PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E BIODIVERSIDADE

COMO QUEIMADAS EM DIFERENTES ÉPOCAS DO ANO AFETAM A RELAÇÃO ENTRE GRAMÍNEAS INVASORAS E A VEGETAÇÃO NATIVA DE CERRADO?

Gabriella De Faria Oliveira Damasceno Ribeiro

Dissertação apresentada ao Instituto de Biociências do *campus* de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de mestre em Ecologia e Biodiversidade

Rio Claro/SP
Junho de 2017

GABRIELLA DE FARIA OLIVEIRA DAMASCENO RIBEIRO

COMO QUEIMADAS EM DIFERENTES ÉPOCAS DO ANO AFETAM A RELAÇÃO ENTRE GRAMÍNEAS INVASORAS E A VEGETAÇÃO NATIVA DE CERRADO?

Dissertação apresentada ao Instituto de Biociências do *campus* de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de mestre em Ecologia e Biodiversidade

Orientadora: Profa. Dra. Alessandra Fidelis

Rio Claro/SP
Junho de 2017

581.5264 Ribeiro, Gabriella de Faria Oliveira Damasceno
R484c Como queimadas em diferentes épocas do ano afetam a relação entre gramíneas invasoras e a vegetação nativa de Cerrado? / Gabriella de Faria Oliveira Damasceno Ribeiro. - Rio Claro, 2017
93 f. : il., figs., gráfs., tabs.

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

1. Cerrados. 2. Manejo de espécies invasoras. 3. Restauração ecológica. 4. Invasão biológica. 5. Melinis minutiflora. 6. Urochloa brizantha. I. Título.

Ficha Catalográfica elaborada pela STATI - Biblioteca da UNESP
Campus de Rio Claro/SP

unesp

UNIVERSIDADE ESTADUAL PAULISTA

Câmpus de Rio Claro

CERTIFICADO DE APROVAÇÃO

TÍTULO DA DISSERTAÇÃO: Como queimadas em diferentes épocas do ano afetam a relação entre gramíneas invasoras e a vegetação nativa do Cerrado?

AUTORA: GABRIELLA DE FARIA OLIVEIRA DAMASCENO RIBEIRO
ORIENTADORA: ALESSANDRA TOMASELLI FIDELIS

Aprovada como parte das exigências para obtenção do Título de Mestra em ECOLOGIA E BIODIVERSIDADE, área de conhecimento: ECOLOGIA pela Comissão Examinadora:

Profa. Dra. ALESSANDRA TOMASELLI FIDELIS
Departamento de Botânica / Instituto de Biociências de Rio Claro - SP

Profa. Dra. VÂNIA REGINA PIVELLO
Departamento de Ecologia / Instituto de Biociências - Universidade de São Paulo / SP

Profa. Dra. GISELDA DURIGAN
Divisão de Florestas e Estações Experimentais - Floresta Estadual de Assis / Instituto Florestal do Estado de São Paulo - Assis/SP

Rio Claro, 04 de agosto de 2017

Dedico este trabalho ao Cerrado: que ele continue (re)existindo!

AGRADECIMENTOS

Agradeço a todos que, de uma forma ou de outra, abriram mão de algo para que este trabalho fosse concluído com sucesso.

Primeiramente, à Alessandra, a quem esta dissertação também pertence. Chefe, obrigada pela presença, parceria, disponibilidade, ensinamentos, oportunidades, correções e pelo crescimento que você incentivou, tanto no aspecto profissional quanto no pessoal.

Às equipes do LEVeg, pretéritas e atual, muito obrigada pela ajuda nas tantas pequenas partes das quais este trabalho é feito: campos, discussões, apresentações, disciplinas, congressos, análises, revisões, hospedagens, botecos, risadas, aprendizados e divertimentos.

Agradeço à SMA/SP pela possibilidade de execução (processo 260108 – 008.914/2012); ao PPG em Ecologia e Biodiversidade, à UNESP e seus funcionários e ao pessoal da Estação Ecológica de Itirapina, pela efetiva realização deste projeto.

Agradeço às instituições que financeiramente viabilizaram este trabalho: à CAPES, pelos dois meses de bolsa; à FAPESP pela bolsa de mestrado (2015/10714-6) e pelo projeto Jovem Pesquisador ao qual ela é vinculada (2015/06743-0); e à Neotropical Grassland Conservancy pela concessão de financiamento adicional.

Agradeço aos meus familiares, especialmente aos meus pais, Raquel e Cláudio, que viabilizaram, incentivaram, apoiaram e acreditaram em tudo que eu me arrisquei a fazer. À minha irmã, Isabella, por ser uma parceria certa mesmo nas distâncias mais remotas. Agradeço aos meus avós, Zezé e Aparecido, por serem sempre um suporte adicional em todos os momentos. A todos aqueles que sempre foram o aconchego de voltar pras Minas Gerais.

Agradeço à Tamires, minha parceira de vida. Obrigada pelo apoio, respeito, carinho, companheirismo e amizade ao longo de todo o nosso caminho e nessa jornada mestrado. Agradeço também a minha família expandida que me incorporou com tanta receptividade: Lê, Carlão, Mu e Gui, obrigada por todos os momentos dos quais eu fiz parte.

Agradeço ainda aos amigos de todos os lugares: obrigada pelo carinho emanado de tanta lonjura. Aos de Araguari, há 12 anos que é bom contar com vocês, Tóix! A todos aqueles que a capital federal me proporcionou: os velhos do Yellow (um salve especial pra Anninha, mãe acadêmica e grande amiga), as sempre presentes Tina e Yara, o companheiríssimo Marcelo. Ao pessoal de Rio Claro, em especial ao Johnny e a Ana, que aceitaram formar uma república-família comigo. Aos amigos de São Carlos, que começaram por não ser meus, mas que agora fazem parte da minha própria lista de pessoas especiais: alô vizinhança!

A todos vocês, os meus mais sinceros e carinhosos agradecimentos! =)

“ – Está aí.
Se aprendesse qualquer coisa,
necessitaria aprender mais,
e nunca ficaria satisfeito.”

Vidas Secas, Graciliano Ramos

RESUMO GERAL

Gramíneas africanas são uma das principais ameaças à conservação da biodiversidade do Cerrado por estarem amplamente dispersas no interior de unidades de conservação. *Melinis minutiflora* e espécies do gênero *Urochloa*, como *U. brizantha* e *U. decumbens,* estão entre as invasoras mais comuns, alterando inclusive, regimes de distúrbio, como queimadas naturais. O fogo é um elemento recorrente em sistemas savânicos e, assim, a vegetação savânica é resiliente e apresenta adaptações ao regime de fogo. Este estudo avaliou 1) o impacto que as gramíneas invasoras *Melinis minutiflora* e *Urochloa brizantha* causam na vegetação nativa de Cerrado; 2) o efeito da época de queima no controle destas duas espécies; e 3) as alterações de diversidade das comunidades invadidas em resposta à queimadas em diferentes épocas do ano. A área de estudo está inserida na Estação Ecológica de Itirapina e, até o ano 1998, foi utilizada para silvicultura de *Pinus caribaea*, sendo que desde, então, fogo e pastejo foram excluídos. O delineamento experimental é composto por 32 parcelas (15x15m) dominadas por uma das duas espécies invasoras (cobertura mínima de 50%) e aleatoriamente submetidas a três tratamentos de queima: precoce (maio), modal (julho) e tardia (outubro), além de parcelas controle não queimadas (4 parcelas/tratamento/espécie invasora = 32 parcelas). Os experimentos de queima ocorreram em 2014 (maio, julho e outubro), sendo a amostragem da vegetação realizada anteriormente às queimas e ao longo de dois anos após sua execução. Realizamos amostragens de biomassa e cobertura da vegetação em subparcelas no interior das parcelas experimentais (15x15m) devido à heterogeneidade do ambiente pós-fogo. Para atender aos objetivos, utilizamos 1) o índice de impacto de Cohen's D; 2) modelos aditivos mistos para analisar a biomassa das invasoras e da vegetação nativa ao longo do tempo; 3) análises multivariadas (PERMANOVA e PcoA) para estimar a diversidade beta entre parcelas queimadas e não queimadas através da cobertura das espécies invasoras e nativas. Ambas as espécies impactaram de forma mais e menos pronunciada as gramíneas e as herbáceas nativas, respectivamente. *Melinis minutiflora* exerceu efeitos mais pronunciados do que *Urochloa brizantha* devido à sua grande produção de biomassa, havendo, ainda uma variação sazonal do impacto. No geral, comunidades invadidas e não-invadidas diferiram entre si em estrutura, assim como diferiram as comunidades

invadidas por diferentes espécies. As queimadas prescritas reduziram a abundância de *M. minutiflora* em todos os tratamentos. Entretanto, a abundância de *U. brizantha* não foi afetada por nenhuma época de queima, apesar de sua biomassa total ter sido temporariamente reduzida até o final da próxima estação chuvosa. Nas parcelas inicialmente invadidas por *M. minutiflora,* queimas no início e no final da estação seca favoreceram uma nova invasão por *U. brizantha* em virtude da disponibilidade de propágulos desta espécie. A biomassa de plantas herbáceas não-graminóides foi aumentada nas parcelas invadidas por *Melinis minutiflora* após queimadas modais. Considerando o efeito da época de queima nas comunidades como um todo, a identidade da espécie invasora foi relevante nas respostas observadas. Nas comunidades invadidas por *M. minutiflora*, a época de queima aumentou a diversidade das parcelas queimadas em relação aos controles não-queimados, com exceção do tratamento tardio, que ao fim de dois anos resultou em comunidades menos diversas. Nas comunidades invadidas por *U. brizantha*, fogo em qualquer época diminuiu a diversidade das parcelas queimadas em relação às parcelas controle, mas após dois anos da realização das queimadas há uma tendência em retomar os valores encontrados no ambiente pré-fogo. Estas respostas das comunidades à época de queima são dependentes da regeneração da invasora inicialmente dominante em cada uma delas. *M. minutiflora* foi reduzida pelas queimas em todas as épocas, criando no interior da comunidade espaços de solo nu, que deram origem a processos estocásticos de colonização, guiados principalmente pela disponibilidade de propágulos de espécies nativas e de *U. brizantha*. Por sua vez, nas comunidades dominadas por esta invasora, sua rápida regeneração inibiu o estabelecimento de espécies nativas em virtude da ocupação do espaço e da sobreposição no nicho temporal. Em função das respostas levantadas neste estudo, recomendamos o uso de queimadas prescritas em julho (meio da estação seca) para controle de *Melinis minutiflora* visando aumentar o sucesso de projetos de restauração de Cerrado. O uso de queimadas prescritas para o controle de *Urochloa brizantha,* entretanto, deve ser realizado apenas para remover temporariamente sua biomassa do sistema, permitindo a implementação de outras ações de restauração, como a semeadura de espécies nativas.

SUMÁRIO

INTRODUÇÃO GERAL

INVASÕES BIOLÓGICAS

Toda e qualquer espécie, em virtude de seu processo evolutivo, foi selecionada a um determinado ambiente, com condições ambientais específicas, que delimitam sua área de ocorrência natural (Kirkpatrick 1996). O processo de invasão biológica é a ampliação da área de ocorrência natural de uma espécie, que é capaz de colonizar ambientes distintos daqueles nas quais sua evolução ocorreu. Esta ampliação pode ser em parte ou totalmente assistida por ações humanas, intencionais ou não. Entretanto, o prosseguimento do processo invasivo é, teoricamente, reversível, dado que modificações do ambiente e/ou ações antrópicas podem alterar o status de uma espécie não-nativa no novo sistema na qual ela se encontra (Richardson et al. 2000).

Richardson et al. (2000) detalharam as etapas do processo de invasão biológica e sintetizaram as barreiras que uma espécie deve vencer para que seja considerada como invasora em um sistema (Figura 1). A primeira delas é a barreira geográfica em larga escala, que se caracteriza simplesmente pela extrapolação da área natural de ocorrência de uma espécie. As espécies que vencem esta barreira são consideradas exóticas, sendo chamadas de casuais quando não são capazes de persistir no novo ambiente. As próximas barreiras a serem vencidas são referentes à reprodução e dispersão, ultrapassadas quando o organismo já estabelecido é capaz de dispersar descendentes no novo ambiente, tornando-se uma espécie naturalizada. Por fim, as últimas etapas do processo de invasão são a superação de barreiras ambientais em escalas locais em sistemas perturbados (antropicamente modificados ou já dominados por outras espécies invasoras) e em sistemas naturais.

Espécies invasoras são um problema global (Vitousek 1992; Pyšek et al. 2012) tanto em sistemas antrópicos quanto em sistemas naturais (Simberloff & Rejmánek 2011; Simberloff 2013). No primeiro caso, uma espécie pode gerar perdas financeiras em sistemas produtivos ao se comportar como praga agrícola (Pimentel et al. 2001; Paini et al. 2016) ou ao impactar atividades econômicas como o funcionamento de usinas hidroelétricas (Connelly et al. 2007). No âmbito da saúde pública, espécies invasoras podem ser responsáveis pela disseminação de doenças (Gubler 2002). Em intersecção aos problemas ambientais, espécies invasoras são capazes de alterar bens e serviços ecossistêmicos, como o ciclo da água e sua disponibilidade para utilização humana (Rossiter et al. 2004; Pejchar & Mooney 2009). Com relação aos sistemas naturais, espécies invasoras são consideradas ameaças por, em última instância, causarem perda de biodiversidade por meio de extinções (Chapin et al. 2000; Gilbert & Levine 2013).

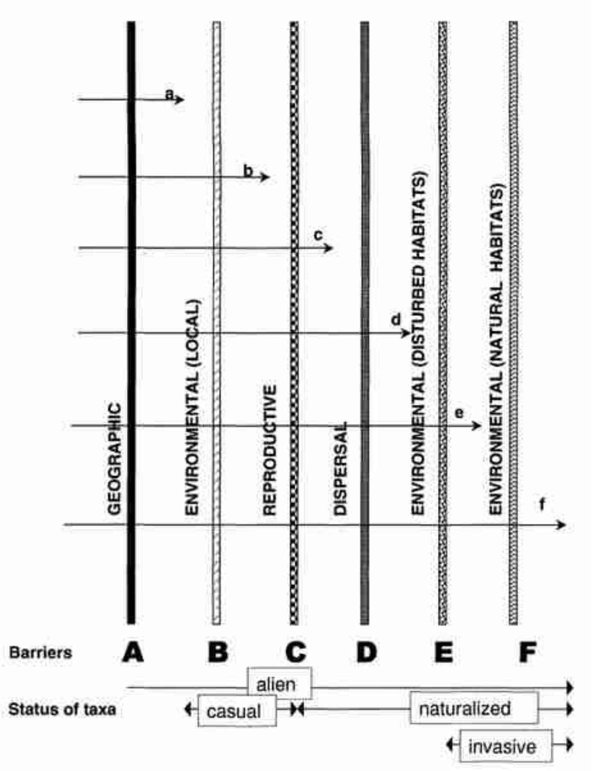

Figura 1. Esquema do processo pelo qual uma espécie torna-se invasora vencendo barreiras geográficas e ambientais sucessivas. As barras verticais representam as barreiras (A) geográfica em larga escala; (B) ambiental local; (C) reprodutiva; (D) de dispersão; (E) ambiental para a colonização de áreas disturbadas; e (F) não disturbadas. As caixas horizontais na parte inferior da figura indicam o status da espécie: exótica (alien); casual (casual); naturalizada (naturalized); e invasora(invasive). Retirado de Richardson et al. (2000).

Nestes sistemas naturais, invasões biológicas de espécies vegetais são mais comuns do que aquelas causadas por animais e tendem a ser mais impactantes em virtude de estarem intimamente relacionadas à configuração do hábitat e à base das cadeias alimentares (Mollot et al. 2017). Espécies vegetais invasoras são capazes de impactar o sistema nativo em níveis de população, comunidade e ecossistema (Mack et al. 2000; Vila et al. 2011; Simberloff et al 2013). Nas populações, interações agonísticas com espécies não-invasoras são capazes de reduzir a abundância e alterar a distribuição das populações nativas (Callaway and Ridenour 2004; Gordon 1998). Já nas comunidade vegetais, são capazes de modificar sua estrutura, diversidade e funcionamento (Gardner et al. 2009; Bernard-Verdier and Hulmes 2015; Flory and Clay 2010), enquanto que no ecossistema acabam por influir em processos como regime de distúrbio natural (Mack & D'Antonio 1998) e ciclagem de nutrientes (Ehrenfeld 2003).

Além disso, estudos sobre espécies invasoras abordam mais plantas como objeto de estudo do que outros organismos: 85% de todos os trabalhos sobre o tema em todo o mundo foram conduzidos com produtores primários (Mollot et al. 2017) enquanto que dos organismos terrestres estudados, 85% foram plantas (Lowry et al. 2013). No Brasil, plantas invasoras são os organismos mais estudados, entretanto, contrariamente ao panorama global, correspondem a apenas 31% do total de trabalhos sobre o tema (Frehse et al. 2016).

O número e o risco de invasões biológicas no Brasil é grande em virtude de sua heterogeneidade de hábitats e da rápida conversão de áreas naturais para fins produtivos (Lövei et al. 2012). Pimentel et al. (2001) estimaram que o número de espécies éxoticas no Brasil seria de cerca de 11709, das quais 11605 espécies seriam de plantas. Zenni (2015) listou 545 espécies de plantas naturalizadas no país, das quais 345 são pertecentes à família Poaceae. Dias et al. (2013), por sua vez, identificaram 54 espécies de plantas invasoras no Brasil, sendo também a maioria pertencente à família Poaceae. Em áreas naturais protegidas, foram identificadas 125 espécies de plantas exóticas invasoras em 163 unidades de conservação por meio de 728 ocorrências (Ziller & Dechoum 2013).

As gramíneas invasoras são principalmente do tipo C_4, oriundas do continente africano (Zenni 2014). Em sistemas nos quais o estrato herbáceo é dominante – como o Pampa e o Cerrado – são capazes de alterar os processos competitivos e modificar a dinâmica da comunidade, sem, entretanto, modificarem a estrutura da vegetação em si (Reed et al. 2005). Nesta família, as espécies invasoras mais abundantes no Brasil são aquelas utilizadas como pastagem para gado, como as do gênero *Urochloa* (capins-braquiária), *Melinis minutiflora* (capim-gordura)*, Megathyrsus maximum* (capim-colonião)*, Hyparrenia rufa* (capim-jaraguá) e *Andropogon gayanus* (capim-andropogon) (Figura 2; Brossard & Barcellos 2005). Em virtude de atributos que conferem vantagens competitivas às espécies invasoras, como, por exemplo, rápido acúmulo de biomassa e altas taxas de sobrevivência e reprodução (Richardson 2006), espécies de gramíneas expandem suas áreas de ocorrência para além das pastagens onde foram intencionalmente inseridas, avançando inclusive sobre áreas de conservação, notadamente daquelas localizadas no bioma Cerrado (Pivello et al. 1999a; Freitas & Pivello 2005).

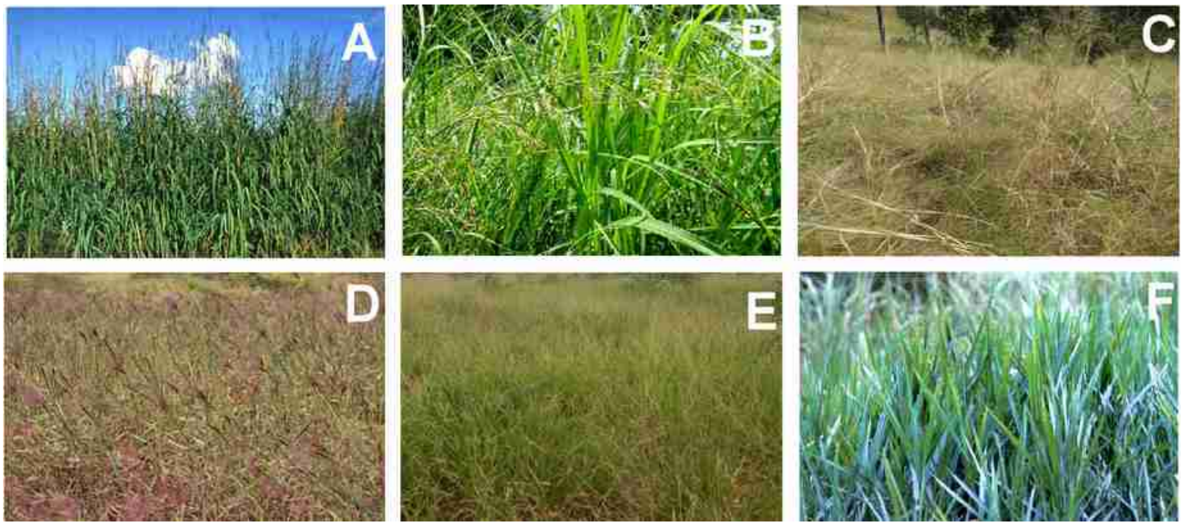

Figura 2. Gramíneas africanas invasoras no Brasil. (A) *Andropogon gayanus;* (B) *Hyparrenia rufa;* (C) *Megathyrsus maximus;* (D) *Melinis minutiflora;* (E) *Urochloa brizantha;* (F) *Urochloa decumbens*. Imagens (A), (B) e (F) foram retiradas do portal de galeria de imagens de gramíneas forrageiras da Organização das Nações Unidas para Agricultura e Alimentação. Endereço: http://www.fao.org/ag/AGP/agpc/doc/Gallery/pic.htm. Acesso em 16/01/2017. Fotos (C), (D) e (E): Alessandra Fidelis.

O CERRADO E O FOGO

O Cerrado é o segundo maior domínio fitogeográfico brasileiro e está localizado na porção central do país, ocupando 22% do território nacional com cerca de 2 milhões km^2 (IBGE 2004). Até o momento foram identificadas mais de 12 mil espécies de plantas, das quais 35% (4252 espécies) são endêmicas ao Cerrado (Brazilian Flora Group - BFG 2015). Sua vegetação é formada principalmente por formações savânicas, mas fitofisionomias campestres e florestais intercalam-se com estas formando um mosaico de acordo com as características físicas do ambiente e suas interações com a biota (Coutinho 2002; Walter 2006).

A proporção geral entre o componente arbóreo-arbustivo e o herbáceo é de 1:7 (BFG 2015), e variações em torno desta proporção caracterizam as diferentes formações vegetais. Segundo o sistema de classificação de Ribeiro & Walter (1998), as fitofisionomias podem ser expressas como um gradiente desta proporção, no qual o campo limpo representa a dominância do estrato herbáceo e o cerradão a do componente arbóreo. Ainda segundo estes autores, o bioma Cerrado é constituído pelo conjunto de todas as suas formações vegetais; o cerrado sentido restrito é composto pelas formações savânicas, enquanto que o cerrado sentido amplo engloba ainda as formações campestres e a formação florestal de cerradão.

O clima predominante no Cerrado é tropical chuvoso, classificado como Aw segundo o sistema de Koppen, caracterizado pela marcada sazonalidade climática com uma estação chuvosa e um período mais seco (Walter 2006). A precipitação média anual gira em torno de 1500mm e está concentrada no período chuvoso, que vai de outubro a março (Walter 2006). A temperatura média anual é de 22,5ºC; a média máxima mensal não varia muito ao longo do ano, e apesar da média mínima mensal do mês mais frio ser superior a 18ºC, geadas podem ocorrer na porção mais ao sul (Coutinho 2002; Walter 2006). Os solos típicos são latossolos profundos, bem drenados, ácidos e distróficos, pobres em bases e ricos em cátions, como alumínio e ferro. Em regiões mais baixas, fora do Planalto Central, como no estado de São paulo, os solos podem ainda ser arenos (Eiten 1972; Furley & Ratter 1998; Coutinho 2002).

Os fatores ambientais solo e fogo, em escala regional, são os determinantes da ocorrência das fitofisionomias de Cerrado, pois influenciam diretamente a disponibilidade hídrica ao longo do ano (altura do lençol freático e sua variação) e os recursos disponíveis no solo e o regime distúrbio do sistema, respectivamente (Simon et al. 2009; Eiten 1972; Coutinho 1990; Ribeiro & Walter 1998; Mistry et al. 2010). Particularmente quanto às fitofisionomias campestres e savânicas, as queimadas são em grande parte responsáveis pela sua manutenção, à medida que possuem uma relação de retroalimentação com a comunidade herbácea (Coutinho 1982; Kauffman et al. 1994). A alta inflamabilidade deste estrato (Rundel 1983) facilita a recorrência de queimadas, que, em ambientes nos quais o intervalo de tempo de recorrência de queimadas é curto, dificulta o estabelecimento e a sobrevivência de espécies lenhosas perenes, favorecendo, assim, a comunidade herbácea sazonal (Hoffmann 1998; Medeiros & Miranda 2005).

O fogo é elemento fundamental e recorrente nos biomas savânicos (Bond and Keeley 2005; Bond et al. 2005; Bowman et al. 2009), tendo exercido pressão seletiva na evolução de sua vegetação em diferentes escalas temporais e espaciais (Pausas & Schwilk 2012) que vão desde a expansão das angiospermas no fim do Cretáceo (Bond & Scott 2010), assim como na expansão de gramíneas C_4 no período Mioceno (Keeley & Rundel 2005) e vão até a era humana do fogo, a partir de 2 milhões de anos atrás (Pausas & Keeley 2009). A passagem das chamas causa impactos nas populações, nas comunidades e também nos processos ecossistêmicos, gerando consequências nesses três níveis (Coutinho 1982; Whelan 1995; Bond & Wilgen 1996). Sua importância na determinação das formações vegetais mundiais (Bond et al. 2005) e evolução das espécies de plantas é comprovada através da análise de atributos das espécies adaptadas a sua ocorrência, como os de semente (Keeley et al. 2011), alta inflamabilidade (Bond et al. 1995), isolamento térmico de tecidos vegetais internos (Lawes et al. 2011), estímulo à floração (Lamont & Downes 2011), proteção de gemas (Charles-Dominique et al. 2015) e história de vida (Pausas & Keeley 2014).

A ocorrência de fogo natural no Cerrado foi datada para pelo menos 4 milhões de anos atrás (Simon et al. 2009), tendo sido intensificada no fim da última era glacial há cerca de 10 mil anos, período no qual houve expansão do Cerrado (Pessenda et al. 2005; Power et al. 2008). Sua importância nesse sistema foi demonstrada através de seus efeitos nos componentes abióticos, como alterações de temperatura do ar e do solo (Miranda et al. 1993; Miranda et al. 2002), assim como dos processos ecossistêmicos, como a ciclagem de nutrientes (Pivello & Coutinho 1992) e o fluxo de carbono (Santos et al. 2003). Por sua vez, sua influência na vegetação é demonstrada pela presença de estruturas protetoras, como cortiça espessa para isolamento térmico dos órgãos internos (Coutinho 1990) e sementes resistentes a altas temperaturas (Le Stradic et al. 2015, Fichino et al. 2016); proteção de gemas subterrâneas (Appezzato-da-glória et al. 2008); e floração e frutificação estimuladas pela ocorrência de queimadas (Munhoz & Felfili 2007; Coutinho 1976).

As características e os efeitos das queimadas são determinadas pelo regime de fogo ao qual a vegetação está submetida (Whelan 1995). Este regime de fogo é composto pelos componentes de frequência, intensidade, extensão, tipo e sazonalidade de ocorrência das queimas (Brooks et al. 2004). Importante ressaltar que o fogo não é apenas um distúrbio físico, mas sim um componente do sistema que influencia e interage com a vegetação em um sistema de retroalimentação (Whelan 1995; Bond and Wilgen 1996). Dessa forma, uma vegetação adaptada à passagem das chamas não está adaptada ao fogo em si, mas sim a todo um regime de queimas, e, portanto, modificações em qualquer um dos componentes do regime podem desencadear características de queimas às quais o sistema não esteja adaptado (Whelan 1995; Brooks et al. 2004).

Espécies invasoras são capazes de alterar o regime de fogo nos novos ambientes em que estão inseridas, criando um ciclo de retroalimentação com a ocorrência de queimadas e sua manutenção nas áreas invadidas (D'Antonio & Vitousek 1992; Gorgone-Barbosa et al. 2015). A partir do ponto no qual este ciclo foi estabelecido, outras propriedades do ecossistema também sofrem modificações e iniciativas de restauração das áreas invadidas devem contar com ações de manejo do próprio regime de fogo de forma a restabelecer as condições pretéritas à entrada das invasoras (Brooks et al. 2004).

Gramíneas invasoras são especialmente problemáticas neste aspecto porque, em virtude de sua história de vida, são organismos inflamáveis e adaptados à passagem de fogo, produzindo grandes quantidades de biomassa morta que se acumula como combustível para queimadas, modificando as características do regime de fogo (Figura 3; Rundel 1983; Gagnon et al. 2010; Gorgone-Barbosa et al. 2015). Por sua vez, a relação de retroalimentação entre a ocorrência de queimadas e a flora local (inclusive as invasoras) abre campo para a utilização do fogo como ferramenta de manejo em virtude do distúrbio que causa na comunidade, modificando a hierarquia competitiva entre as espécies (Tyler 1995; Laterra & Solbrig 2001; Wrobleski & Kauffman 2003).

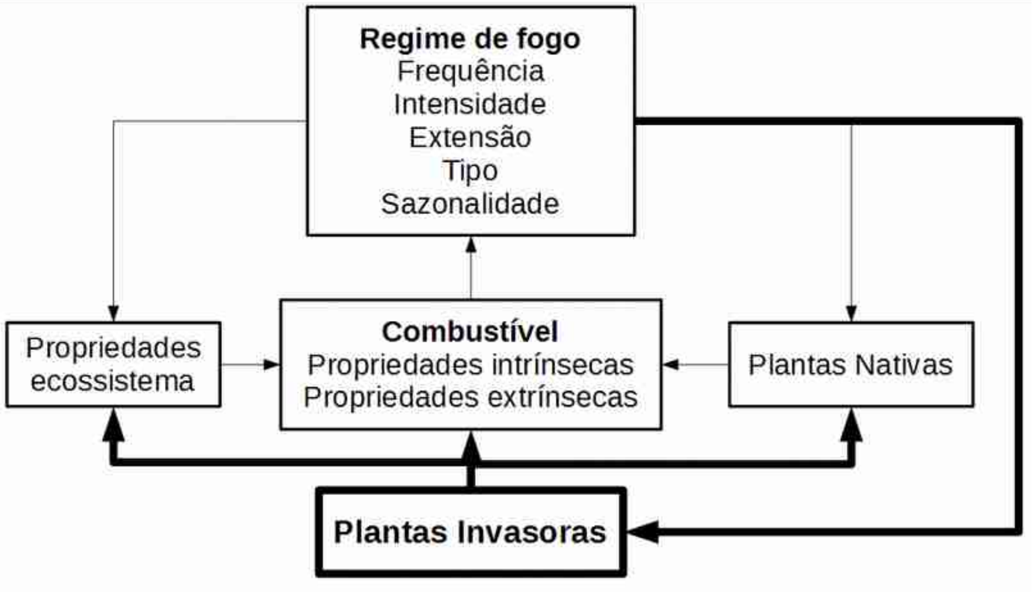

Figura 3. Relação entre regime de fogo, componentes do sistema natural invadido (plantas nativas, propriedades do ecossistema, combustível para queimadas) e plantas invasoras. Modificado de Brooks et al 2004.

O componente de sazonalidade do regime de fogo tem importante papel na dinâmica da comunidade vegetal ao influenciar as interações entre as espécies, pois as modificações do ambiente causadas pelas queimadas podem favorecer ou não a resposta dos indivíduos em função de seu estado fenológico, já que estruturas reprodutivas são mais custosas energeticamente (Bond & Wilgen 1996; Knapp et al. 2009). Queimadas em diferentes épocas do ano constituem-se em distintos regimes de queima, já que conduzem a fogos com características diferentes entre si: fogos no início da estação seca (maio e junho) são mais brandos e frios, pois o material combustível encontra-se úmido; a partir de julho e agosto há acúmulo de biomassa morta no sistema, que possibilita queimadas de maiores temperatura e intensidade em outubro, no início da estação chuvosa (Coutinho 1990; Mistry 1998).

O período de ocorrência de queimadas naturais no Cerrado é na estação chuvosa e na transição entre as estações seca e chuvosa (entre setembro e maio) quando há a incidência de raios que funcionam como fonte ignitora (Ramos-Neto & Pivello 2000). Entretanto, este regime de queima vem sendo modificado pela ação humana, já que as queimadas antrópicas usualmente são aplicadas na estação seca para renovação de pastagens e limpeza de áreas agrícolas (Miranda et al. 2002; Fidelis & Pivello 2011). Alterações do regime de queima, juntamente com a conversão de áreas naturais e as invasões biológicas, constituem as maiores ameaças à conservação do Cerrado (Pivello et al. 1999b; Klink & Machado 2005; Durigan et al. 2007). Dessa forma, compreender a relação entre queimadas em diferentes épocas do ano e espécies invasoras é imprescindível para o entendimento e tomada de decisões para conservação e restauração de áreas de Cerrado.

POR QUE ESTUDAR FOGO E INVASORAS NO CERRADO?

Apesar de ser a maior e mais rica savana do mundo (Klink & Machado 2005), o Cerrado tem sido a principal fronteira agrícola brasileira, motivo pelo qual 53% de sua área original tenha sido convertida para usos agrícolas (Beuchle et al. 2015). Apenas 2,85% de seu território encontra-se integralmente protegido (MMA 2011), além de estar espacialmente desconexo em fragmentos (Carvalho et al. 2009). Em virtude de sua alta biodiversidade e do nível de ameaça a sua conservação, o Cerrado é considerado um *hotspot* mundial (Myers et al. 2000).

Particularmente quanto à conversão de áreas naturais para criação de gado, dados do Ministério da Agricultura e Pecuária (2010), demonstram que o aumento de área destinada às pastagens no Brasil subiu de 122,3 milhões em 1960 para 170 milhões de hectares em 2010, das quais 53 milhões estejam localizadas no Cerrado (MMA 2011). Apesar da enorme biodiversidade de gramíneas nativas que poderiam ser utilizados como alimentação para bovinos (Filgueiras 1992), é comum a retirada desta vegetação para a introdução de outras espécies de forrageiras, principalmente africanas (Brossard & Barcellos 2005; Santos et al. 2005). Esta prática é economicamente justificada pelo melhor conteúdo nutricional e maior resistência destas espécies exóticas ao pastejo (Deschamps & Tcacenco 2000; Valadares-Filho et al. 2013).

Duas espécies muito utilizadas para esses fins são *Melinis minutiflora* P. Beauv e *Urochloa decumbens* (Stapf) R.D. Webster, popularmente conhecidas como capim-gordura e braquiária. No Cerrado estas espécies tornaram-se invasoras dispersando para novas áreas e causando a exclusão competitiva de gramíneas nativas (capítulo I desta dissertação), podendo acarretar perda de biodiversidade e alterações das funções ecossistêmicas (Pivello et al. 1999; Hoffmann et al. 2004; Martins 2006). Além disso, gramíneas invasoras, notadamente as do gênero *Urochloa*, são um dos principais filtros a serem vencidos na restauração ecológica de formações campestres e savânicas do Cerrado, pois excluem competitivamente tanto as espécies nativas da camada herbácea, quanto as plântulas de árvores e arbustos em emergência (Durigan et al. 1998; Melo et al. 2004; Hoffmann & Haridasan 2008).

As medidas adequadas para o controle de espécies invasoras variam para cada tipo de organismo que se deseja manipular. De forma geral, as técnicas adotadas visam promover uma alteração da relação competitiva, favorecendo as espécies nativas e/ou prejudicando as invasoras (Mack et al. 2000; Rejmánek 2000). Para plantas, é comum o uso de práticas de manejo que utilizem regimes de distúrbios naturais da área invadida, partindo do pressuposto que as espécies autóctones – por terem evoluído no ambiente sob distúrbio – sejam menos impactadas do que as alóctones (Daehler 2003). Para fins de restauração, o controle de *M. minutiflora* e *U. decumbens*, assim como de outras gramíneas invasoras, tem sido feito mediante técnicas de arranquio, corte mecânico da parte aérea, aragem do solo, controle químico (aplicação de herbicidas), sombreamento, abafamento, queimadas prescritas e combinações destas técnicas (Palermo et al. 2007; Aires 2009; Barbosa 2009; Horowitz et al. 2014; Assis 2017; Cava et al. 2016; Tomazi & Castellani 2016; Gorgone-Barbosa 2016).

Até o momento, os resultados indicam que para espécies do gênero *Urochloa,* somente o uso de fogo não foi efetivo em controlar esta invasora, sendo que as melhores técnicas seriam a capina manual isoladamente e seu uso consorciado com queimadas prescritas, além da utilização de herbicidas (Assis 2017). Por sua vez, as técnicas que geraram os melhores resultados no manejo de *M. minutiflora* foram o corte mecânico de forma independente (Aires 2009), e a associação entre queimadas prescritas, aplicação de herbicida e capina manual (Martins et al. 2011), o uso isolado queimadas prescritas (Pivello 2006; Palermo et al. 2007), apesar de não haver consenso sobre a eficácia desta última (Martins 2006). Além disso, ambas as espécies são reduzidas pela aplicação de tratamentos de abafamento e de corte mecânico da parte aérea (Martins 2006; Barbosa 2009).

Este estudo portanto, contribui para o entendimento do controle de gramíneas invasoras no Cerrado (*Melinis minutiflora* e *Urochloa brizantha*) ao testar diferentes épocas de queima para esta finalidade, agregando conhecimentos para o desenvolvimento de técnicas de manejo e restauração de Cerrado tanto em Unidades de Conservação (Lei nº9.985/2000) quanto em propriedades particulares que possuam passivos ambientais em suas Áreas de Preservação Permanente (APP) e Reserva Legal (RL). Neste último caso, a obrigatoriedade para recuperação de áreas degradas é imposta por normativas federais (Lei nº12.651/2012; Lei nº6.938/1981; Decreto nº97.632/1989; Resolução CONAMA nº237/1997) e do estado de São Paulo (Lei nº15.684/2015 Portaria CBRN nº01/2015 e da Resolução SMA nº32/2014); além de também ser exigida por órgãos ambientais e pelo Ministério Público.

Assim como para a restauração de áreas degradadas, as invasões biológicas são preocupação das esferas públicas devido ao ônus que causam em programas de conservação e em sistemas produtivos onde tornam-se pragas. Em consonância com Convenção de Diversidade Biológica, o Ministério do Meio Ambiente desenvolve desde o ano de 2001 atividades voltadas à prevenção das introduções, detecção precoce, monitoramento, controle e erradicação de espécies exóticas invasoras que possam afetar ecossistemas, habitats e espécies nativas. Em 2006 foi criada a Câmara Técnica Permanente sobre Espécies Exóticas Invasoras (Deliberação CONABIO nº49/2006); em 2009 foi elaborada a Estratégia Nacional sobre Espécies Invasoras (Resolução CONABIO nº05/2009) e em 2013 o Governo Federal aprovou as Metas Nacionais de Biodiversidade para 2020 (Resolução CONABIO nº06/2013), que em sua Meta 9 assume o compromisso de implementação da Estratégia Nacional sobre Espécies Invasoras.

Dessa forma, a investigação conduzida neste estudo – compreender como a época de queima afeta a relação entre gramíneas invasoras *Melinis minutiflora* e *Urochloa brizantha* e a vegetação nativa de Cerrado – tem motivação e aplicabilidades nas esferas científica, pública e privada em virtude de ser um tema de intersecção entre produção de conhecimento e elaboração de técnicas de manejo para restauração e conservação de formações campestres e savânicas de Cerrado.

COMO E ONDE FOI FEITO ESTE ESTUDO?

O objetivo deste estudo foi avaliar qual o efeito da época de queima em comunidades invadidas de Cerrado, considerando tanto as respostas das gramíneas africanas quanto das espécies vegetais nativas. Para tanto, estabelecemos três épocas de queima ao longo da estação seca: queimas precoces (em maio), modais (em julho) e tardias (em outubro).

O trabalho de campo foi desenvolvido na Estação Ecológica de Itirapina (20°00’ - 22°15’ S e 47°45’ - 48°00 W) localizada no interior do estado de São Paulo na bacia hidrográfica do Médio Tietê Inferior. O clima é temperado, com verões quentes e chuvosos (Cwa) e a temperatura e a precipitação média anual são de 21,9ºC e 1459mm, respectivamente. Os solos são predominantemente do tipo Arenosolos, e a vegetação é de cerrado, composta majoritariamente por formações savânicas e campestres como campo sujo, campo úmido, campo cerrado e campo limpo (Zanchetta e Reis 2006.

A área de estudo tem cerca de 33 hectares e está em regeneração natural desde 1998, quando a então existente silvicultura de *Pinus caribaea* var. *hondurensis* foi encerrada com o corte raso das árvores. A partir de então foram excluídos fogo e pastoreio da área, que atualmente apresenta uma fisionomia de campo sujo com alto grau de invasão pelas gramíneas africanas *Melinis minutiflora* e *Urochloa brizantha* (Figura 4A e 4B; Zanchetta e Reis 2006).

As queimadas prescritas foram realizadas em 2014 (maio, julho e outubro), utilizando-se de queimas a favor do vento (*head-fires*) de modo a simular as características de queimadas naturais (Figuras 4C e 4D). A execução dos experimentos foi realizada após a confecção de aceiros de três metros ao redor de cada parcela e sempre contando com a participação de funcionários e da brigada de incêndio da EEI. Todos os parâmetros de fogo foram amostrados, como intensidade, altura e temperatura da chama (Dairel et al., em preparação).

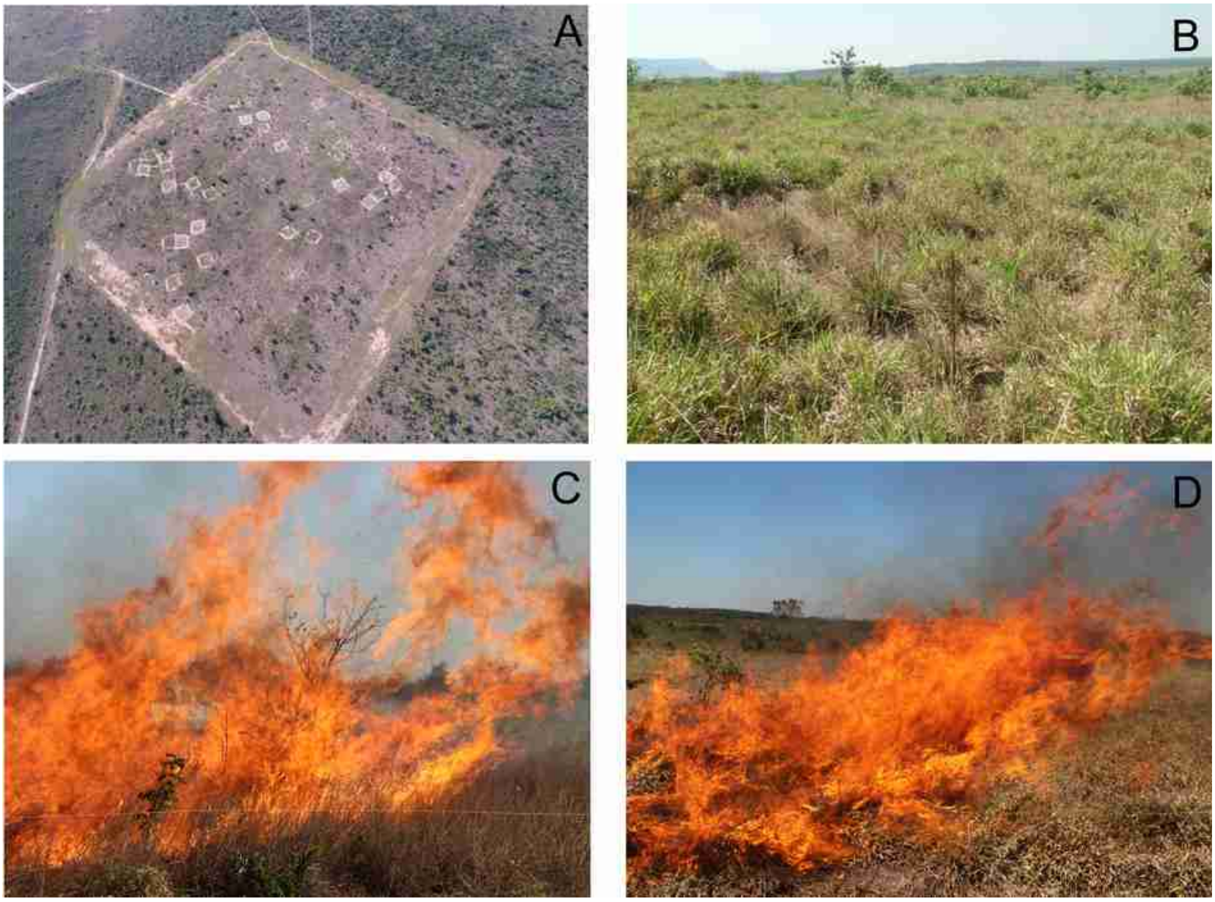

Figura 4. (A) Vista aérea da área de estudo: o quadrado maior é o antigo talhão de *Pinus*, os quadrados menores são algumas das parcelas experimentais de $15m^2$. (B) Vista geral da área de estudo. Realização dos experimentos de queimas modais (julho de 2014) em parcelas invadidas por (C) *Melinis minutiflora* e por (D) *Urochloa brizantha*. Fotografias de (A) Dhemerson Conciani; (B) Gabriella Damasceno; (C) e (D) Alessandra Fidelis.

O delineamento experimental é composto por 32 parcelas experimentais de 15x15m divididas em dois grupos de acordo com a gramínea invasora dominante (ao menos 50% de cobertura da invasora em questão). As parcelas foram estabelecidas em manchas das espécies invasoras encontradas na área. Para cada espécie invasora, aleatoriamente determinamos quatro parcelas a serem queimadas em cada época, mais 4 parcelas controles que não foram queimadas (4 réplicas/tratamento/espécie = 32 parcelas). Todas as parcelas estão fisicamente isoladas e foram queimadas individualmente, configurando-se como réplicas verdadeiras. Em cada parcela experimental foram sorteadas 10 parcelas para avaliação da cobertura vegetal por estimativa visual segundo Braun-Blanquet (Wikun & Shanholtzer 1978; 1x1m) e da biomassa aérea ($g.m^{-2}$, 5 parcelas de 0,5x0,5m) conforme Figura 5.

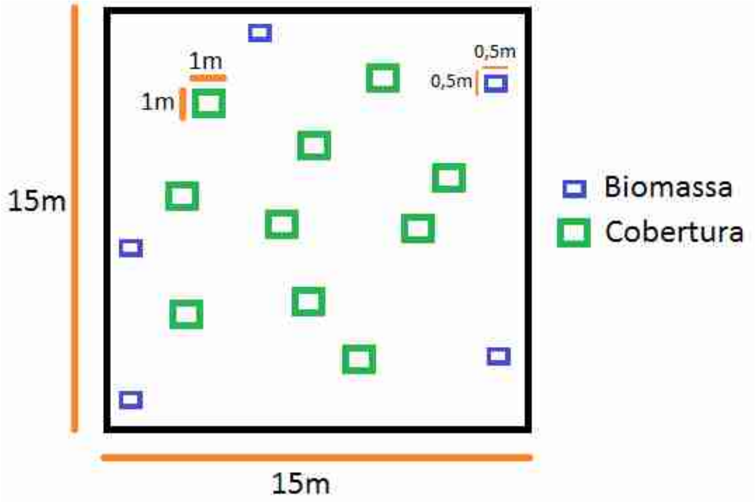

Figura 5. Esquema representando a amostragem da cobertura vegetal e da biomassa em uma parcela experimental de 15x15m.

As amostragens da vegetação (cobertura e biomassa) foram realizadas imediatamente antes das queimadas (maio, julho e outubro de 2014) e ao longo de dois anos após sua realização. Foram realizadas amostragens nas duas estações chuvosas subsequentes (fevereiro de 2015 e 2016), na primeira estação seca subsequente (julho de 2015) e ao se completarem um e dois anos da realização dos experimentos (maio, julho e outubro de 2015 e 2016, para os tratamentos precoce, modal e tardio, respectivamente).

Além das parcelas com invasoras, faz parte deste experimento a avaliação da regeneração da vegetação nativa após o fogo em distintas épocas do ano, com parcelas com dominância de vegetação nativa (4 parcelas/tratamento), estabelecidas em manchas de vegetação nativa. Estes experimentos continuam sendo conduzidos dentro do projeto JP FAPESP 2015/06743-0, sob coordenação da Profa Dra Alessandra Fidelis e portanto, as parcelas estabelecidas são permanente, e tanto os dados de queima, quanto os dados de vegetação continuam sendo avaliados.

COMO FOI ESTRUTURADA A DISSERTAÇÃO?

Para compreender como a época de queima afeta a relação entre gramíneas invasoras *Melinis minutiflora* e *Urochloa brizantha* e a vegetação nativa de Cerrado detalhamos este objetivo geral em três objetivos específicos, cada um correspondente a um capítulo desta dissertação. Todos eles estão redigidos em inglês no formato de manuscritos para publicação em revistas científicas.

O primeiro deles trata sobre a quantificação do impacto das gramíneas invasoras sobre as comunidades nativas de Cerrado, considerando os grupos funcionais de forma de crescimento (graminóides, herbáceas e arbustos) e os parâmetros estruturais de cobertura de solo nu e de biomassa morta. Nossa hipótese é de que o impacto das gramíneas invasoras seja negativo e mais pronunciado no grupo de graminóides nativos em função de sua similaridade funcional. Além disso, esperamos que o impacto varie ao longo do ano em função da sazonalidade climática ocorrente no Cerrado.

O segundo capítulo discorre sobre o possível uso de queimadas prescritas em diferentes épocas do ano para controle das gramíneas invasoras e promoção de oportunidades de restauração do Cerrado. Nossas hipóteses são de que cada espécie invasora seja controlada por queimadas que ocorram em sua época reprodutiva, em virtude da alocação de recursos para este fim. Dessa forma, *M. minutiflora* seria mais reduzida por queimadas precoces e *U. brizantha* por queimadas tardias.

O terceiro capítulo aborda os efeitos a curto prazo da época de queima sobre as comunidades vegetais nativas invadidas de Cerrado. Nossas hipóteses são as de que a identidade da espécie invasora exerça influência nas repostas das comunidades, assim como a ocorrência do fogo e em diferentes épocas resultem em comunidades dissimilares.

Concluindo, no fim desta dissertação apresentamos uma sessão de considerações finais (em português) que terá a função de resumir os principais resultados deste estudo e de servir como material de apoio a gestores de unidades de conservação e a profissionais interessados no controle de gramíneas invasoras e na restauração de formações do Cerrado.

REFERÊNCIAS BIBLIOGRÁFICAS

Abreu, R.C.R. de, Assis, G.B. de, Frison, S., Aguirre, A., & Durigan, G. 2011. Can native vegetation recover after slash pine cultivation in the Brazilian Savanna? *Forest Ecology and Management* 262: 1452–1459.

Aires, F.S. 2009. Desenvolvimento de técnica de manejo, sem uso de agentes químicos, no controle da espécie invasora invasora Melinis minutiflora Beauv. (capim-gordura) para aplicação em áreas de campo sujo. *Dissertação de mestrado.* Universidade de Brasília, Brasília.

Appezzato-da-glória, A.B., Cury, G., Misaki, M.K., Rocha, R., Hayashi, A.H. 2008. Underground systems of Asteraceae species from the Brazilian Cerrado. *The Journal of the Torrey Botanical Society* 135: 103–113.

Assis, G.B., Pilon, N.A.L., Durigan, G., & Siqueira, M.F. 2016. Ecological assessment of different management techniques to control the invasion by Urochloa decumbens in the Brazilian savanna. *59th Annual Symposium of the International Association for Vegetation Science.* Pirenópolis, Brasil.

Barbosa, E.G. 2009. Eficiência do manejo no controle de duas espécies de gramíneas invasoras em Cerrados Paulistas. *Dissertação de mestrado.* Universidade de São Paulo, São Paulo.

BFG. 2015. Growing knowledge: An overview of Seed Plant diversity in Brazil. *Rodriguesia* 66: 1085–1113.

Bond, W.J., Midgley, J.J., & May, N. 1995. Kill Thy Neighbour : An Individualistic Argument for the Evolution of Flammability. *Oikos* 73: 79–85.

Bond, W.J., & Scott, A.C. 2010. Fire and the spread of flowering plants in the Cretaceous. *New Phytologist* 188: 1137–1150.

Bond, W.J., & Wilgen, B. 1996. *Fire and Plants*. Chapman & Hall, London, UK.

Bond, W.J., Woodward, F.. I., & Midgley, G.F. 2005. The Global Distribtuion of Ecosystems in a world without Fire. *New Phytologist* 165: 525–538.

Bowman, D.M.J.S., Balch, J.K., Artaxo, P., Bond, W.J., Carlson, J.M., Cochrane, M. a., D'Antonio, C.M., Defries, R.S., Doyle, J.C., Harrison, S.P., Johnston, F.H., Keeley, J.E., Krawchuk, M. a., Kull, C. a., Marston, J.B., Moritz, M. a., Prentice, I.C., Roos, C.I., Scott, A.C., Swetnam, T.W., van der Werf, G.R., & Pyne, S.J. 2009. Fire in the Earth system. *Science* 324: 481–4.

Brooks, M.L., D'Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, E., Ditomaso, J.M., Hobbs, R.J., Pellant, M., & Pyke, D. 2004. Effects of Invasive Alien Plants on Fire Regimes. *BioScience* 54: 677–688.

Brossard, M., & Barcellos, A.D.O. 2005. Conversão do Cerrado em pastagens cultivadas e funcionamento de latossolos. *Cadernos de Ciência e Tecnologia* 22: 153–168.

Cardoso Da Silva, J.M., & Bates, J.M. 2002. Biogeographic Patterns and Conservation in the South American Cerrado: A Tropical Savanna Hotspot. *BioScience* 52: 225.

Carvalho, F.M. V, De Marco, P., & Ferreira, L.G. 2009. The Cerrado into-pieces: Habitat fragmentation as a function of landscape use in the savannas of central Brazil. *Biological*

Conservation 142: 1392–1403.

Cava, M.G. de B., Isernhagen, I., Mendonça, A.H., & Durigan, G. 2016. Comparação de técnicas para restauração da vegetação lenhosa de Cerrado em pastagens abandonadas. *Hoehnea* 43: 301–315.

Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C., & Díaz, S. 2000. Consequences of changing biodiversity. *Nature* 405: 234–42.

Charles-Dominique, T., Beckett, H., Midgley, G.F., & Bond, W.J. 2015. Bud protection: A key trait for species sorting in a forest-savanna mosaic. *New Phytologist* 207: 1052–1060.

Connelly, N.A., O'Neill, C.R., Knuth, B.A., & Brown, T.L. 2007. Economic impacts of zebra mussels on drinking water treatment and electric power generation facilities. *Environmental management* 40: 105–112.

Coutinho, L.M. 1982. Ecological Effects of Fire in Brazilian Cerrado. In Huntley, B.J. & Walker, B.H. (eds.), *Ecology of Tropical Savannas*,

Coutinho, L.M. 1990. Fire in the ecology of the Brazilian Cerrado. In *Ecological Studies 84 in J. Goldammer (ed) Fire in the Tropical Biota*, pp. 82–105.

Coutinho, L.M. 2002. O bioma Cerrado. In Klein, A.L. (ed.), *Eugene Warming e o cerrado brasileiro: um século depois*,

D'Antonio, C.M., & Meyerson, L.A. 2002. Exotic plant species as problems and solutions in ecological restoration. *Restoration Ecology* 10: 703–713.

D'Antonio, C.M., & Vitousek, P.M. 1992. Biological Invasions By Exotic Grasses, the Grass/Fire Cycle, and Global Change. *Annual Review of Ecology and Systematics* 23: 63–87.

Daehler, C.C. 2003. Performance Comparisons of Co-Occurring Native and Alien Invasive Plants: Implications for Conservation and Restoration. *Annual Review of Ecology, Evolution, and Systematics* 34: 183–211.

Deschamps, F.C., & Tcacenco, F.A. 2000. Parâmetros nutricionais de forrageiras nativas e exóticas no vale do Itajaí, Santa Catarina. *Pesquisa Agropecuária Brasileira* 35: 457–465.

Dias, J., da Fonte, M.A.M.A., Baptista, R., Mantoani, M.C., Holdefer, D.R., & Torezan, J.M.D. 2013. Invasive alien plants in Brazil: A nonrestrictive revision of academic works. *Natureza a Conservação* 11: 31–35.

Durigan, G., Contieri, W.A., Franco, G.A.D.C., & Garrido, M.A.O. 1998. Indução Do Processo De Regeneração Da Vegetação De Cerrado Em Área De Pastagem, Assis, Sp. *Acta boctânica. brasílica* 12: 421–429.

Durigan, G., Ferreira De Siqueira, M., Daher, G.A., & Franco, C. 2007. Threats to the cerrado remnants. *Scientia Agricola* 64: 355–363.

Ehrenfeld, J.G. 2003. Effects of Exotic Plant Invasions on Soil Nutrient Cycling Processes. *Ecosystems* 6: 503–523.

Eiten, G. 1972. The Cerrado vegetation of Brazil. *The Botanical Review* 38: 201–338.

Fichino, B.S., Dombroski, J.R.G., Pivello, V.R., & Fidelis, A. 2016. Does Fire Trigger Seed Germination in the Neotropical Savannas? Experimental Tests with Six Cerrado Species. *Biotropica* 48: 181–187.

Fidelis, A., & Pivello, V.R. 2011. Deve-se usar o fogo como instrumento de manejo no Cerrado e Campos Sulinos? *Biodiversidade Brasileira* 1: 12–25.

Filgueiras, T.S. 1992. Gramineas forrageiras nativas do distrito federal. *Pesquisa Agropecuária brasileira.* 27: 1103–1111.

Frehse, F. de A., Braga, R.R., Nocera, G.A., & Vitule, J.R.S. 2016. Non-native species and invasion biology in a megadiverse country: scientometric analysis and ecological interactions in Brazil. *Biological Invasions* 18: 3713–3725.

Freitas, G., & Pivello, V. 2005. A ameaça das gramíneas exóticas à Biodiversidade. *O Cerrado Pé-de-Gigante (Parque Estadual de Vassununga, SP)*

Furley, P.A.., & Ratter, J.A.. 1998. Soil Resources and Plant Communities of the Central Brazilian Cerrado and Their Development. *Journal of Biogeography* 15: 97–108.

Gagnon, P.R., Passmore, H.A., Platt, W.J., Myers, J.A., Paine, T.C.E., & Harms, K.E. 2010. Does pyrogenicity protect burning plants? *Ecology* 91: 3481–3486.

Gilbert, B., & Levine, J.M.J.M. 2013. Plant invasions and extinction debts. *Proceedings of National Academy of Science* 110: 1–6.

Gorgone-Barbosa, E., Pivello, V.R., Bautista, S., Zupo, T., Rissi, M.N., & Fidelis, A. 2015. How can an invasive grass affect fire behavior in a tropical savanna? A community and individual plant level approach. *Biological Invasions* 17: 423–431.

Govender, N., Trollope, W.S.W., & Van Wilgen, B.W. 2006. The effect of fire season, fire frequency, rainfall and management on fire intensity in savanna vegetation in South Africa. *Journal of Applied Ecology* 43: 748–758.

Gubler, D.J. 2002. Epidemic dengue / dengue hemorrhagic fever as a public health , social and economic problem in the 21st century. *TRENDS in Microbiology* 10: 100–103.

Hoffmann, W.A. 1998. Post-burn reproduction of woody plants in a neotropical savanna: The relative importance of sexual and vegetative reproduction. *Journal of Applied Ecology* 35: 422–433.

Hoffmann, W.A., & Haridasan, M. 2008. The invasive grass, Melinis minutiflora, inhibits tree regeneration in a Neotropical savanna. *Austral Ecology* 33: 29–36.

Hoffmann, W.A., Lucatelli, V.M.P.C., Silva, F.J., Azeuedo, I.N., Marinho, M.S., Albuquerque, Ana Maria S Lopes, A.O., & Moreira, S.P. 2004. Impact of the invasive alien grass Melinis minutiflora at the savanna-forest ecotone in the Brazilian Cerrado. *Diversity and Distributions*. doi: 10.1111/j.1366-9516.2004.00063.x

Horowitz, C., Oliveira, A. dos S., Silva, V. da, Pacheco, G., & Sobrinho, R.I. 2014. Manejo da flora exótica invasora no Parque Nacional de Brasília: contexto histórico e atual. *Biodiversidade Brasileira* 0: 217–236.

Hughes, F., & Vitousek, P.M. 1993. Barriers to shrub reestablishment following fire in the seasonal submontane zone of Hawai'i. *Oecologia* 93: 557–563.

IBGE. 2004. Biomas Brasileiros. Mapa Temático. Instituto Brasileiro de Geografia e Estatística.

Kauffman, J.B., Cummings, D.L., & Ward, D.E. 1994. Relationships of Fire, Biomass and Nutrient Dynamics along a Vegetation Gradient in the Brazilian Cerrado. *The Journal of Ecology* 82: 519–531.

Keeley, J.E., Pausas, J.G., Rundel, P.W., Bond, W.J., & Bradstock, R.A. 2011. Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science* 16: 406–411.

Keeley, J.E., & Rundel, P.W. 2005. Fire and the Miocene expansion of C4 grasslands. *Ecology Letters* 8: 683–690.

Klink, C.A., & Machado, R.B. 2005. Conservation of the Brazilian Cerrado. *Conservation Biology* 19: 707–713.

Knapp, E.E., Estes, B.L., & Skinner, C.N. 2009. *Ecological Effects of Prescribed Fire Season : A Literature Review and Synthesis for Managers*. United States Department of Agriculture, Albany, USA.

Lamont, B.B., & Downes, K.S. 2011. Fire-stimulated flowering among resprouters and geophytes in Australia and South Africa. *Plant Ecology* 212: 2111–2125.

Laterra, P., & Solbrig, O.T. 2001. Dispersal strategies, spatial heterogeneity and colonization success in fire-managed grasslands. *Ecological Modelling* 139: 17–29.

Lawes, M.J., Richards, A., Dathe, J., & Midgley, J.J. 2011. Bark thickness determines fire resistance of selected tree species from fire-prone tropical savanna in north Australia. *Plant Ecology* 212: 2057–2069.

Ledru, M.-P. 2002. Late Quaternary history and evolution of the cerrados as revealed by palynological records. In *The Cerrados of Brazil*, pp. 33–50.

Lövei, Gábor, L., & Lewinsohn, T. 2012. Megadiverse developing countries face huge risks from invasives. *Trends in Ecology and Evolution* 27: 2–3.

Lowry, E., Rollinson, E.J., Laybourn, A.J., Scott, T.E., Aiello-Lammens, M.E., Gray, S.M., Mickley, J., & Gurevitch, J. 2013. Biological invasions: A field synopsis, systematic review, and database of the literature. *Ecology and Evolution* 3: 182–196.

Mack, M.C., & D'Antonio, C.M. 1998. Impacts of biological invasions on disturbance regimes. *Trends in Ecology and Evolution* 13: 195–198.

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M., & Bazzaz, F.A. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications* 10: 689–710.

MAPA. 2010. Agronegócio brasileiro em números. Ministério da Agricultura, Pecuária e Abastecimento

Marinho, M.D.S., & Miranda, H.S. 2013. Efeito do Fogo Anual na Mortalidade e no Banco de Sementes de Andropogon gayanus Kunth. no Parque Nacional de Brasília/DF. *Biodiversidade Brasileira* 3: 149–158.

Martinelli, L.A., Naylor, R., Vitousek, P.M., & Moutinho, P. 2010. Agriculture in Brazil: Impacts, costs, and opportunities for a sustainable future. *Current Opinion in Environmental Sustainability* 2: 431–438.

Martins, C.R. 2006. Caracterização e manejo da gramínea Melinis minutiflora P. Beauv. (capim-gordura): uma espécie invasora do Cerrado. *Tese de doutorado.* Universidade de Brasília, Brasília.

Martins, C.R., Hay, J.D.V., Walter, B.M.T., Proença, C.E.B., & Vivaldi, L.J. 2011. Impact of invasion and management of molasses grass (Melinis minutiflora) on the native vegetation of the Brazilian Savanna. *Brazilian Journal of Botany* 34: 73–90.

Martins, C.R., Leite, L.L., & M., H. 2004. Molasses grass (Melinis minutiflora P . Beauv .), an exotic species compromising the recuperation of degraded areas in conservation units. *Revista Árvore* 28: 739–747.

Medeiros, M.B. De, & Miranda, H.S. 2005. Mortalidade pós-fogo em espécies lenhosas de campo sujo submetido a três queimadas prescritas anuais. *Acta Botanica Brasilica* 19: 493–500.

Melo, A. de, Durigan, G., & Kawabata, M. 2004. Crescimento e Sobrevivência de Espécies Arbóreas

Plantadas em Área de Cerrado, Assis SP.

Miranda, H.S., Bustamante, M.M.C., & Miranda, A.C. 2002. The Fire Factor. In Oliveira, P.S. & Marquis, R.J. (eds.), *The Cerrados of Brazil. Ecology and natural history of a neotropical savanna*,

Miranda, A.C., Miranda, H.S., de Fátima Oliveira Dias, I., & de Souza Dias, B.F. 1993. Soil and air temperatures during prescribed cerated fires in Central Brazil. *Journal of Tropical Ecology* 9: 313.

Mistry, J. 1998. Fire in the cerrado (savannas) of Brazil: an ecological review. *Progress in Physical Geography* 22: 425–448.

Mistry, J., Berardi, A., & Durigan, G. 2010. The influence of fire regime on microscale structural variation and patchiness in Cerrado vegetation. *Revista do Instituto Florestal* 22: 33–49.

Mollot, G., Pantel, J.H., & Romanuk, T.N. 2017. *The Effects of Invasive Species on the Decline in Species Richness: A Global Meta-Analysis*. Elsevier Ltd.

Munhoz, C.B.R., & Felfili, J.M. 2007. Reproductive phenology of an herbaceous-subshrub layer of a Savannah (Campo Sujo) in the Cerrado Biosphere Reserve I, Brazil. *Brazilian journal of biology* 67: 299–307.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., & Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.

Paini, D.R., Sheppard, A.W., Cook, D.C., De Barro, P.J., Worner, S.P., & Thomas, M.B. 2016. Global threat to agriculture from invasive species. *Proceedings of the National Academy of Sciences* 113: 7575–7579.

Palermo, A.C., Musso, C., Borges, G.B.O., Aires, F.S., Andrade, S.M.A., Martins, C.R., Sato, M.N., & Miranda, H.S. 2007. Manejo com fogo em áreas invadidas com capim-gordura visando o aumento da diversidade de gramíneas nativas. *Biotropica* 31: 1–2.

Pausas, J.G., & Keeley, J.E. 2009. A Burning Story: The Role of Fire in the History of Life. *BioScience* 59: 593–601.

Pausas, J.G., & Keeley, J.E. 2014. Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. *New Phytologist* 204: 55–65.

Pausas, J., & Schwilk, D. 2012. Fire and plant evolution. *New Phytologist*. doi: 10.1111/j.1469-8137.2011.04010.x

Pejchar, L., & Mooney, H.A. 2009. Invasive species, ecosystem services and human well-being. *Trends in Ecology and Evolution* 24: 497–504.

Pessenda, L.C.R., Ledru, M.P., Gouveia, S.E.M., Aravena, R., Ribeiro, a. S., Bendassolli, J. a., & Boulet, R. 2005. Holocene palaeoenvironmental reconstruction in northeastern Brazil inferred from pollen, charcoal and carbon isotope records. *The Holocene* 15: 812–820.

Pilon, N.A.L., & Durigan, G. 2013. Critérios para indicação de espécies prioritárias para a restauração da vegetação de cerrado. *Scientia Florestalis* 41(99):389-399.

Pimentel, D., McNair, S., Janecka, J., Wightman, J., Simmonds, C., O'Connell, C., Wong, E., Russel, L., Zern, J., Aquino, T., & Tsomondo, T. 2001. Economic and environmental threats of alien plant, animal, and microbe invasions. *Agriculture, Ecosystems and Environment* 84: 1–20.

Pivello, V.R. 2006. Fire management for biological conservation in the Brazilian Cerrado. *Savannas and dry forests – linking people with nature.* 129–154.

Pivello, V., Carvalho, V., & Lopes, P. 1999. Abundance and distribution of native and alien grasses in a "Cerrado"(Brazilian Savanna) biological reserve. *Biotropica* 31: 71–82.

Pivello, V.R., & Coutinho, L.M. 1992. Transfer off macro nutrients to the atmosphere during burns in Cerrado. *Journal of Tropical Ecology* 8: 487–497.

Pivello, V.R., Shida, C.N., & Meirelles, S.T. 1999. Alien grasses in Brazilian savannas: A threat to the biodiversity. *Biodiversity and Conservation* 8: 1281–1294.

Power, M.J., Marlon, J., Ortiz, N., Bartlein, P.J., Harrison, S.P., Mayle, F.E., Ballouche, A., Bradshaw, R.H.W., Carcaillet, C., Cordova, C., Mooney, S., Moreno, P.I., Prentice, I.C., Thonicke, K., Tinner, W., Whitlock, C., Zhang, Y., Zhao, Y., Ali, A.A., Anderson, R.S., Beer, R., Behling, H., Briles, C., Brown, K.J., Brunelle, A., Bush, M., Camill, P., Chu, G.Q., Clark, J., Colombaroli, D., Connor, S., Daniau, A.L., Daniels, M., Dodson, J., Doughty, E., Edwards, M.E., Finsinger, W., Foster, D., Frechette, J., Gaillard, M.J., Gavin, D.G., Gobet, E., Haberle, S., Hallett, D.J., Higuera, P., Hope, G., Horn, S., Inoue, J., Kaltenrieder, P., Kennedy, L., Kong, Z.C., Larsen, C., Long, C.J., Lynch, J., Lynch, E.A., McGlone, M., Meeks, S., Mensing, S., Meyer, G., Minckley, T., Mohr, J., Nelson, D.M., New, J., Newnham, R., Noti, R., Oswald, W., Pierce, J., Richard, P.J.H., Rowe, C., Sanchez Go??i, M.F., Shuman, B.N., Takahara, H., Toney, J., Turney, C., Urrego-Sanchez, D.H., Umbanhowar, C., Vandergoes, M., Vanniere, B., Vescovi, E., Walsh, M., Wang, X., Williams, N., Wilmshurst, J., & Zhang, J.H. 2008. Changes in fire regimes since the last glacial maximum: An assessment based on a global synthesis and analysis of charcoal data. *Climate Dynamics* 30: 887–907.

Pyšek, P., Jarošík, V., Hulme, P.E., Pergl, J., Hejda, M., Schaffner, U., & Vilà, M. 2012. A global assessment of invasive plant impacts on resident species, communities and ecosystems: The interaction of impact measures, invading species' traits and environment. *Global Change Biology* 18: 1725–1737.

Ramos-Neto, M.B., & Pivello, V.R. 2000. Lightning fires in a Brazilian Savanna National Park: Rethinking management strategies. *Environmental Management* 26: 675–684.

Ratter, J. a., Ribeiro, J.F., & S., B. 1997. The Brazilian Cerrado Vegetation and Threats to its Biodiversity. *Annals of Botany* 80: 223–230.

Reed, H.E., Seastedt, T.R., & Blair, J.M. 2005. Ecological Consequences of C 4 Grass Invasion of a C 4 Grassland: a Dilemma for Management. *Ecological Applications* 15: 1560–1569.

Rejmánek, M. 2000. Invasive plants: approaches and predictions. *Austral Ecology* 25: 497–506.

Ribeiro, J.F., & Walter, B.M.. 1998. Fitofisionomias do bioma Cerrado. In Sano, S.M. & Almeida, S.P. (eds.), *Cerrado: Ambiente e Flora.* Embrapa, Planaltina.

Richardson, D.M., Pysek, P., Rejmanek, M., Barbour, M.G., Dane, F., West, C.J., & Panetta, F.D. 2000. Naturalization and invasion of alien plants: concpets and definitions. *Diversity and Distributions* 6: 93–107.

Rossi, R.D., Martins, C.R., Viana, P.L., Rodrigues, E.L., & Eugênio, J.F.C. 2014. Impact of invasion by molasses grass (Melinis minutiflora P . Beauv .) on native species and on fires in areas of campo-cerrado in Brazil. *Acta Botanica Brasilica* 28: 631–637.

Rossiter, N., Setterfield, S.A., Douglas, M.M., Hutley, L., & Cook, G. 2004. Exotic grass invasion in the tropical savanna of northern Australia: ecosystem consequences. *Fourteenth Australian Weeds Conference* 168–171.

Rundel, P.W. 1983. Impact of fire on nutrient cycles in Mediterranean-type ecosystems with reference to chaparral. In *Mediterranean-type ecosystems.*, pp. 192–207. Springer Berlin Heidelberg.

Sano, E.E., Barcellos, A.O., & Bezerra, H.S. 2000. Assessing the spatial distribuition of cultivated pasture in the Brazilian savana. *Pasturas Tropicales* 22: 2–15.

Santos, S.A., Crispim, S.M.A., Comastri, J.A.F., Pott, A., & Cardoso, E.L. 2005. Substituição de Pastagem Nativa de Baixo Valor Nutritivo por Forrageiras de Melhor Qualidade no Pantanal. *Circular Técnica (EMBRAPA)* 62: 1–5.

Santos, A.J.B., Silva, G.T.D.A., Miranda, H.S., Miranda, A.C., & Lloyd, J. 2003. Effects of fire on surface carbon, energy and water vapour fluxes over campo sujo savanna in central Brazil. *Functional Ecology* 17: 711–719.

Simberloff, D. 2013. *Invasive species: what everyone needs to know.* Oxford University Press.

Simberloff, D., & Rejmánek, M. 2011. *Encyclopedia of biological invasions.* (University of California

Simon, M.F., Grether, R., de Queiroz, L.P., Skema, C., Pennington, R.T., & Hughes, C.E. 2009. Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. *Proceedings of the National Academy of Sciences* 106: 20359–20364.

Tomazi, A.L., & Castellani, T.T. 2016. Artificial perches and solarization for forest restoration : assessment of their value *Tropical Conservation Science*. 9(2): 809–831.

Tyler, C. 1995. Factors contributing to postfire seedling establishment in chaparral: direct and indirect effects of fire. *Journal of Ecology* 83: 1009–1020.

Valadares-Filho, S. de C., da Silva, F.F., Rocha Junior, V.R., & Chapelle, E.R. 2013. Tabelas de composição de alimentos e exigências nutricionais para bovinos no brasil 1. *II Simpósio de Produção de Gado de Corte* 291–358.

Vila, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarok, V., Maron, J.L., Pergl, J., Schaffner, U., Sun, Y., & Py??ek, P. 2011. Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters* 14: 702–708.

Vitousek, P.M. 1992. Effects of Alien Plants on Native Ecosystems. *Biological Invasions of North Maerica and Hawaii* 29–41.

Vitousek, P.M., DAntonio, C.M., Loope, L.L., Westbrooks, R., & D'Antonio, C.M. 1996. Biological Invasions as Global Environmental Change. *The American Naturalist* 84: 468–478.

Walter, B.M.T. 2006. Fitofisionomias do bioma Cerrado : síntese terminológica e relações florísticas. *Tese de doutorado.* Universidade de Brasília. Brasília.

Whelan, R.J. 1995. *The ecology of fire*. Cambridge University Press.

Williams, D.G., & Baruch, Z. 2000. African grass invasion in the Americas: Ecosystem consequences and the role of ecophysiology. *Biological Invasions* 2: 123–140.

Wrobleski, D.W., & Kauffman, J.B. 2003. Initial effects of prescribed fire on morphology, abundance, and phenology of forbs in big sagebrush communities in southeastern Oregon. *Restoration Ecology* 11: 82–90.

Zanchetta, D., & Reis, C.M. 2006. *Plano de Manejo Integrado: Estações Ecológica e Experimental de Itirapina/SP*.

Zenni, R.D. 2014. Analysis of introduction history of invasive plants in Brazil reveals patterns of association between biogeographical origin and reason for introduction. *Austral Ecology* 39: 401–407.

Zenni, R.D. 2015. The naturalized flora of Brazil: A step towards identifying future invasive non-native species. *Rodriguesia* 66: 1137–1144.

Ziller, S.R., & Dechoum, M.S. 2013. Plantas e vertebrados exóticos invasores em unidades de conservação no Brasil. *Biodiversidade Brasileira* 3: 4–31.

Impact of invasive grasses on Cerrado under natural regeneration

Damasceno, G.[1,4] (ORCID: 0000-0001-5103-484X); Souza[2], L; Pivello, V.R. [3] (ORCID: 0000-0001-8063-772X); Gorgone-Barbosa, E.[1] (ORCID:0000-0001-7109-5586); Giroldo, P.Z.[3] ; Fidelis, A.[1] (ORCID: 0000-0001-9545-2285)

1. Universidade Estadual Paulista (UNESP), Instituto de Biociências, Rio Claro. Av. 24A, 1515, 13506-900, Rio Claro, Brazil.
2. Oklahoma Biological Survey & Department of Microbiology and Plant Biology, University of Oklahoma, 111 E. Chesapeake Street, 73019-0390, Norman, Oklahoma, USA
3. Departamento de Ecologia, Universidade de São Paulo, Rua do Matão, Trav. 14, 321,05508-900, São Paulo, Brazil
4. Correspondence author: fariadamasceno@gmail.com +55193526-4218

Manuscript under review in the journal Biological Invasions

Abstract

The Cerrado is a neotropical savanna threatened by invasive African grasses. We aimed to quantify the impact caused by *Melinis minutiflora* and *Urochloa brizantha* on community functional components (native graminoids, forbs and shrubs and bare soil and dead biomass covers). Our major hypothesis was that a negative impact would be stronger on the native-graminoid group given overlap in function. We sampled 120 1m × 1m plots four times a year to capture changes in plant community also due to seasonality. Using the Coenh's D index, we calculated the effect size of invasive grasses on the functional components. Negative values of Coenh's D index indicate that a functional component was reduced by the invasive grasses, while a positive value indicates an increase on this component. Both invasive species negatively affected all the native growth-form groups, also decreasing bare soil and increasing total dead biomass. Native graminoids and native dead biomass were the most negatively affected components. *M. minutiflora* caused stronger impact than *U. brizantha* on bare soil and on total dead biomass. The impacts of *M. minutiflora* on total graminoids ranged from positive in the Early-Dry period to negative in the Mid-Dry season; the negative impact of *U. brizantha* on bare soil became more pronounced from the Mid-Dry to the Mid-Rainy season. The variation in direction and magnitude of invasive species in our system is likely caused by the huge production of biomass by *M. minutiflora;* and by bare soil colonization by *U. brizantha.* Overall, invaded vs. non invaded communities differed in structure, as well as both invaded communities between each other. Our results demonstrate the need to control these species concerning the conservation and restoration of Cerrado.

keywords: neotropical savanna; conservation; restoration; *Melinis minutiflora; Urochloa brizantha*

Introduction

African grasses negatively affect invaded grasslands worldwide, from temperate to tropical ecosystems. At temperate American prairies, *Andropogon bladhii* dominates the system by overcompeting the former native dominant species from the same genus, altering thus, the fire cycle (Reed et al. 2005). In the Venezuelan savannas, *Melinis minutiflora* displaces native species due to its growth dynamics, phenology and biomass allocation (Baruch et al. 1989), and in Australian savannas, *Andropogon gayanus* alters fire regime, nutrient cycling and water use, also conducting the savanna to alternative stable states by affecting the richness and abundance of the understory functional groups (Rossiter et al. 2004; Brooks et al. 2010).

In the Cerrado (Brazilian Neotropical savanna), invasive grasses are responsible for biodiversity loss (Pivello et al. 1999a; Durigan et al. 2007), being mostly represented by C_4 African species like *Melinis minutiflora* P. Beauv. (molasses grass) and *Urochloa* spp. (Pivello et al. 1999b). The ability of *Melinis minutiflora* and *Urochloa* spp. to change the fire behavior

(Gorgone-Barbosa et al. 2015; Rossi et al. 2014) alter the dynamics of native communities by increasing fuel amount (mostly composed by dead biomass), promoting thus, the risk of wildfires (Hoffmann et al. 2004).

Also, in areas undergoing regeneration process, invasive grasses can hinder the vegetation recovery (Durigan et al. 1999; Hoffmann and Haridasan 2008) despite Cerrado's high resilience (Hoffmann 1998; Barreira et al. 2000; Abreu et al. 2011). Therefore, the invasive African grasses not only impact and decrease diversity in the Cerrado, but they also can be considered one of the most important biotic filters regarding the regeneration and restoration of those native systems (Silveira et al. 2013).

The Cerrado, as other tropical savannas, is characterized by a strong seasonality, which is a key characteristic of species' ecophysiology and community dynamics (Eiten 1972; Coutinho 1990; Franco 2002). As a result, the majority of the herbaceous layer dries out during the dry season and resume growing as environmental conditions become favorable (Munhoz and Felfili 2005). Consequently, Cerrado plant communities are very dynamic, changing the amount of dead biomass along the year, which influences thus, vegetation structure (Batmanian and Haridasan 1985). Therefore, the impact of invasive grasses on native plant communities must also be influenced by seasonality, affecting vegetation composition, structure and dynamics throughout the year.

In the present study we aimed to 1) quantify and compare the impact of *Melinis minutiflora* and *Urochloa brizantha* on the native community of an open Cerrado under natural regeneration after the removal of *Pinus caribeaea* plantation; and 2) evaluate the impact variation during the year, since seasonality is one of the major factors affecting tropical savannas. We hypothesized that the invasive grasses would negatively impact different functional groups of native plants, but the magnitude of such negative impacts would be greater on native graminoids due to their intolerance to shading. Additionally, considering variation along seasons, we hypothesized that the impact would be higher in the rainy period, due to a vegetation growth peak, mostly caused by the invasive grasses (Gorgone-Barbosa 2016; Damasceno et al. unpublished data), leading to higher soil cover by invasive species, thus reducing resources available to natives.

As a consequence of invasive species impacts, the structure and composition of native communities would be altered, thus leading to dissimilarity in composition of invaded vs. non-invaded communities; furthermore, invasive grass identity would lead to compositional dissimilarity between invaded communities.

Material and Methods

Study area

The study was conducted at the Itirapina Ecological Station (EEI, 20°00’-22°15’S e 47°45’-48°00W; 710 to 830 m a.s.l.) in São Paulo State, Brazil. Most of the area is composed by grasslands and open physiognomies of the Cerrado: dominant herbaceous layer with forbs and C_4 grasses, scattered shrubs and dwarf trees. The climate is mesothermic with a marked dry winter season. The mean annual temperature is 21.9º C and mean annual precipitation is 1459 mm. The dominant soil type is Arenosol (Zanchetta and Reis 2006). Until the year 2000 the study site was planted with the exotic *Pinus caribaea* var. *hondurensis.* After that, pine trees were removed, grazing was excluded, fire has been avoided, and the area has been left to natural regeneration. *Melinis minutiflora* and *Urochloa brizantha* invaded the area and large patches of these species can be found within the native vegetation (Zanchetta and Reis 2006).

Data acquisition

Vegetation sampling was carried out in three communities respectively dominated by (1) *Melinis minutiflora, (2) Urochloa brizantha,* and (3) mostly native species. For each of these communities we selected four 15x15m patches and randomly established 10 plots

(1x1m) per patch (40 plots/communities, total of 120 plots), avoiding termites, ant nests, armadillo holes and large areas of bare soil. In each plot, using a modified Braun-Blanquet method (Wikum and Shanholtzer 1978) we visually estimated the cover percentage of bare soil, of native dead and of invasive dead; as well as the cover percentage of the functional groups of native graminoids (Poaceae, Cyperaceae), invasive graminoids (*M. minutiflora* and/or *U. brizantha*), forbs, and shrubs. We created two more categories cover of total dead biomass, comprising the sum of the percentage cover of invasive and native species' dead biomasses; and total graminoids cover, corresponding to the sum of invasive and native graminoids' cover.

We conducted the sampling four times in the year: at Early-Dry (May 2014), Mid-Dry (August 2014), Late-Dry (September 2014) and Mid-Rainy seasons (February 2015), in order to capture all changes in plant community due to seasonality.

Data analysis

We used the Coenhs' D index to quantify the magnitude of invasive species' impact on the community by the pooled ratio of response variables in the invaded plots relative to non-invaded ones (Deeks et al. 2001). Negative values of Coenh's D index indicate that a functional component was reduced by the invasive grasses, while a positive value indicates an increase on this component. Then, we used linear mixed-effect models (lme) to investigate the differences of impact according to invasive species and seasonality (two-way analysis) and the effect of seasonality on each of them individually. Further, we assessed differences using pairwise post-hoc general linear hypothesis tests of Tukey HSD type.

To analyze the consequence of invasive species' impacts on composition of native communities, we compared invaded and non-invaded communities using multivariate non-parametric analysis of variance – PERMANOVA (Anderson 2001) – and Principal Coordinates Analysis (PCoA) with the data from the 120 plots considering the cover of all functional components (functional groups+bare soil+invasive and dead biomass cover). As data was expressed as abundance (%) and so upper limited, we used the chord distance to generate the dissimilarity matrix for both analyses (Orlóci 1967).

Statistical analyses were performed in the R program (R Development Core Team 2016) with the packages nlme, vegan and multcomp (Hothorn et al. 2008; Oksanen et al. 2016; Pinheiro et al. 2016).

Results

The impacts of both invasive species were negative on the total soil cover of the community functional components (considering the categories of bare soil, native species and total species dead cover, total graminoids and the native functional groups of graminoids, forbs and shrubs). The two species had a similar effect on communities (p=0.32, Table 1); according to the Coehn's D index, the total impact of *M. minutiflora* and *U. brizantha* was negative (-1.12±2.30 and -0.86±1.77, respectively; mean±SD for all results) and did not change during the year according to the season (Table 1). However, there is a tendency of differentiation of *M. minutiflora* and *U. brizantha* impacts, as the former species had lower values than the latter considering all seasons together and the Early-, Mid- and Late-Dry season.

Table 1 Coehn's D impact index (mean±SD) of *Melinis minutiflora* and *Urochloa brizantha* on communities invaded and dominated by each one of these species. Community functional components were considered altogether (bare soil + total dead biomass cover + native dead biomass cover + total graminoids + native graminoids, forbs and shrubs) along seasons. There is a tendency of differentiation between the two invasive species. No statistical differences were detected across seasons for each species (p>0.05 in all cases). ED= Early-Dry, MD= Mid-Dry, LD= Late-Dry, MR= Mid-Rainy seasons.

Invasive	All-time	Seasons			
		ED	MD	LD	MR
Melinis minutiflora	-1.12±2.30	-0.90±2.49	-1.21±2.40	-1.23±2.32	-1.13±2.08
Urochloa brizantha	-0.86±1.77	-0.59±1.81	-0.75±1.78	-0.98±1.77	-1.14±1.76

Independently from the season, the impact of *M. minutiflora* and *U. brizantha* differed for bare soil (p=0.03; Cohen's D index of -1.94±0.66 and -1.33±0.77, respectively) and total dead biomass cover (p=0.009; 2.93±1.27 and 1.90±0.86). In both cases, *M. minutiflora* had a stronger impact than *U. brizantha*: higher on the percentage of total dead cover and lower on the percentage of bare soil (Figure 1).

Both invasive species negatively affected every native functional group (native dead biomass cover, graminoids, forbs and shrubs) (Figure 1). The two most negatively impacted groups both by *M. minutiflora* or *U. brizantha* were the native graminoids (Coehn's D of -4.24±1.45 and -3.29±1.34, respectively), as well as the native dead biomass cover, with values of -3.28±1.276 and -2.70±0.98, for the former and last species respectively. When we consider the categories where the invasive species contribute (total dead biomass cover and total graminoids) the impact of invasion is positive due to the increase they promote on the cover of those two groups (Figure 1).

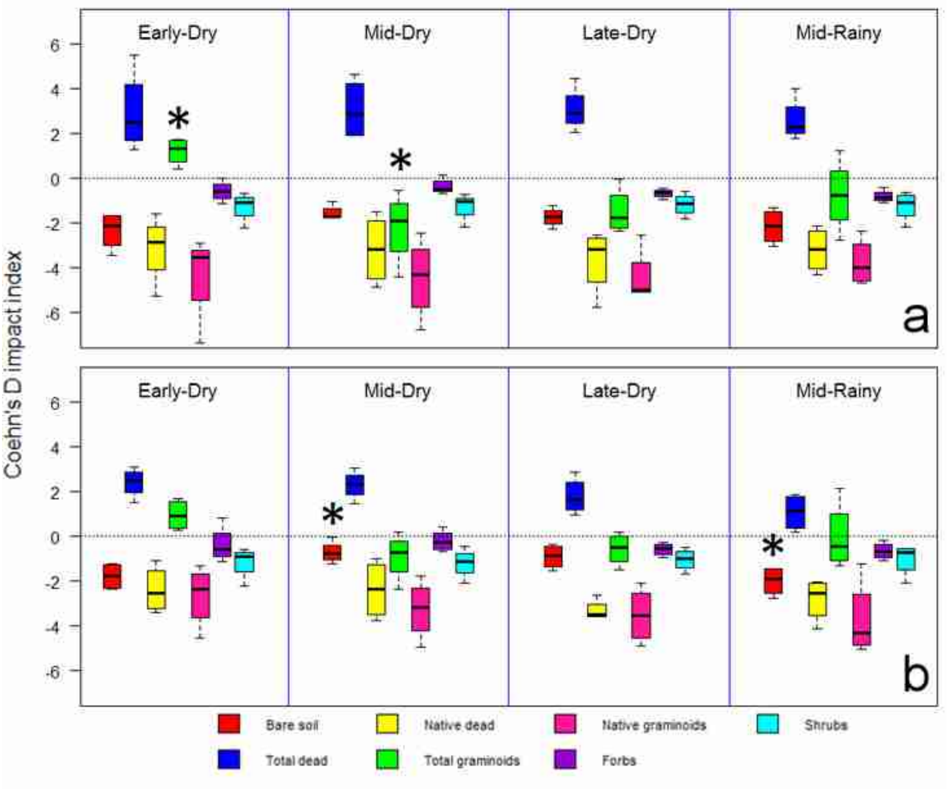

Fig. 1 Coehns' D impact index for *Melinis minutiflora* (a) and *Urochloa brizantha* (b) on communities invaded and dominated by each on of these species. Impact on community functional components

[bare soil + total dead biomass cover (native+invasive) + native dead cover + total graminoids (native+invasive) + native graminoids, forbs and shrubs] are exhibited across seasons. For each invasive species, statistical differences on Coehns' D impact index on a functional component across seasons are marked with *.

Seasonality did not affect the impact of the invasive grasses when we consider all functional components altogether (functional groups + bare soil + total dead biomass cover + total graminoids) across time, (p=0.90; Table 1). Considering each functional component separately, only the total graminoids varied in the communities invaded by *M. minutiflora*, from a positive effect (1.209±0.606) in the Early-Dry period to a negative one (-2.178±1.608) in the Mid-Dry season (p=0.02; Figure 1a). For *U. brizantha* plots, a significant difference was detected for bare soil, changing from -0.697±0.481 in the Mid-Dry to -1.998±0.659 in the Mid-Rainy seasons (p=0.03; Figure 1b).

Therefore, due to the impacts of invasive species on the functional components, their presence led to dissimilarity in composition of invaded vs. non-invaded communities (PERMANOVA, p=0.01); and despite the similar impacts of *M. minutiflora* and *U. brizantha*, communities invaded by them are dissimilar between each other (PERMANOVA, p=0.04). The PCoA elucidate these patterns by the shift in location between invaded and non-invaded communities in two dimensions (axes) that together explained 71.2% of the total variation in functional composition (Figure 2).

Discussion

Urochloa brizantha and *Melinis minutiflora* have a negative impact on the native functional components (native dead biomass cover, graminoids, forbs and shrubs) and these impacts mostly did not change across the seasons during the year, leading to completely different communities where the invasive species is present.

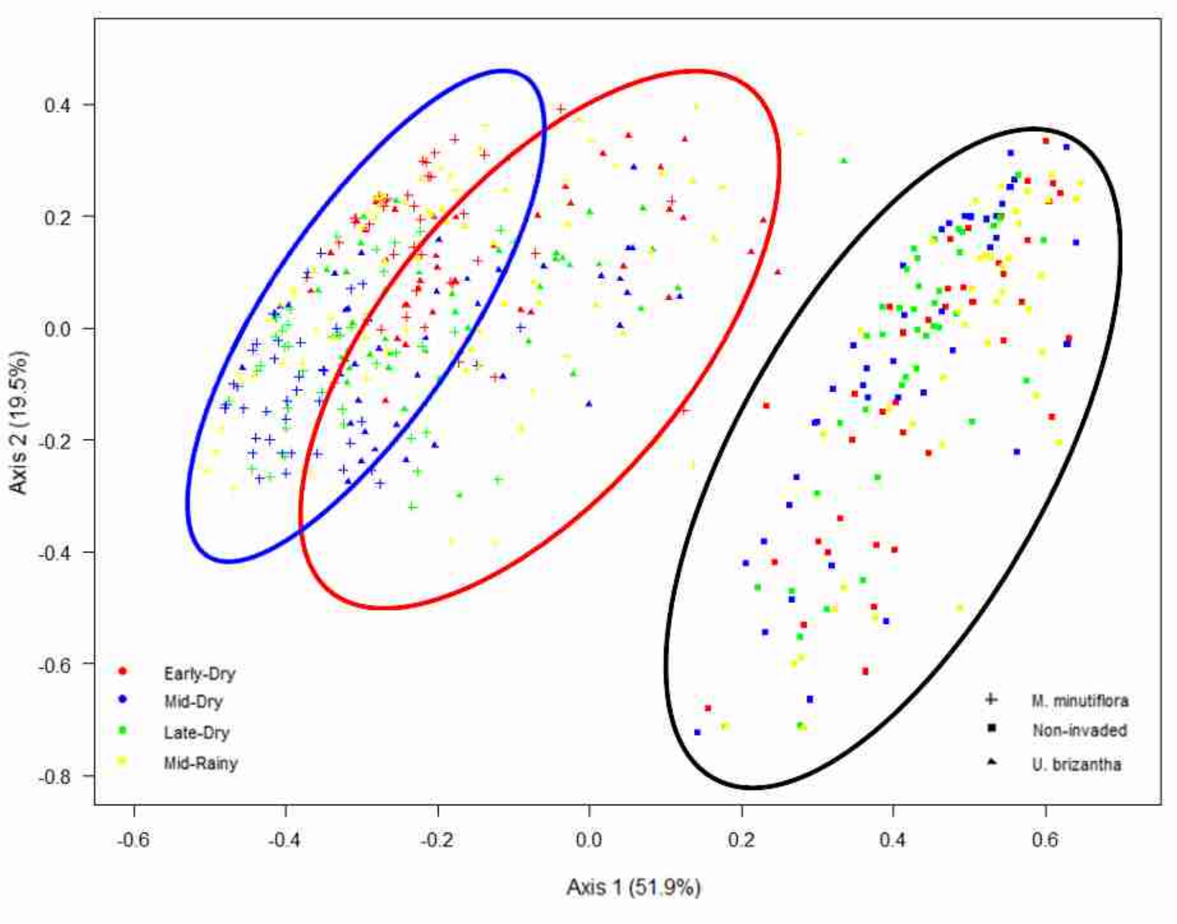

Fig. 2 Principal Coordinates Analysis for functional composition [bare soil + total dead biomass cover (native+invasive) + native dead cover + total graminoids (native+invasive) + native graminoids, forbs and shrubs] of the non-invaded and invaded communities by *Melinis minutiflora* and *Urochloa brizantha.* Each point represents a plot (1m^2) during a sampling event (Early-, Mid- and Late-Dry and Mid-Rainy season). Different symbols refer to distinct communities (dominated by each one of the invasive grasses and non-invaded) and different color refer to distinct times of sampling along a year. Ellipsis are grouping points from the same type of communities: non-invaded (black), invaded by *M. minutiflora* (blue) and invaded by *U. brizantha* (red).

Urochloa spp and *Melinis minutiflora* are two of the most common invasive species in Cerrado (Pivello et al. 1999b; Zenni and Ziller 2011; Ziller and Dechoum 2013; Sampaio and Schmidt 2014). Some authors had already shown negative impacts of these species on the invaded systems (Klink 1994; Pivello et al. 1999a; Almeida-Neto et al. 2010; Martins et al. 2011; Rossi et al. 2014). The presence of *M. minutiflora,* for example, inhibited the establishment of native tree species (Hoffmann and Haridasan 2008), hindering the recovery of degraded areas, by increasing its abundance and excluding native species (Martins et al.

2004). The presence of these African grasses negatively affected the plant communities, such as native grasses (Pivello et al. 1999a) and Asteraceae shrubs (Almeida-Neto et al. 2010). However, the above-mentioned studies have not considered the seasonality of invasives impacts nor quantified their impact on communities functional components.

Our study revealed that presence of *Melinis minutiflora* and *Urochloa brizantha* negatively impacted several functional components, being the strongest impact on the native graminoids. This result is probably related to competition between invasive and native grass species, as they are functional similarly, but also with the sensibility of Cerrado native graminoids to modifications of micro-habitats (Assis 2017; Abreu & Durigan 2011). *Melinis minutiflora* and *Urochloa brizantha* have evolved under grazers' pressure in the African savannas and thus became good competitors on nutrient assimilation and biomass production (Baruch et al. 1985; McNaughton 1985; Lannes et al. 2012), being probably more efficient in resource and water acquisition than the native Cerrado grasses (Rossiter et al. 2004; Mozdzer et al. 2016). They also increase soil cover by biomass production and accumulation, thus altering conditions for native plants seedling and development (Williams and Baruch 2000; Silva and Haridasan 2007; Hoffmann and Haridasan 2008; Assis 2017).

Indeed, *M. minutiflora* inhibits native species recruitment by influencing the dominance in composition of seed banks (Freitas & Pivello 2005) and by acting as a physical barrier blocking emergence of seedlings (Hoffmann and Haridasan 2008) and impeding native seeds to reach the ground (Zorzi 2011). *Urochloa* spp, in turn, can modify light incidence, soil temperature and air moisture, causing diversity losses and hampering native grasses germination (Assis 2017). Additionally, invasive grass species can exhibit ecophysiology advantages over Cerrado native grass species regarding to photosynthetic process and to energetic reserve mobilization on disturbed sites (Souza et al. 2010), thus enhancing their spacial dominance on invaded areas.

As a consequence of the invasive grasses negative impact on native plants, the native dead biomass cover was also negatively affected, while on the other hand the total dead biomass cover (including that of invasive species) was positively affected. These qualitative and quantitative modifications of biomass may alter species dominance on a herbaceous community in succession (Facelli and Facelli 1993), a process occurring at an area recovering from fire. Also, at the ecosystem level, those changes can lead to alterations of decomposition rates and nutrient cycling (Vitousek 1992; Vila et al. 2011), as well as of and fire behavior (Gorgone-Barbosa et al. 2015), thus promoting a positive feedback-cycle between invasive grasses and fire (D'Antonio and Vitousek 1992).

Finally, considering the temporal variation of invasives impact, differently from our hypothesis, seasonality did not change the impact of the invasive species on vegetation. Both invasive species are perennial, producing a high amount of live biomass during the rainy season. Most of that biomass dries out in the dry season but remains attached to the plant (Gorgone-Barbosa 2016). In the next rainy season, the invasive species resprout (Fisher and Kerridge 1996; Zanchi et al. 2009) and negatively impact the native community along the year by decreasing mostly native graminoids cover.

However, considering each particular functional component across time, the negative impact of *M. minutilfora* was only enhanced during the Mid-Dry season on total graminoids, while *Urochloa brizantha* impact was altered in the Mid-Dry and Mid-Rainy seasons on bare soil. These impacts were mainly the result of the natural dynamic of these species that produce huge amount of biomass during the rainy season that dries out in the next dry season (Baruch and Bilbao 1999; Silva and Haridasan 2007)(Baruch and Bilbao 1999; Silva and Haridasan 2007).

Melinis minutiflora and *Urochloa brizantha* invasions lead to functionally dissimilar communities by the production of huge amounts of persistent biomass in detriment mainly of the native grasses. These results could be interpreted as an early stage of the differentiation between the invaded and non-invaded communities, either by changes on the community characteristics (richness, eveness, diversity) or by altering the relationships of co-occurrence among native species (Kuebbing et al. 2014), and consequently, diversity, productivity and seedling establishment (Drake et al. 2008; Kuebbing et al. 2015).

In the long-term perspective, those dissimilarities can lead to modified communities (plant abundance and recruitment) and associated ecosystem properties such as decomposition rates, fire regime and mineral cycling (Vitousek 1992; D'Antonio and Vitousek 1992; Hoffmann and Haridasan 2008; Gorgone-Barbosa et al. 2015), ultimately leading the system to alternative stable states (Brooks et al. 2010).

Particularly in ecosystems under a multiple-pathway succession, invasive species can alter the process trajectory by the loss of species and ecosystem properties (Suding et al. 2004; Suding and Gross 2006; Brooks et al. 2010). Moreover, exotic grasses seem to be a case of persistent invasives that can maintain themselves over time, creating thus, the need of management actions to exclude them from the system in the long-term (D'Antonio and Meyerson 2002). It seems to be the case of invasion by *M. minutiflora* and *Urochloa* spp. in Cerrado, as they are able to promote the transition between open formations and also from preserved areas into a degraded state (Pivello and Coutinho 1996). These invasive species could alter the community diversity-stability mechanisms (Wilsey et al. 2014) to a point where a "degraded land" (sensu Pivello and Coutinho 1996) persists.

The control or eradication of *Melinis minutiflora* and *Urochloa brizantha* is thus needed to redefine the trajectory towards restoration of a diverse community where its own mechanisms of diversity-stability are included.

Acknowledgments

The authors thank Ana Carolina Ferreira, Cíntia Souza, Evaldo Souza, Giovana Chiari, Heloiza Zirondi, Jonathan Galdi Rosa, Karen Castillioni, Lucas Barbosa, Luis Felipe Daibes, Mariana Dairel, Mariana Rissi, Natacha Silva, Priscilla Sperandio, Rafael Consolmagno, Tamires Zepon and Vagner Zanzarini for helping during the field work and the Estação Ecológica de Itirapina staff for their valuable help during the establishment and maintenance of the plots. G.D received financial support from Fundação de Amparo à Pesquisa do Estado de São Paulo (2015/10714-6), V.P and A.F. were granted by Conselho Nacional de Desenvolvimento Científico e Tecnológico (305253/2015-8 and 306170/2015-9). This project was funded by Fundação de Amparo à Pesquisa do Estado de São Paulo (2015/06743-0) and the Neotropical Grasslands Conservancy.

References

Abreu RCR de, Assis GB de, Frison S, Aguirre A, Durigan G (2011) Can native vegetation recover after slash pine cultivation in the Brazilian Savanna? For Ecol Manage 262:1452–1459. doi: 10.1016/j.foreco.2011.06.046

Almeida-Neto M, Prado PI, Kubota U, Bariani JM, Aguirre, GH, Lewinsohn, TM (2010) Invasive grasses and native Asteraceae in the Brazilian Cerrado. Plant Ecol 209:109–122. doi: 10.1007/s11258-010-9727-8

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecol 26:32–46.

Anten NPR, Hirose T (1999) Interspecific differences in above-ground growth patterns result in spatial and temporal partitioning of light among species in a tall-grass meadow. J Ecol 87:583–597. doi: 10.1046/j.1365-2745.1999.00365.x

Barbosa EG, Pivello VR, Meirelles ST (2008) Allelopathic evidence in Brachiaria decumbens and its potential to invade the Brazilian cerrados. Brazilian Arch Biol Technol 51:825–831. doi: 10.1590/S1516-89132008000400021

Barreira S, Alvarenga Botelho S, Scolforo JR, Mello JM (2000) Efeitos de diferentes intensidades de corte seletivo sobre a regeneração natural de Cerrado. CERNE 6:40–51.

Baruch Z, Bilbao B (1999) Effects of fire and defoliation on the life history of native and invader C4 grasses in a Neotropical savanna. Oecologia 119:510–520. doi: 10.1007/s004420050814

Baruch Z, Hernandez ABR, Montilla MG (1989) Dinamica del crecimiento, fenologia y reparticion de biomasa gramineas nativas e introducidas de una sabana neotropical. Ecotropicos 2:1–13.

Baruch Z, Ludlow M, Davis R (1985) Photosynthetic responses of native and introduced C 4 grasses from Venezuelan savannas. Oecologia 67:388–393. doi: 10.1007/BF00384945

Batmanian GJ, Haridasan M (1985) Primary production and accumulation of nutrients by the ground layer community of cerrado vegetation of central Brazil. Plant Soil 88:437–440. doi: 10.1007/BF02197500

Brooks KJ, Setterfield SA, Douglas MM (2010) Exotic grass invasions: Applying a conceptual framework to the dynamics of degradation and restoration in Australia's tropical savannas. Restor Ecol 18:188–197. doi: 10.1111/j.1526-100X.2008.00470.x

Coutinho LM (1990) Fire in the ecology of the Brazilian Cerrado. In: Goldammer J (ed) Fire in the Tropical Biota. Ecological studies, vol 84. Springer, Berlin, pp 82-105

D'Antonio CM, Meyerson LA (2002) Exotic plant species as problems and solutions in ecological restoration. Restor Ecol 10:703–713. doi: 10.1046/j.1526-100X.2002.01051.x

D'Antonio CM, Vitousek PM (1992) Biological Invasions by Exotic Grasses, the Grass / Fire Cycle, and Global Change. Annu Rev Ecol Syst 23:63–87

Daehler CC (2003) Performance Comparisons of Co-Occurring Native and Alien Invasive Plants: Implications for Conservation and Restoration. Annu Rev Ecol Evol Syst 34:183–211. doi: 10.1146/132403

Deeks JJ, Douglas GA, Michael JB (2001) Statistical methods for examining heterogeneity and combining results from several studies in meta-analysis. In: Egger M, Altman DG, Smith GD (eds) Systematic reviews in health care: meta-analysis in context, 2nd edn. BMJ Publishing Group, London, pp 285–312

Dick JTA, Alexander ME, Jeschke JM, et al (2014) Advancing impact prediction and hypothesis testing in invasion ecology using a comparative functional response approach. Biol Invasions 16:735–753. doi: 10.1007/s10530-013-0550-8

Drake JM, Cleland EE, Horner-Devine MC, et al (2008) Do Non-native Plant Species Affect the Shape of Productivity-diversity Relationships? Am Midl Nat 159:55-56. https://www.jstor.org/stable/20491311

Durigan G, Contieri WA, Franco GADC, Garrido MAO (1999) Indução do processo de regeneração da vegetação de Cerrado em área de pastagem, Assis, SP. Acta Bot Brasilica 12:421–429.

Durigan G, Ferreira De Siqueira M, Daher GA, Franco C (2007) Threats to the cerrado remnants. Sci Agric (Piracicaba) 64:355–363. doi: 10.1590/S0103-90162007000400006

Eiten G (1972) The Cerrado vegetation of Brazil. Bot Rev 38:201–338. doi: 10.1007/BF02859158

Emery SM (2007) Limiting similarity between invaders and dominant species in herbaceous plant communities? J Ecol 95:1027–1035. doi: 10.1111/j.1365-2745.2007.01274.x

Emery SM, Gross KL (2007) Dominant species identity, not community evennes, regulates invasion in experimental grassland plant communities. Ecology 88:954–964. doi: 10.1890/06-0568

Engelhardt MJ, Anderson RC (2011) Phenological niche separation from native species increases reproductive success of an invasive species : Alliaria petiolata (Brassicaceae) – garlic mustard. J Torrey Bot Soc 138:418–433.

Facelli JM, Facelli E (1993) Interactions after death: plant litter controls priority effects in a successional plant community. Oecologia 95:277–282. doi: 10.1007/BF00323500

Fargione J, Brown CS, Tilman D (2003) Community assembly and invasion: an experimental test of neutral versus niche processes. Proc Natl Acad Sci USA 100:8916–20. doi: 10.1073/pnas.1033107100

Fargione J, Tilman D (2005) Niche differences in phenology and rooting depth promote coexistence with a dominant C4 bunchgrass. Oecologia 143:598–606. doi: 10.1007/s00442-005-0010-y

Fisher MJ, Kerridge PC (1996) The agronomy and physiology of Brachiaria species. In: Miles JW, Mass BL, Valle CB (eds) Brachiaria: Biology, agronomy and improvement. Centro Internacional de Agricultura Tropical (CIAT) and Empresa Brasileira de Pesquisa Agropecuária/ Centro Nacional de Pesquisa de Gado de Corte (EMBRAPA/CNPGC), Cali, Colombia pp 43–52

Flory SL, Clay K (2010) Non-native grass invasion suppresses forest succession. Oecologia 164:1029–1038. doi: 10.1007/s00442-010-1697-y

Franco AC (2002) Ecophysiology of wood plants. In: Oliveira PS, Marquis RJ (eds) The Cerrados of Brazil: Ecology and natural history of a neotropical savanna, Columbia University Press, New York, pp. 178–198. www.jstor.org/stable/10.7312/oliv12042.13pp 178–200

Gorgone-Barbosa E (2016) A relação entre fogo e uma gramínea invasora no Cerrado: O fogo pode ser utilizado como uma estratégia de controle? Thesis,Universidade Estadual Paulista “Júlio de Mesquita Filho”

Gorgone-Barbosa E, Pivello VR, Bautista S, Zupo T, Rissi MN, Fidelis A (2015) How can an invasive grass affect fire behavior in a tropical savanna? A community and individual plant level approach. Biol Invasions 17:423–431. doi: 10.1007/s10530-014-0740-z

Hoffmann WA (1998) Post-burn reproduction of woody plants in a neotropical savanna: The relative importance of sexual and vegetative reproduction. J Appl Ecol 35:422–433. doi: 10.1046/j.1365-2664.1998.00321.x

Hoffmann W a, Hoffmann W a, Lucatelli VMPC, Silva FJ, Azeuedo INC, Marinho MS, Albuquerque AMS, Lopes AO, Moreira SP (2004) Impact of the invasive alien grass Melinis minutiflora at the savanna-forest ecotone in the Brazilian Cerrado. Divers Distrib 99–103. doi: 10.1111/j.1366-9516.2004.00063.x

Hoffmann WA, Haridasan M (2008) The invasive grass, Melinis minutiflora, inhibits tree regeneration in a Neotropical savanna. Austral Ecol 33:29–36. doi: 10.1111/j.1442-9993.2007.01787.x

Hothorn T, Bretz F, Westfall P (2008) Simultaneous Inference in General Parametric Models. Biometrical J 50:346–363.

Klink CA (1994) Effects of clipping on size and tillering of native and African grasses of the Brazilian savannas (the cerrado). Oikos 70:365–376. doi: 10.2307/3545774

Kuebbing SE, Classen AT, Sanders NJ, Simberloff D (2015) Above- and below-ground effects of plant diversity depend on species origin: An experimental test with multiple invaders. New Phytol 208:727–735. doi: 10.1111/nph.13488

Kuebbing SE, Souza L, Sanders NJ (2014) Effects of co-occurring non-native invasive plant species on old-field succession. For Ecol Manage 324:196–204.

Lannes LS, Bustamante MMC, Edwards PJ, Venterink HO (2012) Alien and endangered plants in the Brazilian Cerrado exhibit contrasting relationships with vegetation biomass and N : P stoichiometry. New Phytol 196:816–823. doi: 10.1111/j.1469-8137.2012.04363.x

Martins CR, Hay JDV, Walter BMT, Proença CEB, Vivaldi, LJ (2011) Impact of invasion and management of molasses grass (Melinis minutiflora) on the native vegetation of the Brazilian Savanna. Brazilian J Bot 34:73–90. doi: 10.1590/s0100-84042011000100008

Martins CR, Leite LL, M. H (2004) Molasses grass (Melinis minutiflora P . Beauv .), an exotic species compromising the recuperation of degraded areas in conservation units. Rev Árvore 28:739–747. doi: 10.1590/s0100-67622004000500014

McNaughton SJ (1985) Ecology of a Grazing Ecosystem : The Serengeti. Ecol Monogr 55:259–294

Mozdzer TJ, Langley JA, Mueller P, Megonigal JP (2016) Deep rooting and global change facilitate spread of invasive grass. Biol Invasions 18:2619–2631. doi: 10.1007/s10530-016-1156-8

Munhoz CBR, Felfili JM (2005) Fenologia do estrato herbáceo-subarbustivo de uma comunidade de campo sujo na Fazenda Água Limpa no Distrito Federal, Brasil. Acta Bot Brasilica 19:979–988. doi: 10.1590/S0102-33062005000400031

Mwangi PN, Schmitz M, Scherber C, et al (2007) Niche pre-emption increases with species richness in experimental plant communities. J Ecol 95:65–78. doi: 10.1111/j.1365-2745.2006.01189.x

Oksanen J, Blanchet FG, Kindt R, et al (2016) vegan: Community Ecology Package. Community Ecol. Packag. version

Oliveira APP, Pereira SR, Cândido ACS, Laura VA, Peres MTLP (2016) Can Allelopathic Grasses Limit Seed Germination and Seedling Growth of Mutambo? A Test with Two Species of Brachiaria Grasses. Planta Daninha 34:639–648. doi: 10.1590/s0100-83582016340400003

Orlóci L. (1967) An Agglomerative Method for Classification of Plant Communities. Br Ecol Soc 55:193–206.

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2016) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-131, https://CRAN.R-project.org/package=nlme.

Pivello V, Carvalho V, Lopes P (1999b) Abundance and distribution of native and alien grasses in a “Cerrado”(Brazilian Savanna) biological reserve. Biotropica 31:71–82. doi: 10.1111/j.1744-7429.1999.tb00117.x

Pivello VR, Coutinho LM (1996) A qualitative successional model to assist in the management of Brazilian cerrados. For Ecol Manage 87:127–138. doi: 10.1016/S0378-1127(96)03829-7

Pivello VR, Shida CN, Meirelles ST (1999a) Alien grasses in Brazilian savannas: A threat to the biodiversity. Biodivers Conserv 8:1281–1294. doi: 10.1023/A:1008933305857

Pokorny ML, Sheley RL, Zabinski CA, Engel RE, Svejcar TJ, Borkowski JJ (2005) Plant functional group diversity as a mechanism for invasion resistance. Restor Ecol 13:448–459. doi: 10.1111/j.1526-100X.2005.00056.x

Prieur-Richard AH, Lavorel S, Linhart YB, Dos Santos A (2002) Plant diversity, herbivory and resistance of a plant community to invasion in Mediterranean annual communities. Oecologia 130:96–104. doi: 10.1007/s004420100774

R Development Core Team (2016) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Reed HE, Seastedt TR, Blair JM (2005) Ecological Consequences of C4 Grass Invasion of a C4 Grassland: a Dilemma for Management. Ecol Appl 15:1560–1569. doi: 10.1890/04-0407

Rossi RD, Martins CR, Viana PL, Rodrigues EL, Eugênio JCF (2014) Impact of invasion by molasses grass (Melinis minutiflora P. Beauv.) on native species and on fires in areas of campo-cerrado in Brazil. Acta Bot Brasilica 28:631–637. doi: 10.1590/0102-33062014abb3390

Rossiter N, Setterfield S a, Douglas MM, et al (2004) Exotic grass invasion in the tropical savanna of northern Australia: ecosystem consequences. Fuel 2004, pp 168–171.

Sampaio AB, Schmidt IB (2014) Espécies exóticas invasoras em unidades de conservação federais do Brasil. Biodiversidade Bras 3:32–49.

Silva JSO, Haridasan M (2007) Acúmulo de biomassa aérea e concentração de nutrientes em Melinis minutiflora P. Beauv. e gramíneas nativas do cerrado. Rev Bras Botânica 30:337–344. doi: 10.1590/S0100-84042007000200016

Silveira ER da, Melo ACG de, Contieri WA, Durigan G (2013) Controle de gramíneas exóticas em plantio de restauração de Cerrado. In: Durigan G, Ramos VSR (eds) Manejo Adaptativo: primeiras experiências na restauração de ecossistemas. Páginas e Letras Editora e Gráfica, São Paulo, pp 5–8

Souza, A., Sandrin, C.Z., Calió, M.F.A., Meirelles, S.T., Pivello, V.R. & Figueiredo-Ribeiro, R.C.L. (2010) Seasonal variation of soluble carbohydrates and starch in Echinolaena inflexa, a native grass species from the Brazilian savanna, and in the invasive grass Melinis minutiflora. *Brazilian journal of biology*, **70**, 395–404.

Suding KN, Gross KL (2006) Modifying native and exotic species richness correlations: The influence of fire and seed addition. Ecol Appl 16:1319–1326. doi: 10.1890/1051-0761(2006)016[1319:MNAESR]2.0.CO;2

Suding KN, Gross KL, Houseman GR (2004) Alternative states and positive feedbacks in restoration ecology. Trends Ecol Evol 19:46–53. doi: 10.1016/j.tree.2003.10.005

Thomsen MS, Wernberg T, South PM, Schiel DR (2016) To include or not to include (the invader in community analyses)? That is the question. Biol Invasions 18:1515–1521. doi: 10.1007/s10530-016-1102-9

Turnbull LA, Rahm S, Baudois O, Eichenberger-Glinz S, Wacker L, Schmid B (2005) Experimental invasion by legumes reveals non-random assembly rules in grassland communities. J Ecol 93:1062–1070. doi: 10.1111/j.1365-2745.2005.01051.x

Vila M, Espinar JL, Hejda M, et al (2011) Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. Ecol Lett 14:702–708. doi: 10.1111/j.1461-0248.2011.01628.x

Vitousek PM (1992) Effects of Alien Plants on Native Ecosystems. In: CP Stone, CW Smith, and JT Tunison (ed) Alien plant species in native ecosystems of Hawai'i: management and research. University of Hawai'i Cooperative National Park Resources Studies Unit, Honolulu pp 29-41.

Wikum DA, Shanholtzer GF (1978) Application of the Braun-Blanquet cover-abundance scale for vegetation analysis in land development studies. Environ Manage 2:323–329. doi: 10.1007/BF01866672

Williams DG, Baruch Z (2000) African grass invasion in the Americas: Ecosystem consequences and the role of ecophysiology. Biol Invasions 2:123–140. doi: 10.1023/A:1010040524588

Wilsey BJ, Daneshgar PP, Hofmockel K, Polley HW (2014) Invaded grassland communities have altered stability-maintenance mechanisms but equal stability compared to native communities. Ecol Lett 17:92–100. doi: 10.1111/ele.12213

Zanchetta D, Reis CM (2006) Plano de Manejo Integrado: Estações Ecológica e Experimental de Itirapina/SP, 1ª Revisão.

Zanchi FB, Waterloo MJ, Aguiar LJG, et al (2009) Estimativa do Índice de Área Foliar (IAF) e Biomassa em pastagem no estado de Rondônia, Brasil. Acta Amazonica 39:335–348.

Zenni RD, Ziller SR (2011) An overview of invasive plants in Brazil. Rev Bras Botânica 34:431–446. doi: 10.1590/S0100-84042011000300016

Ziller SR, Dechoum MS (2013) Plantas e vertebrados exóticos invasores em unidades de conservação no Brasil. Biodiversidade Bras 3:4–31.

Zorzi, V.G. de. (2011) Interferênncia da gramínea invasora Melinis minutiflora Beauv. No Banco De Sementes De Um Campo Sujo De Cerrado. *X Congresso de Ecologia do Brasil*, pp. 1–3.

Fire season implications for management of invasive grasses and savanna restoration: an example from Cerrado

Gabriella Damasceno[1,*] & Alessandra Fidelis[1]

1 Universidade Estadual Paulista (UNESP), Instituto de Biociências, Rio Claro. Av. 24A,1515, 13506-900, Rio Claro, Brazil.

* Correspondence author: fariadamasceno@gmail.com +55193526-4208

Summary

1) Invasive grasses are a common and dangerous threat to savannas worldwide, also being an obstacle for the restoration of these ecosystems. Management techniques to their control usually involve herbicides, hand weeding and prescribed fires. However, there is no consensus about the effect of fire and fire season on invasive grasses at Cerrado, the Brazilian neotropical savanna.
2) We evaluated the effect of fire season on the abundance – measured as above-ground biomass of the invasive grasses *Melinis minutiflora* and *Urochloa brizantha* and native plants functional groups (graminoids, forbs and shrubs). We tested three fire seasons: Early-Dry (May), Mid-Dry (July) and Late-Dry season (October) in relation to unburned control plots. Prescribed burnings were conducted in 2014 on 15x15 m plots (4 plots/treatment/invasive species – total of 32 plots). Biomass samplings were randomly carried out before the experiments and every six months for two years (5 samples of 0.5x0.5 m^2 each) inside each experimental plot. We used additive mixed modeling to investigate the effect of fire season across time for biomass of each functional component and for bare soil cover.
3) All fire season treatments reduced *M. minutiflora* abundance after two years. A new invasion by *U. brizantha* on plots previously dominated by *M. minutiflora* occurred and it was more pronounced on Early-Dry fire plots, although it also seems to be

enhanced on Late-Dry season plots. *U. brizantha* was not affected by fires in any season, but its biomass was reduced in short-term just after fires. Only native forbs biomass were enhanced by Mid-Dry fires on communities dominated by *M. minutiflora.*

4) Fire intensity and environmental conditions may explain the pattern related to *M. minutiflora*, while *U. brizantha* fast growth and high propagule pressure are the explanations for its faster recovery after fires. Also, these influential factors may be mediated by changes in community invasibility due to resources fluctuations.
5) *Synthesis and applications:* Hence, at invaded Cerrado areas we recommend Mid-Dry fires to control *M. minutiflora* and enhance savanna restoration, whilst fire could be used combined with another technique to control *Urochloa brizantha,* since it reduced the amount of this invasive dead biomass.

Keywords: biological invasion; ecological restoration; invasive grasses management; fire season; *Melinis minutiflora*; prescribed burning; savanna restoration; *Urochloa brizantha*

Introduction

Invasive species are a major threat to biodiversity conservation worldwide (Pyšek *et al.* 2012), because they can lead to species extinctions (Sax & Gaines 2008) and promote indirect effects on the environment such as changes in litter properties (Bansal *et al.* 2014), water and mineral cycling (Rossiter *et al.* 2004), and climate regulation (Pejchar & Mooney 2009). Invasive grasses impact different types of systems by altering community structure and composition (Reed, Seastedt & Blair 2005; Flory & Clay 2010a) by modifying competition relationship among species (Flory & Clay 2010b), ecosystem processes (Brooks, Setterfield & Douglas 2010) and disturbance regimes, such as fire (D’Antonio & Vitousek 1992).

Fire is natural and recurrent disturbance on savannas (Bond & Keeley 2005) and fire season is a key-aspect of fire regimes (Govender, Trollope & Van Wilgen 2006), such as in markedly seasonal systems as Cerrado, with its dry winter and rainy summers (Eiten 1972). Consequently, plant responses to fire season may be linked to environmental conditions and plant phenology at the moment of fires (Knapp, Estes & Skinner 2009), since both drought and reproductive structures imply in mobilization of energetic reserves (Vieira & Figueiredo-Ribeiro 1993; Almeida *et al.* 2017). Additionally, the moment of fire occurrence influences plant responses because it determines the proximity of the next growing season, when water availability promotes favorable conditions for plant recovery (Eiten 1992). Furthermore, there is a relationship among environment, plant conditions and fire characteristics, because in dry periods, the plant biomass will dry-out, altering thus, the fuel properties and as a consequence, fire behavior (Whelan 1995). Therefore, fires on different seasons should lead to distinct responses of invasive and native species due to conditions during and after fire.

African grasses as *Melinis minutiflora* and species from the genus *Urochloa*, e.g. *U. brizantha*, are a major threat to Cerrado biodiversity conservation due to their recurrent presence into nature preserves (Pivello, Carvalho & Lopes 1999), where they alter microhabitat structure (Assis 2017), reduce native biomass (Martins *et al.* 2011) and negatively affect native plants (Pivello, Shida & Meirelles 1999), as well as alter fire regimes (Rossi *et al.* 2014) and behavior (Gorgone-Barbosa *et al.* 2015). They are perennials with high production of biomass during the growing season and accumulation of dead biomass during the dry winter (Fisher & Kerridge 1996; Silva & Haridasan 2007). Their reproductive peak is at the beginning (October) and at the end of the rainy season (May) for *Urochloa* spp. (Hopkinson *et al.* 1996) and *M. minutiflora* (Martins 2006), respectively. Both of them produce high quantities of seeds resistant to fires (Martins 2006; Hopkinson *et al.* 1996), showing an increase in germination in post-disturbance environments due to temperature fluctuation (Gorgone-Barbosa *et al.* 2016; Musso *et al.* 2015). *Urochloa* spp produce allelopathic compounds that facilitate its invasion in new areas (Barbosa, Pivello & Meirelles 2008), a fact that is also favored by the intentional improvement of these species to be more competitive, aggressive and resilient (Karia, Duarte & Araújo 2006; Valle *et al.* 2009).

Despite Cerrado's high biodiversity and importance on providing ecosystem services (Myers *et al.* 2000; Honda & Durigan 2016), nearly half of its original distribution area has already been changed into different land uses (Klink & Machado 2005; Sano *et al.* 2008). Legal obligations imposed by Brazilian environmental laws demands that part of these already converted land must be ecologically restored (Lei 12651/2012). Regardless of Cerrado's high resilience and fast natural regeneration (Abreu *et al.* 2011), African grasses poses a huge obstacle to Cerrado restoration because they hamper initial management actions due to their high cover (Durigan *et al.* 1999; Hoffmann & Haridassan 2008; Silveira *et al.* 2013). Moreover, they can initiate a new invasion process during the restoration process, jeopardizing thus, herbaceous species and recruitment of shrubs and trees (Durigan *et al.* 1999; Melo, Durigan & Kawabata 2004; Hoffmann & Haridasan 2008).

Control of invasive plant species is usually the first step on restoration projects and it can be carried out directly by removing individuals, and/or indirectly by promoting disturbance that alter the competitive relationship between native and invasive species, favoring the first over the last one (Mack *et al.* 2000; Catford *et al.* 2012). Fire is a common tool used to control invasive species worldwide (Emery & Gross 2005; Prober *et al.* 2005; DiTomaso *et al.* 2006; Davies & Sheley 2011), but despite its natural occurrence in Cerrado (Simon *et al.* 2009), its efficacy on controlling invasive grasses is still not well understood. Some studies showed that prescribed fires alone did not affect the abundance of African grasses (Martins 2006; Assis 2017). On the other hand, its efficacy as part of an integrated management to control invasive grasses has been demonstrated (Pivello 2006; Palermo *et al.*

2007; Martins *et al.* 2011; Assis 2017), although fire season was not investigated in these previous studies. And since Cerrado has a marked seasonality and fire behavior can differ among seasons (Rissi et al., 2017), fire in different seasons could be used to control African invasive grasses in Cerrado, and at the same time, not hamper native vegetation regeneration.

Therefore, the main aim of this study was to investigate if fire in different seasons (Early-, Mid- and Late-Dry season) would affect the abundance (measured as aboveground biomass) of *Melinis minutiflora* and *Urochloa brizantha*, resulting thus, in distinct scenaria of opportunities to Cerrado restoration. We hypothesized that fires at the moment of the reproduction stage of the invasive species would be more efficient in controlling them, since resources are being allocated to reproductive structures. Consequently, we presume that *M. minutiflora* and *U. brizantha* would be better controlled by fires in Early-Dry and Late-Dry seasons, respectively.

Material and Methods

Study area

The study site was located in Southeastern Brazil, at the Ecological Station of Itirapina (20°00'-22°15'S e 47°45'-48°00W; 710 to 830 m a.s.l) and it was a former *Pinus caribaea* plantation (33 ha). Pine trees were removed in 1998. Since this time, the area is under natural regeneration, excluded from fire and grazing, but it is highly invaded by the African grasses *Melinis minutiflora* and *Urochloa brizantha*. The area is an open savanna, characterized by a continuous herbaceous layer composed mainly by C_4 grasses with scattered shrubs and small tress. Patches of both invasive species can be found within the vegetation. Arenosol is the predominant soil type (Zanchetta & Reis 2006). Climate is marked by seasonality with dry winters and rainy summers, with mean annual precipitation of 1459 mm and temperature 21.9ºC (Zanchetta & Reis 2006).

Experimental design and methods

Within the experimental area we selected patches dominated by the invasive grass species (at least 50% of cover by *M. minutiflora* or *U. brizantha*) and established 16 plots (15x15 m) for each African species. For each type of community (dominated by *M. minutiflora* or by *U. brizantha*) we randomly assigned four plots for each treatment: Controls (C; unburned plots); Early-Dry (ED; burned in May), Mid-Dry (MD; burned in July) and Late-Dry (LD; burned in October), a total of 32 plots (4 plots/treatment/species). All prescribed burnings were conducted in 2014.

Sampling was performed before the execution of prescribed burnings and after it every six months, over two years, in order to cover both dry and rainy season. On every sampling event, aiming to capture spacial variations, we randomly selected five subplots of 0.5x0.5m within each experimental plot ($15m^2$) and collected all above-ground biomass. The biomass was conditioned in paper bags, and at the laboratory, it was sorted into the following functional components: live and dead invasive species (*M. minutiflora* and *U. brizantha*), native live graminoids, forbs, shrubs and native dead biomass. The biomass was dried for 48 hours at 80ºC on a drying oven and weighted after that.

Additionally, in order to monitor the dynamics of empty spaces after fires, we visually estimated the bare soil cover (%) in permanent plots (10 plots of $1m^2$) that were randomly established within each experimental plot (15 x 15m).

Statistical analysis

We used additive mixed modeling to investigate the effect of fire season across time for biomass of each functional component and for bare soil cover. We proceeded to model selection based on the restricted maximum likelihood criteria (REML) and ended up with treatment and time as fixed factors and plot as a random effect due to the nested design of the experiment. We also corrected the models for temporal correlation using ARMA structure and for heterogeneity by leading different variations based on the identity of treatment groups. All statistical analyzes were performed using R program (R Core Team 2016) with the packages vegan (Oksanen *et al.* 2016), lme4 (Bates *et al.* 2015), mgcv (Wood 2011), multcomp (Hothorn, Bretz & Westfall 2008) and ggplot2 (Wickham 2009).

Results

Fire itself was able to control *Melinis minutiflora*, since the total biomass on all treatments differed from controls plots (Table 1), decreasing ca. 65% in relation to pre-fire values on the first rainy season (Fig. 1A). Regeneration of total *M. minutiflora* biomass reached maximum values on the rainy season of 2016 and no differences between treatments could be found: 139±341g.m^{-2}, 88±309g.m^{-2}, and 0±0g.m^{-2} for plots submitted to Early-, Mid- and Late-Dry season fires, respectively.

On the other hand, *U. brizantha* was not affected by fires in any season, because its total biomass did not differ from unburned plots after two year (Table 1). However, considering this component just after fires, on the first rainy season (February 2015), the total biomass was lower in burned than unburned plots, which had a value of 500±353g.m^{-2} (Fig. 1B) on controls. Compared to Early- (193±155g.m^{-2}), Mid- (329±239g.m^{-2}) and Late-Dry fires (200±154g.m^{-2}). Also, Early-Dry fires led to an increase of *U. brizantha* total biomass (627±328g.m^{-2}) in comparison to control plots (404±246g.m^{-2}) during the rainy season of 2016 (Fig. 1B). However, from the mid of the rainy season of 2016 (February) thenceforward, biomass of this invasive species was similar in all treatments, including unburned controls (404±247g.m^{-2}, 627±328g.m^{-2}, 476±349g.m^{-2} and 476±312g.m^{-2} for Control, Early-, Mid and Late-Dry treatments, respectively; Fig. 1B).

Table 1. Differences, two years after the experiments, in total, live and dead biomass of *Melinis*

minutiflora ($g.m^{-2}$) and *Urochloa brizantha* ($g.m^{-2}$), native functional components (native graminoids, forbs and shrubs, $g.m^{-2}$) and cover of bare soil (%) according to the generalized additive mixed modeling (GAMM) in communities initially invaded by either *M. minutiflora* or *U. brizantha* and submitted to fire season treatments: C - Control; ED - Early-Dry; MD - Mid-Dry and LD - Late-Dry. Components that differed among fire treatments ($p \leq 0.05$) are in bold.

Invasive species	**Functional component**	**Treatment**	**C x ED**	**C x MD**	**C x LD**
Melinis minutiflora communities	Total *M. minutiflora*	**<0.001**	**<0.001**	**<0.001**	**<0.001**
	Live *M. minutiflora*	**<0.001**	**0.05**	**<0.001**	**<0.001**
	Dead *M. minutiflora*	**<0.001**	**<0.001**	**<0.001**	**<0.001**
	Native dead biomass	0.7	0.9	0.5	0.4
	Graminois	0.9	0.9	0.9	0.5
	Forbs	**0.05**	0.3	**0.02**	0.7
	Shrubs	0.1	0.09	0.5	0.6
	Total *U. brizantha*	**0.05**	**0.01**	0.6	0.07
	Live *U. brizantha*	0.3	0.2	0.7	0.1
	Dead *U. brizantha*	0.3	0.07	0.6	0.1
	Bare soil cover	**<0.001**	**<0.001**	**<0.001**	**<0.001**
Urochloa brizantha communities	Total *U. brizantha*	0.8	0.3	0.8	0.9
	Live *U. brizantha*	0.8	0.4	0.5	0.9
	Dead *U. brizantha*	0.6	0.3	0.3	0.3
	Native dead biomass	0.2	0.2	0.8	0.06
	Graminoids	0.5	0.6	0.4	0.5
	Forbs	0.06	0.2	0.3	0.5
	Shrubs	0.5	0.8	0.5	0.3
	Bare soil cover	**0.03**	**0.01**	0.2	0.2

In general, the same patterns of fire effects could be observed for both live and dead biomass of the invasive species two years after fire: fires in all season affected live and dead biomass of *M. minutiflora,* whilst no effect could be observed on *U. brizantha* biomass (Table 1). Like *M. minutiflora* total biomass, the live biomass was not affected by fire season (Fig. 1C). However, for live *U. brizantha* biomass, patterns are distinct from the total biomass:

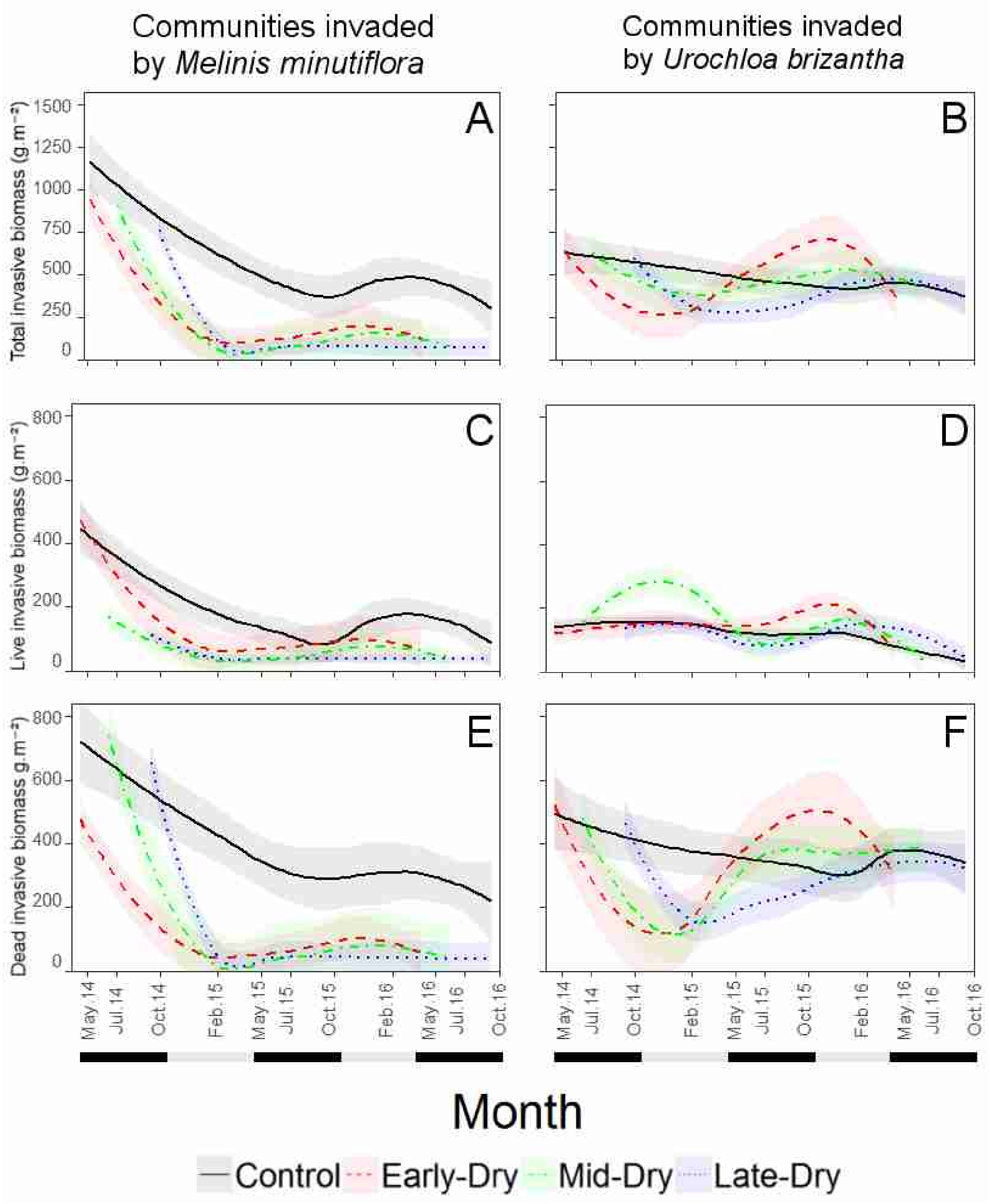

Figure 1. Biomass (g.m^{-2}) over time after fire (months) for invasive functional components on Cerrado invaded communities by *Melinis minutiflora* and *Urochloa brizantha*. Lines are the predicted values by the best fitted GAMM and fills are the confidence interval (95%). The horizontal bars on x axis indicates seasonality in relation to months: black and gray traces are the dry and rainy seasons, respectively. Total biomass (A, B), Live (C, D) and Dead Biomass (E, F).

Mid-Dry fires stimulated the regeneration during the first rainy season (two-fold increase in comparison to controls), and Early-Dry treatment on the second rainy season (18% higher than control). Finally, Late-Dry season fires did not affect *Urochloa brizantha* live biomass (Fig. 1D).

Fire effect on *M. minutiflora* dead biomass was similar in any season, with reductions of 85%, 95% and 97% by Early-, Mid- and Late-Dry treatments on the first rainy season after fires (Fig. 1E). *U. brizantha* dead biomass followed the same pattern of the total biomass, however not significant differences were observed among fire season ($p<0.05$). Moreover, this component was temporarily reduced by fires, as during the first rainy season after experiments, the amount of dead biomass of *U. brizantha* in control plots was 351±258g.m^{-2}, whilst in burned plots it varied from 65±46g.m^{-2} (Late-Dry season fires) to 96±100g.m^{-2} (Early-Dry season fires, Fig. 1F). Additionally, on plots burned at Late-Dry season, the amount of dead biomass was low until the mid of the following dry season (July 2015; 240±175g.m^{-2}). However, in the following dry season (July 2016), an accumulation of dead biomass could be observed in all fire season treatments, reaching the values of control plots during the following rainy season (February 2016), varying from 301±187g.m^{-2} in controls to 440±257g.m^{-2} in Early-Dry season fire plots (Fig. 1F).

Urochloa brizantha invaded plots initially dominated by *M. minutiflora* independently of fire occurrence or season. However, a more intense invasion could be observed in Early-Dry season fire plots, which on the second rainy season (February 2016) after fire experiments had values of total biomass of 352±326g.m^{-2} in relation to 57±135g.m^{-2} on unburned controls (Table 2). Additionally, Late-Dry fires have also promoted the new invasion by *U. brizantha*, but only during 2016 rainy season, when biomass values were 361±340g.m^{-2} (LD plots) and 57±135g.m^{-2} (control plots).

In general, native functional components (e.g. graminoids, forbs, and shrubs) were not

Table 2. Differences, two years after the experiments, in total, live and dead biomass of *Urochloa brizantha* (g.m^{-2}) according to the generalized additive mixed modeling (GAMM) in plots initially invaded by *M. minutiflora* and submitted to fire season treatments: C - Control; ED - Early-Dry; MD - Mid-Dry and LD - Late-Dry. Components that differed among fire treatments ($p \leq 0.05$) are in bold.

Invasive species	Functional component	Treatment	C x ED	C x MD	C x LD
Melinis minutiflora communities	Total *U. brizantha*	**0.05**	**0.01**	0.6	0.07
	Live *U. brizantha*	0.3	0.2	0.7	0.1
	Dead *U. brizantha*	0.3	0.07	0.6	0.1

affected by fires in any season in communities dominated by the African invasive grasses, with exception of forbs on communities invaded by *M. minutiflora* (Table 1). Moreover, in communities invaded by this grass, native dead biomass was immediately reduced by fires by 5% (ED), 27% (MD) and 2% (LD), but did not differ from unburned controls (Fig. 2A). On communities invaded by *U. brizantha,* native dead biomass was reduced to 5% of its initial biomass after all fire treatments (Fig. 2B). On communities invaded by both African grasses, although the biomass of native graminoids was not affected by fire season ($p>0.05$, Table 1), Mid-Dry season fires tended to be less harmful than fires on Early- and Late-Dry season, since a graminoid biomass peak was observed in the rainy season of 2016, showing the same pattern found in control plots (Fig. 2C and 2D).

Forbs biomass increased only after Mid-Dry season fires on communities invaded by *M. minutiflora* ($p=0.05$;Table 1; Fig. 2E) with values of 29±62g.m^2 and 32±78g.m^2 in 2015 and 2016, respectively (Fig. 2E). Contrarily, on communities invaded by *U. brizantha,* forbs was the less affected component by fires in any season, being sampled only in plots that were burned on Late-Dry season (Fig. 2F). Shrubs showed the same biomass values for all treatments ($p>0.05$; Table 1), in communities invaded both by *M. minutiflora* and *U.*

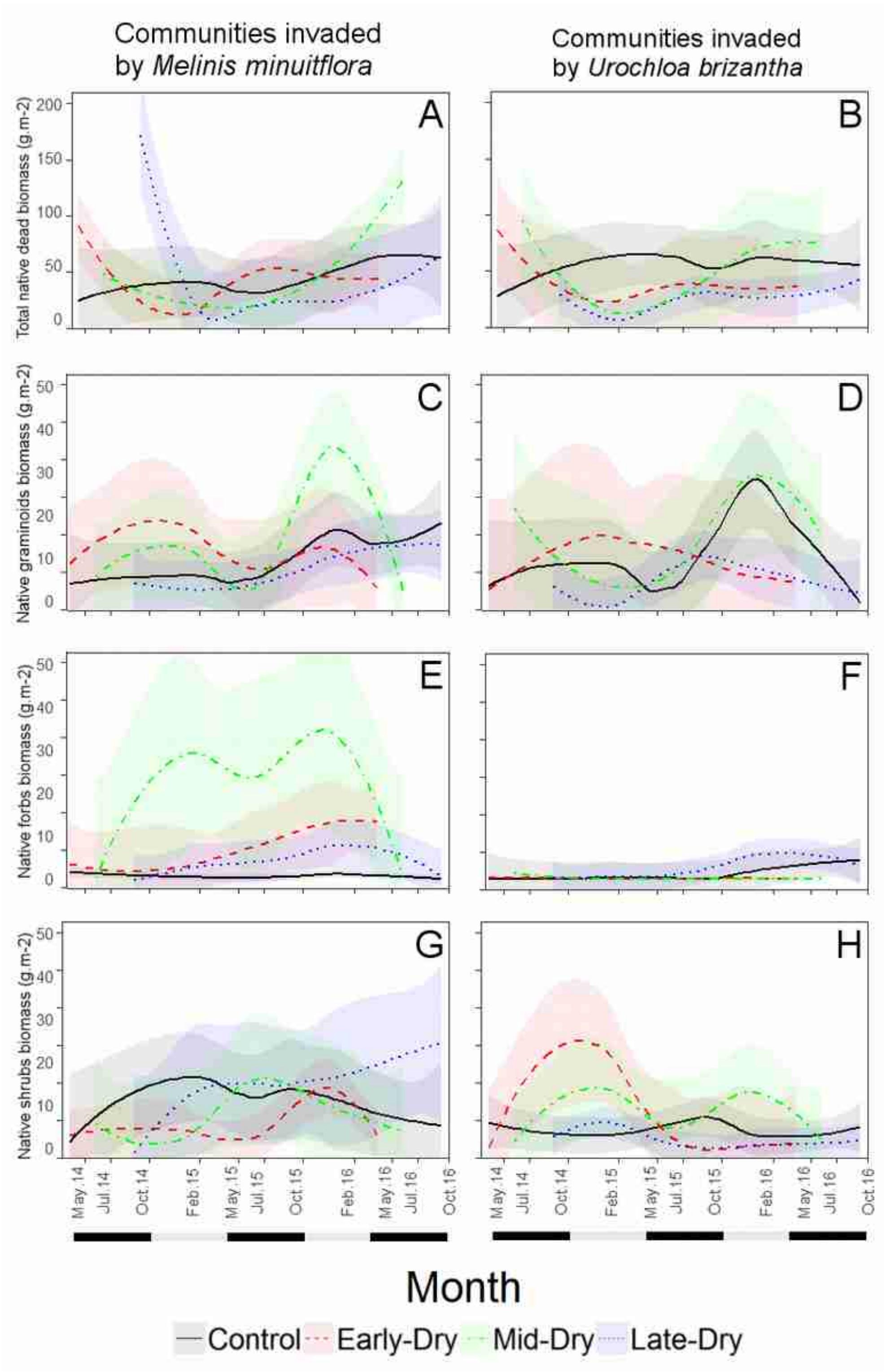

Figure 2. Biomass (g.m^{-2}) across time after fire (months) for invasive functional components on Cerrado invaded communities by *Melinis minutiflora* and *Urochloa brizantha*. Lines are the predicted values by the best fitted GAMM and fills are the confidence interval (95%). The horizontal bars on x axis indicates seasonality in relation to months: black and gray traces are the dry and rainy seasons, respectively. Total native biomass (A, B), native graminoids (C, D), native forbs (E, F) and native shrubs (G, H). *brizantha* (Fig. 2G and 2H).

Finally, fire season differently affected bare soil cover on communities invaded by *M. minutiflora* and *U. brizantha* (Table 1). On the first one, fires in all seasons increased bare soil cover (p<0.001) in 43% (ED), 60% (MD) and 65% (LD) in February 2015 in comparison to pre-fire values, while a less pronounced increase was observed in control plots (8%). On communities dominated by *U. brizantha*, only Early-Dry season fires increased bare soil cover (p=0.02, Table 1) to 39%.

Discussion

Fire was efficient to reduce the abundance of *Melinis minutiflora,* independently of season. However, in the Late-Dry season treatment, there was a tendency to increase *Urochloa brizantha* biomass, like occurred in Early-Dry plots. This new invasion was probably due to the new gaps in the vegetation created by fires and the new income of propagules from neighboring areas. On the other hand, fire did not affect the abundance of *U. brizantha* in any season. However, it was reduced by Early- and Mid-Dry season treatments just after fires, and was increased in Early-Dry season plots during the following rainy season. Native vegetation was only affected by Mid-Dry season fires on communities invaded by *M. minutiflora*, represented by an increase in forbs biomass.

Contrary to our hypothesis, the best time to reduce invasive species abundance was not on their reproductive peak: in Early-Dry season for *M. minutiflora* and Late-Dry season for *U. brizantha.* We believe that other processes might be involved in the responses of the invasive species to fire season other than their reproductive phenology. Such process play different roles on plant responses depending on the identity of the invasive grass, such as 1) differences on fire characteristics, caused by environmental conditions (Knapp *et al.* 2009) and by changes in fire regimes and behavior by the invasive grasses (Gorgone-Barbosa *et al.* 2015); 2) the phenology of the invasive grasses from neighboring areas, via mechanisms of propagule pressure (Lockwood, Cassey & Blackburn 2005) and via seed bank recolonization (Gioria, Pyšek & Moracova 2012); and 3) changes on community invasibility caused by fires due to changes in resources availability (Davis, Grime & Thompson 2000), such as bare soil and mineral nutrients (Pivello & Coutinho 1992).

Reduction of *M. minutiflora* by Early-Dry fires, however, could be a consequence of the reproductive state of this grass at the moment of fires, as already found for other invasive plant species (DiTomaso *et al.* 2006), due to lower reserves (Vieira & Figueiredo-Ribeiro 1993). Additionally, the decrease of biomass of this invasive species by fires at Early-Dry season could be caused by environmental conditions, since it is the beginning of the dry season, and plants would face at least a 3-4 months of drought (Eiten 1992), that could negatively impact the regeneration of possible surviving individuals (Filgueiras 2002).

Environmental conditions could also have influenced the decreased in *M. minutiflora* biomass after Mid- and Late-Dry season fires. Seasonal changes of Cerrado herbaceous layer (Filgueiras 2002) modify quantity and quality the fuel load (Mistry 1998), affecting thus, fire intensity and other fire parameters, such as flame height and temperature (Rissi *et al.* 2017). This process is synergistic with the increase in fuel load and flammability that *M. minutiflora* promote in the invaded system (Rossi *et al.* 2014). Thus, fires were more intense and severe during the Mid- and Late-Dry season (Dairel *et al.* unpublished data), being able to kill the individuals and leading thus, to an increase in gaps within the vegetation for new colonization.

On the other hand, *U. brizantha*, did not cause more intense fires, a fact that is related to its microclimate modification and moisture retention (Gorgone-Barbosa *et al.* 2015; Assis 2017), probably caused by its architecture. As a consequence, effects of high temperatures caused by fires would be buffered, resulting in less damage to its tussocks, but probably killing neighboring plants, as suggested by the “killing the neighbor” theory (Bond &

Midgley 1995). Furthermore, *Urochloa brizantha* individuals can resprout rapidly after fires, independently of season, occupying very quickly the gaps formed in the post-fire vegetation, hampering thus, the native vegetation regeneration. Additionally, *U. brizantha* cultivars that are used for cattle pasture that invaded the nature preserves are more resistant to disturbance and can quickly regrow after fires (Valle *et al.* 2009).

On communities invaded by *Melinis minutiflora,* fire season might also have changed community invasibility by altering resources, as proposed by the theory of fluctuating resources (Davis *et al.* 2000). The main resource increased by fires was space, because the flames consumed the high quantities of dead biomass accumulated in the system. As a result, new invasion by *U. brizantha* occurred in Early-Dry plots, as well as in Late-Dry season plots (although in less intensity). The expansion of *Urochloa* species occur mainly via seed dispersion (Assis 2017), due to traits that favor their high invasiveness as seed quality (influenced by high viability and dormancy) and high seed production (Hopkinson *et al* 1996), fast growth (Fisher & Kerridge 1996), seed resistance to fire (Gorgone-Barbosa 2016) and enhanced germination on post-fire conditions (Goronge-Barbosa *et al.* 2016).

Consequently, the promotion of this new invasion on Early-Dry fire plots may have been enhanced by the recruitment of the viable seeds from the seed bank that was refilled by *U. brizantha* seeds from the last reproductive peak in the previous rainy season. Moreover, these seeds might have resisted to the passage of fire and found good conditions to germinate and to establish after the consumption of above-ground biomass. This mechanism can also explain the decrease on bare soil cover and the short-term increase of *U. brizantha* cover on plots already dominated by this species (ED plots). Nevertheless, the increase of *U. brizantha* invasion on *M. minutiflora* Late-Dry fire plots was probably caused by the increment of propagule pressure at this time of the year (Hopkinson *et al.* 1996) just after the creation of available resources (gaps) by fires and thus, which increased community invasibility (Davis *et* *al.* 2000).

On communities invaded by *Urochloa brizantha*, contrarily to the responses found for *M. minutiflora* communities, fire season did not result on changes in community invasibility. Despite its reproductive peak at the beginning of the rainy season (Hopkinson *et al*. 1996), in our study site, this species was able to produce flowers and seeds all over the year (Gorgone-Barbosa *et al.* unpublished data), resulting thus in an increased propagule pressure over burned areas independently of the season. Seeds were already incorporated to the soil seed bank during the entire year (M. Dairel & A. Fidelis, unpublished data). Moreover, because their seeds are tolerant to fire (Gorgone-Barbosa 2016) and favored by post-fire conditions (Gorgone-Barbosa *et al.* 2016), fire at any season did not harm the seed bank and regeneration by seeds might have enhanced *U. brizantha* post-fire recovery, that was also occurring by resprouting of individuals that survived fire (Gorgone-Barbosa *et al.* 2015). Therefore, the newly formed gaps formed in the vegetation just after fire were quickly colonized by *Urochloa brizantha* tussocks via seedling and resprouting. Although Cerrado vegetation responds quickly after fires at any season, (Rissi 2016), due to its high capacity of regeneration mostly via resprouting (Zupo 2017), only forbs were positively affected by Early-Dry season fires in *Melinis minutiflora* communities. As already mentioned before, during this time of the year, less invasion of *Urochloa brizantha* in these communities was observed, which could have favored forbs establishment and regeneration. In general, where invasive species regenerated well and quickly after fire, native vegetation was hampered by the invasives, showing that their presence is negatively affecting the native vegetation (Damasceno *et al.* submitted) and thus, it should be controlled in order to recover the herbaceous vegetation.

Implications for restoration

One of the major problem in Cerrado nature preserves is the presence of invasive species (Pivello *et al.* 1999a, Sampaio & Schimdt 2013), that are affecting negatively the native plant communities (G. Damasceno *et al.* unpublished data) and hampering restoration efforts (Hoffmann & Haridassan 2008; Silveira *et al.* 2013). Therefore, efforts to implement management plans to control these invasive species are of crucial importance in order to implement restoration actions to recover native vegetation.

Our study showed that fire can be used to control *Melinis minutiflora*, and we would recommend managers to conduct Mid-Dry season fires, as they did not facilitate invasion by *Urochloa* spp. and was the unique fire treatment that promoted an increase on native components. Fires on the Mid-Dry season would also favor regeneration by seeds, since Cerrado forbs and shrubs are dispersing their seeds at this time of the year (Oliveira 1998). Additionally, seeds that were already dispersed and incorporated by the seed bank will not be damaged by fires (Ikeda *et al.* 2008; L. F. Daibes *et al.* unpublished data) and most of them will be able to germinate in the following rainy season (Andrade & Miranda 2014). However, additional actions could be necessary to enhance native vegetation recovery, like seeds sowing (Sampaio *et al.* 2015; Silva *et al.* 2015) and transposition of soil banks of buds (Ferreira *et al.* 2015) and seeds (Pilon, Buisson & Durigan 2017).

On areas invaded by *Urochloa* spp. we would only recommend fire as part of management actions to reduce biomass in the short-term. The temporal control of this invasive species (mainly by reduction of its dead biomass) would be an opportunity to overcome the biotic filter, allowing the implementation of management actions which would conduct the invaded system over a threshold, leading thus to the restoration of Cerrado.

Acknowledgments

The authors thank Ana Carolina Ferreira, Cíntia Souza, Elizabeth Gorgone-Barbosa, Evaldo Souza, Giovana Chiari, Heloiza Zirondi, Jonathan Galdi Rosa, Karen Castillioni, Lucas Barbosa, Luis Felipe Daibes, Mariana Dairel, Mariana N. Rissi, Natacha Silva, Priscilla Sperandio, Rafael Consolmagno, Tamires Zepon and Vagner Zanzarini for helping during the field work. We are also grateful to the Estação Ecológica de Itirapina staff for their valuable help during the prescribed fires, establishment and maintenance of the plots. We also thank Vânia Pivello and Giselda Durigan for their wise comments on this manuscript. G.D received financial support from Fundação de Amparo à Pesquisa do Estado de São Paulo (2015/10714-6), A.F. was granted by Conselho Nacional de Desenvolvimento Científico e Tecnológico (306170/2015-9). This project was funded by Fundação de Amparo à Pesquisa do Estado de São Paulo (2015/06743-0) and the Neotropical Grasslands Conservancy.

Authors' contributions

G. Damasceno wrote the manuscript, collected, manipulated and analyzed data. A. Fidelis was responsible for the experimental design, assisted in data collection and analysis, and reviewed and commented all drafts of this manuscript.

References

Abreu, R.C.R. de, Assis, G.B. de, Frison, S., Aguirre, A. & Durigan, G. (2011) Can native vegetation recover after slash pine cultivation in the Brazilian Savanna? *Forest Ecology and Management*, **262**, 1452–1459.

Almeida, L.V., Ferri, P.H., Seraphin, J.C. & de Moraes, M.G. (2017) Seasonal changes of fructans in dimorphic roots of Ichthyothere terminalis (Spreng.) Blake (Asteraceae) growing in Cerrado. *Science of the Total Environment*, **598**, 404–412.

Andrade, L.A.Z. & Miranda, H.S. (2014) The dynamics of the soil seed bank after a fire event in a woody savanna in central Brazil. *Plant Ecology*, **215**, 1199–1209.

Assis, G.B. de. (2017) Invasão Do Campo Cerrado Por Braquiária (Urochloa Decumbens): Perdas de Diversidade E Experimentação de Técnicas de Restauração. *PhD Thesis.* Instituto de Pesquisas Jardim Botânico do Rio de Janeiro. Rio de Janeiro.

Bansal, S., Sheley, R.L., Blank, B. & Vasquez, E.A. (2014) Plant litter effects on soil nutrient availability and vegetation dynamics: changes that occur when annual grasses invade shrub-steppe communities. *Plant Ecology*, **215,** 1–12.

Barbosa, E.G., Pivello, V.R. & Meirelles, S.T. (2008) Allelopathic evidence in Brachiaria decumbens and its potential to invade the Brazilian cerrados. *Brazilian Archives of Biology and Technology*, **51**, 825–831.

Bates, D., Maechler, M., Bolker, B. & Steve, W. (2015) Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, **67**, 1–48.

Bond, W.J., & Midgley, J.J. 1995. Kill Thy Neighbour : An Individualistic Argument for the Evolution of Flammability. *Oikos* **73,** 79–85.

Bond, W.J., Woodward, F.. I. & Midgley, G.F. (2005) The Global Distribtuion of Ecosystems in a world without Fire. *New Phytologist*, **165**, 525–538.

Brooks, K.J., Setterfield, S.A. & Douglas, M.M. (2010) Exotic grass invasions: Applying a conceptual framework to the dynamics of degradation and restoration in Australia's tropical savannas. *Restoration Ecology*, **18**, 188–197.

Catford, J.A., Daehler, C.C., Murphy, H.T., Sheppard, A.W., Hardesty, B.D., Westcott, D.A., Rejmánek, M., Bellingham, P.J., Pergl, J., Horvitz, C.C. & Hulme, P.E. (2012) The intermediate disturbance hypothesis and plant invasions: Implications for species richness and management. *Perspectives in Plant Ecology, Evolution and Systematics*, **14**, 231–241.

D'Antonio, C.M. & Vitousek, P.M. (1992) Biological Invasions By Exotic Grasses, the Grass/Fire Cycle, and Global Change. *Annual Review of Ecology and Systematics*, **23**, 63–87.

Davies, K.W. & Sheley, R.L. (2011) Promoting Native Vegetation and Diversity in Exotic Annual Grass Infestations. *Restoration Ecology*, **19**, 159–165.

Davis, M.A., Grime, J.P. & Thompson, K.E.N. (2000) Fluctuating resources in plant communities : a general theory of invasibility. *Journal of Ecology.* **88**, 528–534.

DiTomaso, J.M., Brooks, M.L., Allen, E.B., Minnich, R., Rice, P.M. & Kyser, G.B. (2006) Control of Invasive Weeds with Prescribed Burning. *Weed Technology*, **20**, 535–548.

Durigan, G., Contieri, W.A., Franco, G.A.D.C. & Garrido, M.A.O. (1999) Indução do processo de regeneração da vegetação de Cerrado em área de pastagem, Assis, SP. *Acta Botanica Brasilica*, **12**, 421–429.

Eiten, G. (1972) The Cerrado vegetation of Brazil. *The Botanical Review*, **38**, 201–338.

Emery, S.M. & Gross, K.L. (2005) Effects of timing of prescribed fire on the demography of an invasive plant, spotted knapweed Centaurea maculosa. *Journal of Applied Ecology*, **42**, 60–69.

Ferreira, M.C., Walter, B.M.T. & Vieira, D.L.M. (2015) Topsoil translocation for Brazilian savanna restoration: Propagation of herbs, shrubs, and trees. *Restoration Ecology*, **23**, 723–728.

Filgueiras, T.S. (2002) Herbaceous Plant Communities. In: A.L Klein (ed) *The Cerrados of Brazil*, 121–139. São Paulo. Editora da UNESP.

Fisher, M.J. & Kerridge, P.C. (1996) The agronomy and physiology of Brachiaria species. *Brachiaria: Biology, agronomy and improvement* (eds J.W. Miles, B.L. Mass, & C.B. Valle), pp. 43–52.

Flory, S.L. & Clay, K. (2010a) Non-native grass invasion alters native plant composition in experimental communities. *Biological Invasions*, **12**, 1285–1294.

Flory, S.L. & Clay, K. (2010b) Non-native grass invasion suppresses forest succession. *Oecologia*, **164**, 1029–1038.

Gioria, M., Pyšek, P. & Moracova, L. (2012) Soil seed banks in plant invasions : promoting species invasiveness and long-term impact on plant community dynamics. *Preslia*, **84**, 327–350.

Gorgone-Barbosa, E. (2016) A Relação Entre Fogo E Uma Gramínea Invasora No Cerrado: O Fogo Pode Ser Utilizado Como Uma Estratégia de Controle? *PhD Thesis.* Universidade Estadual Paulista 'Júlio de Mesquita Filho'.

Gorgone-Barbosa, E., Pivello, V.R., Baeza, M.J. & Fidelis, A. (2016) Disturbance as a factor in breaking dormancy and enhancing invasiveness of African grasses in a Neotropical Savanna. *Acta Botanica Brasilica*, **30**, 131–137.

Gorgone-Barbosa, E., Pivello, V.R., Bautista, S., Zupo, T., Rissi, M.N. & Fidelis, A. (2015) How can an invasive grass affect fire behavior in a tropical savanna? A community and individual plant level approach. *Biological Invasions*, **17**, 423–431.

Govender, N., Trollope, W.S.W. & Van Wilgen, B.W. (2006) The effect of fire season, fire frequency, rainfall and management on fire intensity in savanna vegetation in South Africa. *Journal of Applied Ecology*, **43**, 748–758.

Hoffmann, W.A. & Haridasan, M. (2008) The invasive grass, Melinis minutiflora, inhibits tree regeneration in a Neotropical savanna. *Austral Ecology*, **33**, 29–36.

Honda, E.A. & Durigan, G. (2016) Woody encroachment and its consequences on hydrological processes in the savannah. *Philosophical transactions of the Royal Society of London. Series B, Biological sciences*, **371**, 115–133.

Hopkinson, J., de Souza, F., Diulgherolff, S., Oriz, A. & Sánchez, M. (1996) Reprodcutive Physiology, Seed Production and Seed Quality of Brachiaria. In J.W. Miles, B.L. Mass, & C.B. Valle (eds)

Brachiaria: Biology, agronomy and improvement, p. 288. Campo Grande. Empresa Brasileira de Pesquisa Agropecuária. Brasília.

Hothorn, T., Bretz, F. & Westfall, P. (2008) Simultaneous Inference in General Parametric Models. *Biometrical Journal*, **50**, 346–363.

Ikeda, F.S., Mitja, D., Vilela, L. & Silva, J.C.S. (2008) Banco de sementes em cerrado sensu stricto sob queimada e sistemas de cultivo. *Pesquisa Agropecuaria Brasileira*, **43**, 667–673.

Karia, C.T., Duarte, J.B. & Araújo, A.C.G. (2006) Desenvolvimento de cultivares do gênero Brachiaria (trin.) Griseb. no Brasil. *Documentos 163.* 58p. Planaltina. Embrapa Cerrados.

Klink, C.A. & Machado, R.B. (2005) Conservation of the Brazilian Cerrado. *Conservation Biology*, **19**, 707–713.

Knapp, E.E., Estes, B.L. & Skinner, C.N. (2009) *Ecological Effects of Prescribed Fire Season : A Literature Review and Synthesis for Managers*. United States Department of Agriculture, Albany, USA.

Lockwood, J.L., Cassey, P. & Blackburn, T. (2005) The role of propagule pressure in explaining species invasions. *TRENDS in Ecology and Evolution*, **20**(5), 223-228.

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. & Bazzaz, F.A. (2000) Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications*, **10**, 689–710.

Martins, C.R. (2006) Caracterização e manejo da gramínea Melinis minutiflora P. Beauv. (capim-gordura): uma espécie invasora do Cerrado. *PhD Thesis.* Universidade de Brasília.

Martins, C.R., Hay, J.D.V., Walter, B.M.T., Proença, C.E.B. & Vivaldi, L.J. (2011) Impact of invasion and management of molasses grass (Melinis minutiflora) on the native vegetation of the Brazilian Savanna. *Brazilian Journal of Botany*, **34**, 73–90.

Melo, A. de, Durigan, G. & Kawabata, M. (2004) Crescimento e Sobrevivência de Espécies Arbóreas Plantadas em Área de Cerrado, Assis SP. *Pesquisas em conservação e recuperação ambiental no oeste paulista.* **18**, 315-324.

Mistry, J. (1998) Fire in the cerrado (savannas) of Brazil: an ecological review. *Progress in Physical Geography*, **22**, 425–448.

Musso, C., Miranda, H.S., Aires, S.S., Bastos, A.C., Soares, A.M., & Loureiro, S. 2015. Simulated post-fire temperature affects germination of native and invasive grasses in cerrado (Brazilian savanna). *Plant Ecology & Diversity* **8,** 219–227.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, **403**, 853–858.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2016) vegan: Community Ecology Package.

Oliveira, P.E.A.M. (1998) Fenologia e biologia reprodutiva das espécies de cerrado. In S.M. Sano, S.P. Almeida, & J.F. Ribeiro (ed) *Cerrado: Ecologia e Flora* pp. 275–289. Brasília, Embrapa Cerrados.

Palermo, A.C., Musso, C., Borges, G.B.O., Aires, F.S., Andrade, S.M.A., Martins, C.R., Sato, M.N. & Miranda, H.S. (2007) Manejo com fogo em áreas invadidas com capim-gordura visando o aumento da diversidade de gramíneas nativas. *Biotropica*, **31**, 1–2.

Pejchar, L. & Mooney, H.A. (2009) Invasive species, ecosystem services and human well-being. *Trends in Ecology and Evolution*, **24**, 497–504.

Pilon, N.A.L., Buisson, E. & Durigan, G. (2017) Restoring Brazilian savanna ground layer vegetation by topsoil and hay transfer. *Restoration Ecology*, 1–9. http://doi.wiley.com/10.1111/rec.12534

Pivello, V.R., & Coutinho, L.M. 1992. Transfer off macro nutrients to the atmosphere during burns in Cerrado. *Journal of Tropical Ecology* **8,** 487–497.

Pivello, V., Carvalho, V. & Lopes, P. (1999a) Abundance and distribution of native and alien grasses in a 'Cerrado'(Brazilian Savanna) biological reserve. *Biotropica*, **31**, 71–82.

Pivello, V.R., Shida, C.N., & Meirelles, S.T. (1999b). Alien grasses in Brazilian savannas: A threat to the biodiversity. *Biodiversity and Conservation* **8,** 1281–1294.

Prober, S.M., Thiele, K.R., Lunt, I.D. & Koen, T.B. (2005) Restoring ecological function in temperate grassy woodlands: Manipulating soil nutrients, exotic annuals and native perennial grasses through carbon supplements and spring burns. *Journal of Applied Ecology*, **42**, 1073–1085.

Pyšek, P., Jarošík, V., Hulme, P.E., Pergl, J., Hejda, M., Schaffner, U. & Vilà, M. (2012) A global assessment of invasive plant impacts on resident species, communities and ecosystems: The interaction of impact measures, invading species' traits and environment. *Global Change Biology*, **18**, 1725–1737.

Reed, H.E., Seastedt, T.R. & Blair, J.M. (2005) Ecological Consequences of C 4 Grass Invasion of a C_4 Grassland: a Dilemma for Management. *Ecological Applications*, **15**, 1560–1569.

Rissi, M.N. (2016) Efeito Da Época Da Queima Na Dinâmica de Campo Sujo de Cerrado. *PhD Thesis.* Universidade Estadual Paulista "Júlio de Mesquita Filho". Rio Claro.

Rissi, M.N., Baeza, M.J., Gorgone-Barbosa, E., Zupo, T. & Fidelis, A. (2017) Does season affect fire behaviour in the Cerrado ? *International Journal of Wildland Fire*, **26**, 427–433.

Rossi, R.D., Martins, C.R., Viana, P.L., Rodrigues, E.L. & Eugênio, J.F.C. (2014) Impact of invasion by molasses grass (Melinis minutiflora P . Beauv .) on native species and on fires in areas of campo-cerrado in Brazil. *Acta Botanica Brasilica*, **28**, 631–637.

Rossiter, N., Setterfield, S.A., Douglas, M.M., Hutley, L. & Cook, G. (2004) Exotic grass invasion in the tropical savanna of northern Australia: ecosystem consequences. *Fourteenth Australian Weeds Conference*, pp.168–171.

Sampaio, A.B. & Schmidt, I.B. (2013) Espécies exóticas invasoras em unidades de conservação federais do Brasil. *Biodiversidade Brasileira*, 32–49.

Sampaio, A.B., Vieira, D.L.M., Cordeiro, A.O.D.O., Aquino, F.D.G., Sousa, A.D.P., Albuquerque, L.B. De, Schmidt, I.B., Ribeiro, J.F., Pellizaro, K.F., Sousa, F.S. De, Moreira, A.G., Santos, A.B.P. Dos, Rezende, G.M., Silva, R.R.P., Alves, M., Motta, C.P., Oliveira, M.C. De, Cortes, C.D.A. & Ogata, R. (2015) *Guia de Restauração Do Cerrado Volume 1 - Semeadura Direta*. Brasília, Rede de Sementes do Cerrado.

Sano, E.E., Rosa, R., Luís, J., Brito, S. & Ferreira, G. (2008) Notas Científicas Mapeamento semidetalhado do uso da terra do Bioma Cerrado. *Pesquisa Agropecuária Brasileira*, **43**, 153–156.

Sax, D.F. & Gaines, S.D. (2008) Species invasions and extinction: the future of native biodiversity on islands. *Proceedings of the National Academy of Sciences*, **105**, 11490–11497.

Silva, J.S.O. & Haridasan, M. (2007) Acúmulo de biomassa aérea e concentração de nutrientes em Melinis minutiflora P. Beauv. e gramíneas nativas do cerrado. *Revista Brasileira de Botânica*, **30**, 337–344.

Silva, R.P.R.P., Oliveira, D.R., da Rocha, G.P.E. & Vieira, D.L.M. (2015) Direct seeding of Brazilian savanna trees: effects of plant cover and fertilization on seedling establishment and growth. *Restoration Ecology*, **23**, 393–401.

Silveira, É.R. da, Melo, A.C.G. De, Contieri, W.A. & Durigan, G. (2013) Controle de gramíneas exóticas em plantio de restauração de Cerrado. In G Durigan & V.S.R Ramos (eds) *Manejo Adaptativo: primeiras experiências na restauração de ecossistemas*, pp. 5–8. São Paulo, Páginas & Lestras Editora e Gráfica.

Simon, M.F., Grether, R., de Queiroz, L.P., Skema, C., Pennington, R.T. & Hughes, C.E. (2009) Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. *Proceedings of the National Academy of Sciences*, **106**, 20359–20364.

R Core Team. (2016) R: A Language and Environment for Statistical Computing.

Valle, C.B., Jank, L. & Resende, R.M.S. (2009) O melhoramento de forrageiras tropicais no Brasil.

Ceres, **56**, 460–472.

Vieira, C.C.J. & Figueiredo-Ribeiro, R.C.L. (1993) Fructose-containing carbohydrates in the tuberous root of Gomphrena macrocephala St.-Hil. (Amaranthaceae) at different phenological phases. *Plant, Cell & Environment*, **16**, 919–928.

Whelan, R.J. 1995. *The ecology of fire*. Cambridge University Press.

Wickham, H. (2009) ggplot2: Elegant Graphics for Data Analysis.

Wood, S.N. (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society (B)*, **73**, 3–36.

Zanchetta, D. & Reis, C.M. (2006) Plano de Manejo Integrado: Estações Ecológica E Experimental de Itirapina/SP, 1ª Revisão.

Short-term effects of fire season on diversity of Cerrado invaded communities

Damasceno, G[1,2]. & Fidelis, A[1].

Universidade Estadual Paulista (UNESP), Instituto de Biociências, Rio Claro. Av. 24A, 1515, 13506-900, Rio Claro, Brazil.

Correspondence author: fariadamasceno@gmail.com +55193526-4208

Manuscript to be submitted to Journal of Vegetation Science

Abstract

Questions: Are Cerrado communities invaded by the African grasses *Melinis minutiflora* and *Urochloa brizantha* differently affected by fire season? Would fire season lead to dissimilar communities, regarding plant diversity? This study evaluated the effects of prescribed fires conducted in the Early-, Mid- and Late-Dry seasons (2014) on savanna-like Cerrado formations invaded by *M. minutiflora* and *U. brizantha.*

Location: Tropical savanna in Southeastern Brazil. 22°15'S, 47°45'00W.

Methods: We sampled four plots (15x15m) for each treatment and four unburned (controls) plots every 6 months from 2014 to 2016, evaluating the percentage cover of each plant species on 1m^2 (10 subplots/plot). Using PERMANOVA and PCoA analyzes we investigated the influence of invasive species and structural components on the responses of community, and the effects of treatments and time as well. We also investigated the temporal variation in beta diversity (calculated from species cover at every sampling event) between burned and unburned plots on communities invaded both by *M. minutiflora* and by *U. brizantha*.

Results: The identity of invasive species was relevant in producing patterns of plant community responses to fire season due to differential post-fire recovery of the African grasses. On communities invaded by *M. minutiflora,* fire increased species diversity in relation to unburned plots, with exception for Late-Dry season. On *U. brizantha* communities, fire decreased diversity in all treatments, which after two years, tended to return to pre-fire values.

Conclusions: Fire season led to different response patterns on invaded communities, mostly because of each invasive species post-fire regeneration. *M. minutiflora* was reduced by fires, creating new gaps within the vegetation and leading to stochastic recolonization, which was probably guided mainly by the availability of native propagules. On communities dominated by *U. brizantha*, this process was linked to the rapid recovery and high invasiveness of this African grass, causing the preemption of native species establishment due to lower complementarity and high overlap in temporal niche.

key-words: community dynamics, fire recovery, neotropical savanna, *Melinis minutiflora*, *Urochloa brizantha*

Introduction

Fire is a common disturbance and an evolutionary force in savanna ecosystems (Bond & Keeley 2005). Interactions between fire regime – composed by frequency, extension, intensity, seasonality and type (Bond & Wilgen 1996) – and environmental factors, such as temperature and precipitation, determine the effects of fire on plant communities (Mistry et al. 2010). Additionally, the presence of invasive species on fire-prone systems may also influence the recovery trajectories of burned communities (Ogden & Rejmánek 2005) due to alterations they can promote on fire regimes (Brooks et al. 2004) and regarding their impact on communities dynamics (Fargione et al. 2003), function (Bernard-Verdier & Hulme 2015) composition and structure (Vila et al. 2011).

Fire season influences community responses because different components of vegetation exhibit particular responses to burning at a specific time of the year (Ansley & Castellano 2001; Laterra & Solbrig 2001), mostly due to plant phenology and post-fire environmental conditions (Bond & Wilgen 1996; Knapp et al. 2009). Therefore, on environments where fire is an intrinsic disturbance, fire season can affect richness (Towne &

Kemp 2003), productivity (Robertson & Hmielowski 2014) and plant dynamics by altering flowering and fruiting production (Lamont et al. 2000).

Short-term effects of fire on plant communities are usually considered until the fifth year since burning and are probably caused by shifts in dominance and competitive relationships during the community regeneration process (Tyler 1995; Laterra & Solbrig 2001) due to shifts in nutrients availability (Certini 2005) and litter removal (Fidelis et al. 2012). On invaded herbaceous plant communities, short-term effects of fire are mediated by the response of the dominant invasive species (Emery & Gross 2005), which when disfavored by fire conditions could became subdominant or even absent (Simmons et al. 2007).

Effects of fire on plant diversity are not homogeneous across fire-prone systems: at Mediterranean (Enright et al. 2014) and tropical savannas systems (Morrinson 2002) they is related to fire regime and environmental conditions; at subtropical savannas (De Coster et al. 199) and pine-forests it usually increases species diversity after a burning (Martinéz-Hernandéz et al. 2008); and at Cerrado (i.e. the Brazilian savanna) it may influence plant diversity (Coutinho 1990) or may have a minor role on it (Rissi et al. 2017). In general, in tropical savannic environments, fire effects alter herbaceous plant diversity (Oyedeji et al. 2016) via alterations of community structure (Higgins et al 2007) and of seed-bank dynamics (Andrade e Miranda 2014).

Regarding fire season, In Mediterranean ecosystems, time of burning produced effects on plant communities mainly due to its effect on seeding (Céspedes et al. 2014a). In African savannas, it does not influences short-term responses of the herbaceous layer such as species richness, diversity and dominant species (Dayamba et al. 2010), despite being able to alter their flowering phenology (Pavlovic et al. 2011). Considering invaded grassland communities, fire season can cause differential consumption of the invasive grass above-ground biomass, resulting thus, in changes on vegetation dynamics (Ruckman et al. 2012).

Invasive grasses impact savanna plant communities from individual to ecosystem levels (Williams & Baruch 2000) by directly influencing the recruitment of species (Hoffmann & Haridasan 2008) and by indirectly affecting herbivory (Pires et al. 2009), water and nutrient cycling (Rossiter-Rachor et al. 2009) and fire regimes (Gorgone-Barbosa et al. 2015). Alterations of fire regimes create a feedback cycle with invasive grasses (D'Antonio & Vitousek 1992) which could lead to modifications of fire season (Brooks et al. 2004), an important factor on the invasives responses after burning (Potts & Stephens 2009).

Particularly, invasive grasses are a major threat to Cerrado (Durigan et al. 2007), mainly represented by the C_4 African grasses *Melinis minutiflora* and *Urochloa* spp. They can directly affect native communities by negatively impacting native functional groups (Pivello et al. 1999; Damasceno et al. submitted) and indirectly, by altering the fire regime (Rossi et al. 2014; Gorgone-Barbosa et al. 2015). Since Cerrado vegetation is affected by fire (Simon et al. 2009) and negatively impacted by the presence of African grasses (Pivello et al. 1999; Damasceno et al. submitted), which are also impacted by fire season (Gorgone-Barbosa 2016, Damasceno & Fidelis, unpublished data), fire season could play an important role on shaping invaded communities.

Therefore, the aim of this study was to investigate the short-term effects of fire season (Early-, Mid- and Late-Dry Season) on the diversity (considered as percentage cover of plant species) of Cerrado communities invaded by the African grasses *Melinis minutiflora* and *Urochloa brizantha.* We hypothesized that 1) community responses would be influenced by the identity of the dominant invasive species; 2) burned communities would be dissimilar from unburned ones; and 3) fire season would lead to dissimilar communities, in both cases regarding communities species composition.

Material and Methods

Study area

This study was conducted at the Itirapina Ecological Station (EEI, 20°00’-22°15’S and 47°45’-48°00W; 710 to 830 m a.s.l.) in Southeastern Brazil. The area is mostly composed by open savannas, with a dominant herbaceous layer and the presence of scattered shrubs and small trees (also known as *campo sujo*). The mean annual temperature and precipitation are 21.9º C, and 1459 mm respectively, having a seasonal climate with a pronounced dry winter. Soils are of the arenosol type (Zanchetta & Reis 2006). The area was used for forestry with the exotic species *Pinus caribaea* var. *hondurensis* until 1998, when the trees were removed and the area has been left to natural regeneration, excluded from cattle and fire. *Melinis minutiflora* and *Urochloa brizantha* invaded the area and large patches of these species can be found (Zanchetta & Reis 2006), negatively impacting the native vegetation (Damasceno et al. submitted).

Experimental design

The experimental area has 33 hectares and we selected different patches dominated by each one of the invasive species, where we established the experimental plots (15x15m). We assigned four plots for Control (C, unburned) and for each fire season treatment: Early-Dry (ED, burned in May), Mid-Dry (MD, burned in July) and Late-Dry (LD, burned in October) seasons (4 plots x 4 treatments x 2 invasive species = 32 plots). Within each plot, we randomly established 10 subplots (1x1m), avoiding the plot borders, old pine trees trunks, termite and ant nests. The prescribed fires were conducted in 2014.

Vegetation sampling was carried out before each prescribed burning in 2014 and every 6 months until 2016 (24 months for each treatment), in order to sample data during the dry and rainy season. We used a modified Braun-Blanquet method (Wikum & Shanholtzer 1978) with percentage cover values of 0, 1, 5 and then every 5% until 100% to evaluate each plant species ground-cover (mainly assessed as morphospecies), including the invasive species *Melinis minutiflora* and *Urochloa brizantha*.

Data analysis

Invasive species are usually dominant on invaded communities, influencing most of the ecological processes (Baruch et al. 1985) and should thus be included in community ecology studies (Thomsen et al. 2016). However, this approach may mask native community patterns and processes, and in order to highlight invasive species roles on community ecology after fire on invaded communities, we conducted a model comparison among structures adding and excluding the invasive species (+I and -I, respectively).

Since we know *a priori* that communities invaded by *M. minutiflora* and *U. brizantha* are distinct in some aspects (e.g. impact on bare soil and native dead biomass, production and accumulation of biomass; Damasceno et al. submitted), we analyzed data separately for each invaded community.

Aiming to test if treatments lead to dissimilar communities, we conducted a two-way non-parametric analysis of variance (PERMANOVA – Anderson 2001), considering fire treatment and time since burnings as main factors. Further, we used a pairwise *post-hoc* general linear hypothesis tests of HSD Tukey type to check for differences between each pair of fire treatment (unburned Control, Early-, Mid- and Late-Dry), including Bonferroni corrections for multiple comparisions. We used species cover mean values from every sampling event to generate the dissimilarity matrix using Bray-Curtis distances.

Using the same dissimilarity matrices, we also calculated beta diversity among burned and unburned plots and conducted Principal Coordinate Analyzes (PCoA) to identify differences among communities burned at different seasons. Finally, we separately calculated beta diversity scores between each pair of burned communities x control plots at every sampling event. All statistical analyzes were performed in the R program (R Core Team 2016) with the packages vegan (Oksanen et al. 2016) and multcomp (Hothorn, Bretz & Westfall 2008).

Results

Invaded communities differed due to fire treatment and due time for both invasive species (p≤0.05), but no interaction withing these factors was detected (p>0.05; Table 1). Moreover, when the invasive species was excluded from the analysis (–I) time became a non-influential factor for communities invaded by *Melinis minutiflora* (p=0.94) and *Urochloa brizantha* (p=1.0, Table 1). In general, treatment was a strong factor explaining the variation found in communities invaded by *M. minutiflora*. On the other hand, when *Urochloa brizantha* was included into the analysis, these invaded communities had their variation better explained by time, probably due to the temporal dynamic of the invasive species (see Table 1).

Table 1. Statistical output of two-way non-parametric analysis of variance (PERMANOVA) for plant communities invaded by *Melinis minutiflora* and *Urochloa brizantha* according to fire treatments (Early-, Mid-, and Late-Dry season fires) and time since fire (in months). Results from two data matrices including (+I) and excluding (-I) the invasive species in the analyzes. Statistical significant values (p≤0.05) are in bold.

Invasive specie	**Factor**	**Model**			
		+I		**-I**	
		Explained variation	**p value**	**Explained variation**	**p value**
Melinis minutiflora communities	Treatment	23.6	***0.001***	22.7	***0.001***
	Time	15.1	***0.001***	6.2	***0.001***
	Treatment:Time	4.8	1.0	4.1	1.0
Urochloa brizantha communities	Treatment	13.1	***0.001***	13.8	***0.001***
	Time	18.3	***0.001***	4.7	1.0
	Treatment:Time	2.1	1.0	2.9	1.0

The inclusion of the invasive species into the PCoA analyses highlight their influence in differentiating burned and unburned plots for both communities dominated by *M. minutiflora* and *U. brizantha* (Figure 1). Therefore, we opted to use the data considering invasive species presence and identity (*M. minutiflora* and *U. brizantha*) due to their importance in shaping invaded communities as suggested by Thomsen et al. (2016). Consequently, both communities invaded *M. minutiflora* and *U. brizantha* exhibited a similar response: fire occurrence itself produced dissimilar communities (burned x unburned; p=0.001), as well as fire season, since communities burned in different times of the year are also dissimilar among themselves (Table 2).

Table 2. Pairwise comparisons from PERMANOVA analysis of invaded communities by their ground-cover and including the invasive species at two years after applications of the fire treatments. Tests of the type general linear hypothesis tests, similar to HDS Tukey. P values are adjusted by Bonferroni correction for multiple comparisons. Treatment legend: C=Control, ED=Early-Dry, MD=Mid-Dry and LD=Late-Dry.

Invasive specie	**Component**	**Pair**					
		C x ED	**C x MD**	**C x LD**	**ED x MD**	**ED x LD**	**MD x LD**
Melinis minutiflora communities	F	12.13	12.39	26.43	3.11	6.48	2.16
	p value	**0.001**	**0.001**	**0.001**	**0.005**	**0.002**	**0.03**
Urochloa brizantha communities	F	4.70	4.15	8.40	4.58	7.23	3.10
	p value	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**	**0.01**

Communities diversity trajectories – measured as the percentage cover of each plant species at every sampling event – were dependent on the identity of the invasive species. Beta diversity between each par of burned communities in relation to unburned controls demonstrated that fires in any season increased diversity in communities invaded by *M. minutiflora* (Figure 2A), but decreased it in communities dominated by *U. brizantha* (Figure 2B). Moreover, only in communities invaded by *M. minutiflora* fire season influenced the beta diversity: Early-, and Mid-Dry season communities were more similar than Late-Dry season plots, which diverged from the others due to the lower diversity (Figure 2A). Thus, two years

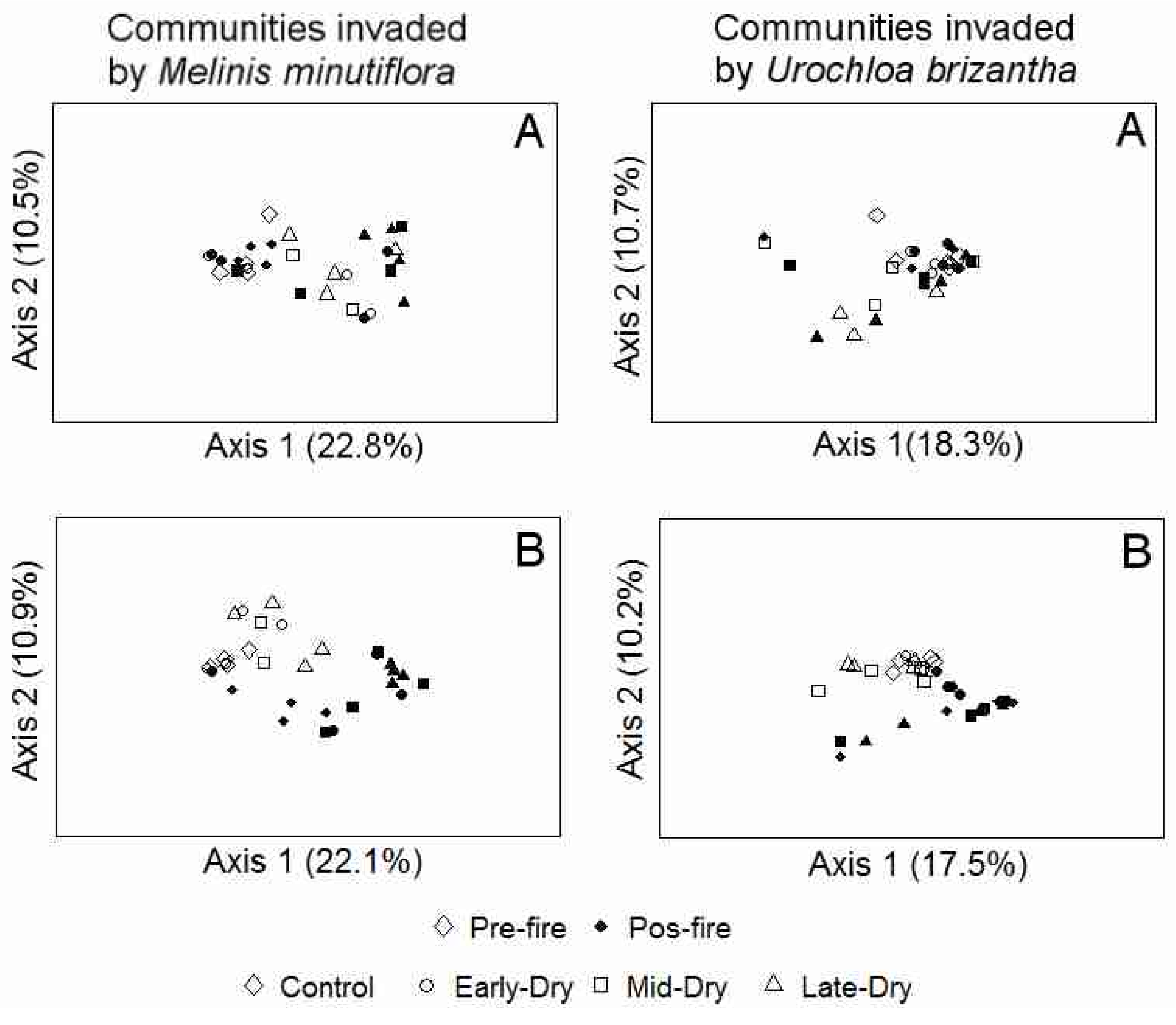

Figure 1: Principal Coordinate Analysis (PCoA) for communities invaded by *Melinis minutiflora* and *Urochloa brizantha* two years after fires on Early-, Mid- and Late-Dry seasons. Data from the percentage ground-cover species composition was used to generate the dissimilarity matrix by the

Bray-Curtis distance. Results from data matrices that have included or not the invasive species are shown in order to demonstrate their influence on community responses. Data that included (A) and not-included (B) the invasive species *Melinis minutiflora* (left column) and *U. brizantha* (right column). Range of all axis is from -1 until 1.

after fire, there was an increase in diversity in Early- and Mid-Dry season plots in relation to control ones. On the other hand, on communities invaded by *U. brizantha,* fire reduced the beta diversity in plots burned in all seasons in comparison to control plots (Figure 2B). Two years after fires, only Late-Dry season plots showed similar values of diversity from pre-fire condition.

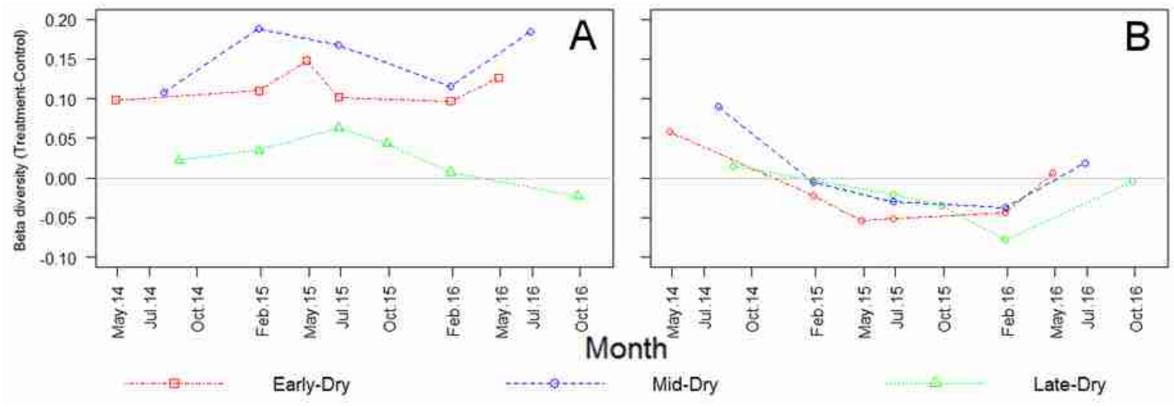

Figure 2: Beta diversity (calculated from the percentage cover of each plant species at every sampling event) among plots submitted to fire season treatments (Early-, Mid-, and Late-Dry season fires) and control plots (unburned) throughout time (two years) in plant communities invaded by *Melinis minutiflora* (A) and *Urochloa brizantha* (B). The first vegetation sampling was conducted before each fire treatment. Positive values indicate that diversity of a treatment is higher than control, negative values show the opposite.

Discussion

On Cerrado invaded systems, fire itself created dissimilar communities regarding percentage cover of plant species in comparison with unburned plots. Corroborating our first hypothesis, the identity of the invasive species was a key factor influencing community dynamics after fire events on different seasons: in general, communities invaded by *Melinis minutiflora* showed an increase in diversity, whilst communities dominated by *Urochloa* *brizantha* decreased in diversity after fire. Finally, fire season played an important role on shaping community composition, since on communities invaded by *M. minutiflora* Early- and Mid-Dry season fires led to more diverse communities two years after fire than Late-Dry season fires did.

One of the most important effects of fire on plant communities is the removal of above-ground biomass and the consequent formation of gaps within the vegetation (Fidelis et al., 2012), creating new possibilities for plant establishment (Grubb 1977), where light incidence and temperature are usually higher than within the vegetation (Fidelis & Blanco 2014). Fires can also affect soil properties, mineral cycling and its availability to plants (Pivello & Coutinho 1992). As results, fires influence plant demographic responses (Bond & Wilgen 1996), their competitive relationship (Bond & Wilgen 1996), herbivory (Tyler 1995) and can also modify hierarchy among species (Laterra & Solbrig 2001).

On invaded systems, the above-mentioned effects of fire on plant communities can be shaped by the different responses of invasive species to fire (Damasceno & Fidelis, in preparation), which in turn, alter the recovery trajectory of plant communities in post-fire environments (Simons et al. 2007). *Melinis minutiflora* was killed by fires, being unable to successfully regenerate and reestablish in burned patches, leading thus, to the formation of large gaps within the vegetation that remained available for stochastic colonization by other species populations (Damasceno and Fidelis, in preparation).

Urochloa brizantha, on the other hand, quickly recovered its biomass after fires (Damasceno & Fidelis in preparation, Assis 2017) both via resprouting and by colonizing newly formed gaps through seedling recruitment from both seed bank and seed rain (Dairel & Fidelis, unpublished data; Gorgone-Barbosa et al. unpublished data). Also, this specie may have successfully initiated a fire/invasive grass cycle, on which the invasive determined fire characteristics that favored itself, such as increasing temperature (Fidelis & Gorgone-Barbosa, unpublished data), which does not affect its buds due to its higher moisture content (Gorgone-Barbosa et al. 2015).

Fire season is a key-factor determining the recovery of a burned community as plants are adapted to particular conditions of fire regimes, that influence their responses, and thus, can modify plant community dynamics (Whelan 1995). Fire season effects on species composition may be a consequence of fire characteristics guided mostly by fuel conditions, that in turn, can influence plants both via above- and belowground mechanisms (Gagnon et al. 2015). Additionally, moisture content and percentage of invsive species dead biomass are also able to change fire behavior (Rossi et al. 2014, Gorgone-Barbosa et al. 2015), probably influencing the regeneration of native plants.

The divergence of communities burned in different seasons may vary from communities invaded by *M. minutiflora* and *U. brizantha.* On the first case, the non-returning of the invasive grass lead to stochastic re-colonization of empty areas left by fires, which were guided mainly by the availability of native propagules (Andrade & Miranda 2014, Dairel & Fidelis unpublished data) and probably from resprouting from the bud bank. As a consequence, plots burned on the Mid-Dry season received a more intense propagule pressure due to the dispersion peak of most Cerrado forb species (Oliveira 2008; Salazar et al. 2011). On the other hand, Late-Dry season plots were more intensely colonized by *U. brizantha,* due to its reproductive peak at this time of the year (Gorgone-Barbosa et al. unpublished data, Dairel & Fidelis unpublished data).

On communities dominated by *U. brizantha*, however, the dissimilarities among fire seasons seemed to be linked to the rapid recovery and high invasiviness of grasses from this genus (Pivello et al. 1999; Durigan et al. 2007; Almeida-Neto et al. 2010) causing the preemption of native species establishment due to lower complementarity and higher overlap in temporal niche as already observed for other invasive grass species (Wilsey et al. 2011).

Phenology and environmental conditions may also play a role on vegetation responses to different fire seasons, because depending on the phenological stage of the plant, the formation of reproductive structures, or even dispersion might be harmed by fire (Robertson & Hmielowski 2014). Moreover, if fire occurs during the reproductive stage, plant is affected by a disturbance on the moment when there is a depletion of reserves (Vieira & Figueiredo-Ribeiro 1993), a condition that also occurs during the dry season due to variations of precipitation and humidity (Almeida et al. 2017).

In other grassy fire-prone ecosystems, fire season was able to shift plant community diversity on a short-term perspective by favoring the response of herbaceous plants from a specific metabolic type (C_3 over C_4 or vice versa), but those responses were usually dependent of time since last fire and fire frequency (Ansley & Castellano 2001). Additionally, short-term effects of fire season on plant responses could interact with other factors to produce no divergence on the long-term responses (Brewer 2006). In other savannas, fire season can alter seedling emergence of different functional groups due the removal of the herbaceous covering layer, creation of gaps and breaking dormancy of seeds incorporated on the seed bank (Williams et al. 2005).

Comparing our results with those environments, it seems to us that fire season is more important on shaping invaded Cerrado communities than in other invaded and non-invaded tropical savanna systems (Gorgone-Barbosa 2016; Céspedes et al. 2014b), despite the role it can exhibit on community species composition (Howe 2011) and on invasive species (Kerns et al. 2006). However, the responses we identified here could only refer to short-term responses of invasive species and their effect on regenerating community dynamics, as in the long-term perspective, they could be evidenced as inter-annual variations (Dayamba et al. 2010) or as results of atypical climatic conditions (Ladwig et al. 2014).

Concluding, the identity of invasive grass species is influential on the diversity trajectory of burned communities, as on communities dominated by *Melinis minutiflora* and by *Urochloa brizantha* fire respectively increased and decreased diversity in species composition. Moreover, only in communities invaded by *M. minutiflora*, fire season lead to dissimilar communities, with Late-Dry resulting in lesser diverse communities when comparing with unburned controls.

Acknowledgments

The authors thank Ana Carolina Ferreira, Cíntia Souza, Elizabeth Gorgone-Barbosa, Evaldo Benetido Souza, Giovana Chiari, Heloiza Zirondi, Jonathan Galdi Rosa, Karen Castillioni, Lucas Barbosa, Luis Felipe Daibes, Mariana Dairel, Mariana Rissi, Natacha Silva, Priscilla Sperandio, Rafael Consolmagno, Tamires Zepon and Vagner Zanzarini for helping during the field work and the Estação Ecológica de Itirapina staff for their valuable help during the prescribed burnings, establishment and maintenance of the plots. G.D received financial support from Fundação de Amparo à Pesquisa do Estado de São Paulo (2015/10714-6), A.F. received grant from Conselho Nacional de Desenvolvimento Científico e Tecnológico (306170/2015-9). This project was funded by Fundação de Amparo à Pesquisa do Estado de São Paulo (2015/06743-0) and the Neotropical Grasslands Conservancy.

References

Almeida, L.V., Ferri, P.H., Seraphin, J.C., & de Moraes, M.G. 2017. Seasonal changes of fructans in dimorphic roots of Ichthyothere terminalis (Spreng.) Blake (Asteraceae) growing in Cerrado. *Science of the Total Environment* 598: 404–412.

Anderson, M.J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26: 32–46.

Andrade, L.A.Z., & Miranda, H.S. 2014. The dynamics of the soil seed bank after a fire event in a woody savanna in central Brazil. *Plant Ecology* 215: 1199–1209.

Ansley, R.J., & Castellano, M.J. 2001. Effects of Summer Fires on Woody, Succulent, and Graminoid Vegetation in Southern Mixed-Prairie Ecosystems : a Review. In Masters, R.E. & Galley, K.E.M. (eds.), *Proceedings of the 23rd Tall Timbers Fire Ecology Conference: Fire in Grassland and Shrubland Ecosystems*, pp. 63–70. Tall Timbers Research Station, Tallahassee, Florida, USA.

Baruch, Z., Ludlow, M., & Davis, R. 1985. Photosynthetic responses of native and introduced C_4 grasses from Venezuelan savannas. *Oecologia* 67: 388–393.

Bond, W.J., & Keeley, J.E. 2005. Fire as a global “herbivore”: The ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution* 20: 387–394.

Bond, W.J., & Wilgen, B. 1996. *Fire and Plants*. Chapman & Hall, London, UK.. 263p.

Brewer, J.S. 2006. Long-term population changes of a fire-adapted plant subjected to different fire seasons. *Natural Areas Journal* 26: 267–273.

Brooks, M.L., D’Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, E., Ditomaso, J.M., Hobbs, R.J., Pellant, M., & Pyke, D. 2004. Effects of Invasive Alien Plants on Fire Regimes. *BioScience* 54: 677–688.

Céspedes, B., Luna, B., Pérez, B., Urbieta, I.R., & Moreno, J.M. 2014a. Burning season effects on the short-term post-fire vegetation dynamics of a Mediterranean heathland. *Applied Vegetation Science* 17: 86–96.

Céspedes, B., Torres, I., Pérez, B., Luna, B., & Moreno, J.M. 2014b. Burning season does not affect post-fire regeneration but fire alters the balance of the dominant species in a seeder-dominated Mediterranean shrubland. *Applied Vegetation Science* 17: 711–725.

Coutinho, L.M. 1990. Fire in the ecology of the Brazilian Cerrado. In J. Goldammer (ed) *Ecological Studies 84 - Fire in the Tropical Biota*, pp. 82–105.

D’Antonio, C.M., & Vitousek, P.M. 1992. Biological Invasions By Exotic Grasses, the Grass/Fire Cycle, and Global Change. *Annual Review of Ecology and Systematics* 23: 63–87.

Dayamba, S.D., Savadogo, P., Sawadogo, L., Tiveau, D., Zida, D., Tigabu, M., & Oden, P.C. 2010. Community dynamics and phytomass of herbaceous species in the Sudaniansavanna-woodlands of Burkina Faso: short-term impact of burning season. *African Journal of Range & Forage Science* 27: 171–177.

Durigan, G., Ferreira De Siqueira, M., Daher, G.A., & Franco, C. 2007. Threats to the cerrado remnants. *Scientia Agricola* 64: 355–363.

Emery, S.M., & Gross, K.L. 2005. Effects of timing of prescribed fire on the demography of an invasive plant, spotted knapweed Centaurea maculosa. *Journal of Applied Ecology* 42: 60–69.

Fargione, J., Brown, C.S., & Tilman, D. 2003. Community assembly and invasion: an experimental test of neutral versus niche processes. *Proceedings of the National Academy of Sciences USA* 100: 8916–20.

Fidelis, A., & Blanco, C. 2014. Does fire induce flowering in Brazilian subtropical grasslands?

Applied Vegetation Science 17: 690–699.

Fidelis, A., Blanco, C.C., Müller, S.C., Pillar, V.D., & Pfadenhauer, J. 2012. Short-term changes caused by fire and mowing in Brazilian Campos grasslands with different long-term fire histories. *Journal of Vegetation Science* 23: 552–562.

Gagnon, P.R., Passmore, H.A., Slocum, M., Myers, J.A., Harms, K.E., Platt, W.J., & Paine, C.E.T. 2015. Fuels and fires influence vegetation via above- and belowground pathways in a high-diversity plant community. *Journal of Ecology* 103: 1009–1019.

Gorgone-Barbosa, E. 2016. A relação entre fogo e uma gramínea invasora no Cerrado: O fogo pode ser utilizado como uma estratégia de controle? *PhD Thesis.* Universidade Estadual Paulista "Júlio de Mesquita Filho". Rio Claro, Brazil.

Gorgone-Barbosa, E., Pivello, V.R., Bautista, S., Zupo, T., Rissi, M.N., & Fidelis, A. 2015. How can an invasive grass affect fire behavior in a tropical savanna? A community and individual plant level approach. *Biological Invasions* 17: 423–431.

Grubb, P.J. 1977. The Maintenance of Species-Richness in Plant Communities: the Importance of the Regeneration Niche. *Biological Reviews* 52: 107–145.

Hoffmann, W.A., & Haridasan, M. 2008. The invasive grass, Melinis minutiflora, inhibits tree regeneration in a Neotropical savanna. *Austral Ecology* 33: 29–36.

Howe, H.F. 2011. Fire Season and Prairie Forb Richness in a 21-y experiment. *Ecoscience* 18: 317–328.

Kerns, B.K., Thies, W.G., & Niwa, C.G. 2006. Season and severity of prescribed burn in ponderosa pine forests: Implications for understory native and exotic plants. *Ecoscience* 13: 44–55.

Knapp, E.E., Estes, B.L., & Skinner, C.N. 2009. *Ecological Effects of Prescribed Fire Season : A Literature Review and Synthesis for Managers*. United States Department of Agriculture, Albany, USA.

Ladwig, L.M., Collins, S.L., Ford, P.L., & White, L.B. 2014. Chihuahuan Desert Grassland Responds Similarly to Fall, Spring, and Summer Fires During Prolonged Drought. *Rangeland Ecology & Management* 67: 621–628.

Lamont, B.B., Swanborough, P.W., & Ward, D. 2000. Plant size and season of burn affect flowering and fruiting of the grasstree Xanthorrhoea preissii. *Austral Ecology* 25: 268–272.

Laterra, P., & Solbrig, O.T. 2001. Dispersal strategies, spatial heterogeneity and colonization success in fire-managed grasslands. *Ecological Modelling* 139: 17–29.

Mistry, J., Berardi, A., & Durigan, G. 2010. The influence of fire regime on microscale structural variation and patchiness in Cerrado vegetation. *Revista do Instituto Florestal* 22: 33–49.

Ogden, J.A.E., & Rejmánek, M. 2005. Recovery of native plant communities after the control of a dominant invasive plant species, Foeniculum vulgare: Implications for management. *Biological Conservation* 125: 427–439.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., & Wagner, H. 2016. vegan: Community Ecology R Package.

Oliveira, P.E.A.M. 2008. Fenologia e biologia reprodutiva das espécies de cerrado. In Sano, S.M., Almeida, S.P., & Ribeiro, J.F. (eds.), *Cerrado: Ecologia e Flora*, pp. 275–289. Embrapa Cerrados, Brasília, Brazil.

Pavlovic, N.B., Leicht-Young, S.A., & Grundel, R. 2011. Short-term effects of burn season on flowering phenology of savanna plants. *Plant Ecology* 212: 611–625.

Pires, A.C.V., Pereira, S.R., Fernandes, G.W., & Oki, Y. 2009. Effect of Brachiaria decumbens on herbivory and development of two Cerrado native leguminosae species. *Planta Daninha*. doi: 10.1590/S0100-83582012000400007

Pivello, V.R. & Coutinho, L.M. 1992. Transfer off macro nutrients to the atmosphere during prescribed burnings in Cerrado. *Journal of Tropical Ecology.* 8(4):487-497.

Pivello, V.R., Shida, C.N., & Meirelles, S.T. 1999. Alien grasses in Brazilian savannas: A threat to the biodiversity. *Biodiversity and Conservation* 8: 1281–1294.

Potts, J.B., & Stephens, S.L. 2009. Invasive and native plant responses to shrubland fuel reduction: comparing prescribed fire, mastication, and treatment season. *Biological Conservation* 142: 1657–1664.

Rissi, M.N., Baeza, M.J., Gorgone-Barbosa, E., Zupo, T., & Fidelis, A. 2017. Does season affect fire behaviour in the Cerrado ? *International Journal of Wildland Fire* 26: 427–433.

Robertson, K.M., & Hmielowski, T.L. 2014. Effects of fire frequency and season on resprouting of woody plants in southeastern US pine-grassland communities. *Oecologia* 174: 765–776.

Rossi, R.D., Martins, C.R., Viana, P.L., Rodrigues, E.L., & Eugênio, J.F.C. 2014. Impact of invasion by molasses grass (Melinis minutiflora P . Beauv .) on native species and on fires in areas of campo-cerrado in Brazil. *Acta Botanica Brasilica* 28: 631–637.

Rossiter-Rachor, N.A., Setterfield, S.A., Douglas, M.M., Hutley, L.B., Cook, G.D., & Schmidt, S. 2009. Invasive Andropogon gayanus (gamba grass) is an ecosystem transformer of nitrogen relations in Australian savanna. *Ecological Applications* 19: 1546–1560.

Ruckman, E.M., Schwinning, S., & Lyons, K.G. 2012. Effects of Phenology at Burn Time on Post-Fire

Recovery in an Invasive C_4 Grass. *Restoration Ecology* 20: 756–763.

Salazar, A., Goldstein, G., Franco, A.C., & Miralles-Wilhelm, F. 2011. Timing of seed dispersal and dormancy, rather than persistent soil seed-banks, control seedling recruitment of woody plants in Neotropical savannas. *Seed Science Research* 21: 103–116.

Simmons, M.T., Windhager, S., Power, P., Lott, J., Lyons, R.K., & Schwope, C. 2007. Selective and non-selective control of invasive plants: The short-term effects of growing-season prescribed fire, herbicide, and mowing in two texas prairies. *Restoration Ecology* 15: 662–669.

Simon, M.F., Grether, R., de Queiroz, L.P., Skema, C., Pennington, R.T., & Hughes, C.E. 2009. Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. *Proceedings of the National Academy of Sciences* 106: 20359–20364.

Team, R.C. 2016. R: A Language and Environment for Statistical Computing.

Thomsen, M.S., Wernberg, T., South, P.M., & Schiel, D.R. 2016. To include or not to include (the invader in community analyses)? That is the question. *Biological Invasions* 18: 1515–1521.

Towne, E.G., & Kemp, K.E. 2003. Vegetation Dynamics from Annually Burning Tallgrass Prairie in Different Seasons. *Society for Range Management.* 56: 185–192.

Tyler, C. 1995. Factors contributing to postfire seedling establishment in chaparral: direct and indirect effects of fire. *Journal of Ecology* 83: 1009–1020.

Vieira, C.C.J., & Figueiredo-Ribeiro, R.C.L. 1993. Fructose-containing carbohydrates in the tuberous root of Gomphrena macrocephala St.-Hil. (Amaranthaceae) at different phenological phases. *Plant, Cell & Environment* 16: 919–928.

Wikum, D.A., & Shanholtzer, G.F. 1978. Application of the Braun-Blanquet cover-abundance scale for vegetation analysis in land development studies. *Environmental Management* 2: 323–329.

Williams, D.G., & Baruch, Z. 2000. African grass invasion in the Americas: Ecosystem consequences and the role of ecophysiology. *Biological Invasions* 2: 123–140.

Williams, P.R., Congdon, R.A., Grice, A.C., & Clarke, P.J. 2005. Effect of season of burning and removal of herbaceous cover on seedling emergence in a eucalypt savanna of north-eastern Australia. *Austral Ecology* 30: 491–496.

Wilsey, B.J., Daneshgar, P.P., & Polley, H.W. 2011. Biodiversity, phenology and temporal niche differences between native- and novel exotic-dominated grasslands. *Perspectives in Plant Ecology, Evolution and Systematics* 13: 265–276.

Zanchetta, D., & Reis, C.M. 2006. *Plano de Manejo Integrado: Estações Ecológica e Experimental de Itirapina/SP*.

CONSIDERAÇÕES FINAIS

Espécies invasoras são um problema global para a conservação da biodiversidade (Pyšek *et al.* 2012). Por sua vez, gramíneas invasoras são uma das principais ameaças à conservação do Cerrado (Pivello *et al.* 1999a; Durigan *et al.* 2007) em virtude da sua ampla distribuição nas unidades de conservação (Pivello *et al.* 1999b; Zenni & Deschoum 2013; Sampaio & Schmidt 2015) e das dificuldades que estabelecem para a restauração de ambientes degradados (Durigan *et al.* 1999; Silveira *et al.* 2013; Hoffmann & Haridasan 2008).

Nesse sentido, este estudo abordou três objetivos específicos: 1) quantificar o impacto que *Melinis minutiflora* e *Urochloa brizantha* exercem sazonalmente sobre os componentes da vegetação nativa; 2) testar a eficácia de queimas no início (precoce), meio (modal) e fim (tardia) da estação seca para controlar a abundância destas duas espécies invasoras; e 3) avaliar o impacto destas mesmas épocas de queima na diversidade de comunidades dominadas pelas duas gramíneas invasoras.

Primeiramente, quantificamos impacto de *M. minutiflora* e *U. brizantha* sobre componentes funcionais e estruturais da comunidade (solo nu, biomassa morta, graminóides, herbáceas e arbustos) avaliados através da porcentagem de sua cobertura relativa. Verificamos que as duas espécies invasoras afetaram negativamente todos os grupos de formas de crescimento de plantas, além de reduzir a cobertura de solo nu e de incrementar a cobertura de biomassa morta.

Os componentes funcionais de gramíneas nativas e de biomassa morta foram os mais negativamente afetados, sendo que *M. minutiflora* causou um impacto maior do que *U. brizantha* na cobertura de solo nu e de biomassa morta total. Além disso, houve uma intensificação sazonal do impacto de *M. minutiflora* sobre as gramíneas nativas do início para o meio da estação seca, causada pela grande produção de biomassa desta espécie invasora.

Por sua vez, o impacto negativo de *U. brizantha* sobre a cobertura de solo nu foi intensificado da estação seca para a chuvosa em virtude da colonização de espaços anteriormente disponíveis.

Os impactos causados por estas espécies resultaram na diferenciação estrutural e funcional das comunidades invadidas e não-invadidas com relação à proporção dos componentes (solo nu, biomassa morta, graminóides, herbáceas e arbustos) que as compõem. Consequentemente, as alterações dos componentes funcionais levaram à divergência entre as comunidades invadidas por cada uma das espécies invasoras. Dessa forma, os resultados relacionados ao nosso primeiro objetivo demonstram a necessidade de controlar estas espécies invasoras no que tange à conservação e restauração de formações de Cerrado.

Atendendo a esta necessidade de manejo de *M. minutiflora* e *U. brizantha*, investigamos a influência das três épocas de queima (precoce, modal e tardia) na abundância (avaliada por meio da biomassa aérea) de cada uma das invasoras, e dos grupos funcionais de plantas nativas do Cerrado (agrupadas por formas de crescimento: graminóides, herbáceas e arbustos), além da biomassa morta total de nativas e cobertura de solo nu.

Dois anos após a realização das queimas prescritas, a abundância de *M. minutiflora* foi reduzida por queimadas, independentemente da época do ano. Nas parcelas inicialmente dominadas por esta espécie, uma nova invasão por *U. brizantha* foi intensificada pelas queimas precoces, tendência também observada para o tratamento tardio e que em ambos os casos pode ser atribuída à disponibilidade de propágulos de *U. brizantha* tanto no banco de sementes quanto da chuva de sementes. Considerando a vegetação nativa, somente o grupo de herbáceas foi afetado pelas queimadas, tendo sido favorecido pelas queimas modais nas comunidades dominadas por *M. minutiflora*.

Nas parcelas inicialmente dominadas por *U. brizantha,* queimas em nenhuma estação afetaram a abundância desta invasora ou de quaisquer componentes nativos após dois anos da realização das queimadas. Entretanto, todas as épocas de queima foram eficientes em reduzir momentaneamente a biomassa desta invasora até o fim da próxima estação chuvosa após as queimadas.

Fenologia, intensidade e severidade do fogo, além das condições ambientais durante e após as queimadas são as explicações para as respostas encontradas em parcelas invadidas por *M. minutiflora*. Por sua vez, nas parcelas dominadas por *U. brizantha*, a agressividade e a alta pressão de propágulo desta espécie conduziram ao seu rápido retorno em todos os tratamentos de queima. Ainda, todos esses efeitos são mediados por modificações da invasibilidade das comunidades (sua susceptibilidade a novas invasões) em virtude da flutuação de recursos (principalmente espaço, representado pelo aumento e/ou diminuição de cobertura de solo nu) causada pela ocorrência de queimadas.

Complementarmente a estes resultados, avaliamos a cobertura relativa de cada espécie – invasoras e nativas – ao longo de dois anos após a execução dos experimentos para compreender como as épocas de queima influenciam a diversidade e composição de espécies nativas em comunidades dominadas por espécies invasoras. Desta forma, poderíamos avaliar como os tratamentos utilizados para controle das invasoras influenciariam também a comunidade nativa, dando desta forma, um melhor embasamento científico para o uso das técnicas de manejo propostas não apenas para controlar as invasoras, mas também para promover a regeneração da vegetação nativa.

As respostas diferenciais de *M. minutiflora* e *U. brizantha* à ocorrência e à época de queima determinaram distintas modificações na diversidade das comunidades de acordo com a identidade da espécie invasora dominante. Em virtude da redução da abundância de *M. minutiflora* e da nova invasão por *U. brizantha*, as queimadas precoce e modal aumentaram a diversidade em relação às parcelas controle, enquanto que queimadas tardias a diminuíram após dois anos nas comunidades invadidas por *M. minutiflora*.

Nas comunidades invadidas por *U. brizantha*, em virtude de sua rápida regeneração após a ocorrência de queimadas, fogos em todas as épocas causaram uma diminuição da diversidade quando comparadas às parcelas não queimadas. Entretanto, dois anos após as queimadas prescritas a diversidade dessas parcelas queimadas parece retornar aos valores encontrados antes das queimas.

Portanto, conforme ilustrado pela Figura 1, podemos resumir os resultados encontrados neste estudo da seguinte maneira:

1) necessidade de controle das gramíneas africanas *Melinis minutiflora* e *Urochloa brizantha* em áreas de Cerrado em virtude do negativo impacto que exercem sobre a vegetação nativa;
2) eficácia do uso de queimadas prescritas no controle de *Melinis minutiflora*;
3) ineficácia do controle de *Urochloa brizantha* por meio de queimadas prescritas;
4) redução momentânea da biomassa acumulada de *Urochloa brizantha*, promovida pela execução das queimadas, independentemente da época do ano;
5) intensificação de novas invasões por *Urochloa brizantha* em comunidades inicialmente invadidas por *Melinis minutiflora* submetidas a queimadas precoces, bem como a tendência de que queimadas tardias também favoreçam esse processo;
6) favorecimento da regeneração de herbáceas nativas em parcelas invadidas por *Melinis minutiflora* quando submetidas à queimadas modais;
7) aumento de diversidade resultante de queimadas precoces e modais, bem como a diminuição de diversidade após queimas tardias nas parcelas invadidas por *Melinis minutiflora*;
8) efeito negativo de queimadas em todas as épocas na diversidade de comunidades invadidas por *Urochloa brizantha* ao longo de dois anos após a execução das queimas, em virtude da rápida regeneração desta invasora.

Figura 1. Comunidades inicialmente invadidas por *Melinis minutiflora*.(colunas da esquerda) e por *Urochloa brizantha* (colunas da direita). Controles não queimados (primeira linha); queimas precoce (segunda linha); modal (terceira linha); e tardia (última linha). Figuras na primeira e terceira coluna representam amostragens durante a estação chuvosa em 2016 (fevereiro) e figuras na segunda e quarta colunas foram tomadas dois anos após a aplicação dos tratamentos (maio, julho e outubro de 2016). A foto das parcelas controles na segunda e quarta colunas representam amostragens durante o final da estação seca de 2016 (outubro).

Assim sendo, recomendamos a utilização de queimadas no meio da estação seca (Julho) para o controle de *Melinis minutiflora*. Adicionalmente, ações que aumentem a regeneração da vegetação herbácea nativa podem ser implementadas visando diminuir as áreas ainda ocupadas por solo nu após a execução das queimadas. Tais ações poderiam ser a semeadura direta (Sampaio *et al.* 2015) e a transposição de bancos de gemas e sementes (Ferreira *et al.* 2015), por exemplo.

Entretanto, duas ressalvas devem ser feitas com relação a nossos resultados e recomendações: a primeira é que nossa área de estudo é uma área em regeneração, com um histórico de perturbação (plantação de *Pinus caribaea*), situação diferente da de áreas naturais invadidas, simplesmente. O segundo destaque é com relação à duração do monitoramento do experimento, pois apesar de o intervalo de 2 anos após as queimadas ser o período no qual há a recuperação da biomassa rasteira de formações savânicas de Cerrado (Andrade 1998), os resultados encontrados podem não persistir a médio e longo prazo.

Por outro lado, não recomendamos o uso de queimadas prescritas de forma isolada para o controle de *Urochloa brizantha*. Entretanto, para esta espécie, queimadas prescritas poderiam ser utilizadas como parte de um plano de manejo para esta espécie para promover a redução da biomassa morta desta espécie que pode levar a queimadas de maiores intensidades (Gorgone-Barbosa et al., 2015). Todavia, mais estudos a longo prazo são necessários para estabelecer quais e como seriam realizadas essas ações de manejo de forma a garantir sua implementação sem o retorno ou estabelecimento de novas invasões. Alguns exemplos bem-sucedidos do controle de espécies de *Urochloa* e estabelecimento de projetos de restauração de Cerrado podem ser encontrados em trabalhos realizados nos últimos anos (Ferreira *et al.* 2015; Sampaio *et al.* 2015; Silva *et al.* 2015; Alves 2016; Pellizaro 2016; Assis 2017).

REFERÊNCIAS BIBLIOGRÁFICAS

Alves, M. 2016. Semeadura direta de ervas, arbustos e árvores para restauração do Cerrado. *Dissertação de Mestrado*. Universidade de Brasília, Brasília.

Assis, G.B. de. 2017. Invasão do campo cerrado por braquiária (Urochloa decumbens): perdas de diversidade e experimentação de técnicas de restauração. *Tese de Doutorado*. Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Rio de Janeiro.

Durigan, G., Contieri, W.A., Franco, G.A.D.C. & Garrido, M.A.O. (1999) Indução do processo de regeneração da vegetação de Cerrado em área de pastagem, Assis, SP. *Acta Botanica Brasilica,* 2, 421–429.

Durigan, G., Ferreira De Siqueira, M., Daher, G.A. & Franco, C. (2007) Threats to the cerrado remnants. *Scientia Agricola*, 64, 355–363.

Gorgone-Barbosa, E., Pivello, V.R., Bautista, S., Zupo, T., Rissi, M.N., & Fidelis, A. 2015. How can an invasive grass affect fire behavior in a tropical savanna? A community and individual plant level approach. *Biological Invasions* 17: 423–431.

Hoffmann, W.A. & Haridasan, M. (2008) The invasive grass, Melinis minutiflora, inhibits tree regeneration in a Neotropical savanna. *Austral Ecology*, 33, 29–36.

Ferreira, M.C., Walter, B.M.T., & Vieira, D.L.M. 2015. Topsoil translocation for Brazilian savanna restoration: Propagation of herbs, shrubs, and trees. *Restoration Ecology* 23: 723–728.

Pellizaro, K.F. 2016. Restauração ecológica por meio de semeadura direta no Cerrado: avaliando espécies de diferentes formas de vida e densidades de plantio. *Dissertação de Mestrado*. Universidade de Brasília, Brasília.

Pivello, V.R., Shida, C.N. & Meirelles, S.T. (1999a) Alien grasses in Brazilian savannas: A threat to the biodiversity. *Biodiversity and Conservation*, 8, 1281–1294.

Pivello, V., Carvalho, V. & Lopes, P. (1999b) Abundance and distribution of native and alien grasses in a ‘Cerrado’(Brazilian Savanna) biological reserve. *Biotropica*, 31, 71–82.

Pyšek, P., Jarošík, V., Hulme, P.E., Pergl, J., Hejda, M., Schaffner, U. & Vilà, M. (2012) A global assessment of invasive plant impacts on resident species, communities and ecosystems: The interaction of impact measures, invading species' traits and environment. *Global Change Biology,* 18, 1725–1737.

Sampaio, A.B. & Schmidt, I.B. (2014) Espécies exóticas invasoras em unidades de conservação federais do Brasil. *Biodiversidade Brasileira*, 32–49.

Sampaio, A.B., Vieira, D.L.M., Cordeiro, A.O.D.O., Aquino, F.D.G., Sousa, A.D.P., Albuquerque, L.B. De, Schmidt, I.B., Ribeiro, J.F., Pellizaro, K.F., Sousa, F.S. De, Moreira, A.G., Santos, A.B.P. Dos, Rezende,G.M., Silva, R.R.P., Alves, M., Motta, C.P., Oliveira, M.C. De, Cortes, C.D.A., & Ogata, R. 2015. *Guia de restauração do Cerrado Volume 1 - semeadura direta.* 40pp. Rede de sementes do Cerrado. Brasília, Brasil.

Silva, R.P.R.P., Oliveira, D.R., da Rocha, G.P.E., & Vieira, D.L.M. 2015. Direct seeding of Brazilian savanna trees: effects of plant cover and fertilization on seedling establishment and growth. *Restoration Ecology* 23: 393–401.

Silveira, É.R. da, Melo, A.C.G. De, Contieri, W.A. & Durigan, G. (2013) Controle de gramíneas exóticas em plantio de restauração de Cerrado. *Manejo Adaptativo: primeiras experiências na restauração de ecossistemas* (eds G. Durigan & V.S.R. Ramos), pp. 5–8.

Ziller, S.R. & Dechoum, M.S. (2013) Plantas e vertebrados exóticos invasores em unidades de conservação no Brasil. *Biodiversidade Brasileira,* 3, 4–31.