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PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS (BIOLOGIA VEGETAL)

Efeito da época da queima na dinâmica de campo sujo de Cerrado

MARIANA NINNO RISSI

Tese apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de doutor em Ciências Biológicas (Biologia Vegetal).

Maio - 2016

Mariana Ninno Rissi

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Orientadora: Prof. Dra. Alessandra Fidelis
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TÍTULO DA TESE: Efeito da época da queima na dinâmica de campo sujo

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Título alterado para "Efeito da época da queima na dinâmica de campo sujo de cerrado".

À pequena Manuela, na esperança de que um dia todas as crianças possam realizar seus sonhos...

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Nessas regiões, encontro gente que não sabe ler livros,
Mas que sabe ler mundo!
Nesse universo de outros saberes,
Sou eu o analfabeto."

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Índice

Resumo

Queimadas descontroladas e de grandes proporções estão entre as principais ameaças à biodiversidade do Cerrado. A época da queima é um dos elementos do regime do fogo, e estudos sobre seus efeitos na dinâmica da vegetação pós-fogo podem auxiliar no uso de queimas prescritas como ferramenta de manejo. Desta forma, o objetivo desta tese foi avaliar os resultados da época da queima no comportamento do fogo e na dinâmica da vegetação herbácea-arbustiva de uma área de campo sujo. Os experimentos foram realizados na Reserva Natural Serra do Tombador (Goiás). Primeiramente, comparamos o comportamento do fogo nas diferentes épocas de queima, dando subsídios para seu uso como ferramenta de manejo. Além disso, investigamos o efeito das épocas de queima nos padrões de recuperação/acumulação da biomassa (total, morta e viva), na fenologia (da comunidade e dos grupos funcionais: graminóides, herbáceas não graminóides e arbustos) e na dinâmica dos diferentes elementos da vegetação herbácea-arbustiva (solo nu, biomassa morta, graminóides, herbáceas e arbustos). Para tal, parcelas experimentais (30x30m) foram estabelecidas e queimadas em maio (queima precoce, início da estação seca), julho (queima modal, meio da estação seca), outubro (queima tardia, final da seca) e controle (não queimada, 4 réplicas/tratamento, total de 16 parcelas). Dentro de cada parcela experimental, dez subparcelas foram sorteadas e estabelecidas (1x1m) para análise da dinâmica e acompanhamento do padrão fenológico pós-fogo. As coletas de biomassa foram realizadas em cinco subparcelas de (0,5x0,5m), sorteadas aleatoriamente na borda das parcelas. O comportamento do fogo (ex: intensidade, taxa de propagação e altura da chama) não diferiu entre as épocas da queima, mas a porcentagem de material combustível morto foi maior no meio (modal) e final da seca (tardia). O material combustível total e a sua composição (porcentagem de material combustível morto) foram os parâmetros que melhor explicaram a intensidade do fogo. A regeneração da biomassa viva não foi afetada por nenhuma época da queima, enquanto que as diferenças na composição da biomassa (entre parcelas queimadas e controle) foi guiada pela quantidade de biomassa morta. A acumulação de biomassa entre as parcelas controles e queimadas foi diferente apenas no primeiro ano após a queima. No entanto, os padrões de biomassa total, viva e morta ao longo do tempo não foram afetados pela época da queima. Quanto à fenologia, queimas precoces promoveram uma maior floração da comunidade, principalmente de graminóides, logo após a queima, enquanto que nas queimas modais mais arbustos floresceram (ao longo do primeiro ano após a queima) e mais espécies frutificaram após um ano. Nas parcelas de queimas tardias mais espécies da comunidade e arbusto floresceram ao longo do ano e mais espécies frutificaram nove meses e um ano após a queima. Além disso, as respostas das espécies após o fogo foram distintas e pudemos agrupá-las de acordo com os padrões de floração pós-queima. A dinâmica da vegetação herbácea parece estar relacionada com a sazonalidade (época seca e chuvosa), em geral a época da queima não modificou os padrões de cobertura, riqueza e diversidade, sugerindo que em curto prazo a época da queima exerce efeitos sutis na dinâmica desta vegetação. Os resultados deste estudo poderão auxiliar na compreensão do comportamento do fogo e da dinâmica da vegetação nas diferentes épocas de queima, auxiliando na elaboração de planos de manejo nos quais o fogo possa ser uma alternativa para o manejo da vegetação campo sujo de Cerrado.

Abstract

Uncontrolled wildfires are one of the major threats to Cerrado biodiversity. Fire season is a component of fire regime and studies regarding fire season effects on vegetation dynamics can provide information on whether fire should be used as a management tool. Therefore, the aim of this study was to evaluate the effects of fire season on fire behavior and the dynamics of the herbaceous vegetation in a *campo sujo* area. The study was conducted at the Reserva Serra do do Tombador (Goiás). We first compared fire behavior in each fire season, aiming to provide information for the use of fire as a management tool. Furthermore, we investigated the effects of fire season in the patterns of biomass regeneration/accumulation (total, dead and live), phenology (community and functional groups: graminoids, forbs and shrubs) and in the dynamics of the different components of the herbaceous vegetation (bare soil, dead biomass, graminoids, forbs and shrubs). For such, plots (30 x 30 m) were established and burned in May (early-, at the beginning of the dry season), July (mid-, at the middle of the dry season), October (late-dry season fire, at the end of the dry season) and control (unburned, C, 4 replicates/treatment; total of 16 plots). In each plot, we randomly established and fixed ten subplots (1x1m) for the vegetation dynamics and phenology studies. Biomass sampling was done in five subplots (0.5x0.5m) randomly established in each plot. Fire behavior (e.g.: fire intensity, rate of spread and flame height) did not differ between fire seasons, but percentage of dead fuel was greater in the mid and late-dry season fires. Fire intensity was mainly influenced by the combination of percentage of dead fuel and fuel load. Live biomass regeneration was not affected by any fire season, while differences in total biomass composition (between control and burned areas) were mainly driven by dead biomass. Differences in biomass accumulation were observed only in the first year after fire. Moreover, the patterns of total, live and dead biomass were not affected by fire season. Regarding species' phenology, early- dry season fires enhanced flowering in more species just after fire, especially for graminoids, while mid and late-dry season fires enhanced flowering of species throughout the first year, mainly shrubs. Moreover, responses to fire and to fire seasons were not similar among species; they were grouped according to their flowering patterns after fire. Herbaceous layer dynamics changed mainly due to seasonality (between dry and rainy season), in general fire season did not change the patterns of cover, richness and diversity, suggesting that in short-time fire season has little effects on herbaceous vegetation dynamics. The results of this study provide information on the understanding of fire season and its effects on both fire behavior and vegetation dynamics, helping the development of management plans where fire could be used as an alternative to the management of Cerrado vegetation.

Introdução Geral

O fogo é considerado um dos controladores globais da estrutura das vegetações, agindo como um fator primário na distribuição dos diferentes ecossistemas pelo mundo (Bond *et al.*, 2005; Bond & Keeley 2005). Dependendo do seu regime (época do ano em que ocorre, intensidade, área e frequência (Whelan 1995), o fogo leva a mudanças como, por exemplo, a substituição de árvores por arbustos/gramíneas, assim como a redução de biomassa e controle da altura da vegetação (Hoffmann & Moreira 2002; Bond *et al.* 2005). O fogo está presente em diversas vegetações do mundo: savanas africanas (Trollope 1982) e australianas (Morgan 1999), os páramos equatorianos (Ramsay & Oxley 1996) e ecossistemas mediterrâneos (Lloret 1998). E, portanto, tem efeitos complexos sobre a estrutura da vegetação, afetando a distribuição de espécies tolerantes e sensíveis a este distúrbio (Bond *et al.* 2005).

Evidências mostram que não poderíamos manter grande parte dos ecossitemas campestres e savânicos do mundo na ausência do fogo sem que a vegetação e os processos ecossistêmicos se alterassem, ou que houvesse incêndios de maiores proporções (Bond *et al.* 2005; Hardesty *et al*. 2005; Bowman *et al.* 2009; Pausas & Keeley 2009). Portanto, o fogo é um importante fator ecológico em tais ambientes e deveria ser considerado como uma ferramenta de manejo em unidades de conservação dos ecossistemas em que ele ocorre, a fim de manter sua dinâmica, estrutura e composição florística e evitando-se incêndios descontrolados (Pivello & Norton 1996; Govender *et al.* 2006; Fidelis & Pivello 2011; Durigan & Ratter 2016).

A resposta individual das plantas ao fogo envolve alterações

morfológicas e fisiológicas, enquanto que na comunidade observam-se mudanças na dinâmica e na composição de espécies (Whelan 1995; Bond & Van Wilgen 1996; Céspedes *et al*. 2014). Nas vegetações campestres e savânicas, as gramíneas são o componente da comunidade mais resiliente ao fogo (Bond 2004), devido ao contínuo crescimento dos meristemas intercalares, que geralmente estão protegidos por bainhas ou abaixo do solo (Bond & Van Wilgen 1996; Filgueiras 2002; Gottsberger & Silberbauer-Gottsberger 2006). O fogo pode ainda promover a floração de algumas espécies (Coutinho 1976; Wrobleski & Kauffman 2003) e atuar nos padrões fenológicos de acordo com a interação entre: estado fenológico da espécie, indução floral e época de ocorrência da queima (Pavlovic *et al.* 2011).

A época da queima é um dos principais componentes do regime do fogo (Gill *et al.* 2002), influenciando além dos padrões de floração (Platt *et al.* 1988), a dinâmica (Whelan & Tait 1995; Knox & Clarke 2006) e as habilidades competitivas das espécies (Whelan 1995; Bond & Van Wilgen 1996). O período em que as condições ambientais estejam favoráveis para o estabelecimento das espécies irá variar de acordo com a época em que o fogo ocorreu (Céspedes *et al.* 2013). Esta dinâmica, entre o distúrbio e a sazonalidade, pode interferir no modo em que as plantas irão regenerar após a queima (Bond & Van Wilgen 1996; Whelan 1995). A mudança da época da queima (Miranda *et al.* 2009) pode levar a alteraçõess na estrutura e dinâmica de vegetações. Encontrar uma época de queima ideal é uma das principais questões para a aplicação do manejo do fogo (e.g. Govender *et al.* 2006; Durigan & Ratter 2016), pois a dinâmica sazonal da vegetação altera o acúmulo de biomassa morta (que serve como material combustível), durante

as estações seca e chuvosa, de modo que toda dinâmica do fogo e suas relações com a vegetação podem mudar ao longo do ano.

O fogo pode ser considerado como um fator importante para a dinâmica da vegetação do Cerrado presente há pelo menos cinco milhões de anos (Simon *et al.* 2009). O fogo natural (por meio de raios) ocorre no início da estação chuvosa (setembro – maio), e as áreas atingidas tendem a ser pequenas, uma vez que o distúrbio é usualmente seguido da chuva (Ramos-Neto & Pivello 2000). Entretanto, o homem alterou a época e a frequência da queima, utilizando-se do fogo durante a estação seca, principalmente para estimular os rebrotes e prover alimento para o gado (Coutinho 1990).

A pressão antrópica no Cerrado é constante, com alta incidência de queimadas não controladas, perda de hábitat e invasão por espécies exóticas (Klink & Machado 2005; Durigan *et al*. 2007). Ele ocupava originalmente uma área de 2 milhões km^2, o que correspondia à aproximadamente 22% do território brasileiro (Ratter & Dargie 1992). A rápida perda de hábitat, em um sistema de alta riqueza de espécies e grande endemismo culminou na classificação do Cerrado como um dos *hotspots* globais de biodiversidade (Myers *et al*. 2000).

A vegetação do Cerrado é caracterizada por sua grande variação fisionômica, formando um mosaico de diferentes tipos vegetacionais que vai desde formações campestre (campo limpo), savânicas (campo sujo, campo cerrado, cerrado *sensu stricto*) até formações florestais (cerradão) (Oliveira-Filho & Ratter 2002). A distribuição de tais fisionomias está relacionada a diferentes fatores como o tipo, a profundidade e a quantidade de nutrientes

no solo, assim como a recorrência do fogo (Coutinho 1978, 1982; Furley 1999).

Além da mudança da estação da queima, a falta de manejo ou supressão do fogo tem levado ao acúmulo de biomassa morta, que pode causar incêndios de grandes proporções, com maior eficiência de combustão e velocidade das chamas (Fidelis & Pivello 2011; Simpson *et al*. 2016). No Cerrado, a maioria dos parques e reservas tem utilizado a prática de supressão do fogo (independentemente da sua origem natural ou antrópica) o que, juntamente com a falta de manejo do material combustível, resulta em incêndios de grandes magnitudes (Fidelis & Pivello 2011; Durigan & Ratter 2016). Estes incêndios têm afetado extensas áreas de Cerrado, chamando a atenção da comunidade científica e de gestores, sobre a necessidade e possibilidade do uso do fogo como ferramenta de manejo (Fidelis & Pivello 2011; Durigan & Ratter 2016). Questões sobre a época da queima e suas consequências, tais como: taxa de acumulação e tempo de recuperação da biomassa pós-fogo, e mudança dos padrões da vegetação herbácea, continuam em análise e com dados insuficientes que possibilitem o manejo adequado destas áreas. Enquanto que em outras vegetações nas quais o fogo é um fator presente, queimadas prescritas são utilizadas para fins de conservação (e.g. Van Wilgen *et al*. 2007), no Brasil, o fogo raramente é visto como uma possibilidade de ferramenta de manejo (Durigan & Ratter 2016).

Estudos de monitoramento que acompanhem as respostas dessa vegetação ao fogo são necessários para o entendimento da dinâmica natural de tais ambientes. Assim, o uso adequado e planejado do fogo pode ser uma estratégia de manejo viável para a manutenção da diversidade e de

fisionomias, principalmente mais aberta, em parques nacionais e reservas biológicas que se destinam à conservação do Cerrado (Fidelis & Pivello 2011). As plantas de Cerrado possuem atributos referentes à resistência e resiliência ao fogo como o súber bem desenvolvido e a capacidade de rebrotar após a queima (Coutinho 1982, Simon *et al.* 2009, Dantas & Pausas 2013). Para muitas espécies, principalmente as herbáceas e graminóides, o fogo pode ser benéfico ao estimular e/ou facilitar diversas etapas de seu ciclo de vida (Keith 1997; Wrobleski & Kauffman 2003).

Portanto, o **objetivo principal** desta tese foi avaliar os efeitos da época da queima na intensidade do fogo, na acumulação/regeneração de biomassa, na fenologia e dinâmica do estrato herbáceo-arbustivo em uma área de campo sujo na região central do Brasil, utilizando-se para isso, queimas controladas no início (maio, precoce), no meio (julho, modal) e no final da estação seca e início da chuvosa (outubro, tardia).

O estudo foi desenvolvido na Reserva Natural da Serra do Tombador (RNST) localizada em Cavalcante, Goiás (13° 35’ e 13° 38’ S e 47° 45’ e 47° 51’ W, 560-1118 m de altitude, Figura 1). O clima da região é tropical, com precipitação anual média entre 1300-1500 mm, com forte sazonalidade. A vegetação da reserva é composta por diversos tipos vegetacionais, com predomínio de fisionomias típicas de Cerrado (por exemplo, campo sujo e cerrado *stricto sensu*, AER 2009).

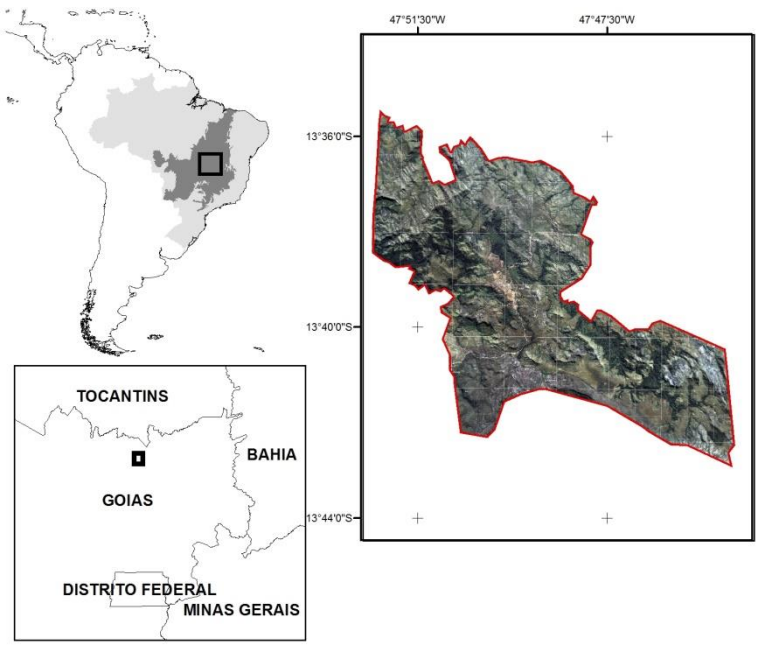

Figura 1. Distribuição original do Cerrado, detalhe da localização e área da Reserva Natural Serra do Tombador, no Estado de Goiás, Brasil (retirado de Gorgone-Barbosa 2016).

A RNST possui uma área de aproximadamente 8.900 ha e atualmente representa a maior reserva particular do patrimônio natural de Cerrado no Brasil (AER, 2009). Entre 2001 a 2010, 82% da área da reserva registrou a presença do fogo. Dentre os fatores responsáveis pela queima, pode-se citar o acúmulo do material combustível, composto principalmente pelo estrato herbáceo-arbustivo. A principal fonte de origem dos incêndios é externa à Reserva, onde os moradores utilizam-se das queimas para manejo das suas pastagens para promover a rebrota da vegetação e aumentar a disponibilidade de alimento para o gado (Daldergan 2014). A área utilizada para o estudo possui fisionomia de campo sujo (Figura 2) e estava excluída de qualquer distúrbio, como o fogo (a última queima na área ocorreu em 2011 e teve origem natural) e o gado (desde 2006).

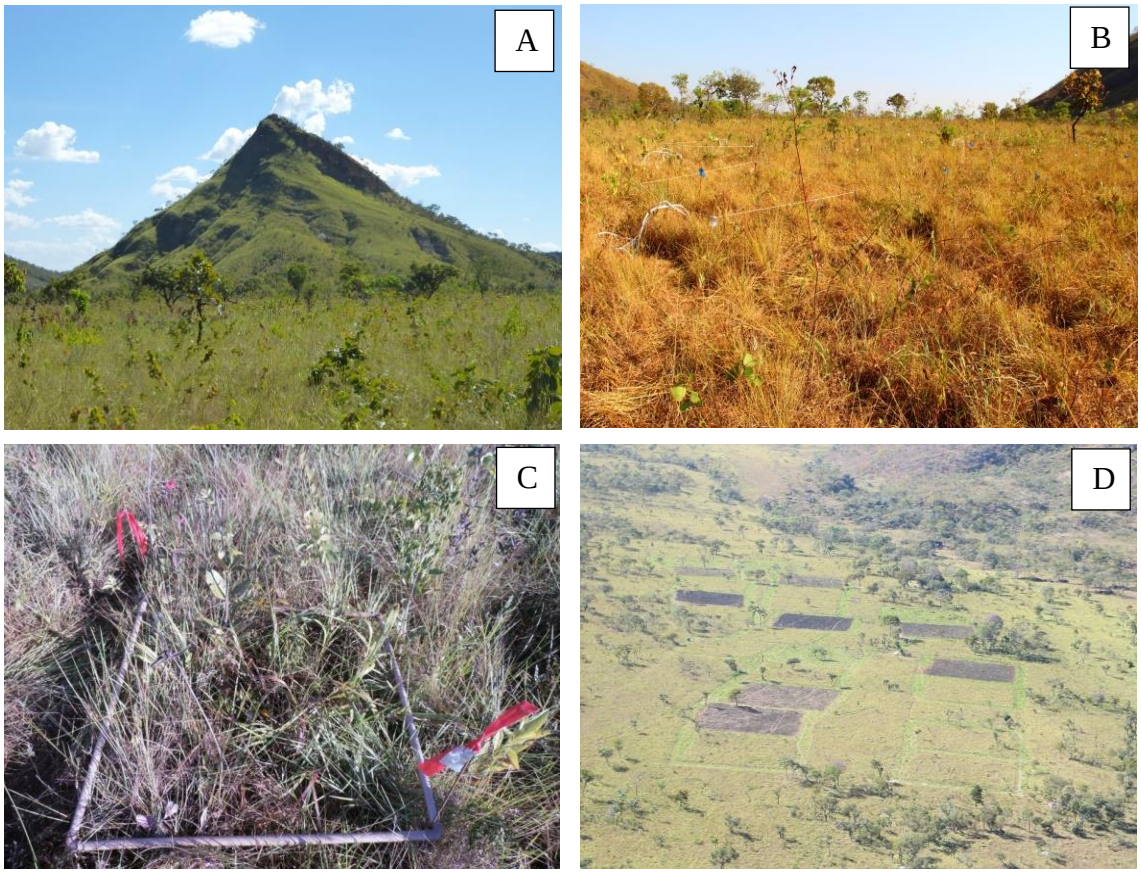

Figura 2. Vista geral da área de estudos (A), detalhe da vegetação (B), exemplo das subparcelas fixas utilizadas para amostragem fenológica e da vegetação (C) e vista aérea dos experimentos (D).

A área onde as parcelas foram estabelecidas possui uma pequena declividade e, para diminuir a influência deste fator e incorporá-lo igualmente em todos os tratamentos, as parcelas foram alocadas em bloco. Cada bloco foi estabelecido de modo que em cada um deles as condições ambientais fossem as mais similares possíveis, cada um em um gradiente de declividade (Figura 2D). Após a alocação dos blocos, as parcelas foram distribuídas de maneira aleatória, de modo que uma única parcela de cada um dos tratamentos fosse atribuída a cada bloco.

Para cada tratamento, foram estabelecidas quatro parcelas de 30x30m. Os tratamentos foram: controle (sem queima), precoce (queimada

em maio de 2013, início da estação seca), modal (queimada em julho de 2013, meio da seca) e tardia (queimada em outubro de 2013, final da seca e início da estação chuvosa), com quatro réplicas/tratamento, totalizando 16 parcelas. Em cada parcela, foram estabelecidas de maneira aleatória através de um sorteio em um grid de subparcelas de 1x1m, dez subparcelas permanentes seguindo alguns critérios: ausência de formigueiro, cupinzeiro, grande quantidade de solo nu (>20%) e presença de grandes árvores. Para a segurança dos experimentos, foram estabelecidos aceiros de 3m de largura ao redor e entre as parcelas durante a estação chuvosa (abril 2013, 2014 e 2015).

As queimas sempre foram realizadas individualmente em cada parcela e o fogo foi colocado a favor do vento (Figura 3A). Medidas ambientais (velocidade do vento, temperatura do ar e umidade ambiental) foram feitas antes, durante e após as queimas (Figura 3B).

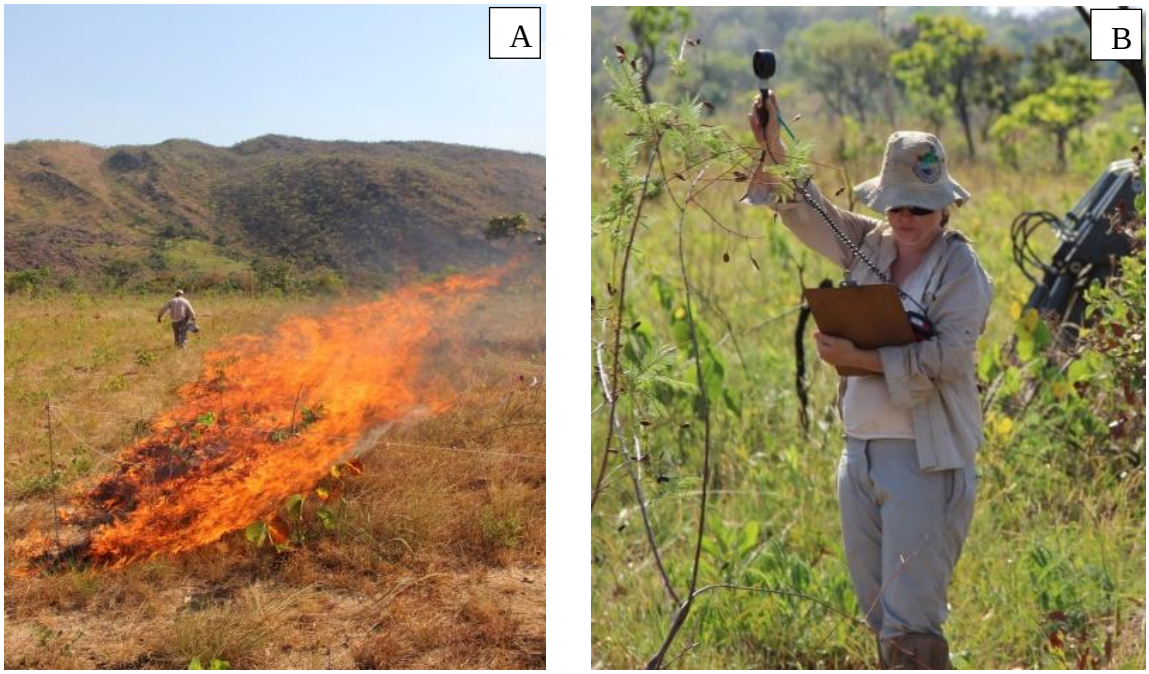

Figura 3. Colocação da linha de fogo (A), detalhe da coleta dos dados ambientais (B).

A tese foi dividida em quatro capítulos, que serão apresentados no formato de artigos.

No primeiro capítulo "**Is the aboveground biomass affected by fire season in Cerrado?"** (Mariana Ninno Rissi, Elizabeth Gorgone-Barbosa e Alessandra Fidelis; a ser submetido ao periódico *Journal of Environmental Management*), verificamos como a época da queima afeta a regeneração da biomassa aérea. A partir deste estudo, podemos inferir quanto tempo é necessário para que o material combustível (total, vivo e morto) seja recuperado. Analisamos também a produtividade e composição da biomassa (1 e 2 anos pós o fogo) e como estes resultados podem ser utilizados para o manejo de biomassa em áreas de campo sujo.

No segundo capítulo **"Does season affect fire behavior in Cerrado? Fire season has little effect on fire behavior in Cerrado"**, de autoria de Mariana Ninno Rissi, M. Jaime Baeza, Elizabeth Gorgone-Barbosa, Talita Zupo e Alessandra Fidelis; e foi submetido ao periódico *International Journal of Wildland Fire* (em revisão). Neste capítulo, analisamos o efeito da época do ano (início, meio e final da seca) nos parâmetros do comportamento do fogo (como por exemplo, intensidade, velocidade e altura das chamas). Além disso, foram avaliadas quais variáveis (ambientais e do fogo) seriam responsáveis pela variação na intensidade e altura do fogo, para um maior entendimento sobre o comportamento do fogo nas diferentes épocas e prover informação para a sua utilização como ferramenta de manejo.

Já no terceiro capítulo "**Are plant communities of open savannas affected by fire season? An example from the Cerrado**" (Mariana Ninno Rissi & Alessandra Fidelis, a ser submetido ao periódico *Journal of*

Vegetation Science), avaliamos a influência da época da queima na riqueza e diversidade das comunidades vegetais, cobertura dos elementos constituintes do estrato herbáceo-arbustivo (solo nu, biomassa morta, arbustos, herbáceas e graminóides). Tais informações são relevantes para um maior conhecimento da dinâmica (em curto prazo) do estrato herbáceo-arbustivo pós-fogo e suas implicações para o manejo.

Por fim, no quarto capítulo investigamos a influência da época da queima na floração e frutificação das espécies e grupos funcionais. "**Does fire season affect the phenological patterns in Cerrado?**" (Mariana Ninno Rissi & Alessandra Fidelis, a ser submetido ao periódico *Journal of Vegetation Science*). Para isso, nós analisamos os efeitos da época da queima na floração e frutificação da comunidade (todas as espécies e grupos funcionais). Neste capítulo, foram analisadas as estratégias fenológicas das espécies da comunidade durante um ano após a queima.

Para a classificação das espécies em cada grupos funcional (graminóide, herbácea e arbusto), utilizamos a literatura de classificação internacionalmente (ver Pérez-Harguindegauy et al. 2013).

Ao final são expostas as conclusões finais desta tese, sobre como a época do ano pode afetar o comportamento do fogo e os padrões da vegetação herbácea-arbustiva (regeneração da biomassa, fenologia, riqueza, diversidade e cobertura dos elementos constituintes do estrato herbáceo-arbustivo). Além disso, discutimos as implicações de tais resultados para o uso do fogo como ferramenta de manejo do Cerrado.

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Capítulo 1

Is the aboveground biomass affected by fire season in Cerrado?

Mariana Ninno Rissi, Elizabeth Gorgone-Barbosa & Alessandra Fidelis.

Abstract

Understanding the effects of fire season on biomass dynamics is critical for its management and vegetation dynamics. We aimed to assess the effects of fire season on aboveground biomass regeneration and accumulation for two years after fire: total (TB), live (TLB) and dead (TDB). We analyzed if biomass productivity is different between burned and unburned plots, one and two years after fire. Also, we provided information about differences in biomass composition between control and burned in different seasons and tested which components (dead biomass, graminoids, shrubs or forbs) should be driving this difference. We established four plots/treatment (30x30m), which were burned separately. Experimental burns were in the following seasons: Early- (May/EF), Mid- (July/MF), Late-dry season fire (October/LF), and control (unburned/C). We collected the aboveground biomass over a year (each tree months), during the next wet season and two years after fire (0.5x0.5m, 5 samples/plot/treatment). Total biomass in EF and MF was similar to control two years after fire, whilst LF was different from control all over the time. Live biomass regeneration was not affect by any fire season. Differences in total biomass composition between control and burned areas were mainly driven by dead biomass. Productivity of biomass in the first year after fire (when compared between burned and unburned plots) was similar in EF, and greater in MF and LF. However, two years after fire, no differences were registered between burned and unburned plots in biomass productivity. In general, patterns of TB, TLB and TDB were not affected by fire season. Independently of fire, TLB registered a seasonal pattern according to dry/rainy season. TB and TDB accumulated over the time in control plots, probably due to the low rates of decomposition, suggesting the importance of fire management in order to avoid hotter and more intense fires. Finally, our results suggest that fire season does not change the accumulation and regeneration of biomass.

Keywords: fuel management, Cerrado, fire season, plant community.

Introduction

In fire-prone ecosystems, disturbance may be the major driver of ecosystem's dynamics (Whelan 1995), since it removes part or all aboveground biomass (Grime 1979). In such ecosystems, the distribution, structure and arrangement of the fuel (biomass) will directly influence how fire spreads (Bond & Van Wilgen 1996; Gagnon *et al.* 2015). For example, total biomass can influence fire rate of spread and combustion efficiency (Simpson *et al.* 2016) and fire behavior can be influenced by the components of biomass, such as the amount of accumulated dead biomass in the plants (Bond & Van Wilgen 1996), which is an important parameter for modeling fire behavior (Pausas & Moreira 2012). However, some of these components may vary according to the season, such as the amount and relationship between dead and live biomass (Oliveras *et al.* 2013; Fidelis *et al.* 2013), which should thus be considered. Moreover, how biomass regenerates after fire may indicate the rate of recovery of vegetation after a particular fire, or series of fires thus contributing to changes in fire intensity and rate of spread of the next fire (Whelan 1995; Marino *et al.* 2011).

Fire has been used as a management tool in different fire-prone ecosystems (Govender *et al*. 2006; Van Wilgen *et al.* 2007). However, fire season may be one of the least understood components of fire regime (Gill *et al.* 2002; Durigan & Ratter 2016), affecting significantly fire behavior (Van Wilgen *et al.* 2007; Knapp *et al.* 2009), community composition (Whelan & Tait 1995; Knox & Clarke 2006) and biomass accumulation (Sarmiento 1984). Identify if there is an ideal season to burn is one of the main questions to improve fire management (Whelan 1995; Durigan & Ratter 2016). Prescribed fires in the most favorable season may lead to different responses of the vegetation according to the aim of the management, such as: control of fuel load, change or maintenance of vegetation structure, maintain the biodiversity and physiognomy, reduce wildfire incidence, fire intensity and fire severity (Govender *et al*. 2006; Van Wilgen *et al.* 2007).

Fire is an important ecological and evolutionary factor in Cerrado (Simon *et al.* 2009). It is already known that 80% of herbaceous layer biomass is recovered in open savannas one year after fire (Andrade 1998), being completely recovered after 2 years (Nascimento Neto *et al.* 1998). Therefore, two years after fire, vegetation has sufficient fuel load to burn again if a fire comes (Nascimento Neto *et al.* 1998). After all, if fire in different seasons will affect biomass recovery is still poorly understood. Since that if fire occurs at the end of the rainy season, vegetation will face three to five months of dry season and thus, vegetation regeneration may be affected differently if fire occurred at the end of the dry season.

Cerrado is characterized by a seasonal climate, with a well-marked dry season (Eiten 1972) which can last 3-5 months (May-September; Coutinho 1982; Furley 1999). Cerrado vegetation is composed by grasslands (campo limpo), savannas (campo sujo, campo cerrado, cerrado *sensu stricto*) and forest formations (cerradão) (Oliveira-Filho & Ratter 2002). Natural fires occur during the rainy season (September - May) and frequently affect small areas since they are usually followed by rain (Ramos- Neto & Pivello 2000). However, anthropic actions, such as setting fire during the dry season to provide food for cattle raising have been changing the season of fire (Coutinho 1982).

Besides the changes in fire season, the lack of management and the policy of fire suppression has caused the accumulation of dead biomass, which can lead to wildfires (Fidelis & Pivello 2011; Durigan & Ratter 2016). Fire should be considered as a management tool in protected areas of Cerrado not only to control fuel load and avoid wildfires (Pivello & Norton 1996; Fidelis & Pivello 2011), but also in order to maintain biodiversity and plant community structure and dynamic (Furley 1999; Durigan & Ratter 2016). It is extremely important to understand the patterns of biomass regeneration after fire (Baeza & Santana 2015) and how they are affected by fire season, since fire regime and behavior will be mostly influenced by quantity and composition of biomass (Trollope 1982; Whelan 1995; Pausas & Moreira 2012).

Therefore, this study aims to: 1) evaluate the differences of total biomass (TB), live biomass (TLB) and dead biomass (TDB) quantity between control and plots burned in different fire seasons; 2) quantify the accumulation of total biomass one and two years after fire experiments; 3) analyze the differences of biomass composition between control and burned plots in one and two years after fire and identify which components of community are driving the major differences between treatments.

We hypothesize that different fire seasons would lead to changes in total biomass productivity, composition and regeneration. We expect that early-dry season fires communities (EF) will have lower total biomass (TB) regeneration and slower accumulation of biomass compared to mid- (MF) and late dry season fires (LF), since fires in MF and LF are followed by the rainy season and thus, biomass regeneration should be enhanced, at least during the first year post-fire.

Methods

Study area

The study was conducted at the RNST (Reserva Natural da Serra do Tombador), in Central Brazil (47°45-51'W and 13°35-38'S, 560-1118m a.s.l.). Mean annual rainfall is between 1300 and 1500 mm, and climate is tropical with a dry season from May to September (AER 2009). The study site is composed by *campo sujo*, which is characterized by a dominant herbaceous layer with scattered shrubs and dwarf trees. The plots were established in an area with no invasive species, dominated by grasses (e.g. *Mesosetum loliiforme*, *Oedochloa procurrens*), forbs (e.g. *Mimosa somnians*, *Ichthyothere terminales*, *Deianira pallescens*), and subshrubs and shrubs (e.g. *Harpalyce brasiliana*, *Mimosa* aff. *leiocephala*, *Bauhinia dumosa*). The area has not been grazed since 2006 and the last fire occurred two years (August 2011) before the beginning of this study (2013). Fire events occurs in a 3-year cycle and the principal cause of fires in the reserve is the accumulation of fuel load and the

origin of fires are external, from neighborhood that uses fire to provide food for cattle (Daldergan *et al.* 2014).

Experimental design and data sampling

We established 30x30m experimental plots (4 plots/treatment, total of 16 plots) distant at least 4m from each other, with 3m-wide fire breaks between plots. Plots were burned in May, at the beginning of the dry season (early-dry, EF), in July (mid-dry, MF) and in October, at the end of the dry season and beginning of the rainy season, (late-dry, LF), as well as control plots (unburned, C). Fire seasons were chosen according to the period of most natural (end of the rainy season and end of the dry sason, Ramos-Neto & Pivello 2000) and anthropogenic fires occurrence in Cerrado (July-August, in the middle of the dry season (Coutinho 1982; Ramos-Neto & Pivello 2000).

The experimental fires were conducted individually in each plot to guarantee the independence of data. Fire was set in wind direction (head fire). For more details about the fire experiments, please see Rissi *et al.* (Capítulo 2).

Aboveground biomass

We collected the aboveground biomass (composed mostly by graminoids, forbs, shrubs <1.5m and dead biomass) in each plot before experiments (May 2013 (M13); July 2013 (J13) and October 2013 (O13)), every three months after fire during one year (M14; J14; O14) and after that, during the next wet season (F15) and 2 years after fire (M15; J15; O15). The aboveground biomass was sampled in 0.5x0.5m subplots, randomly established in each plot. For this, each 30x30m plot was divided into 1x1m quadrats, and then five samples were randomly chosen in each time. We never sampled the same subplot twice.

Vegetation was cut at the ground level (ca 2cm above soil surface) and put in paper bags. In order to evaluate changes in biomass composition, we separated the

biomass in the following components: dead biomass (litter + standing dead biomass), graminoids (Poaceae, Xyridaceae, Iridaceae, and Cyperaceae), forbs and shrubs (<1.5 m). After that, the material was dried at 70°C for three days and weighed.

Data analysis

In order to evaluate the differences of total (TB), live (TLB) and dead biomass (TDB) quantity between treatments (control and burned) in each season (early-, mid-, and late-dry season) for each time of observation, we used mixed linear model. We considered in the analysis the treatments as the fixed factor and the plots as the random factor. To verify in each fire season, how much time is necessary to TB, TLB and TDB to reach the same amount before fire, we compared the values found over the time (three (T3), six (T6), nine months (T9), one year (T12), the following rainy season (T18) and two years after fire (T24)) to the ones found before each fire, by using mixed linear models. We considered in the analysis the time as the fixed factor and the plots as the random factor.

In order to quantify the productivity of total biomass (TB), we used the values of biomass accumulated in one and two years after fire (for each burned plots). For control, we subtracted the values found in one and two years after fire, in relation to values found before fire. After that, we performed mixed models, to test if the accumulation in each fire season was different from control.

To evaluate the differences in total biomass composition of control and each fire treatment (control x early; control x mid; control x late) in time (1 year and 2 years after fire), we used permutational multivariate analysis (Permanova; Anderson 2001), applied to Euclidian similarity matrix generated from biomass components of community structure data (dead, forbs, graminoids and shrubs). We also performed a similarity percentage analysis (SIMPER) to determine the contribution of a particular component of community composition (dead, forbs, graminoids and shrubs) to the overall community composition dissimilarities between fire treatments and control.

Analyses were performed using the R program (R Core Team 2013) with the packages: vegan (Oksanen *et al.* 2013) and nlme (Pinheiro *et al.* 2015). For Simper analysis we used the trial version of software PRIMER (Plymouth Marine Laboratory, UK).

Results

Total biomass (TB) dead biomass (TDB) and live biomass (TLB)

TB from plots burned in early- and mid-dry season (EF and MF) differed from control in each time of observation (P≤0.05) until two years after fire, when the amount of biomass was the same between treatments (EF x control: *P*=0.57; MF x control: *P*=0.3; Fig. 1A and B). TB in control plots was always higher than in LF plots, even two years after fire (*P*<0.05; Fig. 1C). In the following rainy season after fire (February 2014), total aboveground biomass was the same as before fire in EF and MF treatments (P>0.05, EF: T9, MF: T6, Table 1). Moreover, two years after fire, TB was greater than before fire in both fire seasons (EF: *P*=0.01; MF: *P=0.001*). TB regeneration in LF reached the same values of before fire, just three months after (*P*=0.98). In this fire season, higher values of total biomass were found in the next rainy season (February 2015 (T18); *P*=0.001) and two years after fire (*P*=0.001).

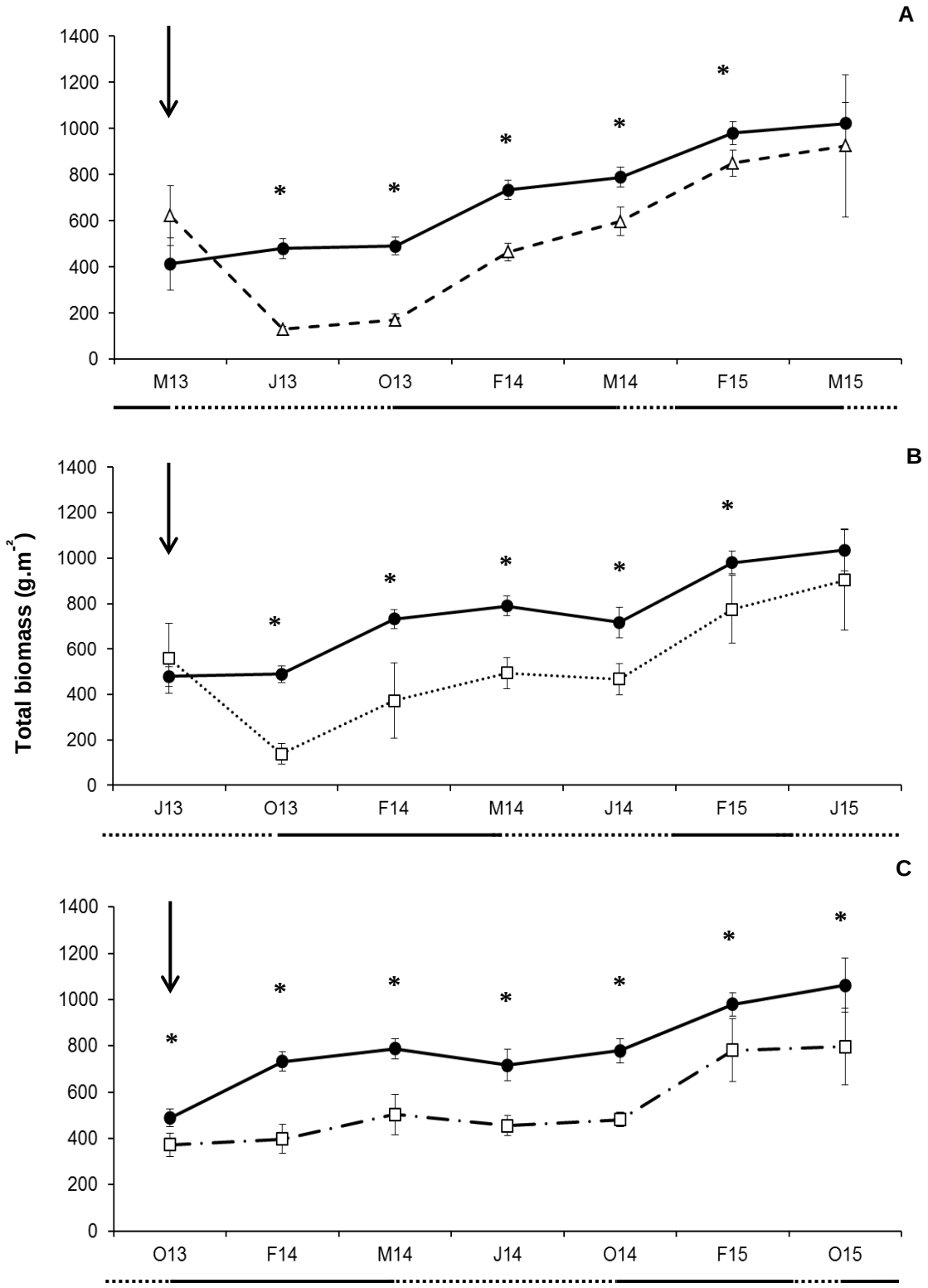

Figure 1. Total biomass (TB; g/m²) in different fire seasons: early- (A), mid- (B) and late-dry season fire (C). Black markers represent control plots and white markers represent burned plots. Before (M13, J13, O13), over one year (each tree months), the next rainy season (F15) and two years after fire (M15, J15, O15), in *campo sujo* areas in Central Brazil. Error bars represent the standard deviation, asterisk represents significant differences between treatments ($p \leq 0.05$). Arrows indicate when he prescribed fires were carried out, dotted line indicate the dry season, continous line indicate the rainy season.

Total dead biomass (TDB) followed the same pattern of the total biomass (Fig. 2): two years after fire in EF and MF values were the same between treatments (Fig. 2A and 2B). However, fires during the late-dry season led to lower values of dead biomass in comparison to control ($P \leq 0.05$, Fig. 2C). Dead biomass (TDB) in EF followed the same pattern of TB: registering similar values as before fire, in the middle of the rainy season (February 2014; T9; $P=0.2$; Table 1), while two years after fire, we found greater values than those found before fire ($P=0.001$). In MF, TDB values were the same as before fire one year after fire (July 14; T12; $P=0.6$) with greater accumulation two years after fire ($P=0.001$). Three months after fire (February 2014), TDB in LF was similar to before fire ($P=0.84$), with greater values in the next rainy season (February 2015; $P=0.001$) and two years after fire ($P=0.001$, Table 1).

When we evaluated the amount of live biomass (TLB), just three months after fire, all burned plots registered the same values of control (EF: $P=0.06$; MF: $P=0.5$; LF: $P=0.16$; Fig. 2D-F), showing that after biomass removal by fire, live biomass regenerated fast independently of season. Additionally, fire enhanced live biomass productivity in plots burned during the early-dry season, in F15 and M15, a higher amount of biomass was found in burned plots (F15: $P=0.04$; M15: $P=0.02$; Fig. 2D). Comparing the time of live biomass to regenerate in each fire treatment, in EF it occurred nine months after fire, in the middle of the rainy season (February 2014; T9; $P=0.9$; Table 1), while in MF, TLB regeneration occurred just three months after fire (MF: October 2013; T3; $P=0.9$). LF not only regenerated three months after fire, but also registered greater values (LF: February 2014; T3; $P=0.001$). The amount of live biomass varied seasonally, both in burned and control plots (Fig 2), showing the same pattern over the dry season and rainy season.

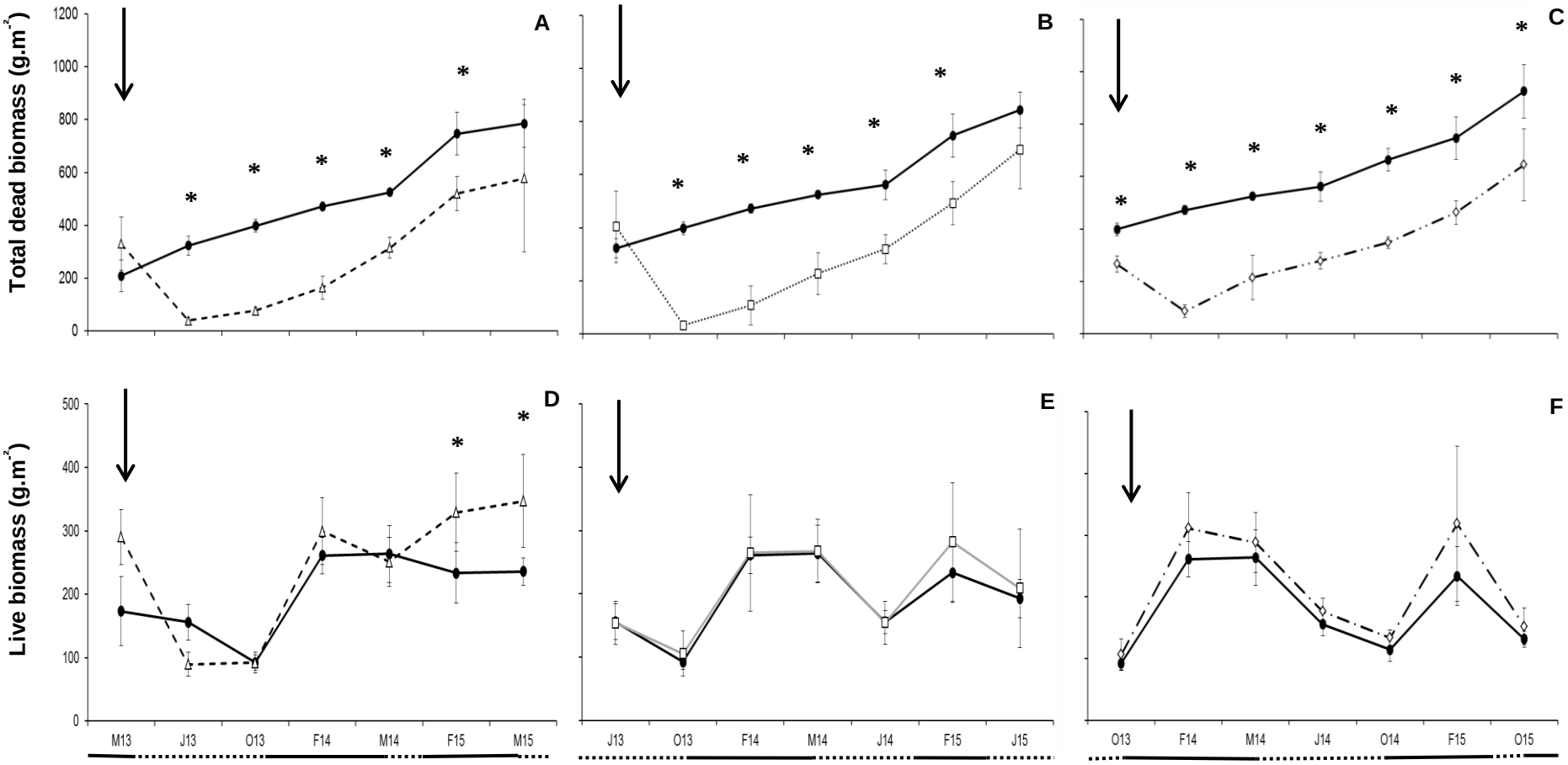

Figure 2. Dead biomass (TDB; g/m²) in different fire season: early- (A), mid- (B) and late-dry season fires (C), and live biomass (TLB; g/m²) in different fire season: early- (D), mid- (BE) and late-dry season fires (F). Black markers represent control plots and white markers represent burned plots. Before (M13, J13, O13), over one year (each tree months), the next rainy season (F15) and two years after fire (M15, J15, O15), in *campo sujo* areas in Central Brazil. Error bars represent the standard deviation, asterisk represents significant differences between treatments ($p \leq 0.05$). Arrows indicate when the prescribed fires were carried out, dotted line indicate the dry season, continous line indicate the rainy season.

Table 1. Total biomass (g/m²; mean±DP), total dead biomass (g/m²; mean±DP) and total live biomass (g/m²; mean±DP), in different fire season: early- (EF), mid- (MF) and late-dry season fires (LF). Before (M13, J13, O13), over one year (every tree months), the next rainy season (F15) and two years after fire (M15, J15, O15). In *campo sujo* areas in Central Brazil. Asterisks represents significat difereences (results of mixed models analysis) in every treatment in relation to values of before fire.

	EF	MF	LF
Total Biomass			
M13	620.91±129.68	----------	----------
J13	128.97±13.12*	557.85±153.71	----------
O13	169.20±26.14*	137.37±45.43*	372.51±49.95
F14	463.6±38.78	372.39±164.78	397.99±63.77
M14	595.72±62.13	494.78±68.39	502.86±87.98
J14	----------	467.67±68.56	455.2±43.41
O14	----------	----------	481.79±33
F15	849.19±57.52	774.72±148.25	781.36±136.68*
M15	924.61±308.64*	----------	----------
J15	----------	903.24±220.23*	----------
O15	----------	----------	797.46±165.11*
Total Dead Biomass			
M13	330.46±99.92	----------	----------
J13	39.35±10.46*	403.75±135.57	----------
O13	76.99±13.32*	31.85±17*	265.81±30.42
F14	164.23±43.86	107.52±74.07*	86.61±24.03
M14	314.44±39.45	227.14±78.31*	214.28±84.56
J14	----------	319.09±53.83	278.48±30.86
O14	----------	----------	348.03±21.86
F15	519.94±64.7	492.71±80.78	464.8±44.25*
M15	577.63±277.74*	----------	----------
J15	----------	694.34±146.31*	----------
O15	----------	----------	645.26±137.29*
Total Live Biomass			
M13	290.45±43.33	----------	----------
J13	89.62±18.84*	154.1±33.8	----------
O13	92.2±15.9*	105.52±35.3	106.7±25.43
F14	299.36±52.54	264.87±92.12	311.38±57.7*
M14	250.95±38.4	267.64±50.53	288.57±48.54*
J14	----------	154.36±34.03	176.72±21.42
O14	----------	----------	133.76±13.14
F15	329.24±61.46	282±93.66	318.55±126.06*
M15	346.97±73.42	----------	----------
J15	----------	208.9±93.71	----------
O15	----------	----------	152.19±30.15

Productivity of total biomass

EF had the same biomass productivity in one year (C=387±161g.m^{-2}; EF=601±53g.m^{-2}; *P*=0.07; Fig. 3A) and two years after fire as control (C=624±162g.m^{-2}; EF=1027±301g.m^{-2}; *P*=0.13; Fig. 3B). Fire in the middle of the dry season (MF) registered greater biomass productivity in the first year than control (C=238±83g.m^{-2}; MF=473±70g.m^{-2}; *P*=0.02; Fig. 3C). However, two years after fire, the productivity in MF and control was the same (C=557±109g.m^{-2}; MF=903±220g.m^{-2}; *P*=0.06; Fig. 3D). The same pattern was found for plots burned in the late-dry season: a higher productivity of biomass in burned plots than control in the first year after fire (C=298±42g.m^{-2}; LF=481±14g.m^{-2}; *P*=0.003; Fig. 3E), and no significant differences between control and burned plots two years after fire (C=572±98g.m^{-2}; LF=797±165g.m^{-2}; *P*=0.1; Fig. 3F).

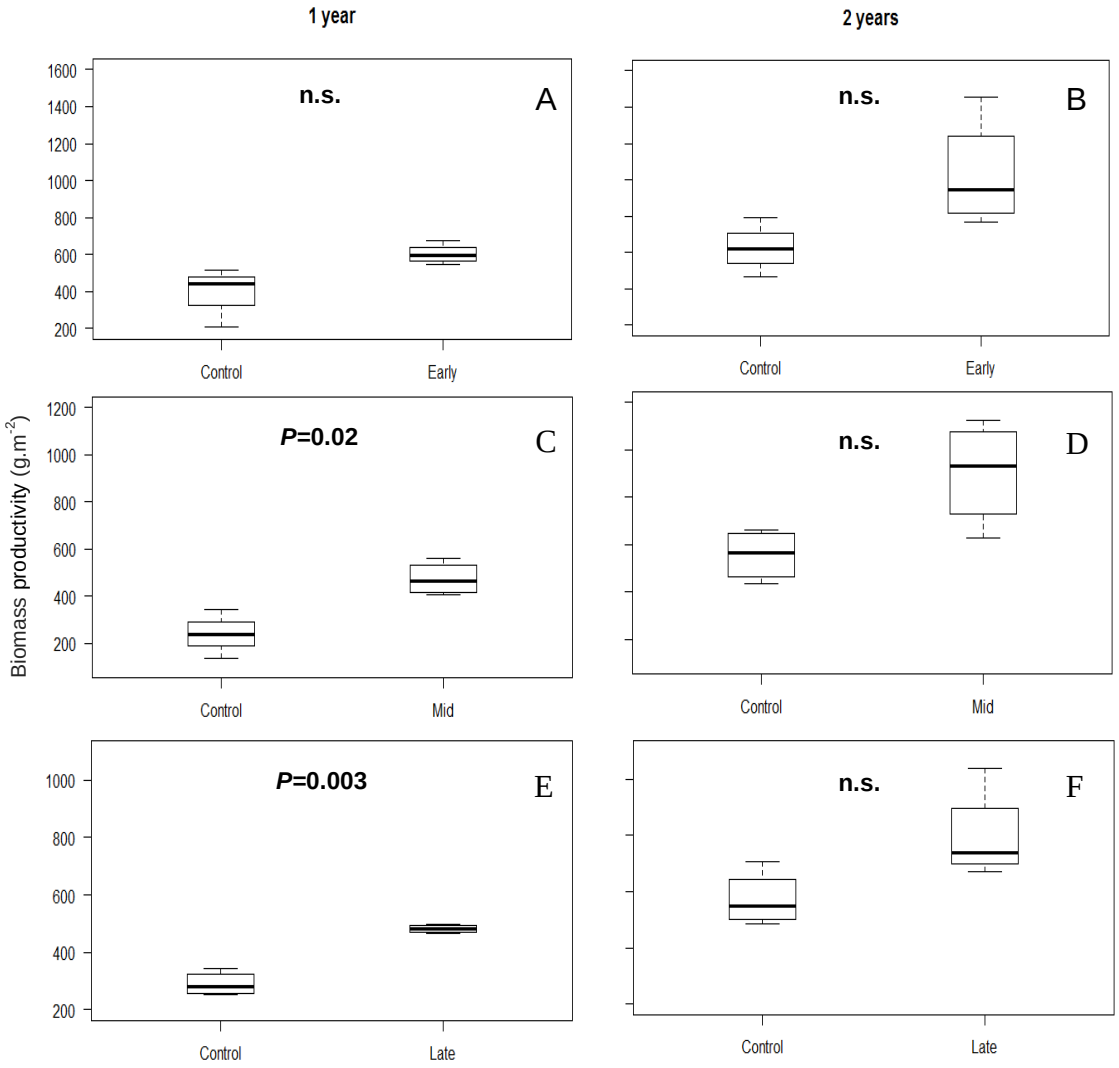

Figure 3. Total biomass productivity in one year in early- (A), mid- (C) and late-dry season fire (E). And two years after fire in early- (B), mid-(D) and late-dry season fire (F). Line between boxes is the median and T-shaped line represents the maximum and minimum values among four experimental plots.

Biomass composition

Biomass composition diverged between control and burned treatments differently in one and two years after fire. One year after fire, biomass composition differed between all fire season treatments and control (Table 2). The dissimilarities found between control and burned treatments were >20% (EF= 20%, MF=26.3%, LF=28.3%). Those differences in all seasons were driven mostly by the amount of dead biomass, which contributed from 68.2% (EF) to 81% (LF) of the dissimilarities. Two years after fire, biomass composition was similar to control in EF and MF (Table 2). However, LF differed from control (LF x control: Pseudo-*F*=10.76*; P*=0.001),

mostly due to the amount of dead biomass that was lower in LF (dissimilarity=17.8%, dead biomass contribution=79.1%).

Table 2. Differences in biomass composition between fire treatments (early- (EF), mid- (MF) and late-dry season fire (LF)) and control, one and two years after fire. Bold values represents significant differences between treatments (P≤0.05).

Time	Treatment	df	Pseudo-F	P
1 year				
	EF x Control	1	22.09	**0.02**
	MF x Control	1	29.516	**0.001**
	LF x Control	1	99.39	**0.03**
2 years				
	EF x Control	1	3.4121	0.13
	MF x Control	1	0.90858	0.57
	LF x Control	1	10.763	**0.001**

Discussion

Biomass regeneration may indicate the rate of vegetation recovery after fire, and will influence intensity and rate of spread of the next fire (Gagnon *et al.* 2015). But, how fast the biomass recover after fire? And, how is the total biomass productivity after the disturbance? These are fundamental questions for fire management, since we can predict the potential of vegetation to be burned again. Fire season can affect biomass regeneration, since the plant community will be in different phenological stages (Knapp *et al.* 2009) and also interfere in the fire intensity (Govender *et al.* 2006), which could implicate in different recoveries after fire.

Our results suggest that, regardless of fire season, live biomass reached the same values as control just after fire (three months). Total live biomass varies according to seasonality in control plots, and this same pattern was found in all burned plots. EF registered greater values of live biomass (than control) in the next rainy season and two years after fire. In prairies this same pattern was found of highest quantities of live biomass in the end of the rainy season, which can be mostly due to year climatic variation (Coppedge *et al.* 1998) and linked to precipitation patterns (Briggs & Knapp 1995). Cerrado has a seasonal climate with dry/rainy season (Eiten 1972) and live biomass seems to vary according to this seasonality. Soil water availability plays an important role in herbaceous aboveground biomass regeneration (Oliveras *et al.* 2013). Just after fire, EF is

followed by the dry season which could affect the biomass regeneration. Fire season also interacts with the plant physiological active periods: plants nutrients are storaged in underground organs at the begging of the dry season, being allocate during the rainy season to growth (when enough water becomes available), fire may lead to dormancy process when setting and followed by the dry season (Oliveras *et al.* 2013), what may explain why TLB in EF just regenerated (in relation to values found before fire) in the middle of the rainy season (February). MF is followed by a short dry season period and when the rainy season began the biomass also regenerates. LF is followed by the rainy season, with greater water availability and in association with plant physiological active period, leads to allocation of resources resulting in faster biomass regeneration.

The patterns of TB were not affected by any fire season. EF and MF registered the same values than control two years after fire. However, for LF this variable was different from control all over the period (including before fire). EF registered lower accumulation in TB in the first years after fire, while MF and LF have greater accumulation than control, despite that, two years after fire, no differences were found in TB accumulation between control and all fire season. These results corroborate with Nascimento Neto *et al.* (1998) that also found that the herbaceous layers in *campo sujo* completely recover 2 years after fire, indicating that biomass regeneration in Cerrado *campo sujo* is fast independently of the season of burning. In our study, most differences in biomass regeneration related to fire season, seems to occur during the first year following fire.

Cerrado is characterized by surface fires that propagate fast and consume most of the herbaceous layer (Miranda *et al.* 2002), that regenerated during the first year after fire. The rapid regeneration of TB, TLB and TDB (over time, in relation to values found before fire) is an important information for managers to evaluate fire risks and biomass dynamics in *campo sujo* areas. The regeneration of biomass over time (in each fire season) shows that the community already reached the potential to burn again (if the environmental conditions were favorable), in the first rainy season just three months after fire, LF, had already recovered all aboveground biomass (total, dead and live), while EF and MF had all biomass components recovered in just one year after fire.

Differences in total biomass composition (between burned and control, 1 and 2 years after fire) were mainly driven by the quantity of dead biomass. The accumulation of dead biomass is considered one of the most relevant traits that affect plant flammability and fire (Keeley *et al.* 2011)

and seems to be not modified by fire season: EF and MF registered the same values than control two years after fire, while, in LF TDB still different from control all over the period. The proportion of dead biomass in vegetation will influence the moisture content of vegetation (Baeza & Santana 2015), which can affect directly fire behavior: since the percentage of dead biomass and fuel load are the community components that best explained fire intensity in the area (Rissi *et al. submitted*) and dead biomass accumulation can lead to more intense fires harder to control (Whelan 1995; Fidelis *et al.* 2013), the use of prescribed burns it is important to reduce and manage biomass.

The amount of total (TB) and dead biomass (TDB) in control plots increased over time and did not vary according to seasonality. However, despite of fire season, live biomass regeneration was very fast and not reduced by any fire treatment. In Cerrado, biomass decomposition rate might be slow (Oliveras *et al.* 2013; Fidelis *et al.* 2013), thus the longer the time since last fire, the higher amount of TB and TDB, as already showed for tropical wet grasslands (Fidelis *et al.* 2013), showing how fire exclusion can influence this accumulation, reinforcing that, if no management is done, the risk of wildland fire will certainly increase over time. Prescribed burning can be used as an effective tool to reduce fuel, biomass accumulation and fire risk (Fernandes & Botelho 2003; Marino *et al.* 2010). Once that, if no management is done, biomass accumulation will affect vegetation and consequently fire behavior responses: mainly fire temperature and duration (Gagnon *et al.* 2015).

Which fire season could be interesting for biomass management? One year after fire, the productivity of TB (in relation to control) was greater in MF and LF, in this same period, biomass (TB, TDB and TLB) was regenerated and reached the potential to be burned again (in all fire plots, in relation to values found before fire). Despite that, we identify that EF will accumulate more live biomass than control in the second year after fire. EF is usually cool and easier to control (Pivello 2011). In the other hand, MF and LF are hotter and harder to control and if implemented should be set at the beginning and end of the day, with larger firebreaks and with help of a greater number of fire fighters. Our results shows that two years after fire, the accumulation of TB was similar between all fire treatments and control, suggesting that after this period fire season does not matter.

Conclusions

Biomass management is important in order to avoid intense fires. After one year, all burned plots reached the potential to be burned again in biomass quantity. Besides that, in general, fire season did not change the patterns of TB, TLB and TDB. Total live biomass changed according to seasonality (rainy/dry season, in all plots), while TDB and TB increased over time (in all treatments). In this context, if no management is done, this biomass can increase, leading to uncontrolled fires with possible negative consequences. To use fire as a tool to control biomass in order to avoid fire risk, our results suggest that fire season does not change the accumulation and regeneration of biomass.

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Capítulo 2

Does season affect fire behavior in Cerrado? Fire season has little effect on fire behavior in Cerrado

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BRIEF SUMMARY

We compared fire behavior in different fire seasons in areas of open savanna aiming to understand fire behavior and to provide information to control fuel and avoid wildfires. No differences were found among fire seasons in most of the fire behavior parameters analyzed.

ABSTRACT

Fire has played an important role in Cerrado for millions of years. We intended to evaluate fire behavior at different fire seasons in areas of open savanna providing information to control fuel and, thus avoid wildfires. It has been hypothesized that early (May – end of the rainy season) will be less intense than fires conducted in the middle and end of the dry season (July and October), due to the moisture content of the fuel. We compared fire behavior in early-, mid- and late-dry season. Fire intensity was mainly influenced by the combination of percentage of dead fuel and fuel load, however, there was no difference in the components of the equation used to calculate intensity: combustion efficiency and rate of spread were similar among treatments. Fire parameters did not differ among fire seasons. Flame height was best explained by the percentage of dead fuel + fuel moisture content, percentage of dead fuel + fuel load and also by the percentage of dead fuel, that means, by the type and quantity of fuel load. We recommend prescribed fires in a mosaic design, to reduce the percentage of dead fuel and to prevent wildfires during the dry season.

Keywords: dead fuel percentage, fire experiments, fire intensity, fuel type, tropical savanna.

INTRODUCTION

Fire plays an important role in determining the structure of different ecosystems worldwide (Bond *et al.* 2005), such as African (Trollope 1982), Australian (Morgan 1999) and Brazilian savannas (Cerrado, Simon *et al.* 2009), Ecuadorian páramo (Ramsay and Oxley 1996) and Mediterranean ecosystems (Lloret 1998; Keeley *et al.* 2012). Evidences in Brazil (Pivello 2011; Fidelis *et al.* 2012) and throughout the world (Bond *et al.* 2005; Hardesty *et al.* 2005; Bowman *et al.* 2009; Pausas and Keeley 2009) reinforces that most of the ecological processes of grasslands and savanna ecosystems are maintained by fire.

Despite the fact that these ecosystems have/had their own natural fire regime, humans have changed the frequency and timing of ignitions, modifying the fuel load and landscape pattern of fuel distribution and in several regions, fire has become more severe (Keeley *et al*. 2012). In other cases, fire has been suppressed, leading to changes in vegetation structure and biodiversity, as for example, the increase in woody cover in open savanna areas (e.g. Moreira 2000; Bond *et al.* 2005; Durigan and Ratter 2016). In fact, fire suppression could cause more intense wildfires due to the accumulation of dead fuel (Whelan 1995). In some areas of wet grasslands in Cerrado, four years of fire exclusion almost doubled the amount of dead biomass, leading to an increase in the dead component of the fuel load which could increase the risk of wildfires and hinder the establishment and survival of other plants (Fidelis *et al.* 2013). Thus, all these shifts in the natural fire regimes could change plant community structure, diversity, and ecosystem processes (Whelan 1995).

Therefore, in some fire-prone ecosystems, prescribed fires have been used as a management tool to reduce fuel levels, control the incidence, intensity and severity of fire (Govender *et al*. 2006), but also to maintain and conserve local biodiversity and vegetation structure (Govender *et al*. 2006; Van Wilgen *et al.* 2007). Moreover, fire management should be supported by scientific research, mostly through the establishment of long-term fire experiments that test different fire regimes, according to the ecosystem natural fire regime and current shifts they have been suffering (see experiences in the Kruger National Park, Van Wilgen *et al*. 2007).

Even though fire has been used as a management tool in many fire-prone ecosystems, fire season may be one of the least understood components of fire regime (Gill *et al.* 2002), although it

can significantly affect fire behavior (Knapp *et al.* 2009; Van Wilgen *et al.* 2007), plant phenology (Platt *et al.* 1988), community composition (Hodgkinson 1991; Whelan and Tait 1995; Knox and Clarke 2006), topkill and influence growth of large juveniles and small saplings (Werner and Prior 2013). The ability of plants to survive and persist to different fire seasons is related to their physiological state at the time of the fire and their growth form (Trollope 1982) and thus, vegetation will respond differently a particular fire season. Moreover, fuel load and moisture can be considered important factors affecting fire season, frequency and intensity in savannas (Trollope 1982) and thus, they should also be evaluated seasonally in order to explain variations in fire behavior.

In Cerrado, fire plays a major role on vegetation dynamics and it is considered one of the main factors maintaining the different physiognomies, together with soil characteristics and water availability (Coutinho 1990; Furley 1999; Moreira 2000; Miranda *et al.* 2009). Cerrado is characterized by a seasonal climate, with the existence of a well-marked dry season (Eiten 1972) that can last 3-5 months (Coutinho 1982; Furley 1999). Fire has been present in Cerrado for at least 10 million years (Simon *et al.* 2009) and has been influencing Cerrado vegetation ever since (Miranda *et al.* 2009). Natural fires in Cerrado are caused by lightning and occur mostly during the rainy season (October – April), but it may also occur in May and September (Ramos-Neto and Pivello 2000). However, as in many other fire-prone ecosystems, current land use, human activities and agricultural practices have considerably changed fire regimes in the Cerrado (Pivello 2011). Currently, anthropogenic fires are increasingly more common and usually set during the dry season to promote new shoots for cattle raising (Fidelis and Pivello 2011). As a consequence, the high incidence of wildfires is one of the major threats to Cerrado's biodiversity (Klink and Machado 2005; Durigan *et al.* 2007). While other fire-prone systems already use prescribe fires for conservation, fire is still not considered as a management tool for Cerrado (Durigan and Ratter 2016, Fidelis and Pivello 2011).

Although information about fire behavior is available for different Cerrado physiognomies (see Miranda *et al.* 2010), the main variables explaining fire were not explored in this non-replicated long-term study. Fire behavior might be influenced not only by fuel load quantity, but also by its structure and arrangement in the plant community, as well as combustion efficiency and

fuel water content (Castro & Kaufmann 1998) and we believe that some of those variables can vary according to the season (e.g. water content). Moreover, the retention of dead biomass by plants is an important property to make ecosystems more flammable and thus, influence fire behavior (Bond & Van Wilgen 1996). Thus, data about dead biomass accumulation and variation in different seasons is crucial. Information about fuel load can be found for Cerrado (Castro and Kauffman l998; Kauffman *et al.* 1994), however seasonality was not considered in most of the studies. Thus, the lack of information about the amount and quality of fuel load and other fire behavior parameters in the different seasons hinders management decisions, since knowing if there is an ideal season to burn is one of the main questions to provide answers to improve fire management (Durigan and Ratter 2016). Prescribed fires in the correct season may lead to different responses of the vegetation according to the aim of the management: change/maintenance of vegetation structure, control of fuel load, avoid fire risk, and/or maximize biodiversity conservation (Whelan 1995). Therefore we believe that our study can provide valuable information about variation of important variables, such as fuel load quantity and quality, and how this would affect fire behavior in the different seasons in open areas of Cerrado.

Therefore, this study aims to evaluate fire behavior in an open physiognomy of Cerrado (*campo sujo*) in different seasons (early-, mid- and late-dry season). We analyzed which variables explain fire parameters (fire intensity and flame height), and evaluated which variables (both environmental and fire) drive fire intensity (regardless to fire season), in order to understand fire behavior in Cerrado and also to provide information for management actions considering fire as a tool. We hypothesize that early- (May) fires will be less intense than fires occurring during mid- and late-dry season (July and October), mostly due to the lower percentage of dead fuel and higher water content.

MATERIAL AND METHODS

Study area

The study was conducted at the Reserva Natural Serra do Tombador (RNST), in Central Brazil (47°45-51'W and 13°35-38'S, 560-1118m a.s.l.). The climate is tropical and mean annual rainfall is between 1300 and 1500 mm (AER 2009) with a dry season from May to October.

The study site is composed by *campo sujo* physiognomy, which is characterized by a dominant herbaceous layer with scattered shrubs and dwarf trees (Coutinho 1978). The plots were established in an area with no invasive species, dominated by C4 grasses (e.g. *Mesosetum loliiforme, M. ferrugineum*, *Onchorahis ramosa*) forbs (e.g. *Deianira pallescens*, *Ichthyothere terminales*, *Mimosa somnians*), and shrubs (e.g. *Bauhinia dumosa*, *Harpalyce brasiliana*, *Mimosa* aff. *leiocephala*). The area has not been grazed since 2006 and last fire was in August 2011, thus the study area had been excluded from fire for two years prior to the beginning of the experiments.

Experimental design and data sampling

We established 30x30m experimental plots with a distance of at least 4m from each other, in a randomized block design. Firebreaks were established among plots (3m) and blocks. Since vegetation is heterogeneous, we established *a priori* the following criteria: plots should not have more than 20% of tree cover (to avoid tree clumps, which would not represent a *campo sujo*); and plots should not contain large patches of termites and bare soil (<1m^2), since the lack of fuel load in large patches could influence fire spread. Moreover, fire shows a high heterogeneity at fine-scale in Cerrado, mostly due to the presence of bare soil (Fidelis *et al.*, unpublished data). Plots were burned in May, at the beginning of the dry season (early, E), in July, mid-dry season (middle, M) and in October, at the end of the dry season and beginning of the rainy season, (late, L) being 4 replicates/treatment; total of 12 plots. We chose these seasons because most of the natural fires in Cerrado occur at the beginning and end of the dry season (Ramos-Neto and Pivello 2000), whilst anthropogenic fires usually occur during July-August, in the middle of the dry season, to improve pastures mainly for cattle ranching (Coutinho 1982).

The experimental fires were conducted individually in each plot to guarantee the independence of data. Fire was set at wind direction (head fire), being burned at the beginning and at the end of the day for security reasons (2 of them in each day period). Weather conditions such as air temperature, relative air humidity and wind speed were measured before, during and after the experiments, in order to evaluate the influence of environmental variables on fire behavior. The maximum height of grasses, forbs and shrubs were measured (according Pérez-Harguindeguy *et al.* 2013) in each plot before fires in ten subplots (1x1m) randomly established within each plot.

Fuel load in *campo sujo* can be composed by 50-80% of graminoids and thus, to evaluate fuel load (all aboveground biomass, $kg.m^{-2}$), we stablished a grid (1x1m, total of 900 subplots) in the plot before the experiments and sampled six samples (0.25x0.25m) along plot margin (to avoid interference in fire spread during experiments). Forbs and shrubs are also present in the vegetation and thus, first we separated the biomass in fine (mainly composed by graminoids) and coarse (diameter >1cm), but since the contribution of coarse biomass was very low (<1%), we considered the entire herbaceous biomass as fuel load. Miranda *et al.* (1996) sampled 25 plots of 0.25x0.25 to characterize fuel load in plots of 4ha in Cerrado, therefore we believe that, although vegetation is heterogeneous at fine-scale (Fidelis *et al.* unpublished data), our sample size will be sufficient to characterize fuel load. Each sample was weighed in the field and then taken to the laboratory where it was separated into dead and live fuel, dried at 70°C for three days and weighed again (to determine fuel moisture content). In our samples, the dead biomass corresponded to the dead standing biomass, considered to be an important factor to turn a plant more flammable (Bond & Van Wilgen 1996), excluding litter due to its low contribution to aboveground biomass in *campo sujo* areas (Rissi et al., *unpublished data*). We considered the total aboveground biomass the fuel load, since 84% of all biomass is consumed during fires in *campo sujo* (Castro & Kaufmann et *al.* 1998). After fires, we sampled another six samples (0.25x0.25m) to determine residuals. The residual biomass samples were dried and weighed in the laboratory and we used it to estimate combustion efficiency (%) and consumed fuel (w, $kg.m^{-2}$).

The maximum temperatures reached during each fire were assessed by using pyrometers made of aluminum plates painted with color-change crayons (ColeParmer®) with temperatures ranging from 120ºC to 600ºC. We randomly selected ten points in each plot (avoiding plot borders) and established ten pyrometers in each three different heights: 1cm below soil surface, at soil surface and 50cm aboveground, where most of the fuel could be found.

The fire parameters measured during and after the experiments were: rate of spread ($m.s^{-1}$), flame height (cm), and fire intensity ($kW.m^{-1}$, Byram's equation). To measure flame height and the rate of spread, we established a line along the outer border of the plot and marked four observation points (10, 15, 20 and 25m). We measured the time taken for the fire line to reach each of these points and the flame height at each point. From these values we calculated the

average rate of spread per plot. Fire intensity was calculated using the equation I=h.w.r, where h: is the heat yielded of fuel ($kJ.kg^{-1}$), w: consumed fuel ($kg.m^{-2}$), and r: rate of spread ($m.s^{-1}$). The value of 15500 $J.g^{-1}$ was used for heat yield (Griffin and Friedel 1984), the same used to calculate fire intensity in other Cerrado fire experiments (Miranda *et al.* 1996, 2010).

Statistical analyses

We used one-way analysis of variance (ANOVA) applied to randomization tests (Euclidean distance between sampling units, 10000 iterations) to evaluate differences among treatments (factor: fire season) for the following variables: air temperature (°C), air humidity (%), wind speed ($m.s^{-1}$), fuel load ($kg.m^{-2}$), amount of dead and live fuel ($kg.m^{-2}$), fuel moisture content (%), percentage of dead fuel (%), flame height (cm), fire intensity ($kW.m^{-1}$), combustion efficiency (%), rate of spread ($m.s^{-1}$), and height of graminoids (cm).

In order to determine which variables (or group of variables) best explained the two fire parameters, fire intensity and flame height, we constructed GLM models (Gaussian distribution) using single and combined variables. For the models, we did not consider fire season separately.

To evaluate which variables can be driving fire intensity, besides the ones used to calculate fire intensity, we selected single (percentage of dead fuel, fuel moisture content, relative air humidity, wind speed, fuel load and temperature), and possible combinations of variables (fuel load + percentage of dead fuel, fuel load + fuel moisture content, percentage of dead fuel + fuel moisture content, temperature + relative air humidity, temperature + wind speed and wind speed + relative air humidity).

For flame height we also constructed models using single variables (percentage of dead fuel, fuel load, graminoid average height, shrub average height, relative air humidity and wind speed) and combinations of variables (fuel load + percentage of dead fuel, fuel load + fuel moisture content, percentage of dead fuel + fuel moisture content and graminoids average height + shrubs average height). We included a null model for both fire intensity and flame height.

Models were selected using Akaike´s information criterion corrected for small sample sizes (AICc) and thus, we compared the models based on ΔAICc and Akaike weights**.** ΔAICc values <2 indicate equally plausible models (Burnham and Anderson 2002). The probability that each model

is the best of a set of proposed models can be evaluated by Akaike´s model weight (wAICc, Anderson *et al.* 2000). All analyses were performed using the R program (R Core Team 2013) with the vegan package (Oksanen *et al*. 2013) and the software MULTIV (Pillar 2005).

RESULTS

The experimental fires were conducted under similar conditions in all seasons (Table 1): air temperatures varied from 31 to 35ºC and wind speed was lower than 1.5 $m.s^{-1}$. Relative air humidity was lower during mid-dry season fires in relation to early- and late-dry season fires ($p=0.01$, Table 1).

Table 1. Environmental parameters (mean±EP) measured during the experiments of early- (May 2013), mid- (July 2013) and late-dry season fires (October 2013), in *campo sujo* areas in Central Brazil. Different letters represent significant differences between treatments ($p \leq 0.05$).

Fire Season	Air temperature	Air humidity	Wind speed
Early	31.0±1.2 [a]	50.0±3.3[a]	0.9±0.07 [a]
Mid	34.3±4.0 [a]	25.8±10.4[b]	1.5±0.4 [a]
Late	35.4±0.5 [a]	43.1±1.8[a]	1.4±0.7 [a]

Total amount of fuel load (dead + live) and the moisture content are not significantly different among fire seasons ($p=0.48$, $p=0.15$, respectively, Table 2). Combustion efficiency was greater than 89% in all seasons and was similar among treatments ($p=0.46$, Table 2). Rate of spread and flame height were the same for all fire seasons ($p=0.3$, $p=0.69$, respectively). However, percentage of dead fuel was higher in mid- ($p=0.02$, 63%) and late-dry season ($p=0.05$), corresponding to 73% of the total fuel load during the late-dry season (L).

Table 2. Fire parameters (mean±EP) in early- (E), mid- (M) and late-dry season fires (L) in *campo sujo* areas in Central Brazil. Different letters represent significant differences between treatments (p≤0.05).

Fire parameters	E	M	L
Fuel load ($kg.m^{-2}$)	0.73±0.03 [a]	0.75±0.05 [a]	0.65±0.06 [a]
Dead fuel ($kg.m^{-2}$)	0.41±0.02 [a]	0.47±0.04 [a]	0.48±0.04 [a]
Percentage of dead fuel (%)	56.41±2.68 [a]	63.47±3.35 [b]	73.83±2.63 [b]
Live fuel ($kg.m^{-2}$)	0.32±0.02 [a]	0.27±0.03 [a]	0.17±0.02 [b]
Fuel moisture content (%)	25.54±1.45 [a]	15.12±2.83 [a]	18.15±3.86 [a]
Rate of spread ($m.s^{-1}$)	0.05±0.01 [a]	0.23±0.13 [a]	0.35±0.15 [a]
Flame height (cm)	250±40 [a]	260±40 [a]	320±60 [a]
Combustion efficiency (%)	89.89±1.99 [a]	91.97±2.52 [a]	89.38±1.26 [a]

Independently of season, most pyrometers 1cm below soil surface did not change color and thus, temperatures were <120ºC (96.6% E, 100% M and 100% L, Fig. 1A). At soil surface, temperatures over 600^{o}C were registered in both E and M plots (6.7% and 5%, respectively, Fig. 1B). In E plots, the most frequent temperature was >360°C (60%), while in mid-dry season, temperatures >470°C were more frequent (42.5%). In L plots, pyrometers at soil surface registered a maximum temperature of 470ºC (42.5% of pyrometers), and no temperatures ≥600ºC were observed. However, at 50cm aboveground, temperatures ≥600°C were recorded for all fire seasons (10%, 17.5% and 15% of all pyrometers for early-, mid- and late-dry season, respectively).

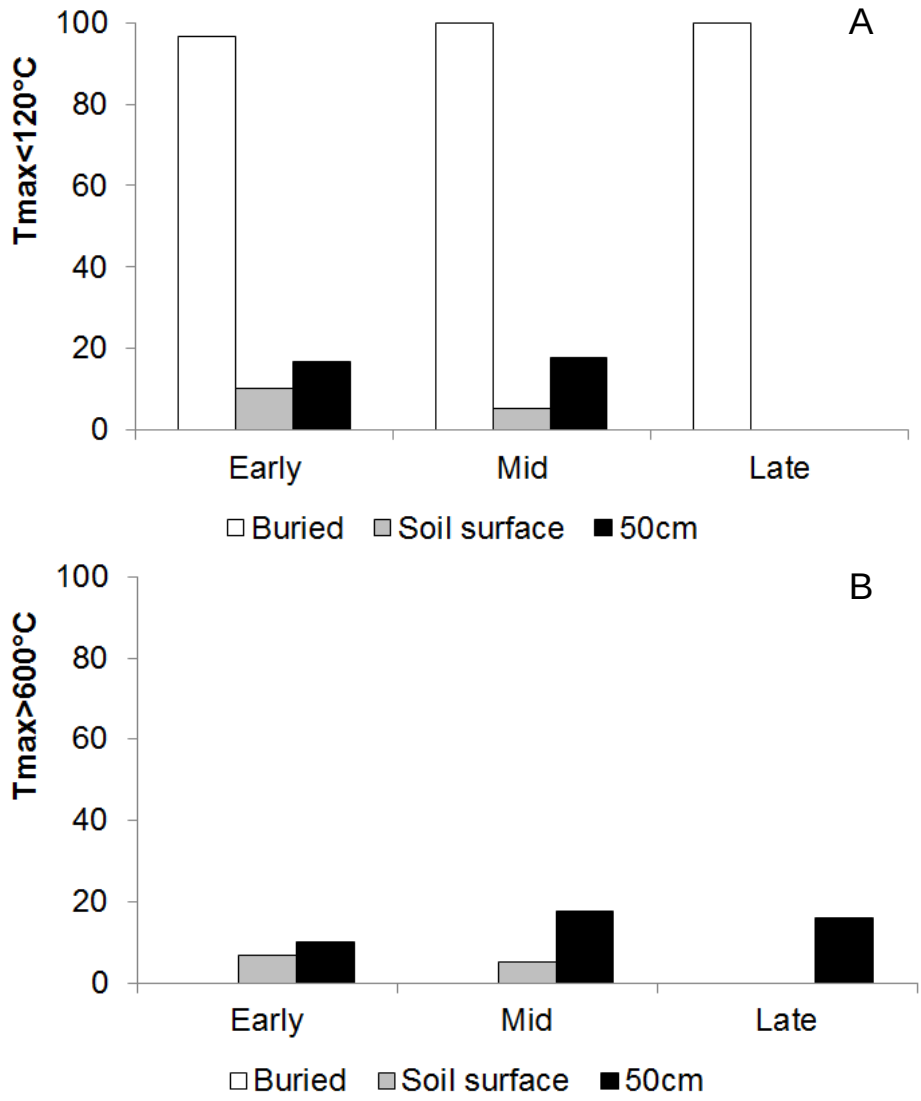

Figure 1. Frequency of pyrometers with maximum temperature (Tmax) <120°C (A) and frequency of pyrometers with maximum temperature (Tmax) ≥600°C (B) buried (1 cm below soil surface), at soil surface and 50 cm above soil surface in early, mid and late-dry season fires in *campo sujo* areas in Central Brazil.

Fire intensity varied from 503±119 kW.m^{-1} during the early-dry season, to 2707±1899 kW.m^{-1} (mid-dry season) and 3009±1408 kW.m^{-1} in the late-dry season (p=0.38, Fig.2).

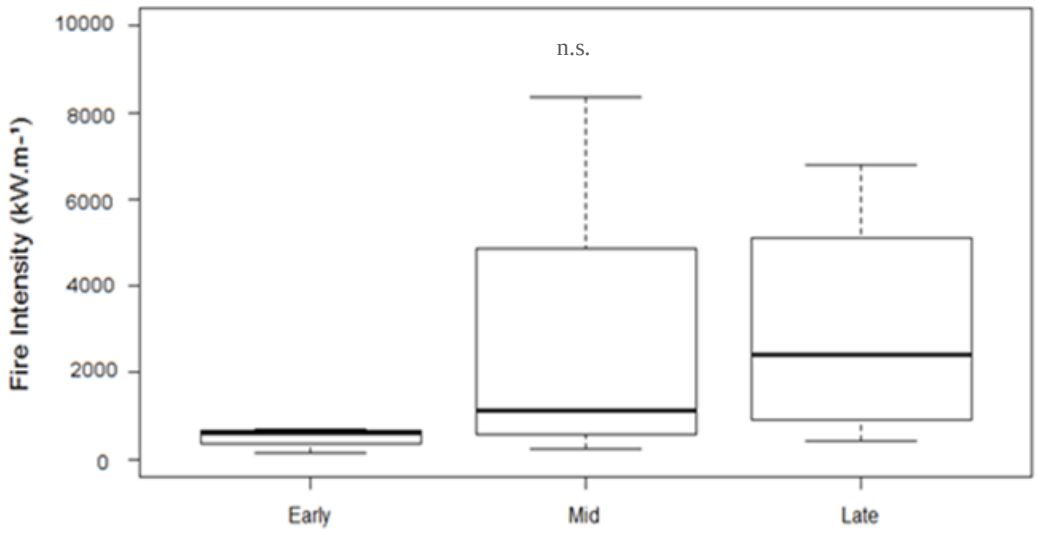

Figure 2. Fire intensity ($kW.m^{-1}$) in the different seasons: early, mid and late-dry season fires, in *campo sujo* areas in Central Brazil. Line between boxes is the median and T-shaped line represents the maximum and minimum values among four experimental burned plots.

The combination of fuel load and percentage of dead fuel was the best model to explain fire intensity variability in our experiments, accounting for 71% of the Akaike weights in the model set (ΔAICc=0.0, wAICc =0.71, Table 3).

Table 3. Results from model selection for fire intensity in all seasons in *campo sujo* areas in Central Brazil, using Gaussian distribuition. ΔAICc: difference in AICc units between the model and the most parsimonious model of the candidate set (smallest AICc value; the most parsimonious model is displayed in bold face). wAICc: Akaike weight, indicate the relative probability of a given model being the best model out of those compared for the observed data.

Models	ΔAICc	wAICc
Percentage of dead fuel + fuel load	**0.0**	**0.71**
Percentage of dead fuel + fuel moisture content	2.7	0.18
Percentage of dead fuel	3.7	0.11
Fuel moisture content + fuel load	14.1	<0.001
Fuel moisture content	14.7	<0.001
Wind speed + Relative air humidity	16.2	<0.001
Wind speed + Temperature	16.8	<0.001
Wind speed	16.8	<0.001
Relative air humidity + Temperature	17.9	<0.001
Relative air humidity	17.9	<0.001
Temperature	19.2	<0.001
Fuel load	19.3	<0.001
Fire Intensity.null	204.1	<0.001

Flame height was best explained by the combination of percentage of dead fuel and fuel moisture content (ΔAICc=0.0, wAICc =0.30, Table 4, Fig. 4A). In addition to this model, the combination of fuel load and percentage of dead fuel (ΔAICc=0.1, wAICc =0.29, Table 4), followed by the percentage of dead fuel (ΔAICc=0.2, wAICc =0.27, Table 4) were also good predictors for flame height, showing, thus, that fuel load (both type and quantity) is the most important variable explaining fire intensity and flame height.

Table 4. Results from model selection for flame height in all seasons in *campo sujo* areas in Central Brazil, using Gaussian distribuition. ΔAICc: difference in AICc units between the model and the most parsimonious model of the candidate set (smallest AICc value; the tree most parsimonious models are displayed in bold face). wAICc: Akaike weight, indicate the relative probability of a given model being the best model out of those compared for the observed data.

Models	ΔAICc	wAICc
Percentage of dead fuel + fuel moisture content	**0.0**	**0.30**
Percentage of dead fuel + fuel load	**0.1**	**0.28**
Percentage of dead fuel	**0.2**	**0.27**
Wind speed	2.9	0.07
Graminoids average height + shrubs average height	6.3	0.01
Fuel moisture content + fuel load	6.9	0.01
Relative air humidity	6.9	0.00
Shrubs average height	7.4	0.00
Fuel load	7.5	0.00
Graminoids average height	7.7	0.00
Flame height.null	142.4	<0.001

DISCUSSION

Fire behavior is well studied in different ecosystems in the world. However, information about how fire season affects it and the most important variables explaining fire intensity are usually lacking. We have not found significant differences of fire intensity, flame height, fuel load and rate of spread between fire seasons. However, when we analyzed fire intensity and flame height, independently of fire season, we observed that percentage of dead fuel load, composed mostly by dead biomass of graminoids, is one of the most important variable related to fire intensity and flame height in Cerrado, regardless of fire season. Since we observed a tendency of higher intensity at the mid- and late-dry season and the proportion of dead fuel may vary among seasons (e.g. Fidelis *et al.* 2013), local managers should also consider this variable when elaborating management plans using fires in their areas. Therefore, fuel load should not only be evaluated as total fuel load, but it should be separated into dead and live fuel, as well as having its moisture content analyzed.

More than 55% of the fuel load was composed by dead fuel and the total amount of fuel load was similar for all treatments. However, the percentage of dead fuel from the total fuel load

was higher in mid- and late-dry season fires (Table 2). Due to the seasonality, many graminoid and forb species usually dry out during winter (dry season), which causes standing dead fuel accumulation and could promote more intense and hotter fires in long-term and especially with greater intervals between fires (Whelan 1995; Oliveras *et al.* 2013). The time since last fire contributes for the dead fuel accumulation. In a *campo sujo* area excluded from fire for two years, around 40% of total fuel was composed by dead fuel while in areas excluded from fire for seven years, the amount of fuel load almost doubled, varying from 45 to 75% of dead fuel (Chiari *et al*. unpublished data). In Cerrado wet grasslands, Fidelis *et al.* (2013) also reported a greater accumulation of dead fuel in areas excluded from fire for four years (460 $g.m^{-2}$) in relation to areas excluded from fire for two years (255 $g.m^{-2}$), probably due to low decomposition rates. Thus, not only season, but time since last fire influence the accumulation of fuel load and dead biomass. Since fire intensity and flame height are best explained by the amount of dead fuel, then, areas that have been excluded from fires for greater periods could have more intense fires especially during seasons where dead fuel accumulation is higher, increasing the risk of wildfires. Our experiments were set only two years after the last fire and thus, differences among fire intensity might not have been observed due to the shorter time without fire. If fires were set when exclusion time was longer (e.g. 4-5 years), differences among fire seasons might have been found.

Not only the composition (percentage of dead and live fuel) and the amount of fuel load, but its vertical and horizontal distribution can also influence fire parameters, especially, the temperature (Bond and Van Wilgen 1996). The vertical distribution of temperature is a key factor for individual plants and plant parts survival (Whelan 1995), and is mainly influenced by the vertical distribution of vegetation (Bilbao and Medina 1996). In our study area, percentage of temperatures above 600°C at soil level were observed for early and mid-dry season fires, while 50cm aboveground temperatures >600°C were found in all seasons. Miranda *et al.* (1993, 1996) registered temperatures around 500°C at 60cm aboveground (in areas protected from fire for 15 years), however in an area of *campo sujo* burned annually, maximum temperatures at this same height reached between 197°C and 221°C. Since this type of vegetation is very heterogeneous, temperature distribution will highly depend on vegetation structure, the accumulation of dead fuel and time since last fire and, therefore, will be highly variable within an area (Fidelis *et al.*

unpublished data). The longer the exclusion of fire, the higher the temperatures reached during fire (Oliveras *et al.* 2013), which could influence nutrient loss (Pivello & Coutinho 1992, Kauffmann *et al*. 1994), species regrowth, seed survival (Daibes *et al.* unpublished data), germination and individual plant survivorship (Whelan 1995).

Cerrado is characterized by surface fires that propagate fast and consume most of the herbaceous layer. The combustion efficiency in our study was 89%, where most of fuel consumed was from the herbaceous layer, confirming the high flammability of this vegetation only two years since last fire, allowing frequent fires to occur regardless of season. Additionally, these fires rarely kill the woody vegetation due to their low flame height (Miranda *et al.* 1993), which is between 1.2 and 2.9m (Castro and Kauffmann 1998). In our study, flame height varied from 2.5m (EF) to 3.2m (LF). Gorgone-Barbosa *et al.* (2015) found that the presence of an invasive species in *campo sujo* areas led to higher flames, which could affect tree survival in the area. Since fuel load can affect vertical spread of fire (Whelan 1995), we showed that not only total amount of fuel load, but its properties (moisture content and % of dead fuel) should also be considered, since they influenced flame height.

In African savannas, the density of both trees and shrubs is not affected by different fire regimes (Higgins *et al.* 2007, Van Wilgen *et al.* 2007). However, the herbaceous layer can be significantly affected by fire season (Van Wilgen *et al.* 2007) and since most of the Cerrado diversity is in the herbaceous layer, decision-makers should consider it when planning the management in Cerrado nature reserves. Nevertheless, the aim of fire management, when present, in Brazilian nature reserves is to prevent wildfires (by fire suppression) and not to maintain biodiversity and vegetation structure (Durigan & Ratter 2016). Even actions to control fuel, as for example, burning in a patch mosaic are not considered. These suppression policies would lead to an increase in the fuel load (and dead fuel), leading to more intense fires (as a consequence, difficult to control), which could threaten Cerrado biodiversity (Oliveras *et al.* 2013).

Fire management can have different objectives: hazard-reduction, maintenance of ecological roles of fire, flower harvesting, protect/maintain target species or control invasive ones (Whelan 1995; Pivello & Norton 1996), and human protection purposes (Bradstock *et al.* 2012; Keeley *et al.* 2012). It should adapt to land use, climate change, and be based on research and on

the knowledge of the local community (Cook *et al.* 2012). Thus, decision-makers in Cerrado nature preserves should first set their objectives when they are plaining to use fire as a management tool in their conservation unit (Pivello & Norton 1996).

Managers in Cerrado preserves should also consider fuel load and percentage of dead fuel when evaluating fire risk and planning for fire management. Cerrado physiognomies vary in type and quantity of fuel load: from grassland (with more fine fuels) to forest types (almost no fine fuels and more trees) and thus, decision-makers should also evaluate fire risk and the use of fire in these different physiognomies. We believe that fire can be used in grassland and savanna physiognomies, not only to control fuel load but also to maintain biodiversity. One should also remember that most of the biomass of these physiognomies is found belowground (Castro & Kaufmann 1998) and vegetation regenerates very fast after fire (Coutinho 1990), and thus, fire would not affect the carbon storage of Cerrado.

Fire season did not change fire behavior, but we believe that if the area is excluded from fire for a longer period, the higher accumulation of dead biomass at the mid- and late-dry season might lead to more intense fires. Thus, for applying prescribed fires there are some implications to consider: 1) if the management aim is to reduce wildfire risk by fuel reduction, managers should evaluate annually both the fuel and percentage of dead fuel accumulated in the area. 2) fires during the early-dry season would be less intense and easier to control. However, if the aim is also to maintain biodiversity, managers should be aware that early-dry season fires also tend to have lower rates of spread (in our study early-dry season fires registered a rate of spread between 0.01 and 0.06 $m.s^{-1}$) and possibly higher residence times, which could affect bud banks (Clarke *et al.* 2013) and lead to higher mortality rates of saplings and juveniles (Werner and Prior 2013). Additionally, fire in this season will be followed by a dry season (3-4 months) which can possibly cause additional restrains for vegetation regeneration. On the other hand, mid- and late-dry season fires showed to have higher variation on fire parameters such as rate of spread and flame height. We have not measured residence time of fire, but we have observed in other experiments that temperatures >200ºC do not last more than 3 minutes (Rissi *et al.* unpublished data, Fidelis *et al.* unpublished data), as already showed by Miranda *et al.* (1993). Seeds of some species of Cerrado can survive such temperatures (see Fichino *et al.* 2016) and buds are usually well-protected

belowground (Appezzato-da-Gloria *et al.* 2008), thus fires during these periods may not have negative effects on vegetation. Although a positive aspect of burning the vegetation in the late-dry season is the rain in the following months, these fires are more difficult to control. Therefore, if managers choose to use fire during this season, they should use larger fire breaks and set fires at the beginning and end of the day. If the aim of the management is to suppress woody vegetation in open physiognomies, fires should also be set during the middle and end of the dry season once that flame height, in all models, was best explained by the percentage of dead fuel, which was greater in the middle and in the end of the dry season.

We believe that the best use of fire in open physiognomies of Cerrado should combine a mosaic of different sizes, burned in different seasons and frequency, in order to maintain biodiversity, reduce fuel load and fire risk. However, we assure that, if no management is performed in these areas, dead fuel will accumulate and wildfires will take place, affecting negatively the local fauna and flora.

Conclusion section

No significant difference was found related to fire behavior and fire season in short-time since the last fire (2 yrs). However, if areas are excluded from fire for longer periods, we believe that burning during the mid- and late-dry season would lead to more intense fires, due to the higher accumulation of dead fuel. Once that, this variable was the best one to explain variation in fire intensity in our study site. However, for applying prescribed fires there are some implications to consider according to management aim: to reduce wildfire risks and fuel load, fire could be set in any season. However, if the aim is to maintain biodiversity and/or suppress woody vegetation: mid and late fires are better, but, fires during mid and late-dry season are difficult to control and spread very fast and is recommended to use larger fire breaks and set fires at the beginning and end of the day. We believe that the best use of fire in open physiognomies of Cerrado should combine a mosaic of different sizes, burned in different seasons and frequency.

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Capítulo 3

Are open savannas plant communities affected by fire season? An example from the Cerrado

Mariana Ninno Rissi & Alessandra Fidelis.

Abstract

Questions: Does fire season affect the vegetation structure in short-term in Cerrado communities? Does fire season change the vegetation and functional groups (graminoids, forbs and shrubs) cover, diversity and richness in post-fire communities?

Location: Open savannas from Cerrado ("campo sujo"), Central Brazil (Reserva Natural da Serra do Tombador, Brazil).

Methods: We established 16 plots with different fire season treatments (4 plots/treatment, 10 subplots/plot): early- (EF, burned in May – begin of the dry season), mid- (MF, burned in July – middle of the dry season), late-season fires (LF, burned in October – end of the dry season and beginning of the rainy season) and control (not burned). At each time of observation, bare soil, dead vegetation and species cover were visually estimated. Later, species were grouped according to their functional group (graminoids, forbs and shrubs) for statistical analyses. Total richness and each functional group richness were calculated for all treatments over time. Vegetation survey was carried out before experiments, every tree months during the first year, the following wet season and two years after fire.

Results: The most important effect of fire treatments was the removal of dead vegetation and consequently increased in bare soil during the first year after fire. EF enhanced total species richness, six months after fire, and the same pattern was found between all burned plots and control. All functional group recovered fast in all fire seasons, forbs cover was greater in LF during the middle of the dry season. In EF shrub cover was greater during the middle of the dry season and during the rainy season, in MF shrub cover was greater two years after fire, while in LF shrub showed a rapid answer regenerating just after fire. Functional groups richness was not higher in any fire treatment and showed the same pattern of control. In general species composition (presence/absence of species) and species cover, vary during rainy and dry season in all treatments and fire season did not change those patterns.

Conclusions: Fire (regardless of season) removed dead vegetation and consequently opened gaps in vegetation, maybe decreased the competition and enhanced the available of nutrients and contributed to the rapid regeneration of vegetation. Herbaceous layer dynamics (in fire absence) changed mainly due to seasonality (between dry and rainy season). In general, fire season did not

change the patterns of cover, richness and diversity, suggesting that (in short-time) fire season had little effects on herbaceous vegetation dynamics. Therefore, studies considering fire set more times in each fire season are essential to a better understanding of Cerrado herbaceous vegetation dynamics after fire.

Keywords: prescribed fire; functional groups; herbaceous layer; tropical savanna; fire management; fire season, community patterns.

INTRODUCTION

Fire season is an important component of fire regime (Gill *et al.* 2002), which can significantly affect plant community assembly (Hodgkinson 1991; Hodgkinson 1998; Knox & Clarke 2006) and change the competitive abilities of plants (Bond & Van Wilgen 1996; Whelan 1995). Therefore, how vegetation and functional groups respond to fire in different seasons, as well as the strategies used by plants can be critical to community composition and dynamics (Bond & Van Wilgen 1996; Whelan 1995). Plant responses will depend on if and when they regenerate after fire (Bond 2004).

After fire, one of the most important effects in post-fire communities is the removal of litter and standing dead vegetation, following by the opening of gaps in the area (Bond & Van Wilgen 1996; Fidelis *et al.* 2012). Moreover, there is an input and consequent increase in nutrient availability (Coutinho 1982; Whelan 1995), which can lead to competition among species to occupy these new sites (Boughton *et al.* 2013), as well as increases in plant growth rates and productivity (Whelan 1995). At the individual level, some savanna grasses registered rapid regrowth, which may give a competitive advantage for their establishment (Ripley *et al.* 2015). At community level, changes in species richness (such as increase/decrease), composition (as species being lost/replaced/new species) and plant community structure (such as change in functional groups cover) can be observed (Whelan 1995; Fidelis *et al.* 2012; Boughton *et al.* 2013).

The persistence of species in post-fire environments may be determined by phenological and physiological state (Pavlovic *et al.* 2011). Distinct patterns of regrowth and plant establishment can be observed depending when fire was set (Russell *et al.* 2015), since when fire occurs, vegetation regeneration will be affected through distinct mechanisms in seasonal climates, such as water availability, soil and plant moisture content, fire intensity, seasonality and residence time (Sarmiento 1984; Whelan 1995; Govender *et al.* 2006; Céspedes *et al.* 2013). Fire season interacts with plant physiological active periods: plant nutrients may be stored in underground organs at the begging of the dry season, being reallocated to aerial parts during the rainy season (when enough water becomes available, Oliveras *et al.* 2013). Although, how fire season affect the herbaceous layer in Cerrado is not well understood, in order to determine if there is an ideal fire season to set prescribed fires (Durigan & Ratter 2016). The studies about fire season and

community changes looked to the woody layer (Sato *et al.* 2010; Reis *et al.* 2015), to a specific fire season or to the effect of presence/absence of fire (Hoffmann 1999).

Fire has been influencing Cerrado vegetation since at least 4 million years (Simon *et al.* 2009), and can be considered an important ecological and evolutionary factor. Natural fires in Cerrado are mostly caused by lightning at the end of the dry season (September-October), but also in the rainy season (September– May; Ramos-Neto & Pivello 2000). However, anthropogenic fires are mostly set during the dry season (Ramos-Neto & Pivello 2000) to promote new shoots for cattle raising (Coutinho 1982), what may be changing the natural fire regime in Cerrado (Fidelis & Pivello 2011). Coupled with these changes, fire suppression has also been greatly altering composition, richness and physiognomy of plant communities in this vegetation (Hoffmann & Moreira 2002; Miranda *et al.* 2009; Dantas *et al.* 2013). Studies conducted to evaluate herbaceous layer vegetation responses to fire season in Cerrado are essential, since they provide essential information about community functioning and ecological issues (Durigan & Ratter 2016), which can be used in fire management and to give a better understanding of this fire-prone ecosystem.

Therefore, this study aims to evaluate in short-term the influence of fire season (early-, mid- and late-dry season) on vegetation richness structure, and dynamics in post-fire community. We hypothesized that fire at different seasons lead to different responses in species recovery and therefore will affect the structure and dynamics of communities, as well as species composition. We expected that fires set at the beginning of the dry season will delay vegetation recovery (plant cover) due to the following months with water restrictions (ca 3-4 months of dry season), whilst plots where fire was set at the end of the dry season (late-dry season fire), will show faster regeneration, greater cover, richness and diversity, due to the rainy that will happen just after fire. Answering these questions could be relevant for Cerrado open physiognomies management and also provide a better understanding of vegetation patterns and dynamics following fire season.

MATERIAL AND METHODS

Study area

The study was conducted at the Reserva Natural Serra do Tombador (RNST), in Central Brazil (13°35-38'S and 47°45-51'W, 560-1118m a.s.l.). The study area is dominated by *campo*

sujo, which is characterized by the dominant herbaceous layer with scattered shrubs and small trees. The herbaceous layer is rich in plant species, composed mainly by C4 grasses, sedges, forbs and shrubs from different botanical families, e.g. Asteraceae, Lamiaceae, Lythraceae and Poaceae. Climate is tropical, with a marked dry season (usually from May to September), with mean annual rainfall between 1300 and 1500 mm (AER 2009). The last fire occurred in the area in August 2011 and the experimental fires were carried out in 2013.

Experimental design and data sampling

We established 30x30m experimental plots (4 replicates/treatments; total of 16 plots) in a randomized block design in the area with at least 4m distance from each other. A firebreak (3m wide) was established around each plot and block to prevent fire to spread. The following fire treatments were established: burning in May, at the beginning of the dry season (early-dry season fire, EF), burning in July, at the middle of the dry season (mid-dry season fire, MF), burning in October, at the end of the dry season and beginning of the rainy season (late-dry season fire, LF), and control (unburned, C). The experimental fires were conducted individually in each plot to guarantee the independence of data. For more details about the fire experiments, please see Rissi *et al.* (Capítulo 2).

Vegetation sampling

In each plot, we randomly established and fixed ten subplots (1x1m), for which we used some rules as: absence of cattle paths, termites, anthill, shrubs greater than 1.5m or other condition different from the others subplots. In the subplots, we visually estimated the cover of bare soil, dead vegetation (litter + standing dead vegetation) and plant species. Only shrubs <1.5m were sampled, to characterize the area. Later, species were grouped into different functional groups according to the growth form: graminoids (grasses, sedges, Xyridaceae), forbs and shrubs (shrubs + subshrubs). The amount of lianas and palm trees was negligible and therefore, species of these groups were not considered.

All sampling was conducted before each experiment (2013: May-M, July-J, October-O) and every three months, during one year (May 2014 – M14, July 2014 – J14 and October 2014 – O14).

After that, the next vegetation sampling was conducted in the middle of the wet season (February 2015 – F15) and two years after fire experiments (May 2015 – M15, July 2015 – J15 and October 2015 –O15). Burned and unburned (control) plots were sampled at each time of observation.

Statistical analyses

In order to evaluate differences in cover (%, bare soil, dead vegetation, graminoids, forbs, and shrubs), and richness (total and for each functional group) in each season for each time of observation, we performed mixed linear model analysis. We considered treatments (burned x unburned) as the fixed factor and the plots as the random factor. To verify changes, we also performed mixed linear models, we considered in the analysis time as the fixed factor and the plots as the random factor.

In order to verify changes in the percentage of gain/loss of species in relation to values found before fire, we also performed mixed linear models.We considered in the analysis time as the fixed factor and the plots as the random factor.

To find patterns of changes in vegetation through time, we performed principal coordinate analyses (PCO), with sampling units described by species cover at each time of observation for each treatment (Chord distance as resemblance measure). We used the first PCO axis, which accounted for the greater part of data variation, to illustrate treatment differences overtime. We also performed principal coordinate analyses, with sampling units described by species presence/absence at each time of observation and treatment (Jaccard as resemblance measure) to illustrate changes in plant communities composition.

To evaluate the differences in species cover in control plots (dry x rainy season), we used Permanova analysis (Anderson 2001), applied to Bray Curtis similarity matrix generated from species cover of community structure data (graminoids, forbs and shrubs). To all treatments, in each time, we calculated Simpon´s diversity, after that, we performed mixed linear models (to compare diversity between buned x unburned). Treatment was used as fixed factor and plots as the random factor.

All analyses were performed using the R program (R Core Team 2013) with the packages: vegan (Oksanen *et al.* 2013), multcomp (Hothorn *et al.* 2008), analogue (Simpson & Oksanen 2015), labdsv (Roberts 2016) and nlme (Pinheiro *et al.* 2015).

RESULTS

Effects of fire season on plant community structure and richness

Fire affected the cover of bare soil by increasing the gaps available in all fire treatments during the first year after fire ($p \leq 0.05$). In all fire treatments, bare soil cover decreased to the same value as control plots in February 15 (EF: $p=0.54$; MF: $p=0.4$; and LF: $p=0.22$) and two years after fire (EF: $p=0.78$; MF: $p=0.28$; and LF: $p=0.15$). In all treatments, two years after fire, bare soil cover was lower than before fire (EF: $p=0.001$; MF: $p=0.01$; LF: $p=0.02$ and C: $p=0.001$). Plots burned in the EF and LF showed lower dead vegetation cover than controls, even two years after fire ($p \leq 0.05$, Fig. 1D, 1F). However, in MF, dead vegetation cover was the same as control two years after fire experiments ($p=0.39$, Fig. 1E). Dead vegetation cover also increased in all treatments two years after fire (EF: $p=0.02$; MF: $p=0.03$; LF: $p=0.02$ and C: $p=0.01$)

Species richness in control plots varied with seasonality: more species were found during the rainy season (February) than in the dry season (July or October; J13xF14: $p=0.01$; O13xF14: $p=0.01$; F14xO14: $p=0.01$ and F15xO15: $p=0.01$). When compared to control, the patterns of species richness were similar in all fire treatments (Table 1). Species richness was higher in control than in EF three months after fire ($p=0.01$; Table 1). No differences were found in number of species between control and MF, LF (Table 1). Simpson´s index did not change between treatments (burned x unburned) over time. The patterns of diversity were very similar in all fire treatments and control (Table 1).

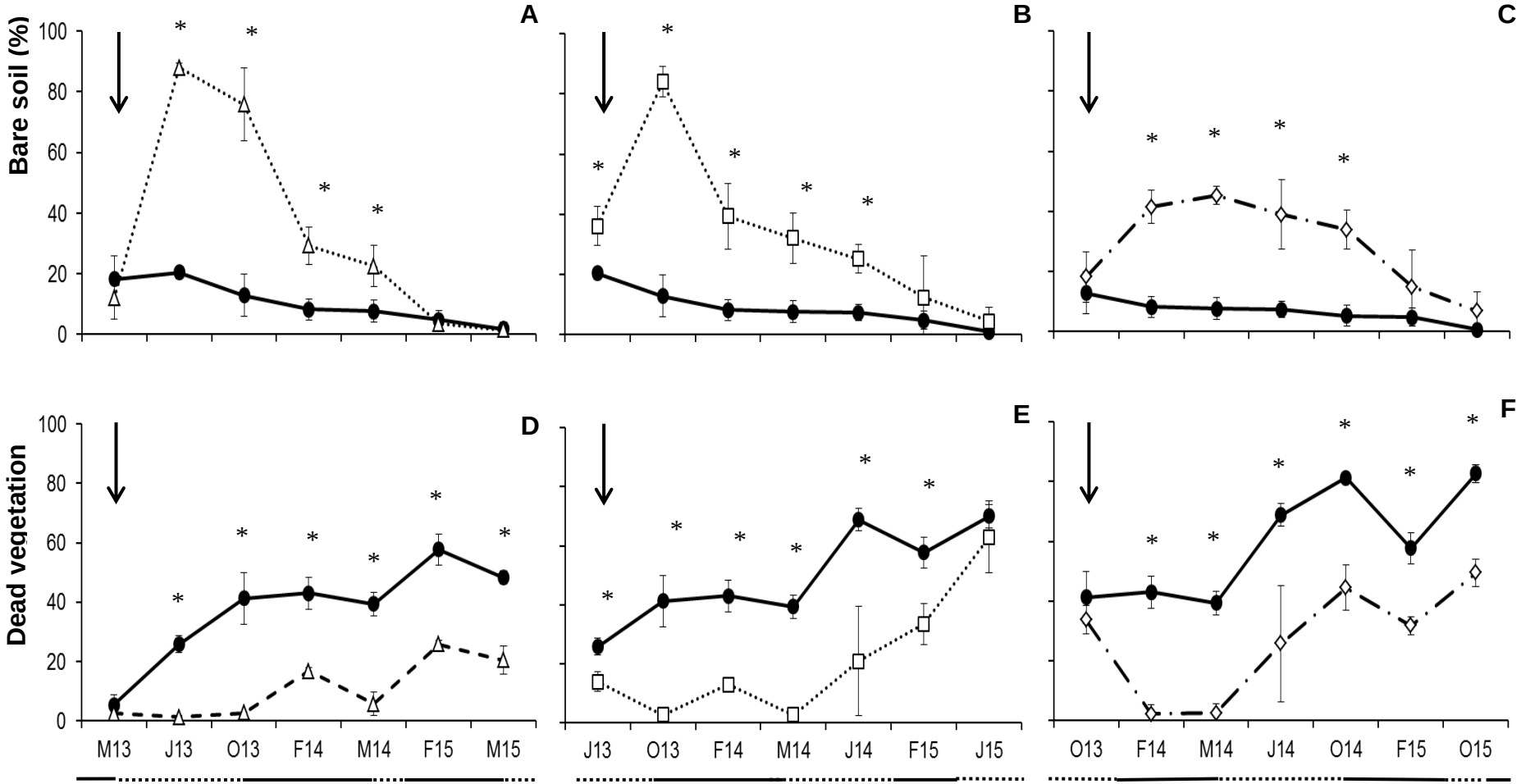

Figure 1. Bare soil (%) in: early- (A), mid- (B) and late-dry season fires (C), dead vegetation (%) in: early- (D), mid- (E) and late-dry season fires (F). Over the first year, the following rainy season and two years after fire, in *campo sujo* areas in Central Brazil. Arrows indicate when the experimental fires were carried out, dotted lines indicate the dry season, continuous lines indicate the rainy season. Error bars represent the standard deviation, asterisk represents significant differences between treatments ($p \leq 0.05$).

Table 1. Simpson´s index (m²) and species richness (m²) in: control, early- (EF), mid- (MF) and late-dry season fire (LF). Before (T0), over the first year, the following rainy season (T18) and two years after fire (T24), in *campo sujo* areas in Central Brazil. Different letters represents significant differences between treatments (p≤0.05).

Simpson´s index (m²)	EF	Control EF	MF	Control MF	LF	Control LF
T0	0.966±0.002[a]	0.974±0.002[a]	0.964±0.005[a]	0.969±0.003[a]	0.965±0.004[a]	0.967±0.006[a]
T3	0.957±0.005[a]	0.969±0.003[b]	0.950±0.007[a]	0.967±0.006[a]	0.970±0.003[a]	0.981±0.004[a]
T6	0.95±0.008[a]	0.967±0.006[a]	0.972±0.003[a]	0.981±0.004[a]	0.974±0.003[a]	0.980±0.007[a]
T9	0.969±0.006[a]	0.981±0.004[a]	0.972±0.003[a]	0.980±0.007[a]	0.966±0.008[a]	0.981±0.001[a]
T12	0.963±0.006[a]	0.980±0.007[a]	0.957±0.001[a]	0.981±0.001[a]	0.961±0.007[a]	0.969±0.006[a]
T18	0.956±0.004[a]	0.966±0.001[a]	0.955±0.005[a]	0.966±0.001[a]	0.961±0.003[a]	0.966±0.001[a]
T24	0.973±0.001[a]	0.972±0.001[a]	0.945±0.009[a]	0.96±0.003[a]	0.935±0.005[a]	0.943±0.003[a]
Richness (m²)						
T0	12.62±1.21[a]	12.54±1.34[a]	10.97±0.78[a]	12.35±0.66[a]	10.57±1.61[a]	11.85±1.86[a]
T3	10.52±0.55[a]	12.35±0.66[a]	10.41±1.55[a]	11.85±1.86[a]	14.62±0.90[a]	15.2±2.13[a]
T6	9.75±1.06[a]	11.85±1.86[a]	14.72±1.57[a]	15.2±2.13[a]	15.81±1.32[a]	16.11±1.57[a]
T9	13.76±0.78[a]	15.2±2.13[a]	16.05±1.79[a]	16.11±1.57[a]	14.7±1.32[a]	11.21±1.67[a]
T12	14.71±1.27[a]	16.11±1.57[a]	14.72±1.67[a]	11.21±1.67[a]	9.95±0.31[a]	10.05±2.66[a]
T18	12.2±0.5[a]	10.16±5.34[a]	13.2±0.76[a]	10.16±5.34[a]	11.62±1.16[a]	10.16±5.34[a]
T24	12.17±1.19[a]	10.78±3.87[a]	9.97±1.26[a]	8.66±3.26[a]	7.87±0.76[a]	7.24±0.76[a]

Fire season and post-fire changes in functional groups cover and richness

Responses of different functional groups varied according to the fire season treatment. Graminoids in plots burned in the early-dry season had the same cover as control plots one year after fire experiments ($p=0.12$; Fig. 2A), whilst in MF and LF, graminoids were already similar to control plots nine months after fire (MF: $p=0.12$; Fig. 3B; LF: $p=0.39$; Fig. 2C). However, fire season did not affect forbs cover: three months after fire experiments, independently of fire season, forbs cover in all burned plots was the same as in control plots ($p>0.05$; Fig. 2D-F). In LF forbs cover was higher in burned plots than in control (in the middle of the dry season; $p=0.01$; Fig. 2F). Shrubs registered lower cover in EF just after fire (T3; $p=0.04$; Fig. 2G). Nevertheless, in the next rainy season (F14; M14), cover of shrubs in EF plots was higher than control plots ($p\leq0.05$). Two years after fire, MF plots showed higher cover of shrubs than control plots ($p=0.01$; Fig. 3H). Fire in the late-dry season also increased shrubs cover three months after fire ($p=0.004$; Fig. 2I).

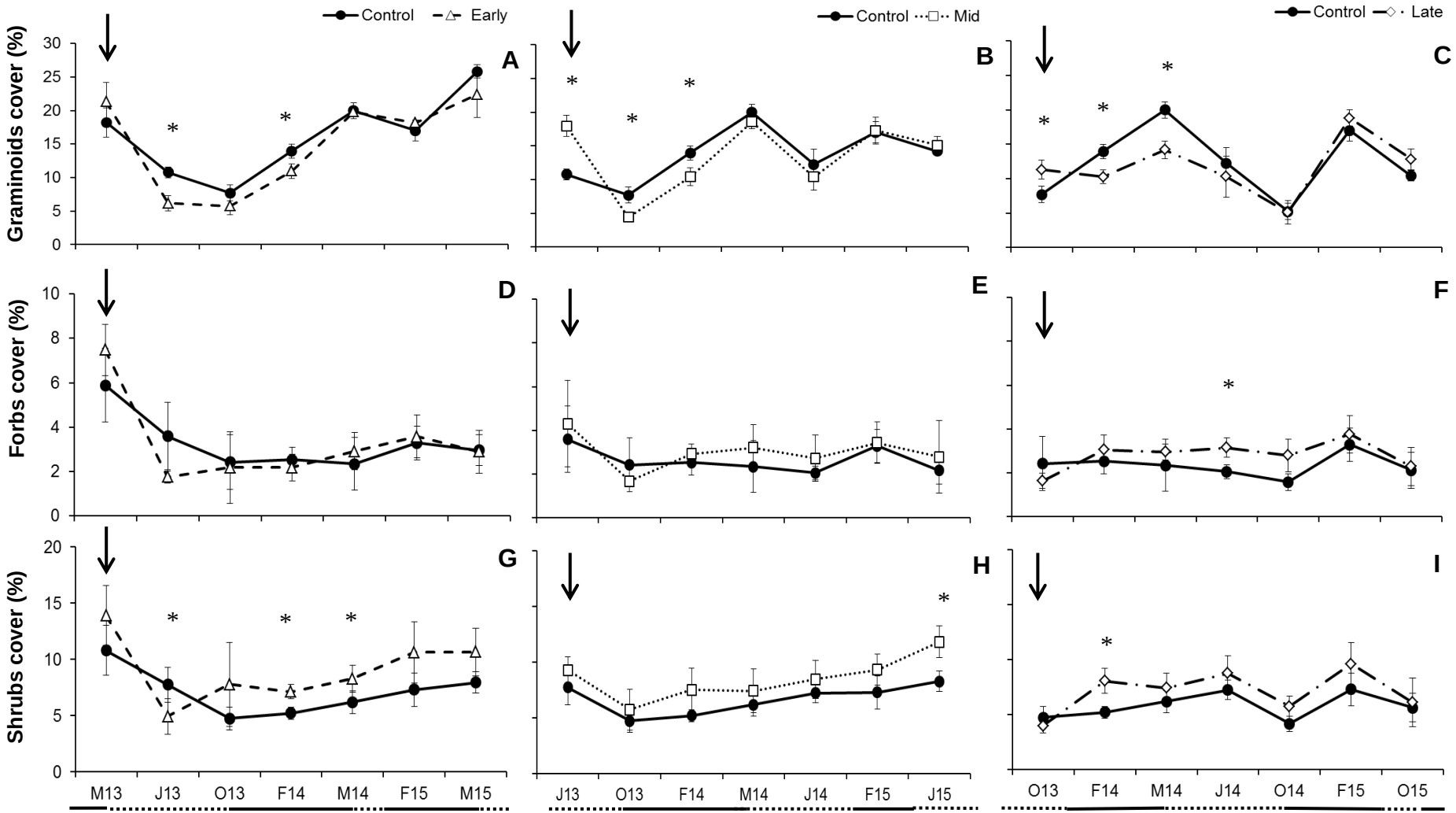

Figure 2. Functional groups cover (%) in different fire season: graminoids (early- (A), mid- (B) and late-dry season fire (C)), forbs (early- (D), mid- (E) and late-dry season fire (F)) and shrubs (early- (G), mid- (H) and late-dry season fire (I)). Over the first year, the following rainy season and two years after fire, in *campo sujo* areas in Central Brazil. Arrows indicate when the experimental fires were carried out, dotted lines indicate the dry season, continuous lines indicate the rainy season. Error bars represent the standard deviation, asterisk represents significant differences between treatments ($p \leq 0.05$).

Number of species of each functional group varied between fire plots and control according to seasonality. Just after fire, one can observe a lower number of species.m^{-2} in burned plots when compared to control (EF: p= p=0.009 Fig. 3A; MF: p=0.03, Fig. 3B). On the other hand, species richness in plots burned in the late-dry season was not affected by fire (p>0.05, Fig. 3C). Forbs and shrubs richness richness was not affected by fire season (Fig 3D-I). Besides that, the patterns of species richness (of all functional groups) all over the period did not vary, being very similar between burned and unburned plots.

In general, in control plots, functional groups richness varied according to seasonality. Such as: graminoids richness (less species over the dry season and more species during the rainy season: O14xF14: p=0.01; O15xF15: p=0.02; M14xO14: p=0.01) as well as forbs richness (F14xO13: p=0.01; F14xJ13: p=0.01; M15xJ15: p=0.03; M14xO14: p=0.01) and shrubs richness (F14xO13: p=0.01; F15xO15: p=0.01; M14xO14: p=0.01).

Two years after fire, EF and MF showed the same number of species as before fire to total, graminoids, forbs and shrubs (p>0.05). LF also registered the same values of richness to forbs and shrubs (p>0.05), but lower number of total (p=0.001) and graminoids (p=0.02).

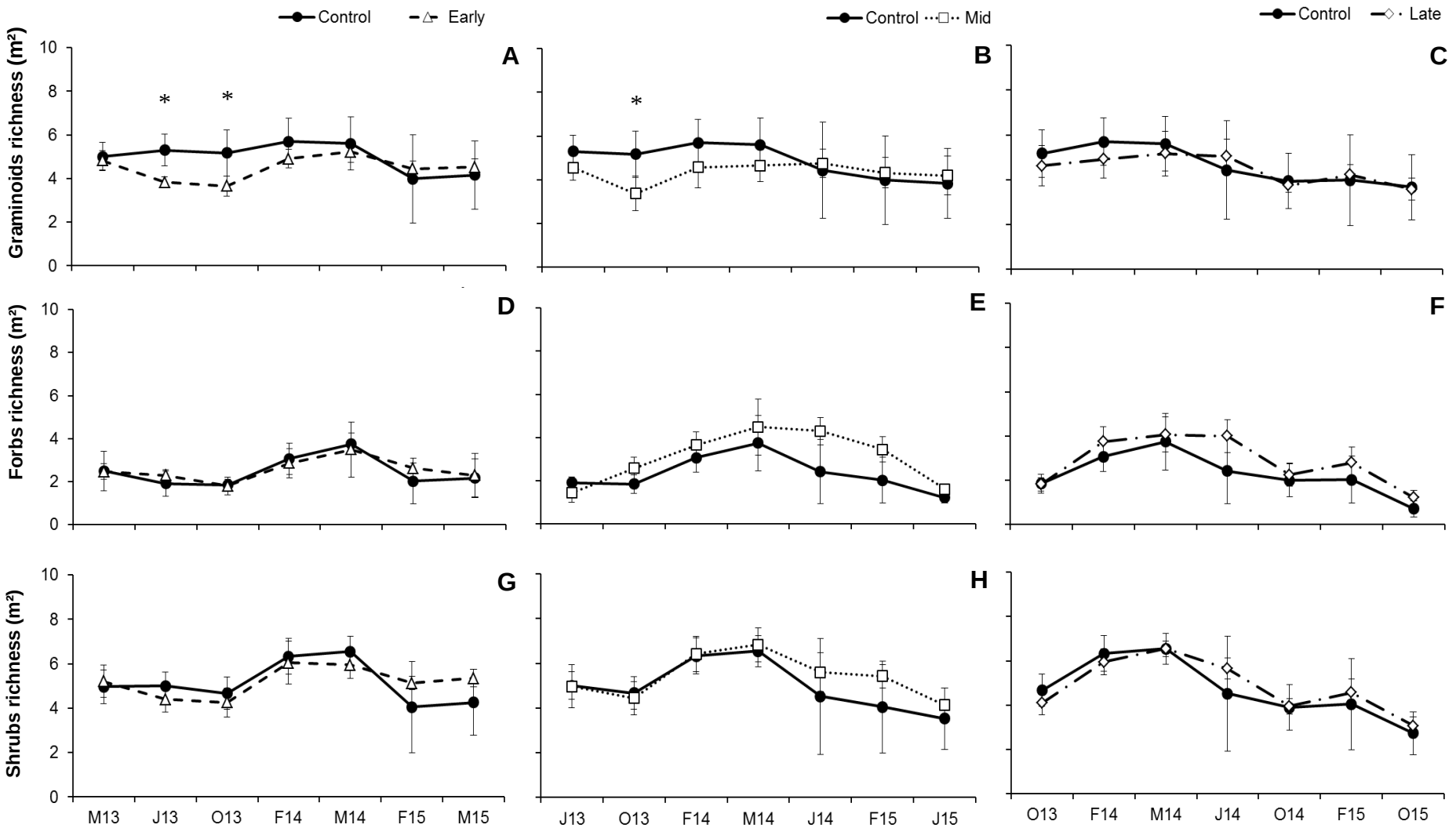

Figure 3. Functional groups species richness in different fire season: graminoids (early- (A), mid- (B) and late-dry season fire (C)), forbs (early- (D), mid- (E) and late-dry season fire (F)) and shrubs (early- (G), mid- (H) and late-dry season fire (I)). Over the first year, the following rainy season and two years after fire, in *campo sujo* areas in Central Brazil. Error bars represent the standard deviation, asterisk represents significant differences between treatments ($p \leq 0.05$).

Species dynamics after fire

The pattern of species cover over in the time in control plots varied according to the season: higher species cover was found during the rainy season (M13xO13: Pseudo-F=78.7; p=0.001; O13xM14: Pseudo-F=88.9; p=0.001; M14xO14: Pseudo-F=152.4; p=0.001; O14xM15: Pseudo-F=155; p=0.001; M15xO15: Pseudo-F=52.5; p=0.001; Fig. 4A).

The first axis of PCO account for 17% of data variation. Control plots varied along the years, showing marked differences between rainy and dry season. Burned plots, independently of fire season, showed the same pattern. At the end of the rainy season (M14), fire plots (EF, MF, LF) seems more close to each other than to control. This differences probably occured due to the high cover of some species in unburned plots, as such: *Calliandra dysantha* (Fabaceae), *Cipura xanthomelas* (Iridaceae) and *Tibouchina* sp. (Melastomataceae). At the middle of the second rainy season (F15), the proportion of species cover was very similar between all treatments.

When the presence and absence of species is analyzed, the same pattern is found (Fig. 4B, axis1=16%), the gain/loss of species occurred in all treatments over time. Control plots registered an increase of species during the first year of sample in the middle of the rainy season (O13xF14: 5.61%; p=0.01) and in the end of the rainy season (O13xM14: 9.78%; p=0.01). Three months after fire, in EF and MF there was a loss of 27.7% and 14.28% species (EF: p=0.6; MF: p=0.7), while in LF an increase of species was found (O13xF14; 17.07%; p=0.01). An increment of species also occurred in fire plots: in EF one year after fire (M13xM14: 12.65%; p=0.03), in MF during the first rainy season (J13xF14: 16.27%; p=0.001; J13xM14: 20.87%; p=0.001) and in the middle of the dry season (J13xJ14: 12.19%; p=0.01). In LF the species gain occurred during the first nine months (O13xF14: 17.07%; p=0.001; O13xM14: 22.72%; p=0.001; O13xJ14: 21.83%).

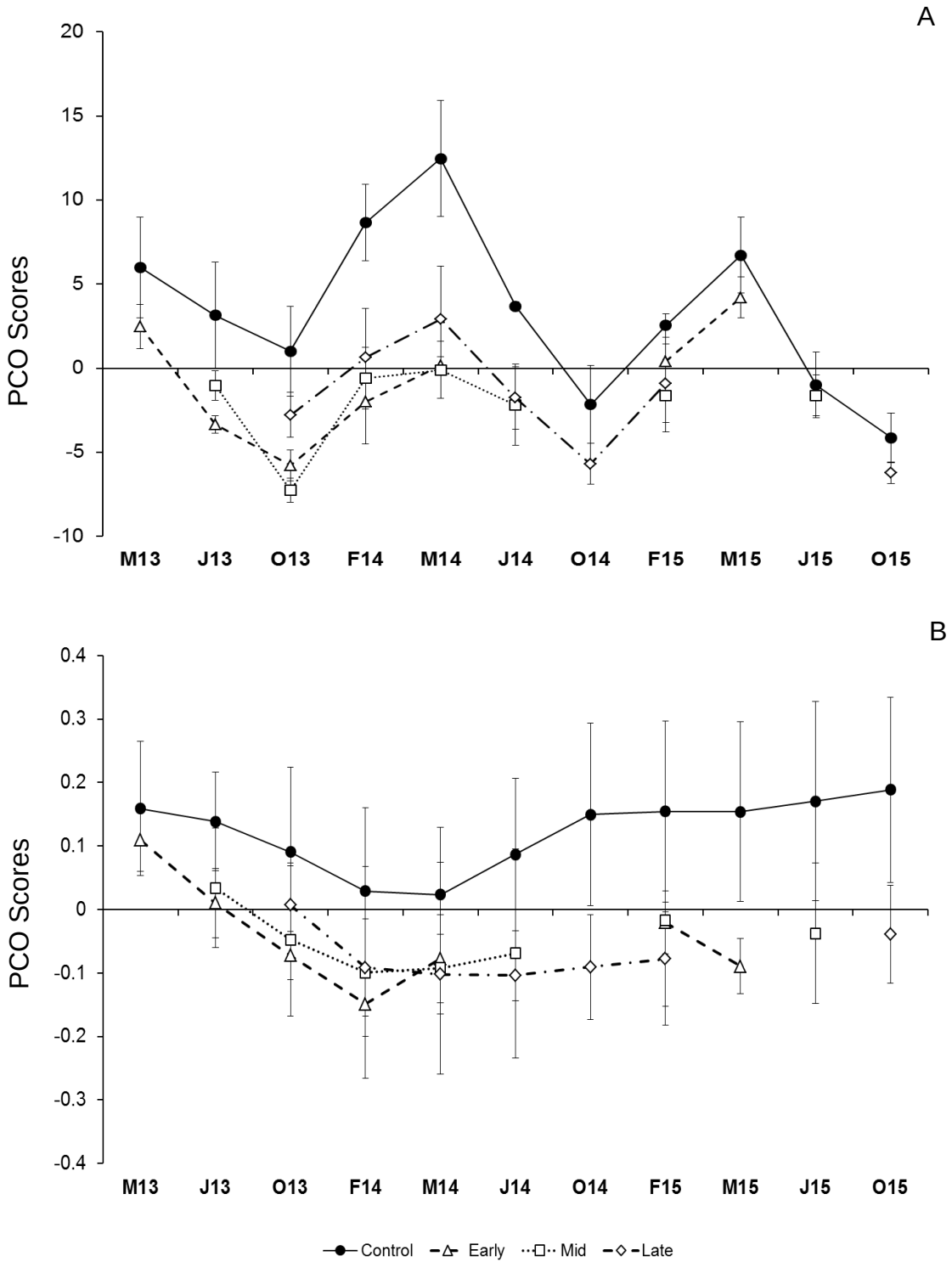

Figure 4. Principal coordinate analysis (PCO) species cover (%, Chord distance, A); presence/absence (Jaccard distance, B) at the different fire season. Black balls represents control plots, white triangles represents early-, white squares represents mid- and white lozenge represents late-dry season fires. Values are the mean and T lines are the standard deviation of PCO scores.

DISCUSSION

Fire has an important role in community dynamics, since it consumes the aboveground vegetation, promoting the opening of gaps and thus enhancing the space available for species regeneration and establishment (Whelan 1995; Bond *et al.* 2005). In all fire treatments, during the first year after fire, there was an increase in bare soil cover, but in the next rainy season (EF and MF) and two years after fire (LF), values between fire plots and control was the same, showing that vegetation had already recovered and occupied the empty spaces that were available just after fire. Dead vegetation cover was lower in EF and LF when compared to control all over the study, MF values of dead vegetation was the same as control just two years after fire.

In short-term, fire did not enhance species richness (number of total species) and diversity when compared to unburned plots. The same results were found in prairie, which plots burned in May (spring) and July (summer) did not differ in overall richness (Howe 2011). In shrublands, fire season also did not alter the various variables (cover, richness) of plant community made during the first three post-fire years, suggesting that species richness dynamics were not related to fire season (Céspedes *et al.* 2014). However, in others fire-prone ecosystems richness increased after fire (Christensen 1985; Bond & Van Wilgen 1996). An alteration in species richness implieschanges in species composition, some species may be lost and others included. This increase in richness observed after fire in many fire-prone ecosystems is mainly due to species recovering from underground organs (Whelan 1985). Pattern of richness in control plots (total, graminoids, forbs and shrubs), varied with seasonality with greater number of species in the rainy season. Total richness and richness of each functional groups did not change two years after fire (in relation to before) in EF and MF. This same tendency was found to LF (to forbs and shrubs), but not to graminoids and total richness, which registered lower number of those groups two years after fire.

Compared to control, graminoids richness was lower in EF (until nine months after fire) and in MF just after fire (three months), in prairie this same pattern of less graminoids richness was found in burned plots in relation to control (Rogers & Hartnett 2001). When compared to control, forbs and shrubs richness was not greater/lower, besides that, fire did not change the patterns of richness between unburned and burned plots. In other savanna, fire season also did not change the number of forbs species (Owens *et al.* 2002). In prairie, more species of forbs was also found in burned areas (Rogers & Hartnett 2001). In grasslands, the richness of forb species was increased by spring burns (Brockway *et al.* 2002), and this functional group can be also better maintained by July fires (Howe 2011).

Functional groups cover was also little affected by fire and it varied according to season, in the same way as control plots. Grasses in grasslands (Bond 2004) and Cerrado (Coutinho 1990) are known as the functional group most resilient to changes in fire regime (Smith *et al*. 2012), which show rapid capacity of recovery (Naveh 1975). Despite that, graminoids cover was similar to control just nine months (MF and LF) and one year after fire (EF). Forbs species cover registered greater values just in LF in the middle of the dry season (nine months after fire). Water availability, due to the rainy season just after fire (October until May; Quesada *et al.* 2008) and the new microsites should propitiated this enhance in cover, despite that, fire season and seasonality also can affect the patterns of biomass regrowth (Capítulo 1) and phenological patterns and flowering strategies in Cerrado (Capítulo 4) .

Shrub cover in EF has higher during the rainy season (F14 and M14). MF cover was greater than control 2 years after fire (in the middle of the dry season). In LF, shrubs cover was greater just after fire, at the middle of the rainy season (February). This pattern seems to be liked to rainy season and water availability to their establishment, despite that many of this species have underground storage organs (Rissi *unpublished data*) and may resprout using these reserves after fire.

Our study showed that the herbaceous layer is very dynamic. The patterns of unburned areas varied according to season (dry/rainy) and fire season did not affect this dynamics. Therefore, the herbaceous vegetation is very resilient to fire, showing that the Cerrado vegetation were adapted to fire.

Conclusions

After fire dead vegetation was removed and as a consequence, gaps within the herbaceous layer could be observed, which would be regeneration niches for new species. The removal of aboveground biomass and consequently decrease in competition might have contributed to the fast recovery of vegetation. In short-term, fire did not enhance total species richness when compared to unburned plots, but all treatments increased the total number of species during the first year after fire when compared to values found before fire (inclusive control). The vegetation is very dynamic, which is probably mainly driven by seasonality. In general, fire did not change the patterns of vegetation (diversity, richness, cover and composition), but showed some little differences between control and fire treatments in short-term, such as functional groups cover. This information is extremely important for a better understanding of Cerrado dynamics and ecological process after fire. We reinforce that it is extremely important the establishment of long-term studies evaluating the impact of season on vegetation, in order to verify its effects on plant community structure over time in particular with repeated application of fire in the same season.

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Capítulo 4

Does fire season affect the phenological patterns in Cerrado?

Mariana Ninno Rissi & Alessandra Fidelis.

ABSTRACT

Questions: Will fire season affect the phenological pattern of flowering and fruiting in Cerrado communities? Do species of different functional groups show differences in their phenological pattern according to the fire season? Are phenological patterns being driven by fire only, or by fire season? What are the flowering strategies of species after fire?

Location: Open savannas ("campo sujo", Cerrado) in Central Brazil (Reserva Natural da Serra do Tombador, Brazil).

Methods: We established 16 plots with different fire season treatments (4 plots/treatment, 10 subplots/plot): early- (EF, burned in May – begining of the dry season), mid- (MF, burned in July – middle of the dry season), late-season fires (LF, burned in October – end of the dry season) and control (unburned). We counted the number of species flowering and fruiting in different times since fire (0, 3, 6, 9 and 12 months) and compared between treatments (burned x unburned). We first did this for the entire community and then, we compared functional groups (graminoids, forbs and shrubs).

Results: Fire changed the patterns of flowering and fruiting in all treatments. Early-dry season fires enhanced flowering just after fire (community and graminoids), while late-dry season fires more species were flowering three and nine months after fire and more species were fruiting nine months and one year after fire. Burning the vegetation in the middle of the dry season promoted flowering in shrubs and more community species fruiting one year after fire. We also found different flowering strategies as: species that just flowered in control (fire sensitive), those that just flowered in the presence of fire (fire dependent), species that flowered in all treatments (fire independent) and species that just flowered in dry or rainy season, regardless to fire season (season dependent).

Conclusions: Fire changed phenological patterns both for the plant community and for the different functional groups. Moreover, responses to fire and to fire seasons were not similar to the different species, and we could group them according to their flowering patterns after fire. As a conclusion, fire in general enhanced flowering in the entire communities, and some species flowered just after fire occurred.

Keywords: prescribed fire; functional groups; herbaceous layer; tropical savanna; fire management; phenological strategies.

Running head: Effects of fire season on flowering and fruiting phenology in a tropical savanna

INTRODUCTION

Fire season is one of the least understood fire regime components (Gill et al. 2002), significantly affecting plant phenology (Platt et al. 1988) and plant community assembly (Hodgkinson 1991; Whelan and Tait 1995; Knox & Clarke 2006). How vegetation and functional groups respond to different fire seasons, as well as which strategy is used after fire can be critical to community composition, since fire can change the competitive abilities of plants (Bond & Van Wilgen 1996; Whelan 1995).

The effects of fire on flowering of savanna species are dependent on the interaction between species phenology, floral induction and fire season (Pavlovic et al. 2011). The death of aboveground parts followed by resprouting when the rainy season begins is an important phenological strategy for several herbaceous species in Cerrado, althought it is mostly as a response to seasonality (Moraes et al. in press). Additionally, in order to resprout and flower, plants need to allocate their reserves, which are many underground and composed mostly by soluble carbohydrates in herbaceous species of Cerrado (Moraes et al. in press) and their amount can vary according to season and phenological stages (Machado de Carvalho & Dietrich 1993, Jones & Laude 1960). Therefore, fire season can also affect the flower production and timing of flowering (Platt et al. 1988) probably due to the phenological stage in which the species is during that particular fire season, thus affecting its response. For example, in prairie, fire in the growing season can increase the dominance of forbs flowering and delay the fall peak flowering (Platt et al. 1988). Summer fires (July), on the other hand, can favor early-flowering species, while late-flowering species can be favored by late-winter fires (Howe 1994). Despite that, after fire there is an increase on nutrient availability in ashes, among them: phosphorus, potassium, and calcium (Pivello & Coutinho 1992) which could be used by plants favouring the flowering.

The phenological strategies of species after fire are crucial to guarantee their persistence (Monasterio & Sarmiento 1976). Species with similar phenological patterns can be grouped, each one representing a unique phenological strategy that will allow species to deal to different environmental conditions (Sarmiento & Monasterio 1983).

In Brazilian subtropical grasslands, an increase in forbs species flowering after fire was observed, while most graminoids flowered throughout the year, showing that functional groups had different phenological strategies in post-fire environments (Fidelis & Blanco 2014). Although an intense post-fire flowering of herbaceous species is known to occur in the Cerrado (Coutinho 1976), less is known about phenological strategies after fire and the role of fire season on plant community phenology. The Cerrado is composed by a mosaic of physiognomies, from open savannas to forest (Oliveira-Filho & Ratter 2002). Fire has been influencing this vegetation since at least 4 million years (Simon et al. 2009), and the open savannas are those with the highest fire frequency (Coutinho 1982). Natural fires in Cerrado are caused by lightning and occur mostly during the rainy season (September– May; Ramos-Neto & Pivello 2000). However, anthropogenic fires are usually set during the dry season to promote new shoots for cattle raising, what may be changing the natural fire regime in Cerrado (Fidelis & Pivello 2011, Ramos-Neto & Pivello 2000).

The natural flowering peak of Cerrado herbaceous layer (wihout fire), occurs mainly in the rainy season (Munhoz & Felfili 2005; Tannus et al. 2006), when most of natural fires occurred (Ramos-Neto & Pivello 2000). Understanding how fire season affects flowering and fruiting of herbaceous species of Cerrado is important to predict the effects of long-term changes in herbaceous communities and functional groups, since it may affect seedling and recruitment of different functional groups and, as a consequence, change the herbaceous community dynamics and composition.

Therefore, this study aims to evaluate the influence of fire season (early-, mid-, and late-dry season) on the flowering and fruiting patterns of an open savanna of Cerrado (*campo sujo*) and to analyze the phenological strategies in response to fire. We examined the following questions: (1) Does fire season affect the pattern of flowering and fruiting of the community? (2) Does plant species of different functional group show differences in their phenological patterns according to the fire season? (3) Are phenological patterns being driven by fire only or by fire season? (4) What are the phenological strategies of species in relation to fire? We hypothesize that fire in different seasons will affect plant species and functional groups in different ways: plants flowering and fruiting during the dry season will have their phenology affected by delaying flowering and fruiting, while species reproducing during the rainy season will not be affected. Additionally, we believe that fire will stimulate flowering and fruiting, thus inducing an increase of the number of reproducing species in the community immediately after fire.

MATERIAL AND METHODS

Study area

The study was conducted at the Reserva Natural Serra do Tombador (RNST), in Central Brazil (47°45-51'W and 13°35-38'S, 560-1118m a.s.l.). The climate is tropical with a marked dry season from May to September and mean annual rainfall between 1300 and 1500 mm (AER 2009). *Campo sujo* is the dominant vegetation in the study site, which is composed by an almost continous herbaceous layer mainly composed by graminoids with scattered shrubs and small trees. The area has not been grazed since 2006 and there is an absece of invasive species. In August 2011 the entire area burned accidentally and the experimental fires were carried out in 2013.

Experimental design and data sampling

We established 30x30m experimental plots in a randomized block design, surrounded by a 3m wide fire break. Plots were at least 4m distant from each other. The following fire treatments were stablished: fire in May, at the beginning of the dry season (early-dry season fire, EF), fire in July, at the middle of the dry season (mid-dry season fire, MF), fire in October, at the end of the dry season and beginning of the rainy season (late-dry season fire, LF), and control (unburned, C, 4 replicates/treatments; total of 16 plots). The experimental fires were conducted individually in each plot to guarantee the independence of data. For more details about the fire experiments, please see Rissi et al. (Capítulo 2).

Within each plot, we randomly established and fixed ten subplots (1x1m). In the subplots we counted the total number of species and the number of species flowering and/or fruiting. We performed all calculations using the percentage of species flowering and/or fruiting from the entire plant community (plot level).

All the species were collected and incorporated at the Herbarium Rioclarense, located at Universidade Estadual Paulista (UNESP), Rio Claro, SP, Brazil. The vouchers of each specie are given at supporting information. The taxonomists that help the identification was: Angela Borges Martins, Angela Studart da Fonseca Vaz, Bruno Walter, Elysiane Marinho, Gustavo Shimizu, Igor Azevedo, João Aguiar Nogueira Batista, João Bernando de Azevedo Bringel, José Floriano Barêa Pastore, Juliana Rando, Júlio Lombardi, Leonardo Borges, Letícia Lima, Marcelo Fragomeni Simon, Marcos Sobral, Marcelo Trovó Lopes de Oliveira, Moises Mendoza, Pedro Fiaschi, Nara Mota, Rafael Trevisan, Regina Célia de Oliveira, Renato de Mello-Silva, Rodrigo Camargo, Taciana Barbosa Cavalcanti e Tarciso Filgueiras.

Phenological observations

All phenological observations were conducted before each experiment (May, July, October; burned and control) and every three months, during one year.

We first evaluated the phenological pattern for the community (percentage of species flowering/fruiting, independently of the functional group). And subsequently these species were grouped into graminoids, forbs and shrubs in order to describe these patterns in different functional groups. The amount of lianas and palm trees was negligible and therefore, species of these groups were not considered.

Statistical analyses

Differences in the percentage of species flowering and/or fruiting from the community between treatments for each time of observation were tested using a mixed linear model. The fixed factor was treatment (burned x unburned, for each fire season) and the random factor was the plot.

We performed multivariate analysis, using ordination methods (Principal Coordinate Analysis – PCO) to find patterns in the community over time. We used Jaccard distance as resemblance measurement among sampling using presence/absence data of flowering and fruiting species in the community. All analyses were performed using the R program (R Core Team 2013) with the packages: vegan (Oksanen et al. 2013) and nlme (Pinheiro et al. 2015).

RESULTS

Phenological patterns in plant community

Just after fire (3 and 6 months, during the dry season), a higher percentage of species were flowering in plots burned in May (EF) than control ($P=0.04$, $P=0.03$, respectively, Fig. 1A), whilst plots burned in the middle of the dry season were not affected by fire ($P<0.05$, Fig. 1B). LF communities also registered a greater percentage of species flowering three months after fire experiments, during the rainy season ($P=0.04$), and also nine months after fire (during the dry season, $P=0.02$, Fig. 1C).

Although a tendency in having a higher percentage of species fruiting was observed in EF plots, no significant differences were found ($P>0.05$, Fig. 1D). However, MF and LF plots had higher percentage of species fruiting one year after fire ($P=0.02$; $P=0.01$, respectively, Fig. 1E-F). More species were producing fruits in the middle of the dry season (July) in plots burned in the late-dry season ($P=0.02$, Fig. 1F).

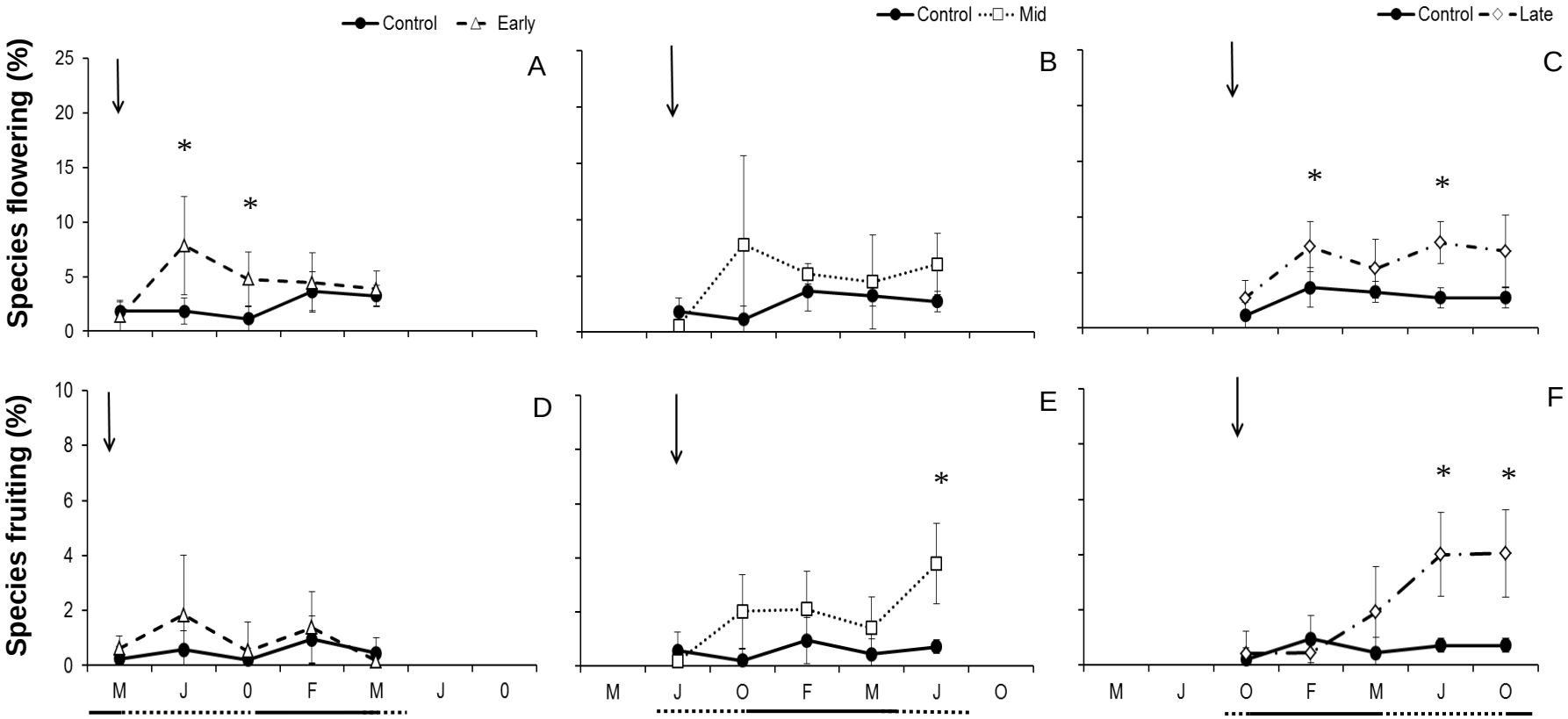

Figure 1. Species flowering (%) in: early- (A), mid- (B) and late-dry season fires (C) and species fruiting (%) in: early- (D), mid- (E) and late-dry season fires (F), during one year in a *campo sujo* areas in Central Brazil. Arrows indicate when the experimental fires were carried out, dotted lines indicate the dry season, continuous lines indicate the rainy season. Error bars represent the standard deviation. Asterisk represents significant differences between treatments (P≤0.05).

In relation to flowering presence/absence, a similar pattern in relation to control was found along the year for all fire treatments and control species flowering in the community (Fig. 2A).

The first two axes of the PCO considering the presence and absence of flowering species in control and all fire season accounted for 15% of data variation. Three months after fire (July), burned plots in EF were not similar to control ones, mostly due to the flowering of some species, such as *Davilla elliptica* (Dilleniaceae), *Diplusodon punctatus* (Lythraceae), *Mesosetum ferrugineum* and *Oedochloa procurrens* (both Poaceae). This same pattern was found for MF and control plots, three months after fire, *Croton antisyphiliticus* (Euphorbiaceae), *Camarea ericoides* (Malpighiaceae) and *Turnera incana* (Passifloraceae), were not flowering in unburned plots. Communities in plots burned during the late-dry season had similar species flowering than in control plots. However, in the middle of the dry season, LF plots had species flowering, which were not found in the control, such as *Ichthyothere terminalis* (Asteraceae) and *Polygala abreui* (Polygalaceae).

The first two axes of the PCO considering the presence and absence of fruiting species in control and all fire season accounted for 13% of data variation. EF and control registered different patterns in relation to species fruiting (presence/absence, Fig. 2B): three and nine months after fire, species fruiting was not the same in both treatments. Some species just fruited in EF plots, such as: *Mimosa* aff. *pteridifolia* (Fabaceae) and *Trimezia juncifolia* (Iridaceae) (T3); and *Mimosa* aff. *flavocaesia* (Fabaceae) (T9). Before fire, fruiting species composition was very similar between MF and control all over the time, except two years after fire, when some species just fruited in MF plots (such as: *Bauhinia dumosa* (Fabaceae) and *Medusantha mollissima* (Lamiaceae)). Late-dry season fire species fruiting composition was very similar to control before and two years after fire, except

one year after fire, when some species, such as: *Harpalyce brasiliana* (Fabaceae) and *Chamaecrist calussenii* (Fabaceae) just fruited in fire plots.

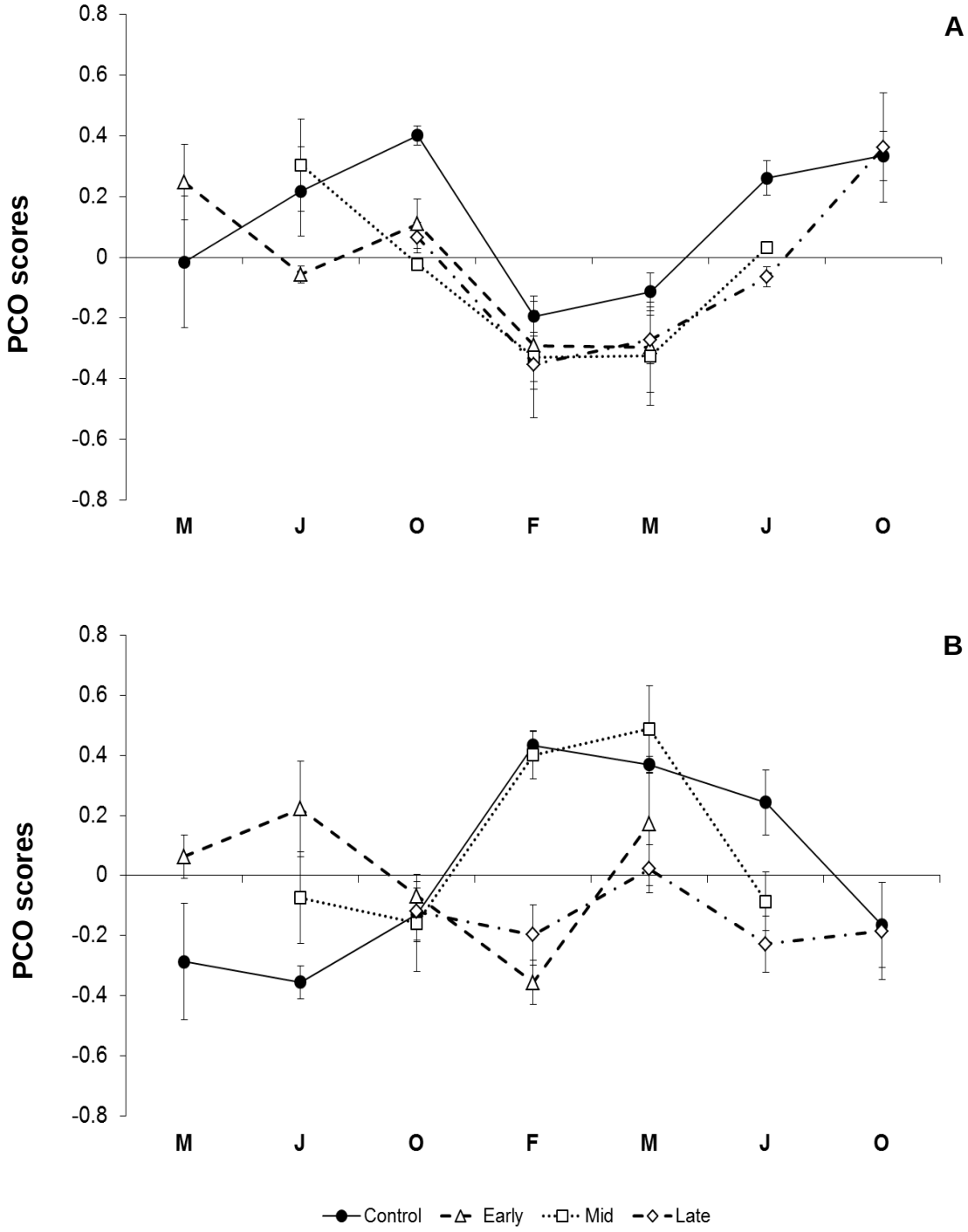

Figure 2. Principal Coordinate Analysis (PCO, resemblance measurement among sampling units: Jaccard) of burned and control plots, according to the presence/absence of species flowering (A) and presence absence of species fruiting (B) during the early, mid-, and late-dry season. Before experiments and each three months over the year after fire.

Flowering and fruiting: functional groups

Graminoids had few species flowering in control plots throughout the year. However, when plots were burned in the early-dry season, graminoid species were stimulated to flower just after fire, even though it was in the middle of the dry season (EF=15.27±8.91%, C=0.22±0.45%, P=0.01, Fig. 3A). MF communities showed the same pattern of higher graminoids species flowering just after fire, although no significant differences were observed (Fig. 3B, P=0.2). However, when plots were burned at the end of the dry season (October), there was no increase in number of graminoid species flowering (P>0.05, Fig. 3C). Forb species tended to have more species flowering after fire, however no significant difference between burned and unburned could be observed for any fire season (P>0.05, Fig. 3D-F). Shrub species, on the other hand, were stimulated to flower and showed a significant higher percentage of species flowering one year after fires in MF plots (P=0.005, Figure 3H). When fire occurred at the end of the dry season (LF), shrubs flower immediately after fire (three months, P=0.02), and during the next dry season (July and October, P=0.02, P=0.02, respectively Fig. 3I).

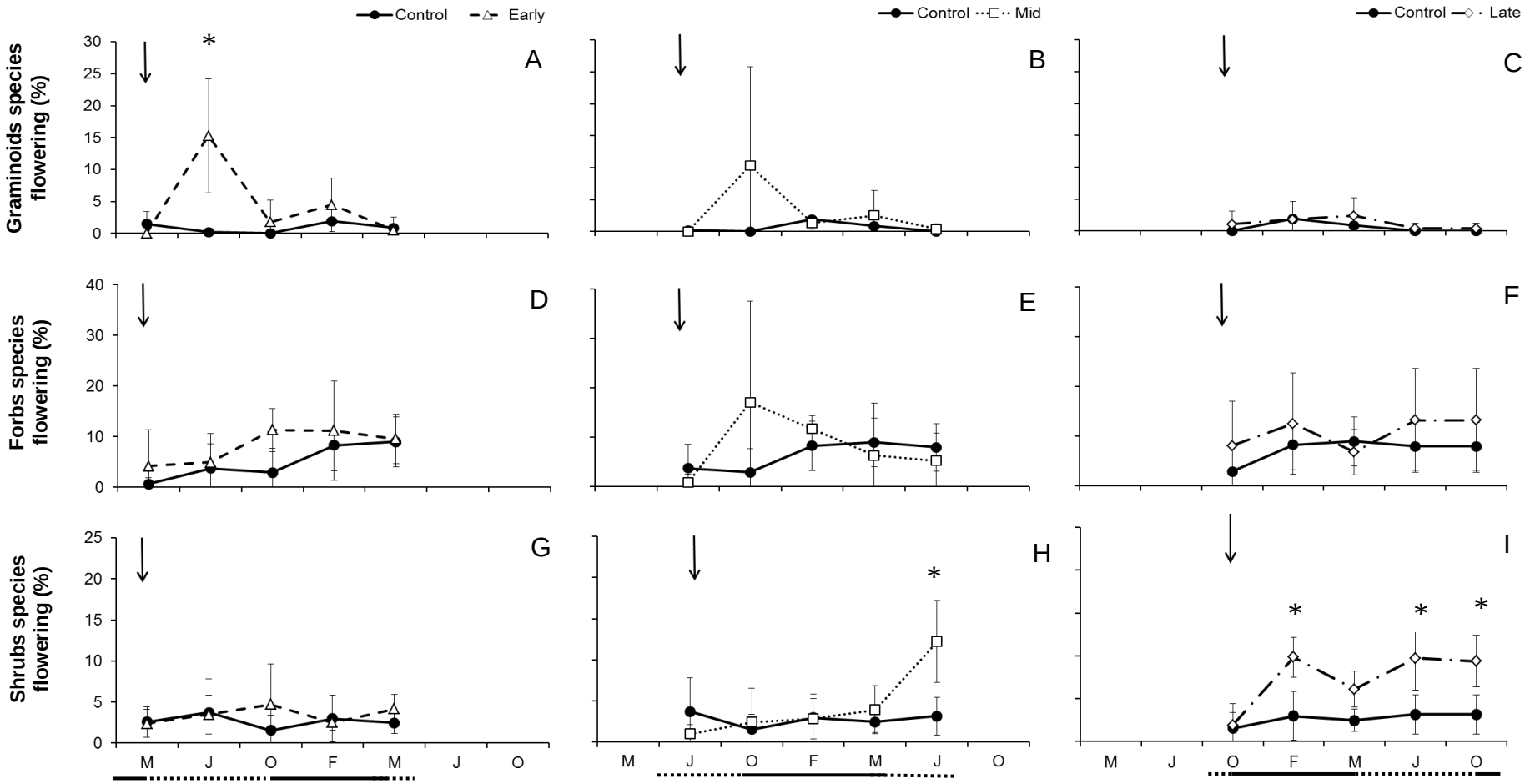

Figure 3. Flowering species (%) according to the different functional groups in different fire seasons: graminoids (early- (A), mid- (B) and late-dry season fire (C)), forbs (early- (D), mid- (E) and late-dry season fire (F)) and shrubs (early- (G), mid- (H) and late-dry season fire (I), during one year in a *campo sujo* areas in Central Brazil. Arrows indicate when the experimental fires were carried out, dotted lines indicate the dry season, continuous lines indicate the rainy season. Error bars represent the standard deviation. Asterisk represents significant differences between treatments (P≤0.05).

Although graminoids fruiting only ocurred in fire plots (all over the year), no statistical differences were found between treatments (EF x control, MF x control and LF x control, Table 1). Forbs and shrubs fruiting did not differ in relation to control and any fire treatment.

Table 1. Community species fruiting (%) according to the different functional groups in different fire seasons: early- (EF), mid- (MF), late-dry season fires (LF) and control in each time of observation: before (T0), three (T3), six (T6), nine (T9), and one year after fire experiments (T12) in *campo sujo* areas in Central Brazil. Different letters represents significant differences between treatments (control and fire treatments).

Functional groups / Time	EF	Control EF	MF	Control MF	LF	Control LF
Graminoids species fruiting						
T0	0 [a]	0 [a]	0 [a]	0 [a]	0 [a]	0 [a]
T3	1.12±2.25 [a]	0 [a]	0 [a]	0 [a]	0.41±0.83 [a]	0 [a]
T6	0 [a]	0 [a]	0.62±1.25 [a]	0 [a]	0.66±1.33 [a]	0 [a]
T9	0.5±1 [a]	0 [a]	0.41±2.25 [a]	0 [a]	1.19±2.38 [a]	0 [a]
T12	0.5±1 [a]	0 [a]	0.35±0.71 [a]	0 [a]	1.19±2.38 [a]	0 [a]
Forbs species fruiting						
T0	0 [a]	0 [a]	0 [a]	0.5±1 [a]	2.5±5 [a]	0 [a]
T3	4.10±5.42 [a]	0.5±1 [a]	4.79±3.49 [a]	0 [a]	0.83±1.66 [a]	1.25±2.5 [a]
T6	1.25±2.5 [a]	0 [a]	0 [a]	1.25±2.5 [a]	3.2±2.96 [a]	0.65±1.25 [a]
T9	4.87±5.48 [a]	1.25±2.5 [a]	1±2 [a]	0.65±1.25 [a]	2.81±2.6 [a]	0 [a]
T12	0 [a]	0.65±1.25 [a]	1.75±3.5 [a]	0 [a]	2.81±2.6 [a]	0 [a]
Shrubs species fruiting						
T0	1.43±1.08 [a]	0.41±0.83 [a]	0.41±0.83 [a]	0.41±0.83 [a]	0 [a]	0.65±1.25 [a]
T3	0.62±1.25 [a]	0.41±0.83 [a]	1.12±1.31 [a]	0.65±1.25 [a]	0 [a]	1.64±1.52 [a]
T6	0.83±1.66 [a]	0.65±1.25 [a]	4.8±2.14 [a]	1.64±1.52 [a]	1.58±1.54 [a]	0.72±0.85 [a]
T9	0.85±1.01 [a]	1.64±1.52 [a]	2.39±2.5 [a]	0.72±0.85 [a]	7.71±6.14 [a]	2.14±1.03 [a]
T12	0 [a]	0.72±0.85 [a]	8.09±3.3 [a]	2.14±1.03 [a]	7.62±6.11 [a]	2.14±1.03 [a]

Phenological strategies

We classified the species in the following phenological strategies, according to their responses to fire and fire season (Table 2): fire dependent - species that occur in all treatments, but just flower in the presence of fire; fire independent - flowered in all treatments; fire sensitive – species that flowered only in the control plots, without fire; season dependent – species that occurred in both burned and unburned plots and flowered only in the rainy or dry season, independently of fire.

Table 2. Strategies of flowering species, over one year, in *campo sujo* areas in Central Brazil.

Strategy	Description	Species
Fire dependent	Flower only in fire presence	
all fire seasons		
		Bauhinia dumosa
		Bulbostylis pardoxa
		Calliandra dysantha
		Croton antisyphiliticus
		Digitaria insularis
		Eriochloa sp.
		Hyptis sp.
early-dry season fires		
		Davilla elliptica
		Diplusodon punctatus
		Mimosa gracilis
mid-dry season fires		
		Brosimum gaudichaudii
		Deianira pallescens
		Euphorbia sp1
		Heteropteris pannosa
		Justicia lanstyakii
		Merremia digitata
		Turnera incana
late-dry season fires		
		Chamaecrista ochrosperma
		Polygala abreui
Fire independent	Flowered in all treatments	
		Borreria sp.
		Camarea affinis
		Chamaecrista claussenii
		Hypenia sp.
		Ichthyothere terminalis
		Medusantha mollissima
		Mimosa aff. *pteridifolia*
		Mimosa somnians
		Oxalis goyazensis
		Tibouchina melastomoides
		Trimezia juncifolia
Fire sensitive	Flowered without fire	
		Annona crasiflora
		Myrcia laruotteana
Season dependent	Flowered in the rainy or dry season , independently of fire	
rainy season		*Bulbostylis junciformis*

Strategy	Description	Species
		Manihot kalungae
		Mimosa diminuta
dry season		
		Serjania trichomisca

DISCUSSION

Phenology and fire can interact in two ways: the direct effect of fire on vegetation will depend of the phenological stage of the species; and the phenological patterns and the availability of resources to vegetation will be influenced by fire (Andersen et al. 1998). Fire affected the phenological patterns in *campo sujo* communities of Cerrado by increasing the number of species flowering, mostly three months after fire (in EF and LF). Moreover, plots burned at the end of the dry season (October) also showed a higher percentage of species flowering and fruiting during the dry season. Even though plots burned in May (begin of the dry season) faced the entire dry season after fire, more species flowered during this period in burned plots than control, showing that plants invested in both resprouting and flowering during the dry season, probably to have seeds to be dispersed when the rain begins. Most of these species were graminoids: in the absence of fire, almost no graminoids species could be observed flowering (the greater value found in control was of 1.9%). However, after early- and mid-dry season fires, 15.2 % and 10.2% of species showed flowers.

Most grasses and sedges can resprout immediately after fire (Sarmiento 1984). This fast regrowth is due to the rapid resource imobilization, which may lead graminoids to have competitive advantages in post-fire environments (Bond 2004). Some savanna grasses cannot persist without fire (Canales et al. 1994, Silva et al. 1991), others are highly dependent of fire to flower and very few flowers in the absence of fire (Sarmiento 1992). Fidelis and Blanco (2014) observed in subtropical grasslands that graminoids did not show a high number of species flowering

immediately after fire, but in the following year when more species were flowering in burned plots than in unburnt. In savannas, the natural pattern of grass flowering phenology seems to be limited to the rainy season (Monasterio & Sarmiento 1976). However, Munhoz and Felfilli (2005) adressed an interesting pattern in *campo sujo*: grass and sedge species flowered just after fire (*Andropogon bicornis*, *Bulbostylis paradoxa* and *Anthaenantia lanata*), suggesting that fire could change the patterns of grass flowering. In our study, *Bulbostylis paradoxa* (Cyperaceae) had the most amazing response to fire: in the next day of fire experiments, the species could already be found flowering in the experimental plots, showing the rapid response of this species to fire. We also never observed this species flowering in control plots and when we came back to the plots, three months after fire, seeds were already dispersed and only the rest of the inflorescence could be found.

Moreover, graminoid species fruiting were only observed in burned plots, which means that the few species flowering in control plots did not form fruits or dispersed them very fast, whilst in burned plots, flowering and/or fruiting stage were longer, since our observations were only carried out every three months. Flowering and fruiting just after fire would give an extra advantage to grasses: they can resprout very fast (Bond 2004) and refill the seed bank and establish new seedlings in the gaps formed after fire by the removal of vegetation and standing dead biomass (Canales et al. 1994). Most of the Cerrado grasses synthetize non-structural carbohydrates (NSC, mainly free glucose, sucrose and malto-oligosaccharides but not fructans) (Moraes et al. 2012), which could be an advantage to mobilize rapidly resources to both resprout and flower.

In Cerrado, forbs flowering normally starts in the middle of the rainy season (Tannus et al. 2006, Munhoz & Felfili 2005). We found this tendency for all control plots, while in fire treatments, flowering occurred just after fire, but more vigorous in the beginning and during the rainy season. This behavior could be related to the

strong water stress during the dry season (Barbosa & Sazima 2008) or also to competition reduction and the opening of new sites (Fidelis & Blanco 2014). Despite that, fructans (present in some Cerrado herbaceous species (Mantovani and Martins 1988)) is related to fire tolerance (Hendry 1993) being the responsible by the water balance maintenance over the dry season (Moraes et al. *in* press).

Shrubs in MF registered a greater number of species flowering one year after fire and in LF more species flourished three, nine months and one year after fire. Shrubs may have more plastic responses, and thus they can respond better to changes in the environment (Paritsis et al. 2006). Besides that, as also reported by Sarmiento (1984), shrubs have storage organs, which allow completing the reproductive cycle without first developing the photosynthetic tissues, in this way; seeds are ready to be dispersed at the beginning of rainy season when the conditions of humidity would be favorable to germination. After fire, the number of shrubs flowering in Cerrado did not decrease (Munhoz & Felfili 2005).

Cerrado species showed different phenological strategies: some of them just flowered in fire absence (fire sensitive species). However, since our sampling was only every three months, species may have flowered and formed fruits in the intervals between observations, showing thus a very rapid flowering/fruiting stage.

The category fire independent (those species that flowered in control and all fire treatments) and season dependent (species that flowered during the same season (dry/rainy) despite of any treatment), seem to be indifferent to burn or not, once that fire season did not affect flowering or the season when this phenological phase occurs. Coutinho (1976) also pointed that the period of flowering of some species are not changed by fire.

Fire dependent species only flowered in fire presence. The flowering of species in all fire seasons can be due to the gaps and the new conditions after fire as competition reduction (Sarmiento & Monasterio 1983). In addition, species that only

flowered after a specific fire season can be due to some other factor related to each fire season (as an example, shorter days of winter or lower temperatures for MF; Coutinho 1976) Still, other species were affected by EF/MF/LF (not flowering) maybe due to direct/indirect effects of this specific fire season.

Burns occurring too frequently in the same season could negatively affect future flowering and/or reproduction of these plant species (affect by EF/MF/LF) and enhance the flowering of species that are fire season dependent.

Fire affected the patterns of flowering, fruiting according to fire season. Flowering and fruiting did not occur throughout the year, reflecting the seasonality of the Cerrado (Sarmiento & Monasterio 1983). The relation of fire season and the phenological stage of the plant can be important, because if fire occurs too early it could damage flowering buds or developing flowers and thus abort the next generation of seeds (Whelan 1995). Species that have their reproductive period interrupted by fires may lose the resources invested in flower production and would reduce propagules productionl, affecting the fauna and local communities. Our study shows how the patterns of flowering and fruiting (of entire community and functional groups) can vary over time, providing information about the dynamics of Cerrado herbaceous layer following fires.

Conclusions

Our study was one of the few to demonstrate the influence of fire season in the flowering and fruiting patterns of communities and functional groups in areas of open savannas, revealing distincts effects. EF would trigger flowering of graminoids and other community species just after fire. MF would favor shrub species flowering 1 yr after fire. Shrubs certainly would benefit by LF as well as communities species (during the middle of rainy and dry season). Strategies after fire can be diverse, fire dependent (just flower with fire), fire sensitive (just flower without fire) or seems to be

not affected by fire: fire independent (flowered in all treatments) and season dependent (flowered in the same season (dry/rainy), regardless to fire presence or season). So, fire season can affect not only the flowering patterns of community and functional groups but also the species strategies, suggesting that very frequent fires in a specific fire season could favor some groups or species.

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Supporting Information 1. List of family and species flowering in different periods in each fire season, over one year after fire, in *campo sujo* areas in Central Brazil. EF= early-dry season fire, MF=mid-dry season fire, LF=late dry season fire and Control. n.p.=species not present in the plot, dotted line indicate presence of species, but the absence of flower. M13: May 2013, J13: July 2013, O13: October 2013, F14: February 2014, M14: May 2014, J14: July 2014, O14: October 2014, F15: February 2015, M15: May 2015, J15: July 2015 and O15: October 2015. HRCB= resgistration number at "Herbarium Rioclarense", Rio Claro, SP, Brazil. n.c. = not collected.

Family	Species	Control	EF	MF	LF	HRCB
Acanthaceae						
	Justicia chrysotrichoma Pohl ex Nees	n.p.	n.p.	-------	n.p.	63855
	Justicia lanstyakii Rizzini	-------	-------	J14	-------	63905
	Ruellia angustior Lindau	n.p.	-------	n.p.	n.p.	63908
	Ruellia nitens (Nees) Wassh.	-------	O13	J14	-------	63807
Annonaceae						
	Annona crassiflora Mart.	M14	-------	-------	-------	63813
Apocynaceae						
	Hemipogon acerosus Decne.	n.p.	F14	M14	n.p.	63371
	Mandevilla tenuifolia (J.C.Mikan) Woodson	-------	n.p.	n.p.	n.p.	63814
Arecaceae						
	Syagrus sp.	-------	-------	-------	-------	n.c.
Asteraceae						
	Aldama bracteata (Gardner) E.E.Schill. & Panero	-------	F14/M14	M14	-------	63924
	Aldama grandiflora (Gardner) E.E.Schill. & Panero	J13/M14	-------	O13	-------	63842
	Ayapana amygdalina (Lam.) R.M.King & H.Rob.	J13/M14	F14	-------	J14	63925
	Calea elongata (Gardner) Baker	n.p.	-------	-------	n.p.	59687
	Chresta curumbensis (Philipson) H.Rob.	n.p.	n.p.	n.p.	-------	n.c.
	Chrysolaena simplex (Less.) M. Dematteis	-------	-------	n.p.	n.p.	63859
	Echinocoryne holosericea (Mart.) H.Rob.	-------	-------	-------	n.p.	63293
	Gochnatia paniculata (Less.) Cabrera	-------	n.p.	-------	-------	63850
	Ichthyothere terminalis (Spreng.) S.F.Blake	F14	O13/F14	F14	F14/J14	63309

Family	Species	Control	EF	MF	LF	HRCB
	Lessingianthus durus (Mart. ex DC.) H.Rob.	-------	n.p.	-------	-------	63297
	Lessingianthus warmingianus (Baker) H. Rob.	-------	n.p.	-------	n.p.	63845
	Praxelis kleinioides (Kunth) Sch.Bip.	n.p.	n.p.	-------	n.p.	63294
	Senecio adamantinus Bong.	-------	n.p.	n.p.	n.p.	n.c.
	Spilanthes nervosa Chodat	-------	n.p.	-------	-------	63829
	Trichogonia cinerea (Gardner) R.M.King & H.Rob.	-------	-------	n.p.	n.p.	63496
Bignoniaceae						
	Distictella elongata (Vahl) Urb.	-------	-------	-------	n.p.	63264
	Fridericia platyphylla (Cham.) L.G.Lohmann	-------	-------	-------	n.p.	56938
	Jacaranda caroba (Vell.) A.DC.	n.p.	-------	n.p.	-------	n.c.
Cactaceae						
	Brittonia sp.	-------	-------	-------	-------	63353
Calophyllaceae						
	Kielmeyera rubriflora Cambess. var. *major* Saddi	n.p.	F14	O13/F14	n.p.	63864
Caryocaraceae						
	Caryocar brasiliense Cambess.	n.p.	n.p.	-------	n.p.	n.c.
Connaraceae						
	Connarus suberosus Planch.	n.p.	n.p.	n.p.	-------	63901
Convolvulaceae						
	Ipomoea fiebrigii Hassl. ex O'Donell	-------	O13/F14	-------	F14	63376
	Ipomoea sp.	-------	-------	-------	-------	64389
	Merremia digitata (Spreng.) Hallier f.	-------	-------	F14	-------	63375
	Merremia digitata (Spreng.) Hallier f. var. *digitata*	-------	-------	n.p.	-------	n.c.
Cyperaceae						
	Bulbostylis junciformis (Kunth) C.B.Clarke	F14	F14	F14	n.p.	64379

Family	Species	Control	EF	MF	LF	HRCB
	Bulbostylis paradoxa (Spreng.) Kunth ex C.B.Clarke	-------	-------	-------	-------	n.c.
	Cyperaceae sp.	F14	n.p.	O13	n.p.	63467
	Cryptangium verticillatum (Spreng.) Vitta	-------	n.p.	-------	n.p.	63451
	Rhynchospora sp1	J13	n.p.	M14	F14	63456
	Rhynchospora sp2	-------	-------	-------	-------	63453
Dilleniaceae						
	Davilla elliptica A.St.-Hil.	-------	J13	-------	-------	63897
Eriocaulaceae						
	Paepalanthus koernickei (Ruhland) Trovó	-------	n.p.	n.p.	n.p.	63801
Erythroxylaceae						
	Erythroxylum suberosum A.St.-Hil.	-------	n.p.	n.p.	-------	63370
Euphorbiaceae						
	Dalechampia sp.	-------	n.p.	n.p.	-------	63851
	Croton antisyphiliticus Mart.	-------	J13	O13	O14	63860
	Croton sp.	n.p.	-------	-------	-------	63363
	Euphorbia sp1	-------	-------	O13	-------	63938
	Euphorbia sp2	-------	n.p.	-------	n.p.	63941
	Manihot kalungae M.J.Silva & R.C.Sodré	F14/M14	-------	-------	F14	64377
	Manihot sp. new specie	-------	-------	n.p.	n.p.	59733
	Sebastiana sp.	n.p.	n.p.	n.p.	-------	63846
Fabaceae						
	Bauhinia dumosa Benth.	-------	M14	M14/J14	M14/J14/O14	63497
	Calliandra dysantha Benth.	-------	J13	O13/F14	M14	63911
	Chamaecrista claussenii (Benth.) H.S.Irwin & Barneby	J13	M14	M14/J14	M14/J14	65891
	Chamaecrista aff. *fagonioides* (Vogel) H.S.Irwin & Barneby	n.p.	-------	J14	-------	63893

Family	Species	Control	EF	MF	LF	HRCB
	Chamaecrista isidorea (Benth.) H.S.Irwin & Barneby	n.p.	-------	n.p.	n.p.	63895
	Chamaecrista ochrosperma (H.S.Irwin & Barneby) H.S.Irwin & Barneby	-------	-------	-------	M14	63920
	Cenostigma sp.	-------	n.p.	n.p.	n.p.	63786
	Eriosema rufum (Thonn.) Baill.	-------	-------	-------	-------	63891
	Galactia sp.	-------	-------	F14	J14	63811
	Harpalyce brasiliana Benth.	-------	F14	-------	F14	64365
	Mimosa diminuta Marc. F. Simon & C.E. Hughes	M14	M14	M14	-------	63935
	Mimosa aff. *flavocaesia* Barneby	O14	-------	F14	-------	63789
	Mimosa gracilis Benth.	-------	O13	-------	-------	63791
	Mimosa aff. *leiocephala* Benth.	-------	-------	-------	-------	63769
	Mimosa macrocephala Benth.	-------	-------	n.p.	-------	63766
	Mimosa oligosperma Barneby	-------	n.p.	n.p.	n.p.	63772
	Mimosa aff. *pteridifolia* Benth.	F14	F14	F14	F14	63767
	Mimosa somnians Humb. & Bonpl. ex Willd.	F14/O14	F14	F14	F14	63787
	Mimosa sp1 new species	-------	O13	n.p.	n.p.	63914
	Mimosa sp2 new species	-------	-------	-------	-------	63895
	Senna corifolia (Benth.) H.S.Irwin & Barneby var. *corifolia*	-------	M14	-------	M14	63894
Gentianaceae						
	Deianira pallescens Cham. & Schltdl.	-------	-------	J14	-------	63940
Iridaceae						
	Cipura xanthomelas Maxim. ex Klatt	-------	F14	-------	F14	56931
	Sisyrinchium luzula Klotzsch	n.p.	n.p.	-------	n.p.	63282
	Trimezia juncifolia (Klatt) Benth. & Hook.f.	F14	O13	F14/M14	F14/M14	n.c.
Lamiaceae						
	Amasonia hirta Benth.	-------	n.p.	n.p.	n.p.	n.c.
	Hypenia sp.	J13/O13/F14/M14/J14/O14	O13	O13/J14	J14/O14	63871

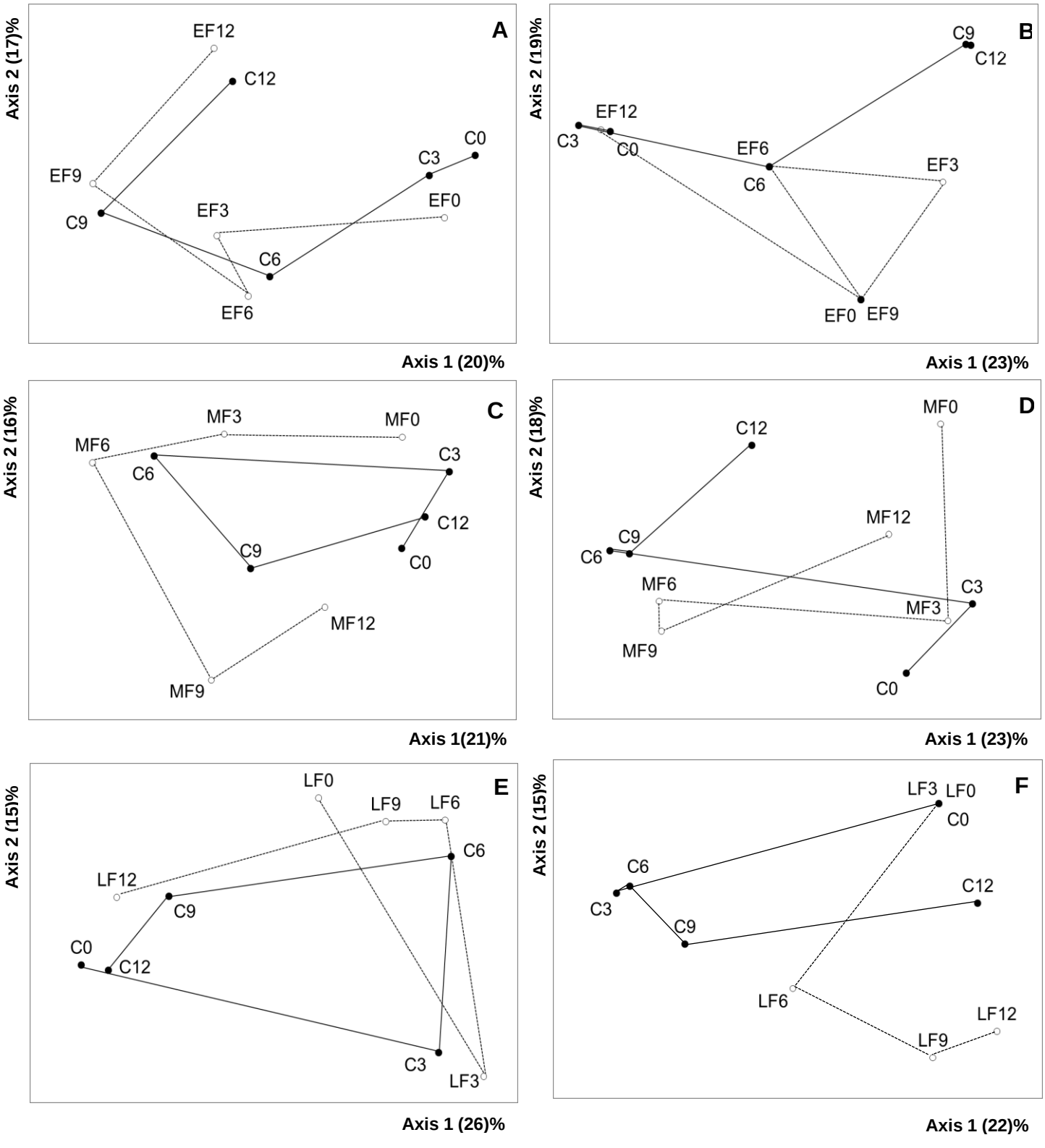
Family	Species	Control	EF	MF	LF	HRCB
	Hyptis sp.	-------	M14	F14/M14/J14	F14/M14	63291
	Medusantha mollissima (Benth.) Harley & J.F.B.Pastore ex Benth.	J13/O13/J14	O13	J14	J14/O14	63854
	Gymneia sp.	-------	-------	-------	n.p.	63367
Lythraceae						
	Cuphea sp.	-------	J13/F14	O13	-------	63852
	Diplusodon longipes Koehne	-------	n.p.	-------	-------	63836
	Diplusodon punctatus Pohl	-------	J13	-------	-------	63289
	Diplusodon sp.	-------	n.p.	O13/F14	n.p.	64374
	Lythraceae sp1	F14/M14	-------	-------	J14	56934
	Lythraceae sp2	-------	-------	-------	-------	63832
	Lythraceae sp3	-------	n.p.	n.p.	-------	63831
	Lythracea sp4	n.p.	n.p.	-------	n.p.	63288
Malpighiaceae						
	Banisteriopsis vernoniifolia (A.Juss.) B.Gates	n.p.	n.p.	n.p.	-------	63798
	Byrsonima guilleminiana A.Juss.	n.p.	n.p.	n.p.	-------	65456
	Byrsonima sp.	-------	-------	-------	-------	65458
	Camarea affinis A.St.-Hil.	F14/M14	M14	F14/M14/J14	F14/M14/J14	63875
	Camarea ericoides A.St.-Hil.	-------	J13	O13	-------	56935
	Heteropteris pannosa Griseb.	-------	-------	J14	-------	63887
	Heteropteris sp.	-------	n.p.	-------	n.p.	63899
	Pterandra pyroidea A.Juss.	-------	-------	n.p.	n.p.	63840
Malvaceae						
	Abutilon sp.	J13	M14	n.p.	M14	63313
Maranthaceae						
	Myrosma cannifolia L.f.	n.p.	F14	n.p.	n.p.	n.c.
Melastomataceae						

Family	Species	Control	EF	MF	LF	HRCB
	Microlicia sp1	-------	-------	-------	n.p.	63286
	Microlicia sp2	n.p.	-------	n.p.	n.p.	63306
	Tibouchina aegopogon Cogn.	M14	n.p.	n.p.	n.p.	63312
	Tibouchina melastomoides Cogn.	M14	M14	O13	M14/J14	63305
Moraceae						
	Brosimum gaudichaudii Trécul	-------	-------	J14	-------	n.c.
Myrtaceae						
	Myrcia guianensis (Aubl.) DC.	-------	-------	-------	-------	63890
	Myrcia laruotteana Cambess.	J14	-------	-------	-------	63885
	Myrcia sp.	n.p.	n.p.	n.p.	-------	n.c.
	Myrtaceae sp.	n.p.	-------	-------	n.p.	64386
	Psidium firmum O.Berg	-------	-------	n.p.	n.p.	n.c.
Ochnaceae						
	Ouratea sp.	O13/O14	-------	J14	M14	63882
Orchidaceae						
	Cleistes paranaenses (Barb. Rodr.) Schltdl.	-------	n.p.	n.p.	n.p.	63937
	Habenaria sp.	n.p.	n.p.	-------	n.p.	63816
	Habenaria tamanduensis Schltr.	-------	-------	-------	n.p.	64385
Oxalidaceae						
	Oxalis goyazensis Turcz.	O13/F14/J14	F14	F14/J14	F14	63824
Passifloraceae						
	Turnera incana Cambess.	-------	-------	O13	-------	63869
Phyllanthaceae						
	Phyllanthus sp.	n.p.	-------	n.p.	n.p.	63272
Poaceae						
	Anthaenantia lanata (Kunth) Benth.	-------	J13/F14	O13	O14	63459

Family	Species	Control	EF	MF	LF	HRCB
	Aristida setifolia Kunth	n.p.	-------	M14	n.p.	63482
	Axonopus marginatus (Trin.) Chase ex Hitchc.	-------	-------	-------	-------	63475
	Digitaria sp.	-------	J13	O13	n.p.	n.c.
	Elyonurus muticus (Spreng.) Kuntze	-------	J13	O13	-------	63458
	Mesosetum ferrugineum (Trin.) Chase	-------	J13	O13	-------	63446
	Mesosetum loliiforme (Hochst. ex Steud.) Chase	-------	-------	-------	M14	65451
	Oedochloa procurrens (Nees ex Trin.) C. Silva & R.P. Oliveira	-------	J13/O13	O13	-------	63469
	Oncorachis ramosa (Zuloaga & Soderstr.) Morrone & Zuloaga	M14	-------	M14/J14	-------	63485
	Panicum campestre Nees ex Trin.	-------	J13	O13	M14	63470
	Paspalum gardnerianum Nees	-------	-------	-------	-------	63473
	Paspalum pectinatum Nees ex Trin.	-------	-------	-------	-------	63468
	Poaceae sp.	-------	J13	-------	M14	n.c.
	Trachypogon spicatus (L. f.) Kuntze	-------	-------	-------	-------	63931
	Trichanthecium cyanescens (Nees ex Trin.) Zuloaga & Morrone	M14	M14	-------	M14/J14	63457
Polygalaceae						
	Polygala abreui Marques & J.F.B.Pastore	-------	-------	-------	J14	64372
	Polygala coriacea A.St.-Hil. & Moq	-------	-------	-------	-------	63847
Rubiaceae						
	Galianthe sp.	n.p.	n.p.	-------	-------	63867
	Borreria sp.	M14/J14	M14	M14	M14/J14	63866
	Diodia sp.	n.p.	n.p.	n.p.	-------	63301
	Palicourea rigida Kunth	-------	-------	-------	-------	63849
	Sabicea brasiliensis Wernham	n.p.	-------	-------	n.p.	63265
	Tocoyena formosa (Cham. & Schltdl.) K.Schum.	-------	n.p.	n.p.	n.p.	63856
	Rubiaceae sp.	-------	-------	-------	-------	64559
Salicaceae						

Family	Species	Control	EF	MF	LF	HRCB
	Casearia sylvestris Sw.	n.p.	-------	-------	-------	n.c.
Sapindaceae						
	Serjania trichomisca Radlk.	J14	n.p.	M14/J14	M14/J14	63805
Velloziaceae						
	Vellozia squamata Pohl	n.p.	-------	n.p.	n.p.	63436
	Vellozia tubiflora (A. Rich.) Kunth	-------	-------	-------	n.p.	63929
Verbenaceae						
	Lippia sp.	-------	-------	-------	-------	63837
	Stachytarpheta sp .	-------	n.p.	n.p.	n.p.	63364
Vochysiaceae						
	Vochysia pumila Pohl	-------	-------	-------	-------	63495

Supporting Information 2. Ordination of sampling units described by the species composition (presence/absence of flowering species (A, C, E) / presence/absence of fruiting species (B, D, F)) in early- (EF), mid- (MF), late-dry season fires (LF) and controls (C). Over one year (0: before fire (C0, EF0, MF0, LF0), 3: tree monts after fire (C3, EF3, MF3, LF3), 6: six months after fire (C6, EF6, MF6, LF6), 9: Nine months after fire (C9, EF9, MF9, LF9) and 12: one year after fire (C12, EF12, MF12, LF12)) in *campo sujo* areas in Central Brazil. The ordination method was Principal Analysis (PCO) and the resemblance measure applied between sampling units was Jaccard.



Considerações finais

Considerações finais

O fogo pode ser considerado como um fator de extrema importância para diversas vegetações ao redor do mundo (Trollope 1982, Ramsay & Oxley 1996, Lloret 1998, Morgan 1999) e exerce efeitos complexos sobre a dinâmica da vegetação (Bond *et al.* 2005), inclusive no Cerrado, estando presente há pelo menos 5 milhões de anos (Simon *et al.* 2009). O fogo natural (por meio de raios) ocorre no Cerrado na estação chuvosa (setembro – maio) e as áreas atingidas tendem a ser pequenas, pois geralmente os raios são seguidos da chuva (Ramos-Neto & Pivello 2000). Porém, o homem alterou a época da queima, utilizando-se do fogo durante a estação seca para prover alimento para o gado (Coutinho 1990). No Brasil, além da mudança na época da queima, grande parte das unidades de conservação tem utilizado a prática de supressão do fogo, levando a um grande acúmulo de material combustível, resultando em incêndios de grandes magnitudes (Fidelis & Pivello 2011).

Enquanto que em outras vegetações onde o fogo é um fator presente utilizam-se de queimadas prescritas para a conservação, o fogo ainda não é utilizado como uma ferramenta de manejo no Brasil (Durigan & Ratter 2016). Saber se há uma época de queima ideal é uma das principais questões para a aplicação do manejo do fogo (Durigan & Ratter 2016). Por essa razão, o objetivo principal desta tese foi estudar as respostas da vegetação herbáceo-arbustiva do Cerrado quando submetida a diferentes épocas de queimas.

<u>Época da queima e sua influência no comportamento do fogo e recuperação da biomassa:</u>

Nos dois primeiros capítulos discutimos a influência da época da queima no comportamento do fogo e como a biomassa se regenera e acumula após cada época de queima ao longo de dois anos.

A produtividade da biomassa total, um ano depois da queima, foi maior nas queimas modais e tardias, enquanto que na queima precoce o acúmulo foi menor em relação às áreas controles. Dois anos depois, a produtividade entre áreas controle e queimadas foi a mesma. A composição da biomassa total entre controle e tratamentos foi diferente um ano (entre controle e todos os tratamentos) e dois anos após a queima (entre controle e tardias), essa diferença deve-se principalmente à quantidade de biomassa morta (menor nas parcelas de queima). A regeneração da biomassa (total/morta e viva) foi rápida sem ser prejudicada por nenhuma das queimas. Nas parcelas controle, a acumulação de biomassa total e morta ao longo do tempo demonstra a lenta taxa de decomposição da biomassa. Sem um manejo adequado deste material, essa biomassa irá aumentar ao longo do tempo, favorecendo fogos mais intensos e difíceis de controlar.

A época da queima não resultou em diferenças significativas entre os principais parâmetros do fogo (por exemplo: intensidade, velocidade da chama, altura da chama e eficiência de queima). No entanto, a porcentagem de material combustível morto foi maior no meio e no final da estação seca (queimas modal e tardia) em relação ao início da estação seca (queimas precoce), o que poderia resultar em diferenças na intensidade do fogo (com um maior tempo de exclusão desde o último fogo). A intensidade do fogo foi explicada pela combinação de material combustível total e porcentagem de material combustível morto. A altura da chama foi melhor explicada pelos

modelos: 1) porcentagem de material combustível morto e umidade do material combustível, 2) porcentagem de material combustível morto e material combustível total e 3) pela porcentagem de material combustível morto.

Época da queima e as respostas da vegetação herbácea:

No terceiro capítulo verificamos se o fogo nas diferentes épocas influenciaria os padrões da comunidade (riqueza, diversidade, cobertura) e dos elementos que a compõem (solo nu, biomassa morta, graminóide, herbácea e arbusto). Logo após a queima, o fogo removeu a biomassa morta, aumentando os espaços (solo nu) para o reestabelecimento da vegetação. Há uma dinâmica natural das comunidades na ausência do fogo, na qual os padrões variam de acordo com a sazonalidade (época seca e época chuvosa). De maneira geral, o fogo (independentemente da época) não alterou esses padrões de cobertura, riqueza e diversidade, sugerindo que a curto-prazo a época da queima tem pouco efeito sobre a dinâmica dessas comunidades. Apesar da pouca influência da época da queima nestes padrões, efeitos sutis foram observados: a cobertura de todos os grupos funcionais foi recuperada, queimas tardias favoreceram maior cobertura de espécies de herbáceas no meio da estação seca. A cobertura de espécies de arbustos foi favorecida em todas as épocas da queima em diferentes momentos: nas precoces ao longo da estação chuvosa (fevereiro e maio), após dois anos nas queimas modais (meio da estação seca) e no meio da estação chuvosa nas queimas tardias. A riqueza total e de cada grupo funcional assim como a diversidade não foram maiores nas parcelas de queima (independentemente da época). A composição e

cobertura de espécies variam ao longo do ano em todos os tratamentos e seus padrões também não foram alterados devido às queimas.

Finalmente, no último capítulo, discutimos o efeito da época da queima na floração e frutificação de comunidade do estrato-herbáceo, bem como dos distintos grupos funcionais. Além disso, podemos constatar e exemplificar diferentes estratégias de floração pós-fogo, como: espécies que só floresceram na presença (fogo dependentes) ou ausência do fogo (sensíveis ao fogo), florescimento nos tratamentos de queima e controle (fogo independente) e florescimento sempre na mesma época do ano (seca/chuvosa) independente do fogo ou da época da queima. A porcentagem de floração da comunidade foi maior nas queimas precoces (logo após o fogo: três e seis meses) e tardias (três e nove meses após o fogo). A frutificação da comunidade foi maior nas queimas modais (um ano depois) e tardias (nove meses e um ano após a queima). Queimas precoces tendem a aumentar o florescimento de espécies de graminóides logo após a queima, enquanto que, queimas modais e tardias favoreceriam o florescimento de espécies de arbustos.

Neste estudo de queimadas controladas em um curto prazo (dois anos após as queimas) foi observado que a época da queima, de maneira geral, não altera a dinâmica e os padrões das comunidades vegetais, as diferenças são sutis e ocorrem a curto período de tempo (Figura 1).

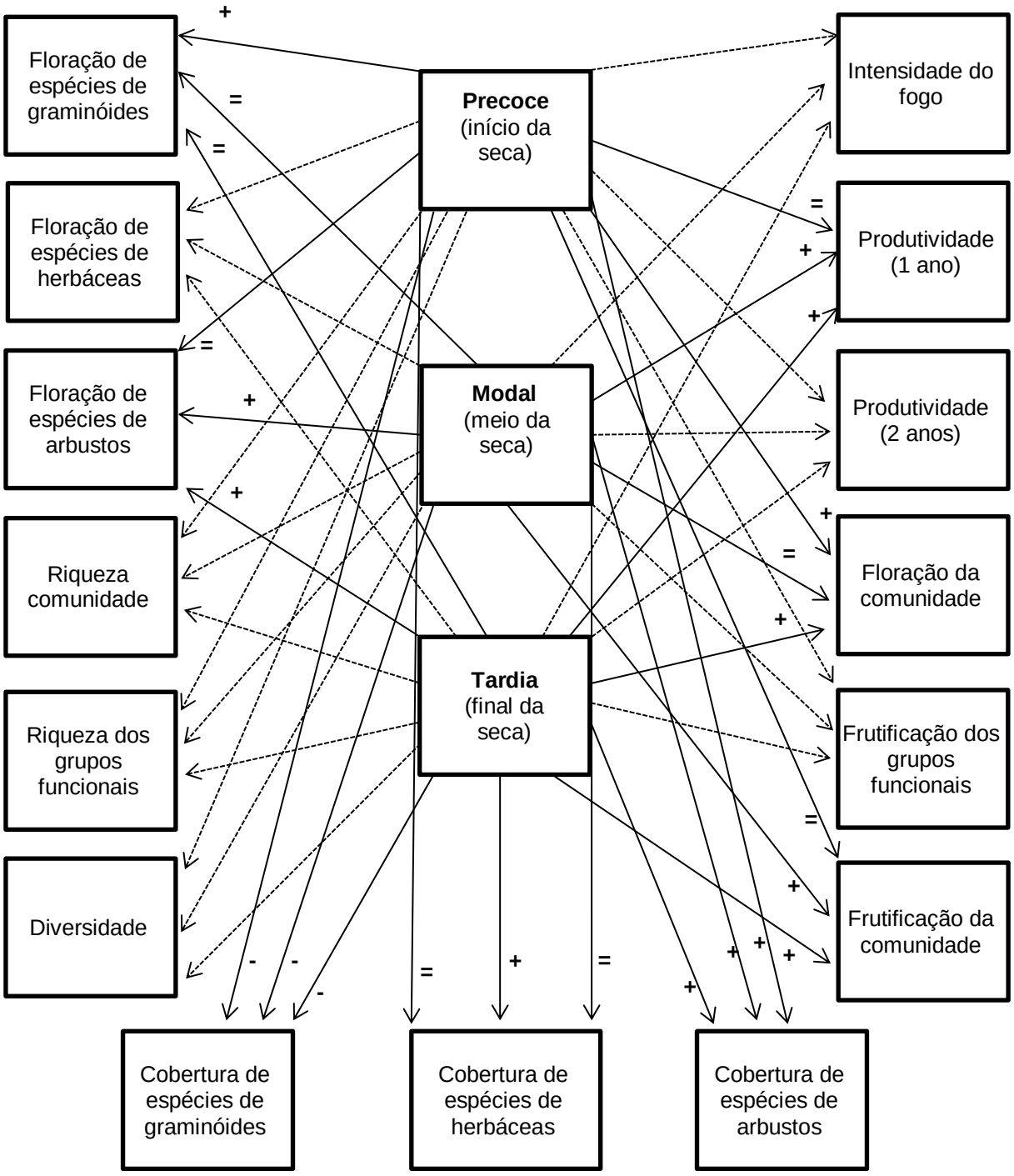


Figura 1. Representação da relação entre época da queima (precoce, modal e tardia) nos principais parâmetros avaliados neste trabalho. Flechas pontilhadas indicam que nenhuma das épocas aumentou/diminui o parâmetro analisado, o sinal de igual (=) representa a não alteração do parâmetro, sinal positivo (+) indica aumento, enquanto que o sinal negativo (-) indica diminuição.

A recuperação da biomassa e da vegetação são importantes parâmetros que irão influenciar o comportamento do fogo. Com base nos resultados alcançados, para a aplicação de queimas prescritas, elucidamos algumas implicações de acordo com o objetivo do manejo:

- para a redução do material combustível e incêndios de grandes proporções: a queima controlada pode ser realizada em qualquer época do ano.

- manutenção da fisionomia campestre: as poucas mudanças nos padrões de regeneração (da vegetação e da biomassa) e na estrutura da vegetação sugerem que a época da queima pouco altera a dinâmica destas vegetações.

- para o uso do fogo como ferramenta de manejo e manutenção da vegetação herbácea, sugerimos que a queima seja realizada em mosaicos utilizando diferentes épocas e frequências. Uma vez que as respostas da comunidade e dos grupos funcionais diferiram de acordo com a época, principalmente em relação à floração, frutificação e cobertura. Além disso, maiores amplitudes de intensidade, taxa de propagação do fogo e altura das chamas foram amostradas apenas nas parcelas modais e tardias.

O fogo deve ser utilizado como ferramenta de manejo a fim de prevenir incêndios de maiores áreas e com grandes intensidades. Além disso, queimas prescritas também podem ser utilizadas para a manutenção de fisionomias e diversidade das comunidades vegetais nativas. Dessa forma, os resultados desta tese possibilitam uma visão dos efeitos em curto prazo da época da

queima, a fim de possibilitar o manejo desta vegetação. Acreditamos que a melhor maneira para o uso do fogo como ferramenta de manejo seja através da queima em mosaicos utilizando diferentes épocas e frequências, uma vez que os grupos funcionais apresentaram respostas diferentes de acordo com cada época da queima. Estudos de longo prazo e que observem outros componentes do regime de queima (histórico e frequência, por exemplo) são de extrema importância para o conhecimento do manejo através do fogo.

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