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

**O EFEITO DO HISTÓRICO DO FOGO NA FENOLOGIA REPRODUTIVA E
ATRIBUTOS DE SEMENTES E GERMINAÇÃO EM ESPÉCIES DE CERRADO**

HELOIZA LOURENÇO ZIRONDI

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

**Junho
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(Biologia Vegetal).

Orientadora: Prof^a. Dra. Alessandra Fidelis
Coorientador: Dr. Mark Ooi

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Z81e

Zirondi, Heloiza Lourenço

O efeito do historico do fogo na fenologia reprodutiva e atributos de sementes e germinacao em especies de Cerrado / Heloiza Lourenço Zirondi.

-- Rio Claro, 2019

85 f. : tabs., fotos

Dissertação (mestrado) - Universidade Estadual Paulista (Unesp), Instituto de Biociências, Rio Claro

Orientadora: Alessandra Fidelis

Coorientador: Mark Ooi

1. Fenologia reprodutiva pós-fogo. 2. Germinacao. 3. Atributos de sementes. 4. Floracao pos-fogo. 5. Cerrado. I. Título.

Sistema de geração automática de fichas catalográficas da Unesp. Biblioteca do Instituto de Biociências, Rio Claro. Dados fornecidos pelo autor(a).

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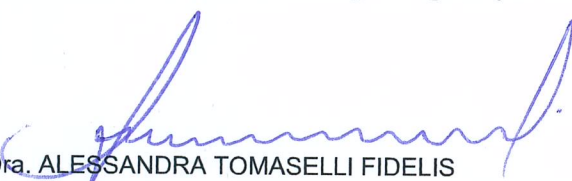
TÍTULO DA DISSERTAÇÃO: O efeito do histórico do fogo na fenologia reprodutiva e atributos de sementes e germinação em espécies de cerrado

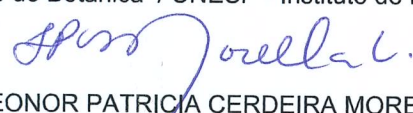
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Rio Claro, 26 de junho de 2019

Aos meus avós *Maria, Deley e Quelé (in Memoriam)*

pelo amor, carinho e ensinamentos!

AGRADECIMENTOS

Agradeço primeiramente à Deus que me deu forças para alcançar mais um objetivo.

Aos meus pais, Miriam e Eliel, pelos ensinamentos, amor, incentivo e suporte. Obrigada por me impulsionaram a trabalhar pelos meus sonhos e me inspirarem a seguir sempre em frente. Aos meus irmãos Beatriz e Leandro pelo amor e por estarem sempre ao meu lado.

Aos meus familiares e amigos que sempre estiveram ao meu lado me aconselhando, apoiando e fazendo rir, deixando assim o caminho mais leve.

À minha professora, orientadora e amiga Ale! que confiou em mim desde a graduação e ao longo dos anos me ensinou, corrigiu e guiou no caminho da ciência, me inspirando com sua paixão e dedicação nesse mundo de descobertas. Obrigada por humildemente abrir as portas desse mundo e me fazer alçar vôo!

To my co-supervisor Mark for all contributions, knowledge, and kindness. I learned so much with you!

À família LEveg (ex e atuais integrantes): Aline, Ana, Cassy, Daniel, Gabi, Giovana, Jhony Galdi, Ju, Marco, Mari, Soizig e Vagner, pelo suporte, orientação e ajuda dedicados a mim e a este trabalho. Agradeço principalmente pelas “reuniões de cúpula”, contagens de perfilhos, coleta de sementes (eu sei que não foi fácil), discussões estatísticas e até análise de imagens. Vocês são a melhor equipe do mundo! Obrigada pelas risadas sinceras e escandalosas e por compartilhar essa experiência comigo!

Às pessoas de Brasília e Cavalcante que foram essenciais para realização desse trabalho: Mylene M. da Silva, Raquel Vieira, Mauricio Cunha e os empregados da Reserva Natural Serra do Tombador: Whatson F. Rezende, Anderson F. Terra, Gilson de A. Berberino, Rogério B. de Almeida e Silvanio A. Borges.

Ao Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq 130344/2017-6) pela bolsa concedida no início do projeto.

À Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) pelo financiamento dos projetos FAPESP 2017/16149-4, FAPESP 2015/06743-0 e BEPE 2018/08017-3 os quais fazem parte desta pesquisa. E também à Fundação Grupo Boticário (0153_2011_PR).

Ao Programa de Pós-Graduação em Ciências Biológicas (Biologia Vegetal) e ao departamento de Botânica da UNESP-Rio Claro pela oportunidade.

Enfim, a todos aqueles que fizeram parte da minha vida nesta caminhada meu
Muitíssimo Obrigada!

RESUMO GERAL

No Cerrado, um dos fatores abióticos que influenciam na fenologia das plantas é o fogo, o qual é um distúrbio natural que interfere em diversos ecossistemas do mundo. O fogo altera as condições do habitat podendo afetar a floração, frutificação, atributos das sementes e germinação. Portanto, esse projeto visou compreender o efeito do fogo na fenologia reprodutiva e nos atributos de semente e germinação da comunidade do Cerrado. Para isso, foram realizadas a contagem do número de ramos (vegetativos e reprodutivos) por espécie, realizados em 30 subparcelas de 1x1m em áreas com diferentes históricos de fogo (C=6 anos sem queima e FB=recentemente queimada). Também foram marcados indivíduos de diferentes espécies dominantes em ambas as áreas. A comunidade e os indivíduos tiveram sua floração acompanhados a cada 15 dias durante 3 meses após a queima e então aos 6, 9 e 12 meses. Os seguintes atributos das sementes e germinação foram medidos: forma e peso da semente, teor de água, germinabilidade, tempo médio de germinação e sincronia. Nossos resultados mostraram que o fogo aumentou a floração nas áreas queimadas. Já nos primeiros 30 dias até 3 meses após a queima houve até 2 vezes mais espécies que floresceram nas áreas FB comparados a C. Também houve um aumento significativo na proporção de ramos reprodutivos aos 3 meses pós-fogo na comunidade, mostrando que a profusão reprodutiva ocorre nos primeiros meses após queima. Dentre as espécies da comunidade 66,39% podem ser consideradas estimuladas pelo fogo. Os atributos de semente e germinação foram afetados pela frequência de fogo, resultados mostraram que 67% das espécies apresentaram pelo menos uma de seus atributos de germinação alterados na área FB quando comparadas à área C. Algumas espécies mostraram um aumento e outras uma diminuição na germinação no FB. No entanto, a viabilidade foi menor e a germinação mais rápida nas sementes das áreas FB. Atributos das sementes (peso, forma e conteúdo de água) de oito espécies também diferiram entre as áreas. Dentre essas espécies, a maioria apresentava sementes menores com maior teor de água nas áreas FB em relação a C. Portanto, o fogo não somente altera a fenologia reprodutiva, principalmente, estimulando a floração e frutificação de muitas espécies como também a frequência de fogo pode levar a mudanças rápidas nos atributos de germinação e sementes. Isso fornece alguns indicativos sobre a evolução dos atributos das plantas do Cerrado frente ao fogo.

Palavras-chave: fenologia reprodutiva, germinação, atributos de sementes, floração pós-fogo, fogo, Cerrado.

ABSTRACT

In Cerrado one of the abiotic factors that influences plant phenology is fire, which is a natural disturbance that interferes with several ecosystems in the world. Fire changes the conditions of the habitat and can affect flowering, fruiting and seeds and germination traits. Therefore, this project aimed to understand the effect of fire on reproductive phenology and on seed and germination traits of Cerrado community. For this purpose, the counting of the number of branches (vegetative and reproductive) by species was carried out in 30 subplots of 1x1m in areas with different fire histories (C = 6 years without burning and FB = recently burned). We also marked individuals of different dominant species in both areas. The community and individuals had their flowering counted every 15 days for 3 months after burning and then at 6, 9 and 12 months. The following seed and germination traits were measured: seed shape and mass/weight, water content, germinability, mean germination time and synchrony. Our results showed that fire increased flowering in burned areas. Already after 30 days up to 3 months after the burning there were up to 2-fold more species flowering in the FB areas compared to C. There was also a significant increase in the proportion of reproductive shoots at 3 months post-fire in the community, showing that the reproductive profusion occurs in the first few months after burning. Among the species of the community 66.39% can be considered stimulated by fire. Seed and germination traits were affected by fire frequency. Results showed that 67% of the species presented at least one of their germination altered in FB area when compared to area C. In general, some species showed an increase and others a decrease in germination in FB. However, viability was lower and germination faster in seeds of FB areas. Seed traits (mass/weight, shape and water content) of eight species also differed between areas. Among these species, the majority presented smaller seeds with higher water content in burned areas compared to C. Therefore, fire not only alters the reproductive phenology, mainly stimulating flowering and fruiting of many species but also fire frequency can lead to rapid changes in germination and seed traits. This provides some insight on the evolution of Cerrado plant traits facing fire.

Keywords: reproductive phenology, germination, seed traits, post-fire flowering, fire, Cerrado.

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INTRODUÇÃO GERAL

O fogo é um processo natural integrado nas funções de diversos ecossistemas. Age como força seletiva que altera as condições do habitat e consequentemente, afeta os processos vitais dos organismos (Keeley et al., 2011; Whelan, 1995). Tal distúrbio pode provocar mudanças na hierarquia de competição, assim como mudanças na estrutura e dinâmica de populações e comunidades vegetais, nos processos ecológicos, na disponibilidade de substrato e na diversidade de espécies (Whelan 1995; Bond e van Wilgen 1996). Essas alterações ocorrem pois a queima remove a serapilheira abrindo espaço para novas espécies (Fidelis et al. 2012), altera condições de microclima (Fidelis e Blanco 2014), além de modificar quimicamente o solo, estimula o rebrotamento e a ciclagem de nutrientes (Whelan 1995; Bond e Wilgen 1996; Hoffmann 1996). Após tantas mudanças causadas pela passagem do fogo, muitos ecossistemas ainda são capazes de se regenerar, enquanto outros são radicalmente alterados (Cochrane e Ryan 2009).

Em vegetações onde o fogo é um distúrbio recorrente, muitas plantas possuem adaptações morfológica e/ou fisiológicas à passagem do fogo como, meristemas protegidos, cascas grossas (Gignoux et al., 1997; Keeley et al., 2011), aumento e antecipação da floração (Lamont and Downes, 2011; Pyke, 2017) e estímulo da germinação (Auld and O'Connell, 1991; Auld and Ooi, 2009), assegurando portanto a persistência das plantas após o fogo.

Em muitos ecossistemas inflamáveis é possível observar diversas espécies, principalmente monocotiledôneas, que necessitam do fogo para florir ou que florescem em maior quantidade em áreas queimadas (Lamont and Downes, 2011; Pyke, 2017). A passagem do fogo também pode afetar a sincronia de floração como observado em herbáceas e arbustos de uma floresta de pinheiros nos Estados Unidos

(Platt et al., 1988) e em indivíduos de *Vellozia sincorana* no campo rupestre (Conceição et al., 2013; Conceição and Orr, 2012).

Algumas plantas apresentam adaptações em seus propágulos e respostas germinativas. Os compostos químicos presentes na fumaça podem estimular germinação e aumentar sincronia de diversas espécies de ambientes pirofíticos (Çatav et al., 2018; Moreira et al., 2010). As altas temperaturas ocasionadas nas queimas podem agir quebrando a dormência física de sementes impermeáveis ao romper o tegumento permitindo a entrada de água na semente e possibilitando o processo a germinação (Baskin and Baskin, 2001; Keeley et al., 2011; Moreira et al., 2010; Paula and Pausas, 2008). No entanto, nem sempre os efeitos do fogo são positivos na vegetação. Hoffmann (1998) observou uma queda na produção de frutos e sementes de quatro espécies lenhosas três anos após o fogo, o que poderia estar associado à estratégia de investimento energético na reposição de órgãos vegetativos danificados durante a passagem do fogo (Hoffmann 1998; Medeiros e Miranda 2008; Palermo e Miranda 2012).

Na verdade, as plantas não apresentam adaptações ao fogo e sim ao regime do fogo (Keeley et al., 2011), ou seja, adaptações às características do fogo como intensidade, frequência, estação e histórico (Bond and van Wilgen, 1996; Keeley et al., 2011; Whelan, 1995). Por exemplo, comunidades vegetais expostas a regimes de fogo com queimas mais frequentes tendem a apresentar maior porcentagem de plantas rebrotadoras, enquanto uma menor frequência de fogo permite uma maior presença de plantas germinadoras, já que o estabelecimento por sementes demanda um intervalo entre queimas geralmente maior (Bond and Midgley, 2001; Pausas et al., 2004). Desta forma, o estudo do efeito do regime do fogo se torna importante para compreender os reais efeitos do fogo nos atributos das plantas e consequentemente na dinâmica das comunidades vegetais.

Um dos atributos que pode ser alterado pelo regime de fogo é a fenologia reprodutiva das plantas (Coutinho, 1990; Fidelis and Blanco, 2014; Lamont and Downes, 2011; Pyke, 2017). Em muitos casos, a floração e/ou frutificação podem ser adiantadas e/ou aumentadas e essas respostas diferem de acordo com as características do fogo daquele ambiente. O estímulo da floração pós-fogo foi observado para 386 espécies (em sua maioria plantas da vegetação Mediterrânea), sendo que a floração pós-fogo foi mais estimulada em áreas com uma frequência moderada de queimas e alta intensidade (Lamont and Downes, 2011). Knox e Morrison (2005) relataram um aumento no output reprodutivo de proteáceas devido intervalos de queimas menores na vegetação australiana. No Cerrado, observou-se o estímulo e mudança no padrão floração de plantas de diversos grupos funcionais (Pilon et al., 2018; Rissi, 2016; Souza, 2011) após a passagem do fogo. Algumas espécies mostraram certa dependência da queima, como por exemplo, *Bulbostylis paradoxa* que necessita do fogo para que a fenofase reprodutiva ocorra (Fidelis et al., 2019). Já nos Campos Sulinos, o histórico do fogo afetou diferentemente a floração da comunidade campestre, aumentando o número de espécies herbáceas florindo logo 30 dias após a queima enquanto que para as gramíneas esse aumento da floração foi observado depois um ano (Fidelis e Blanco, 2014). Assim sendo, o regime de fogo pode influenciar de maneira distinta os diferentes grupos funcionais (Fidelis e Blanco, 2014), afetando desta forma a montagem das comunidades.

Para algumas espécies, a época da queima pode afetar negativamente os processos reprodutivos (Hoffmann, 1998), afetando de maneira positiva ou negativa a floração, influenciando assim, os processos de recrutamento pós-fogo. Por exemplo Rissi (2016) observou um aumento na floração das gramíneas com a queima precoce (começo da estação seca) enquanto que a floração de arbustos foi beneficiada com as queimas tardias (final da seca) no Cerrado (Rissi, 2016).

O regime de fogo não somente altera o fitness das espécies vegetais ao alterar as condições básicas para o estabelecimento no ambiente (por exemplo disponibilidade de espaço, recursos e luminosidade) como também as características do fogo poderão afetar os atributos de germinação e propágulos/sementes (Bond and van Wilgen, 1996; Keeley and Fotheringham, 2000; Whelan, 1995).

Atributos das sementes são importantes pois estão diretamente conectados às fases essenciais de sobrevivência e propagação das espécies (Jiménez-Alfaro et al., 2016), pois permitem que as espécies germinem em condições propícias ao seu estabelecimento (Saatkamp et al., 2019). Por exemplo, alguns estudos indicam que o tamanho da semente estaria diretamente conectado com a capacidade de sobrevivência das plantas, onde sementes maiores resistiriam às altas temperaturas e teriam vantagens de estabelecimento sobre as pequenas ao originarem plântulas maiores e melhores competidoras (Bradstock et al., 1994; Daibes et al., 2019; Escudero et al., 2000; Gashaw and Michelsen, 2002; Lahoreau et al., 2006; Ribeiro et al., 2015). Porém, Hanley et al. (2003) mostraram que sementes menores possuem uma capacidade maior de germinar e são estimuladas quando expostas a altas temperaturas quando comparadas com sementes maiores. Portanto, mudanças em características do fogo, como a intensidade seriam capaz de selecionar espécies com sementes maiores ou menores ou até mesmo estimular a germinação (ver Moreno e Oechel, 1991). Da mesma maneira, a forma da semente estaria associada com as frequências das queimas, uma vez que sementes mais arredondadas seriam selecionadas por altas frequências de fogo (Gomez-Gonzalez et al., 2016, 2011).

O Cerrado é considerado uma vegetação susceptível ao fogo (“fire-prone ecosystem”), possuindo uma vegetação considerada pirofítica (Coutinho, 1990). A influência do fogo na vegetação do Cerrado já foi observada por grandes naturalistas como Saint-Hilaire e Eugen Warming desde os anos 1800, principalmente no estímulo

da floração pós-fogo (Saint-Hilaire, 2011; Warming and Ferri, 1973). E apesar de já existirem alguns estudos sobre como o fogo afeta a floração (Massi et al., 2017; Neves and Damasceno-Junior, 2013; Pilon et al., 2018) e germinação de espécies do Cerrado (ver Le Stradic et al. 2015; Fichino et al. 2016; Daibes et al. 2017; Daibes et al. 2018; Zironi, Silveira, et al. 2019; Zironi et al. 2019) a influência do regime de fogo na floração e nos atributos de sementes e germinação de espécies herbáceas e arbustivas do Cerrado ainda é pouco estudada.

É necessário ressaltar que alterações no regime de fogo irão resultar na mudança da comunidade vegetal (Keeley and Pausas, 2019). No Cerrado, o regime de fogo é alterado pela ação do homem sendo que, dentro da maioria das unidades de conservação ainda persiste a política de supressão do fogo (Durigan and Ratter, 2016; Fidelis et al., 2018) enquanto que fora delas, em áreas não protegidas, as queimadas realizadas em pastos e plantios alteram o regime natural de queima (Coutinho, 1990). Consequentemente, é visível a diferença na estrutura e composição de espécies em áreas com características de fogo distintas, como por exemplo diferentes históricos de fogo. Desta maneira, devido às diferentes respostas da vegetação em relação ao regime do fogo, é necessário entender seu efeito sobre as plantas do Cerrado e principalmente sobre a germinação a fim de utilizar esse conhecimento como subsídio para estratégias de manejo e conservação da diversidade do Cerrado.

Portanto, este trabalho visou avaliar o efeito do fogo na fenologia reprodutiva e da frequência e histórico do fogo (recentemente e frequentemente queimado x excluídas do fogo) nos atributos de sementes e germinação de espécies do Cerrado. Para tal, objetivou-se responder as seguintes perguntas: i) Existe diferença na fenologia reprodutiva de plantas do Cerrado entre áreas queimadas recentemente e excluídas do fogo?, ii) O fogo afeta a produção de flores das espécies na área

queimada?, iii) O histórico do fogo altera os atributos de semente e germinação dessas espécies? Esperamos que nossos resultados possam contribuir para um melhor entendimento dos processos envolvidos nas primeiras etapas da regeneração da vegetação após a passagem do fogo.

Estrutura da dissertação

Os capítulos foram elaborados em forma de manuscrito, redigidos em inglês e na formatação da revista científica de interesse, da seguinte forma:

Capítulo I: “*Fire affects flowering and fruiting of Cerrado species*”. Neste capítulo avaliamos a influência do fogo na fenologia reprodutiva, principalmente na floração de espécies do estrato herbáceo-arbustivo do Cerrado. Também comparamos como o fogo afeta a floração e frutificação dessas espécies de acordo com diferentes históricos de fogo (exclusão de fogo por seis anos x área recentemente queimada). Finalmente, criamos uma classificação de estratégias de floração pós-fogo e classificamos as espécies da comunidade de acordo com tal classificação. Tem-se como hipótese que haverá uma maior quantidade de espécies e uma maior profusão de floração e frutificação na área recentemente queimada quando comparada com a área de exclusão de fogo. Também haverá uma grande porcentagem de espécies que seriam estimuladas e dependentes do fogo para florescer no Cerrado. Este capítulo será submetido para *Journal of Vegetation Science*.

Capítulo II: “*Effects of fire frequency on seed and germination traits of Cerrado species*”. Neste capítulo avaliamos a influência da frequência de fogo (exclusão de fogo por seis anos x. área recentemente e frequentemente queimada) nos atributos de semente e germinação de espécies herbáceas e arbustivas do Cerrado. Tem-se como hipótese que espécies de áreas recentemente e frequentemente queimadas terão atributos de sementes e germinação alteradas direta ou indiretamente (efeito materno) quando comparadas a áreas com exclusão de fogo, uma vez que o fogo exerce uma pressão seletiva sobre os atributos da planta. Este capítulo será submetido para *Seed Science Research*.

Delineamento experimental

Área de estudo

Os experimentos foram realizados na Reserva Natural Serra do Tombador (RNST, 13° 35-38' S e 47° 45'-51' W) Cavalcante, Goiás (Fig.1). A Reserva é a maior RPPN de Cerrado do Brasil, com aproximadamente 8900 ha. O clima predominante para a região da RNST é tropical, com estação seca no inverno e chuvosa no verão, precipitação anual média entre 1500 e 1750mm e temperaturas médias máximas entre 26 e 36 °C e mínimas entre 8 e 14°C (Antonelli-Filho, 2011). Os solos são ácidos e pedregosos sendo classificados como Neossolos Litólicos Distróficos (Antonelli-Filho, 2011). Na RPNN podem ser encontrados diversas fisionomias de Cerrado, que vão desde fisionomias abertas como o *campo limpo* até fisionomias florestais como o *Cerradão*, porém os experimentos de queima foram realizados em áreas de *campo sujo* (Fig.2) que ocupam cerca de 31% da reserva. O *campo sujo* é uma fisionomia caracterizada pela dominância de gramíneas e plantas herbáceas, possuindo também arbustos esparsos e poucas árvores isoladas ao longo da paisagem (Coutinho, 1978).

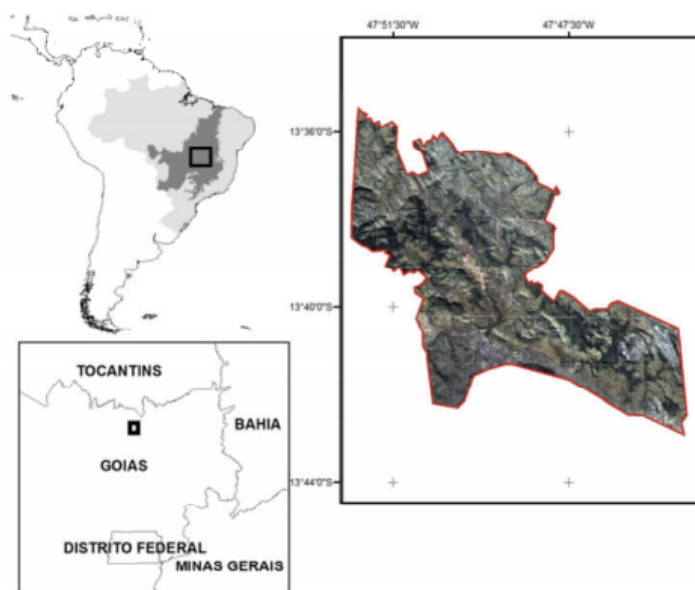


Figura 1. Localização da Reserva Nacional Serra do Tombador, no Estado de Goiás. Retirado de Gorgone-Barbosa (2016).

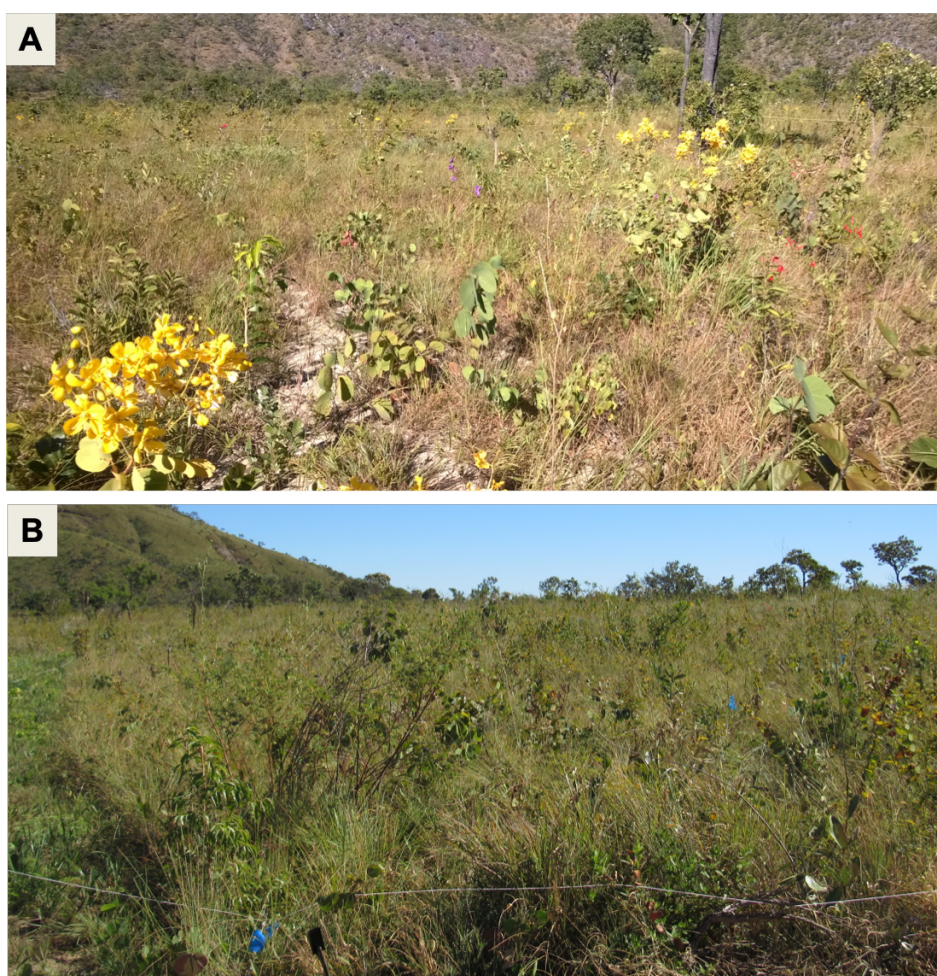


Figura 2. Fisionomias de campo sujo da área experimental na Reserva Natural Serra do Tombador, Cavalcante, Goiás.

Parcelas experimentais e Queimas

Foram utilizadas parcelas experimentais (30x30m) já estabelecidas na área desde 2013 (Fig.3a). Nesta área, há quatro tratamentos distribuídos aleatoriamente: controle (sem queimar desde 2011), queimais bienais (desde 2013) em Maio (precoces), Julho (modais) e Outubro (tardias). Para este experimento foram utilizadas as três parcelas experimentais controle (C) e três bienais modais (FB) (totalizando 6 parcelas) (Fig.3b-c). As parcelas modais foram queimadas pela terceira vez em Julho de 2017 quando tiveram início os levantamentos. As queimas de cada parcela experimental foram realizadas individualmente com o fogo sendo colocado em linha e a favor do vento (Fig.4). O fogo nessa área é de superfície, baixa intensidade e temperaturas (Rissi et al., 2017), com pulsos de calor acima de 100°C não ultrapassando 1 minuto em média (Daibes et al., 2017).

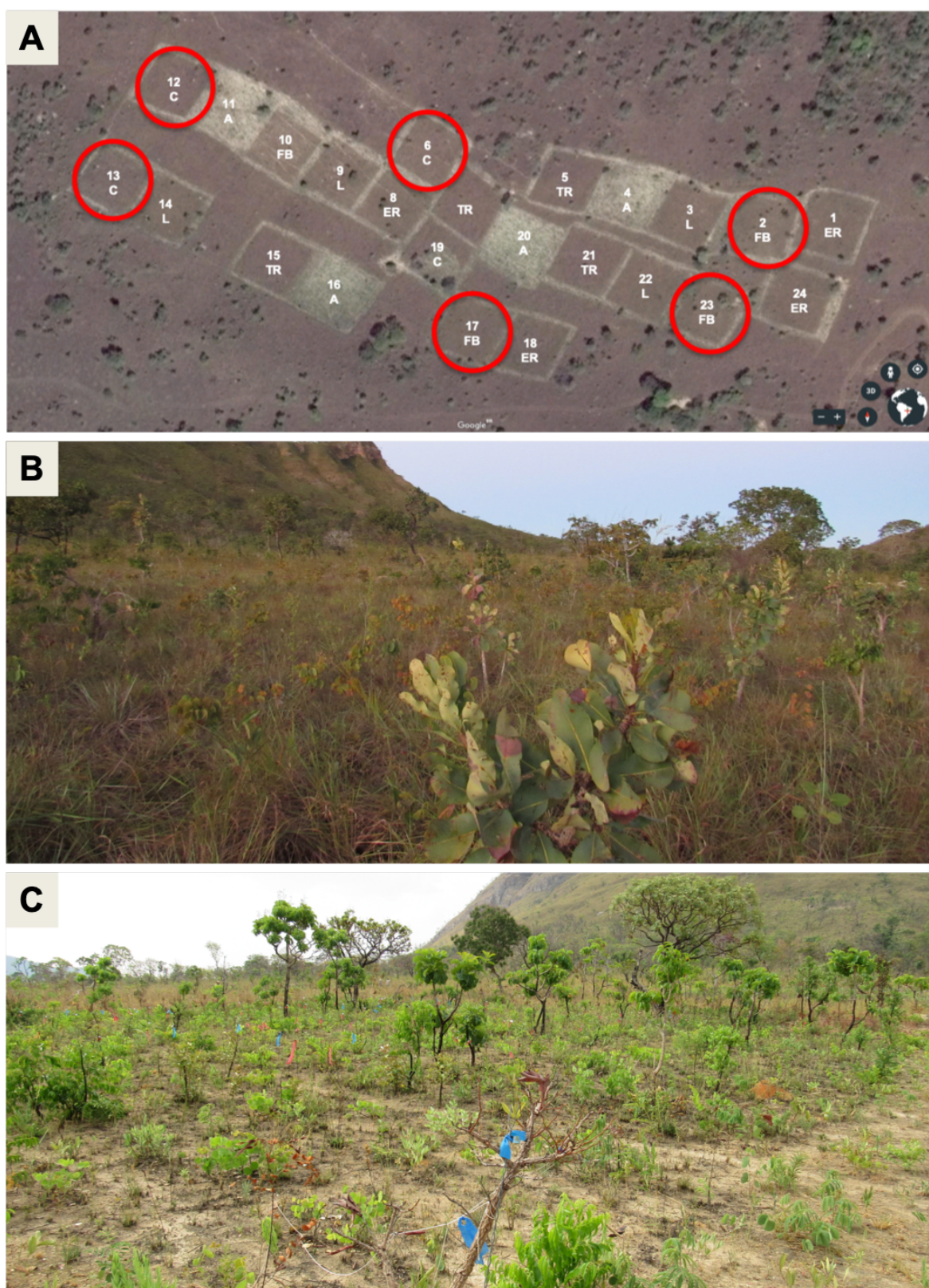


Figura 3. Área experimental. A) As parcelas circuladas em vermelho foram utilizadas nos experimentos. (C) são as parcelas com exclusão de fogo por seis anos e (FB) são as parcelas bienais queimadas em julho 2017; B) Parcela com exclusão de fogo e C) Parcela bienal recém queimada, três meses pós-fogo de julho 2017.



Figura 4. Experimento de queima. A) linha de fogo colocada na parcela no início da queima, B) queima da parcela sendo monitorada.

Em cada uma das seis parcelas de 30x30m foram estabelecidas 10 subparcelas fixas de 1x1m (Fig. 5) distribuídas aleatoriamente para levantamento da comunidade vegetal, contagem de ramos reprodutivos e vegetativos das espécies (ver Capítulo I). As campanhas de campo foram realizadas após a queima quinzenalmente

até três meses e depois a cada três meses até completar um ano. Para investigar o efeito do histórico de fogo nos atributos de sementes e germinação foram coletadas sementes de espécies presentes em ambas as áreas (ver Capítulo II). Detalhes dos materiais e métodos para cada objetivo serão descritos a seguir em cada capítulo.

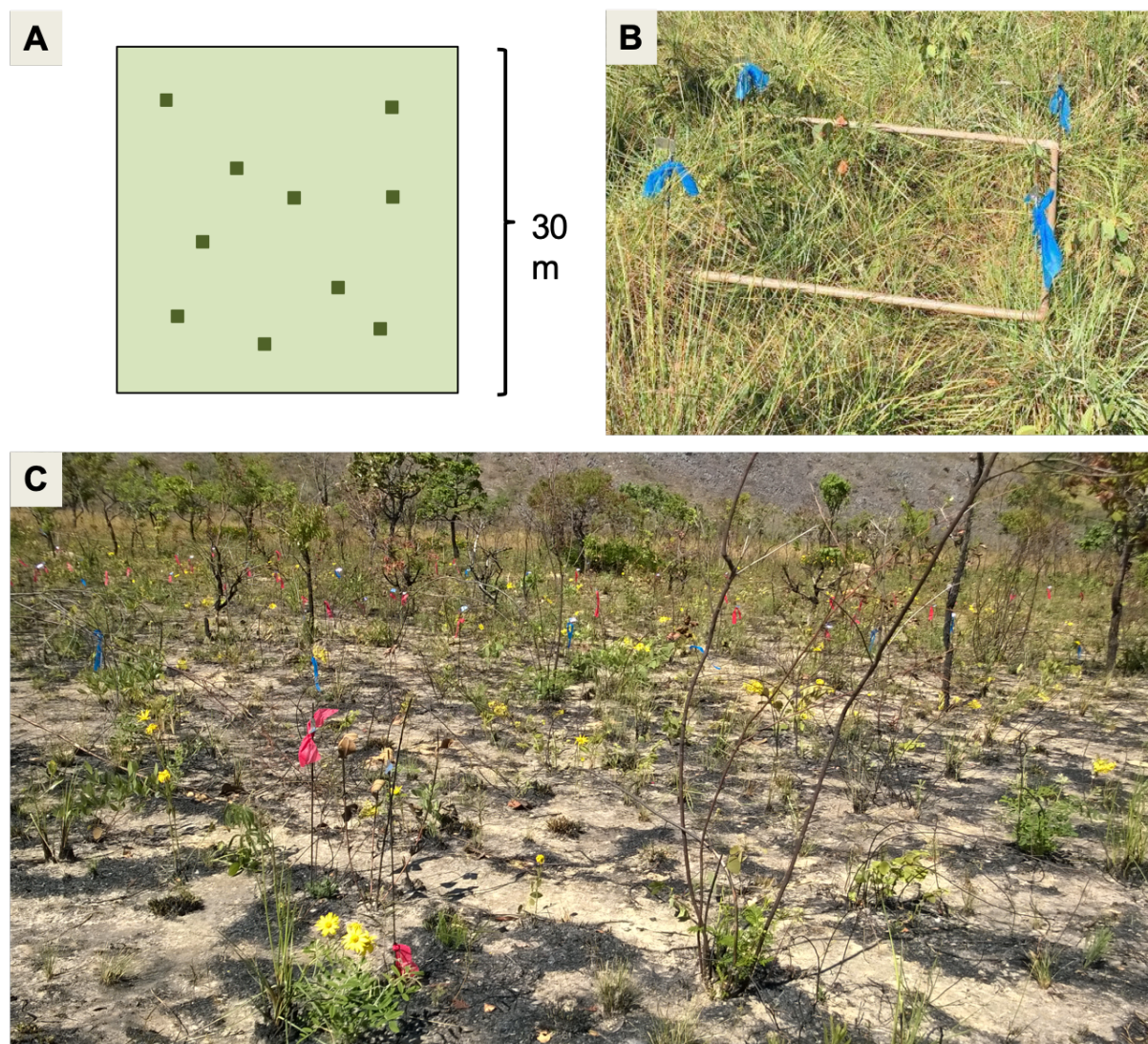


Figura 5. A) Esquema da parcela de 30x30m com as dez subparcelas fixas de 1x1m; B) Exemplo das subparcelas de 1x1m utilizadas nos levantamentos da vegetação e C) Parcela recém queimada com os indivíduos marcados. Vergalhões com fitas vermelhas são posicionados a frente de cada indivíduo estudado.

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Fire affects flowering and fruiting of Cerrado species

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Abstract

In fire-prone ecosystems around the world fire can enhance the flowering and fruiting of many species. This can contribute to determining the reproductive phenology of plants, with fire able to accelerate these processes. Therefore, we evaluated fire effects on number and profusion of flowering and fruiting of Cerrado's species.

Location

Reserva Natural Serra do Tombador, Cavalcante-GO, Central Brazil

Methods

We established 6 plots (30x30m) in open savannas in Central Brazil, with the following treatments: fire exclusion (C, excluded from fire for 6 years) and burned (FB, recent and frequently burned). In all treatments, the number of species flowering, and fruiting was counted every 15 days for 3 months and then at 6, 9 and 12 months after fire. We also counted the number of reproductive and vegetative shoots in 30 subplots (1mX1m) in each area.

Results

Our results showed that fire enhanced flowering in general. Already in the first 30 days up to 3 months after fire there was up to 2-fold more species flowering in the FB than C areas. After 12 months there was still a higher percentage of species flowering in the burned area (C=18.85%, FB=27.87%). At the community level, there was significant increase in the ratio of reproductive shoots at 3 months post-fire, showing that that mass response of flowering happened in the first 3 months after fire. Both areas shared less than 50% of common species flowering at each time post-fire. We also classified species according their responses to fire in: sensitive, fire-triggered (dependent and stimulated) and independent and we found 66.39% of species to be fire-triggered, since they flowered only in the burned area or was stimulated by fire.

Conclusions

Therefore, although the mechanism of flowering in post-fire environments is not known our results showed that fire changes the reproductive phenology mainly stimulating and enhancing flowering and fruiting of many species thus altering the dynamics and diversity of the plant community in Cerrado.

Key words: Post-fire flowering, *campo sujo*, reproductive phenology, Cerrado, fruiting increase

Introduction

Reproductive stages, such as flowering and fruiting (phenophases) are of critical importance to ensure the recruitment and survival of species (Lieth 1974; Primack 1985; Fenner 1998) and driving the regeneration of plants after disturbance (Grubb 1977; Primack 1985). These phenophases are influenced by biotic and abiotic factors (Lieth 1974; Fenner 1998). Among the biotic factors one can find herbivory, pollinators, seed dispersion, whilst availability of nutrients and water, luminosity and temperature are some of the abiotic factors that influence plant phenology (Fenner 1998).

In flammable ecosystems, fire is capable of changing the conditions and dynamics of the environment, while also acting as an evolutionary pressure that can alter the phenology of plant individuals (Trabaud 1987; Whelan 1995; Bond & van Wilgen 1996; Keeley et al. 2011; Pyke 2017). Fire affects reproductive phenology mainly by stimulating and/or increasing the number, synchrony and profusion of flowering (Trabaud 1987; Whelan 1995; Bond & van Wilgen 1996; Keeley et al. 2011; Pyke 2017). Although the physiological mechanisms involved in this stimulation are not yet fully elucidated (Pyke 2017), post-fire flowering stimulus can be attributed to the availability of nutrients and the increased incidence of light in the environment (Trabaud 1987; Whelan 1995; Bond & van Wilgen 1996; Lamont & Downes 2011). In other cases, this stimulus is associated to the chemical compounds released in the environment after burning, especially to the ethylene present in the smoke (Gill & Ingwersen 1976; Bond & van Wilgen 1996). However, Keeley (1993) observed that an *Amaryllidaceae* species was stimulated by smoke but not by ethylene, showing that the effect of another smoke chemical might be responsible for flowering stimuli.

First records of fire on Earth dates back to Silurian (ca 440mya) although greater charcoal evidence only appears about 345 mya (Pausas & Keeley 2009; Keeley et al.

2012). Evolutionarily, there are records of fire-stimulated flowering appearing on Mediterranean vegetation about 14mya when fire was already present in the environment (ca. 20 to 70mya) evidencing in this case flowering being an adaptive response to the fire regime (Bytebier et al. 2011; Lamont & He 2017; Pyke 2017). Flowering stimulus by fire is generally reported for monocotyledonous plants, especially for the families Orchidaceae, Poaceae, Cyperaceae, Iridaceae, Liliaceae and Haemodoraceae (Le Maitre & Brown 1992; Bond & van Wilgen 1996; He et al. 2016; Lamont et al. 2018). One extraordinary case was reported for a sedge species from the Cerrado (*Bulbostylis paradoxa*), which is able to start flowering just 24hs after fire (Fidelis et al. 2019). Many cases of post-fire flowering have been reported for the Mediterranean-climate vegetation with effects (e.g. enhancing and/or accelerating flowering) appearing within 12 months or in some cases, after a couple of years (Pyke 1983; Wroblewski & Kauffman 2003; Bowen & Pate 2004; Paritsis et al. 2006; Lamont & Downes 2011). In some cases, it is also possible to observe an increase in fruiting after fire as well, with fruit set being larger in burned areas (Paritsis et al. 2006), perhaps as a consequence of enhanced flowering. In savannas, flowering stimulus has been less observed and most studies focused on single species responses rather than on the community (e.g. Franceschinelli & Bawa 2005; Conceição & Orr 2012; Dodonov et al. 2018; Shearman et al. 2019; Sousa & Cunha 2019). In the Cerrado, where fire has been present for about 4 million years (Simon et al. 2009), it is possible to observe massive post-fire flowering events (Coutinho 1976; Coutinho 1990), being this an unique event among the tropical savannas. Since the 1800s, European naturalists such as Saint-Hilaire and Warming have written about their observations of fire effects on Cerrado vegetation and both were amazed by the flush of flowering after fire events (Warming & Ferri 1973; Saint-Hilaire 2011). Eugen Warming described one of the burning effects as an “earlier spring” due to the presence of “many beautiful flowers

arising from the black surface” after fire (Warming & Ferri 1973). Moreover, he pointed out that, during the rainy season, the Cerrado vegetation was not a “flowering garden” as one could see in Europe, due to the lower number of plants flowering (Warming & Ferri 1973). Some studies have shown this increase in flowering in Cerrado areas already in the first post-fire months (Neves & Damasceno-Junior 2013; Massi et al. 2017; Pilon et al. 2018) while others observed mass synchrony such as for *Vellozia sincorana* (Conceição & Orr 2012; Conceição et al. 2013).

Since fire regime interferes in phases of the reproductive cycle (e.g. genetic diversity) and survival of plants, understanding and quantifying this effect is of extreme importance to protect the biodiversity of the plant community as well as to give subsidy for decision making to manage these areas. Based on the premise that fire stimulates flowering and fruiting and in the absence of fire, there would be a lower number of species flowering, the main objective of this study was to analyze the effect of fire on the reproduction of a range of species from the Cerrado vegetation by answering the following questions: (i) Are there differences in the reproductive phenology of Cerrado plants between recently burned areas and areas with six years fire exclusion? (ii) How does fire affect flowering one year after the burn? And (iii) What are the range of post-fire flowering strategies possessed by Cerrado species? We hypothesize that a greater number of species with flowers will be present in the recently burned area compared to plants excluded from fire. Additionally, the flush of flowering will be observed just after fire and most of the species will have a flowering strategy related to fire events.

Material and Methods

Study area

We used fire experiments established since 2013 in Central Brazil (RNST, 13 ° 35-38 'S and 47 ° 45'-51' W) to evaluate post-fire flowering in open savannas communities. The climate is tropical and strongly seasonal, with dry winters and wet summers with averages of minimum temperatures from 8 -14°C and maximum from 26-36°C. Average annual precipitation is between 1500 and 1750 mm. Soil is acid with a pH of 4-5 and predominantly classified as Litho-Dystrophic Neosols (Antonelli-Filho 2011). The study site where the fire experiments are established is characterized by the dominance of graminoids and herbaceous plants and trees and shrubs isolated along the vegetation (*campo sujo*) (Coutinho 1978).

Reproductive phenology of the plant community

All sampling was conducted in experimental plots established in the area since 2013. We used three plots (30x30m) for fire exclusion which we called control (C, excluded from fire since 2011) and three burned plots (FB, burned every two years since 2013, last burned in July). FB plots were burned for the third time in July 2017, using the methods described by Rissi et al. (2017).

To compare the difference in richness of reproductive species on plant community between plots burned and excluded from fire the number of species in their reproductive stage (flowering and fruiting phenophases) were counted for each plot after fire experiments every 15 days up to three months. After that, we conducted the surveys every three months up to one year after fire. Due to logistical reasons, we skipped the survey 75 days after fire.

In addition, in each one of the six plots we established 10 fixed subplots of 1x1m randomly distributed for surveying the reproductive ratio (reproductive/total) of shoots in the plant community. In each subplot, the total number of species (with and without reproductive structures) was surveyed, and the reproductive and vegetative shoots counted. Shoots presenting buds, open flowers and/or fruits/seeds were considered as reproductive shoots. Surveys were carried out before and after fire (July 2017) every three months up to one year after fire.

In order to evaluate how fire affects flower and fruit production of Cerrado species, fifteen dominant species were chosen (Table 1) in both areas (C and FB) belonging to different growth forms, including grasses, forbs and shrubs. For each species, the number of flowers and fruits was counted before and after fire, according described for richness (see above).

Table 1. Family and growth form of dominant species marked and surveyed for 12 months in both areas, C and FB.

Family	Species	Growth form
Poaceae	<i>Axonopus aureus</i>	Graminoid
Poaceae	<i>Elionurus muticus</i>	Graminoid
Poaceae	<i>Mesosetum ferrugineum</i>	Graminoid
Poaceae	<i>Mesosetum loliiforme</i>	Graminoid
Poaceae	<i>Oncorachis ramosa</i>	Graminoid
Bignoniaceae	<i>Anemopaegma arvense</i>	Forb
Lamiaceae	<i>Eriope glandulosa</i>	Forb
Euphorbiaceae	<i>Euphorbia potentilloides</i>	Forb
Asteraceae	<i>Ichthyothere hirsuta</i>	Forb
Convolvulaceae	<i>Ipomoea fiebrigii</i>	Forb
Fabaceae	<i>Bauhinia dumosa</i>	Shrub
Moraceae	<i>Brosimum gaudichaudii</i>	Shrub
Lythraceae	<i>Diplusodon punctatus</i>	Shrub
Lamiaceae	<i>Medusantha mollissima</i>	Shrub
Fabaceae	<i>Mimosa pteridifolia</i>	Shrub
Acanthaceae	<i>Ruellia nitens</i>	Shrub

Finally, species were classified according to their post-fire flowering strategy. We defined this strategies according to their responses until one year after the fire event: *fire-sensitive* (S) if fire inhibited flowering in burned areas (species did not flower after fire in burned plots, only in excluded plots); *fire-independent* (I) if fire did not affect flowering (species flowered in both excluded and burned plots at the same period); *fire- dependent* (FD) when species only flowered after fire (species never flowered in excluded plots, only in burned ones) and *fire -stimulated* (FS) when flowering was accelerated or enhanced by the fire (species flowered more profusely or flowering was accelerated in the burned plots in comparison to the excluded ones).

Statistical analyses

Differences in the ratio of reproductive shoots, and number of flowering and fruiting shoots between treatments were tested using GLMM (generalized linear mixed models) with a Poisson error structure. Species was treated as random factors. Differences of reproductive shoots between treatments of dominant species according growth forms were tested using GLMM (generalized linear mixed models) with a poisson error structure. Individuals was treated as random factors.

Statistical analyses were performed using *multicomp*, *lme4* and *lsmeans* packages in the R software (Hothorn et al. 2008; Bates et al. 2015; Lenth 2016; R Core Team 2016).

Results

Results showed that richness of reproductive species was higher in FB areas compared to C, except at six months after fire (wet season) (Fig.1a). Thirty days after fire there was 20.49% species flowering in the burned area and 3.28% in the fire exclusion area, with the greatest difference between areas at 60 days where 17.21% of total species were flowering in the FB and only 0.82%, at C areas (Fig.1b). The percentages of species with fruits also followed the same pattern with the greatest difference between areas at 60 days (C=8.26% and FB=24.77% of total species, Fig.1c). Twelve months after fire there was 27.87% of species flowering at FB and 18.85% at C and 20.49% with fruits at FB against 10.66% at the fire exclusion area (Fig.1b, c).

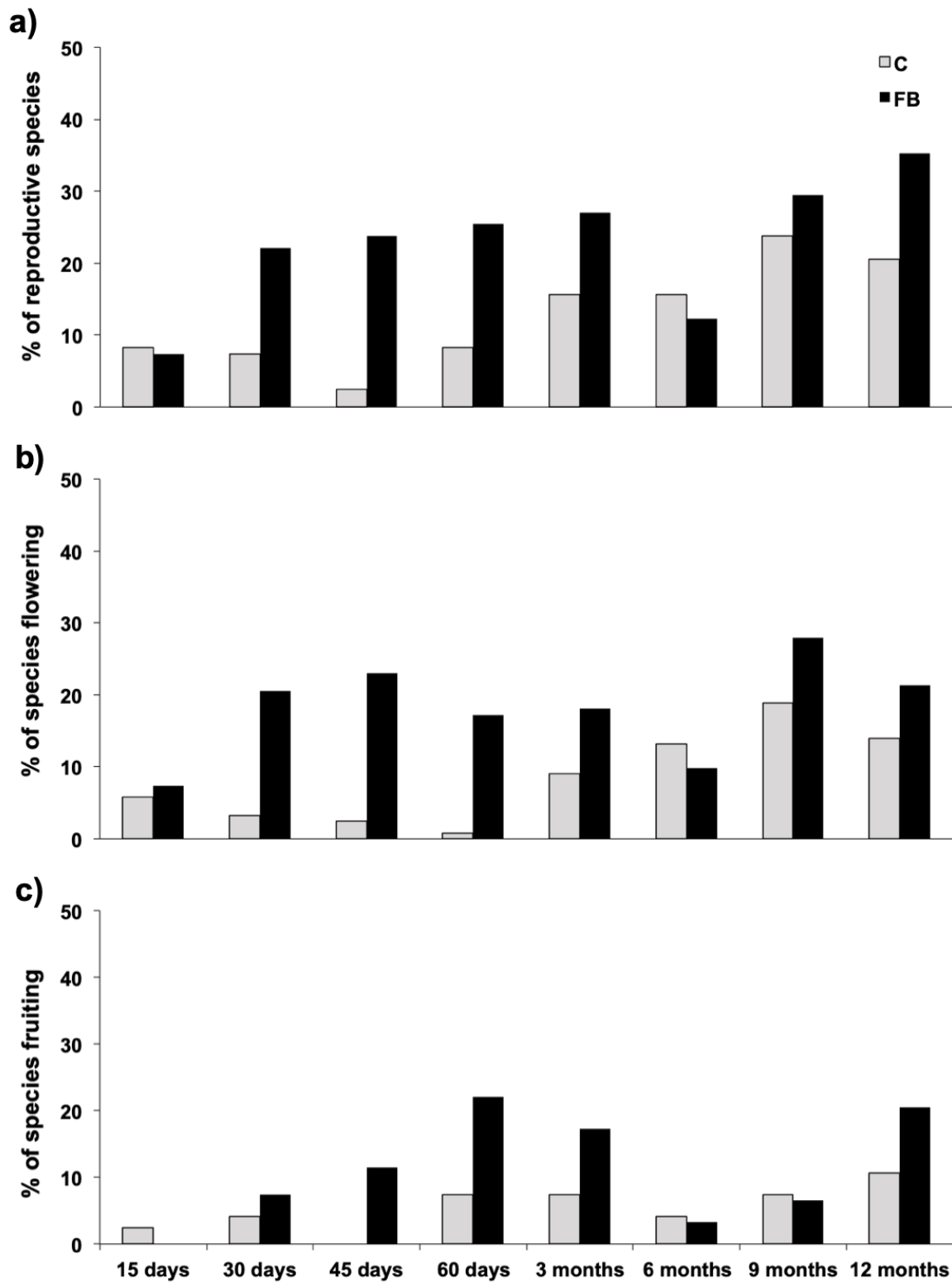


Figure 1. Percentages of the number of a) reproductive (total average of species flowering plus fruiting) b) flowering and c) fruiting species in relation to the total number of species in the community. C=fire exclusion area; FB= burned area.

In relation to the ratio of reproductive/total shoots, there was a significant increase in the ratio of reproductive shoots only at three months after fire in FB areas when compared to C, showing that mass response of flowering happened within three months after fire (Fig.2). The same pattern was found accounting for the average number of flowering shoots, with graminoids having 9-fold more flowering tillers in FB than in C areas ($E=1\pm0$, $FB=9.81\pm1.69$). Forbs showed the same pattern, having 3-fold more flowering shoots three months after fire than in excluded areas ($C=1.25\pm0.13$, $FB=3\pm0.34$). There was no significant difference in the ratio of reproductive shoots or number of flowering at six, nine and 12 months after fire. Moreover, both areas shared less than 50% of common species flowering at each time post-fire.

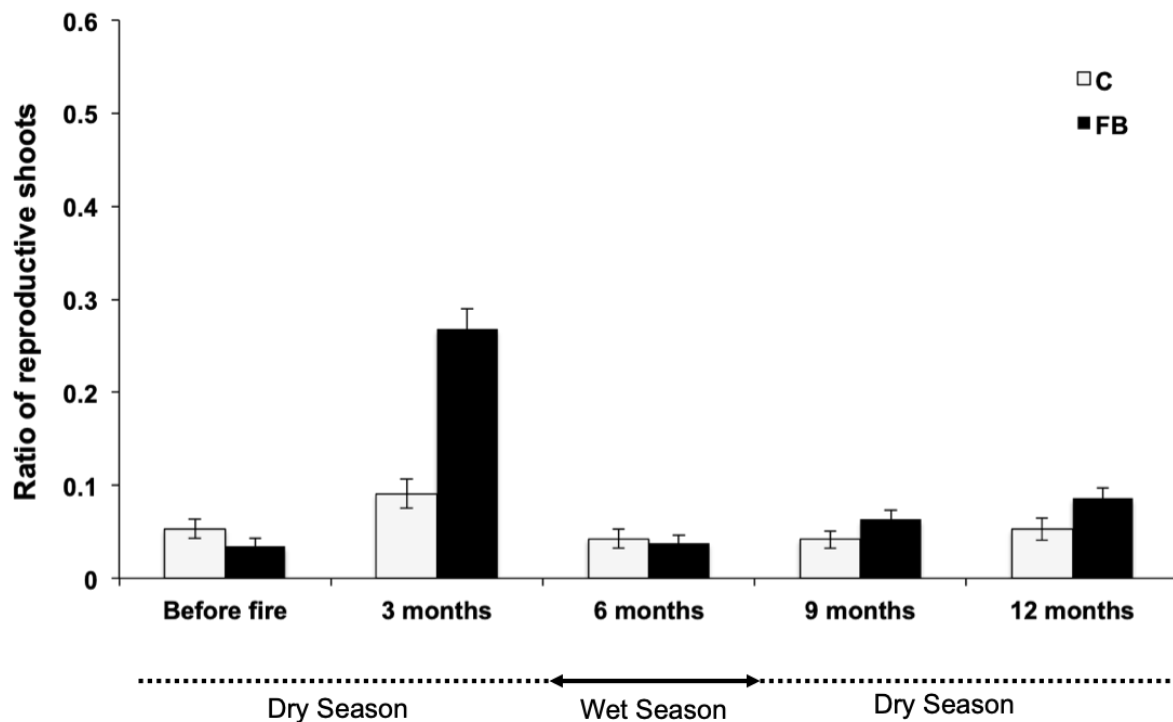


Figure 2. Ratio of reproductive shoots at the community level. C=fire exclusion area; FB=burned area. *Indicates significant difference between the areas at each time.

Dominant species

First, we analyzed the sixteen dominant species (Table 1) surveyed for 12 months according growth forms. Graminoids from FB area presented a higher average of reproductive tillers from 30 days up to three months (Fig. 3). The average of flowering tillers followed the same pattern, whilst fruiting on FB was higher at 60 days up to three months (Fig.3). The ratio of reproductive shoots was also significantly higher for FB with 11-fold more reproductive tillers than C at 30 days and 21-fold more at three months after fire (Table 2). Three species only flowered in burned areas and in the period from 30 days to three months: *Elionurus muticus*, *Mesosetum ferrugineum* and *Oncorachis ramosa*. *Axonopus aureus* was the only species that flowered in both areas, during the first 60 days at the exclusion area and at nine months in FB. *Mesosetum loliiforme* was the only graminoid that did not flower or fruit during 12 months of survey.

Forbs at FB had higher flowering shoots from 15 days up to three months and also at 12 months (Fig.3). The average number of fruiting was higher at FB comparing to C only at 45 days up to three months (Fig.3). Average number of reproductive shoots (Fig. 3) and reproductive ratio was higher at every time of observation, except six (wet season) and nine months (Table 2). *Ipomoea fiebrigii* was the only reproductive species before the burn, thus it was reproductive in C from 15 days to 60 days and in FB only at nine and 12 months (8-fold more than in C). Within the first three months *Anemopaegma arvense* and *Euphorbia potentilloides* presented reproductive shoots only in FB. At three months the reproductive ratio of *A. arvense* was 51-fold higher in FB and 3-fold more for *E. potentilloides* in FB compared to C. *Eriope glandulosa* only flowered on burned areas and within the first three months post-fire. On the other hand, *Ichthyothere hirsuta* flowered in both areas at 6 months.

Shrubs showed a higher average of reproductive shoots for FB at six, nine and 12 months (Fig.3) although the reproductive ratio was only affected at from 15 days up to three months, mainly because the shrubs were still resprouting in the burned area while fruiting at C (Table 2). However, the number of vegetative shoots was greater at FB at all times. All species were reproductive before being burned and maintained at C area until three months. At six months only *Mimosa pteridifolia* was flowering in both areas but 2-fold more at FB. Nine months after fire, *Diplusodon punctatus* and *Mimosa pteridifolia* presented reproductive shoots, and by one year after fire most shrubs (*Bauhinia dumosa*, *Brosimum gaudichaudii*, *Medusantha mollissima* and *Mimosa pteridifolia*) had reproductive structures.

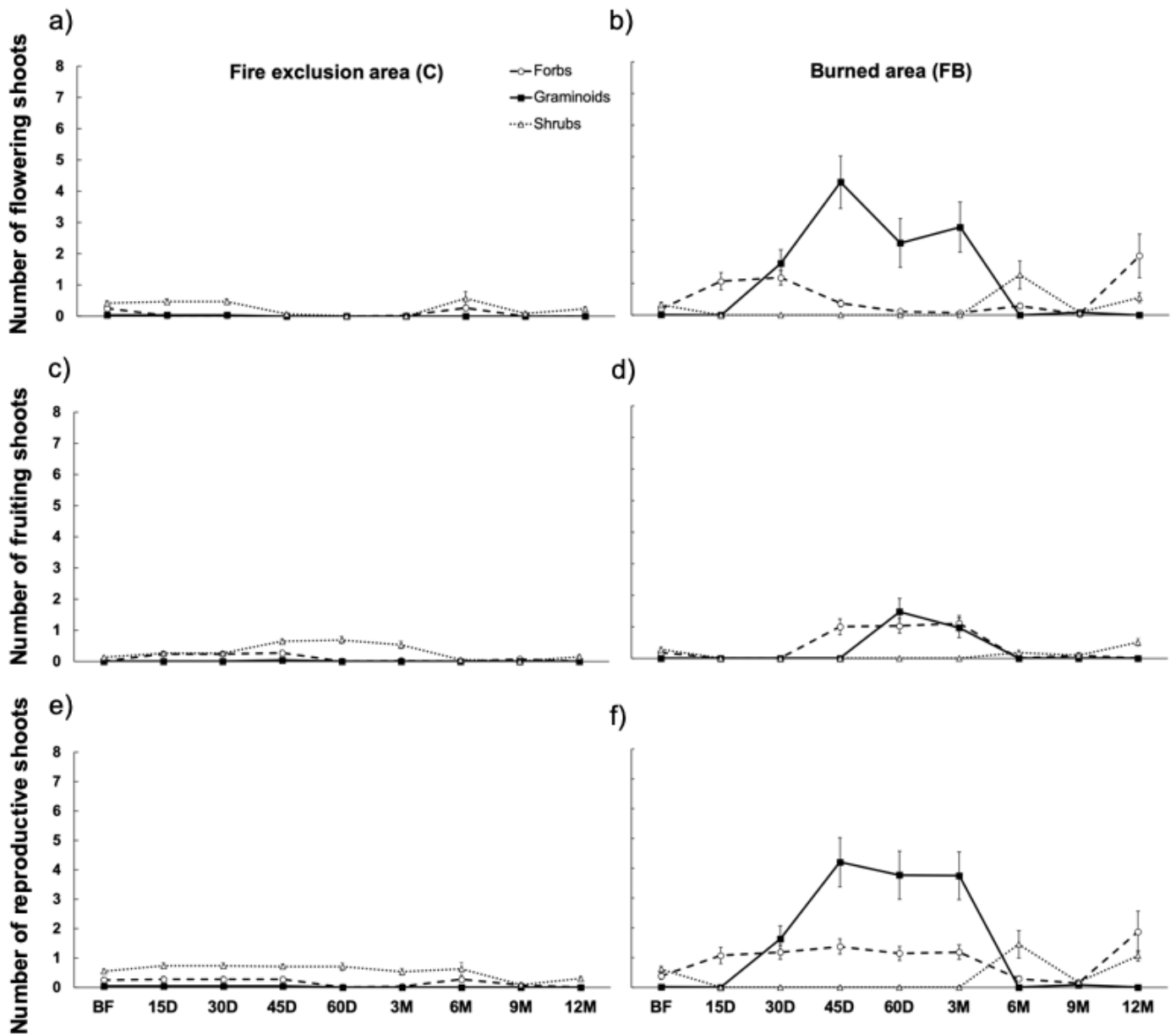


Figure 3. Number of flowering (a,b), fruiting (c,d) and reproductive (e,f) (flowering+fruiting) shoots (mean $\pm$ SE) at each sample time for each area (C and FB) according growth form. C=fire exclusion area; FB= burned area.

Table 2. Ratio of reproductive shoots (total number of reproductive shoots/total number of shoots, mean $\pm$ SE) at each sample time for each area (C and FB) according growth form. C=fire exclusion area; FB= burned area. *Indicates significant difference between C and FB for each growth form at each time. *, P < 0.05; **, P < 0.01; ***, P < 0.001

Time after fire	Forbs		Graminoids		Shrubs	
	C	FB	C	FB	C	FB
Before fire	0.11 $\pm$ 0.04	0.13 $\pm$ 0.04	0.01 $\pm$ 0.01	0 $\pm$ 0	0.36 $\pm$ 0.05	0.30 $\pm$ 0.04
15 days	0.10 $\pm$ 0.03	0.21 $\pm$ 0.05***	0.01 $\pm$ 0.01	0 $\pm$ 0	0.42 $\pm$ 0.05	0 $\pm$ 0***
30 days	0.10 $\pm$ 0.03	0.26 $\pm$ 0.05***	0.01 $\pm$ 0.01	0.11 $\pm$ 0.03***	0.42 $\pm$ 0.05	0 $\pm$ 0***
45 days	0.10 $\pm$ 0.03	0.31 $\pm$ 0.05**	0.01 $\pm$ 0.01	0.21 $\pm$ 0.03***	0.41 $\pm$ 0.05	0 $\pm$ 0***
60 days	0.01 $\pm$ 0.01	0.31 $\pm$ 0.05***	0 $\pm$ 0	0.22 $\pm$ 0.04***	0.38 $\pm$ 0.05	0 $\pm$ 0***
3 months	0.01 $\pm$ 0.01	0.35 $\pm$ 0.05***	0 $\pm$ 0	0.21 $\pm$ 0.03***	0.30 $\pm$ 0.05	0 $\pm$ 0***
6 months	0.16 $\pm$ 0.05	0.13 $\pm$ 0.04	0 $\pm$ 0	0 $\pm$ 0	0.14 $\pm$ 0.05	0.15 $\pm$ 0.04
9 months	0.04 $\pm$ 0.03	0.04 $\pm$ 0.02	0 $\pm$ 0	0.01 $\pm$ 0.01	0.09 $\pm$ 0.04	0.07 $\pm$ 0.02
12 months	0 $\pm$ 0	0.11 $\pm$ 0.03	0 $\pm$ 0	0 $\pm$ 0	0.23 $\pm$ 0.05	0.26 $\pm$ 0.04

We found 66.39% species to be fire-triggered: 35.25% were fire-dependent (FD) and 31.15% were fire-stimulated (FS). A quarter of species (25.41%) did not have flowering affected by fire thus being classified as independent, whereas 10% were shown to be fire sensitive as they only flowered in the exclusion area (Fig. 4a, Table 1S). Among the 28 families with fire-triggered (FD or FS) flowering, the ones with more species were: Poaceae (11 spp.), Fabaceae (10 spp.), Asteraceae (7 spp.), Euphorbiaceae (6 spp.), Cyperaceae (5 spp.), Lamiaceae (5 spp.) and Polygalaceae (5 spp., Table 1S). Taking into account the total number of species in the study area this represents: 73.33% of Poaceae, 52.63% of Fabaceae, 63.64% of Asteraceae, 85.71% of Euphorbiaceae, 83.33% of Cyperaceae 71.43% of Lamiaceae and 100% of Polygalaceae species stimulated or dependent of fire for flowering (Fig.4b).

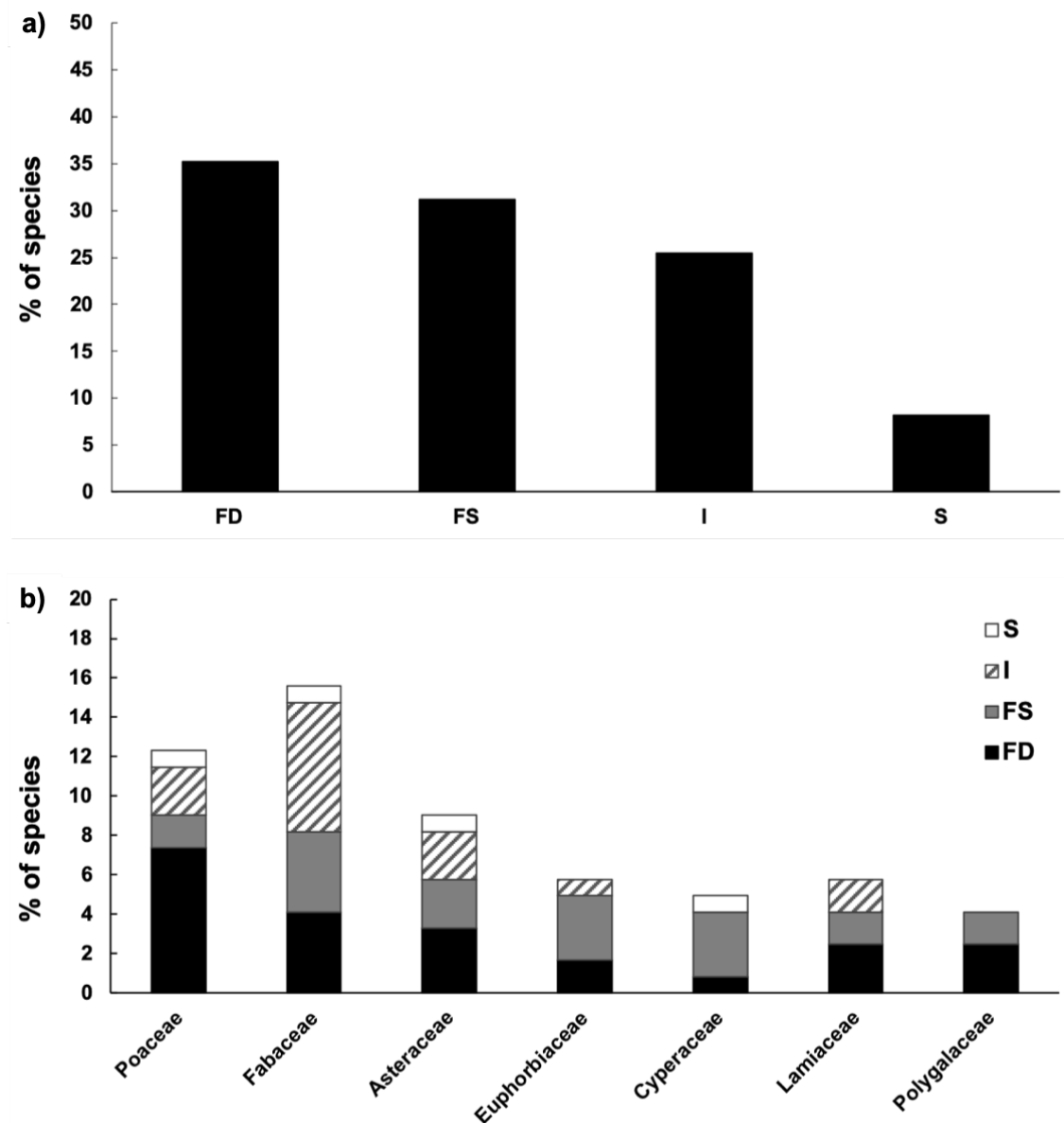


Figure 4. Classification of species according to fire effect on flowering within one year after fire event. a) Percentage of species of each category, b) Percentage of species of each category within families with most fire-triggered species. Sensitive (S) if fire inhibited flowering in burned areas; Independent (I) if fire did not affected flowering; Fire-dependent (FD) when species only flowered after burn and stimulated and fire-stimulated (FS) when flowering were accelerated or enhanced by the fire.

Discussion

The noticeable difference in reproductive phenology, especially in the flowering of the burned areas of *campo sujo* compared to fire excluded areas, demonstrates the importance of fire in driving reproduction and the role that evolutionary pressure has

played on these processes in the Cerrado (Simon et al. 2009; Keeley et al. 2011; Lamont & He 2017). For the majority of species, fire increased the profusion of reproductive structures and produced some shifts in reproductive phenology of Cerrado species.

As already seen for other fire-prone ecosystems, fire regime affects stages of reproduction of plants such as flowering and fruiting (Trabaud 1987; Whelan 1995; Bond & van Wilgen 1996; Keeley et al. 2011; Pyke 2017). In the literature we can find a range of examples, mainly for Mediterranean ecosystems, where post-fire flowering area stimulated (see Borchert & Tyler 2009) or dependent of fire (e.g. Keeley 1993) but also for other vegetation types such as woodlands and shrublands (Pyke 1983; Wroblewski & Kauffman 2003; Bowen & Pate 2004; Paritsis et al. 2006; Lamont & Downes 2011). For example, Lamont and Downes (2011) compiled information of 386 species of Australasia and South Africa where 40.2% only flowered in the presence of fire (obligate). Generally, the peak of the stimulus caused by fire can vary between 5 to 18 months, or even after few years, after fire in many Mediterranean-climate regions (Lamont & Downes 2011). In the savannas this effect is more pronounced in the first months after fire (Lamont & Downes 2011), a finding supported by our results.

Post-fire flowering in savannas is less studied and most observations have been made for specific, mainly shrub, species (e.g. Franceschinelli & Bawa 2005; Conceição & Orr 2012; Dodonov et al. 2018; Shearman et al. 2019; Sousa & Cunha 2019 but see Pilon et al. 2018). From the few studies that have focused on the broader range of savanna species, overall there seems to be a very fast post-fire flowering response. Our data corroborate these findings, as in our sites the peak of flowering stimulus was observed in the first three months after fire for the herbaceous stratum, and up to a year post-fire for the shrubs. Some species such as *Lippia horridula*, *Turnera emendata*, *Pombalia lanata* and *Euphorbia* sp. flowered within fifteen days after fire

and never flowered in the fire exclusion areas. Remarkably, the fastest response in Cerrado was found by Fidelis et al. (2019) for a sedge species that started flowering 24 hours after burning. Moreover, although the abundance of flowering species is greater in the burned areas, in almost all the survey periods during the year of study (except at six months – during the wet season), the number of flowering shoots is only significantly higher at three months post-fire, with grasses and forbs the groups driving this difference. Thus, flowering in the Cerrado is one of the most important and fast responses to fire, with species flowering within the first weeks/months after fire, hence being hard sometimes to find these species (most of graminoids and some forbs) in flower if one visits the areas many months after fire, or even in areas where fire has been excluded.

The dominant species also showed a pattern in the floral stimulus according to the growth form. In general, forbs begin to bloom as soon as fifteen days after the burning with its peak at 30 days. A similar pattern was found for grasses that begin to flower at 30 days with a peak at 45 days after fire. Fidelis and Blanco (2014) showed that forbs responded within 30 months flowering after fire, while grasses showed significant post-fire flowering only one year after fire in subtropical grasslands. Post-fire flowering stimulation of grasses and forbs was also found for savannas in other studies (Cardoso et al. 2000; Munhoz & Felfili 2007; Massi et al. 2017; Pilon et al. 2018), confirming thus that our results demonstrate that Cerrado herbaceous species are capable of rapid regeneration and stimulation of sexual reproduction in the face of this disturbance. In relation to the shrubs the effects of fire in the flowering are observed only after six months of the burning since they need more time to resprout and to begin to produce flowers. Although in some cases a negative effect of the fire regime on the reproductive phenology of woody species has already been recorded (Hoffmann 1998; Miranda & Sato 2004; Palermo & Miranda 2012) our results resemble those found by

Franceschinelli & Bawa (2005) who observed increasing flower density for a savanna shrub, *Helicteres sacarolha*.

Within the 36 families of the study area 28 had flowering positively affected by fire. According to results of other flammable ecosystems most fire-stimulated species are among monocotyledonous plants including two families Poaceae and Cyperaceae (Le Maitre & Brown 1992; Bond & van Wilgen 1996; He et al. 2016; Lamont et al. 2018) that was also within our findings. However, fire not only affects most of the monocots (mainly Poaceae) but also has a great influence on the dicots of *campo sujo* (e.g. Fabaceae). Thus, fire affects the reproduction of the most dominant families in this Cerrado area.

The specific mechanisms involved in the flowering stimulus remain unknown (Pyke 2017) and some other factors or their combination such as the availability of nutrients and increasing the incidence of light in the environment (Trabaud 1987; Whelan 1995; Bond & van Wilgen 1996; Lamont & Downes 2011), hormonal and chemical cues (Coutinho 1977; Keeley 1993; Lamont & Downes 2011) could be considered responsible for this response. Even the plant traits such as height and age could affect the reproductive response to fire (Pyke 2017). Interestingly, Taylor et al. (1998) found a higher percentage of *Xanthorrhoea fulva* crowns flowering in the plants that were burned, even when compared with plants subjected to a clipping treatment. The difference between these two treatments suggests that fire provides cues besides biomass removal alone that cues flowering.

Fruiting was also affected in burned areas following a similar pattern to that found for flowering. Forbs had their peak of fruiting at three months and grasses at 60 days post-fire, while shrubs presented a higher amount of fruits only one year after fire. The increase of flowering could be responsible for enhance of fruiting after fire as found in a shrubland in Argentina, where the fruit set of three species was larger in the burned

areas (Paritsis et al. 2006). Increased pollination could play a role, however as we did not monitor the presence of pollinators, we cannot say if the increase in burned areas is due to the increase of pollinators or to other environmental factors.

When fire affects the phenophases of plant reproductive cycles, it is acting directly on the survival and propagation of the species as well as on diversity and dynamics of the community. As the number of blooming individuals increases, the possibility of cross-fertilization increases consequently, as a result this will increase the genetic diversity of species as seen for *Helicteres sacarolha* that had the outcrossing rate increased post-fire (Franceschinelli & Bawa 2005). The increase in fruit yield may also positively influence the propagation of the species. In addition, accelerated flowering (e.g. Wroblewski & Kauffman 2003; Paritsis et al. 2006) confers species another advantage to utilize first the abundant resources in the post-fire environment (Lamont & Downes 2011). Results such as this solidify the already well-known importance of fire in the flammable savanna ecosystems (Coutinho 1976; Coutinho 1990; Ramos-Neto & Pivello 2000; Simon et al. 2009).

Finally, of particular importance to note regarding the management of natural ecosystems, Brazil has a “zero fire” policy. Although this has begun to change in recent times (Schmidt et al. 2018; Fidelis et al. 2018), our work provides further evidence that Cerrado needs fire to maintain biodiversity and prevent the loss of herbaceous species richness in particular (Durigan & Ratter 2016; Abreu et al. 2017). Therefore, since fire can have a significant impact on reproductive output, with some Cerrado species dependent on fire to promote flowering and reproduction, further research to understand and quantify this effect is of extreme importance both to inform decision making for management of these areas and to protect biodiversity of savanna plant communities.

Funding

This work was supported by Fundação Grupo Boticário (0153_2011_PR) and FAPESP (2015/06743-0). H.L.Z. received financial support from FAPESP (2017/16149-4). AF received a productivity grant from CNPq.

Acknowledgments

We thank LEVeg (Lab of Vegetation Ecology) members and friends: Cassy Anne S. Rodrigues, Gabriella Damasceno, Mariana Dairel, Juliana Teixeira, Vagner Zanzarini, Mylene M. da Silva, Raquel Vieira and Mauricio Cunha for helping with field work and experiments. We also thank the employees of Reserva Natural Serra do Tombador: Whatson F. Rezende, Anderson F. Terra, Gilson de A. Berberino, Rogério B. de Almeida and Silvanio A. Borges for the support during the experiments.

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Supplementary Information

Table 1S. Classification of species according to fire effect on flowering within one year after fire event. Sensitive (S) if fire inhibited flowering in burned areas; Independent (I) if fire did not affected flowering; Fire-dependent (FD) when species only flowered after burn and stimulated and fire-stimulated (FS) when flowering were accelerated or enhanced by the fire.

Family	Species	Growth form	Classification
Acanthaceae	<i>Justicia lanstyakii</i>	shrub	I
Acanthaceae	<i>Ruellia angustior</i>	shrub	FS
Acanthaceae	<i>Ruellia nitens</i>	shrub	FS
Acanthaceae	<i>Ruellia</i> sp	shrub	S
Acanthaceae	<i>Stenandrium irwinii</i>	forb	FS
Amaranthaceae	<i>Gomphrena</i> sp	forb	FD
Annonaceae	<i>Annona tomentosa</i>	shrub	I
Apocynaceae	<i>Hemipogon acerosus</i>	forb	FD
Arecaceae	<i>Syagrus acaulis</i>	palm	S
Asteraceae	<i>Aldama bracteata</i>	forb	S
Asteraceae	<i>Aldama grandiflora</i>	forb	FS
Asteraceae	<i>Ayapana amygdalina</i>	shrub	I
Asteraceae	<i>Chresta exsucca</i>	forb	FD
Asteraceae	<i>Chresta speciosa</i>	forb	FD
Asteraceae	<i>Eremanthus goyazensis</i>	shrub	I
Asteraceae	<i>Ichthyothere hirsuta</i>	forb	I
Asteraceae	<i>Lessigianthus buddleifolius</i>	forb	FD
Asteraceae	<i>Lessigianthus durus</i>	forb	FS
Asteraceae	<i>Lessigianthus warmingianus</i>	shrub	FS
Asteraceae	<i>Porophyllum obscurum</i>	forb	FD
Bignoniaceae	<i>Adenocalymma</i> sp	shrub	FD
Bignoniaceae	<i>Anemopaegma arvense</i>	forb	FD
Calophyllaceae	<i>Kielmeyera abdita</i>	shrub	FD
Calophyllaceae	<i>Kielmeyera rubiflora</i>	shrub	FS
Convolvulaceae	<i>Ipomoea echioides</i>	forb	S
Convolvulaceae	<i>Ipomoea fiebrigii</i>	forb	FS
Cyperaceae	<i>Bulbostylis junciformis</i>	graminoid	S
Cyperaceae	<i>Bulbostylis paradoxa</i>	graminoid	FD
Cyperaceae	<i>Rhynchopora consanguinea</i>	graminoid	FS
Cyperaceae	<i>Rhynchospora elatior</i>	graminoid	FS
Cyperaceae	<i>Rhynchospora globosa</i>	graminoid	FS
Cyperaceae	<i>Rhynchospora</i> sp	graminoid	FS
Erythroxylaceae	<i>Erythroxylum campestris</i>	shrub	FD
Euphorbiaceae	<i>Bernardia hirsutissima</i>	forb	FS
Euphorbiaceae	<i>Croton gracilescens</i>	forb	FS

Euphorbiaceae	<i>Croton odontadenius</i>	shrub	FD
Euphorbiaceae	<i>Dalechampia linearis</i>	forb	FS
Euphorbiaceae	<i>Euphorbia</i> sp.	forb	FD
Euphorbiaceae	<i>Euphorbia potentilloides</i>	forb	FS
Euphorbiaceae	<i>Manihot kalungae</i>	forb	I
Fabaceae	<i>Aeschynomene</i> sp.	forb	FD
Fabaceae	<i>Bauhinia dumosa</i>	shrub	I
Fabaceae	<i>Calliandra dysantha</i>	shrub	FS
Fabaceae	<i>Chamaecrista clausenii</i>	shrub	I
Fabaceae	<i>Chamaecrista fagonoides</i>	shrub	I
Fabaceae	<i>Chamaecrista isidoria</i>	shrub	S
Fabaceae	<i>Chamaecrista ochrosperma</i>	shrub	I
Fabaceae	<i>Clitoria guianensis</i>	forb	FD
Fabaceae	<i>Desmodium platycarpum</i>	forb	FD
Fabaceae	<i>Eriosema congestum</i>	shrub	I
Fabaceae	<i>Eriosema</i> sp.	shrub	FD
Fabaceae	<i>Galactia</i> sp.	forb	FD
Fabaceae	<i>Harpalyce tombadorensis</i>	shrub	FS
Fabaceae	<i>Mimosa gracilis</i>	forb	I
Fabaceae	<i>Mimosa leioccephala</i>	shrub	FS
Fabaceae	<i>Mimosa longipes</i>	forb	I
Fabaceae	<i>Mimosa macrocephala</i>	forb	I
Fabaceae	<i>Mimosa pteridifolia</i>	shrub	FS
Fabaceae	<i>Senna corifolia</i> var. <i>corifolia</i>	shrub	FS
Gentianaceae	<i>Calolisianthus speciosus</i>	forb	FS
Gentianaceae	<i>Deianira pallescens</i>	forb	FS
Iridaceae	<i>Cipura xanthomelas</i>	forb	I
Iridaceae	<i>Trimezia juncifolia</i>	forb	FS
Lamiaceae	<i>Amasonia hirta</i>	forb	FD
Lamiaceae	<i>Eriope glandulosa</i>	forb	FD
Lamiaceae	<i>Gymneia chapadensis</i>	forb	I
Lamiaceae	<i>Hypenia</i> sp.	forb	FS
Lamiaceae	<i>Hyptis remota</i>	forb	I
Lamiaceae	<i>Marsypianthes</i> sp.	forb	FD
Lamiaceae	<i>Medusantha mollissima</i>	shrub	FS
Lythraceae	<i>Cuphea ericoides</i>	forb	I
Lythraceae	<i>Cuphea linearoides</i>	forb	FD
Lythraceae	<i>Diplusodon paraísoensis</i>	shrub	FS
Lythraceae	<i>Diplusodon punctatus</i>	shrub	I
Malpighiaceae	<i>Camarea ericoides</i>	forb	FD
Malpighiaceae	<i>Basniteriopsis pannosa</i>	shrub	FS
Malpighiaceae	<i>Byrsonima</i> sp.	shrub	S
Malvaceae	<i>Byttneria jaculifolia</i>	forb	I
Malvaceae	<i>Pavonia grandiflora</i>	shrub	I

Malvaceae	<i>Pelteia macedoi</i>	shrub	I
Melastomataceae	<i>Stenodon suberosum</i>	shrub	FS
Melastomataceae	<i>Stenodon campestris</i>	shrub	FS
Melastomataceae	<i>Tibouchina melastomoides</i>	forb	FS
Moraceae	<i>Brosimum gaudichaudii</i>	shrub	I
Ochnaceae	<i>Ouratea lanceolata</i>	shrub	I
Oxalidaceae	<i>Oxalis goyazensis</i>	forb	FD
Oxalidaceae	<i>Oxalis pyreneae</i>	forb	S
Poaceae	<i>Anthaenantia lanata</i>	graminoid	FD
Poaceae	<i>Aristida setifolia</i>	graminoid	I
Poaceae	<i>Axonopus aureus</i>	graminoid	I
Poaceae	<i>Axonopus marginatus</i>	graminoid	FD
Poaceae	<i>Axonopus pressus</i>	graminoid	FS
Poaceae	<i>Elionurus muticus</i>	graminoid	FD
Poaceae	<i>Mesosetum ferrugineum</i>	graminoid	FD
Poaceae	<i>Mesosteum loliforme</i>	graminoid	S
Poaceae	<i>Oedochloa procurrens</i>	graminoid	FD
Poaceae	<i>Oncorachis ramosa</i>	graminoid	FD
Poaceae	<i>Paspalum pectinatum</i>	graminoid	FD
Poaceae	<i>Paspalum vallsii</i>	graminoid	FS
Poaceae	<i>Sporobolus cubensis</i>	graminoid	FD
Poaceae	<i>Trachypogon spicatus</i>	graminoid	FD
Poaceae	<i>Trichantheum cyanescens</i>	graminoid	I
Polygalaceae	<i>Asemia marquesiana</i>	forb	FD
Polygalaceae	<i>Polygala abreui</i>	forb	FD
Polygalaceae	<i>Polygala sp.</i>	forb	FD
Polygalaceae	<i>Polygala coriacea</i>	forb	FS
Polygalaceae	<i>Polygala longicaules</i>	forb	FS
Rhamnaceae	<i>Crumenaria choretroides</i>	forb	FS
Rubiaceae	<i>Borreria poaya</i>	forb	I
Rubiaceae	<i>Declieuxia lancifolia</i>	forb	I
Rubiaceae	<i>Palicourea rigida</i>	shrub	I
Rubiaceae	<i>Spermacoce tenella</i>	forb	FS
Salicaceae	<i>Casearia sylvestris</i>	tree	S
Sapindaceae	<i>Serjania trichomisca</i>	shrub	FS
Turneraceae	<i>Piriqueta breviseminata</i>	forb	FD
Turneraceae	<i>Turnera emendata</i>	forb	FD
Velloziaceae	<i>Vellozia squamata</i>	vellozia	FD
Verbenaceae	<i>Lippia horridula</i>	forb	FD
Verbenaceae	<i>Stachytarpheta villosa</i>	forb	FD
Violaceae	<i>Pombalia lanata</i>	forb	FD
Vochysiaceae	<i>Vochysia pumila</i>	shrub	I
Xyridaceae	<i>Xyris sp.</i>	forb	FD

Effects of fire frequency on seed and germination traits of Cerrado species

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Abstract

In fire-prone ecosystems, reproduction and establishment of plants can be affected by changes promoted by fire. By altering the environmental conditions, fire can therefore influence seed and germination traits. We investigated the effect of fire history, specifically fire frequency, on seed and germination traits of species from the Cerrado community. Seeds from 15 species were collected in two areas with distinct fire history: recently and frequently burned area (> 2 fires in 6 yrs, first seed production after fire, FB) and the other excluded from fire for six years (C). Seeds underwent germination trials under optimal conditions (27°C, 12/12 hs light) for 30 days. Seed and germination traits were also measured and compared between the two areas. This included seed size and shape, water content, germinability, viability, mean germination time (MGT) and synchrony (Z). The results showed that 67% of the species had at least one of their germination traits altered in the FB area when compared to the C area. Some clear differences in traits were identified in our study, despite species-specific variation in our results. Viability was lower and germination faster in seeds from FB areas. Seed traits (seed mass, shape and water content) of eight species also differed between treatments. Within this species, most of them had smaller seeds with greater water content in FB areas compared to C, while seed shape varied as two species presented more rounded seeds and other three less rounded. Thus, our results suggest that, for a few species, frequent fires can lead to rapid changes in germination and seed traits. This provides some insight into the evolution of seed traits and the effects of fire.

Key words: Cerrado, Germination, Fire frequency, Fire history, Seed traits

Introduction

Plants inhabiting fire-prone ecosystems have traits that allow post-fire persistence and recovery including thick bark, meristems and buds insulated from heat (Gignoux *et al.*, 1997; Pausas *et al.*, 2018), vigorous resprouting and rapid flowering (Coutinho, 1990; Fidelis and Blanco, 2014; Pausas and Keeley, 2014; Lamont and He, 2017; Pyke, 2017) and high temperature requirements for breaking seed dormancy (Moreira *et al.*, 2010; Keeley *et al.*, 2011; Lamont and He, 2017). However, although such morphological and physiological traits allow persistence of individuals (Coutinho, 1982; Simon *et al.*, 2009; Simon and Pennington, 2012), plants from these systems are adapted to persist under a particular fire regime, rather than simply fire occurrence (Keeley *et al.*, 2011).

Fire regime elements include frequency, intensity and season, and all can drive both a plant population's response to disturbance and the frequency that particular adaptive traits will appear in the community (Bond and van Wilgen, 1996; Keeley *et al.*, 2011). Fire frequency is one of the most important aspects of the fire regime and can act as a filter by selecting species with certain persistence traits, thus affecting community assembly and diversity. For instance, some habitats with a high fire frequency may benefit species with a rapid resprouting and flowering response, as seen for example with *Vellozia sincorana* in *campos rupestres* (Conceição and Orr, 2012; Souza *et al.*, 2017). Areas with high fire frequency therefore generally have a greater proportion of resprouting species inhabiting the community, while habitats with a lower frequency of fire allows obligate seeders (i.e. species which above-ground plants are killed and recovery after fire only occurs through germination) to persist, since establishment to reproductive age and replenishment of the seed bank requires a longer burn interval (Bond and Midgley, 2001; Pausas *et al.*, 2004). The persistence of species adapted to a low fire frequency may therefore

be compromised if frequency is increased (Bradstock, 2008; Keeley *et al.*, 2011). However, some evidence suggests that the traits themselves could be altered by changes to the fire frequency (e.g. Gomez-Gonzalez *et al.*, 2011). As such, the study of the effect of fire frequency becomes an important tool for understanding how plants traits vary under various fire regimes and thus its impact on plant communities.

The direct effects of fire cues on germination, such as temperature shock breaking dormancy and smoke stimulating germination of some species in inflammable ecosystems, is well known (Whelan, 1995; Paula and Pausas, 2008; Moreira *et al.*, 2010; Keeley *et al.*, 2011). However, how changes to the fire regime provides a selective force that affects germination and other seed traits is less well studied. How some aspects of the fire regime, particularly fire intensity, influences germination have been the focus of some study. For example, Moreno and Oechel (1991) observed accelerated germination for *Ceanothus greggii* as a result of increasing fire intensity in the California Chaparral. Others seed traits, such as size, have also been shown to respond to variation in fire intensity experienced in the mother environment. One of the few examples investigating how selective pressure of fire frequency may alter seed traits found that shape and pubescence of seeds of species occurring in areas of high frequency burnings were considerably different to lower frequency burnt sites; this change in traits had occurred over relatively short time scales (Gomez-Gonzalez *et al.*, 2011, 2016; Ruprecht *et al.*, 2015).

Considering that few studies investigating fire regime effects on germination and seed traits focus on fire frequency, it raises the questions: Would fire frequency influence key seed traits related to regeneration? The fire regime experienced by the mother plant, particularly for resprouting species, has an indirect effect on seed and germination traits. Since maternal effect is when the phenotype of the mother plant affects the phenotype of the offspring and that environmental factors affects the

mother plant traits (Roach and Wulff, 1987; Gutterman, 2000; Räsänen and Kruuk, 2007; Donohue, 2009) one could expect that fire frequency would affect plant traits consequently altering and selecting their progeny traits.

The effect of fire frequency on germination in the Cerrado (Neotropical savanna) has not been described yet. Although there are some studies investigating how fire cues directly affect the germination of Cerrado species (e.g. Fichino *et al.* 2016; Daibes *et al.* 2017, 2018; Zironi *et al.* 2019), the alteration of seed and germination traits as a result of different fire regimes is yet to be clarified. Understanding of how seed and germination traits are affected by fire regime is of the utmost importance for improving the knowledge of the processes involved in the first stages of vegetation regeneration after the passage of fire (Grubb, 1977; Jiménez-Alfaro *et al.*, 2016).

Therefore, the objective of this work was to evaluate the effect of fire frequency (frequently burned vs fire exclusion) on seed and germination traits of species from the Cerrado community. Our hypothesis is that species of frequently burned areas will have seeds and germination traits altered when compared to areas with fire exclusion since fire exerts a selective pressure on plant traits.

Material and Methods

Study area and seed collection

Seeds from 15 species (see Table 1) with different growth forms (forbs and shrubs) were collected from the Serra do Tombador Natural Reserve (RNST, 13 ° 35-38 'S and 47 ° 45'-51' W, Central Brazil). The predominant climate for the RNST region is tropical, with a dry season predominant in the winter and maximum temperatures between 26 and 36°C and minimum between 8 and 14°C (Antonelli-Filho, 2011). Seeds were collected from areas of *campo sujo*, which is characterized by the presence of herbaceous plants and trees and isolated shrubs and dwarf trees (Coutinho, 1978).

Table 1. Study species according to their family, growth-form, presence of dormancy (ND: non-dormant; PY: physical dormancy) and the experiments to which species of C and FB areas were submitted. C, control areas with six years of fire exclusion; FB, frequently burned areas. All species are resprouters.

Species	Family	Growth-form	Dormancy	Experiments in both C and FB areas			
				Germination traits	Seed Mass	Seed shape	Water content
<i>Bauhinia dumosa</i>	Fabaceae	Shrub	ND	✓	✓	✓	✓
<i>Chamaecrista clausenii</i>	Fabaceae	Shrub	PY	✓	-	-	-
<i>Gymneia chapadensis</i>	Lamiaceae	Forb	ND	✓	✓	✓	✓
<i>Harpalyce</i> sp.	Fabaceae	Shrub	PY	✓	✓	✓	✓
<i>Hyptenia</i> sp	Lamiaceae	Forb	ND	✓	✓	✓	✓
<i>Hyptis remota</i>	Lamiaceae	Forb	ND	✓	-	-	-
<i>Kielmeyera rubriflora</i>	Calophyllaceae	Shrub	ND	✓	-	-	-
<i>Lessingianthus durus</i>	Asteraceae	Forb	ND	✓	-	-	-
<i>Medusantha mollissima</i>	Lamiaceae	Shrub	ND	✓	✓	✓	✓
<i>Mimosa gracilis</i>	Fabaceae	Forb	PY	✓	✓	✓	✓
<i>Mimosa leioccephala</i>	Fabaceae	Shrub	PY	✓	✓	✓	✓
<i>Mimosa pteridifolia</i>	Fabaceae	Shrub	PY	✓	✓	✓	✓
<i>Senna corifolia</i>	Fabaceae	Shrub	PY	✓	✓	✓	✓
<i>Tibouchina melastomoides</i>	Melastomataceae	Forb	ND	✓	✓	✓	✓
<i>Trimezia juncifolia</i>	Iridaceae	Forb	ND	✓	✓	✓	✓

Seeds were acquired from *campo sujo* areas with two distinct fire frequencies: recently and frequently burned areas (FB, burned >2 times in the last six years) and areas excluded from fire for six years which we called control (C). Before fire exclusion, both areas had the same fire frequency. Seeds from FB were from the first production after fire whereas plants from C areas had been producing seeds presumably for the previous six years.

Seed and germination traits

We investigated how fire history affected the following germination traits: germinability (%), viability (%), mean germination time (MGT, days) and synchrony (Z). Seeds from both areas (C and FB) were collected from at least five individuals/treatment (as suggested by Pérez-Harguindeguy *et al.* 2013). Then seeds were sorted in the laboratory and separated into five replicates of 20 seeds.

Seeds were placed to germinate in germination chambers at a constant temperature of 27°C and 12 / 12h light / dark photoperiod (see Fichino *et al.* 2016). Observations were made daily for 30 days to verify the number of seeds germinated in each plate. Seeds were considered germinated with the appearance of a radicle and/or cotyledons. After the completion of the experiments, viability tests were performed with the seeds that did not germinate, using 1% tetrazolium solution. The seeds stained pink were considered viable (adapted from Lakon 1949). In this way, the germinability was given as the percentage of seeds germinated in the treatment, and the viability, by the sum of the germinated plus viable seeds at the end of the experiments.

The mean germination time (MGT) and synchrony (Z) for each species were calculated according to adapted formulas from Ranal and Santana (2006):

$MGT = \frac{\sum_{i=1}^k ni \cdot ti}{\sum_{i=1}^k ni}$, where: ti = incubation time (days); ni = number of seeds germinated per day; k = last germination time of the seeds.

$Z = \frac{\sum Cni,2}{N}$, where: $Cni,2 = \frac{ni(ni-1)}{2}$ and $N = \sum ni(\sum ni - 1)/2$, where $Cni,2$ = combination of seeds germinated in the time i , two by two, and ni : number of seeds germinated in the time i . Therefore, if $Z = 1$, all seeds germinate at the same time. If $Z = 0$, at least two seeds could germinate, one at each time.

To evaluate if fire frequency affected seed traits, we measured seed shape, mass and water content, following and adapting trait protocols (Cornelissen *et al.*, 2003; Pérez-Harguindeguy *et al.*, 2013; AL-Tam *et al.*, 2013):

1. Seed shape was obtained using the software P-TRAP software (AL-Tam *et al.*, 2013). For each species from both areas (control and frequently burned), a hundred seeds were scanned at 800dpi and 1200dpi using an Epson Perfection v800 scanner. Then the images were analysed using P-TRAP software and the shape (width:length ratio) obtained.
2. Seed mass (mg): seeds were weighed individually before being placed in an oven at 80°C for 48 hours and the weighed again, thus obtaining the fresh and dry weight respectively. We measured 20 seeds / individual and averaged the seeds of the individuals, when there were enough seeds/individual. Otherwise, we measured 100 seeds for the population.
3. Water content (%): calculated by the fresh weight of the seed subtracted from the dry weight after 48 hours at 80°C in an oven. From this value was calculated the percentage of water that the seed had. At least 20 seeds / individual were used, when there were enough seeds/individual. Otherwise, we measured 100 seeds for the population. The value for the species was the average of the individuals (>10).

Statistical analyses

Differences in germination percentages between treatments were tested using GLMM (generalized linear mixed models) with a binomial error structure and a logit link function for each species to compare final germination and viability averages. The fire histories were treated as the fixed factor and replicate as the random factor. In addition, to analyse MGT between treatments a GLM with a Gamma error structure and an inverse link function for each species was performed, while for comparing Z we used Poisson family due to the amount of zeros in the data that needed to be accounted for.

Differences in seed mass (fresh and dry weight), water content and seed shape between treatments were tested using GLM with a Gamma error structure and an inverse link function for each species. Fire frequency was treated as a fixed factor.

Statistical analyses were performed using *multcomp*, *lme4* and *lsmeans* packages in the R software (Hothorn *et al.*, 2008; Bates *et al.*, 2015; Lenth, 2016; R Core Team, 2016).

Results

Germination traits

Results showed that 67% of the species had at least one of their germination traits altered in the frequently and recently burned area (FB) when compared to the fire exclusion (C) area.

The two species that had the highest germination percentages, both in control and burned areas, were *Bauhinia dumosa* (>80%) and *Trimezia juncifolia* (>90%) while *Harpalyce* sp. and *Lessingianthus durus* had no germination at control and the

lowest percentages on the burned area ($4\pm 2.67\%$, $4\pm 2.45\%$, respectively) (Table 2). *Lessingianthus durus* showed low values of germinability and viability due to the high amount of empty seeds ($>60\%$).

Out of the fifteen species, only four had germination significantly different between the two fire frequencies. *B. dumosa* and *H. remota* had an increase in germination in the burned area seeds compared to control, 13.15% more for *B. dumosa* and 87.85% more for *Hypstis remota* (Table 2, $p<0.05$). The opposite could be observed for *M. gracilis* and *G. chapadensis*, where the germination decreased at the FB site (decrease of 37% and 20.3%, respectively) (Table 2).

The viability results showed differences in the percentages for six species when comparing both frequencies. For five of them there was a decrease in viability in seeds of burned area where *Harpalyce* sp. and *M. gracilis* had a decrease greater than 50% in viability compared to C while for *M. leiocephala*, *M. pteridifolia* and *G. chapadensis* this decrease was lower than 35% (Table 2). Most of these species were from the Fabaceae family. In the other side, *T. melastomoides* had a higher viability for seeds of the recently burned area compared to the control (increase of 27.24%, $p\leq 0.05$) (Table 2).

Synchrony (Z) was not affected by fire history for any of the species. However mean germination time (MGT) was significantly affected in the frequently burned treatment for five species (*B. dumosa*, *T. juncifolia*, *H. remota*, *M. mollissima* and *M. gracilis*) with germination occurring from two to eight days earlier than control (Table 2).

Table 2. Germination traits of all studied species. Germination and Viability percentages, Mean germination time (MGT) in days and Synchrony (Z) (mean±SE) for both fire histories; C= control areas with 6 years of fire exclusion; FB= frequently burned areas; NA=not available. * means significant difference from the respective control where *P≤0.05 **P < 0.01, ***P < 0.001.

Species	Germination (%)		Viability (%)		MGT(days)		Z	
	C	FB	C	FB	C	FB	C	FB
<i>Bauhinia dumosa</i>	83.58±4.18	94.57±3.18*	100±0	96.44±2.54	18.53±0.42	13.22±0.9***	0.12±0.01	0.13±0.02
<i>Chamaecrista clausenii</i>	14.9±6.19	10±4.08	85.61±5.3	67.5±16.01	2.67±0.67	4.5±2.33	0.33±0.33	0±0
<i>Gymneia chapadensis</i>	70.23±4.21	55.97±2.78*	73.05±4.45	57.88±3.82*	8.63±0.9	8.17±0.8	0.11±0.06	0.1±0.04
<i>Harpalyce</i> sp.	0±0	4±2.67	43.5±2.69	14.76±4.86***	0±0	2.9±1.78	0±0	0±0
<i>Hypenia</i> sp	8.48±4.12	11.67±5.87	32.57±3.51	42±8.6	10.3±4.42	6.47±3.01	0±0	0.07±0.07
<i>Hyptis remota</i>	29.39±9.56	55.21±7.93**	56.67±8.21	59.03±8.31	14.22±1.69	6.4±0.5***	0.03±0.02	0.12±0.05
<i>Kielmeyera rubriflora</i>	79.63±5.46	84.36±3.92	79.63±5.46	84.36±3.92	6.47±0.2	5.05±0.68	0.46±0.09	0.38±0.05
<i>Lessingianthus durus</i>	0±0	4±2.45	3.82±2.34	4±2.45	0±0	2.4±1.5	0±0	0±0
<i>Medusantha mollissima</i>	71.6±10.55	71.78±5.94	75.66±9.33	73.78±5.71	12.69±1.05	10.23±0.76*	0.06±0.03	0.09±0.03
<i>Mimosa gracilis</i>	46±9.27	28.92±5.14*	76±6.78	34.36±6.92***	14.93±2.01	8.35±0.91**	0.06±0.04	0.11±0.05
<i>Mimosa leiocephala</i>	8.11±2.67	5.56±5.56	92.14±3.21	61.11±18.22***	8.6±4.09	2.33±2.33	0±0	0.33±0.33
<i>Mimosa pteridifolia</i>	16.26±3.07	8.04±2.04	79.68±3.1	61.62±11.05*	8.47±1.72	6±2.17	0.09±0.06	0±0
<i>Senna corifolia</i>	4.64±2.04	2±1.22	92.49±3.19	85.51±1.31	6.6±2.89	5.4±3.4	0±0	0±0
<i>Tibouchina melastomoides</i>	58±9.17	68±6.44	58±9.17	73±8*	4.87±0.32	4.26±0.31	0.15±0.13	0.28±0.09
<i>Trimezia juncifolia</i>	90.59±2.59	94±4	95.27±0.11	98±2	18.01±0.46	15.87±0.51**	0.14±0.06	0.16±0.07

Seed traits

At least one seed trait of eight of the studied species differed between treatments. Seed mass was measured for only eleven of the species due to seed availability. In general, seed mass (fresh weight) was higher for Fabaceae species, *B. dumosa* being the species with largest seed size ($65.32 \pm 1.1 \text{ mg}$). On the other hand, seeds of *G. chapadensis*, *M. mollissima* and *T. melastomoides* were so small that they needed to be weighed in groups of ten seeds. The smallest seeds were from *T. melastomoides* with a fresh weight of approximately 0.189 mg (Table 3).

Comparing seed mass/size between control and frequently burned areas, we found significant differences for five species. Four of them, *G. chapadensis*, *M. pteridifolia*, *S. corifolia* and *T. juncifolia* presented smaller seeds at the FB area, whereas for *Hyphenia* sp. showed an opposite trend (Table 3).

Water content (WC) of seeds varied between 3.46 to 22.62% in control areas and from 5.08 to 10.35% in FB areas. Six species had WC values altered according to fire history. *B. dumosa*, *M. gracilis*, *M. pteridifolia*, *S. corifolia* and *T. juncifolia* presented higher percentages of water content in the FB areas compared to control whereas for *Hyphenia* sp., the water content for seeds from C was almost three times higher than for FB areas ($C = 8.81 \pm 0.83\%$, $FB = 22.62 \pm 2\%$, $p < 0.001$) (Table 3).

Seed shape (width:length ratio) results showed that fire frequency affected the shape of five species. Values of the ratio decreased for *B. dumosa*, *G. chapadensis* and *Hyphenia* sp. indicating more elongated seeds on FB areas. The opposite happened with seeds from *S. corifolia* and *T. melastomoides* ($p < 0.05$) and seeds from FB areas were more rounded compared to control. There were no significant changes in shape for the remaining species (Table 3).

Table 3. Seed Traits. Average (mean+SE) seed mass (fresh and dry weight), seed water content and seed shape for all studied species in both fire histories. Seed shape is the width:length ratio. C= control areas with 6 years of fire exclusion and FB= frequently burned areas. NA=not available. * means significant difference from the respective control where, *P<=0.05, **P < 0.01, ***P < 0.001.

Species	Fresh weight (mg)		Dry weight (mg)		Water content (%)		Seed Shape (mm)	
	C	FB	C	FB	C	FB	C	FB
<i>Bauhinia dumosa</i>	65.32±1.1	66.63±1.22	59.99±0.99	60.14±1.1	8.13±0.09	9.73±0.07***	0.86±0.01	0.82±0.01***
<i>Chamaecrista clausenii</i>	NA	16.29±0.41	NA	15.02±0.38	NA	7.76±0.26	0.79±0.01	0.81±0.01
<i>Gymneia chapadensis</i>	2.35±0.11	1.89±0.13*	2.27±0.11	1.79±0.12**	3.46±1.1	5.08±1.27	0.67±0.01	0.64±0.01**
<i>Harpalyce</i> sp.	30.93±0.54	31.42±0.66	28.98±0.51	29.53±0.63	6.36±0.18	6.03±0.18	0.65±0.02	0.65±0.01
<i>Hypenia</i> sp.	1.63±0.16	2.44±0.12***	1.28±0.14	2.23±0.11***	22.62±2	8.81±0.83***	0.76±0.01	0.72±0.01**
<i>Hyptis remota</i> .	NA	7.03±0.8	NA	6.41±0.82	NA	10.35±2.75	±NA	0.61±0.01
<i>Kielmeyera rubriflora</i>	NA	NA	NA	NA	NA	NA	0.83±0.01	0.81±0.01
<i>Medusantha mollissima</i>	2.57±0.15	2.74±0.10	2.35±0.14	2.42±0.10	8.56±1.12	11.67±1.88	0.44±0.005	0.44±0.01
<i>Mimosa gracilis</i>	8.06±0.76	9.05±0.2	7.63±0.74	8.35±0.19	5.47±0.48	7.82±0.36*	0.75±0.02	0.79±0.01
<i>Mimosa leioccephala</i>	31.45±0.57	NA	30.22±0.52	NA	3.72±0.3	NA	0.81±0.01	0.77±0.03
<i>Mimosa pteridifolia</i>	9.78±0.19	8.16±0.21***	9.29±0.18	7.64±0.21***	4.9±0.43	6.58±0.5*	0.83±0.01	0.82±0.02
<i>Senna corifolia</i>	32.58±0.48	30.9±0.68*	31.31±0.46	29.11±0.61**	3.81±0.4	5.6±0.3**	0.6±0.01	0.65±0.01***
<i>Tibouchina melastomoides</i>	1.89±0.14	2.05±0.07	1.7±0.14	1.87±0.06	10.38±2.11	8.61±1.51	0.75±0.01	0.78±0.02*
<i>Trimezia juncifolia</i>	5.42±0.13	4.68±0.1***	5.09±0.12	4.33±0.1***	5.8±0.41	7.5±0.53***	0.77±0.01	0.78±0.01

The weight presented for *G. chapadensis*, *M. mollissima* and *T. melastomoides* is based on ten seeds.

Discussion

Some clear differences in traits were identified in our study, despite species-specific variation in our results. We showed that fire frequency affects germination and seed traits of Cerrado species. Overall, ten of the fifteen species had at least one of their germination traits altered in the recent frequently burned (FB) area when compared to the area with fire exclusion (C). More specifically, species within the Fabaceae and/or shrub growth form tended to have lower viability, faster germination and smaller seed size in recently and frequently burnt sites, some characteristics that are required for faster establishment in frequently disturbed environments (Keeley and Fotheringham, 2000). Both germination and seeds traits are critical elements of the regeneration niche of species (Grubb, 1977; Ranieri *et al.*, 2012; Marques *et al.*, 2014) and evaluating how fire can influence them can give us an insight into their evolution and help us to understand the effects of changes to the fire regime. In turn, this can help us understand the influence of ecological and evolutionary filters in community assembly (Jiménez-Alfaro *et al.*, 2016; Saatkamp *et al.*, 2019).

Most studies focus on how fire cues such as heat shock and smoke affects germination traits and how those responses vary (e.g. Keeley and Fotheringham 2000; van Staden and Brown 2000; Keeley *et al.* 2011). Species from fire-prone ecosystems that have dormancy could have this dormancy broken (Ooi *et al.*, 2006; Baskin and Baskin, 2014) and the germination stimulated by high temperatures (Auld and O'Connell, 1991; Auld and Ooi, 2009), while seeds with permeable coat or physiological dormancy would have the germination enhanced by chemicals compounds derived from smoke (Flematti, 2004; Light *et al.*, 2009; Keeley and Pausas, 2016). However, in our study we aimed to observe whether fire frequency would affect the germination traits and not on the fire cues effects per se. Our results show a complex species-specific pattern of fire frequency effects on these

germination traits, however despite this variation it appears that certain groups are likely to be impacted more by changes to fire frequency.

Most information on post-fire regeneration strategies have been addressed from crown-fire and Mediterranean ecosystems (e.g. Pausas *et al.* 2004), where quite high proportions of species are obligate seeders (i.e. adult plants die in response to high intensity fires and are dependent on seeding for populations to persist). Savanna species, on the other hand, face low intensity surface fires, usually very frequent in the grassy layer (Bond *et al.*, 2005) and resprouting is the most favoured post-fire recruitment strategy (Bond and Midgley, 2003). This is reported for many Cerrado species which maintain from underground systems that bear buds (Appenzato-da-Glória *et al.*, 2008; Simon and Pennington, 2012) . As such, the effects we found in our study is not a result of populations being subjected to pressure selecting for faster germinating and smaller seeded genetic individuals, but of the direct influence of higher frequency burning of the same individuals. This could lead to changes as a result of pressure on plant resourcing or other factors.

The seed mass/size of five species was altered according to fire history, with seeds from FB areas generally smaller except for for *Hypenia* sp. which reversed this trend. Seed size can be linked as an adaptation to disturbance, and a well-studied hypothesis is that larger seeds would prevail in high frequency fires because larger seeds lead to more vigorous seedlings with a great likelihood to survive (Westoby *et al.*, 2002; Moles *et al.*, 2004; Moles and Westoby, 2006; Lahoreau *et al.*, 2006). Thus, high intensity disturbance as frequent fires would select larger seeds (Ribeiro *et al.*, 2015) but that is the opposite that we found for most studied species that had seed size altered. Four species (*Gymneia chapadensis*, *Mimosa pteridifolia*, *Senna corifolia* and *Trimezia juncifolia*), presented smaller seeds at the frequently burned area compared to control. This suggests that rather than the high fire frequency

producing a response that provides any benefit to the species, it is perhaps more of a result of reduced resourcing towards reproductive effort. Either recent or recurrent resprouting could reduce the resources maintained by individual plants, therefore resulting in reduced seed resourcing.

Seed shape of five species was significantly different between FB and C areas. Seeds of *B. dumosa*, *G. chapadensis* and *Hyphenia* sp. were more elongated on FB areas while seeds from *S. corifolia* and *T. melastomoides* were more rounded compared to control. Generally it is expected that seeds from plants exposed to higher fire frequencies would be more rounded since this shape helps to protect the embryo from the high temperatures as well as facilitates it buries in the soil (Gomez-Gonzalez *et al.*, 2011, 2016; Ruprecht *et al.*, 2015). However, seed shape can be modulated by the sum up of different factors such as soil type, seed dormancy and other fire parameters. For example as seen by Gomez-Gonzalez *et al.* (2011) where more rounded seeds were selected by fire when analysing the regional pattern whereas when seeds were analysed within-population more elongated seeds were the prominent ones.

Perhaps the explanation for the diversity in traits according fire history lays on the maternal effect, where habitat conditions such as variations in temperature, availability of mineral nutrients and water affects the mother plant phenotype thus altering the progeny phenotype (Roach and Wulff, 1987; Donohue, 2009). Since C and FB plants were exposed to the same climatic conditions species exposed to higher fire frequency would have traits shaped by the disturbance pressure consequently altering the progeny traits (seed and germination traits). Considering that the environmental conditions directly affect plants responses, another explanation for our findings would be that after repeatedly allocating resources towards resprouting because of the burnings the seed traits would be negatively

affected. For example a study with *Sorghum stipoides* from north Australia found that the nutrient level of its seeds was lower in areas with high fire frequency (Weier *et al.*, 2017). Also fire frequency could be affecting the trade-off where plants with small seeds produce a greater number of it (Moles *et al.*, 2004) and thus not directly affecting the measured seed size and shape. But this finding cannot be affirmed since it was not properly investigated in this study.

In a closer look to the results it seems that most of Fabaceae species were negatively affected by frequent fires and it might be due to the repeated resprouting ability and how it can relocate resources to resprout that otherwise was going to seed production. It is already known that generally non-resprouters species of fire-prone environments has a better seed set, germination and heat tolerance than resprouters (Paula and Pausas, 2008). Perhaps resprouters species subject to a shorter fire interval have to use stored resources for regrowth thus affecting seed production, quality and germination since it was already hypothesised as the trade-off between vegetative and reproductive regeneration (Bellingham and Sparrow, 2000; Knox and Morrison, 2005). Although, some authors state that the seed set would not be negatively affected by resprouting because while regrowth of vegetative would depend on stored carbon the seed set would likely be dependent on nutrients (Lamont *et al.*, 2011).

Altering fire regime where these traits were selected will affect the fitness of the species and consequently the composition and diversity of this community (Whelan, 1995; Bond and van Wilgen, 1996; Bradshaw *et al.*, 2011; Keeley *et al.*, 2011). As we could observe this response is species-specific, where some species were not affected, some were impaired and a few benefited by a higher fire frequency, nonetheless fire is exerting a selective pressure on these plant traits at a fast rate (within six years). Summarizing, changing the fire history alter the germination traits

of these species when facing a higher fire frequency thus further studies with different fire frequencies are essential to understand the evolution of seed traits.

Acknowledgements

We thank LEVeg (Lab of Vegetation Ecology) members specially: Aline Bombo, Soizig Le Stradic, Cassy A.S. Rodrigues, Gabriella Damasceno, Mariana Dairel, Juliana Teixeira, Vagner Zanzarini, Ana Carolina F. Conceição, Jonathan Galdi and Mauricio Cunha for helping with field work, collection of seeds and germination experiments. We also thank the employees of Reserva Natural Serra do Tombador: Whatson F. Rezende, Anderson F. Terra, Gilson de A. Berberino, Rogério B. de Almeida and Silvanio A. Borges for the support during the experiments. We thank Fundação Grupo Boticário for the permit to work at the Reserva Natural Serra do Tombador.

Financial support

This study received financial support from Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP 2015/06743-0). H.L.Z. received financial support from FAPESP (2017/16149-4, 2018/08017-3). A. F. received research grant from CNPq (306170/2015-9).

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CONSIDERAÇÕES FINAIS

Nos ambientes inflamáveis o fogo modifica a dinâmica do ambiente, afetando a comunidade vegetal e os atributos das plantas (Whelan 1995; Bond & van Wilgen 1996). No entanto, o regime de fogo é responsável por agir como força seletiva sobre as plantas, selecionando as características que garantem o fitness das espécies (Bond & van Wilgen 1996; Keeley et al. 2011).

O fogo pode atuar diretamente na fenologia vegetativa e reprodutiva de espécies de plantas, ocasionando mudanças nos padrões de floração como por exemplo o estímulo na produção de flores e frutos e antecipação no período de floração após a passagem do fogo (Lamont & Downes 2011; Pyke 2017). Além disso, mudanças nos atributos das sementes e de germinação (ex. peso, forma, germinabilidade) também podem ser observados em ambientes inflamáveis (ex. Gomez-Gonzalez et al. 2011; Gomez-Gonzalez et al. 2016). Assim sendo, devido o fogo ser um fator presente no Cerrado há pelo menos 4 milhões de anos (Simon et al. 2009), faz-se necessário entender sua influência e importância nos processos reprodutivos, utilizando como base as respostas destes atributos. Portanto, esse projeto visou compreender o efeito das queimas na fenologia reprodutiva e da frequência de fogo nos atributos de semente e germinação da comunidade do Cerrado.

Considerando os resultados do primeiro capítulo onde avaliamos a influência do fogo na fenologia reprodutiva é possível concluir que muitas espécies do estrato herbáceo-arbustivo têm sua floração e frutificação afetada pelas queimas (Fig. 1). Foi observado um maior número de espécies florindo e frutificando nas áreas queimadas quando comparadas às áreas de exclusão do fogo. Três meses após a queima a profusão da floração, ou seja, o número de ramos floridos também foi maior nas áreas queimadas mesmo na época seca. Dentre as espécies dominantes

estudadas viu-se que as gramíneas e as herbáceas são afetadas positivamente nos três primeiros meses após a queima enquanto os arbustos após 6 meses.

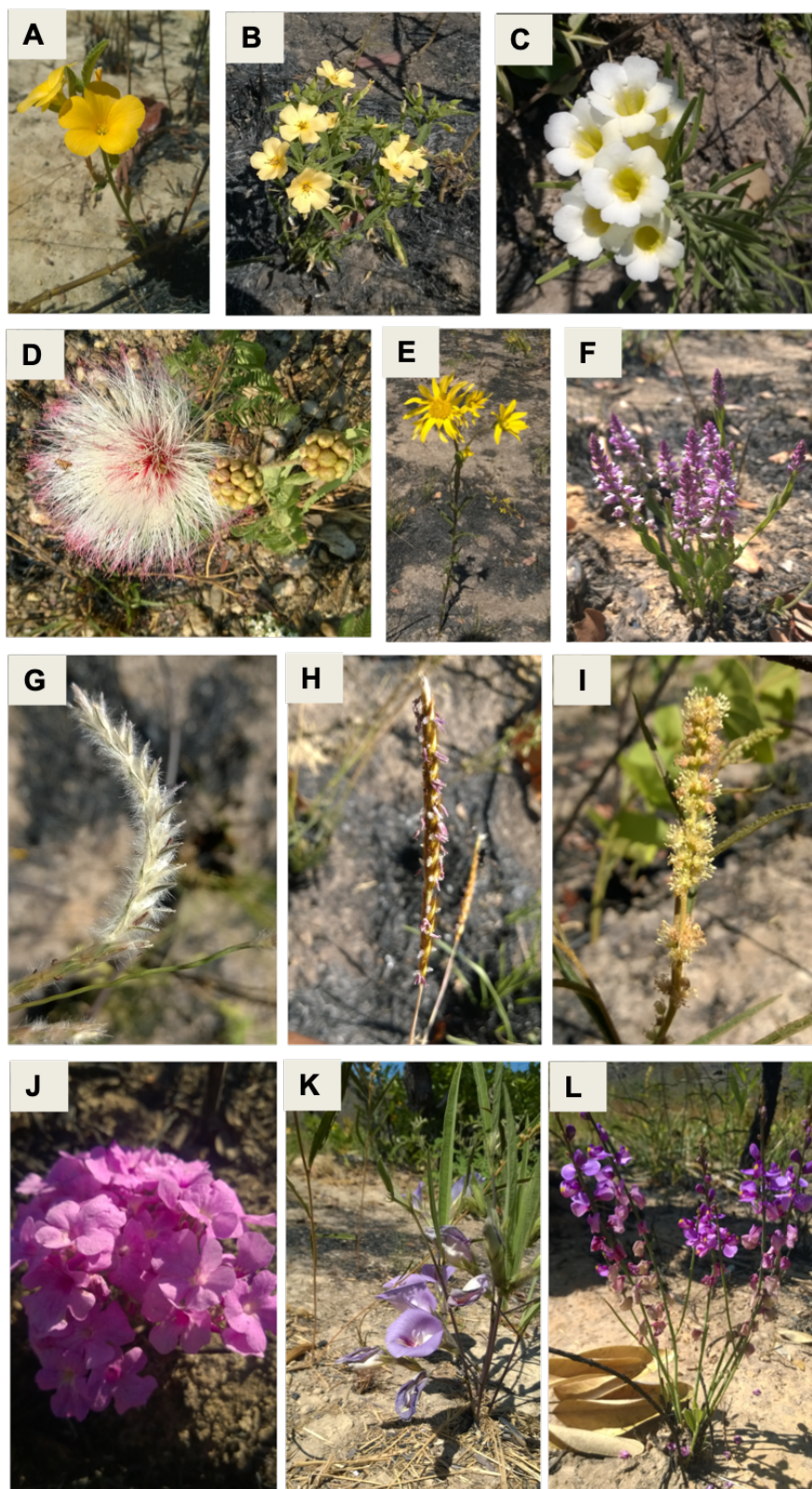


Figura 1. Espécies do campo sujo florescendo pós-fogo. A) *Turnera emendata*, B) *Piriqueta breviseminata*, C) *Anemopaegma arvense*, D) *Calliandra dysantha*, E) *Aldama grandiflora*, F) *Polygala coriácea*, G) *Elionurus muticus*, H) *Mesosetum ferrugineum*, I) *Croton gracilescens*, J) *Lippia horridula*, K) *Clitoria guianensis* e L) *Asemia marquesiana*.

Além disso, foi possível classificar as espécies de acordo sua resposta de floração pós fogo. Vimos que 66,4% das espécies pertencentes a 28 (das 36 encontradas na área) famílias tiveram a floração estimulada pelo fogo sendo que 35,3% delas são dependentes da queima para que reprodução sexuada ocorra.

No capítulo dois, avaliamos a influência da frequência de fogo nos atributos de semente e germinação. Os resultados mostraram que 67% das espécies tiveram pelo menos um dos seus atributos de semente ou germinação afetadas pela frequência do fogo. No entanto, para a maioria das espécies a viabilidade foi menor e a germinação mais rápida nas sementes das áreas queimadas mais frequentemente. Atributos das sementes (peso, forma e conteúdo de água) de oito espécies também diferiram entre as frequências, sendo que a maioria apresentou sementes menores com maior teor de água nas áreas queimadas em relação a espécies da área de exclusão de fogo.

A avaliação de atributos de germinação e sementes é uma importante ferramenta para se entender processos em comunidades vegetais (Jiménez-Alfaro et al. 2016; Saatkamp et al. 2019). Portanto, apesar das variações espécie-específica encontrada em nossos resultados algumas diferenças claras nos atributos foram observadas em nosso estudo. Além disso a alteração nos atributos de plantas da área queimada pode indicar uma pressão seletiva do fogo ocorrendo em rápida escala e em resposta a alta heterogeneidade das queimas.

Sumarizando, a floração de mais de 60% da comunidade vegetal do Cerrado é estimulada rapidamente pelo fogo, ocorrendo logo nos primeiros meses após a queima. Além disso é importante ressaltar que esse estímulo ocorre mesmo na estação seca. Também podemos observar que a frequência do fogo altera os atributos de semente e germinação e essa resposta pode-se dever tanto a pressão seletiva ocorrendo em rápida escala e/ou ao trade-off entre rebrotar e produzir

propágulos, já que todas as espécies da área são rebrotadoras e podem estar alocando mais energia para rebrotar frequentemente ao invés de investir na parte reprodutiva. Tais respostas ainda não foram relatadas para outras savanas. Portanto podemos considerar o fogo um fator importante agindo na comunidade vegetal e na biodiversidade do Cerrado.

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