

Aboveground biomass of functional groups in the ground layer of savannas under different fire frequencies

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Abstract. Savannas with different fire histories should have differences in aboveground biomass due to varying responses of functional groups. We investigated the effects of different fire frequencies on total aboveground biomass and also the biomass of functional groups (the tussock grass *Tristachya leiostachya* Nees, other grasses, small woody individuals) and dry biomass in savannas subjected to annual fires, biennial fires, and protected from fire for 12 years. Total biomass in the protected area was more than twice that of the annually burned area. *T. leiostachya* aboveground biomass was higher in the protected area than in annually and biennially burned areas, which were not different. Biomass of other grasses was lower in the protected area, whereas woody biomass values did not differ among areas. In the biennially burned and protected areas, we found a positive relationship between *T. leiostachya* and dry biomass. In the annually burned area, *T. leiostachya* biomass was negatively correlated with the biomass of other grasses and woody individuals. This negative correlation supports the idea that frequent fires favour the former, and may indicate an outcompeting effect. Knowledge not only about biomass but especially about its functional components is necessary to understand the processes and management consequences of different burning strategies.

Introduction

Fire plays a critical role in savanna ecology through direct and indirect effects on interactions between woody and grass species (Moreira 2000). Most savanna fires are surface fires and burn mainly the ground layer of the vegetation (Miranda *et al.* 2002). As a consequence, the accumulation of grass biomass determines the future fire intensity and rate of spread (Miranda *et al.* 1993; Whelan 1995). Accumulation of biomass in the ground layer, especially grasses, increases the probability of ignition, fire intensity and fire extent (Williams *et al.* 2003; Gardner 2006). In contrast, woody biomass accumulation – especially tree cover and stem density – has a negative effect on grasses through shading and competition for resources (see Gardner 2006 for a conceptual model of factors influencing tree–grass coexistence in savannas).

Fire promotes primary productivity by accelerating nutrient cycling (Frost and Robertson 1987; Miranda *et al.* 2002). Fire decreases growth rates and seedling survival of woody species (Hoffmann 1996, 1998), but also has an indirect positive effect via the release of nutrients to the soil (Singh 1993; Silva and Batalha 2008). This pulse of available nutrients is rapidly acquired by shallow-rooted grass species. Hence, fire can transfer nutrients from woody species to grasses (Coutinho 1990).

In general, savanna plant communities recover much faster after fire than fire-prone temperate communities (Whelan 1995). In frequently burned savannas, ground layer species – mainly grasses – recover quickly because their underground meristems are protected from fire (Gottsberger and Silberbauer-Gottsberger 2006) and because nutrient availability in soil increases after

fires (Coutinho 1990). For example, in the Brazilian cerrado, aboveground herbaceous biomass is regained within a fire-free interval of ~1.5 years, contingent on fire severity (Miranda *et al.* 2002). Such recovery is mainly due to resprouting from underground organs (Whelan 1995; Hoffmann 1998). Even though woody species present adaptations to fire, such as strong suberisation of trunks and branches that protect living tissues from high temperatures, these features usually appear only in larger and older individuals (Miranda *et al.* 2002). Consequently, the life stage when woody individuals are within the ground layer is critical for establishment and survival (Williams *et al.* 2003). Therefore, different fire regimes may favour distinct functional groups of species (Whelan 1995; Pivello and Norton 1996).

In Neotropical savannas, biomass production is high during the wet season due to an increase in water availability, whereas almost all grasses and herbs are desiccated, with their living tissues reduced to underground organs, during the dry season (Cianciaruso *et al.* 2005; Gottsberger and Silberbauer-Gottsberger 2006). Most studies on the response of savanna vegetation to fire have examined woody species mortality, regeneration through seedlings, or resprouting from epicormic meristems or lignotubers (Frost and Robertson 1987; Hoffmann 1996; Moreira 2000; Williams *et al.* 2003). These studies concluded that, in the absence of fire or with a reduction in fire frequency, woody species increase in abundance with a coincident reduction in grass biomass. However, these studies usually do not account for young individuals of woody species within the ground layer.

Knowledge about long-term biomass accumulation under different fire frequencies, especially within functional groups, is necessary to understand community responses after disturbance. Moreover, in Neotropical savannas, almost all studies used the 'time since last fire' approach: biological responses are investigated with knowledge of last time of burning but often with little information about the actual fire history (Whelan 1995). Fire history is important because not all fire regimes are suitable for specific needs, such as wildfire control, food supply to native fauna, weed control, and the maintenance of biodiversity and ecological processes (Whelan 1995; Pivello and Norton 1996).

Here we investigated how three different fire frequencies (annual fire, biennial fires and 12 years of fire exclusion) affect total aboveground biomass of ground layer species, aboveground biomass of functional groups (the tussock grass *Tristachya leiostachya*, other grasses, small woody individuals), and dry (dead) biomass of the ground layer in savannas. We considered *T. leiostachya* as a separate functional group, because it likely drives the fire regime within our study area due to both vegetative and reproductive phenological patterns (Coutinho 1990; Ramos-Neto and Pinheiro-Machado 1996; Ramos-Neto and Pivello 2000). Furthermore, this species has two remarkable features: it produces a very tall (to 3 m) inflorescence and it is a tussock grass, an uncommon life-form among cerrado grasses.

We expected to find higher biomass, especially dry biomass, under fire exclusion. Since fire exclusion favours woody species (Moreira 2000), we also expected to find more woody biomass in the ground layer with decreasing fire frequency and, a negative relationship between woody and grass biomass. Thus, we answered the following questions: (1) Are there differences in total aboveground biomass in the ground layer of savannas with different fire frequencies? (2) Are there differences in aboveground biomass of different functional groups? (3) Within each fire frequency, is the biomass of these functional groups correlated?

Materials and methods

Study area

We carried out this study in Emas National Park (ENP), located in the Brazilian Central Plateau, approximately at 17°49'–18°28'S; 52°39'–53°10'W. The park comprises 132 941 ha and is one of the largest and most important reserves in the cerrado region. Regional climate is humid tropical with wet summers and dry winters. Annual rainfall varies from 1200 to 2000 mm, concentrated from October to March, and mean annual temperature is $\approx 24^{\circ}\text{C}$ (Ramos-Neto and Pivello 2000). Three-quarters of the ENP consist of flat tableland, 820–888 m asl, and the remaining area consists of hilly terrain, 720–820 m asl (Ramos-Neto and Pivello 2000). In the park, open savanna (cerrado) physiognomies prevail, covering 68.1% of the total area, especially on the flat tableland (Ramos-Neto and Pivello 2000). The more closed cerrado covers 25.1% of the reserve, mainly on the hilly terrain. Soils in ENP are mainly Oxisols (Silva and Batalha 2008).

Historically, ENP was exploited by farmers for cattle ranching, and annual dry season fires were used to promote forage regrowth. After 1984, the park was completely fenced,

cattle were no longer allowed inside, and a fire exclusion policy was established (Ramos-Neto and Pivello 2000). As a consequence, catastrophic fires occurred every 3 years in ENP, burning $\sim 80\%$ of its area (França *et al.* 2007). Starting in 1994, firebreaks have been installed and maintained, and anthropogenic fires have been controlled (França *et al.* 2007). As a result, catastrophic fires no longer occur, and the total area burned each year in ENP was reduced (França *et al.* 2007). Currently, only 20% of the ENP is burned each year, and fire return interval at any given point is ~ 7 years (França *et al.* 2007).

Vegetation sampling

In March 2006, at the end of the growing season, we sampled the ground layer in three nearby areas with different fire frequencies and with the same open savanna physiognomy (*campo cerrado*), that is, with an almost continuous ground layer, interrupted only by sparse trees. We randomly placed our sample units (20 0.25 m² quadrats) within: (1) a 50 000 m² area burned annually since 1994 (midpoint approximately at 18°18'50"S and 52°54'00"W); (2) another 50 000 m² area burned approximately every 2 years since 1994, specifically in 1994, 1996, 1999, 2001, 2002, and 2003 (midpoint approximately at 18°19'01"S and 52°54'10"W); and (3) another 50 000 m² area unburned for 12 years. The annually and biennially burned areas bordered the protected area (see Silva and Batalha 2008 for a map and more details about the areas). This design increased the likelihood that significant differences between areas were caused by different fire frequencies and not due to pre-existing differences in vegetation cover, species composition, soil features, or rainfall (see Pucheta *et al.* 1998 for a similar design).

The first two areas are completely burned during the dry season as a management tool to avoid large wildfires inside the park (França *et al.* 2007). As a consequence, tree cover is slightly different among the areas, being higher in the protected area and lower in the annually burned area. However, canopy cover was within the range expected for this type of savanna in all three areas (10–25%, Ottmar *et al.* 2001). Average tree height was higher in the protected site (1.4 m) and decreased with increasing fire frequency (1.2 m in the biennially burned area and 0.7 m in the annually burned area; M. Cianciaruso, unpubl. data). Nevertheless, our aim here in relation to woody species was to investigate the response of this functional group in the ground layer (that is, small woody species or young individuals of woody tree species). Even though tree cover is important to the dynamics of the ground layer, none of the savannas we studied had a tree layer dense enough to prevent sunlight reaching the understorey or significantly contribute litter to dry biomass.

We removed all aboveground plant material within each quadrat, excluding trees (that is, woody individuals with diameter at soil level higher than 3 cm). We sorted the aboveground biomass harvested into three functional groups: the tussock grass *Tristachya leiostachya*, which is the dominant species in ENP's savannas; other grasses; small woody individuals (including shrubs, saplings, woody geophytes, and other dicots); and dry biomass (dry or decomposing plant debris, including litter). We oven-dried all the collected material at 80°C for 48 h before weighing. This method was successfully used to estimate the relative contribution of plant

functional groups to total ground layer biomass in other savannas (Ottmar *et al.* 2001).

We compared biomass values of each functional group, as well as total biomass, among fire frequencies using a one-way analysis of variance and Tukey's post-hoc test (Zar 1999). In addition, we examined the relative change in biomass of the functional groups as a proportion of total biomass and a proportion of living biomass. For this, we applied a G-test (Sokal and Rohlf 1995) to assess whether the functional group's biomass proportions were different among fire frequencies ($\alpha=0.05$). We also used Pearson's correlation (Zar 1999) to assess possible associations among functional groups under each fire frequency, using the biomass values found in each of the 20 quadrats for each group. A negative relationship between the biomass of two coexisting functional groups may be evidence of local exclusion by competition for resources, while a positive relationship may indicate facilitation (Perry *et al.* 2008).

Results

Total and *Tristachya leiostachya* aboveground biomass values were higher in the protected area than in the annually and biennially burned areas, which did not differ (Table 1). Biomass of other grasses was lower in the protected area, whereas woody biomass values did not differ significantly among areas. Dry biomass was highest in the protected and lowest in the annually burned area.

As a ratio of total ground layer biomass, *T. leiostachya* biomass was constant in contrast to the decline of the other grasses with protection from fire (Table 2). Interestingly, woody biomass also declined with decreasing fire frequency. In contrast, the ratio of dry biomass more than doubled with protection from fire. When we analysed the patterns as a ratio of total living biomass, we found some differences: *T. leiostachya* biomass doubled, while woody biomass remained constant. For other grasses, we found the same pattern described above.

In the annually burned area, *T. leiostachya* biomass was negatively correlated with other grasses and woody individuals, but we did not observe any relationship among the biomass values of other functional groups (Table 3). In the biennially burned and protected areas, we found a significant positive relationship only between *T. leiostachya* and dry biomass.

Discussion

An overall consensus about the effects of different fire frequencies in savannas, without accounting for herbivory effects, is that

biomass of ground layer species remains similar in burned and unburned areas after a full growing season (Sarmiento and Vera 1979; Coutinho 1990; Singh 1993). Since we found similar amounts of total biomass under annual and biennial fires, our results supported this general assertion. Neotropical savannas burn generally at intervals of 1–3 years (Coutinho 1990; Hoffmann 1999), and, in physiognomies similar to those we studied, biomass of ground layer ranges from 350 to 550 g m⁻² after 1–3 years since the last fire (Sarmiento and Vera 1979; Kauffman *et al.* 1994; Ottmar *et al.* 2001). Thus, total biomass values we found in the annually and biennially burned areas are within the expected range for these savannas.

Fire exclusion leads to an increase in the ground layer biomass (Ottmar *et al.* 2001; Govender *et al.* 2006). We observed higher total biomass after 12 years of fire exclusion due to an increase in dry and *T. leiostachya* biomass values. Such an increase, especially due to the accumulation of dry biomass, is a matter of concern, because it increases the probability of severe fires (Miranda *et al.* 1993; Kauffman *et al.* 1994). Herbaceous species, which have a combustion factor higher than 90%, are the principal fuel load in these savannas (Kauffman *et al.* 1994). Severe fires have a greater effect on woody species because crown fires are more common (Coutinho 1990; Moreira 2000). In addition, severe fires may spread rapidly and cover large areas, becoming harmful to the fauna and sometimes reaching vegetation types not adapted to fire (Ramos-Neto and Pivello 2000; França *et al.* 2007). Thus, long-term biomass accumulation within protected natural areas may result in uncontrollable fires.

Long-term fire exclusion can immobilise nutrients in inert dry biomass (Frost and Robertson 1987), leading to an impoverishment of surface soil layer. Rapid nutrient turnover caused by frequent fires is expected to favour herbaceous species with superficial roots (Coutinho 1990). In contrast, nutrient immobilisation is expected to favour woody species that exploit nutrients from deeper soils (Coutinho 1990). As expected, soil fertility in ENP is lower in the protected than in the annually burned area (Silva and Batalha 2008).

Our findings indicate that some herbaceous species may also take advantage of fire exclusion, outcompeting other herbaceous species and preventing the growth of woody species. We observed higher *T. leiostachya* and dry biomass values in the protected area, as well as a positive relationship between them in the biennially burned and protected areas. Frequent fires not only remove accumulated dry biomass that constrains the growth of ground layer species by shading (Canales *et al.* 1994), but may also reduce interspecific competition among grasses (Inchausti 1995). Because most of the dry biomass was composed of dead

Table 1. Total and functional groups biomass values (g m⁻² ± s.d.) of the ground layer in Neotropical savannas with different fire frequencies in Emas National Park, central Brazil
Different letters within a row denote significant differences ($P < 0.05$, Tukey's post hoc test)

Biomass	Annually burned	Biennially burned	Protected	F	P
<i>Tristachya leiostachya</i>	125.44 ^a ± 91.00	105.00 ^a ± 90.84	261.04 ^b ± 200.72	7.48	0.001
Other grasses	116.00 ^a ± 75.16	102.64 ^a ± 117.28	40.00 ^b ± 35.64	4.77	0.012
Woody individuals	113.56 ± 74.48	66.68 ± 46.08	82.16 ± 68.40	2.77	0.071
Dry	127.52 ^a ± 88.48	249.88 ^b ± 92.52	739.44 ^c ± 267.04	71.73	0.001
Total	482.52 ^a ± 146.52	524.20 ^a ± 152.24	1122.64 ^b ± 441.00	32.19	0.001

Table 2. Relative contribution of functional groups of the ground layer to total and living biomass in Neotropical savannas with different fire frequencies in Emas National Park, central Brazil

	Annually burned	Biennially burned	Protected	G	P
<i>As a proportion of total herbaceous biomass</i>					
<i>T. leiostachya</i>	25.9	20.0	23.3	0.78	0.677
Other grasses	24.1	19.5	3.6	9.86	0.007
Woody individuals	23.4	12.6	7.3	16.10	0.001
Total living	73.6	52.1	34.1	14.79	0.001
Dry	26.4	47.9	65.9	17.41	0.001
<i>As a proportion of total living biomass</i>					
<i>T. leiostachya</i>	35.3	38.5	68.2	13.15	0.001
Other grasses	32.8	37.4	10.4	17.90	0.001
Woody individuals	31.9	24.2	21.4	2.25	0.325

G, goodness of fit statistics.

leaves and reproductive structures of *T. leiostachya*, the lower biomass value of other grasses we found in the protected area may be due to intense competition from the tussock grass.

Identifying a species or functional group that is the main driver of community function – in our case, one that is related to fire – is a challenging task, but is necessary to understand the coexistence and maintenance of biological diversity in natural assemblages and to manage natural reserves (Duckworth *et al.* 2000). In general, grass biomass increases in savannas under fire exclusion, which increases the likelihood and the intensity of the next fire (Ramos-Neto and Pivello 2000). Here we showed that a single grass species (*T. leiostachya*) alone contributes six times more biomass than all the other grasses combined. While we did not find a relationship between other grasses and dry biomass (as would be expected if grasses in general were the main source for dry biomass in our study sites), *T. leiostachya* was highly associated with dry biomass, emphasising its unique contribution to fire dynamics in these assemblages.

Tristachya leiostachya is favoured by frequent fires (Ramos-Neto and Pinheiro-Machado 1996; Ramos-Neto and Pivello 2000) and is the dominant grass in almost all open physiognomies within the park (França *et al.* 2007), reaching

up to 80% of the community living biomass (Cianciaruso and Batalha 2009). In Neotropical savannas, dominance by a single grass species is uncommon (Filgueiras 2002) and is generally related to frequent fires in the past (Baruch and Bilbao 1999; Ramos-Neto and Pivello 2000). The negative correlation of *T. leiostachya* with other grasses and small woody individuals in the annually burned area supports the idea that even under frequent fires this species is still a strong competitor locally, excluding other functional groups, allowing us to speculate about the process of its establishment and dominance. *T. leiostachya* sprouts vigorously in the year after fire, reaching a high aerial biomass and being negatively associated with other grasses and small woody individuals, which may indicate an outcompeting effect on the local scale. As time since last fire increases, *T. leiostachya* seems to be the main source of dry biomass, which will ultimately shade neighbouring individuals and immobilise nutrients that otherwise would be available to other species.

Tristachya leiostachya seems to have a life cycle well adapted to different fire frequencies: it reproduces sexually every 2–3 years after a fire and vegetatively between fire events (Ramos-Neto and Pinheiro-Machado 1996; França *et al.* 2007). When fire is excluded, vegetative reproduction may maintain this species' dominance. Considering the fire history of ENP in the past (decades of annual burning by cattle ranchers followed by more than a decade of a fire exclusion policy), and the patterns observed for *T. leiostachya*, we have evidence that this species was initially favoured by the frequent fires (much more frequent than what would be expected under natural conditions) and then by the fire exclusion policy, when uncontrollable fires burned the park every 3–4 years (França *et al.* 2007).

Contrary to our initial expectation that fire exclusion would favour woody species, we did not find an increase in woody biomass within the ground layer in the protected area (Moreira 2000). Again, *T. leiostachya* may prevent the growth of shrubs and saplings through shading and nutrient competition, even in otherwise favourable conditions for woody individuals (that is, absence of fire). *T. leiostachya* forms relatively large tussocks (leaves up to 1 m high and tussocks of up to 0.7 m in

Table 3. Pearson correlation values among functional groups biomass values of the ground layer in Neotropical savannas with different fire frequencies in Emas National Park, central Brazil

Values in bold denote significant values $\alpha=0.05$

	Other grasses	Woody individuals	Dry biomass
<i>Annually burned area</i>			
<i>Tristachya leiostachya</i>	-0.58 (P=0.007)	-0.52 (P=0.017)	0.35 (P=0.120)
Other grasses	–	0.41 (P=0.070)	-0.24 (P=0.296)
Woody individuals	–	–	0.16 (P=0.485)
<i>Biennially burned area</i>			
<i>Tristachya leiostachya</i>	-0.38 (P=0.091)	-0.29 (P=0.218)	0.69 (P=0.001)
Other grasses	–	-0.29 (P=0.199)	-0.29 (P=0.203)
Woody individuals	–	–	-0.10 (P=0.667)
<i>Protected area</i>			
<i>Tristachya leiostachya</i>	0.18 (P=0.481)	-0.22 (P=0.348)	0.85 (P=0.000)
Other grasses	–	0.04 (P=0.870)	-0.27 (P=0.259)
Woody individuals	–	–	-0.08 (P=0.749)

circumference, Cianciaruso and Batalha 2009), with inflorescences that can reach more than 3 m high. These morphological traits, and the considerable dry biomass that *T. leiostachya* produces each year, can reduce nutrient availability to small woody plants and can shade those plants.

The amount of woody biomass we found in the unburned area was similar to the observed values in other savannas unburned for 2–3 years (Ottmar *et al.* 2001). Since woody species in these savannas are heliophilous (Coutinho 1990), they are not able to germinate and grow properly under shaded conditions created by the overdominance of grasses (and the resultant dry biomass accumulation under fire exclusion), a pathway that should be included in tree-grass models (for example, Gardner 2006). As discussed previously, this biomass accumulation may also explain the reduction of biomass values of other grasses under fire exclusion. Similar findings were reported from other savannas where fire exclusion lead to a decline in population growth rates of several grass species (Silva and Castro 1989; Silva *et al.* 1990). Moreover, in the absence of fire, some species may outcompete others (Inchausti 1995), which seems to be the case for *T. leiostachya*. An alternative explanation for the lower biomass of other grasses and lack of change in woody biomass is that the sexual reproductive system of many plants may be disrupted under fire suppression. Several savanna plants depend on fire to trigger flowering and to release their diaspores (Coutinho 1990). Therefore, fire suppression would decrease the regeneration capacity of these populations.

We showed that *T. leiostachya* biomass was positively related to the amount of dry biomass and, thus, its life cycle was intimately related to the fire regime within ENP, as previously postulated by Coutinho (1990). Under fire exclusion, *T. leiostachya* may grow by vegetative reproduction and rapidly accumulates dry biomass. This accumulated biomass favours fire occurrence and spread (Ramos-Neto and Pivello 2000; França *et al.* 2007), which, in turn, favours *T. leiostachya* sexual reproduction 2–3 years after a fire (Ramos-Neto and Pinheiro-Machado 1996). The frequent fires in the past may have favoured *T. leiostachya*, explaining its current dominance in the park (Ramos-Neto and Pivello 2000). Therefore, knowledge not only about total biomass, but especially about its functional components, is important to provide a better understanding of the processes and management consequences of different burning strategies.

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