UNIVERSIDADE ESTADUAL PAULISTA
“JÚLIO DE MESQUITA FILHO”
INSTITUTO DE BIOCIÊNCIAS – RIO CLARO

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

QUANTAS VEZES DEVEMOS QUEIMAR O CERRADO? O EFEITO DA FREQUÊNCIA DO FOGO EM COMUNIDADES VEGETAIS DE CAMPO SUJO DE CERRADO

CASSY ANNE DOS SANTOS RODRIGUES

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

Orientadora: Profª. Dra. Alessandra Fidelis

Rio Claro
2019

R696q

Rodrigues, Cassy Anne dos Santos
Quantas vezes devemos queimar o Cerrado? O efeito da frequência do fogo em comunidades vegetais de campo sujo de Cerrado. / Cassy Anne dos Santos Rodrigues. -- Rio Claro, 2019
88 p. : il., tabs.

Dissertação (mestrado) - Universidade Estadual Paulista (Unesp), Instituto de Biociências, Rio Claro
Orientadora: Alessandra Tomaselli Fidelis

1. Frequência do fogo. 2. Comportamento do fogo. 3. Comunidades vegetais de campo sujo de Cerrado. 4. Diversidade de espécies. 5. Produtividade. 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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CERTIFICADO DE APROVAÇÃO

TÍTULO DA DISSERTAÇÃO: QUANTAS VEZES DEVEMOS QUEIMAR O CERRADO? O EFEITO DA FREQUÊNCIA DO FOGO EM COMUNIDADES VEGETAIS DE CAMPO SUJO DE CERRADO

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Aprovada como parte das exigências para obtenção do Título de Mestra em CIÊNCIAS BIOLÓGICAS (BIOLOGIA VEGETAL), área: Biologia Vegetal pela Comissão Examinadora:

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Rio Claro, 29 de novembro de 2019

Dedico este trabalho à quem me deu asas e me ensinou a voar,

à quem todas as minhas conquistas também pertence, mãe.

AGRADECIMENTOS

São tantos a agradecer, pois desde a intenção até a conclusão deste trabalho nunca me faltou apoio ou incentivo.

Agradeço, primeiramente a Alessandra, que confiou desde o começo que eu teria as competências necessárias para desenvolver este trabalho e que me ajudou a desenvolver as que ainda me faltavam. Agradeço pela generosidade em incentivar e providenciar o crescimento profissional de seus alunos e pela total compreensão durante os piores momentos desta jornada.

Agradeço aos amados companheiros do LEVeg, aprendo muito com cada um de vocês. Compartilhar a rotina diária do laboratório e tê-los como equipe no campo foi sem dúvida um privilégio. Obrigada por toda a contribuição com este trabalho, que chegou de tantas maneiras e por me permitirem, de alguma forma, contribuir com vocês. Vocês são um dos grupos mais queridos do qual já fiz parte! Quantas boas memórias.

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

À todos os taxonomistas que contribuíram para a identificação das espécies, em especial aos Drs. Marcelo Fragomeni Simon e Bruno Machado Teles Walter, que além das inestimáveis contribuições para com este estudo, nos receberam com muita atenção e prestabilidade no Herbário da Embrapa Cenargen.

Aos queridos funcionários, da Reserva Natural da Serra do Tombador: Anderson F. Terra, Rosileide A. Berberino, Whatson F. Rezende, Gilson de A. Berberino, Silvanio A. Borges, Rogério B. de Almeida e Adenilton A. F. Figueredo, sem os quais este trabalho não seria possível. Obrigada pela disposição, bom humor e todo o aprendizado.

Ao Sr. Juraci Francisco Maia e toda a sua equipe por todo apoio durante a realização das queimas e pela agradável convivência no alojamento durante as campanhas de campo.

Ao Mauricio Bolliger Andrade da Cunha cuja contribuição foi fundamental para que este trabalho pudesse ser realizado.

À Fundação Grupo Boticário de Proteção à Natureza por apoiar logisticamente

a realização dos experimentos na Reserva Natural Serra do Tombador (0153_2011_PR).

O presente trabalho foi realizado com apoio da Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Código de Financiamento 001.

À Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) pelo financiamento dos projetos FAPESP 2017/22618-7, FAPESP 2015/06743-0 os quais fazem parte desta pesquisa.

Agradeço especialmente à minha família, foram tempos difíceis mas nos mantivemos fortes e unidos para apoiar os sonhos uns dos outros. Dany, minha irmã, obrigada por ser tão presente, tão especial e tão fácil de amar. E obrigada por você e o Matraka, me permitirem vivenciar o amor mais puro, doce e incondicional do mundo ao me tornarem tia, o Henrique é luz, calma, refúgio e ternura. Agradeço ao meu pai pelo exemplo de como podemos transformar nossa vida, contrariando todas as expectativas. Ao meu irmão, Marcelo, por todo afeto ao longo da minha vida, você tem um lindo coração e foi minha referência em muitos aspectos. Agradeço, em especial, minha mãe. De quem eu sinto saudades todos os dias, mas sem tristeza, pois sei o tamanho do privilégio que foi tê-la ao meu lado, ainda que por tão pouco tempo. Mãe, obrigada por tanto, pelo amor sem medidas, por me ensinar a ter coragem diante da vida e por me fazer acreditar que eu posso alcançar tudo o que eu sonhar, desde que eu me dedique. Você foi a pessoa mais linda que eu já conheci e a maior amiga que eu tive. Te amo, para sempre!

Agradeço, meu amor e parceiro de vida, Anderson. Obrigada pelo apoio diário e pelo incentivo sempre que necessário. Obrigada pelo cuidado e paciência, principalmente nos dias mais difíceis. Enquanto realizamos um projeto outras tantas coisas acontecem na nossa vida e algumas são realmente bem difíceis, mas saber que tenho você ao meu lado e contar com sua ajuda sempre que precisei, tornou tudo muito mais possível de enfrentar, pois você me faz mais forte.

Agradeço também, a querida Edna por cuidar de tudo com tanto carinho e estar sempre pronta a ajudar. Minhas idas a campo foram bem mais tranquilas por saber que podia contar com você pra cuidar de tudo e todos por mim.

E as minhas 2 meninas queridas, Cindy e Biluca, que sempre foram as melhores companhias nas horas de trabalho a fio na frente do computador. Minhas batalhas com o R e com as planilhas intermináveis foram muito mais alegres com

vocês por perto.

Agradeço a Deus, pela coragem para começar e a força para terminar!

Por fim, agradeço a todos que estiveram ao meu lado em algum momento durante o desenvolvimento deste trabalho e que por isso o tornaram possível!

RESUMO GERAL

O Cerrado é formado por fisionomias campestres e savânicas, evoluiu na presença do fogo e depende dele para manter suas fisionomias e biodiversidade. O regime de fogo influencia diretamente na montagem da comunidade vegetal, na regeneração e nas habilidades competitivas das plantas. A frequência é um dos fatores do regime de fogo e alterações nela podem ser prejudiciais até mesmo para plantas e comunidades adaptadas ao fogo. Portanto, este estudo busca compreender os efeitos de diferentes frequências de fogo em comunidades de campo sujo de Cerrado. Para isso, foram realizados levantamentos da vegetação e coleta de biomassa em áreas com diferentes históricos de fogo (excluído do fogo, queimadas anualmente e bienalmente), o que forneceu os dados de composição e produtividade da comunidade. Os levantamentos, incluindo a cobertura (%) por espécie, foram realizados em 10 subparcelas de 1x1m por tratamento (10 subparcelas/tratamento,3 tratamentos, 4 parcelas/tratamento). Avaliamos também através da taxa de propagação (m.s-1), eficiência de queima (%) e intensidade (kW.m-1) entre outros parâmetros do fogo, os efeitos de diferentes frequências no comportamento do fogo. Nossos resultados mostraram que a riqueza de espécies das comunidades vegetais foi maior nas áreas com frequência anual de fogo do que nas excluídas, 6 meses após o fogo e maior para as bienais do que as excluídas 12 meses após o fogo. O índice de diversidade foi maior no tratamento anual de queima antes e 12 meses após as queimas. Quanto ao número de espécies por grupo funcional, apenas as herbáceas apresentaram aumento e apenas nas parcelas com queimas. Além disso, encontramos diferenças na porcentagem de cobertura de acordo com a forma de crescimento, apenas as herbáceas entre os tratamentos de queima e as parcelas de exclusão. Em relação à cobertura, são as porcentagens de biomassa morta e solo nu que variam entre os históricos de fogo. As parcelas com menor frequência de queima apresentaram cerca de 7 vezes mais cobertura de biomassa morta do que os outros tratamentos. Estes resultados sugerem que 6 anos de exclusão de fogo começam a causar perda e mudanças no padrão de cobertura das espécies. Quanto ao comportamento do fogo encontramos para as comunidades com queimas anuais menos biomassa morta e total e porcentagens mais altas de solo nu do que com queimas bienais. Quanto aos parâmetros de queima, a intensidade, altura da chama, temperaturas máximas e tempo de permanência foram menores nas parcelas anuais. Maior frequência de fogo mudou a estrutura da vegetação e os parâmetros de queima responderam a essas mudanças. Concluímos que a frequência da queima influencia o comportamento do fogo, afetando o aumento da biomassa morta. As comunidades vegetais sob queimas anuais não acumularam a mesma quantidade de biomassa morta que as bienais e, portanto, elas têm porcentagens mais altas de solo nu. Essa combinação afeta o comportamento do fogo devido a uma diminuição e descontinuidade da carga de combustível disponível, o que dificulta a sustentação e a propagação do fogo. Assim, buscou-se através deste estudo compreender a influência e importância da frequência do fogo na dinâmica e montagem de comunidades vegetais de Cerrado, bem como no comportamento do fogo. O que deve contribuir com o desenvolvimento de estratégias de manejo de fogo para conservação deste ecossistema.

Palavras-chave: comportamento do fogo; intensidade do fogo; quantidade de material combustível, distribuição do material combustível, composição da comunidade vegetal; regeneração pós-fogo.

ABSTRACT

The Cerrado is formed by grasslands and savannah physiognomies, evolved in the presence of fire and depends on it to maintain its physiognomies and biodiversity. The fire regime influences the plant community assembly, the regeneration and the competitive abilities of the plants. Frequency is one of the factors of the fire regime and changes in it can be detrimental even to fire-adapted plants and communities. Therefore, this study aimed to understand the effects of different fire frequencies in campo sujo of Cerrado communities. For this, vegetation surveys and biomass collection were carried out in areas with different fire histories (excluded from fire, burned annually and biennially), which provided community composition and productivity data. Surveys, including coverage (%) by species, were performed on 10 1x1m subplots per treatment (10 subplots / treatment, 3 treatments, 4 plots / treatment). We also evaluated through propagation rate (m.s-1), firing efficiency (%) and intensity (kW.m-1) among other fire parameters, the effects of different frequencies on fire behavior. Our results showed that species richness of plant communities was higher in areas with annual fire frequency than in excluded areas 6 months after fire and higher for biennials than those excluded 12 months after fire. The diversity index was higher in the annual burn treatment before and 12 months after the burns. Regarding the number of species per functional group, only the forbs presented increase and only in the plots with burns. Moreover, we found differences in the percentage of coverage according to the growth form, only the forbs between the burn treatments and the exclusion fire plots. Regarding the cover, the percentages of dead biomass and bare soil vary among fire histories. The plots with lower burning frequency showed about 7 times more dead biomass coverage than the other treatments. These results suggest that 6 years of fire exclusion begin to cause loss and changes in species cover pattern. Regarding fire behavior, we found for communities with annual burns less dead and total biomass and higher percentages of bare soil than with biennial burns. Regarding the burning parameters, the intensity, flame height, maximum temperatures and residence time were lower in the annual plots. Higher frequency of fire changed vegetation structure and burning parameters responded to these changes. We conclude that the frequency of burning influences fire behavior, affecting the increase of dead biomass. Plant communities under annual burns have not accumulated the same amount of dead biomass as biennial burns, therefore they have higher percentages of bare soil. This combination affects the fire behavior due to a decrease and discontinuity of available fuel load, which makes it difficult to sustain and spread the fire. Thus, we aimed through this study to understand the influence and importance of fire frequency on the dynamics and assembly of Cerrado plant communities, as well as on the behavior of fire. This should contribute to the development of fire management strategies for the conservation of this ecosystem.

Keywords: fire behavior; fire intensity; amount of fuel load, distribution of fuel load, composition of the plant community; post-fire regeneration.

SUMÁRIO

INTRODUÇÃO GERAL

O fogo é um processo ecológico que contribui para moldar as comunidades vegetais, influenciando sua estrutura e função. Além disso, o fogo também atua na distribuição de ecossistemas pelo mundo todo há centenas de milhões de anos (Pausas 2012; Bond e Keeley 2005). Ao longo de milhões de anos, espécies com adaptações morfológicas e fisiológicas foram selecionadas pelo fogo, assim como processos ecológicos que permitem a sobrevivência e regeneração das espécies, o que mantém o regime de fogo (Lamont e He 2016; Christensen 1985).

No Cerrado, o fogo está presente há pelo menos 10 milhões de anos e influenciou a diversificação de espécies savânicas (Simon et al. 2009). O grande aumento da população humana que ocorreu durante o Holoceno, há cerca de 5000 anos alterou o regime de fogo no Cerrado, aumentando sua frequência, extensão e mudando a época de ocorrência (Fiedel ,1992). A mudança do regime do fogo vem causando alterações no Cerrado, tanto sua exclusão (Abreu et al., 2017), como mudanças em propriedades do seu regime (Durigan e Ratter 2016; Pivello 2011).

Alterações na frequência, intensidade e na época de queimadas podem ser prejudiciais até mesmo para plantas e comunidades a elas adaptadas, uma vez que as adaptações encontradas na vegetação são relativas aos regimes de fogo (Whelan 1995). Por exemplo, comunidades que evoluíram em áreas frequentemente queimadas e que, portanto, apresentam dominância do estrato graminóide, com uma fisionomia mais aberta, ao passar por exclusão do fogo apresentarão um aumento da cobertura lenhosa o que acarretará em perda de espécies herbáceas e em drásticas mudanças na fitofisionomia (Moreira 2001; Abreu et al. 2017).

De acordo com Abreu et al. (2017), áreas de Cerrado excluídas do fogo há 30 anos tiveram uma perda de 70% de espécies de plantas (principalmente do estrato herbáceo) e 80% de espécies de formiga endêmicas. Além disso, se durante esse processo de exclusão houver uma fonte de ignição (natural ou antropogênica) podem ocorrer queimas descontroladas devido ao grande acúmulo de biomassa morta (Fidelis et al.

2018). Como consequência poderá ocorrer incêndios de copa, destruição de propágulos, morte de indivíduos e a diminuição da produção de frutos e sementes no período pós-fogo (Pivello e Norton 1996; Pivello 2006).

Por sua vez o aumento da frequência de queimas, pode provocar alterações na composição e estrutura da comunidade e na distribuição do material combustível e estas desencadearem alterações no comportamento do fogo (de Castro e Kauffman 1998). A frequência de queimas, a intensidade, as temperaturas alcançadas e os tempos de residência do fogo são parâmetros do comportamento do fogo determinantes para o recrutamento pós-queima e para o estado nutricional do solo (Malanson e Trabaud, 1988; 2000; Whelan 1995) e por isso afetam a manutenção dos padrões de composição e estrutura das comunidades bem como sua produtividade (Vale e Lopes 2011; Higgins et al. 2000; Whelan 1995).

Gill (1975) descreveu a frequência de fogo como uma função do número de incêndios experimentados por uma determinada comunidade dentro de um determinado período de tempo. Compreender como os intervalos entre os incêndios e tempo desde o último incêndio afetam a composição e a produtividade da comunidade permite traçar estratégias de manejo de fogo que mantenham na comunidade a presença de uma grande variedade de plantas, inclusive aquelas vulneráveis a queimadas (Morrinson et al. 1995).

A frequência do fogo é uma importante ferramenta no manejo dos diferentes ecossistemas inflamáveis do mundo. Na região da Planície de Areia de Anoka, Minnesota (EUA), um ecossistema temperado com elevada cobertura de carvalhos por exemplo, a alta frequência de queimadas se mostrou positiva para a restauração e manutenção de savanas. A queima frequente (pelo menos três incêndios a cada dez anos) impediu o desenvolvimento de uma camada de plântulas e do crescimento do dossel de carvalhos, provocando ainda reduções significativas na densidade excessiva e área basal (Peterson e Reich, 2001). A partir deste estudo, Peterson e Reich (2001) sugeriram queimas frequentes objetivando a supressão de arbustos e a promoção de uma maior cobertura de gramíneas e outras espécies herbáceas a fim de preservar as savanas na região.

Todos os anos, grandes proporções de paisagens de savana tropical australiana são queimadas. Trata-se de fogo prescrito utilizado no manejo de fogo contra incêndios de alta intensidade (Andersen et al. 2005). Neste âmbito, a fim de analisar os efeitos da alta frequência de fogo sobre a biodiversidade das savanas australianas, Andersen e colaboradores (2005) realizaram um estudo em Kapalga, no Parque Nacional de Kakadu (Território Norte) e verificaram que grande parte da biota de savana é extremamente resistente ao fogo, ainda que de alta intensidade. A abundância da maioria dos grupos de invertebrados e vertebrados não sofreu alteração. E não foi detectado nenhum efeito do fogo na composição florística do estrato graminóide.

Por outro lado, queimas muito recorrentes também podem ser prejudiciais, levando a alterações no solo e também podem impedir que algumas espécies tenham tempo hábil para se regenerar e estabelecer, o que leva à diminuição da riqueza e abundância da comunidade (Pivello 2011). Russel-Smith et al. (1998) em seu estudo para avaliar os efeitos dos regimes de fogo na vegetação do Arnhem Plateau, norte da Austrália, demonstraram que áreas queimadas com uma alta frequência (pelo menos a cada 1 - 3 anos) teriam perdas substanciais de espécies germinadoras, compreendendo 54% da flora de arbustos amostrada e solos com menor fertilidade que as áreas há mais tempo sem fogo.

Portanto, a importância de conhecer e considerar as estratégias, das espécies que compõem a comunidade frente aos diferentes regimes de fogo, no caso, de diferentes frequências, são fundamentais ao desenvolver um plano de manejo de fogo para uma região. As espécies vulneráveis a queimadas frequentes, em geral não são capazes de rebrotar após a queima, dependem da germinação para manter sua população. Assim um segundo fogo dentro do período juvenil poderia eliminar essas espécies, levando a uma perda de diversidade local (Watson e Wardell-Johnson 2004).

O Cerrado é muito rico em espécies, com alta taxa de endemismo, sendo considerado um *hotspot* de biodiversidade (Myers et al. 2000). A vegetação do Cerrado não é composta por uma fisionomia única e uniforme, mas sim por um mosaico formado por formações campestres (campo limpo), savânicas (campo sujo, campo cerrado e cerrado sensu stricto) e florestal (cerradão). Tamanha diversidade de fisionomias bem como sua distribuição está relacionada, entre outros fatores, com a frequência do fogo (Coutinho 1978). O cerradão, por exemplo, com predomínio de espécies arbóreas e ausência de estrato graminóide (material combustível) não é uma fisionomia susceptível ao fogo, enquanto a frequência de fogo é maior em fisionomias campestres e savânicas (Ratter 1992). Portanto, a manutenção das fisionomias de Cerrado pode estar relacionada com o regime de fogo, principalmente a sua frequência. Desta maneira, faz-se necessário compreender a influência dos fatores do regime de queimas, mais especificamente da frequência do fogo na vegetação, a fim de desenvolver estratégias de manejo que preservem a variedade de fisionomias e a biodiversidade do Cerrado.

No presente estudo, investigamos como diferentes frequências de fogo influenciam a regeneração pós-fogo de comunidades de plantas de campo sujo, afim de ampliar a compreensão acerca da resiliência ao fogo de comunidades que compõem as fisionomias abertas de savana. Buscamos entender como os diferentes grupos funcionais, cujas espécies evoluíram sob um regime de fogo, respondem a frequências muito elevadas de queimas e a exclusão do fogo da comunidade.

Avaliamos também se a frequência de queimas modifica o comportamento do fogo, alterando fatores como a intensidade e a temperatura das chamas os quais podem ser determinantes para as dinâmicas de regeneração da comunidade.

Para isso, buscou-se responder as seguintes perguntas: 1- O comportamento do fogo difere entre áreas com queimadas anuais e bienais? 2 – A riqueza, diversidade e composição de espécies das comunidade vegetais é afetada pela frequência de fogo? 3 – A frequência de fogo altera o incremento e composição da biomassa da comunidade?

Estruturação da dissertação

A dissertação foi dividida em dois capítulos que foram redigidos já em formato de artigo científico, em língua inglesa e de acordo com a formatação da revista cientifica a serem submetidos.

Capítulo I – "Fire frequency affects fire behavior in open savannas in the Cerrado". Neste capítulo, analisamos como queimas anuais e bienais afetam diferentemente a quantidade, distribuição e qualidade do material combustível da comunidade vegetal e como isto influencia os parâmetros do comportamento do fogo, como intensidade, altura das chamas, taxa de propagação, temperaturas alcançadas e tempos de residência das altas temperaturas. Trabalhamos com a hipótese inicial de nas parcelas com queimas bienais haverá um acúmulo maior de material combustível o que levará a chamas mais altas, uma maior velocidade de propagação do fogo, temperaturas mais altas e um fogo mais intenso em comparação com áreas com queimadas anuais. Este capítulo será submetido ao *Journal of Environmental Management.*

Capítulo II – "How many times can we burn the Cerrado? A fire experiment in open savannas". Neste Segundo capítulo, abordamos a influência da frequência de queima na riqueza de espécies, diversidade e na cobertura dos grupos funcionais das comunidades. Investigamos também os efeitos das queimas anuais e bienais na produção de biomassa vegetal total e por grupos funcionais, bem como o incremento de biomassa morta e serapilheira na comunidade, comparando com as áreas não queimadas. Avaliamos também se as diferentes frequências de queimas influenciaram na contribuição dos grupos funcionais na composição da biomassa viva total. Tivemos como hipótese que: 1) parcelas com queimas anuais apresentam uma menor cobertura vegetal, assim como menor riqueza, em comparação com parcelas com queimadas bienais. Porém, a riqueza é maior do que a encontrada em parcelas exclusão (excluídas do fogo há 7 anos); 2) as parcelas exclusão apresentam maior cobertura de biomassa morta, enquanto que as parcelas com queimadas anuais e bienais terão maior cobertura de graminóides e herbáceas; 3) as áreas que queimam anualmente tem menor produtividade que as com queimas bienais e exclusão; 4) os componentes funcionais serão diferentes nas áreas com distintos regimes de queima: as parcelas exclusão terão um maior acúmulo de biomassa morta em comparação com as parcelas queimadas (tanto anuais como bienais). Este capítulo será submetido ao *Journal of Ecology.*

Ao final desta dissertação são apresentadas as considerações finais, sobre como a frequência de queimas pode afetar o comportamento do fogo e os padrões das comunidades vegetais de campo sujo. Além disso, discutimos as possíveis contribuições dos resultados deste trabalho para o uso do fogo como ferramenta de manejo nas fisionomias abertas do Cerrado.

Delineamento experimental

O presente estudo foi conduzido na Reserva Natural da Serra do Tombador (RNST, 13° 35-38’ S e 47° 45’- 51’ W, 560 - 1118m) no município de Cavalcante, Goiás. Trata-se de uma RPPN de Cerrado, com uma área total de 8900 ha. O clima é tropical, com estação seca de inverno, com precipitação anual média entre 1300-1500 mm e temperaturas médias máximas entre 26 e 36°C e mínimas entre 8 e 14°C (AER 2009) (Figura 1a).

Diferentes fisionomias de Cerrado compõem a vegetação da RNST, como campo limpo, campo sujo, cerrado rupestre, cerrado *sensu stricto*, veredas, além de florestas de vale (AER 2009). Para este estudo trabalhamos em áreas de campo sujo. O campo sujo é uma fisionomia de Cerrado composta por um substrato herbáceo-arbustivo, sendo esparsa a distribuição de arbustos e espécies arbóreas (Ribeiro & Walter,1998), e portanto, com material combustível fino contínuo e frequência de fogo de 1-3 anos (Eiten, 1972, Figura 1b).

O principal componente do estrato herbáceo é o grupo de gramíneas C4, composto principalmente por *Oncorachis ramosa, Axonopus aureus, Elionurus muticus, Aristida setifolia, Mesosetum lolliforme, Mesosetum ferrugineum e Paspalum pectinatum* (Rodrigues *et al.,* em preparação).

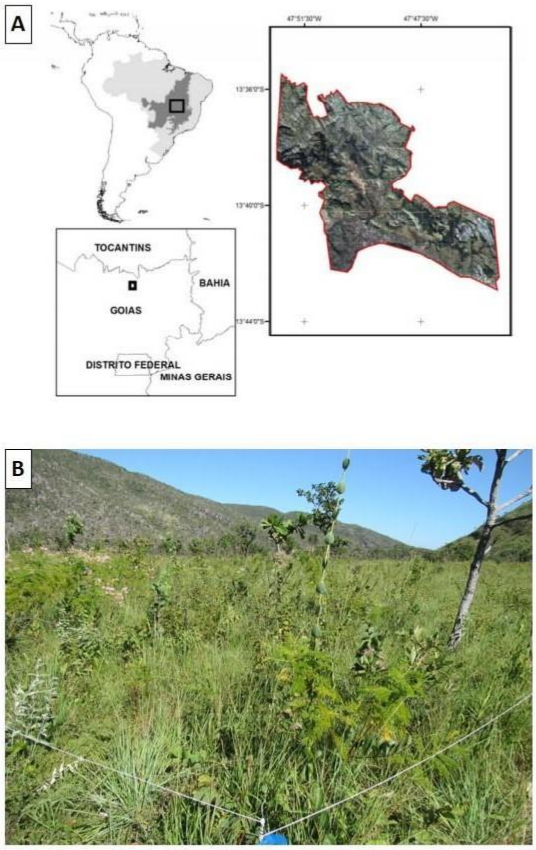

Figura 1. A) Localização da Reserva Nacional Serra do Tombador, no Estado de Goiás. Retirado de Gorgone-Barbosa (2016). B) Fisionomias de campo sujo da área experimental na Reserva Natural Serra do Tombador, Cavalcante, Goiás

Trabalhamos em parcelas de 30x30m, do experimento estabelecido na área e com tratamentos com queimas em andamentos desde 2013 (Figura 2). Tais experimentos fazem parte do projeto coordenado pela Profa. Dra. Alessandra Fidelis, intitulado: Como a época da queima afeta a vegetação do Cerrado?, financiado pela FAPESP (JP 2015/067430). Para maiores detalhes do delineamento de todo experimento, ver Rissi et al. (2017).

Os tratamentos de queima utilizados para este estudo foram: anuais (4 parcelas, queimadas 5 vezes entre 2013 e 2017), bienais (4 parcelas, queimadas 3 vezes no mesmo período) e exclusão (2 parcelas, excluídas do fogo há 6 anos). Apenas duas parcelas de exclusão foram utilizadas em razão das outras duas terem queimado acidentalmente em 2014 e 2017.

Figura 2. Área experimental na Reserva Natural Serra do Tombador, Cavalcante, Goiás. (A) São as parcelas com queimas anuais; (B) são as com queimas bienais e (E) são as excluídas do fogo há 6 anos

Em cada parcela experimental foram estabelecidas aleatoriamente 10 subparcelas permanentes de 1x1m, sorteadas em um grid, para levantamento da cobertura das espécies, da biomassa morta e de solo descoberto, seguindo alguns critérios: ausência de formigueiro, cupinzeiro e de grandes árvores (Figura 3).

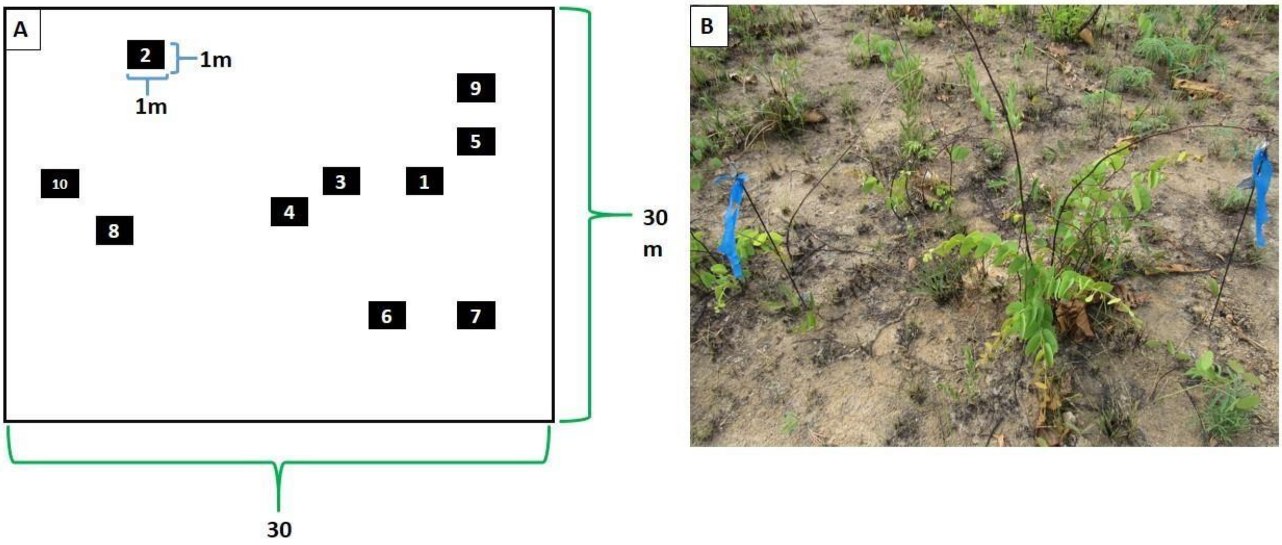

Figura 3. A) Esquema da parcela de 30x30m com as dez subparcelas fixas de 1x1m; B) Exemplo de subparcela de 1x1m, utilizada para os levantamentos da vegetação.

Ao redor de todas as parcelas foram realizados aceiros de 3 metros para evitar a propagação do fogo para outras áreas durante os experimentos.

As queimas experimentais descritos no capítulo 1, ocorreram em julho de 2017, no meio da estação seca e foram realizadas separadamente para evitar a pseudoréplica. O fogo foi colocado sempre na direção do vento e os fatores ambientais temperatura (ºC) e velocidade do vento ($m.s^{-1}$), foram monitorados antes, durante e logo após os experimentos com o auxílio de um anemômetro de digital (Figura 4).

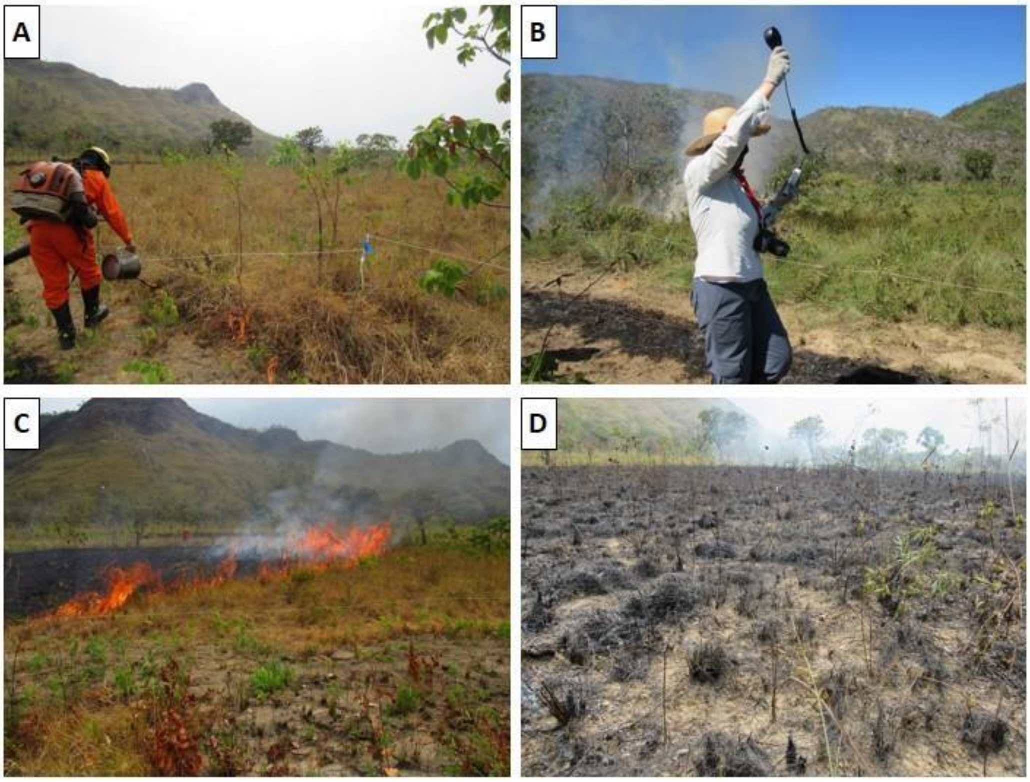

Figura 4. A) Colocação da linha de fogo, a favor do vento; B) coleta de dados ambientais; C) frente de fogo na parcela e D) parcela após o experimento de fogo.

Os levantamentos da comunidade vegetal e as coletas de biomassa ocorreram imediatamente antes das queimas, novamente após 6 meses, durante a estação chuvosa e uma última amostragem foi realizada após 1 ano das queimas, na estação seca. Cada capítulo traz descrito em detalhes seus respectivos material e métodos.

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Fire frequency affects fire behavior in open savannas in the Cerrado

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Abstract

Fire is an ecological process that helps shape plant communities, influencing their structure and function. Frequency is an important aspect of the fire regime. In tropical savannas, fire frequency is high due to the high production and accumulation of fuel load, which is composed mainly of grasses, a dominant group in open physiognomies such as the *campo sujo* of the Cerrado. We evaluated how the quantity, quality and horizontal and vertical distribution of fuel load influence fire behavior. We performed fire experiments with different fire frequencies (annual and biennial, since 2013) in open savannas in the Cerrado (Central Brazil). Before each experimental fire, we sampled the quantity and distribution of the fuel load, as well as their moisture content, and estimated the percentage of bare soil, dead biomass and grass cover in the community. During the experiments, we measured environmental data and fire behavior parameters, such as flame height, fire propagation rate, flame temperature and residence time of fire; finally, we calculated fire intensity. Areas with annual fires showed less dead and total biomass and higher percentages of bare soil. Regarding the fire parameters, the intensity, flame height, maximum temperatures and residence time were lower in the annual plots. Higher fire frequency changed vegetation structure, and the fire parameters responded to these changes. We conclude that fire frequency influences fire behavior mostly by affecting the amount of dead biomass, which will be the main fuel load for the next fire. Plant communities under annual fires did not accumulate the same amount of dead biomass as biennials, and, therefore, they have higher percentages of bare soil. This combination affected fire behavior through a decrease and discontinuity of available fuel load, resulting in fires that could not be sustained and propagated in the same way, which in turn affected the plant community.

Keywords: fire intensity; fuel load quantity; fuel load distribution; plant community structure; residence time of fire; fire temperatures.

Introduction

Fire is an ecological process that shapes plant communities, affecting their structure and function, and influences the distribution of ecosystems around the world

(Bond & Keeley, 2005). Over millions of years, species with morphological and physiological adaptations have been selected by fire and by ecological processes that allow species' survival and regeneration (Lamont & He 2017, Christensen, 1985). The adaptations found in vegetation are related to fire regimes; therefore, changes in parameters of fire regime and fire behavior can negatively affect plant communities (Whelan, 1995).

A fire regime is characterized by season, intensity, type, extent and frequency (Gill, 1975; Whelan, 1995). Fire frequency is the number of fires experienced by a community within a given period (Gill, 1975). For example, tropical savannas have a high fire frequency, with a fire return of 1 to 5 years (Hoffmann et al., 2012; Trollope et al., 1982). This is because these ecosystems have a high production of fuel load, with a continuous distribution that accumulates rapidly during the rainy season and dries out in the prolonged and well-marked dry season (Govender et al., 2006). Also, sources of ignition are abundant, which can be either natural (lightning) or anthropogenic (Ramos-Neto & Pivello, 2000; Pivello & Coutinho, 1996).

High fire frequency in grassland and savanna ecosystems can act beneficially to maintain open physiognomies (Whelan, 1995). However, recurrent fires can also be harmful, leading to changes in the soil properties, preventing some species from having time to regenerate and establish, and causing a decrease in community richness, abundance, and productivity (Pivello, 2011). Furthermore, frequent fires can deplete the amount of reserves stored in the roots (Miyanishi & Kellman, 1986) and other underground storage organs, which can affect resprouting vigor (Paula & Ojeda, 2006). Consequently, a higher percentage of bare soil may also affect the fire regime (Conceição & Pivello, 2011) by changing fire intensity, flame height, maximum temperatures, residence time, severity and extent of fire (Kauffman et al., 1994; Christensen, 1985).

On the other hand, changes in fire frequency can also cause changes in the composition and structure of the community and the distribution of fuel load, which triggers changes in fire behavior (de Castro & Kauffman, 1998). Fire frequency, intensity, temperatures and residence times are determinant factors of post-fire recruitment and soil nutrients (Malanson & Trabaud, 1988; 2000; Whelan, 1995). Fire temperatures and residence time influence tissue, propagules and plant survival directly (Bova & Dickinson, 2005; Bilbao et al., 2006; Cirne & Miranda, 2008; Coutinho, 1990) and, thus, affect plant persistence. Therefore, these factors play an important role in maintaining community composition, structure and productivity (Vale & Lopes, 2011; Higgins et al., 2000; Whelan, 1995).

However, fire regimes in fire-prone ecosystems around the world have undergone significant modifications caused by human activities. In the Cerrado, for example, anthropogenic fires as a result from agricultural practices are frequent and are generally performed in the dry season (Pivello, 2011). Such changes in fire frequency and season influence the amount of fuel load, the structure and distribution of plant communities, combustion efficiency, and the fuel load’s moisture content (de Castro & Kauffman, 1998). These are important properties that affect the system’s flammability, altering fire behavior in the tropical savanna (Bond & van Wilgen, 1996; Pausas et al., 2016; Rissi et al., 2017).

In open savannas in the Cerrado, the continuous herbaceous layer and the dominance of grass species beget a high fire frequency, with a fire return interval of 1–3 years (Eiten, 1972). They are surface fires, with high combustion rates, essentially consuming all the fine fuel load of the herbaceous stratum. Most herbaceous species are fire-resistant and resprout a few days after fire (Miranda et al., 2009). Therefore, two years after fire, the dead biomass already represents 30% to 60% of the total fuel load, suggesting that, given a source of ignition, a fire can occur and spread in the area (Fidelis et al., 2013; Rissi et al., 2017; Miranda et al., 2009).

Therefore, due to the importance of fire behavior in maintaining the structure, composition, and ecological processes of plant communities in tropical grasslands and savannas, this study aimed to analyze fire behavior of different frequencies (annual x biennial) in open savannas in the Cerrado. Thus, we hypothesized that fire behavior will be distinct between the different frequencies because of vegetation modifications related to the amount and distribution of fuel load. Therefore, in the biennially burned plots, a higher amount of fuel load, a lower percentage of bare soil and a higher percentage of dead biomass will lead to higher flames, higher rate of spread, higher temperatures, and longer residence time of fire at higher intensity and temperatures compared to areas with annual fires. Finally, we evaluated fire parameters at each frequency and sought to understand which ones most influence fire behavior.

Material and methods

Study area

The study was conducted at Serra do Tombador Nature Reserve (RNST, 13° 3538' S and 47° 4551' W, 8900 ha, 560–1118 m a.s.l., Central Brazil). The climate is tropical, with a dry winter season, average annual rainfall of 1300–1500 mm, maximum average temperatures between 26 and 36 °C and minimum temperatures between 8 and 14 °C (AER, 2009).

At the RNST, different physiognomies of Cerrado can be found, from grasslands (e.g. *campo limpo*) to savannas (e.g. *campo sujo*) and forests (AER, 2009). For this study, we established our experimental fire plots in open savannas (*campo sujo*). The *campo sujo* is composed of a dominant herbaceous layer (mostly C4 grasses and forbs), with scattered shrubs and small trees (Ribeiro & Walter, 1998). The fuel bed is continuous and fire frequency is every 1–3 years. (Eiten, 1972).

The main component of the herbaceous stratum is the C4 grass group, mainly composed of *Oncorachis ramosa, Axonopus aureus, Elionurus muticus, Aristida setifolia, Mesosetum ferrugineum* and *Paspalum pectinatum* (Rodrigues and Fidelis, unpublished).

Experimental design

We used 30 x 30-m plots established in *campo sujo* areas since 2013, when we initiated the fire experiments (for more details on the methods, see Rissi et al. 2017). We used the following fire frequencies: annual (four plots burned in July 2013, 2014, 2015, 2016) and biennial (four plots burned in July 2013, 2015). The results of this study refer to the fire experiments carried out in 2017. We established firebreaks (3 m) around each experimental plot to prevent fire from escaping during experiments.

In each experimental plot, 10 permanent 1 x 1-m subplots were randomly established in grid, where we visually estimated the cover (%) of dead biomass, graminoids and bare soil cover to evaluate the type and continuity of fuel load.

Before fire, we sampled biomass (0.5 x 0.5 m, five samples/plot) randomly at the edges of each plot, put it in paper bags and weighed it in the field to determine the fresh weight. In the laboratory, biomass was sorted into dead, graminoid, forbs, shrub and litter (collected separately in the field). The samples were then dried in an oven at 80 ºC for 48 hours and were subsequently weighed again to determine the amount and type of fuel load ($kg.m^{-2}$) and its moisture content (%).

Each of the experimental fires were performed separately, to avoid pseudoreplication, and were set in the wind direction (head fires). Environmental factors, such as temperature (ºC) and wind speed ($m.s^{-1}$), were monitored before, during and after the experiments using a digital anemometer.

To measure the fires' temperature and residence time, temperature sensors (thermocouples type K) were distributed across 14 points (10 corresponding to subplots and 4 randomly allocated) within each plot, at two heights: on the soil surface and at 50 cm from soil surface, where most of the fuel load is accumulated. The thermocouples were coupled with data loggers, which measured temperatures every 2 seconds Variables such as fire propagation rate ($m.s^{-1}$), flame height (cm) and residence time of fire (s) were measured. After fire, five samples of residual biomass (0.5 x 0.5 m) were randomly collected at the edges of each plot, placed in paper bags and then oven-dried and weighed. We then calculated burn efficiency (%) and fire intensity (Byram's fireline, $kW.m^{-1}$).

To calculate fire rate of spread ($m.s^{-1}$), we established three observation points (10, 20 and 30 m) along the side of each plot and measured the time that fire took to reach each point. At the same observation points, we visually estimated flame height (cm). We calculated fire intensity through Byram's equation (1959).

Statistical analysis

Fire variables (fire intensity, the temperature at different heights, flame height, propagation rate, amount of fuel load, percentage of bare soil and coverage of dead fuel load, as well as environmental variables) were compared between the different fire frequencies. Differences were tested using generalized linear models (GLM) with Gamma distribution. To analyze which parameters would influence fire intensity and temperature, we performed model selection (Akaike, 1987).

To compare the variation of fire temperature over time between annual and biennial burning, we use a generalized additive model (GAM).

The analyses were performed using the R software and packages stats (R Development Core Team, 2018), graphics (R Development Core Team, 2018), nlme (Pinheiro et al., 2015) and lme4 (Bates et al., 2015).

Results

Environmental conditions during fire experiments were similar between treatments. The air temperature ranged from 25.6 to 32.2 °C, and the wind speed varied from 0.97 to 2.84 $m.s^{-1}$ (Table 1, $p > 0.05$).

Fire frequency	Wind speed ($m.s^{-1}$)	Air Temperature (°C)
Annual	2.05±0.37	28.25±0.90
Biennial	1.98±0.37	27.87±1.47

Table 1: Wind speed ($m.s^{-1}$) and air temperature (ºC, mean ± standard error) during the annual and biennial burning experiments in a *campo sujo* area, Central Brazil

Total fuel load in biennial plots was 72% higher than in plots burned annually (Figure 1, $p < 0.001$), and the dead fuel load was 118% higher in the areas of biennial fires (Figure 1, $p < 0.0001$). Fuel moisture content was not significantly different between fire treatments ($p = 0.09$), ranging from 33.6 ± 5.4% in biennial plots to 39.7 ± 1.9% in annual plots.

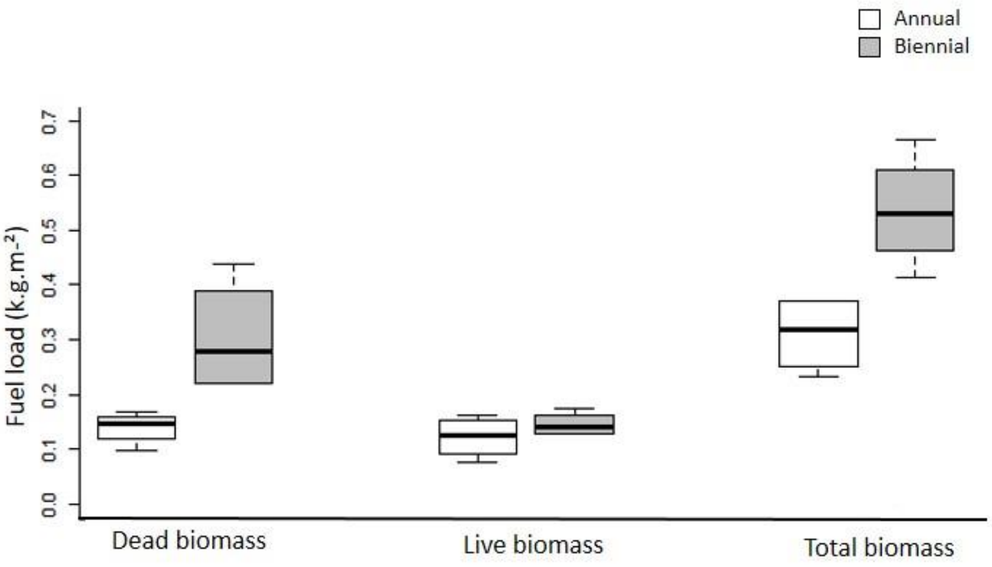

Figure 1: Dead biomass, live biomass and total biomass (kg.m-²) in plots with annual and biennial fires in open savannas (campo sujo) in Central Brazil

Bare soil cover was 3 times higher (p <0.0001) in the annual fire plots. The cover of dead biomass was 2 times higher (p <0.0001) in biennial fire plots. Grass cover was the same in both areas (p = 0.1).

Flame height in the plots burned annually were 2 times lower compared to the biennial treatment. Burn efficiency and rate of spread were the same in both treatments. However, fire intensity of the biennial fires was 2-fold higher than that of annual fires (Table 2).

Fire frequency	Annual	Biennial	p
Fire intensity ($kW.m^{-1}$)	669.3 ± 241.6	1850.2 ± 192.5	0.04*
Flame height (m)	1.3 ± 0.2	2.3 ± 0.3	0.01*
Fire rate of spread (m,s^{-1})	0.15 ± 0.05	0.25 ± 0.05	0.34
Burn efficiency (%)	87 ± 12.4	95 ± 3.34	0.28

Table 2: Fire behavior parameters (mean ± standard error) annual and biennial fire treatments in open savannas (campo sujo), Central Brazil

Fire intensity was best explained by the amount of dead biomass and moisture content of fuel load, representing 45% of Akaike weights (ΔAICc = 0.0, wAICc = 0.45) and by dead fuel and grass fuel, representing 20% of Akaike weights (ΔAICc = 1.6, wAICc = 0.20, table 3).

Models	ΔAICc	wAICc
Dead fuel + fuel moisture content	**0.0**	**0.45**
Dead fuel + grass fuel	1.6	0.20
Total fuel load + fuel moisture content	2.1	0.15
Total fuel load	2.8	0.11
Dead fuel	3.8	0.06
Null	6.7	0.01

Table3: Results of model selection of fire intensity in open savannas (campo sujo) in Central Brazil, using Gamma distribution. ΔAICc: difference in AICc units between the model and the most parsimonious model of the candidate set (lowest AICc value; the most parsimonious model is shown in bold). wAICc: Akaike weight, indicates the relative probability of a given model being the best model of those compared to the observed data

Maximum temperatures on the soil surface and at 50 cm were both higher in plots burned biennially. The maximum recorded surface temperature was 548 °C for biennial fire treatments and 391°C for annual fire treatments. At 50 cm above soil surface, the maximum recorded temperatures were 511 °C and 457 °C for biennial and annual fire treatments, respectively. Residence time of fire at soil surface differed between fire frequencies and was consistently higher in plots with biennial fires. However, residence time of fire was never higher than 250 s (> 60 ºC, at soil surface) and 150 s (> 100 ºC, soil surface, Table 4).

Treatment	Maximum temperature (ºC)		Residence time (s)			
			> 60°C		> 100°C	
	0 cm	50 cm	0 cm	50 cm	0cm	50 cm
Annual	374.5 ± 10.7	328.5 ± 43.6	166 ± 13.7	94.2 ± 1.6	86.5 ± 14.1	49. 2 ± 9
Biennial	497 ± 23.3	470 ± 16.9	250.2 ± 10.6	116.5 ± 8.5	146.2 ± 10.4	72.5 ± 5.7
p	0.01	0.001	0.001	0.1	0.0001	0.01

Table 4: Maximum temperatures (° C); residence time of fire (s) of temperatures ≥ 60ºC and ≥ 100ºC at soil surface (0 cm) and 50 cm above soil surface (mean ± standard error) measured during experimental fires in annually and biennially burned plots in open savannas (campo sujo), Central Brazil

We also found that the temperatures recorded during the burns varied over time differently in each treatment, both on the soil surface ($p < 0.0001$) and at 50 cm above the soil surface ($p < 0.001$) (Fig S1 and S2). Variations in recorded soil surface temperatures responded to the percentage of bare soil: as the percentage of bare soil increased, the maximum temperatures and residence times of temperatures ≥ 60 °C and ≥ 100 °C decreased (Figure 2). In addition to the influence of the percentage of bare soil, we found at 50cm above the soil surface a relationship with the percentage of dead fuel: a higher percentage of dead fuel coverage increased the maximum temperatures and the residence times of temperatures ≥ 60 °C and ≥ 100 ºC (Figure 3). The percentage of grass cover was not related to temperature data.

These relationships become clearer when we analyze the results of the model selections made to explain maximum temperature variations and temperature residence times (Table S1). On the soil surface, the percentage of bare soil explained 63% of variations in maximum temperature and 49% of variations in residence time of temperatures ≥ 100 ºC. At 50 cm from the soil surface, the combination of the percentage of bare soil and dead fuel cover was the best model to explain variations in these parameters, explaining 60% of variations in maximum temperature and 44% of variations in residence time of temperatures ≥ 100 ºC.

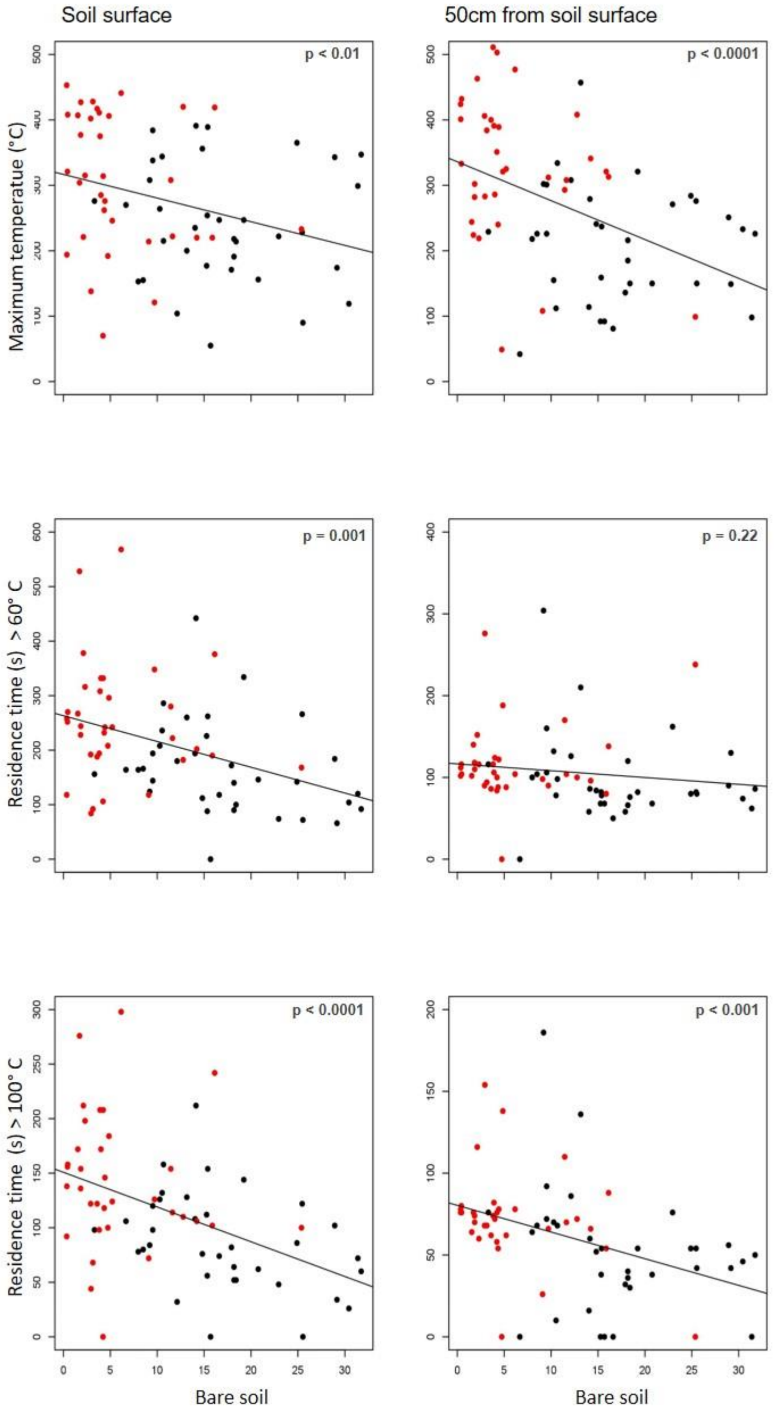

Figure 2: Relationship between bare soil cover and maximum temperature, residence time of fire >60ºC and >100ºC during fire experiments in annually (black dots) and biennially fires (red dots) at soil surface and at 50cm above soil surface in open savannas (campo sujo), Central Brazil

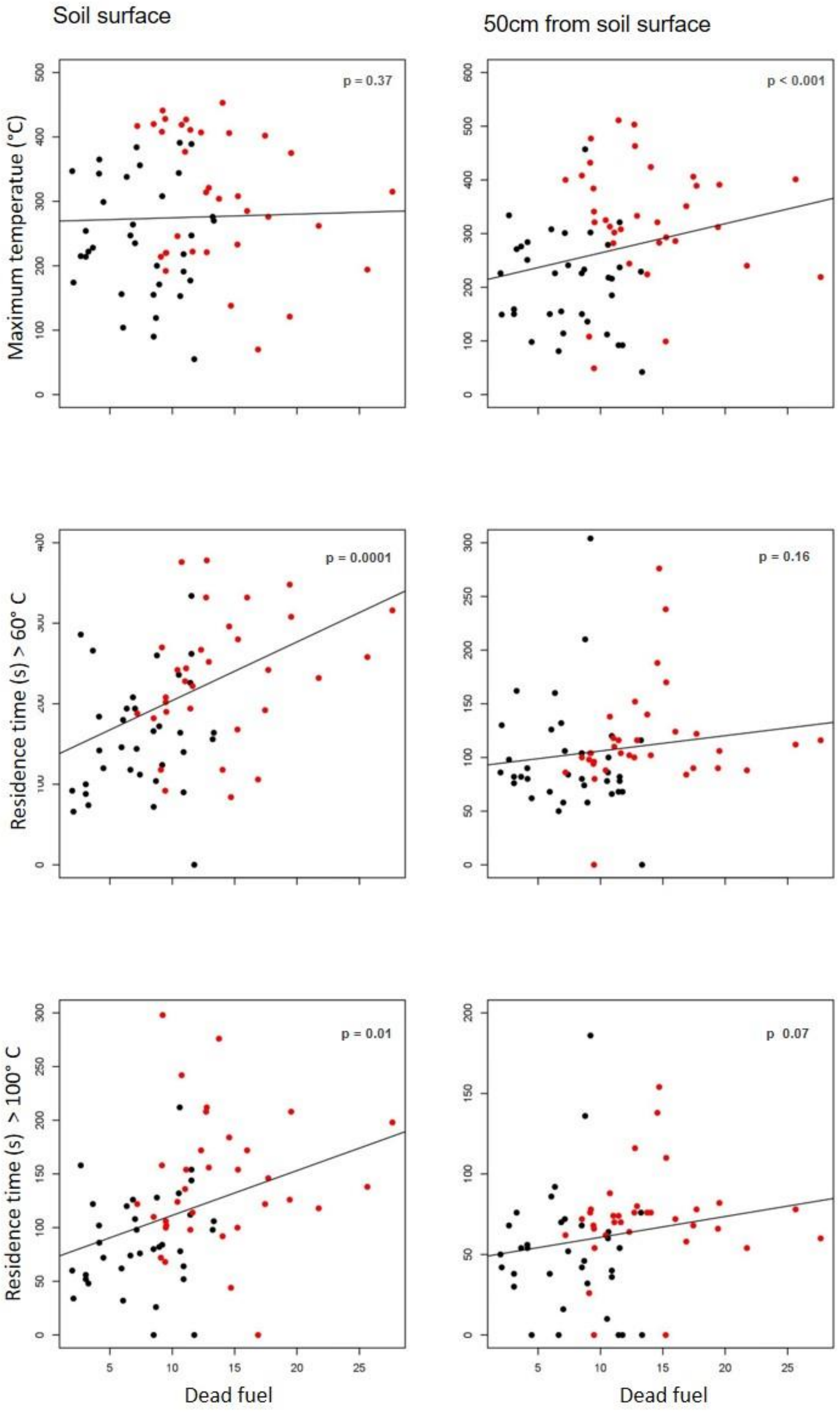

Figure 3: Relationship between dead fuel cover and maximum temperature, residence time of fire >60ºC and >100ºC during fire experiments in annually (black dots) and biennially fires (red dots) at soil surface and at 50cm above soil surface in open savannas (campo sujo), Central Brazil

Discussion

Different fire frequencies altered important fire behavior characteristics such as intensity, flame height, maximum temperature and residence time of fire. These characteristics responded to variations in the amount and moisture content of the available fuel load, and to its distribution. We observed that the highest fire frequency caused a reduction in biomass increment and an increase of bare soil cover. This is possibly explained by the fact that most of the biomass accumulation in open physiognomies occurs in the first two to three years after fire (Govender et al., 2006); thus, when areas are burned every year, there is not enough time between fires for fuel load recovery.

Although the plant community in annually burned plots accumulated enough fuel load to burn again just one year after fire, the accumulation of fuel load in biennially burned plots was 118% greater, resulting in altered fire behavior parameters. This substantial increase in the amount of biomass (mostly dead biomass) in such a short period was also recorded in the South African savannas of Kruger Park, where biennially burned plots accumulated 34% more fuel load than annually burned areas (Govender et al. 2006). Finally, when areas that typically burn annually do not burn for 2–4 years, there is a 100% increase in fuel load, as observed in Kapalga (Northern Australia, Williams et al. 1998; Cook 1994; Cook et al. 1995).

Dead biomass increases fire intensity and flame height but also improves fire sustainability, since increased accumulation of fuel load lengthens the time it takes to consume all that biomass (Simpson et al., 2016). Consequently, temperatures and residence time of fire are greater, interfering in the vertical distribution of flame temperatures, which could lead to the tissue death and, thus, woody vegetation mortality (Kauffman et al., 1994).

Continuity in the distribution of biomass also affects the maximum temperatures reached and the residence time of high temperatures. We showed in this study that bare soil cover influences fire behavior parameters, such as maximum temperatures and residence time of temperatures ≥ 60 °C and ≥ 100 °C. These variables are important for vegetation regeneration, since fire temperature and exposure duration may influence seed germination and survival in fire-prone ecosystems (Moreira & Pausas, 2012; Ooi et al., 2014, Auld & O'Connell, 1991; Herranz et al., 1998; Williams et al., 2003).

Annually burned areas developed a discontinuous fuel bed distribution, unlike biennially burned areas. High fire frequency increased the extent of bare soil, thus interfering in the spread and sustainability of flames, which presented lower temperatures and residence times on the soil surface. As shown by Daibes et al. (2018), fire temperature is highly dependent on the percentage of bare soil, which can directly affect seed survival in savanna areas. Gaps with higher percentages of bare soil had lower maximum temperatures, shorter residence times at temperatures ≥ 60 °C and ≥ 100 °C and, therefore, lower seed mortality. On the other hand, dead biomass cover was the major factor influencing fire temperature parameters at 50 cm above soil surface. Greater dead biomass cover resulted in higher maximum temperatures and longer residence times of fire. Therefore, the different vegetation components and structures influenced fire both horizontally and vertically, demonstrating that fire burns heterogeneously in open savannas. Consequently, the vertical distribution of temperatures affects the distinct savanna layers differently.

Nevertheless, we observed that the maximum temperatures and highest residence times occurred on the soil surface, possibly because grasses are the major component of these plant communities and are responsible for the high flammability of the system. Grasses can accumulate large amounts of biomass, and they have a continuous arrangement and an architecture that result in traits of high flammability (Simpson et al., 2016; Lehman et al. 2019; Zanzarini et al. unpublished). Also, the largest proportion of biomass accumulates at the base of the tussock, which remains attached to the plant even after the dry season (Govender et al., 2006), increasing the amount of dead fuel load.

In summary, this study showed that the major variable affecting fire behavior in open savannas is the accumulation of dead biomass. Although communities with different fire frequencies have similar productivity (Rodrigues and Fidelis, unpublished), areas under annual fires cannot accumulate the same amount of dead biomass as areas burned every two years, for example, because there is not enough time to accumulate sufficient biomass. Moreover, after a long period of being burned every year, vegetation cannot regenerate as fast and vigorously as before (especially grasses, Rodrigues and Fidelis, unpublished data); consequently, the percentage of bare soil within the fuel bed is higher than in areas with lower fire frequency. With time, the combination of a lower amount of dead biomass and a higher percentage of bare soil limits the sustainability and spread of fire, resulting in less intense fires, lower flames, lower temperatures and shorter residence times.

Acknowledgments

The authors thank the staff of the Reserva Natural Serra do Tombador: Anderson F. Terra, Whatson F. Rezende, Gilson de A. Berberino, Silvanio A. Borges, and Rogério B. de Almeida for their support during fire experiments. We also thank Aline Martins, Mariana Dairel, Natacha Silva, Rafael Consolmagno and Vagner Zanzarini for helping during the field work. C.R received financial support from Fundação de Amparo à Pesquisa do Estado de São Paulo (2017/22618-7) and from CAPES/DS (1735266), H.Z. received financial support from Fundação de Amparo à Pesquisa do Estado de São Paulo (2017/16149-4) and from CNPq (130344/2017-6), A.F. receives grant from (CNPq 303988/2018-5). This study was supported by FAPESP (2015/06743-0) and Fundação Grupo o Boticário de Proteção à Natureza (0153_2011_PR).

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Supplementary information

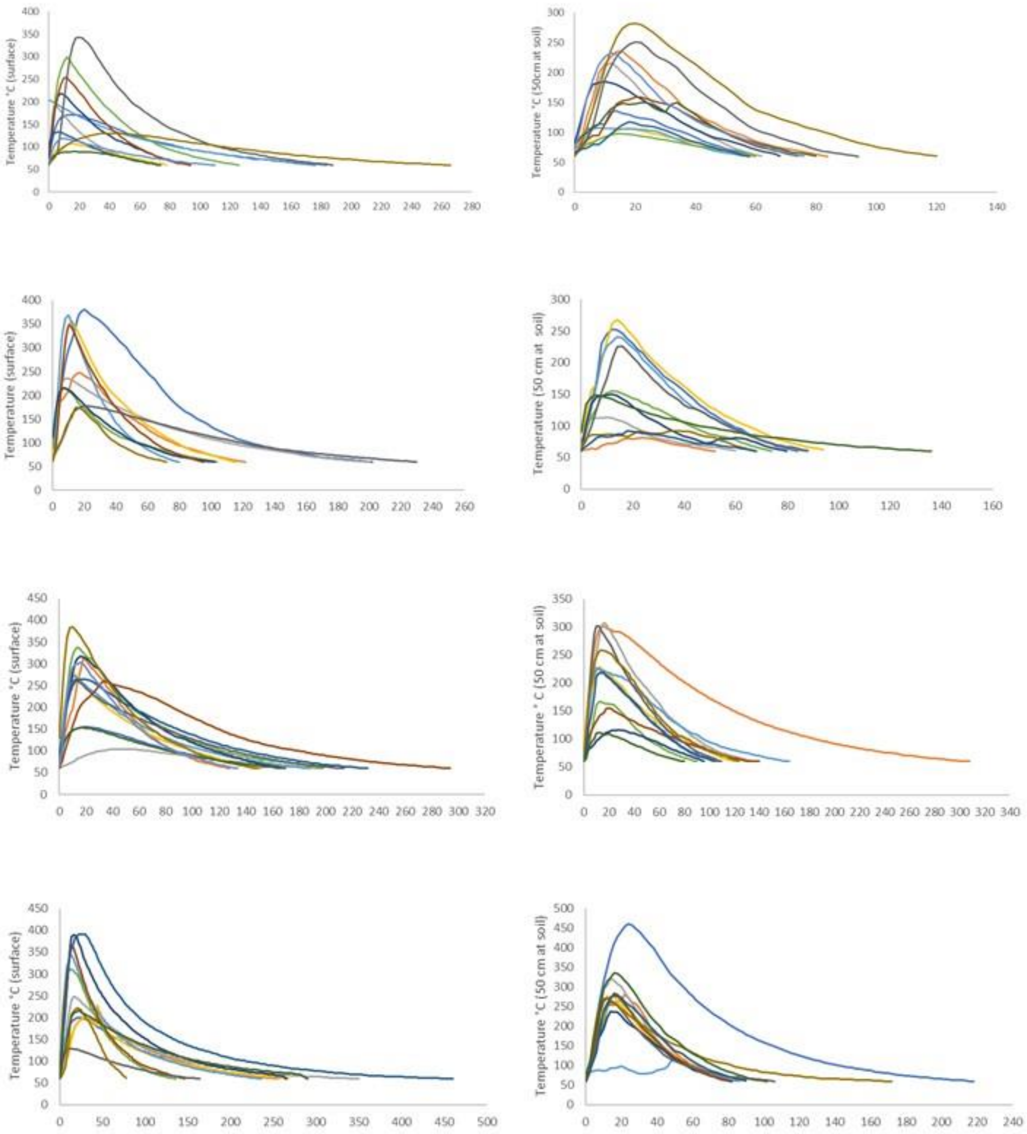

Figure S1.: Temperature variation (ºC) in seconds measured at the soil level and at 50 cm above soil level during experimental fires in annually burned areas in open savannas (campo sujo), Central Brazil. Each line represents the temperature measured by one sensor in the plot during the fire experiments

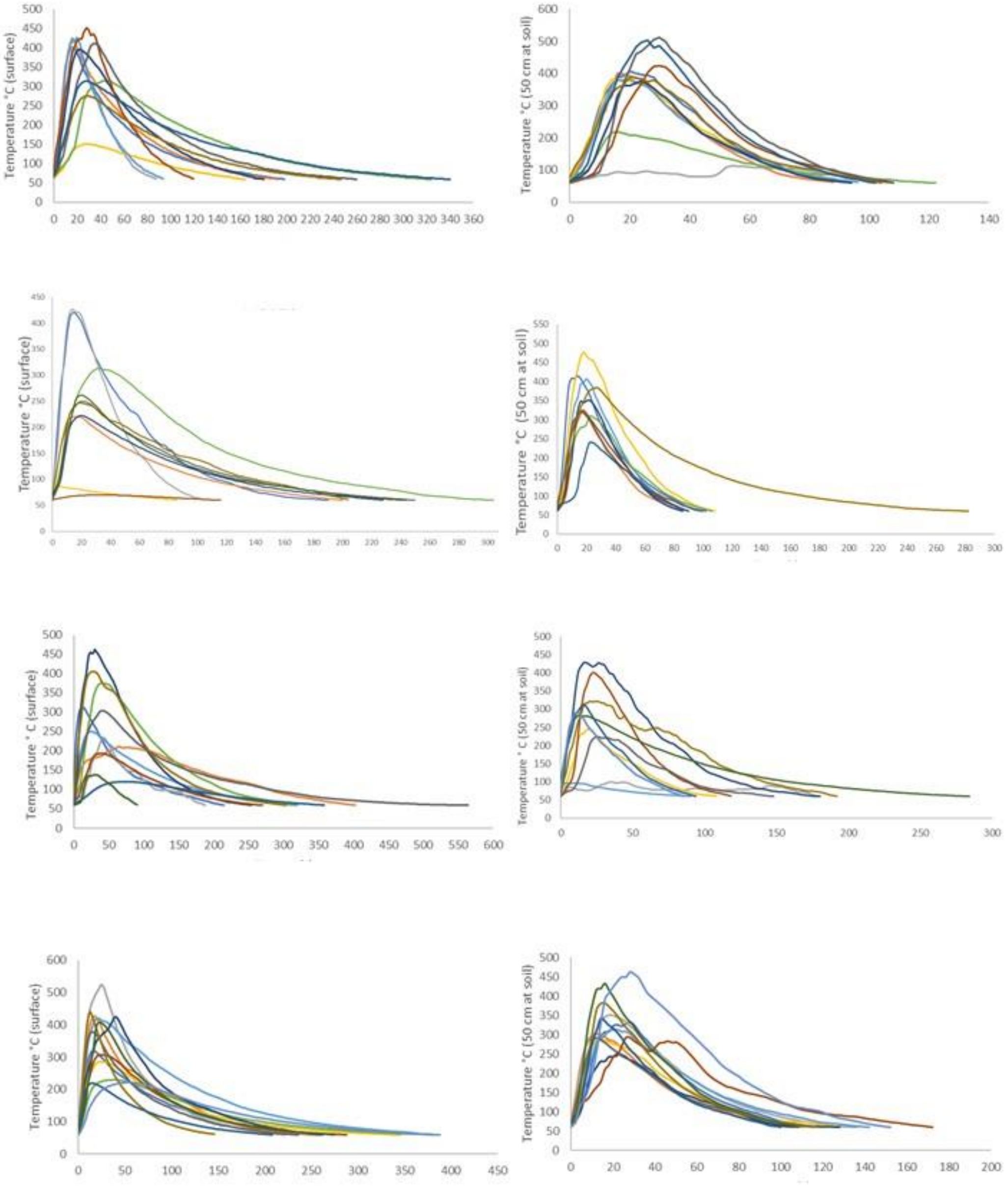

Figure S2: Temperature variation (ºC) in seconds measured at the soil level and at 50 cm above soil level during experimental fires in biennially burned areas in open savannas (campo sujo), Central Brazil. Each line represents the temperature measured by one sensor in the plot during the fire experiments.

Maximum temperature (surface)		
Models	ΔAICc	wAICc
% bare soil	**0.0**	**0.63**
% bare soil + % cover dead fuel	1.9	0.23
% bare soil + % cover dead fuel + % cover grass	3.9	0.08
Null	4.9	0.05
Residence time ≥60° C (surface)		
% bare soil + % cover dead fuel + % cover grass	**0.0**	**0.49**
% bare soil	0.6	0.35
% bare soil + % cover dead fuel	2.5	0.13
Null	9.8	0.003
Residence time ≥100° C (surface)		
% bare soil	**0.0**	**0.49**
% bare soil + % cover dead fuel + % cover grass	1.0	0.29
% bare soil + % cover dead fuel	1.6	0.21
Null	14.0	0.0004
Maximum temperature (50 cm at soil)		
% bare soil+ % cover dead fuel	**0.0**	**0.60**
% bare soil + % cover dead fuel + % cover grass	1.4	0.30
% bare soil	3.6	0.09
Null	17.3	0.0001
Residence time ≥60° C (50 cm at soil)		
% cover dead fuel	**0.0**	**0.53**
% bare soil + % cover dead fuel + % cover grass	1.4	0.26
% bare soil + % cover dead fuel	1.9	0.19
Null	12.9	0.0008
Residence time ≥100° C (50 cm at soil)		
% bare soil + % cover dead fuel	**0.0**	**0.44**
% bare soil + % cover dead fuel + % cover grass	0.21	0.39
% bare soil	2.0	0.16
Null	12.18	0.001

Table S1: Model selection to explain maximum temperature, residence time of temperatures ≥ 60 °C and ≥ 100 °C at soil surface and 50 cm above soil surface during fire experiments in areas burned annually and biennially in open savannas in Central Brazil, using the gamma distribution. ΔAICc: difference in AICc units between the model and the most parsimonious model of the candidate set (lowest AICc value; the most parsimonious model is shown in bold). wAICc: Akaike weight, indicates the relative probability of a given model being the best model of those compared to the observed data

How many times can we burn the Cerrado? A fire experiment in open savannas

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Abstract

1. The Cerrado is composed by grassland, savanna and forest ecosystems that evolved in the presence of fire, depending on it to maintain its physiognomies and biodiversity. Fire events alter environmental conditions of the plant community as well as the interspecific relationships of plants. An important aspect of the fire regime is frequency, which can influence the regeneration of plant communities and the most important question is how many times can we burn a system that will be still resilient?

2. Thus, this study aimed to analyze the effects of different fire frequencies on the composition, structure, and productivity of open savannas plant communities. We conducted surveys in areas with different fire frequencies (fire exclusion (FE), burned annually (AF) and biennially (BF) in a 5-year interval). Vegetation sampling was carried out before fire experiments, six and 12 months post-fire. Species were identified and had their cover (%) estimated visually and later grouped into graminoids, shrubs, and forbs, as well as bare soil and dead biomass. We also calculated the Simpson diversity index for each treatment in all seasons.

3. Our results showed that fire affected positively species richness and diversity, independently if burned every year or two years. In the different growth forms, only forbs had their species richness affected positively by fire. In addition, we found differences in cover only for forbs between both burned and fire exclusion plots. The percentage of dead

biomass and bare soil varied among fire history: plots with lower fire frequency of burning showed about 7-fold more dead biomass than frequently burned areas.

4. *Synthesis* These results suggest that fire exclusion is leading to species loss and changes in species cover patterns in open savannas, showing the importance of fire in these ecosystems. Additionally, burning annually for six years started to show some changes in plant cover (mostly forbs), but still, the major differences were among burned x unburned plots.

Introduction

Tropical grassy biomes cover approximately 20% of the global land surface and they are important for biodiversity, carbon sequestration (Parr, Lehmann, Bond, Hoffmann, & Andersen, 2014; Shimel et al., 1994) and many ecosystem services such as the regulation of climate and ground and surface water recharge (Honda & Durigan, 2016. An important characteristic of these biomes is the presence of a continuous layer composed mostly by C4 grasses, the dominant group in these plant communities, which produces a singular set of ecological processes and interactions such as the occurrence of fire (Parr et al., 2014).

According to the grass cover, grassy biomes range from open grassland to densely canopied savanna (Sankaran et al., 2005). Woody encroachment can occur rapidly in response to changes in climate, atmospheric chemistry, herbivory, and soil fertility, but mostly related to fire exclusion (Bond, 2008; Lehmann et al., 2014; Stevens, Lehmann, Murphy, & Durigan, 2017). These factors strongly influence the maintenance of open physiognomies and community assembly in grassy biomes (Bond 2008; Lehmann et al. 2014).

The Cerrado is a grassy biome composed by grassland, savannas and forest physiognomies that evolved in the presence of fire, thus depending on it to maintain its physiognomies and biodiversity (Simon et al., 2009; Coutinho, 1990; Pivello, 2011; Abreu et al. 2017; Durigan & Ratter, 2016). In the Cerrado, open physiognomies burn frequently, every 1-3 years (Eiten, 1972) and thus, changes in the fire frequency can affect the composition patterns and structure of the plant community, their productivity (Vale & Lopes, 2011; Higgins, Bond, & Trollope, 2000; Whelan, 1995) and the distribution of fuel load (de Castro & Kauffman, 1998). As a consequence, these changes can trigger alterations in the local fire behavior (Rodrigues et al. 2019 in prep.). Fire intensity, temperatures, and the residence time of the fire are crucial for post-fire recruitment and soil nutritional status (Malanson & Trabaud, 1988; 2000; Whelan, 1995) and thus, modifications in the fire behavior can influence the community post-fire regeneration.

Fire events alter the environmental conditions of the plant community as well as the interspecific relationships of plants and therefore, may affect its composition and dynamics (Laterra & Solbrig, 2001; Marcos, Calvo, & Luis-Calabuig, 2009). Fire removes a great amount of live and dead aboveground plant biomass, exposing the soil (Bond & Van Wilgen, 1996; Fidelis, Blanco, Müller, Pillar, & Pfadenhauer, 2012) and promoting an increase in nutrient availability (Coutinho, 1982; Whelan, 1995) and at the same time, a decrease in interspecific competition (Boughton, Bohlen, & Steele, 2013). Such conditions may result in higher plant growth and productivity rates (Whelan, 1995), that favor the occupation of vegetation gaps.

In post-fire environments, particular plant traits are critical for species capacity to persist and regenerate in the community (Chapin et al., 1997; Bond & Midgley, 1995). For example, fast-growing species (e.g. graminoids) may be favored in the occupation of space, and thus, in their establishment in post-fire environments (Ripley et al., 2015).

Forbs and shrubs with belowground bud-bearing organs may also have advantages of the favorable conditions of these environments, since they can rapidly resprout (Bond & Midgley, 2001; Clarke et al., 2013). Thus, it is common to observe changes in species richness, composition, and growth forms after fire events (Whelan, 1995; Fidelis et al., 2012; Boughton et al., 2013). These changes are expected in communities on different fire frequencies, since species from different growth forms have distinct strategies to couple with different fire regimes (Whelan, 1995; Pivello & Norton, 1996).

Differences in aboveground plant biomass can be found in areas with different fire frequencies due to variable responses of growth forms (Cianciaruso, da Silva, & Batalha, 2010). For example, in open savannas, fine fuel load fully recovers just two years after fire (Neto, Andrade, & Miranda, 1998), having restored 80% of its biomass from the herbaceous stratum after just one year (Andrade, 1998). This recovery is mainly due to the regrowth of graminoids (Whelan, 1995; Hoffmann, 1998). Graminoids have their meristems protected from fire by the soil (Gottsberger & Silberbauer-Gottsberger, 2006) or leaf sheaths, which protect their buds from high temperatures (Fidelis et al., 2012). Moreover, they can assimilate available nutrients rapidly from the soil, since their roots are shallow and most of the nutrients are concentrated in the first centimeters of the soil layers (Coutinho, 1990).

However, under recurrent fire, woody species suffer a decrease in seedling growth and survival rates (Hoffmann, 1996, 1998). Although these species are fire-adapted, possessing buds protected and strong suberization of trunks and shoots (Charles-Dominique, Beckett, Midgley, & Bond, 2015) that protect the living tissues from high temperatures, these traits usually appear only in adult individuals (Miranda, Bustamante, Miranda, Oliveira, & Marquis, 2002; Charles-Dominique et al., 2015; Clarke et al., 2013). Therefore, the occurrence of fire during the life stage in which woody individuals are within the herbaceous stratum may be determinant for their establishment and survival (Williams, Gill, & Moore, 2003). Finally, extreme high frequencies can be harmful, causing changes in the depth and water retention soil and can also prevent some species from having time to regenerate and reestablish, leading to diminished community richness, abundance and productivity (Pivello, 2011).

Thus, this study aimed to analyze the effects of different fire frequencies on the composition, structure, and productivity of open savannas plant communities (*campo sujo*). We hypothesized that areas burned annually would have lower vegetation cover and richness compared to areas with burned biennially. However, the richness would be greater than in areas excluded from fire, since fire maintain plant diversity. Moreover, differences in the cover of functional vegetation components will differ according to fire frequency: areas excluded from fire would have higher dead biomass cover, while annually and biennially burned areas would have higher graminoid and forb cover. Shrubs would be negatively affected by annual fires, while their cover would increase in excluded areas. Finally, areas that burn annually would have lower productivity than those with biennial fires and fire exclusion.

Material and methods

Study area

This study was conducted at the Reserva Natural Serra do Tombador (RNST, 13° 35-38 'S and 47 ° 45-51' W, 8900 ha, 560–1118m a.s.l., Central Brazil). The climate is tropical, with dry winters and rainy summers, average annual rainfall between 1300-1500 mm, maximum average temperatures between 26 and 36°C, and minimum temperatures between 8 and 14°C (AER, 2009). The study site where the fire experiments are established is a *campo sujo* area (open savannas), characterized by the dominance of graminoids and forbs, with scattered trees and shrubs (Coutinho, 1978), and therefore with a continuous fine fuel load bed and high fire frequency (every 3 years) until 2006, year of the creation of the reserve (Daldegan et al. 2014). Fire was excluded in the area until 2011, when there was a wildfire in the area. Thus, fire experiments began in 2013, two years after the wildfire. The main component of the herbaceous stratum is the C4 grasses, mainly composed by *Oncorachis ramosa, Axonopus aureus, Elionurus muticus, Aristida setifolia, Mesosetum ferrugineum* and *Paspalum pectinatu*m.

Experimental design

For this study, 30x30 m plots were established in areas of open savannas. Fire treatments began in 2013, with different fire frequencies: annual (AF - four plots, burned annually since July 2013), biennial (BF - four plots,burned biennially since July 2013) and fire exclusion (FE - two plots, excluded from fire since 2011). Experimental burns were always performed independently to avoid pseudoreplication. Only two fire exclusion plots were used because two of them burned accidentally in 2014 and 2017 and thus, they were eliminated from the analysis.

Vegetation was sampled before each fire of July 2017 (T0) in the dry season, 6 months post- fire (T6) in the rainy season and 12 months after the establishment of experiments (T12), in the dry season. In each of the experimental plots, 10 fixed subplots were randomly established in a 1x1m grid. In these subplots, vegetation cover was estimated visually (%) for bare soil, dead biomass (standing + litter) and for each species. Covers were later adjusted to sum up 100%. We grouped species according to their growth form: graminoids (Poaceae, Cyperaceae), forbs, and shrubs.

For the analysis of post-fire regeneration, we sampled aboveground biomass in 0.5x0.5 m subplots within each experimental plot, before and after the experiments, at the same time of vegetation sampling (rainy and dry season) for one year. At each sampling, new subplots were randomly selected to avoid the resampling in the same subplot. The collected material was stored in paper bags in the field and in the laboratory, it was sorted into dead biomass, graminoid, forbs, shrubs and litter (collected separately in the field). Afterwards, samples were oven-dried at 80ºC for 48 hours and weighed.

Data analysis

To assess differences in cover by growth form (%, bare soil, dead biomass, graminoid, forbs and shrub) and diversity (Simpson diversity index and richness, total and for each growth form) among treatments for each observation time and over time for each treatment, mixed linear models were performed (GLMM, fixed factor: treatment, random factor: plots, family: Poisson).

We used the Coenh's D index to quantify the magnitude of the impact of fire frequency on the community by pooling the ratio of response variables from each fire treatment (annual and biennial) relative to the fire exclusion treatment (Deeks et al. 2001). Negative values of Coenh's D index indicate that the treatment had a negative effect on that variable, while a positive value indicates a positive effect.

In order to find patterns of changes in vegetation across time, we performed principal coordinate analysis (PCoA), with sampling units described by species cover at each time of observation for each treatment, using Chord distance as resemblance measure among sampling units.

To evaluate the differences in the amount of total, live and dead biomass, as well as the biomass of the different growth form among treatments (fire exclusion, annual and biennial fires) for each observation time, mixed linear models were used (fixed factor:

treatment, random factor: plot, family: gaussian). We used the same model to evaluate the differences in the amount of total biomass, dead biomass, live biomass and each growth form over time for each treatment.

Finally, we quantified the productivity of total biomass and by growth form in 1 year for the fire treatment areas. Then we compared the productivity between the annual and biennial fires using mixed linear models (fixed factor: treatment, random factor: plot, family: gaussian). All analyses were performed using the R program (R Core Team, 2013) with the packages: vegan (Oksanen et al., 2013), multcomp (Hothorn, Bretz, & Westfall, 2008) and Nlme (Pinheiro, Bates, Dedroy, Sarkar, & R Core Team, 2015).

Results

We identified 120 morphotaxa (106 species and 14 genera) in the surveys six (rainy) and 12 (dry season) months post-fire in all treatments. Of these 120 species, 13 occurred only in the rainy season and 11 only in the dry season. In the rainy season, 48% of species occurred in the three treatments. However, eight species occurred only in the FE plots and 37 species occurred only in burned plots, with eight species being exclusive to BF and 18 to AF areas (Table S1). In the dry season, 50% of species occurred in all three treatments, and seven species occurred only in the fire exclusion areas, whilst 42 species only occurred burned areas (12 exclusively in BF and 11 exclusively in AF, Table S1).

Species richness of plant communities differed among treatments only 6 months after fire experiments (T6, rainy season), when the number of species of annually burned plots was higher than in biennially burned ($p = 0.03$). One year after fire, BF plots had more species than FE ($p = 0.04$, Figure 1). In all treatments, an increase in species richness was observed during the next rainy season (and six months after fire). However, one year after treatments (dry season), FE showed the same number of species than before the experiments (Table S2). Regarding the number of species per growth form, only forbs increased the number of species in the AF and BF areas (Figure 1, p = 0.04 and p = 0.002 to AF and BF, respectively). Graminoids and shrubs did not change their number of species mean in none of the treatments (Figure 1, p > 0.05).

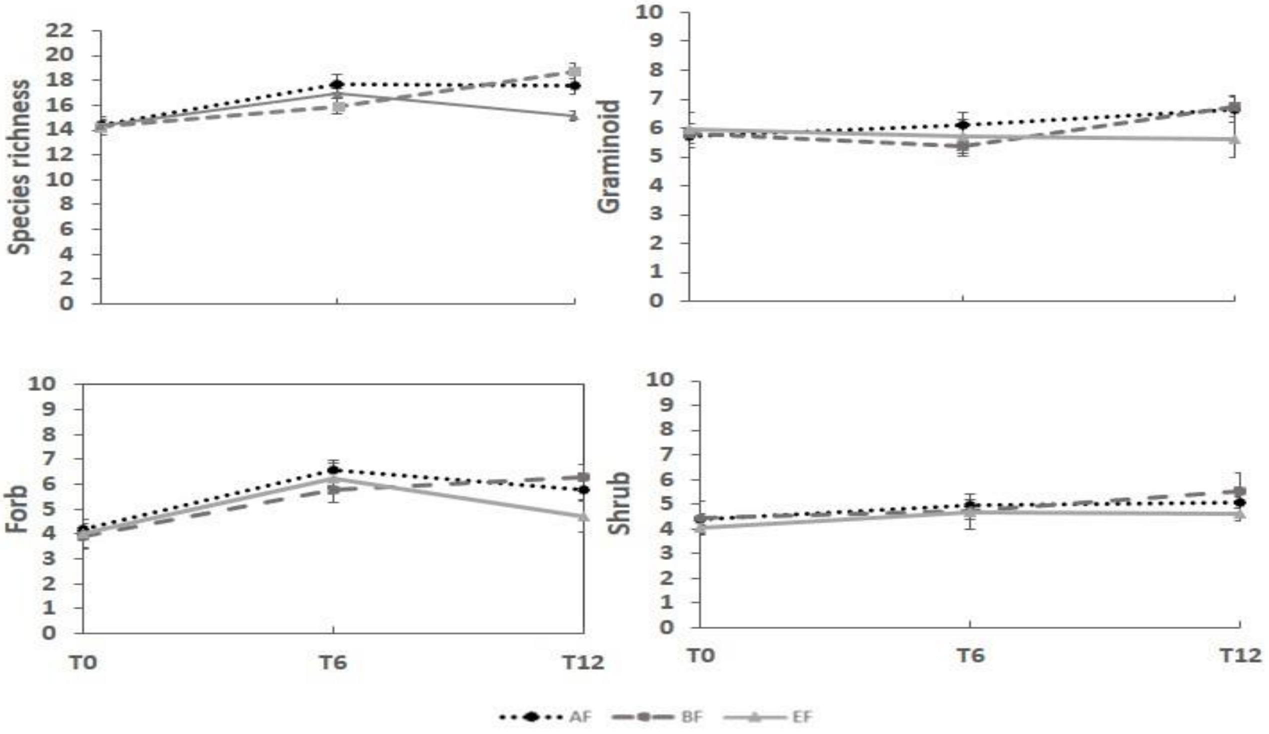

Figure 1. Species richness (species.m-^{2}) per treatment (AF – annually burned, BF – biennially burned, and FE – fire exclusion) before T0 (dry season, before of fire), 6 (T6, rainy season,) and 12 months post-fire (T12, dry season). Total species richness and for each growth form: graminoids, forbs and shrubs in open savanna, Central Brazil. Error bars represent the standard error

However, the impacts of both fire treatments 12 months after fire were positive on both total species richness and by growth forms on plant community (Figure 2).

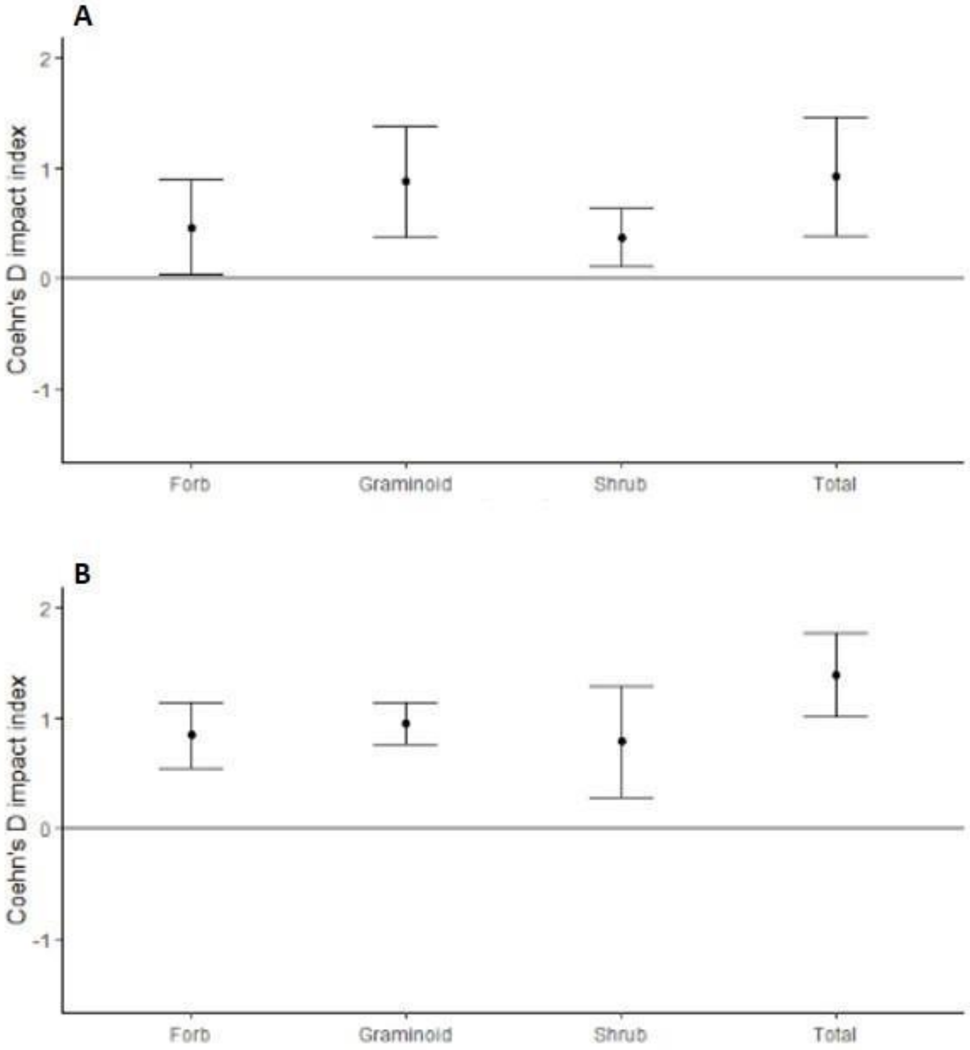

Figure 2. Coenh's D impact index for annual (A) and biennial (B) fires on species richness (species.m-^{2}): total and by growth forms (graminoid, forb, and shrub) 12 months after fire experiments in open savannas in Central Brazil. Error bars represent the standard error

Simpson's index was higher in AF than BF areas ($p = 0.01$) and FE ($p < 0.0007$) treatments before fire, and higher in the AF in comparison to FE areas one year after fire ($p=0.02$). The diversity increased over time, independently of fire treatment. In T6 and T12 the diversity was higher than T0 experiments for all treatments, varying from 0.94 (FE) to 0.96 (BF and AF).

Species composition differed among fire frequency treatments, and two groups could be recognized in the ordination: burned (AF and BF) and fire excluded sites. The two axes together explained 72.4% of the total variation in species composition (Figure 3). Before fire experiments (T0), BF plots were separated from AF sites. After fire (T6 and T12), however, they showed abrupt changes in species composition and thus, BF plots were more similar to AF plots. The excluded fire sites showed to be more stable, showing some changes only across seasons (Figure 3). We could identified some species being more related to some areas than to other ($r > 0.5$). Smaller forbs correlated with the burned sites, such as *Crumenaria choretroides* (Rhamnaceae), *Cuphea ericoides* (Lythraceae), *Eriope glandulosa* (Lamiaceae), *Hyptis remota* (Lamiaceae), and *Lippia horridula* (Verbenaceae). On the other hand, small trees and large shrubs were more related to areas with fire exclusion, such as *Annona tomentosa* (Annonacea), *Connarus suberosus* (Connaraceae), *Hancornia speciosa* (Apocynaceae), *Mimosa leiocephala* (Fabaceae), and *Palicourea rigida* (Rubiaceae).

These changes can be viewed more clearly in terms of species composition by comparing species turnover between sites under different treatments. There was a loss of 23.5% and 24.3% of species in FE plots six and 12 months after fire, respectively. Biennially burned plots lost 20.3% of their species just after fire (six months, rainy season), and 19.7% one year after fire. However, they gained 21% and 31.2% in the same period. AF plots showed lower losses of species (12.3% and 14.5 %, T6 and T12 respectively), but gained 28.9% of new species.

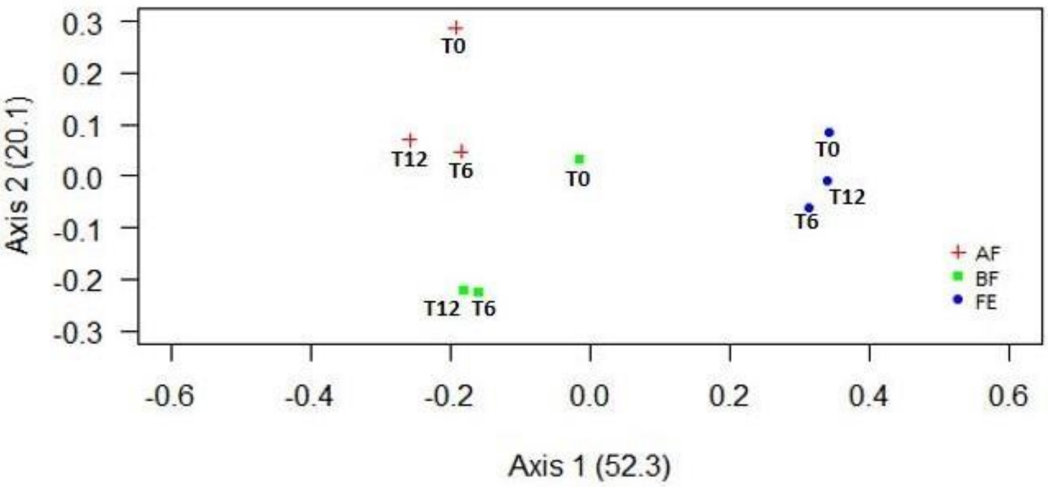

Figure 3. Principal coordinate analysis (PCoA) according to sampling units described by species cover at each observation time in open savannas: T0 (dry season, before fire), T6 (rainy season, 6 months post-fire) and T12 (dry season, 12 months post-fire). The resemblance measure used among sampling units was Chord distance

Frequent fires increased cover of forbs one year after fire: there was a higher cover of forbs in burned than FE areas (Figure 4 and Table S3). Graminoids and shrubs did not show differences in cover over time among treatments.

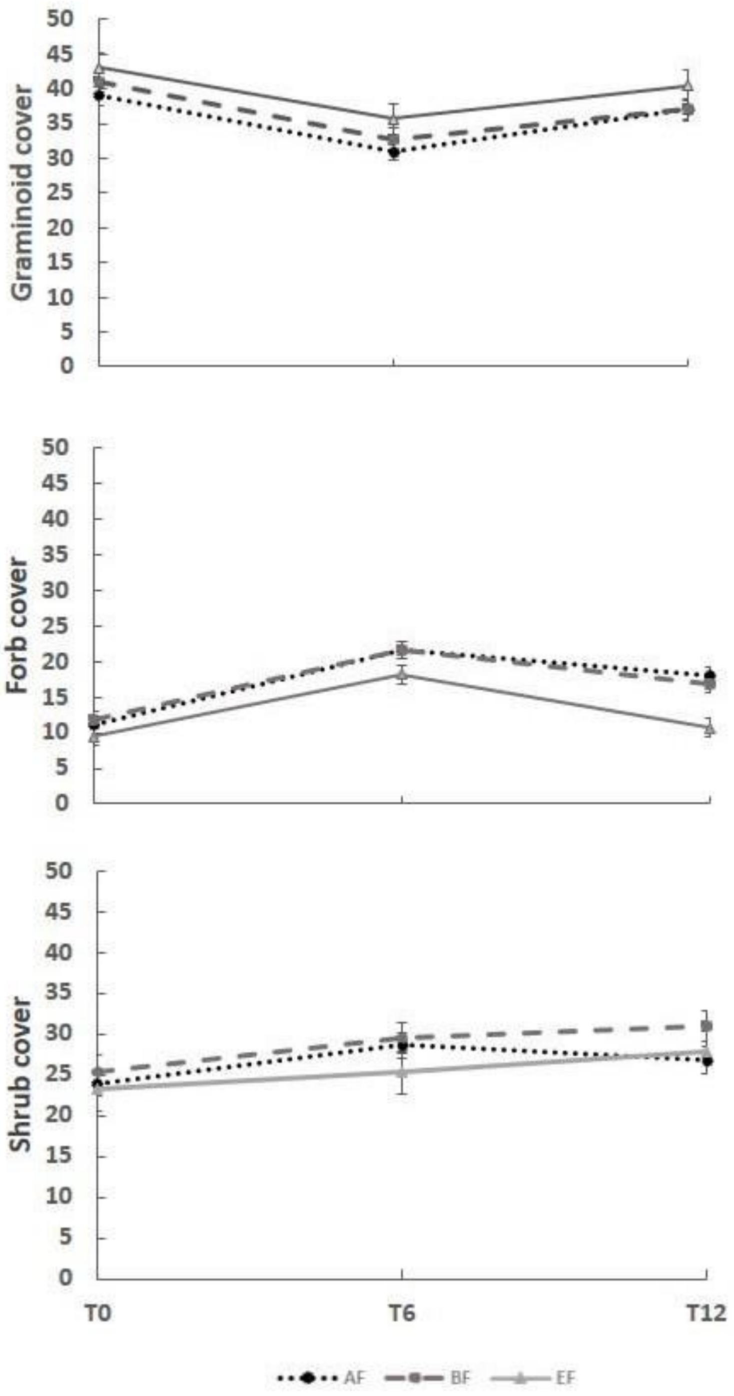

Figure 4. Graminoid, forbs and shrub cover (%) per treatment (AF – annually burned, BF – biennially burned, and FE – fire exclusion) before T0 (dry season, before of fire), six (T6, rainy season,) and 12 months post-fire (T12, dry season) in open savannas in Central Brazil. Error bars represent the standard error.

However, we found higher values of dead biomass cover and lower percentage of bare soil in the fire exclusion plots than in both fire treatments in all times of observation. Only before fire (T0), there was no difference in dead biomass cover between FE and BF plots. Biennially burned sites showed higher values of dead biomass cover and a lower percentage of bare than AF in T0 (Figure 5 and Table S3). AF had higher dead biomass cover than BF in T6 e higher bare soil in T12 (Figure 5 and Table S3).

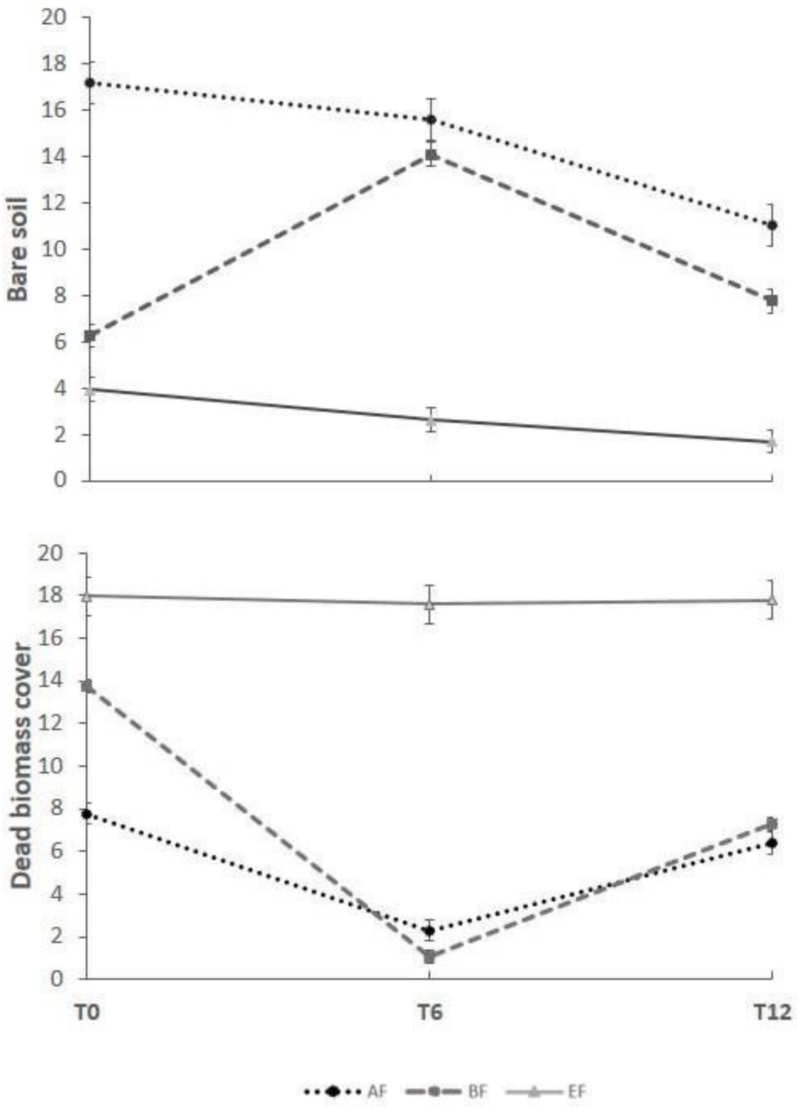

Figure 5. Bare soil and dead biomass cover (%) per treatment (AF – annually burned, BF – biennially burned, and FE – fire exclusion) before T0 (dry season, before of fire), six (T6, rainy season,) and 12 months post-fire (T12, dry season) in open savannas in Central Brazil. Error bars represent the standard error

One year after fire, the impacts of both fire treatments were positive on forb and bare soil cover, but neutral on shrub. On the other hand, AF had a negative impact on graminoid cover while the BF had a neutral impact on this group cover (Figure 6). Finally, dead biomass was negatively affected by both fire treatments.

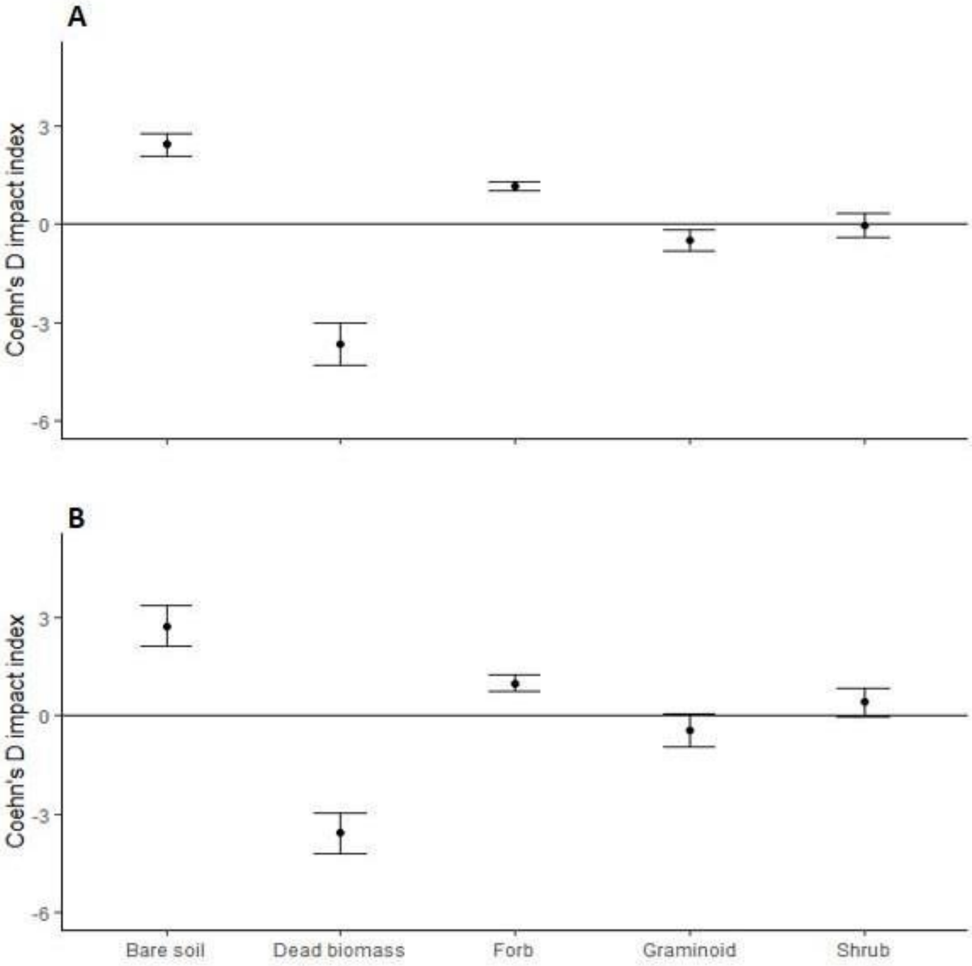

Figure 6. Coenh's D impact index for for annual (A) and biennial (B) fires on bare soil, dead biomass and growth form cover (% forb, graminoid, and shrub) 12 months after fire experiments in open savannas. Error bars represent the standard error

Total live biomass values only differed between AF and FE plots at T12, being higher in FE plots. Total dead fuel (standing dead + litter) and total biomass (total live + total dead) were lower in the burned treatments (AF and BF) in all the sampled periods

(Table 6). Also, annually burned plots showed to have less total dead and total biomass than biennially burned areas before fire (Table 6).

Litter and standing dead biomass differed between the burned and fire exclusion treatments in the three sampled periods. Before fire, annually burned plots already had less litter and dead fuel than the FE plots. In the first rainy season after fire (six months), FE plots had 7 times more accumulated dead fuel and 3-fold more litter than both burn treatments. One year after fire, fire exclusion plots had 3 times more dead fuel accumulated and the double amount of litter than burned plots. Moreover, the dead biomass differed between burned treatments only before fire experiments, when the biennially burned plots had 2 times more dead fuel and almost the double of litter than annually burned plots (Table 6).

Biomass of growth forms revealed significant differences between the burned and unburned treatments only for graminoids (Table 6). Before fire experiments, AF had less graminoid biomass than fire exclusion sites. After the experiments, both fire treatments showed a lower amount of graminoid biomass than FE, both during the rainy (six months) and dry season (12 months after fire). There was no difference between the biomass of growth forms between AF and BF treatments in any of the sampled periods.

Table 6. Biomass (g.m-2, mean±SE) sampes in open savannas before fire (T0, dry season), six months (T6, rainy season) and 12 months after fire (T12, dry season) in plots with annual (AF), biennial fires (BF) and fire exclusion (FE). DB = dead biomass; L = litter G = graminoids; S = shrub; F = forbs; TDB = total dead biomass; TLB = total live biomass; TB = total biomass. Different letters mean significant differences between treatments in each time ($p \leq 0.05$).

Time	Treatment	DB	L	G	S	F	TDB	TLB	TB
T0	FE	386.76 ±62.11^{a}	69.46 ± 11.11^{a}	117.23 ± 21.97^{a}	26.61 ± 8.76^{a}	0.92 ± 0.51^{a}	612.9 ± 10.2^{a}	162.9 ± 26.7^{a}	775.7± 129.1^{a}
	AF	139.2±12.84^{b}	49.3 ± 10.46^{b}	61.7 ± 6.95^{b}	57.7 ± 14.98$_{a}$	2.32 ± 1.39^{a}	182.6 ± 18.3^{b}	133.9 ± 17.9^{a}	316.6 ± 31.2^{b}
	BF	304.5±38.75^{c}	85.2 ± 10.08^{a}	88.3 ± 12.57^{ab}	54.5 ± 14.4^{a}	2.23 ± 0.79^{a}	397 ± 39.9^{c}	146.5 ± 16.1^{a}	543.5 ± 45.6
T6	FE	335.07± 33.58^{a}	78.42 ± 9.04^{a}	127.7 ± 19.39^{a}	23 ± 6.9^{a}	1.28 ± 0.55^{a}	465.3 ± 57.7^{a}	182.4 ±25.1^{a}	647.7 ± 72.6^{a}
	AF	50.8 ±10.78^{b}	28.8 ± 12.27^{b}	92 ± 9.42^{b}	53.95 ± 14.58^{a}	1.7 ± 0.9^{a}	102.9 ± 16.5^{b}	155.7 ± 16.9^{a}	258.6 ± 24.1^{b}
	BF	33.5 ± 37.94^{b}	20.88 ± 4.58^{b}	93.11 ± 9.34^{b}	61.44 ± 13.79^{a}	1.44 ± 0.89^{a}	52.2 ± 11.7^{b}	152.5 ± 13.5^{a}	204.8 ± 18.6^{b}
T12	FE	468.87 ± 69.76^{a}	74.5 ± 16.75^{a}	216.3 ± 37.92^{a}	33.25 ± 9.77^{a}	0.62 ± 0.49^{a}	454.7 ± 65^{a}	237.9 ± 37.4^{a}	692.6 ± 96.3^{a}
	AF	135.25 ± 11.10^{b}	24 ± 5.44^{b}	118.4 ± 11.19^{b}	57.45 ±18.78^{a}	0.8 ± 0.33^{a}	156.2 ± 13.9^{b}	163.7 ± 16.6^{b}	319.9 ± 22.3^{b}
	BF	113 ± 13.52^{b}	29.47 ± 5.29^{b}	129.6 ± 13.87^{b}	56.52 ± 19.1^{a}	1.26 ± 0.45^{a}	153.8 ± 14.6^{b}	226 ± 40.6^{ab}	379.9 ± 43.8^{b}

Regarding the contribution of the growth form to the composition of live biomass of each treatment, the FE had a larger amount of graminoids than shrubs or forbs in all the sampled periods. The AF and BF, before burning, presented a similar amount of graminoids and shrubs, therefore these two groups have contributed equally to the total live biomass. However, after burning, the amount of graminoids increased substantially in burnt plots, doubling in the annuals, in contrast, shrubs, even though they also have shown rapid growth, just recovered their biomass before burning. As a consequence the graminoids turned to represent most of the live biomass in the AF and BF plots.

We found similar values of total productivity ($p = 0.3$) and graminoid ($p = 0.7$), shrub ($p = 0.4$) and forb ($p = 0.4$) productivity between AF and BF treatments one year post-fire (Table 6, T12 values), showing that vegetation regenerated equally independently of fire frequency

Discussion

Noble and Slatyer (1980) recognized two stages of post-fire regeneration. The first is characterized by the “race” for the occupation of the area when there is little competition, associated with the increased availability of resources. The second stage, when competition for resources becomes progressively more important and species need more effort to persist in the community. By assessing the effects of the first year after fire in areas with different fire frequencies on the plant community, we were able to identify increases in species richness, changes in composition pattern and an indicator of increased productivity proper of first regeneration stage in post-fire communities.

These changes have also been previously reported in studies in other fire-prone ecosystems (Bond & van Wilgen, 1996; Keeley, Pfaff, & Safford, 2005; Ghermandi, Guthmann, & Bran, 2004; Heinl, Frost, Vanderpost, & Sliva, 2007; Overbeck, Müller, Pillar, & Pfadenhauer, 2005) and may be related to favorable post-fire environmental conditions and changes in the dominance relationships among species caused by varied plant-specific responses to fire (Suding, 2001; Laterra, Vignolio, Linares, Giaquinta, & Maceira, 2003). Post-fire conditions differ significantly from those found in disturbance-free areas (Carrington & Keeley, 1999; Safford & Harrison, 2004) and are characterized by increased light incidence, higher temperatures (Fidelis & Blanco, 2014), as well as water availability, elevated nutrient levels (Whelan, 1986; Neary, Klopatek, DeBano, & Ffolliott, 1999), more gaps and consequent decrease in interspecific competition (Neary et al., 1999).

Many species have mechanisms that allow them to capture and assimilate resources in the post-fire environment, such as dormant seed banks and resprouting from belowground structures (Trabaud & Prodon, 1993; Bond & van Wilgen, 1996; Bradstock, Williams, & Gill, 2002) which favors their establishment during the process of community post-fire regeneration. The removal of dominant species is also an important factor affecting positively richness after the disturbance (Connell, 1980; Huston, 1979; Pickett, 1980), since it prevents the extinction of species with poor competitive ability. These species can return to the community because fire can buffer the structural predominance of other species and eliminate dense layers of litter and dead biomass that prevent their germination and regrowth (Collins, 1987; Facelli & Pickett 1991).

In open savannas (*campo sujo*), graminoid species compose the dominant group, accumulating large amounts of dead biomass near their bases in the absence of fire (Coutinho, 1990). Because of that, this group is responsible for the increase of dead biomass in the community. As we hypothesized, there was a reduction in dead biomass cover (standing + litter) and an increase in bare soil in burned when compared to unburned areas. This structural change of the burned communities can allow the establishment of new species that are suppressed in areas without fire (Bond & van Wilgen, 1996), especially forbs, which showed a significant increase in the number of species and cover in burned areas. Keeley et al. (2005) also reported an increase in the number of post-fire forb species in shrublands of California and found that almost half of the variation in richness was explained by the availability of resources. Contrary to our hypothesis, shrubs were not affected by fire: neither they decreased in cover in annually burned areas nor they increased in areas excluded by fire. However, large shrub species were more related to FE sites than burned ones and thus, the longer fire is excluded, the more dominant they will be in these areas.

However, the number of species tended to decrease with increasing time after fire. Larger periods without fire are related to a decline in fire-tolerant species due to increased size, cover and biomass of graminoid and woody plants (Guo & Rundel, 1997; Keeley et al., 2005), which results in decrease of the abundance of forbs and small shrubs (Tilman, 1988). According to our results, the loss of species might be related to forbs, which might be negatively affected by the increase in dead biomass cover and shading caused by large shrub species.

In the early stages of post-fire regeneration, it is not only species richness and diversity that increases, but also biomass productivity (Guo, 2003). We found an increase in the amount of graminoid biomass after fire. Shrub productivity was also high. In the rainy season following fire, the burned communities had already recovered graminoid, shrub and forb biomass, reaching the same amount as before the fire, showing the high productivity and resilience of these communities. We hypothesized that areas burned annually would show lower productivity in comparison to areas with biennial fires, but we could not corroborate our hypothesis. Maybe, six years of fire experiments is still not long enough to observe the effects of annual fires on vegetation productivity. However, our results show that open savannas in the Cerrado are extremely resilient to fire, even to high-frequency fires, such as the annual fires.

The high capacity of grassy biomes to regrowth rapidly after disturbance might be linked to a viable bud bank (Clarke et al., 2013, Knapp & Smith, 2001). This is because the main regeneration strategy in these communities is resprouting from surface and belowground bud banks (Coutinho, 1990; Bond & Midgley, 2001; Clarke et al., 2013). Moreover, disturbance maintains a viable and large bud bank, as well as a higher diversity and number of bud-bearing organs than in undisturbed areas, which allows the fast regrowth of graminoids, forbs, and shrubs in the system if the viable bud bank is maintained (Fidelis, Appezzato-da-Glória, Pillar, & Pfadenhauer, 2014).

Therefore, despite the constant discussion about the negative impacts of frequent fires (1-3 years), we found that annual and biennial fires were beneficial for the plant community in comparison to the fire exclusion. This can be explained by the high resilience to fire that is characteristic of grassy biomes (Buisson et al., 2019). Additionally, frequent fires will have lower temperatures and residence time of fire, as well as milder fire intensities (Frost, 1984; Rodrigues, Zirondi, & Fidelis, unpublished data) in comparison to fires occurring in areas with longer periods of exclusion due to the higher accumulation of fuel load (Fidelis, Alvarado, Barradas, & Pivello, 2018). In addition, there are many species that are restricted to post-fire conditions and therefore disappear after the first or second year and do not reappear until the next fire (Keeley, 1999). As shown in this study, we identify 37 species that occurred only in burned plots, mostly forbs and shrubs, such as *Polygala longicaulis (*Polygalaceae*), Spermacoce tenella (*Rubiaceae*), Deianira pallescens (*Gentianacea*), Oxalis goyasensis (*Oxalidaceae*),* and *Ruellia angustior (*Acanthaceae*).*

However, contrary to our hypothesis, we observed that annual fires impacted negatively the graminoid cover. Although the impact was low, it suggests a decrease in regrowth capacity after fire, indicating a probable loss of resilience to this group, since graminoids are the dominant group in open savannas. The decline in abundance of a specific growth form can confer a loss of functional diversity in the plant community that can lead to decreased resilience (Lavorel, 2009). Besides, this decrease in graminoid cover may influence fire behavior and regime in the future, since graminoids are the most important component of fuel load, driving community flammability (Simpson et al., 2014; Zanzarini & Fidelis, unpublished data).

On the other hand, when fire is suppressed for longer periods, the ecological impacts may be more severe, since with the accumulation of fuel load (mostly dead biomass) can lead to higher fire temperatures and intensity if fire occurs in these areas (Gibson, Hartnett, & Merrill, 1990; Rissi, Baeza, Gorgone-Barbosa, Zupo, & Fidelis, 2017), which may cause more tissue and propagule deaths (Bradstock & Auld, 1995), hampering thus, post-fire vegetation regeneration. Moreover, even species that persist in the community in the form of seeds or underground organs can eventually become locally extinct if fire is excluded (Specht et al 1958). In grassy biomes, reducing the biomass of the dominant groups is critical to maintain an open physiognomy and plant species diversity (Collins & Gibson, 1990; Belsky, 1992; Morgan & Lunt, 1999), and thus, the exclusion of disturbance may cause an excessive litter and dead biomass accumulation and reduced plant productivity, and as a consequence, it may result in ecosystem collapse and susceptibility to biological invasions (Knapp & Seastedt, 1986; Morgan & Lunt, 1999).

Thus, in a regime where fire is recurrent, the impact of the dominant groups is reduced, maintaining a state of compositional equilibrium, which would not exist at low fire frequencies, since open ecosystems may be subject to invasion of shrub and forest species if they are in an alternative stable state (Oliveira & Pillar 2004; Staver, Archibald, & Levin, 2011). Therefore, the presence of fire and how often the area is burned will influence both the maintenance of Cerrado open physiognomies and the species composition patterns of the plant communities.

We conclude that burning open savannas in the Cerrado is important for maintenance of plant species diversity, especially of the herbaceous stratum. Communities with high fire recurrence proved to be highly resilient, not only maintaining much of their species but also recruiting a significant number of new post-fire species, increasing their richness, as predicted in our hypothesis. In addition, both biennially and annually burned areas showed rapid regrowth and high post-fire productivity, rapidly regenerating the community at pre-fire levels after the first rainy season. However, we observed that annual fires may be subtly changing community patterns, because after the fifth consecutive fire, we began to observe a decline in graminoid cover while there was an increase on the recruitment of new species. Differently from our hypothesis, annually burned sites did not show lower richness and diversity of species than biennially ones, demonstrating great resilience to fire. In contrast, areas excluded from fire presented lower biomass increment, greater losses and lower recruitment of new species. Therefore, these areas are becoming dominated by fewer species, suggesting the loss of resilience.

These results support two intriguing questions: How much longer under an annual burn frequency will the community be able to accumulate fuel load to sustain fire? And over time, how different will the community composition pattern of annually burned sites will be? However, there is no doubt about the necessity to burn open savannas of the Cerrado, because the lack of fire is more harmful than burning it. Therefore, fire should be considered as an important ecological factor in the Cerrado and used as a management tool in protected areas not only to reduce fuel load and prevent future fires, but be considered in a pyrophilic approache (prescribed burning) that promote the maintenance of Cerrado physiognomies, biodiversity and their valuable ecosystem services.

Acknowledgments

The authors thank the staff of the Reserva Natural Serra do Tombador: Anderson F. Terra, Whatson F. Rezende, Gilson de A. Berberino, Silvanio A. Borges, and Rogério B. de Almeida for their support during fire experiments. We also thank Aline Bombo, Gabriela Dasmaceno, Gionana Chiari, Heloiza Zirondi, Juliana Teixeira, Marco Chiminazzo, Mariana Dairel, Nubia Vilela and Vagner Zanzarini for helping during the field work. C.R received financial support from Fundação de Amparo à Pesquisa do Estado de São Paulo (2017/22618-7) and from CAPES/DS (1735266) and A.F. receives grant from (CNPq 303988/2018-5). This study was supported by FAPESP (2015/06743-0) and Fundação Grupo o Boticário de Proteção à Natureza (0153_2011_PR).

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Supplementary Material

Table S1. List of families and species that occurred after the burns in areas with annual and biennial burnings and fire exclusion in T6 (rainy season, 6 months post-fire) and T12 (dry season, 12 months post-fire) in *campo sujo* areas, Central Brazil. The "x" indicates the occurrence of the species in the treatment

		wet season			**dry season**		
Species	**Family**	**AF**	**FE**	**BF**	**AF**	**FE**	**BF**
Justicia lanstyakii Rizzini	Acanthaceae	x	x	x	x	x	x
Ruellia angustior (Nees) Lindau	Acanthaceae				x		x
Ruellia nitens (Nees) Wassh.	Acanthaceae	x	x	x	x	x	x
Ruellia sp	Acanthaceae	x	x	x	x	x	x
Annona tomentosa R.E.Fr.	Annonaceae	x	x	x	x	x	x
Hancornia speciosa Gomes	Apocynaceae		x			x	
Hemipogon acerosus Decne.	Apocynaceae	x	x	x	x	x	x
Syagrus sp	Areacacea	x	x	x	x	x	x
Aldama grandiflora (Gardner) E.E.Schill. & Panero	Asteraceae	x	x	x	x	x	x
Ayapana amygdalina (Lam.) R.M.King & H.Rob	Asteraceae				x	x	x
Eremanthus goayzesnsis (Gardner) Sch.Bip.	Asteraceae	x			x		
Ichthyothere hirsuta Gardner	Asteraceae	x	x	x	x	x	x
Ichthyothere terminalis (Spreng.) S.F.Blake	Asteraceae	x					
Lessingianthus durus (Mart. ex DC.) H.Rob.	Asteraceae	x			x		
Porophyllum obscurum (Spreng.) DC	Asteraceae	x	x		x		x
Praxelis kleinioides (Kunth) Sch. Bip.	Asteraceae			x			
Anemopaegma arvense (Vell.) Stellfeld ex de Souza	Bignoniaceae	x	x	x	x	x	x
Kielmeyera abdita Saddi	Calophyllaceae	x			x	x	x
Kielmeyera rubriflora Cambess.	Calophyllaceae	x	x	x	x	x	x
Caryocar brasiliense Cambess.	Caryocaraceae			x			x
Connarus suberosus Planch.	Connaraceae		x			x	
Ipomoea echioides Choisy	Convolvulaceae	x	x	x		x	x
Ipomoea fiebrigii Hassl. ex O'Donell	Convolvulaceae			x			x
Merremia ericoides (Meisn.) Hallier f.	Convolvulaceae		x			x	
Bulbostylis junciformis (Kunth) C.B.Clarke	Cyperaceae		x		x		

Bulbostylis paradoxa (Spreng.) Lindm.	Cyperaceae	x	x	x	x	x	x

		wet season			dry season		
Species	**Family**	**AF**	**FE**	**BF**	**AF**	**FE**	**BF**
Rhynchospora consanguinea (Kunth) Boeckeler	Cyperaceae	x	x	x	x		x
Rhynchospora elatior Kunth	Cyperaceae		x	x	x		x
Rhynchospora globosa (Kunth) Roem. & Schult.	Cyperaceae	x	x	x	x	x	x
Rhynchospora sp	Cyperaceae	x					
Erythroxylum suberosum A.St.-Hil.	Erythoxylaceae	x			x	x	
Bernardia hirsutissima (Baill.) Müll.Arg.	Euphorbiaceae	x	x	x	x	x	x
Croton gracilescens Müll.Arg.	Euphorbiaceae	x	x	x	x	x	x
Dalechampia linearis Baill.	Euphorbiaceae	x	x			x	x
Euphorbia potentilloides Boiss.	Euphorbiaceae	x	x	x	x	x	x
Euphorbia sp	Euphorbiaceae	x					x
Manihot kalungae M.J. Silva & R.C. Sodré	Euphorbiaceae	x	x	x	x		x
Manihot tombadorensis M. Mend. & T.B. Cavalc.	Euphorbiaceae	x					
Aeschynomene sp	Fabaceae	x		x	x	x	x
Bauhinia dumosa Benth.	Fabaceae	x	x	x	x	x	x
Calliandra dysantha Benth.	Fabaceae	x		x	x	x	x
Chamaecrista claussenii (Benth.) H.S.Irwin & Barneby	Fabaceae	x	x	x	x	x	x
Chamaecrista fagonioides (Vogel) H.S.Irwin & Barneby	Fabaceae	x		x	x		x
Chamaecrista isidorea (Benth.) H.S.Irwin & Barneby	Fabaceae	x	x	x	x	x	x
Chamaecrista ochrosperma (H.S.Irwin & Barneby) H.S.Irwin & Barneby	Fabaceae	x		x	x		x
Clitoria sp	Fabaceae		x	x			
Desmodium platycarpum Benth.	Fabaceae			x			x
Eriosema congestum Benth.	Fabaceae		x	x		x	x
Eriosema sp	Fabaceae		x	x		x	x
Galactia sp	Fabaceae	x	x	x	x	x	x
Harpalyce tombadorensis São-Mateus, L.P.Queiroz & D.B.O.S.Cardoso	Fabaceae	x	x	x	x	x	x

		wet season			dry season		
Species	**Family**	**AF**	**FE**	**BF**	**AF**	**FE**	**BF**
Mimosa diminuta M.F.Simon & C.E. Hughes	Fabaceae		x				
Mimosa flavocaesia Barneby	Fabaceae	x	x	x	x	x	x
Mimosa gracilis Benth.	Fabaceae	x	x	x	x	x	x
Mimosa leiocephala Benth.	Fabaceae	x	x	x	x	x	x
Mimosa longipes Benth.	Fabaceae			x			
Mimosa macrocephala Benth.	Fabaceae	x		x	x		x
Mimosa pteridifolia Benth.	Fabaceae	x	x	x	x	x	x
Senna corifolia (Benth.) H.S.Irwin & Barneby var. *corifolia*	Fabaceae				x	x	x
Deianira pallescens Cham. & Schltdl.	Gentianaceae	x	x		x		x
Cipura xanthomelas Klatt	Iridaceae	x	x				x
Sisyrinchium luzula Klotzsch ex Klatt	Iridaceae	x	x	x	x	x	x
Trimezia juncifolia (Klatt) Benth. & Hook.	Iridaceae	x					
Amasonia hirta Benth.	Lamiaceae	x	x	x	x	x	x
Eriope glandulosa (Harley) Harley	Lamiaceae	x	x	x	x	x	x
Gymneia chapadensis Harley	Lamiaceae		x				
Hypenia brachystachys (Pohl ex Benth.) Harley	Lamiaceae				x	x	x
Hypenia sp	Lamiaceae	x	x	x	x	x	x
Hyptis remota Pohl ex Benth.	Lamiaceae	x	x	x	x	x	x
Medusantha mollissima (Benth.) Harley & J.F.B.Pastore	Lamiaceae	x	x	x	x	x	x
Cuphea ericoides Cham. & Schltdl.	Lythraceae					x	
Cuphea sp	Lythraceae			x			
Diplusodon longipes Koehne	Lythraceae	x	x	x	x	x	x
Diplusodon paraisoensis Lourteig	Lythraceae	x	x	x	x		x
Diplusodon punctatus Pohl	Lythraceae	x	x	x	x	x	x
Banisteriopsis pannosa Griseb.	Malpighiaceae				x	x	x
Byrsonima sp	Malpighiaceae	x			x		x

		wet season			dry season		
Species	**Family**	**AF**	**FE**	**BF**	**AF**	**FE**	**BF**
Camarea ericoides A.St.-Hil.	Malpighiaceae	x			x		x
Byttneria jaculifolia Pohl	Malvaceae	x	x	x		x	
Pavonia grandiflora A.St.-Hil.	Malvaceae						x
Peltaea macedoi Krapov. & Cristóbal	Malvaceae	x		x	x	x	x
Tibouchina melastomoides (Naudin) Cogn.	Melastomataceae	x	x	x	x	x	x
Brosimum gaudichaudii Trécul	Moraceae		x	x	x	x	
Eugenia paracatuana O.Berg	Myrtaceae	x	x	x	x	x	x
Myrcia laruotteana Cambess.	Myrtaceae	x		x	x		x
Ouratea lanceolata (Pohl) Engl.	Ochnaceae	x			x		
Habenaria tamanduensis Schltr.	Orchidaceae	x		x	x		x
Oxalis goyazensis Turcz.	Oxiladiceae	x	x		x		
Oxalis pyrenea var. *macrochaeta* Lourteig	Oxiladiceae	x			x		
Andropogon lateralis Nees	Poaceae	x	x	x	x	x	x
Anthaenantia lanata (Kunth) Benth.	Poaceae	x	x	x	x	x	x
Aristida setifolia Kunth	Poaceae				x	x	x
Arthropogon villosus Nees	Poaceae	x	x	x	x	x	x
Axonopus aureus P. Beauv.	Poaceae		x	x		x	
*Axonopus brasiliensis (*Spreng.) Kuhlm.	Poaceae			x			
Axonopus pressus (Nees ex Steud.) Parodi	Poaceae	x	x	x	x	x	x
Elionurus muticus (Spreng.) Kuntze	Poaceae	x	x	x	x	x	x
Mesosetum ferrugineum (Trin.) Chase	Poaceae	x	x	x	x	x	x
Mesosetum loliiforme (Hochst.) Chase	Poaceae	x	x	x	x	x	x
Oncorachis ramosa (Zuloaga & Soderstr.) Morrone & Zuloaga	Poaceae	x	x	x	x	x	x
Panicum sp	Poaceae						x
Paspalum pectinatum Nees ex Trin.	Poaceae						x
Schizachyrium sp	Poaceae	x	x	x	x	x	x

		wet season			**dry season**		
Species	**Family**	**AF**	**FE**	**BF**	**AF**	**FE**	**BF**
Trachypogon spicatus (L.f.) Kuntze	Poaceae	x	x	x	x	x	x
Trichanthecium cyanescens (Nees ex Trin.) Zuloaga & Morrone	Poaceae	x			x		x
Polygala abreui Marques & J.F.B.Pastore	Polygalaceae			x			
Polygala sp	Polygalaceae	x		x	x		
Polygala coriacea A.St.-Hil. & Moq.	Polygalaceae	x			x		
Polygala longicaulis Kunth.	Polygalaceae	x		x	x		x
Crumenaria choretroides Mart. ex Reissek	Rhamnaceae	x					
Borreria poaya (A.St.-Hil.) DC.	Rubiaceae	x	x		x		x
Declieuxia lancifolia J.H.Kirkbr.	Rubiaceae		x			x	
Palicourea rigida Kunth	Rubiaceae				x		x
Spermacoce tenella Kunth	Rubiaceae	x			x		x
Casearia sylvestris Sw.	Salicaceae	x	x	x	x	x	x
Serjania trichomisca Radlk.	Sapindaceae	x			x		
Vellozia squamata Pohl	Velloziaceae	x	x	x	x	x	x
Lippia grandiflora Mart. & Schauer	Verbenaceae	x			x		
Lippia triphylla (L'Hér.) Kuntze	Verbenaceae	x	x	x	x	x	x
Vochysia pumila Pohl	Vochysiaceae						x

Table S2. Differences in the number of species (m^2) for each treatment over time T0 (dry season, before of fire), T6 (rainy season, six months post-fire) and T12 (dry season, 12 months post-fire), in campo *sujo* areas, Central Brazil

Treatment		**p**
FE	T0 x T6	0.001
FE	T0 x T12	0.06
BF	T0 x T6	0.01
BF	T0 x T12	<0.0001
AF	T0 x T6	0.02
AF	T0 x T12	0.03

Table S3. Differences in cover of growth form (G = graminoids; S = shrubs and F = forbs), DB = dead biomass and BS = bare soil (%) between treatments. T0 (dry season, before of fire), T6 (rainy season, 6 months post-fire) and T12 (dry season, 12 months post-fire), in *campo sujo* areas, Central Brazil

Time		**DB**	**BS**	**G**	**S**	**F**
T0	FE x AF	< 0.0001	< 0.0001	0.19	0.77	0.31
	FE x BF	0.006	0.11	0.49	0.51	0.13
	AF x BF	< 0.0001	< 0.0001	0.30	0.50	0.62
T6	FE x AF	< 0.0001	< 0.0001	0.12	0.35	0.36
	FE x BF	< 0.0001	< 0.0001	0.33	0.27	0.38
	AF x BF	0.0001	0.32	0.33	0.71	0.98
T12	FE x AF	< 0.0001	< 0.0001	0.44	0.92	< 0.0001
	FE x BF	< 0.0001	< 0.0001	0.43	0.41	0.0003
	AF x BF	0.13	0.002	0.94	0.09	0.40

CONSIDERAÇÕES FINAIS

O Cerrado é um ecossistema inflamável, que evoluiu na presença do fogo e que depende dele para manter suas fisionomias e biodiversidade (Simon et al., 2009; Coutinho, 1990; Pivello, 2011; Abreu et al., 2017; Durigan e Ratter, 2016). A frequência é um dos parâmetros do regime de fogo que influencia diretamente a composição, estrutura e produtividade das comunidades vegetais (Vale e Lopes, 2011; Higgins et al., 2000; Whelan, 1995). O adensamento da vegetação, extinção de espécies e incêndios descontrolados provocados pela exclusão do fogo (Moreira 2001; Abreu et al. 2017), bem como os efeitos degradantes no solo e eliminação de espécies provocados por queimas muito frequentes, afetam não apenas a biodiversidade, mas também os muitos serviços ecossistêmicos prestados pela vegetação nativa do Cerrado (Pivello, 2011). Importantes exemplos destes serviços, incluem a regulação do clima e da água para grande parte do Brasil, incluindo a Amazônia e países vizinhos, contribuindo para a recarga do sistema subterrâneo do aquífero Guarani (Durigan 2010).

Atualmente existe uma grande discussão sobre o uso do fogo como ferramenta de manejo em unidades de conservação de Cerrado (Durigan e Ratter 2016; Fidelis e Pivello 2011). Já há desde 2014 a implementação do Manejo Integrado de Fogo em diversas unidades de conservação, baseados em mapas de acúmulo de biomassa (Schmidt et al. 2018). Desta maneira, estudos baseados em experimentos de campo que possam contribuir para um melhor planejamento destes planos de manejo integrado de fogo são de extrema importância para os gestores de unidades de conservação.

Os resultados apresentados no primeiro capítulo mostram o quanto o incremento de biomassa morta, bem como a continuidade da distribuição do material combustível respondem ao tempo desde o último fogo, ou seja, ao acúmulo de biomassa morta principalmente. Ainda que ambos os tratamentos (queimadas anuais e bienais) sejam considerados de alta frequência, conseguimos observar valores superiores de biomassa morta nas parcelas bienais quando comparadas às anuais, em conjunto com a significativa diminuição de porcentagem de solo descoberto. Isto refletiu em importantes parâmetros do comportamento do fogo, como intensidade, altura da chama, temperaturas máximas registradas e tempo de residência do fogo.

Alterações nestes parâmetros trazem consequências ecológicas, uma vez que podem ocasionar morte de tecidos (Bova e Dickinson, 2005), de propágulos ou de toda a planta (Bradstock e Auld, 1995; Cirne & Miranda, 2008; Coutinho, 1990), afetar o recrutamento de espécies pós-fogo, provocar alterações em características ambientais tais como condições nutricionais do solo (Malanson & Trabaud, 1988; 2000;Whelan, 1995) e estimular a germinação de sementes a partir da quebra de dormência (Moreira e Pausas, 2012), ou mesmo levar a morte de algumas sementes (Daibes et al. 2018).

De qualquer maneira, ainda que as diferenças tenham sido significativas, ambas as frequências de queimas apresentaram intensidades e temperaturas de fogo consideradas moderadas (Govender et al., 2006). No entanto, se considerarmos os dados de incremento de biomassa morta e solo descoberto nas parcelas excluídas do fogo, encontrados no segundo capítulo, podemos inferir que uma queima nessas áreas provavelmente seria muito mais intensa e as temperaturas máximas alcançadas e o tempo de residência do fogo seriam superiores aos encontrados para as demais frequências, o que poderia provocar danos muito mais severos a comunidade.

Além disso, como vimos, a exclusão do fogo há mais de seis anos da comunidade está resultando em perda de biodiversidade e diminuição no incremento de biomassa viva, principalmente de pequenos arbustos e herbáceas. Com isso a dominância de gramíneas tende a aumentar e agravar a perda de espécies da comunidade (Connell, 1980; Huston, 1979; Pickett, 1980). Complementar a isso, é importante considerarmos que o aumento do tempo de exclusão do fogo também pode levar à extinção de espécies que estão dormentes na comunidade nos bancos de sementes e de gemas e que dependem dos estímulos provocados por eventos de fogo para germinarem e/ou rebrotarem (Specht et al., 1958).

Em contrapartida, observamos nas áreas frequentemente queimadas maior riqueza e diversidade de espécies. As parcelas com queimas anuais apresentaram as menores porcentagens de perda de espécies entre os tratamentos. Quanto a composição de espécies das comunidades, as áreas com exclusão do fogo foram as que menos se alteraram, com uma pequena mudança durante a estação chuvosa, mas retornando à composição anterior na próxima estação seca. As áreas com queimas bienais após as queimadas sofreram uma abrupta alteração na composição de espécies, o que as tornaram mais similares às comunidades em áreas com queimadas anuais antes das queimas e durante a estação chuvosa, seis meses após o fogo. As comunidades vegetais queimadas todos os anos, por sua vez, mostraram uma grande mudança nas suas comunidades logo após o fogo, distanciando-se do padrão observado antes e seis meses após as queimas. Esta alteração das comunidades sob queimadas anuais um ano após os experimentos de fogo não foi observada nas bienais e levanta o seguinte questionamento: mantida a alta frequência de queimas, estas comunidades continuarão passando por mudanças em sua composição, diferenciando-se das comunidades sob queimadas bienais, tanto na riqueza quanto na cobertura das espécies que compõem os diferentes grupos funcionais?

Ainda que não tenhamos encontrado diferenças na cobertura dos grupos funcionais entre os tratamentos, exceto para as herbáceas que estão aumentando a cobertura nas áreas frequentemente queimadas, observamos um impacto negativo das queimas anuais na cobertura de graminóides, o que no futuro pode levar a uma diminuição deste grupo na comunidade e que possivelmente afetaria levaria a alterações no comportamento do fogo nestas parcelas, já que o principal componente responsável pela continuidade da distribuição do material combustível na vegetação são os graminóides (Simpson et al., 2016). Com menos material combustível e maior porcentagem de solo descoberto, o fogo teria dificuldade para se propagar e se sustentar, diminuindo a intensidade, as temperaturas e os tempos de residência das queimas. Desta forma, as áreas já não apresentariam uma alta eficiência de queima como no momento e portanto, tais áreas já não queimariam mais como antes.

Em resumo os resultados deste estudo indicam que as comunidades sob altas frequências de queimas mostram-se resilientes ao fogo. As mudanças encontradas nas parcelas com queimas anuais encorajam a continuidade no acompanhamento destas comunidades afim de compreender se elas indicam diminuição da resiliência ao fogo ao longo do tempo, com mais queimadas sendo feitas regularmente.

Por sua vez, a exclusão do fogo mostrou-se prejudicial à comunidade, uma vez que encontramos um número menor de espécies, dominância do grupo funcional dos graminóides e diminuição no incremento de biomassa viva. Finalmente, o grande acúmulo de biomassa morta (principalmente de graminóides) nessas áreas pode levar a queimadas de maiores intensidades e severidades.

Deste modo, recomendamos queimas prescritas com intervalos não superiores há 3 anos como ação de manejo, visando manter a diversidade de espécies das comunidades de fisionomias abertas de Cerrado, evitando-se assim, danos severos à vegetação (Pivello 2006a, 2006b), à saúde humana (Bowman et al., 2009), sociais e econômicos (Gill et al. 2013; Benali et al.,2017; Moritz et al., 2014) que são próprios de queimas descontroladas. No entanto, não sugerimos o uso de queimas anuais, principalmente a longo prazo, pois encontramos neste estudo indicativos de alterações nos padrões da comunidade.

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