
PROGRAMA DE PÓS-GRADUAÇÃO EM CIÊNCIAS BIOLÓGICAS
BIOLOGIA VEGETAL

**A relação entre fogo e uma gramínea invasora no Cerrado: O fogo pode
ser utilizado como uma estratégia de controle?**

Elizabeth Gorgone Barbosa

Dissertação/tese apresentada
ao Instituto de Biociências do
Câmpus de Rio Claro,
Universidade Estadual Paulista,
como parte dos requisitos para
obtenção do título de doutor em
Ciências Biológicas - Biologia
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Orientadora: Prof. Dra. Alessandra Fidelis

Co-Orientadora: Prof. Dra. Vânia Regina Pivello

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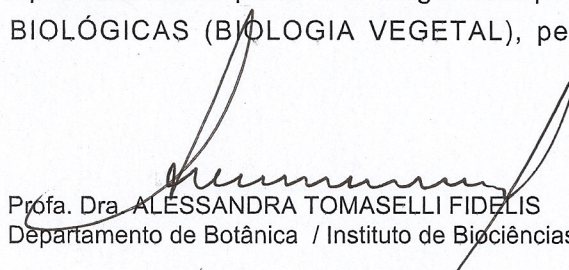
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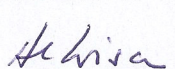
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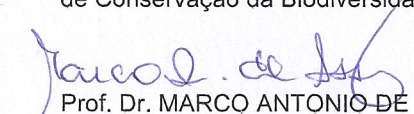
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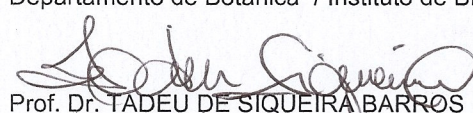
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Rio Claro, 24 de março de 2016

*Aos meus pais, Olívar e Sueli,
e à Alice, dedico esta tese.*

*“Sertão. Sabe o senhor:
sertão é onde o pensamento
da gente se forma mais
forte que o poder do lugar. (...)”*

“(...) Fui aprendendo a achar graça no desosssego (...)”

João Guimarães Rosa – Grande Sertão Veredas





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Resumo

Espécies invasoras e queimadas não-controladas são consideradas atualmente grandes ameaças à diversidade do Cerrado. Gramíneas invasoras podem alterar propriedades do material combustível, afetando o comportamento e regime do fogo em áreas invadidas. Para algumas invasoras, no entanto, o uso do fogo, dependendo de sua época e intensidade, pode auxiliar no manejo e controle dessas espécies. Desta forma, o objetivo desta tese foi avaliar a relação de retroalimentação entre uma gramínea invasora, *Urochloa brizantha* e o fogo no Cerrado. Para isso, foram realizados experimentos de queima controlada (2012-2015) em uma área de campo sujo na Reserva Natural Serra do Tombador (Goiás), a fim de verificar como *U. brizantha* afeta o comportamento do fogo, comparando queimadas em áreas invadidas e não invadidas e, em diferentes estações do ano. Além disso, foi avaliado como o fogo em diferentes frequências (anual, bienal e não queima) e épocas (meio e final da seca) afetam a invasora e as espécies nativas. Ainda, por meio de experimentos em laboratório, foram testados os efeitos indiretos (flutuação de temperatura) e diretos (choques térmicos) do fogo em sementes de *U. brizantha* e de outras invasoras (*U. decumbens* e *Melinis minutiflora*), assim como em sementes de gramíneas nativas, a fim de verificar como a germinação destas espécies é afetada pelo fogo. A presença de *U. brizantha* modifica o comportamento do fogo no meio da estação seca, aumentando o tamanho das chamas. No entanto, no final da estação seca, o fogo em áreas invadidas é mais intenso. Verificamos também que, independentemente da frequência ou época, o fogo reduz a biomassa morta de *U. brizantha*. Queimadas bienais no final da estação seca reduziram a cobertura de *U. brizantha*, mas não sua biomassa, enquanto que queimadas bienais no meio da seca tendem a facilitar a invasão em novas áreas. Com exceção dos gramínoides, que tiveram sua cobertura reduzida, as espécies nativas não foram afetadas pelo fogo. Sementes de *U. brizantha* e *U. decumbens* têm sua dormência quebrada com as flutuações de temperatura, independente do fogo, aumentando desta forma, sua porcentagem de germinação. Quando submetidas a choques térmicos (altas temperaturas), as sementes de *Melinis minutiflora* se mostraram resistentes, enquanto que as sementes de *U. brizantha* resistem e germinam com temperaturas menores de 200°C. Por outro lado, a germinação de *U. decumbens* não é afetada, mas a viabilidade das sementes diminui a partir de 100°C. *U. brizantha* afeta o comportamento do fogo e se regenera rapidamente pós-fogo, o que indica que o fogo sozinho não poderia controlar esta espécie, mas poderia ser utilizado como controle de material combustível. Os resultados deste estudo poderão auxiliar na compreensão dos processos de invasão de *U. brizantha* e, sua relação com o fogo e assim, subsidiar ações de manejo em unidades de conservação.



Abstract

Biological invasions and wildfires are considered major threats to the Cerrado biodiversity. Invasive grasses can change fuel properties, affecting the behavior and the fire regime in invaded areas. However, for some invasive species, prescribed fires could be used to manage and control them. Thus, the aim of this thesis was to evaluate the feedback relationship between an invasive grass, *Urochloa brizantha*, and fire in the Cerrado. Experimental burns were performed (2012-2015) in a “campo sujo” area at the Tombador Natural Preserve (Goiás), to evaluate how *U. brizantha* affects fire behavior, comparing invaded and non-invaded areas and different seasons. We also sought to verify how fire in different frequencies (annual, biennial and control) and seasons (mid-dry and late-dry) affect the invasive and native species. Moreover, we tested, in the laboratory, indirect (temperature fluctuation) and direct (heat shocks) effects of fire on seeds of invasive (*U. brizantha*, *U. decumbens* and *Melinis minutiflora*) and native grass species to verify how germination of these species was affected by fire. The presence of *U. brizantha* changed fire behavior in the mid-dry season by increasing flame height and in the late-dry season by increasing fire intensity in invaded areas. We also observed that, regardless of the fire frequency or season, fire reduced the dead biomass of *U. brizantha*. Biennial fires in the late-dry season reduced the cover of *U. brizantha*, but not its biomass, while biennial fires in the middle of the late-dry season tended to facilitate invasion into new areas. Except for graminoids, which had its cover reduced, native species were not affected by fire events. Regarding the germination experiments, temperature fluctuation, independent of fire, broke dormancy of *U. brizantha* and *U. decumbens* seeds, increasing their germination. When submitted to heat shocks *M. minutiflora* seeds were resistant, while *U. brizantha* seeds were able to germinate and resist temperatures lower than 200°C. On the other hand, germination of *U. decumbens* was not affected by the heat shocks, but the viability of its seeds decreased with 100°C. Finally, the results found in this study have shown that *U. Brizantha* affects fire behavior and regenerates rapidly after fire, indicating that fire by itself could not be used to control this species. However, fire, in this case, could be used as fuel control to avoid wildfires. These results are valuable in understanding the invasion process of *U. brizantha* and its relationship with fire and thus aid in future management decisions and actions in protected areas.



Introdução Geral

Espécies exóticas são consideradas espécies invasoras quando transportadas e introduzidas à novos ambientes, conseguem ultrapassar barreiras geográficas e de cultivo, sendo então capazes de se estabelecerem, ultrapassando as barreiras de sobrevivência e reprodução no novo ambiente e, por fim se dispersam, expandindo-se a à novas áreas, distantes da área de introdução, ultrapassando além da barreiras de dispersão, também barreiras ambientais (abióticas e bióticas), resultando em impactos negativos às comunidades nativas presentes no ambiente invadido (Richardson *et al.* 2000; Blackburn *et al.* 2011).

Diversos ecossistemas do mundo encontram-se atualmente descaracterizados e degradados devido a processos de invasão biológica e, por isso, a invasão biológica é considerada uma das maiores ameaças à biodiversidade (Sheil 2001). Os impactos negativos decorrentes da dominância de espécies invasoras podem ocorrer em diferentes níveis ecológicos e promover mudanças nas espécies, comunidades e/ou ecossistemas (Byers *et al.* 2000; Vilà *et al.* 2010; Vilà *et al.* 2011).

Plantas invasoras costumam atingir altas densidades e dominar a comunidade invadida, produzindo alterações significativas na composição, estrutura e processos dos ecossistemas naturais (Cronk & Fuller 1995; Vilà *et al.* 2011; Gaertner *et al.* 2014). São também capazes de modificar características do solo, a ciclagem de diversos nutrientes, a produtividade, a disponibilidade de luz e de água, o microclima e a dinâmica de distúrbios, especialmente do fogo (D'Antonio & Vitousek 1992; Hughes & Vitousek 1993; Mack *et al.* 2000).

Embora as invasões biológicas sejam fenômenos mundiais preocupantes, poucos estudos foram desenvolvidos em ambientes tropicais, sendo que cerca de 7% dos estudos mundiais sobre invasão biológica foram realizados nas Américas do Sul e Central

(Pauchard *et al.* 2004; Petenon & Pivello 2008). No Brasil, atualmente há cerca de 525 espécies de plantas catalogadas como exóticas naturalizadas, invasoras ou potenciais invasoras, sendo que destas, 223 estão presentes no Cerrado e 32% são gramíneas (Zenni 2015).

No Cerrado, várias espécies de gramíneas de origem africana foram introduzidas acidentalmente ou para fins forrageiros – destacando-se *Melinis minutiflora* P.Beauv. (capim-gordura), *Urochloa* spp. (braquiárias), *Andropogon gayanus* Kunth, *Hyparrhenia rufa* (Nees) Stapf (capim-jaraguá), *Panicum maximum* Jacq. (capim-colonião) – e se tornaram invasoras, principalmente nas fitofisionomias mais abertas (Pivello *et al.* 1999a; Martins *et al.* 2004, Fernandes *et al.* 2015) por serem heliófilas e apresentarem metabolismo fotossintético do tipo C4 (Klink & Joly 1989). O Cerrado é a savana tropical mais rica em espécies vegetais (Silva & Bates 2002), sendo considerado um *hotspot* de biodiversidade (Myers *et al.* 2000), porém, a invasão por gramíneas africanas constitui uma séria ameaça à sua biodiversidade (Pivello *et al.* 1999a; 1999b; 2006; Klink & Machado 2005; Durigan *et al.* 2007).

Diferentes estudos constataram que, principalmente, as gramíneas *Melinis minutiflora* e *Urochloa decumbens*, competem e afetam negativamente a abundância de espécies da comunidade herbácea (Pivello *et al.* 1999a; 1999b; Freitas & Pivello 2005, Almeida-Neto *et al.* 2010). As espécies do gênero *Urochloa* têm se mostrado frequentes e dominantes em comunidades vegetais em unidades de conservação de Cerrado no estado de São Paulo (Pivello *et al.* 1999a; 1999b), apresentando um potencial alelopático sobre a germinação e o crescimento de outras espécies (Barbosa *et al.* 2008, Kobayashi & Kato-Noguchi 2015). Já a espécie *Melinis minutiflora*, no centro-oeste do Brasil, sempre foi considerada uma das espécies invasoras mais agressivas e prioridade para manejo em unidades de conservação do Cerrado (Martins 2006; Martins *et al.* 2011), diminuindo a riqueza nas comunidades nativas e a reduzindo a regeneração de espécies arbórea (Hoffman *et al.* 2004; Martins *et al.* 2011). No entanto, espécies do gênero *Urochloa*,

atualmente vêm sendo constatadas em processos avançados de invasão nos Cerrados do Centro-Oeste (Horowitz *et al.* 2013; Ziller & Dechoum 2013; Sampaio & Schmidt 2013) e áreas alagadas do Pantanal (Bao *et al.* 2015).

Experimentos e modelagens vêm mostrando que algumas destas gramíneas invasoras, como *Urochloa* sp. e *M. minutiflora*, além de serem competidoras eficientes, produzem grande quantidade de biomassa altamente inflamável, aumentando o risco de incêndios durante a estação seca (Berardi 1994; Castro-Neves 2000), modificam o comportamento e o regime do fogo no Cerrado (Berardi 1994; Castro-Neves 2000; Mistry & Berardi 2005; Rossi *et al.* 2014; Gorgone-Barbosa *et al.* 2015) e rebrotam rapidamente após o fogo, ocupando os espaços abertos na vegetação (Gorgone-Barbosa *et al.* dados não publicados) degradando desta maneira, ainda mais o sistema.

No Cerrado, assim como em diversos outros ecossistemas no mundo, o fogo é um importante fator ecológico, responsável pela manutenção, distribuição e evolução desses ecossistemas (Bond *et al.* 2005; Pausas & Keeley 2009). A dependência da vegetação em relação ao fogo podem ser observadas nas savanas africanas (Trollope 1982), australianas (Morgan 1999) e neotropicais (Coutinho 1990; Sarmiento 1993; Simon *et al.* 2009), nas pradarias americanas (Hanes 1971), nos ecossistemas mediterrâneos (Keeley *et al.* 2012). Cada um destes ecossistemas possui um regime de fogo específico, que é caracterizado por sua frequência (intervalo de retorno do fogo), sua intensidade (quantidade de calor liberada), época (quando ocorre) e extensão (área total queimada) (Whelan 1995; Bond & Van Wilgen 1996). Além disso, a severidade (efeitos no solo e/ou vegetação) e o tipo do fogo (de superfície, de copa ou subterrâneo) podem influenciar nas respostas da vegetação e são também característicos dos diferentes ecossistemas (Bond & Van Wilgen 1996; Bond & Keeley 2005).

Sabe-se que, dentre os impactos causados por espécies invasoras, a alteração no regime de fogo é um dos mais significativos, levando à alteração dos ecossistemas invadidos (Brooks *et al.* 2004; D'Antonio 2000). Após a passagem de fogo, há um aumento

na incidência de luz no nível do solo e na disponibilidade de nutrientes (Oliveras *et al.* 2013), assim como mudanças no microclima (Whelan 1995; Knox & Clarke 2006; Fidelis & Blanco 2014). Além disso, o fogo também pode estimular a floração e a germinação de algumas espécies (Bond & Van Wilgen 1996; Miranda *et al.* 2002; Paula & Pausas 2008; Moreira *et al.* 2010). Deste modo, o recrutamento de espécies é afetado no ambiente pós-fogo, influenciando significativamente a dinâmica e a estrutura da comunidade vegetal, levando a alterações nas frequências de espécies raras e na dominância de espécies comuns ou invasoras (D' Antonio 2000; Bond & Keeley 2005).

A relação do fogo com as espécies invasoras pode ser positiva, favorecendo a invasão por meio de aberturas de novos espaços para seu estabelecimento, diminuição da competição interespecífica e aumento na disponibilidade de nutrientes. Uma vez estabelecidas, espécies exóticas geralmente apresentam uma alta produção de biomassa e consequente dominância na comunidade de plantas (Bilbao & Medina 1996; Setterfield *et al.* 2010), podendo causar grandes alterações no regime e comportamento do fogo (Gaertner *et al.* 2014), levando a grandes mudanças nos ecossistemas invadidos (D'Antonio 2000; Brooks *et al.* 2004). No entanto, a relação do fogo com as espécies invasoras também pode ser negativa, diminuindo sua abundância na comunidade invadida (D'Antônio 2000; Brooks *et al.* 2004), podendo o fogo, portanto, ser uma eficiente ferramenta de manejo no controle destas espécies. Essa relação entre fogo e espécie invasora pode ser afetada tanto pela época em que ocorrem os incêndios, quanto pela sua frequência. Fischer *et al.* (2009) demonstraram que incêndios frequentes em vegetação australiana dominada por *Banksia* sp. (Proteaceae) favoreceram o processo de invasão de duas espécies herbáceas sul-africanas (*Ehrharta calycina* e *Pelargonium capitatum*), diminuindo a cobertura, riqueza e diversidade de espécies nativas. O mesmo ocorre na região centro sul do Chile, onde um arbusto invasor (*Teline monspessulana*) não é apenas favorecido pelos incêndios, mas também cria condições favoráveis para incêndios mais intensos e contínuos (Pauchard *et al.* 2008). Por outro lado, em vegetação de *Mallee* na Austrália, onde os solos

são pobres em nutrientes, o fogo não promoveu o aumento de gramíneas invasoras e poderia, portanto, ser utilizado como ferramenta de manejo para a conservação da biodiversidade nestes ecossistemas (Gosper *et al.* 2011).

Desta forma, existe uma importante relação de “mão dupla” entre o fogo e as espécies invasoras em ecossistemas suscetíveis a incêndios, onde tanto a presença da espécie invasora pode afetar o regime e o comportamento do fogo, como também os diferentes regimes de fogo podem afetar a abundância, o estabelecimento e a distribuição das espécies invasoras. As diferentes respostas dessas interações dependerão do tipo de comunidade vegetal, da espécie invasora em questão e do regime de fogo do local. Portanto, o objetivo principal desta tese foi investigar essa relação de “mão dupla” entre o fogo e a gramínea invasora *Urochloa brizantha* em uma área campo sujo (Cerrado), localizada na Reserva Natural Serra do Tombador, Cavalcante, Goiás (Figura 1). Para tal, a tese foi dividida em quatro capítulos onde no primeiro **“How can an invasive grass affect fire behavior in a tropical savanna? A community and individual plant level approach”**, analisamos o efeito da presença de espécies invasoras em diversos parâmetros do comportamento do fogo (como por exemplo, altura das chamas, intensidade, temperatura máxima), por meio de queimadas prescritas. Neste capítulo também avaliamos se a época do ano (meio e final da seca) influenciaria o comportamento do fogo em áreas invadidas por braquiária. O segundo e terceiro capítulo foram dedicados a investigar, em laboratório, o que acontece com as sementes de espécies invasoras quando submetidas a efeitos diretos (exposição a altas temperaturas) e indiretos (flutuações de temperatura) do fogo. No segundo capítulo **“Disturbance as a factor in breaking dormancy and enhancing invasiveness of African grasses in a Neotropical Savanna”**, analisamos o efeito do aumento de temperatura (solo) devido à passagem do fogo afetaria a germinação de sementes de *Urochloa brizantha* e *Urochloa decumbens* presentes no banco de sementes do solo. Como o fogo causa remoção da vegetação aérea e mudanças no microclima, como maiores amplitudes de flutuações de temperaturas, também testamos o efeito de flutuações

térmicas na germinação destas duas espécies. Já no terceiro capítulo “**The role of heat shocks in the germination of native and invasive grasses in Cerrado**”, verificamos como a exposição a altas temperaturas (choques térmicos) durante as queimas afetam a viabilidade e germinação de sementes de espécies invasoras e nativas do Cerrado, verificando a resistência e a capacidade de persistir no ambiente destas espécies, assim como as possíveis implicações na recolonização pós-fogo. Por fim, o quarto capítulo “**Can fire be used as a management tool to control invasive grasses in Cerrado? The effects of fire regime on invaded and native plant communities**”, avaliamos as respostas da invasora *Urochloa brizantha* a diferentes frequências de queimas em diferentes épocas do ano, em uma de campo sujo, assim como as respostas da vegetação nativa que coexistem com esta espécie invasora na área de estudo. Neste capítulo, também discutimos a possibilidade do uso do fogo como instrumento de manejo para controle de *Urochloa brizantha*.

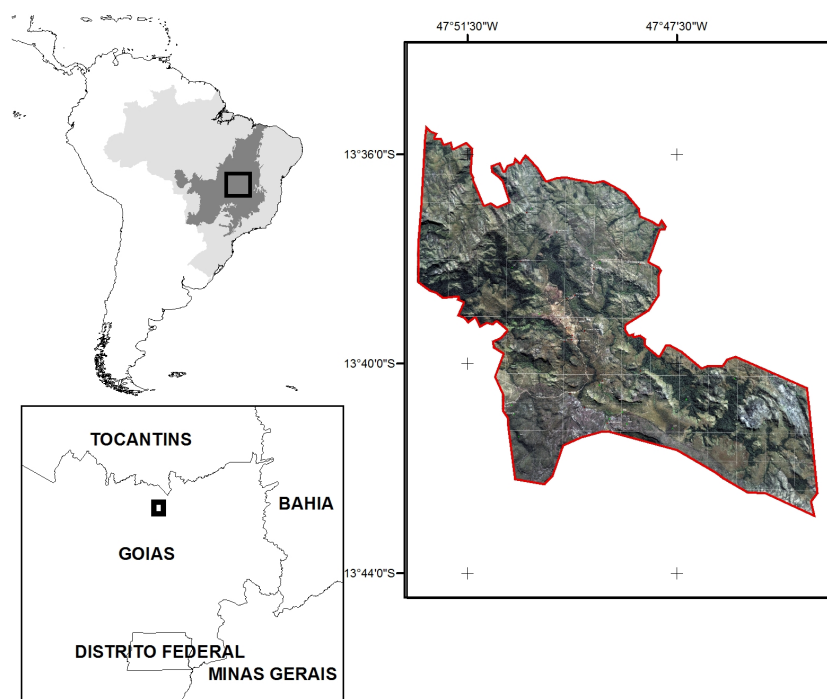


Figura 1. Localização da Reserva Nacional Serra do Tombador, no Estado de Goiás.

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1

How can an invasive grass affect fire behavior in a tropical savanna? A community and individual plant level approach

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ABSTRACT

Some invasive grasses have been reported to change fire behavior in invaded plant communities. *Urochloa brizantha* is an aggressive invasive grass in the Brazilian Cerrado, an ecosystem where fire is a common disturbance. We investigated the effects of *U. brizantha* on fire behavior in an open Cerrado physiognomy in Central Brazil. Using experimental burnings we compared fire behavior at both the community and the individual plant level in invaded (UJ) and non-invaded (NJ) areas burned in July. We also assessed the effect of fire season in invaded areas by comparing July (UJ) and October (UO) burnings. We evaluated the following variables: fuel load, fuel moisture, combustion efficiency, maximum fire temperature, flame height, and fire intensity. Additionally, we evaluated the temperatures reached under invasive and native grass tussocks in both seasons. Fuel load, combustion efficiency, and fire intensity were higher in NJ than in UJ, whilst flame height showed the opposite trend. Fuel amount and fire intensity were higher in October than in July. At the individual plant level, *U. brizantha* moisture was higher than that of native species, however, temperatures reaching $\geq 600^{\circ}\text{C}$ at ground level were more frequent under *U. brizantha* tussocks than under native grasses. At the community level, the invasive grass modified fire behavior towards lower intensity, lower burning efficiency, and higher flame height. These results provide essential information for the planning of prescribed burnings in invaded Cerrado areas.

Keywords: African grass; Cerrado; fire behavior; fire intensity; fuel load; *Urochloa brizantha*.

INTRODUCTION

Invasive plants cause significant changes in the composition, structure and processes of natural ecosystems (Cronk and Fuller 1995; Pimentel *et al.* 2000; Vilà *et al.* 2011; Pyšek *et al.* 2012b). They can reach high densities and dominance in invaded communities, thus being able to modify soil properties and functions, plant productivity, microclimate, fire regime, and interspecific relationships in the community (D'Antonio and Vitousek 1992; Mack *et al.* 2000; Setterfield *et al.* 2010; McGranahan *et al.* 2012). In fire-prone environments such as savannas, invasive grasses may considerably change the nature of the fuel bed, and consequently affect fire behavior and severity (Mack and Antonio 1998; D'Antonio 2000; Mack *et al.* 2000; Brooks *et al.* 2004; Klinger 2011).

The impact of invasive grasses on fire regimes, as well as their influence on post-fire species interactions and ecosystem processes, have been studied and documented for a variety of ecosystems (e.g., Hughes and Vitousek 1993; Bilbao and Medina 1996; D'Antonio *et al.* 1998; Rossiter *et al.* 2003; Setterfield *et al.* 2010). By increasing horizontal fuel continuity, invasive exotic grasses may greatly increase fire extent and frequency (D'Antonio and Vitousek 1992). Furthermore, areas invaded by exotic grasses normally burn at higher fire intensities than areas of native vegetation (Rossiter *et al.* 2003; McDonald and Mcpherson 2013), since invasive grasses can greatly increase the fuel load (Bilbao and Medina 1996; Rossiter *et al.* 2003; Setterfield *et al.* 2010).

The Brazilian tropical savannas – Cerrado – are considered a biodiversity hotspot (Myers *et al.* 2000). However, it is estimated that 55% of the original area of Cerrado has been changed to monocultures and planted pastures (Klink and Machado 2005). The spread of exotic grasses and dry season wildfires are the major threats to the biodiversity of Cerrado (Klink and Machado 2005; Pivello 2006; Durigan *et al.* 2007). Fire has been an important agent of evolution in Cerrado for at least 4 million years (Simon *et al.* 2009). The structure of plant communities influences fire behavior and frequency. In turn, fire characteristics influence the regeneration and structure of post-fire communities, resulting in a feedback

process between fire and the Cerrado plant community (Kauffmann *et al.* 1994; Miranda *et al.* 2009).

Several African grass species (C₄) were introduced in Brazil for cattle grazing, and later became a serious threat to the Cerrado plant community (Klink 1994; VR Pivello *et al.* 1999; Vânia Regina Pivello *et al.* 1999). Nowadays, most of these African grasses (e.g. *Melinis minutiflora* P. Beauv., *Hyparrhenia rufa* (Nees) Stapf, *Panicum maximum* Jacq. *Urochloa* spp.) can be found in almost every Cerrado nature reserve (Vânia Regina Pivello *et al.* 1999; Pivello 2006). *Urochloa* species are the most common and aggressive invasive grasses in Cerrado areas (VR Pivello *et al.* 1999; Almeida-Neto *et al.* 2010; Lannes *et al.* 2012), and can drastically decrease the abundance of native grasses (VR Pivello *et al.* 1999) and forbs (Almeida-Neto *et al.* 2010) and dominate the herbaceous community.

Given that fire plays an important role in the Cerrado, and that extensive Cerrado areas are invaded by *Urochloa* species, it is of crucial importance to understand how these invasive grasses affect fire behavior, especially focusing on the management of such areas. Therefore, the aim of this study was to investigate how the invasive grass *Urochloa brizantha* (A.Rich.) R.D.Webster may affect fire behavior in Cerrado, as well as the potential mechanisms involved. By using experimental burnings we assessed the effect of *U. brizantha* on the fuel bed and on fire behavior at both the community (plot) and the individual plant level (IPL) scales. We also evaluated if and how fire would differ between seasons (dry season and beginning of rainy season) in the invaded areas. We hypothesized that the presence of *U. brizantha* in the herbaceous community would affect fire behavior by increasing fire intensity through changes in the fuel load. Additionally, we expected that fire at the beginning of the rainy season would be more intense due to the accumulation of dead fuel generated by the invasive grass after the dry season.

METHODS

Study area

The study was conducted at the Serra do Tombador Nature Reserve (RNST), in Central Brazil (47°45 ' ; 47°51' W and 13°35 ' ; 13°38' S; 560-1118m a.s.l.). The regional climate is tropical with wet summers and dry winters, and average annual rainfall between 1300 and 1500 mm (AER 2009). The RNST comprises approximately 8900 ha, which encompasses different Cerrado physiognomies, where the *campo sujo* – a grassland type with scattered forbs and small shrubs (Coutinho 1978) – prevails.

Before becoming a nature reserve, in 2007, the RNST was a cattle ranching farm, and for this reason invasive grasses, such as *Urochloa* spp and *Melinis minutiflora*, dominate several disturbed and degraded areas. The entire reserve has patches with different fire histories; most fire events were accidental or criminal and occurred during the dry season (June to October). All experiments were carried out in *campo sujo* physiognomy, where many patches of *U. brizantha* can be found. The experimental area has not been burned or grazed since 2007.

Experimental design and data sampling

Fire behavior in invaded versus non-invaded sites

In the study area, the invasive species was found in patches of different sizes separated by areas of native grasses. To conduct the experimental fires, we selected individual patches of invaded and non-invaded areas and established one single plot per patch. In July 2012 (dry season), we established ten plots of 20x15 m: six with *U. brizantha* covering at least 30% of the plot (UJ treatment), and four plots without *U. brizantha*, having only native vegetation (NJ treatment). To guarantee the independence of experimental units and treatments, head fires were conducted individually on each plot. To avoid the spread of fire to the nearby vegetation, 3 m wide firebreaks were established around each plot. All experimental fires were carried out with the assistance of the reserve's fire brigade and were conducted at the beginning and/or end of the day.

Weather conditions such as air temperature, relative air humidity and wind speed were measured before and during the fires with a portable digital Thermo-Hygrometer (HT-300 Instruthem®) and a digital Thermo-Anemometer (TAD-500 Instruthem®), respectively.

Before the fires, we determined fuel load (kg.m^{-2}) for each plot by sampling aboveground biomass in six 0.25x0.25 m subplots. In the invaded plots, we used a stratified random sampling (three subplots were located on tussocks of *U. brizantha* and three subplots on tussocks of native species). Each sample was weighed in the field to determine fuel moisture (live+dead biomass). Biomass was then separated into the following classes: dead biomass, dead and live *U. brizantha* biomass, coarse biomass (stems + graminoid crowns), and fine biomass (leaves + culms). Biomass was dried at 70°C for three days and weighed to constant dry weight. The fuel load value obtained for each plot was adjusted with weighted averages according to the percentage of *U. brizantha* cover on each plot.

Maximum height (including the reproductive structures) of *U. brizantha*, herbaceous plants (forbs and native grasses), and shrubs were also measured on each plot before the fires. After the fires, residual biomass was sampled on six subplots of 0.25x0.25 m, dried and weighed. We then estimated combustion efficiency by comparing pre- and post-fire biomass. The maximum temperatures reached during the fires were assessed by using pyrometers made of aluminum plates painted with color-change crayons (ColeParmer®) with a temperature range of 120 °C - 600 °C. The pyrometers were placed 2 cm belowground, at soil surface, and 50 cm aboveground, where most of the biomass was found. In UJ plots, pyrometers were placed, at each of the three heights described above, under five *U. brizantha* tussocks and under five tussocks of native grasses; in NJ plots, pyrometers were randomly placed. We also used open-calorimeters made of aluminum cans (350 ml) following methods proposed by Pérez and Moreno (1998). The cans were filled with 200 ml of water and sealed. They were unsealed just before the burnings and sealed again right after fires, when they were weighed to calculate the amount of water evaporated during the passage of fire. We used 10 calorimeters for each plot, five under *U. brizantha* tussocks and five under tussocks of native grasses. Furthermore, ten calorimeters were used as a control,

being left outside the experimental plots, and sealed/ unsealed at the same time as the ones that were in experimental plots.

To measure fire rate of spread (m.s^{-1}) we established three observation points (5, 10 and 15 m) on one side of the plot and measured the time taken for the fire line to reach each of the points. From these values, we calculated the average rate of spread per plot. From the same three observation points and with the aid of a 5 m long scale, we visually estimated flame height (cm). Finally, we estimated fire-line intensity (kW.m^{-1}) for each plot using the Byram's equation and considering a constant value of heat yield for savannas, of 15500 kJ.kg^{-1} (Griffin and Friedel 1984).

Fire behavior in invaded sites at different seasons

In October 2012 (early-rainy season), we conducted a second set of experimental burnings on invaded plots (UO treatment; six 20x15 m plots on patches where *U. brizantha* covered at least 30% of the ground), and compared results with those from the burnings conducted in July (UJ treatment; dry season; six 20x15 m plots). The experimental fires in October were carried out as described above for UJ burnings; the same variables were assessed in both seasons.

Statistical analyses

We used one-way analysis of variance (ANOVA) applied to randomization tests (Euclidean distance between sampling units, 10000 iterations) to evaluate differences between invaded and non-invaded plots (community level), *U. brizantha* and native species tussocks (individual plant level), and between July and October fires (fire season). We also performed linear regression modeling to analyze the relationships between some fuel load properties and fire intensity, and between the amount of water evaporated from the calorimeters and the frequency that the pyrometers registered at least 600°C . All statistical analyses were performed using the software MULTIV (Pillar 2005) and Statistica (StatSoft 2011).

RESULTS

Fire behavior in invaded and non-invaded communities

Weather conditions were similar for all experimental fires, including both NJ and UJ treatments: high air temperatures ($29.7 \pm 1.0^\circ\text{C}$ and $28.9 \pm 1.8^\circ\text{C}$ for UJ and NJ, respectively), low relative air humidity ($36.5 \pm 6.0\%$ in UJ and $31.3 \pm 2.4\%$ in NJ plots) and low wind speed (0.8 ± 0.2 and $0.9 \pm 0.3 \text{ m.s}^{-1}$ for UJ and NJ, respectively).

U. brizantha tussocks (ranging from 109 to 159 cm in height) were significantly taller ($P < 0.001$) than both native grasses/forbs (49 to 55 cm) and shrubs (40 to 79 cm). However, total fuel load was higher in NJ plots (Table 1). Most of the total biomass in the NJ plots consisted of dead and fine live biomass (78% and 16%, respectively), whilst coarse live biomass corresponded to only 5%. In UJ plots, native species biomass accounted for 65% of total biomass, (where 48% was dead biomass), *U. brizantha* biomass represented about 35% (dead+live), and coarse biomass represented only 8% (Table 1). Total fuel moisture (dead+live) did not differ between UJ and NJ plots ($24 \pm 2\%$ and $29 \pm 1\%$, respectively, $P = 0.56$). However, considering only the invaded plots, total fuel moisture was higher for *U. brizantha* ($30 \pm 2\%$) than for native grasses ($18 \pm 3\%$, $P < 0.001$).

Table 1 Fuel load (kg.m^{-2} , mean $\pm$ SE) per fuel class in non-invaded plots (NJ), invaded plots in July fires (UJ), and invaded plots in October fires (UO) at Serra do Tombador Nature Reserve, Central Brazil. * $P \leq 0.05$

Fuel load	Treatments			<i>P</i> values (NJx UJ)	<i>P</i> values (UJ x UO)
	NJ	UJ	UO		
Dead native	0.47 ± 0.11	0.17 ± 0.01	0.26 ± 0.03	0.04 *	0.04 *
Dead <i>Urochloa brizantha</i>	-	0.11 ± 0.02	0.23 ± 0.04	-	0.02 *
Total dead	0.47 ± 0.11	0.28 ± 0.02	0.49 ± 0.06	0.49	0.01 *
Live fine native	0.10 ± 0.03	0.03 ± 0.01	0.04 ± 0.01	0.05 *	0.20
Live coarse native	0.02 ± 0.02	0.03 ± 0.01	0.04 ± 0.01	0.16	0.35
Live <i>Urochloa brizantha</i>	-	0.01 ± 0.01	0.05 ± 0.01	-	0.04 *
Total <i>Urochloa brizantha</i> (dead + live)	-	0.12 ± 0.02	0.26 ± 0.04	-	0.006 *
Total Fuel Load	0.61 ± 0.14	0.35 ± 0.02	0.62 ± 0.06	0.01 *	0.001*

In both invaded and non-invaded plots, maximum temperature at soil level and 50 cm aboveground reached values higher than 600°C, but temperatures >600°C were most frequent at soil surface. Temperatures 2 cm belowground were lower than 120 °C in all experimental plots. Flame height was significantly higher ($P=0.001$, Fig. 1A) in UJ (478±33 cm) than in NJ plots (266±31 cm).

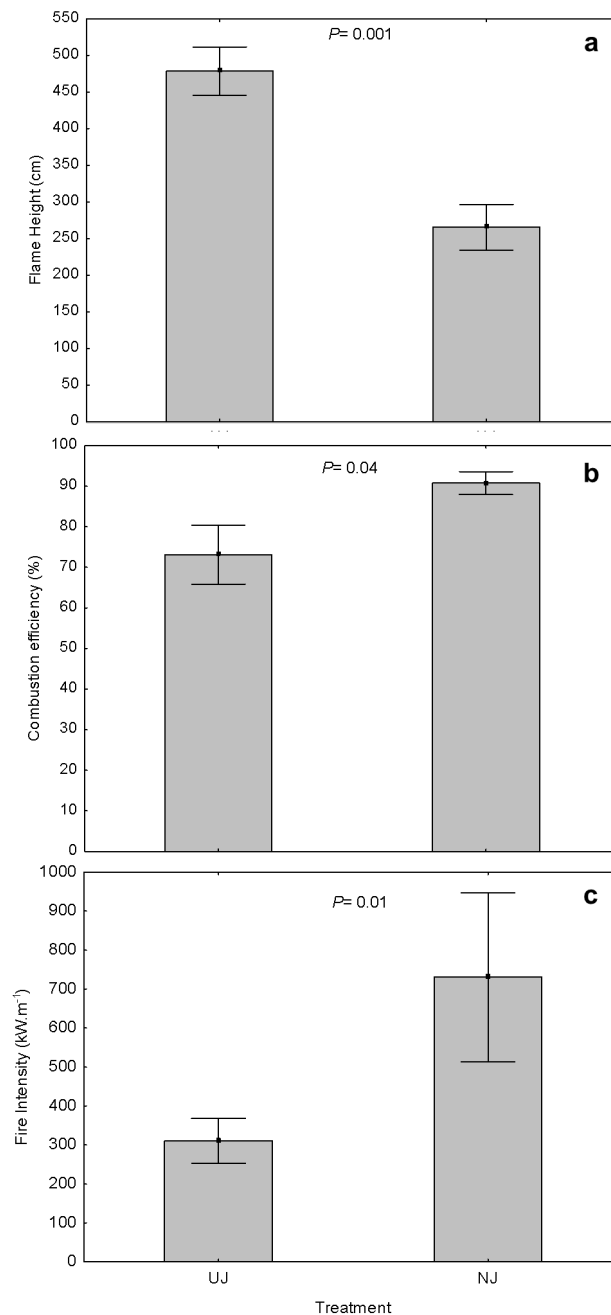


Fig 1 Fire characteristics of experimental burnings in the invaded (UJ) and non-invaded plots (NJ, mean±SD) at the Serra do Tombador Nature Reserve, Central Brazil: (A) Flame height (cm), (B) Combustion efficiency (%), (C) Fire Intensity (kW.m⁻¹).

Nevertheless, combustion efficiency in UJ plots was on average 73%, while in NJ plots it was ca. 90% (Fig. 1B, $P=0.04$). The rate of flame spread was not significantly different between treatments ($P=0.7$) and fire-line intensity was lower in the UJ ($310\pm58 \text{ kW.m}^{-1}$) compared to the NJ plots ($731\pm217 \text{ kW.m}^{-1}$, Fig. 1C, $P=0.001$).

Fire behavior under different seasons and *U. brizantha* effects

Weather conditions were similar between dry (July) and early rainy seasons (October) ($p>0.05$ for all variables). In general, air temperature was higher than 29°C , relative air humidity was lower than 40%, and wind speed varied from 0.8 ± 0.2 to $1.3\pm0.3 \text{ m.s}^{-1}$.

No significant difference was found in the height of *U. brizantha* between UJ ($132\pm10 \text{ cm}$) and UO ($101\pm6 \text{ cm}$, $P=0.06$). Total fuel load in UO was twice the amount sampled in UJ ($P=0.007$), and was mainly composed of dead biomass (*U. brizantha* and natives, Table 1). Total fuel moisture (dead+live) was similar in both seasons ($29\pm2\%$ in July and $27\pm3\%$ in October; $P=0.55$). As in UJ, maximum temperatures registered in UO fires were higher than 600°C in all plots, both at soil level and 50 cm aboveground, while temperatures belowground did not exceed 120°C . All measured fire variables did not differ significantly between UJ and UO (Table 2). However, fire intensity in UJ (dry season) was lower (from 140 to 499 kW.m^{-1}) than in the early rainy season (UO, from 212 to 1611 kW.m^{-1} , $P=0.03$) (Table 2).

Table 2 Fire-behavior variables (mean $\pm$ SE) in invaded plots in July, dry season (UJ), and October, beginning of the rainy season (UO), at the Serra do Tombador Nature Reserve (RNST), Central Brazil. * $P\leq 0.05$

Fire parameters	UJ	UO
Flame height (cm)	478 ± 30	404 ± 51
Combustion efficiency (%)	73 ± 7	87 ± 5
Fire intensity (kW.m^{-1})	310 ± 57	$788 \pm 196^*$
Frequency of temperature $>600^{\circ}\text{C}$ (%) (under tussocks of <i>Urochloa brizantha</i>)	66 ± 4	80 ± 7
Frequency of temperature $>600^{\circ}\text{C}$ (%) (under tussocks of native grasses)	40 ± 8	40 ± 13

The dead fuel of natives explained 48% ($P=0.01$) of the variation of fire intensity. Moreover, dead fuel and moisture content of *U. brizantha* were also good predictors, both explaining more than 30% of the variation of fire intensity independently of the season ($P=0.05$ for both, Fig 2A and 2B). Relationships between fire-line intensity and other fuel properties such as fine, coarse and live *U. brizantha* biomass were not significant.

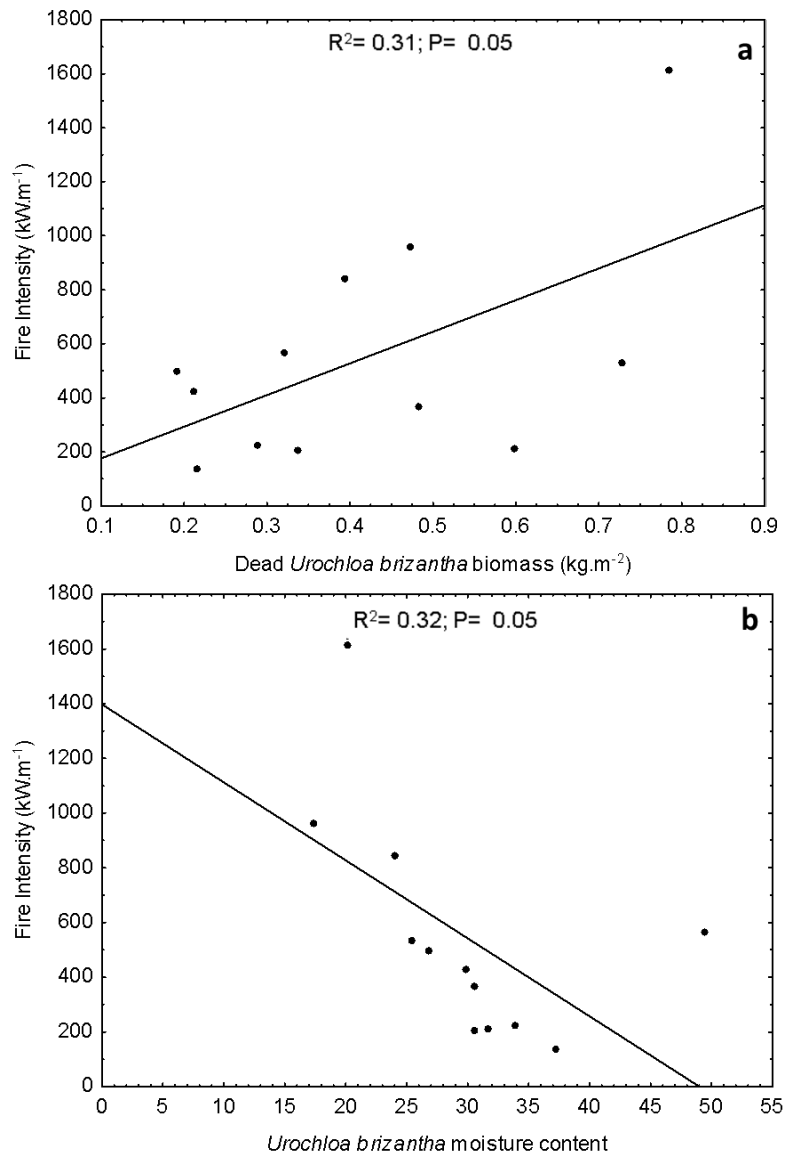


Fig 2 Relationship between (A): fire intensity and dead biomass of *Urochloa brizantha* (kg.m⁻²) in UJ + UO treatments, and (B): fire intensity and moisture content of *Urochloa brizantha* (live+dead biomass,%) in UJ + UO treatments at the Serra do Tombador Nature Reserve, Central Brazil.

Fire behavior at the individual plant level (IPL): tussocks of *U. brizantha* and native grasses

The volume of water lost in calorimeters under *U. brizantha* and under native species did not differ in either July or October fires ($P=0.14$ and $P=0.17$, respectively). However, pyrometers at soil surface under *U. brizantha* reached 600°C more frequently (70% of pyrometers in both July and October – Fig 3) when compared to those under the tussocks of native grasses (40%, $P=0.03$ and $P=0.05$ for July and October, respectively). At 50 cm aboveground and 2 cm belowground there was no significant difference between *U. brizantha* and tussocks of native grasses.

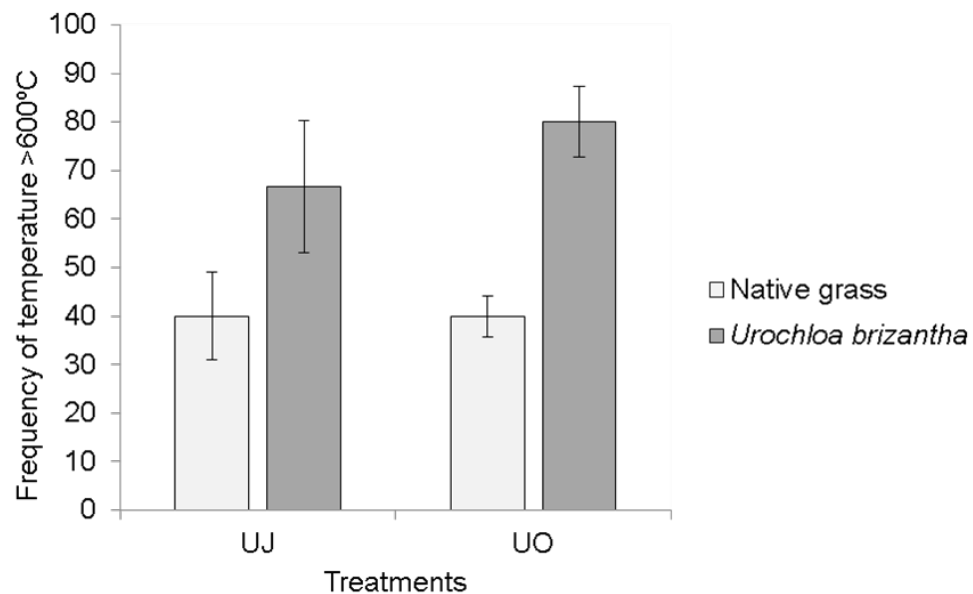


Fig 3 Frequency of temperatures exceeding 600°C under tussocks of native grasses and tussocks of *Urochloa brizantha* both in July fires (UJ) and October fires (UO, mean±SD) at the Serra do Tombador Nature Reserve, Central Brazil (mean ± SE).

DISCUSSION

Fire behavior in invaded and non-invaded communities and at the individual plant level

The presence of the invasive grass *Urochloa brizantha* in the Cerrado *campo sujo* modified fire behavior towards lower fire intensity, lower combustion efficiency, and higher flame height at the community level, and increased the frequency of high temperatures at the individual plant level (IPL).

The type, amount, and moisture content of the fuel load are strongly related to fire behavior, especially fire intensity and rate of spread (Whelan 1995). The amount and type of fuel in Cerrado is related to the physiognomy (Castro and Kauffmann 1998; Miranda *et al.* 2002) and to time since last fire (Oliveras *et al.* 2013; Fidelis *et al.* 2013): open physiognomies have more fine fuel and accumulate dead fuel if not burned frequently. According to Miranda *et al.* (2002), fuel load in *campo sujo* varies from 0.60 – 0.96 kg.m⁻², similar values to those found in the non-invaded plots (NJ) of this study. Several studies show that invasive grasses usually increase the amount of fine fuel (D’Antonio and Vitousek 1992; D’Antonio *et al.* 1998; Brooks *et al.* 2004). However, there have been cases where the invasive grass reduced the fuel load of the invaded areas (Mcgranahan *et al.* 2013). Surprisingly, we found lower fuel load in invaded plots (UJ) than in non-invaded plots. *Urochloa brizantha* forms dense and tall tussocks (Milles *et al.* 1996), an architecture quite different than most native grasses in the area, giving this species great potential for changing fuel characteristics of invaded *campo sujo* areas. The presence of the invasive grass also decreases the native fuel load, especially biomass of native grasses and forbs (Gorgone-Barbosa, unpublished data), which contributed to the change in fuel load and could partially explain the lower fire intensity found in UJ plots.

At the community level, total fuel moisture was not significantly different between UJ and NJ. However, the moisture content of *U. brizantha* biomass was higher than that of native species, also contributing to lower combustion efficiency and lower fire intensity in the invaded plots. Modeling simulations with another African grass invasive of the Cerrado,

Melinis minutiflora, showed that it could promote more intense fires (Mistry and Berardi 2005), which could be related to plant architecture, fuel moisture, and higher fuel load promoted by the invasive species. In Australian eucalypt-dominated savannas, *Andropogon gayanus* doubled the moisture content of the fuel load. However, it increased fire intensity in these savannas (Setterfield et al. 2010).

Nevertheless, temperatures above 600°C were more frequently reached under tussocks of *U. brizantha* than under native grasses, for both July and October fires. High temperatures can lead to high plant mortality rates, since plant tissues usually die at 60°C (Bova and Dickinson 2005). Seed and bud mortality could also increase after being exposed to high temperatures, which would negatively affect the regeneration of native vegetation. As postulated by the “kill the neighbor” theory (Bond and Midgley 1995), more flammable individuals would have an advantage, since they would kill their neighbors and facilitate their own regeneration after fire. Our results suggest that at the individual plant level, *U. brizantha* can alter fire temperatures, killing their neighbors, and thus, creating more open space to regenerate and spread out after fire. High fire temperatures do not seem to affect the resprouting ability of *U. brizantha* (Gorgone-Barbosa, unpublished data), which could be related to its capacity to retain more moisture (compared to native grasses), resulting in a more efficient insulation of buds and protection of living tissues.

Cerrado fires are surface fires: they spread very fast, consume nearly all the herbaceous layer and rarely topkill the woody vegetation (Miranda et al. 1993). We showed in this study that *U. brizantha* doubled the height of flames; this may increase the mortality of shrubs and trees by topkill, favoring the dominance of the herbaceous layer, a typical feedback process of savanna environments (Kauffmann et al. 1994). In Cerrado, the presence of *U. brizantha* will probably lead to increasingly open physiognomies and to vegetation homogenization, and consequently, the diversity of physiognomies, habitats and species would decrease. The maintenance of the mosaic of phytophysiomies that compose the Cerrado (grasslands, savanna-like vegetations and forest, Coutinho 1978) is essential to maintain its huge biodiversity. However, more studies are needed, not only in different physiognomies of

Cerrado, but also evaluating shrub and tree survival after fires in the presence of *U. brizantha* in order to corroborate our hypothesis. In addition, higher flames can also increase the risk of fire nearby, since they could jump to neighboring areas more easily.

It is important to consider that the patterns we found and report here resulted from a moderate level of *U. brizantha* invasion. In our study area, the invasion of *U. brizantha* occurred in patches of different sizes interspersed in a matrix of native vegetation. In general, Cerrado nature reserves may have higher proportions of invasive grasses, such as *U. brizantha* and other *Urochloa* species, which create large and continuous invaded areas. Thus, in such areas, the effects of the invasive species on fire behavior might be intensified, leading to different results from the ones we found.

Fire behavior under different seasons

The fire season greatly influenced fire intensity, with more intense fires at the beginning of the rainy season (October fires). This can be mostly attributed to differences in fuel load. For the invaded sites, total fuel load was significantly higher in UO than in UJ, and dead biomass almost doubled between July and October, particularly for *U. brizantha*. Due to the lack of rain in the region from June to September, the aerial tissues of graminoids and forbs dry out (Filgueiras 1992) and, if fire does not occur, dead biomass accumulates from one season to the other, increasing the risk and intensity of fires in the following dry season. In Cerrado wet grasslands dead biomass can also accumulate during the rainy season and is attributed to low decomposition rates (Fidelis et al. 2013). The amount of live biomass of *U. brizantha* was also higher in UO than in UJ, while live biomass of native species hardly varied. These results indicate that *U. brizantha* resprouts and grows fast at the beginning of the rainy season, faster than native graminoids. This is an advantageous strategy in this ecosystem, since *U. brizantha* can rapidly use the nutrients available after the first spring rains and exclude other species that were not able to establish (by resprouting or germination) so quickly. However, more studies should be performed in order to quantify and test this hypothesis.

Implications for management

Fire properties such as intensity and rate of spread influence the post-fire distribution and abundance of plants in the community. In turn, the species composition is also an important factor affecting fire characteristics (Kauffmann *et al.* 1994). Invasive species alter the community species composition and may lead to changes in fire behavior that reinforces such changes in community composition. Thus, it is important to understand how these invasive grasses will change fire behavior in order to estimate fire risk and vegetation responses to fire.

Urochloa species are aggressive invasive species and a major concern regarding the conservation of Cerrado, being present in almost all protected areas of Cerrado (Pivello 2006). Our results showed that *U. brizantha* has a great potential to influence fire behavior – both at the community and the individual plant level - and modify the post-fire plant community. This potential seems to be modulated by factors such as the abundance of the invasive grass and the stage of degradation (amount of bare ground) of the area. Thus, the effects of *U. brizantha* we found in this study can be intensified in places where invasion is more severe. Moreover, this invasive species could increase the risk of fire and alter the frequency of fires in Cerrado at the end of dry season, due to the prolonged production of biomass, extending into the beginning of the dry season, and to the high amount of dead biomass accumulated during this period. Therefore, further studies considering the effects of different levels of *U. brizantha* infestation on fire regime (frequency, season, intensity) are needed to fully understand the overall role of this species in relation to fire.

Regardless of the presence of the invasive species, decisions about fire management in Cerrado areas must consider fire season as an important factor. The large amount of biomass (especially dead biomass) that is available at the beginning of the rainy season led to more intense and hotter fires, which are harder to control and potentially more damaging for Cerrado ecosystems.

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2

Disturbance as a factor in breaking dormancy and enhancing invasiveness of African grasses in a Neotropical Savanna

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ABSTRACT

The Cerrado is threatened by wildfires and invasive species. We aimed to evaluate in laboratory conditions whether temperature fluctuation at the soil surface, resulting from the absence of vegetation due to fire, can affect the germination of *Urochloa decumbens* and *U. brizantha*, two invasive African grasses. Seeds of both species were submitted to simulations: 1) temperature during fire at 1cm belowground (F); 2) temperature fluctuation at 1cm belowground without vegetation cover for a month (TF); 3) (F) + (TF); 4) control at 25°C. After treatments, seeds were put to germinate at 25°C for 40 days. We had four replicates per treatment and three temporal replicates. We compared germination percentage and the mean germination time among treatments using ANOVA. The treatments TF and F+TF had the highest germination values for both species. The results showed that fire *per se* could not stimulate seed germination, however, they suggest that a disturbance that produces a pattern of temperature fluctuation is able to break dormancy and enhance seed germination and, consequently, increase the invasiveness of the study species. Vegetation gaps resulting from disturbance may become new sites of invasion. This information is important for making management decisions regarding the control of these species.

Keywords: Cerrado, fire, germination percentage, invasive species, physiological dormancy, seed dormancy, temperature fluctuation, *Urochloa brizantha*, *Urochloa decumbens*

Introduction

One of the major challenges in invasion ecology is whether it is possible to identify a set of traits that enables a species to be invasive. Reproductive traits are important determinants of the success of invasive species (Rejmánek 1996; Pyšek *et al.* 2015). The most relevant plant traits related to invasiveness are those associated with seed germination and seed bank longevity. These traits are related to germination capability as well as to the extended germination over time. Together, they enable fast establishment and allow the species to wait for better environmental conditions (Pyšek and Richardson 2007).

Disturbance is well recognized as a triggering factor in a number of cases of biological invasion (Hobbs & Huenneke 1992). Species whose seeds can germinate in both intact and disturbed environments are more likely to spread and occupy new habitats than those with restricted germination requirements. Thus, the ability to germinate in a wide range of environmental conditions should also be mentioned as a trait associated with plant invasiveness (Luo & Cardina 2012).

Events of disturbance create open spaces within the vegetation and lead to alterations in the microclimate (mainly through soil temperature and moisture), and usually increase the availability of soil nutrients or change in the soil microbiota (Davis *et al.* 2000; Carvalho *et al.* 2010). Disturbance may also alter a number of species interactions, and thus favor invasibility in the plant community (Lonsdale 1999; Davis *et al.* 2000). In addition, the type and intensity of a disturbance are critical in determining the success of exotics and their impact on the invaded community (Lockwood *et al.* 2007).

Fire is a natural disturbance in many ecosystems and it has been an important selective force in the evolution of seeds of fire-prone plant species (Keeley & Fortheringham 2000; Bond & Keeley 2005). High temperatures can break the physical dormancy of seeds resulting in higher germination (Hanley & Lamont 2000; Auld & Denham 2006; Keeley *et al.* 2012). Still, the physiological dormancy of seeds may be broken by chemical compounds released in the smoke (Ooi *et al.* 2014). High temperatures have also been reported to break

physiological dormancy of grasses (Whiteman & Mendra 1982; Adkins *et al.* 2002) and other permeable seeds (Luo & Cardina 2012). On the other hand, some studies have shown decreased germination (Auld & O'Connel 1991; Ribeiro *et al.* 2013), or no relevant effect (e.g. Le Stradic *et al.* 2015; Fichino *et al.* 2016).

Besides fire direct effects on germination through high temperatures and smoke (Santana *et al.* 2012; Moreira & Pausas 2012), it also promotes indirect effects by changing the environmental conditions: gaps are open in the vegetation, that lead to higher solar radiation and light spectrum, as well as greater temperatures at the soil surface. In consequence, the range of daily soil temperatures is changed, as shown in different ecosystems (Coutinho 1990; Fidelis & Blanco 2014; Santana *et al.* 2012). The fluctuation of soil temperature can also break seed dormancy (Baeza & Roy 2008; Santana *et al.* 2012; Musso *et al.* 2015) and increase the germination of some “gap dependent” species (Ooi *et al.* 2014). Therefore, the establishment and persistence of invasive species in a community can be directed by fire through its influence on seed germination and seed bank longevity, and according to the burning regime and fire parameters.

In the Cerrado (Brazilian Tropical Savanna), fire has been acting as a selective force on plant communities since millions of years (Simon *et al.* 2009), and several species – especially in the herb layer – are believed to be fire-dependent (Coutinho 1982; 1990). Tolerance or enhanced germination at high temperatures have been reported for some Cerrado species (Coutinho 1982; Gottsberger & Silberbauer-Gottsberger 2006; Ribeiro & Borghetti 2014).

Therefore, the aim of this study was to evaluate in laboratory conditions whether the increase of soil temperature (direct effect of fire) and/or the daily fluctuation of soil temperature (indirect effect of fire) would affect the germination of two African grasses, *Urochloa brizantha* and *U. decumbens*, which show very aggressive invasive behavior in the Cerrado (Pivello *et al.* 1999 a; b). The results of this study will help us to understand the germination strategies of invasive grasses in disturbed environments, giving support to

management actions regarding the adequacy of prescribed fires in Cerrado invaded by these grasses.

Materials and Methods

Climate and fire in Cerrado

Cerrado has a tropical climate with wet summers and dry winters. The mean annual rainfall varies from 1200 to 1800 mm, and mean annual temperatures are 22-23°C (Coutinho 2002). The maximum temperatures do not vary much throughout the year and can reach more than 40°C, however, minimum temperatures may vary greatly and reach values close to zero in the coldest months (May-July), producing high temperature amplitudes in the coldest months (Coutinho 2002). The vegetation of Cerrado is characterized by a mosaic of different formations that include grasslands (*Campo limpo*), savanna-like vegetation (e.g. *Campo sujo*; Cerrado *sensu stricto*), and forest formations (*Cerradão*) (Coutinho 1982; Furley 1999). In a *Campo sujo* physiognomy in Central Brazil, Fidelis *et al.* (unpubl. res.) registered temperatures of 50°C at soil surface during the hottest hours of the day, which decreased to 12 - 17°C at night during the dry season (September).

Fires in the Cerrado are 'surface fires', which run fast over the soil and rapidly consume the herbaceous biomass, causing no intense heating belowground. In Cerrado physiognomies the temperatures registered during a fire at 1 cm aboveground ranged from 85°C to 840°C (for more details, see Miranda *et al.* 1993) but belowground they increased only a few degrees, being the maximum values registered by Miranda *et al.* (1993; 2002) between 29°C (3 cm) and 55°C (1 cm) (Miranda *et al.* 2002) (Miranda *et al.* 2002).

Study species

We used two African species that are considered some of the most common and severe invasive species in the Cerrado: *Urochloa decumbens* (Stapf) R.D.Webster (signal grass)

and *Urochloa brizantha* (Hochst. ex A. Rich.) R.D.Webster (palisade grass) (Pivello *et al.* 1999 a; b; Almeida-Neto *et al.* 2010; Lannes *et al.* 2012). They are C₄ perennial grasses widely used in tropical pastures due to their high palatability, productivity and resistance to intensive grazing and trampling (Loch 1977; Kissmann 1997). *Urochloa* species were introduced in Brazil in the mid-1950s as cattle fodder (Kissmann 1997), and readily adapted to the low-fertile and aluminum-rich soils of Cerrado (Rao *et al.* 1996). The seeds of *U. decumbens* disperse in December/January and of *U. brizantha* from April to June. However, some individuals of both species continue to disperse all over the year (personal observation). These invasive species have a strong competitive ability and they can rapidly dominate the Cerrado herbaceous community (Pivello *et al.* 1999 a; Almeida-Neto *et al.* 2010). In addition, the presence of *Urochloa* spp. in Cerrado can change fire behavior by affecting fire intensity, maximum temperature and flame height (Gorgone-Barbosa *et al.* 2015).

In the experiments of this study we used commercialized seeds of *Urochloa decumbens* and *Urochloa brizantha*, since they are widely used in planted pastures. The seeds were not submitted to any previous treatment, being stored at room temperatures of 25°C.

Temperature treatments and simulated curves

We submitted the seeds of both species to four different treatments to simulate both the effect of belowground temperatures during the passage of fire and the daily temperature fluctuations after the removal of vegetation by fire. The seeds were placed in Petri dishes in an incubator (Binder KB E5.1) where all temperature treatments occurred. We applied the following treatments: *Fire* (F) = simulation of fire temperatures at 1 cm belowground: the initial temperature was 25°C, rose up to 50°C in 20 minutes (based on previous data from Miranda *et al.* 1993) and then decreased continuously to 25°C in the following 30 minutes; *Temperature fluctuations* (TF)= simulation of the daily temperature fluctuation at 1 cm belowground without vegetation cover: seeds were subjected to alternating temperature (10°C to 40°C, that represent the mean range of soil temperatures after fire during the dry

season, measured in the field by A. Fidelis *et al.*, (unpubl. res.) during thirty days; *Fire + Temperature fluctuations* (F + TF) = combination of the two treatments, to simulate both the passage of fire and daily temperature fluctuations resulting from vegetation removal; and *Control* (C): seeds were stored at a constant temperature of 25°C until put to germinate. According to the manual for the analyses of seeds of the Brazilian Ministry of Agriculture (Brasil 2009), temperatures recommended for germinating *U. decumbens* and *U. brizantha* must be between 15 and 35°C. As the mean temperature in open cerrados is around 25°C (Coutinho 2002) we chose it as the control temperature in our experiments, although it has been reported in the literature that germination and dormancy breaking of *Urochloa* spp. was not influenced by light or temperature (Adkins *et al.* 2002).

Seed germination experiments

Before starting the experiments we tested the seed viability through the Tetrazolium test 1%. The mean viability was 81% for *U. decumbens* and 87% for *U. brizantha*.

Urochloa decumbens and *U. brizantha* seeds were divided into four samples for each treatment (30 seeds/replication/treatment) and temporal replication. We replicated the experiment three times (temporal replication) to avoid pseudoreplication, since we had only one incubator (30 seeds x 4 samples x 4 treatments x 3 temporal replications = 1440 seeds/species). The entire duration of the experiment was 90 days (30 days for each replicate). Although a single species viability analysis was performed, the time elapsed between replicates was not considered to have influenced the results of the experiment, as it was depicted from previous tests. Seeds were placed in Petri dishes, covered with one layer of filter paper, moistened with distilled water, and put in germination chambers at 25°C and dark conditions to simulate the buried seeds. The germination was recorded every other day, for 40 days. We considered germinated those seeds with 1 mm long radicle, and removed them from the Petri dishes after being counted. Seeds that did not germinate in 40 days were submitted to Tetrazolium test to check their viability.

Analyses

We calculated the percentage of germination and the mean germination time (MGT) in days, according to Ranal & Santana (2006).

To compare percentage of germination, MGT and viability between treatments, we used one-way analysis of variance (ANOVA, factor = treatment) applied to randomization tests (Euclidean distance between sampling units, 10000 interactions). All statistical analyses were performed using the software MULTIV (Pillar 2005).

Results

Seeds of both *U. decumbens* and *U. brizantha* showed percentage of germination which varied from 45% to 75%, independently of the treatment. Moreover, both species showed a similar pattern of response to the different treatments. A significant increase in the percentage of germination of both species was observed after TF and F+TF treatments when compared to the control (Fig.1).

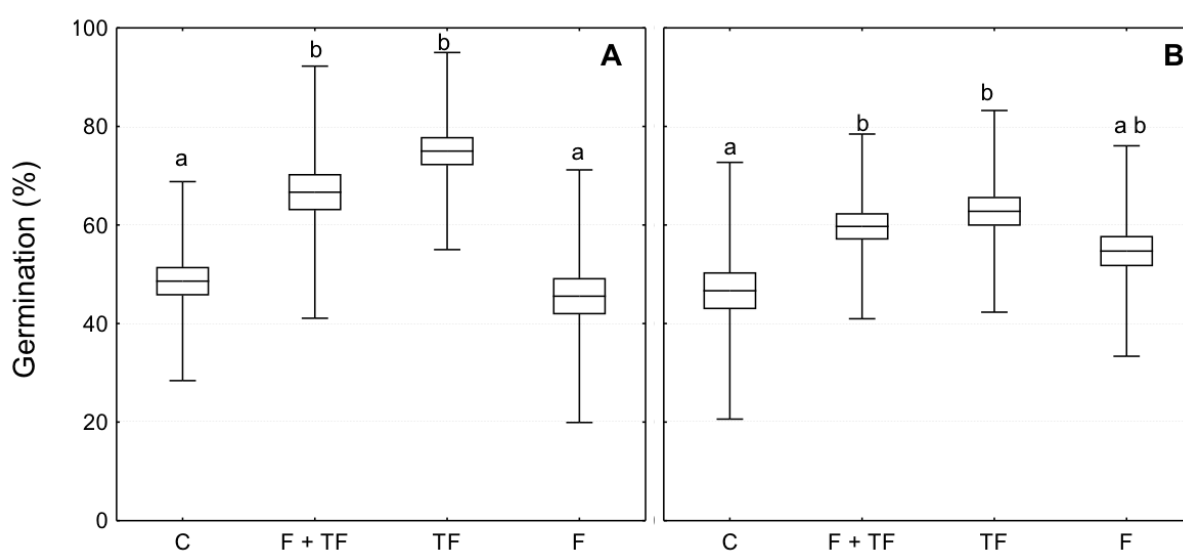


Figure 1. Percentage of germination (%) (mean, standard error and mean + 2* standard deviation) after the treatments: C = Control; F = fire; TF = temperature fluctuation; F+TF = fire followed by temperature fluctuation for (A) *Urochloa decumbens* and (B) *Urochloa brizantha*. Different letters represent significant differences, $P \leq 0.05$.

The percentages of germination of *U. decumbens* were $75 \pm 10\%$ and $66 \pm 12\%$ respectively for TF and F+TF, and not statistically different ($P = 0.09$), whereas the control (C, $48 \pm 10\%$) and F treatment ($45 \pm 12\%$) values were lower ($P < 0.0001$, for all comparisons) and statistically similar to each other ($P = 0.64$) (Fig. 1A). The seeds of *U. brizantha* also showed the highest percentages of germination after TF and F+TF treatments ($62 \pm 10\%$ and $59 \pm 9\%$, respectively) and not statistically different between each other ($P = 0.10$), but significantly differed from the control ($46 \pm 13\%$, $P = 0.004$ and $P = 0.02$, respectively, Fig. 1B) while F treatment resulted in percentage of germination ($54 \pm 10\%$) not statistically different from those of the other treatments ($P > 0.05$, Fig. 1B). Considering all the viable seeds (germinated + not germinated, but still viable), the TF and F+TF treatments proportionally increased the percentage of germination for both species, since viability between the treatments did not differ (Tab. 1, *U. decumbens*, $P = 0.31$ and *U. brizantha*, $P = 0.80$).

The mean germination time (MGT) did not differ between the treatments for both species (Fig. 2 - *U. decumbens*, $P = 0.83$ and *U. brizantha*, $P = 0.63$). The MGT of *U. decumbens* varied from 4.8 ± 1.9 days in C to 3.7 ± 1.1 days in F+TF.

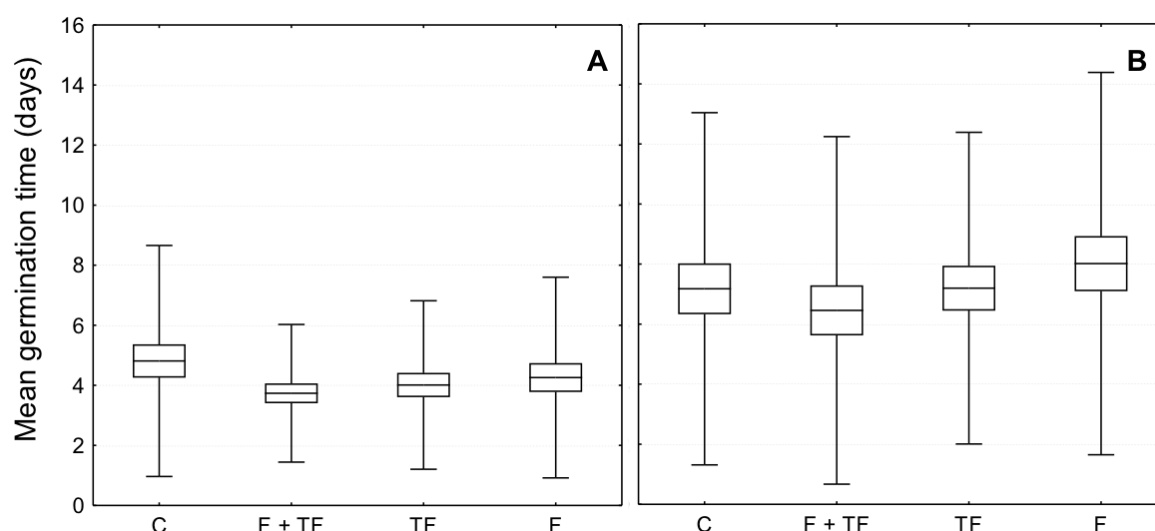


Figure 2. Mean germination time (MGT, days) (mean, standard error and mean + 2* standard deviation) in the treatments: C = Control; F = fire; TF = temperature fluctuation; F+TF = fire followed by temperature fluctuation for (A) *Urochloa decumbens* and (B) *Urochloa brizantha*.

Discussion

The ability to successfully germinate in a wide range of environments and to withstand disturbances are key reproductive traits that increase invasiveness of alien species (Pyšek & Richardson 2007; Luo & Cardina 2012). The two study species germinate more than 40%, which could be already advantageous to colonize and spread in invaded sites. Nevertheless, our results support the idea that part of both species' seeds (14-37%, considering the viable seeds of the treatments) are dormant, and such dormancy could be broken by daily fluctuation of temperature, generated for example, after disturbance events that remove the aboveground vegetation. Such temperature fluctuation enhanced germination, and consequently their invasiveness by increasing the probability of establishment of the species and therefore increasing the chance of a successful invasion.

Several grass species are known to have physiological dormancy (Baskin & Baskin 2004), as already reported for the genus *Urochloa* (Whiteman & Mendra 1982; Adkins *et al.* 2002). This strategy allows for long-term survival of populations by maintaining a persistent soil seed bank and delaying germination until the microclimatic conditions are optimal for seedling establishment (Baskin & Baskin 2004), being advantageous for the invasive species.

Temperature is the main environmental variable involved in the development, control, and the breaking of seed dormancy of species from different ecosystems (Moreira & Pausas 2012; Santana *et al.* 2012; Presotto *et al.* 2014). In our study we simulated the heating effect caused by Cerrado fires on seeds stored in the soil seed bank at 1 cm depth, and that mild temperature of 50°C (F treatment) affected neither *U. decumbens* nor *U. brizantha* germination. A similar result was found by Martins & Silva (2001), where temperatures of 40°C and 55°C were not effective on stimulating the germination of *U. brizantha*. Recent studies showed that fire did not enhance the germination of grasses and forbs of open physiognomies of Cerrado but seeds were resistant to high temperatures (Le Stradic *et al.*

2015; Fichino *et al.* 2016). Also, heat-shock of 100 °C did not affect germination percentages of invasive species in the Chilean matorral (Gómez-González *et al.* 2011).

In this study, we found an indirect effect of fire, since both TF and F+TF were able to break seed dormancy and enhance germination. Thus, fire did not affect directly the germination of *U. decumbens* and *U. brizantha* seeds from the soil seed bank, but the temperature fluctuation during one month was the effective triggering element. Musso *et al.* (2015) also found that *Aristida setifolia* and *Echinolaena inflexa*, two native Cerrado grasses, had their germination increased by temperature fluctuations (10-45°C). However, *Melinis minutiflora*, another Cerrado invasive grass, was not affected by temperature fluctuations (Musso *et al.* 2015).

Our results agree with the idea that disturbance events could facilitate the invasion process of *U. decumbens* and *U. brizantha* in Cerrado, not only by enhancing invasibility due to the increased resources and changes in competition, but also by enhancing the invasiveness of the species by breaking seed dormancy and facilitating germination. High percentage of germination directly affects the process of invasion by increasing recruitment and reproductive success of the invasive species, and as a consequence, its abundance, subsequent spread and colonization of new areas. Moreover, the pool of seeds in the soil may promote a considerable seed bank to maintain the invasive species in the community (as shown by Carmona 1995; Silva & Dias-Filho 2001). Therefore, the post-disturbance behavior of both *Urochloa* species can be pointed out as an advantage over natives and probably other Cerrado invasive species, such as *Melinis minutiflora*.

It is important to highlight that we used commercial seeds with a high viability, and it is expected that seeds collected in the field would have lower viability. But even so, a percentage of these seeds would be stimulated by post-fire conditions. In fact, a great number of *U. decumbens* seedling was observed after fire in an invaded *campo sujo* in São Paulo state (E. Gorgone-Barbosa, unpubl. res.).

Our study revealed an important mechanism of the invasion process: increased germination and seedling recruitment after disturbance, which explains in part the invasion success of these species in the burned Cerrado. Local managers should thus consider the gaps created in the vegetation by any kind of disturbance as a potential new site of invasion, if seeds of invasive species are available in the area.

Conclusion

Mild temperatures (around 50°C) caused by Cerrado fires in the soil seed bank at 1 cm depth do not affected the germination percentage of both *U. decumbens* and *U. brizantha*, aggressive invasives in that ecosystem. An important ecological mechanism that relates fire to the invasion of *Urochloa* species in disturbed cerrados is the post-fire fluctuation of daily temperatures at the soil level, which may facilitate their initial germination, enhance the percentage of germinated seeds, and probably increase the establishment success in recent burned areas.

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3

The role of heat shocks in the germination of native and invasive grasses in Cerrado

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Abstract

Several plants can persist in flammable ecosystems by germinating after disturbance. We evaluated the effect of high temperatures on seed germination of invasive grasses (*Melinis minutiflora*, *Urochloa decumbens* and *U. brizantha*) and native grasses (*Axonopus pressus*, *Aristida setifolia* and *Gymnopogon foliosus*) in Cerrado, to verify if seeds resist and/or be stimulated to germinate after fire. We performed heat shock treatments using temperatures of 60°C, 100°C and 200°C and a control. Five replicates of 20 seeds were used for each treatment, and seeds were put to germinate under optimal conditions. Differences between treatments were evaluated using one-way ANOVA. None of the species was stimulated by fire but, amongst the invasive grasses, *Melinis minutiflora* seeds resisted to high temperatures and germinated (>60%) in all treatments. *U. decumbens* seeds germinated between 25-42%, with a reduction in viability after 100°C. *U. brizantha* germination was severely affected by 200°C (Control= 58%; 200°C= 22%). The native species resisted to the exposure to high temperatures. *Axonopus pressus* showed low germination percentages in all treatments (<20%), whilst *Aristida setifolia* and *Gymnopogon foliosus* always germinated more than 60%. Our results also showed up that seeds of invasive grasses have lower germination times than the native ones, been a good strategy after the fire. Fire resistant seed is a key trait to persist after fire events in the Cerrado for both native and invasive grasses. However, the invasion process of these invasive grasses could be related to different strategies of post-disturbance regeneration.

Key words: African grasses; *Urochloa*; *Melinis*; fire; resistance; persistence

Introduction

Disturbance events are recognized as a key-cause of the invasive plant species establishment and spreading (Hobbs and Huenneke 1992). The disturbance affects the survival, competitive ability and interactions between species and changes the availability of resources for the surviving individuals (Huston 2004). The effects of disturbance on native and invasive species will depend of the type and intensity of the disturbance, as well as on particular adaptations of the species involved (Huston 2004; Lockwood and Hoopes 2007). A competitive advantage resulting in a successful invasion process occurs when invasive species are more resistant than natives to altered conditions and have the capacity to survive and reproduce in a new disturbed environment (Facon et al. 2006).

Fire is an important ecological factor in fire-prone ecosystems, such as savannas, and has been an important driver in the reproductive evolution of plant species (Keeley et al. 2011). The complex effects of fire on plant reproduction can be related to the enhancement of flowering, as well as on stimulating seed germination and seedling recruitment. On the other hand, it can also decrease reproduction in sensitive species (Bond and van Wilgen 1996). Common issues explored in the fire ecology research are the effects of high temperatures and smoke on the germination of seeds, and the recruitment of different species in different fire-prone ecosystems all over the world (Tavşanoğlu et al. 2015). Experiments using heat shocks, for example, are expected to break dormancy impermeable seeds from fire-prone ecosystems (Moreira et al. 2010). However, if seeds survive the exposure to high temperatures, it could be related to the resistance and survival of propagules post-disturbance (Paula and Pausas 2008; Jaureguiberry and Díaz 2015), being thus an important trait in fire-prone ecosystems (Fichino et al. 2016).

The ability of native and exotic species to deal with such factors and conditions (e.g. persistence and survival after fire events) in a given community can be a key factor in determining the beginning of a biological invasion after fire events in fire-prone systems (Adkins and Peters 2001; Figueroa et al. 2009; Figueroa and Cavieres 2012; Arán et al.

2013). However, the relationship involving fire, invasive and native species still remains elusive (Gómez-González et al. 2011). D'Antonio et al. (2001) highlighted the importance of understanding the relative role of native and invasive species facing fire - such as the supply and survival of propagules after fire, and how this relates to invasion patterns, for effective management and conservation of native communities.

In Cerrado, fire has been acting as a selective force on plant communities since millions of years (Simon et al. 2009). Fire can affect the persistence of species and interfere positively or negatively in the invasion processes (Gómez-González et al. 2011; Musso et al. 2015), which is usually driven by African grasses (Pivello et al. 1999a; Pivello et al. 1999b). Some studies have shown that seeds of native species from Cerrado can resist high temperatures (e.g. Vieira et al. 2007; Fichino et al. 2012; Le Stradic et al. 2015; Fichino et al. 2016) and that indirect effects of fire (e.g. daily temperature fluctuation) may increase the germination of invasive species (Musso et al. 2015; Gorgone-barbosa et al. 2016). Nonetheless, the germination and resistance of grass propagules in relation to fire remains unclear in open savannas worldwide. Thus, species from open savannas in Cerrado could be used as models to test ecological patterns comparing invasive and native grasses after fire events, helping thus to elucidate the first stage of biological invasion process in fire-prone systems.

Therefore, we aimed to evaluate the effects of high temperatures, using heat shocks experiments on the seeds of three common invasive grass species in the Cerrado (*Melinis minutiflora*, *Urochloa decumbens* and *U. brizantha*) and three native grasses (*Axonopus pressus*, *Aristida setifolia* and *Gymnopogon foliosus*), identifying if seeds of both invasive and natives are fire resistant and if there are any mechanisms related to increase of germination that could improve a post-fire competitive advantage of the invasive species over the native ones. If a higher percentage of seeds of the invasive species could resist to the exposure to high temperatures (>100°C), it could enable them to germinate and establishing more rapidly their populations in a recently disturbed environment, facilitating thus, invasion. Understanding the relationship of fire and germination of invasive and native

grass species would help to clarify the first stages of invasion process and thus, help to plan management plans to control invasion and manage the native vegetation of Cerrado.

Material and Methods

Species selection and seed collection

We tested three of the most common and aggressive invasive grass species in the Cerrado open savannas (Pivello et al. 1999 a,b; Gorgone-Barbosa et al. unpublished data: *Melinis minutiflora*, *Urochloa decumbens* and *Urochloa brizantha*. They are C₄ African grasses, introduced in Brazil for cattle raising that have spread from the pastures and became invasive, threatening especially the herbaceous layer species of Cerrado (Pivello et al. 1999a; Pivello et al. 1999b; Gorgone-Barbosa et al. unpublished data). They can also change fire behavior (i.e. flame height and temperature) and damage the native community (Mistry and Berardi 2005; Gorgone-Barbosa et al. 2015). Since the three invasive species are widely commercialized (for pasture), we used commercial seeds, obtained from certified producers.

The three native species – *Axonopus pressus*, *Aristida setifolia* and *Gymnopogon foliosus* – are common and abundant in open Cerrado physiognomies, where they co-occur with the invasive species. They were also selected due to the availability of their seeds for the experiments.

The seeds of native species were collected in areas of *campo sujo*, which is an open savanna, dominated by grasses and forbs with scattered shrubs and dwarf trees in Southeast Brazil (Itirapina Experimental Station, 22°15'S and 47°49'W) and Northern Brazil (Jalapão State Park, 10°22'S and 46°40'W). Seeds were collected from at least 20 adults for each species and only intact seeds were selected for the experiments.

Germination experiments

To verify the germination responses of the study species (invasive and natives) to high temperatures, we submitted their seeds to dry heat shocks at 60°C, 100°C and 200°C for one minute in a pre-heated electric oven. We chose these temperatures because fires in Cerrado are fast and rapidly consume the herbaceous biomass, causing no intense heating belowground (Miranda et al. 1993; Miranda et al. 2002).

We used five replicates of 20 seeds/replicate/treatment, placing them separately into the oven to avoid pseudo-replication (Morrison and Morris 2000). For the control, we did not expose seeds to heat shocks. After the treatments, seeds were placed in Petri dishes (60mm diameter), over moistened filter paper (distilled water), and put to germinate in germination chambers at a constant temperature of 27°C and light cycle of 12h.

The observations were made every three times a week for 30 days. We counted and removed the germinated seeds, those which had the primary root protrusion (Bewley et al. 2013). By the end of germination experiments, we tested the non-germinated seeds for viability, using a tetrazolium solution at 1% (pH 7).

Data analysis

We calculated the percentage of germination and the mean germination time (MGT), according to Rana and Santana (2006). We performed one-way analysis of variance with permutation tests (10,000 iterations, Euclidean distance between sampling units) to verify the effect of treatments on germination percentage and MGT, and also to verify differences in the MGT between the species. All statistical analyses were performed using the software MULTIV (Pillar 2005).

Results

High temperatures had no effect on the germination percentage and MGT of both the invasive and the native species (Table 1, Figure 1), except for *Urochloa brizantha*, which had a decrease in germination at 200°C compared to the control ($P = 0.0005$, Figure 1).

The invasive *Melinis minutiflora* showed high germination percentages (>60%) regardless of the treatment ($P= 0.44$, Figure 1a). Moreover, the exposure to high temperatures did not affect their viability ($P= 0.52$, Figure 1a). MGT was 5.1 ± 1 days for all treatments ($P= 0.46$, Table 1).

Table 1. Mean germination time (MGT, days, mean $\pm$ standard deviation) of invasive and native species submitted to dry heat shock treatments at 60°C, 100°C and 200°C for one minute, and the control (not exposed to high temperatures).

Species	Control	60°C	100°C	200°C
Invasive				
<i>Melinis minutiflora</i>	5.4 $\pm$ 1.0	4.7 $\pm$ 0.5	4.9 $\pm$ 0.9	5.4 $\pm$ 1.3
<i>Urochloa decumbens</i>	4.3 $\pm$ 0.8	3.5 $\pm$ 0.3	4.1 $\pm$ 0.8	4.3 $\pm$ 0.3
<i>Urochloa brizantha</i>	4.5 $\pm$ 0.8	4.7 $\pm$ 0.9	4.9 $\pm$ 1.3	4.9 $\pm$ 0.6
Native				
<i>Aristida setifolia</i>	9.0 $\pm$ 1.2	8.3 $\pm$ 0.6	7.5 $\pm$ 2.7	6.3 $\pm$ 0.9
<i>Axonopus pressus</i>	15.4 $\pm$ 6.4	12.9 $\pm$ 7.2	15.2 $\pm$ 5.8	13.7 $\pm$ 3.4
<i>Gymnopogon foliosus</i>	2.3 $\pm$ 0.1	2.3 $\pm$ 0.2	2.4 $\pm$ 0.2	2.9 $\pm$ 0.6

For *Urochloa decumbens*, the germination percentage tended to be lower at 100°C (25 $\pm$ 9%) and 200°C (25 $\pm$ 12%) in comparison to the control (42 $\pm$ 13%, $P= 0.12$, Figure 1b). Nonetheless, the viability of *U. decumbens* seeds was significantly lower at 100°C (32 $\pm$ 13%) and 200°C (35 $\pm$ 12%), indicating a mortality after these treatments (control= 59%, $P= 0.05$, Figure 1b). MGT, (4 $\pm$ 0.5 days for all treatments) was not affected by temperature ($P= 0.11$, Table 1). Seeds of *Urochloa brizantha* showed germination percentages higher than 50% and resisted to temperatures up to 100°C. However, we observed a significant decrease in germination at 200°C ($P= 0.0005$, Figure 1c). The viability of *U. brizantha* seeds also decreased when submitted to 200°C ($P< 0.0001$, Figure 1c). Despite the significant decrease in germination percentage, 20% of the tested seeds still resisted to 200°C and were able to germinate. MGT was the same for all treatments (4.75 $\pm$ 0.7 days, $P= 0.24$, Table 1).

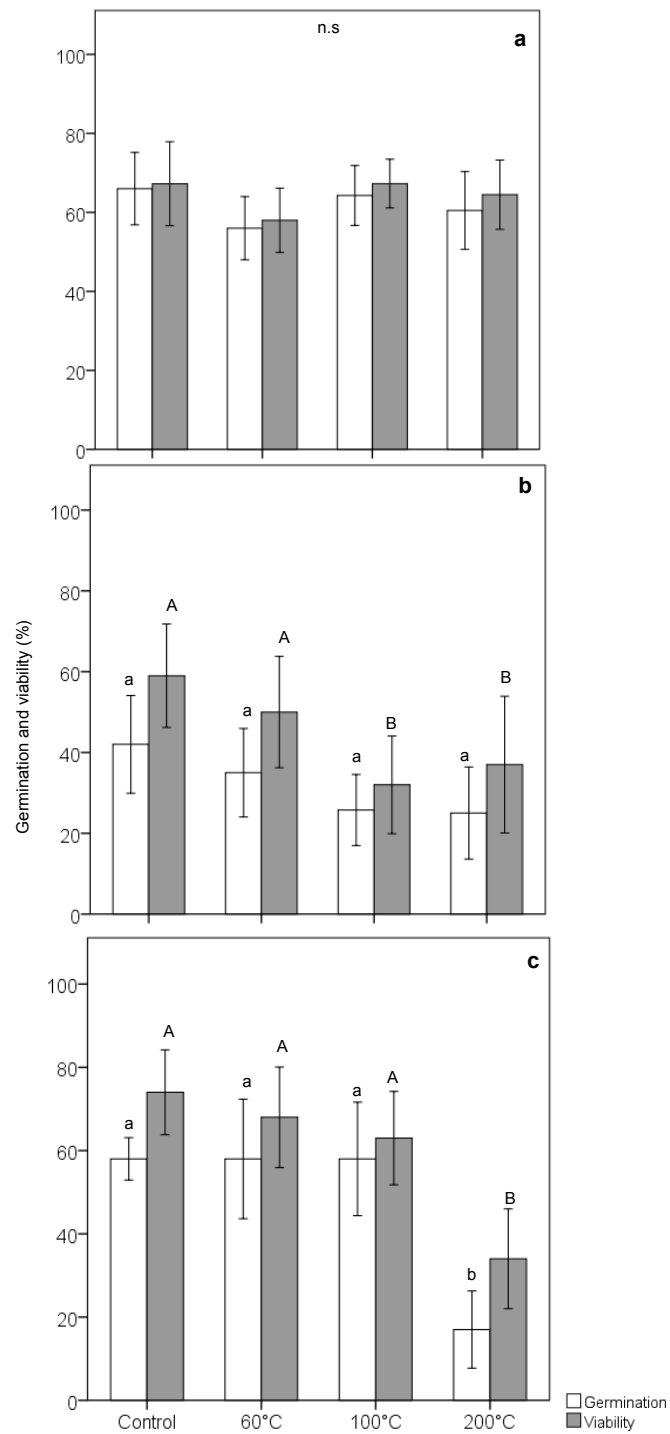


Figure 1. Germination and viability (%; mean $\pm$ standard error) of invasive species (a) *Melinis minutiflora*, (b) *Urochloa decumbens* and (c) *Urochloa brizantha* submitted to dry heat shock treatments at 60°C, 100°C and 200°C for one minute, and the control (not exposed to high temperatures). Different letters mean significant differences among treatments in the percentage of germination (small letters) and viability (capital letters) ($P \leq 0.05$).

Seeds of the native grass *Aristida setifolia* germinated from $75\pm 10\%$ (control) to $63\pm 20\%$ (100°C) and were not affected by the heat treatments ($P= 0.30$, Figure 2a). Viability was higher than 70% for all treatments ($P= 0.40$, Figure 2a).

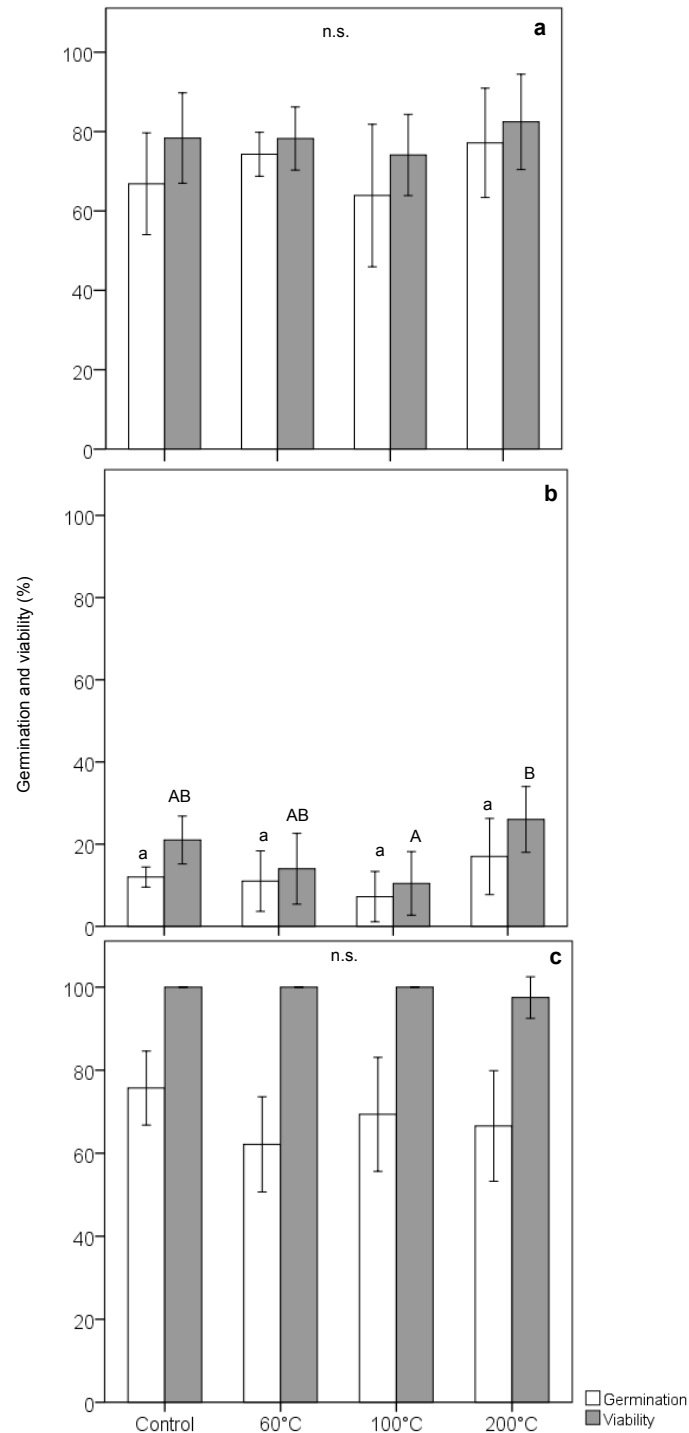


Figure 2. Germination and viability (%; mean $\pm$ standard error) of the native species (a) *Aristida setifolia*, (b) *Axonopus pressus* and (c) *Gymnopogon foliosus* submitted to dry heat shock treatments at 60°C , 100°C and 200°C for one minute, and the control (not exposed to

high temperatures). Different letters mean significant differences among treatments in the percentage of germination (small letters) and viability (capital letters) ($P \leq 0.05$).

MGT showed a tendency to decrease with the heat shock treatments, from approximately 9 days in the control and 6 days when submitted 200°C (Table 1), but no statistical difference was found ($P = 0.98$). Low germination percentages (<20%) and high MGT (14.3 days) were observed for the native species *Axonopus pressus* in all treatments ($P = 0.22$ and $P = 0.54$ respectively, Figure 2b and Table 1). However, its seeds viability was lower at 100°C ($10 \pm 5\%$) compared to 200°C ($26 \pm 8\%$, $P = 0.045$; Figure 2b). Seeds of *Gymnopogon foliosus* were not affected by the exposure to high temperatures, showing high germination percentages at control ($75 \pm 9\%$), 100°C ($64 \pm 20\%$) and 200°C ($77 \pm 15\%$, $P = 0.66$, Figure 2c). Its seeds also showed a fast germination (2.4 ± 0.3 days, $P = 0.48$, Table 1), as well as a high viability ($P = 0.98$, Figure 1c), independently of treatment.

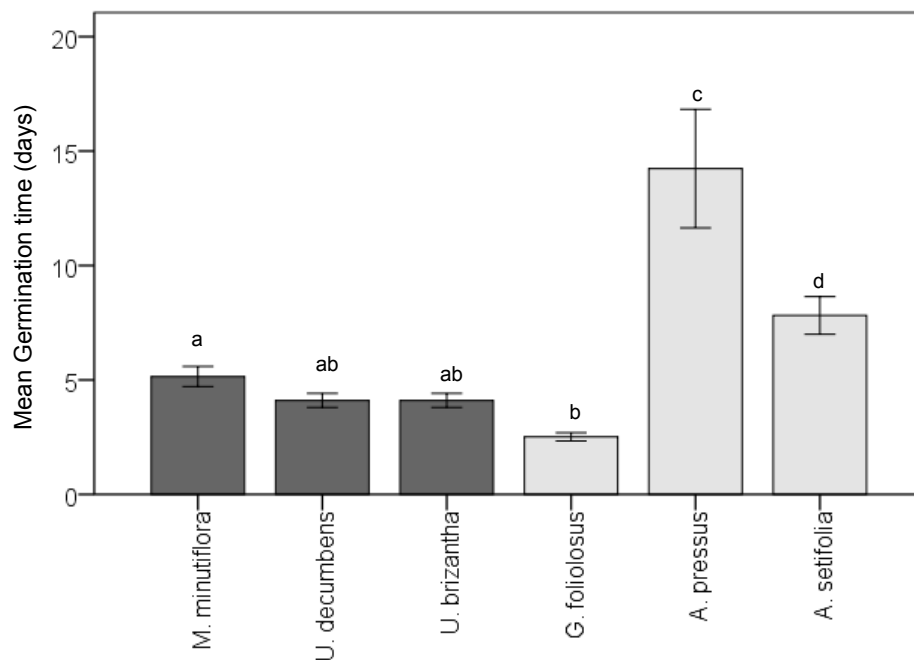


Figure 3. Mean germination time (days, mean $\pm$ standard error) of invasive (dark gray) and native species (light gray) independently of the treatment. Different letters mean significant differences between species ($P \leq 0.05$).

When we compared the MGT between the six study species independently of the treatment, we observed that seeds of invasive species germinated faster than the native ones ($P < 0.0001$ for all comparisons), except for *G. foliosus*, which is a native one and presented the lowest MGT value (2.5 days) ($P < 0.001$, Figure 3).

Discussion

Fire may be one of the driving factors of the Cerrado vegetation evolution (Coutinho 1978; Coutinho 1990; Simon et al. 2009), playing also an important role as an evolutionary force in the African savannas (Bond and Keeley 2005). Moreover, as the African grasses are the major invasive species in the Cerrado (Pivello et al. 1999a; Pivello et al. 1999b), and since fire can be an important factor for the establishment and spread of exotic species (D'Antonio et al. 2001; Jauni et al. 2015), it is fundamental to understand and to compare fire effects on both the African and the Cerrado species, in the search for managing such invasions.

The exposure to high temperatures (heat shocks) is recognized as important factor enhancing the germination of dormant seeds (both invasive and native) (Adkins and Peter 2001; Figueroa et al. 2009; Aran et al. 2013). However, the resistance of seeds to high temperatures can also be used as an important trait in fire-prone ecosystems (e.g. Ribeiro and Borghetti 2014; Jaureguiberry and Díaz 2015; Fichino et al. 2016), helping us thus to understand invasion process after fire events in these systems. Fire-resistance traits would be advantageous in frequently burned areas such as the Cerrado (Fichino et al. 2016; Zupo et al. unpublished data) and here we highlight that those heat shock treatments can also be used to determine the resistance of seed species to fire, as a trait.

Heat shocks did not stimulate germination of neither invasive nor native specie. However, our study showed that a considerable percentage of seeds of the native and invasive species are resistant to the exposure high temperatures, being able to survive the exposure to temperatures $>100^{\circ}\text{C}$. Therefore, these species can survive fire events and persist in the soil. Seeds from other Cerrado native species, including trees (Ribeiro et al. 2013), shrubs,

forbs and grasses, have been reported as being heat tolerant (Schmidt *et al.* 2005; Fichino *et al.* 2012, Fichino *et al.* 2016). In the case of the African grasses, the most aggressive invasive species in the Cerrado – *Urochloa decumbens* and *Melinis minutiflora* (Pivello *et al.* 1999a) – are able to maintain their germination percentages and MGT when exposed to 200°C, and *U. brizantha* to 100°C (there was a significant decrease in the germination when submitted to 200°C). However, only seeds of *Melinis minutiflora* showed to be fire-resistant, maintaining the same germination and viability of seeds when exposed to temperatures >100°C. Both *Urochloa* species decreased in viability when exposed to 100°C (*U. decumbens*) and 200°C (*U. brizantha*), and thus, approximately 20% of their viable seeds might die after fire events.

According to Ramula *et al.* (2015), in the early stages of invasion, the availability of propagules may be more important than the presence of suitable microsites, being thus, propagule persistence and subsequent germination advantageous in colonizing new areas. Fire in sites invaded by these *Urochloa* species might hinder seedling recruitment and persistence of invasive species populations may depend mainly on resprouting. However, Cerrado's fire temperatures below the soil surface it is usually not higher than 55°C (-1-2 cm; Miranda *et al.* 1993), thus, once the seeds of *Urochloa* species are in the seed soil bank, they might as well to survive.

Germination speed is an important trait related to invasiveness (Pyšek and Richardson 2007), and thus, the time needed for seed germination becomes critical for post-fire recolonization. The invasive species we tested showed lower MGT when compared to the natives – except for the annual *G. foliosus* – that allows them a quick establishment and as a consequence, a higher competitiveness over the natives, facilitating thus, the spread of invasion (Lake and Leishman 2004; Tierney and Cushman 2006) and potentially hampering the subsequent recolonization by the native species (Jauni *et al.* 2015).

The removal of aboveground vegetation changes the amplitude of daily temperatures (Fidelis and Blanco 2014), and that temperature fluctuation during the day can stimulate the

germination of some species (e.g. Baeza and Roy 2008; Santana et al. 2012; Gorgone-barbosa et al. 2016). Fires in Cerrado occur mainly in the mid-late dry season (Miranda et al. 2009), period in which there is a severe water deficit, and that could explain why the species do not show any stimulus from fire cues (see Fichino et al. 2016). It would be more important for seeds to survive heat shocks and remain in the soil for successfully colonizing vegetation gaps by quickly germinating at the beginning of the rainy season. Furthermore, seeds that persist during the first months after fire are exposed to temperature fluctuations from 15 to 50°C at the soil surface (Fidelis et al., unpublished data), which can enhance seed germinability and break physiological dormancy of both invasive and native species (Musso et al. 2015; Gorgone-Barbosa et al. 2016). Therefore, surviving the passage of fire is very important, even if a low percentage of seeds survive, giving the species an advantage in post-fire environments, especially if they can germinate fast, as showed for invasive species in our study.

It is well recognized that disturbance – such as fire – facilitates invasions (Hobbs and Huenneke 1992; Jauni et al 2015), however, the responses of invasive species to disturbances may vary with environmental conditions (Hobbs and Huenneke 1992; Lake and Leishman 2004; Price et al. 2015). Our results showed that fire would not directly promote the invasion process by increasing germination of invasive species, differently from other studies (Arán et al. 2013; Cóbar-Carranza et al. 2015). The invasive species we studied have different main strategies post-fire. *M. minutiflora*, for example, shows a lower resprouting ability after fire (Damasceno et. al. unpublished data), but its high percentage of germination and survival, coupled with a low MGT, warrant the species to persist and recolonize open spaces in recently burned environments. The *Urochloa* species, despite the decrease in viability after heat shocks, have also low MGT's which allow the remaining seeds to rapid germinate. Additionally, both *Urochloa* species have a high resprouting capacity after fire (Gorgone-Barbosa et al. unpublished data), which shows up to be their principal strategy for regeneration, benefiting their persistence.

In conclusion, the native species can be resistant to Cerrado fires, as well as the invasive *Melinis minutiflora*, while the seeds of *Urochloa* species are more sensitive to fire, but a small percentage of the seeds population could resist, and persist in the soil, especially if they are in the seed soil bank. However, invasive species showed the ability to germinate faster than the natives, which could be a relevant factor to explain the ongoing process of persistence and invasion of these grasses in the Cerrado and could be an important advantage for their establishment and spread after fire. Such information is fundamental to predict the community dynamics in the invaded Cerrado, in order to control the invasive species and maintain the natural biodiversity.

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4

Can fire be used as a management tool to control invasive grasses in Cerrado? The effects of fire regime on invaded and non-invaded plant communities

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Abstract

Fire regimes can be modified by the presence of invasive species and in the other hand, changes in fire regime can affect positively or negatively the invasive species in a new environment. In the Cerrado, fire is an important ecological factor and therefore, we used prescribed burns, applying different fire regimes to understand how fire affects the African invasive, *Urochla brizantha*, and the native community, in order to evaluate if fire could be used to manage this species. From 2012 to 2014 we applied the following fire treatments: Annual, Biennial and Control (no fire), in two seasons Mid-Dry (MD) and Late-Dry (LD, 4 replicates x treatments, total of 24 plots). We estimated plant cover in 10 subplots (1 × 1 m) and collected six subplots (0.5 × 0.5 m) of biomass, which we separated into the following categories: dead *U. brizantha*, dead native species, *U. brizantha*, graminoids, forbs, and shrubs. We performed analyzes comparing the fire frequencies in each season. We used linear mixed effect models to analyze the effect of the treatment in biomass/cover and permutational multivariate metrics to verify community composition structure in each treatment. Independently of the frequency and season, fire led to the decrease of dead biomass of *U. brizantha*. Moreover, the major difference between burned and Control communities was the amount of dead biomass. Biennial Late-Dry fires tended to reduced the cover of live *U. brizantha*, but not the biomass, whilst, Biennial Mid-Dry fires showed a positive feedback with *U. brizantha*. The non-invaded communities were not affected by any treatment, except for the cover of graminoids, that were lower in all burn treatments when compared to the Control. Fire alone, probably, will not Control the invasive species. However, Late-Dry fires could help in reducing dead biomass, avoiding thus, wildfires and enhancing some native groups. However, it is important to highlight that the Late-Dry fires are also more intense and more dangerous, therefore it application should be cautious. Our study brings new insights and knowledge to understand and predict the assembly of vegetation communities (invaded and non-invaded) and their post-fire regeneration to guide management strategies for conservation of the open areas in Cerrado.

Key words: Fire season; Fire frequency; biological invasion; *Urochloa* sp; *Brachiaria*; Neotropical Savanna; post-fire regeneration; management

Introduction

Invasive plants play an important role in changing native plant communities, being one of the major threats to biodiversity across ecosystems (Pyšek *et al.* 2012). The negative impacts of invasive species can range from different levels of organization: from individuals to ecosystems (Parker *et al.* 1999). For example, invasive plants can directly alter community structure and composition by reducing the abundance and richness of native species (Hejda, Pyšek & Jarosik 2009; Vilà *et al.* 2011), which may affect ecosystem properties (such as nutrient pools), and processes (e.g. nutrient cycling and fire regimes) (D'Antonio & Vitousek 1992; Ehrenfeld 2010).

Fire regimes can be modified by the presence of invasive species through changes in the fuel continuity, properties and/or amount, which consequently change fire intensity and/or frequency (Brooks *et al.* 2004). These changes could result in a positive fire-invasion feedback (D'Antonio & Vitousek 1992; Brooks *et al.* 2004; Didham *et al.* 2005). For example, in temperate forest, the invasive grass, *Microstegium vimineum* interacted with fire by increasing its intensity and reducing the establishment of native trees, promoting thus its own persistence (Flory *et al.* 2015). Many invasive grasses changed the fire regime and, consequently, the natural equilibrium between species in the system, which in turn altered the community structure and light availability. As a result, the new conditions were favorable to the maintenance and spread of the invasive species (D'Antonio & Vitousek 1992; Vilà *et al.* 2001; Rossiter *et al.* 2003; Rossiter-Rachor *et al.* 2009, Flory *et al.* 2015). This positive feedback between fire and invasive species has been registered in several other ecosystems such as woodland forests, savannas, deserts and Mediterranean shrublands (Masocha *et al.* 2011; McDonald & McPherson 2011; Keeley & Brennan 2012; Wagner & Fraterrigo 2015). There are also evidences of negative and neutral feedbacks between invasive plants and fire (Brooks *et al.* 2004; Havill, Schwinning & Lyons 2015) which will depend on the characteristics of both invasive and native species and their interactions, as well on the properties of the invaded ecosystems.

Since fire is a complex factor, different fire regimes will result in different post-fire responses of invasive and native species and communities' recovery. Therefore, the manipulation of fire regime can be used as a management tool to control invasive species by reducing their dominance and/or promoting better conditions for the native species, especially in fire-prone environments (D'Antonio 2000). For example, hot fires and optimal time of burning (according to plant phenology) were effective in reducing the number of tillers of the C₄ invasive perennial grass *Bothriochloa ischaemum*, but it did not affect the native grass in a North-American prairie (Havill, Schwinning & Lyons 2015). Fire may also control invasive grasses by killing their seeds, if they cannot resist to high temperature, or by killing the plant before it reproduces (DiTomaso, Kyser & Hastings 1999). Prescribed burns are often used to manage the vegetation focusing on the conservation of species and physiognomies, as well as for fuel reduction to minimize wildfire risk, and/or to control of exotics (Whelan 1995). However, the effects of prescribed burns on invasive species and on the assemblage of native plant communities varies from one vegetation type to the other (Price *et al.* 2015), making difficult to predict outcomes, since there are several complex elements that will directly or indirectly influence fire, such as the heterogeneous fuel structure and the weather after fire when the species are regenerating or recruiting in burned sites (Pyke, Brooks & D'Antonio 2010).

The Cerrado is a hotspot of biodiversity (Myers *et al.* 2000) and it has been threatened by habitat loss, invasion of African grasses and wildfires (Klink & Machado 2005; Durigan, Siqueira & Franco 2007). There are several African C₄ perennial grasses – such as *Melinis minutiflora* P. Beauv., *Hyparrhenia rufa* (Nees) Stapf, *Panicum maximum* Jacq and *Urochloa* spp. – that were introduced in the Cerrado and became invasive by impacting the native communities (Pivello, Carvalho & Lopes 1999; Pivello, Shida & Meirelles 1999). *Urochloa* species have been recognized as one of the most severe invasive species in the Cerrado, especially by reducing the abundance of native species (Pivello, Shida & Meirelles 1999;

Almeida-Neto *et al.* 2010; Zenni & Ziller 2011; Lannes *et al.* 2012; Gorgone-Barbosa *et al.* unpublished data).

Urochloa brizantha (Hochst. ex A. Rich.) R.D.Webster is an aggressive competitor that reduces the abundance of native species in invaded sites, especially graminoids, (Gorgone-Barbosa *et al.* unpublished data). Besides, once the shoots of *U. brizantha* are incorporated in the soil, they release allelopathic compounds that may inhibit the growth of several species (Kobayashi & Kato-Noguchi 2015). This invasive grass can also change fire behavior, by increasing fire intensity at the end of the dry season and flame height (Gorgone-Barbosa *et al.* 2015). Further, a percentage of seeds population of *Urochloa brizantha* could resist high temperatures (Gorgone-Barbosa *et al.* unpublished data) and their germination can be indirectly stimulated by fire, because in post-fire environments, gaps will experience temperature fluctuations that can be responsible for breaking the dormancy of these seeds (Gorgone-barbosa *et al.* 2016). Following Gaertner *et al.* (2014), *Urochloa brizantha* could be considered as a high-impact invader (intensively transform ecosystems), since this species does not only reduce the abundance of native species but also change the natural fire behavior (Gorgone-Barbosa *et al.* 2015). Because of that, it is essential to understand how this species respond to fire in order to identify the best management strategies to control it without negatively affecting the native plant community.

Fire is an important ecological and evolutionary factor in Cerrado for millions of years (Simon *et al.* 2009). Also, fire is a fundamental factor for the maintenance of the structure, diversity and functioning of Cerrado ecosystems (Durigan & Ratter 2016). Therefore, we used prescribed burns, applying different fire regimes (Mid-Dry and Late-Dry season, and Annual and Biennial) to understand how fire affects non-invaded and invaded communities by *Urochla brizantha*. We aimed to answer the following questions: (1) How does seasonality (Mid-Dry vs. Late-Dry season), affect the invasive species cover and biomass? (2) How do fire frequencies (no fire, Annual and Biennial fires) affect the invasive species cover and biomass in the within seasons (Mid-Dry vs. Late-Dry) and (3) Do fire regimes affect *U.*

brizantha reproductive traits? (4) How do fire frequencies (no fire, Annual and Biennial fires) affect plant functional groups (cover and biomass) and dead biomass of native species in the invaded and native areas in different seasons (Mid-Dry and Late-Dry)? (5) How do fire frequencies affect the whole plant community biomass composition, similarity and composition turnover in invaded and non-invaded communities in the different seasons? And finally, (6) Can we use fire as a management tool to control the invasive species *Urochloa brizantha* without affecting the native community?

We would expect to find a great impact of seasonality in the invasive species cover and biomass, especially in the dead biomass, that would be increased in the late-dry season. Also, *U. brizantha* would be negatively affected by annual fires in the Late-Dry season, by reducing its cover, biomass and consequently, the flowering culms and seeds, since this is the season that the invasive species is starting to allocate resources for reproduction. Annual fires, especially in Mid-Dry season would affect negatively the native community when compared to Biennial fires because plants would not have enough time to regenerate due to rapid return of Annual fire and they would experience a longer period without rain. Besides, different fire frequencies would influence the non-invaded community structure and composition similarity and turnover, by reducing the senescent biomass.

Methods

Study area

The study was conducted at the Serra do Tombador Nature Preserve (RNST) in Goiás State, central Brazil (47°45 ' ; 47°51' W and 13°35 ' ; 13°38' S; 560-at 1118 m a.s.l.). The RNST comprises ca 9000 ha, where we can find different Cerrado physiognomies. The experiments were conducted in a *campo sujo* physiognomy, characterized by a species-rich herbaceous layer with scattered shrubs and small trees (Coutinho 1990). The regional climate is tropical with a marked seasonality, with wet summers and dry winters, and

average annual rainfall between 1300 and 1500 mm (AER 2009) and mean annual temperatures are 22-26°C (Rissi unpublished data).

Portions of the RNST were used for cattle ranching in the past, before it became a nature preserve, and because of that, African invasive grasses such as *Urochloa* spp. and *Melinis minutiflora* dominate disturbed and degraded areas in the preserve, occurring in patches. However, the time of introduction of such grasses is unknown. Fire (both natural and anthropogenic) is recurrent in RNST, forming a mosaic with patches with different fire histories. However, the largest fire events occur in a 3-year cycle (Daldegan *et al.* 2014), mostly during the dry season (June to October). Our study site has not been burned or grazed since 2006.

Experimental design

The experiments were carried out in an invaded *campo sujo* where the invasive *U. brizantha* occurs in patches. We established experimental plots (20 x 15 m) in different patches with all plots being 30-70% covered by *U. brizantha* at the beginning of the experiments. From 2012 to 2014 we applied three fire frequency treatments: 1 – Annual (2012, 2013, 2014), 2 – Biennial (2012, 2014) and 3 - Control (no fire since 2006), in two seasons: Mid-Dry (MD, July) and Late-Dry (LD, October). We had four replicates per treatment (4 replicates x 5 treatments, total of 20 plots). All the experimental fires were head-fires (wind direction), set at mornings, with the assistance of the Preserve fire brigade. In order to maintain independence of the sampling units, the prescribed burns were conducted individually by plot, and the fire parameters (flame height, intensity and temperature) were measured (for more detail about the fire experiments, see Gorgone-Barbosa *et al.* 2015).

Vegetation sampling cover and biomass

To estimate plant cover we established 10 subplots (1 × 1 m) within each 20 x 15 m plot (stratified random). Since *U. brizantha* covered 30-70% of the plots at the beginning of the experiments, we established five subplots in the invaded part of the plot (IP) and five in the non-invaded portion (NIP). In each subplot, we measured the height of vegetation by functional group (*U. brizantha*, native graminoids, forbs and shrubs) and estimated the cover of the following groups: live *U. brizantha*, total dead biomass (native + dead biomass of *U. brizantha*), native graminoids, forbs and shrubs. In six subplots (0.5 × 0.5 m) of each plot we randomly collected the aboveground biomass following a stratified random sampling (three samples were in the invaded patches and three in the native patches). At the laboratory, we separated the biomass into the following categories: dead *U. brizantha*, dead native species, live *U. brizantha*, live native graminoids, live forbs, and live shrubs. All material was dried (70°C for three days) and weighed. We sampled biomass and vegetation cover in the plots before the experiments started (year 2012) and every year after establishing the experiments until July/ 2015 for MD and October/ 2015 LD. We also sampled the data in during the rainy season (January/February) during these years.

Reproductive traits

In the study area, some *U. brizantha* individuals reproduce all over the year (E. Gorgone-Barbosa, personal observation). Thus, to verify the effects of fire regimes on reproductive traits we counted the number of flowering culms and the number of rests of dispersed spikelets in the subplots in the rainy (February) and dry season (August) of 2015. In the rainy season (February), we collected 20 flowering culms per plot to count the number of flowers. In the dry season, we collected four soil samples per plot of each treatment (20 x 20 x 2 cm) to verify the soil seed bank of *U. brizantha*. Soil samples were sieved and washed, and the damaged and intact *U. brizantha* seeds were separated and counted. Since here we aimed to compared all the treatments applied in the same season (rainy or dry) we used another acronyms for the treatments: 1 - Annual Mid-Dry season fire (AMD); 2 - Biennial

Mid-Dry season fire (BMD); 3 – Annual Late-Dry season fire (ALD); 4 – Biennial Late-Dry season fire (BLD) and; 5 – Control, no fire (C).

Data analyses

Due to peculiarities of the invaded (IP) and non-invaded plots (INP), such as the amount of native graminoids (lower in IP) and total productivity (higher in IP), identified in a previous study (Gorgone-Barbosa et al. unpublished data), we assessed the effects of treatments separately for these plots. Since we believe that seasonality is an important factor affecting plant community as a whole in Cerrado, we previously run linear mixed effect models with two factors (season and fire frequency) and we found no interaction between them. Therefore, we performed the analyses separately according to (1) effect of season (MD vs LD) and (2) effect of fire frequency (Annual, Biennial or Control) in each season.

To evaluate the effects of season and fire on the cover and biomass of *U. brizantha* and native functional groups (graminoids, forbs and shrubs) we used the data collected in 2015. We used the linear mixed effect models to analyze the effect of the factors for each dependent biomass variable: live *U. brizantha*, live native graminoids, live forbs and live shrubs, dead *U. brizantha*, dead native species. For cover we used the same vegetation variables except for dead biomass, that was considered the total dead biomass (dead *U. brizantha* + dead native species). Season and frequency were used as fixed factors in the model and the plot, as the random factor. When the effect was significant, we performed pairwise comparisons, using 95% of confidence interval for difference and LSD post hoc with the estimated marginal means of the fitted model.

We also applied linear mixed effect models to test the effect of the fixed factors (season or frequency) on height and cover data. We calculated pairwise comparisons in the same way described above for significant differences.

To look for effects of the fire frequency in each season (LD and MD) on the community composition structure (cover and biomass of NIP and IP) we used permutational multivariate metrics (PERMANOVA; Anderson 2001), applied to Bray-Curtis similarity matrix generated

from biomass and cover groups data and the fire frequency as independent variables in each season. We also performed a similarity percentage analysis (SIMPER) to determine the contribution of particular groups to the overall community composition (dead biomass and functional groups) dissimilarities between burn treatments assemblages. Using the biomass data, we performed a series of principal coordinate analyses (PCO) for each treatment year by year based on the Bray-Curtis similarity matrix to illustrate functional groups composition in multivariate space. We used the first PCO axes, which accounted for a significant proportion of total variation in compositional similarities, to illustrate treatment differences overtime. We quantified the community functional groups dissimilarity (inverse of the square-root transformed Bray Curtis similarity index, based on the biomass abundance of each group) on the biomass of each treatment Bray Curtis matrix and calculated the annual percentage of the biomass turnover per plot overtime from 2012 to 2015. To evaluate the dissimilarity of each treatment community we calculated one-way ANOVA with 10000 permutations.

To evaluate the effects of fire regimes (AMD, BMD, ALD, BLD and C) on the reproductive traits of *U. brizantha* - number of flowering culms or dispersed spikelets and number of flowers per panicle produced during the rainy season – we used one-way ANOVA with randomization tests. We also used one-way ANOVA with randomization tests to compare the number of seeds of *U. brizantha* in the seed soil bank according to the treatments in the dry season (August 2015).

We used SPSS software to perform the linear mixed effect models. To run PERMANOVA analyses we used vegan package for R and R 2.15.0 (R Development Core Team 2013); we used PRIMER version 1.0.3 (Plymouth Marine Laboratory, UK) for Simper analysis, and Multiv (Pillar 2005) for one-way ANOVA with permutations (10,000 iterations, Euclidean distance applied between sampling units).

Results

The effect of seasonality on dead biomass, *U. brizantha* and native functional groups

We found a seasonality effect on the cover of *U. brizantha* and on total dead biomass in IP. For example, *U. brizantha* cover was 5% higher in MD than LD ($P= 0.006$, Table 1) while total dead biomass cover was approximately 10% higher in the LD than in MD ($P= 0.006$, Table 1). In NIP, the cover of graminoids varied from 35 to 65%, being higher in MD ($P= 0.005$; Table 1), whilst the cover of shrubs and forbs did not vary between MD and LD (Table 1). The cover of native species dead biomass was also affected by seasonality (NIP, $P= 0.04$, Table 1), being 8% higher in LD than MD. Seasonality did not affect the cover of bare soil, being similar in both seasons in invaded and non-invaded plots ($P> 0.05$, Table 1). Finally, native functional groups cover was the same between seasons in the IP ($P> 0.05$ for all; Table 1).

Table 1. Bare soil dead biomass and of the native functional groups cover: graminoids, forbs and shrubs (% , mean $\pm$ standard error) in the year 2015, in both invaded (IP) and non-invaded plots (NIP) at different seasons (Mid-Dry: July and Late-Dry: October) in the Serra do Tombador Nature Preserve (Central Brazil).

Groups	Invaded Plots (IP)			Non-Invaded plots (NIP)		
	Mid-Dry	Late-Dry	<i>P</i>	Mid-Dry	Late-Dry	<i>P</i>
Bare soil	15.1 $\pm$ 5.2	15.2 $\pm$ 5.1	0.23	20.0 $\pm$ 5.1	15.1 $\pm$ 5.3	0.35
Dead Biomass	66.0 $\pm$ 5.0	74.3 $\pm$ 6.0	0.006	55.2 $\pm$ 6.1	60.3 $\pm$ 4.2	0.04
<i>Urochloa brizantha</i>	55.1 $\pm$ 7.3	35.4 $\pm$ 7.2	0.006	10.1 $\pm$ 5.2	5.1 $\pm$ 3.0	0.15
Graminoids	20.1 $\pm$ 4.2	15.1 $\pm$ 7.0	0.15	55.5 $\pm$ 6.2	45.2 $\pm$ 6.1	0.005
Shrubs	25.0 $\pm$ 5.1	30.2 $\pm$ 8.1	0.21	40.2 $\pm$ 5.0	45.3 $\pm$ 6.4	0.87
Forbs	2.1 $\pm$ 1.0	4.0 $\pm$ 1.1	0.09	10.1 $\pm$ 2.3	15.2 $\pm$ 5.3	0.15

We found 52% more live biomass of *U. brizantha* in MD compared to LD ($P < 0.0001$, Figure 1A). Differently from the cover data, we did not find the effect of seasonality on *U. brizantha* dead biomass ($P = 0.51$, MD = 939 ± 246 g.m⁻²; LD = 853 ± 171 g.m⁻², Figure 1B). Similarly, the biomass of native functional groups in IP was not affected by seasonality (Graminoids: $P = 0.40$; Shrubs: $P = 0.89$; Forbs: $P = 0.74$). In NIP, the biomass of graminoids was higher in MD (43% higher, $P = 0.002$, Figure 2A) and no differences could be observed between seasons for forbs and shrubs ($P > 0.05$, Figure 2B and C.). Moreover, the dead biomass in NIP did not change with seasonality ($P = 0.56$, Figure 2D).

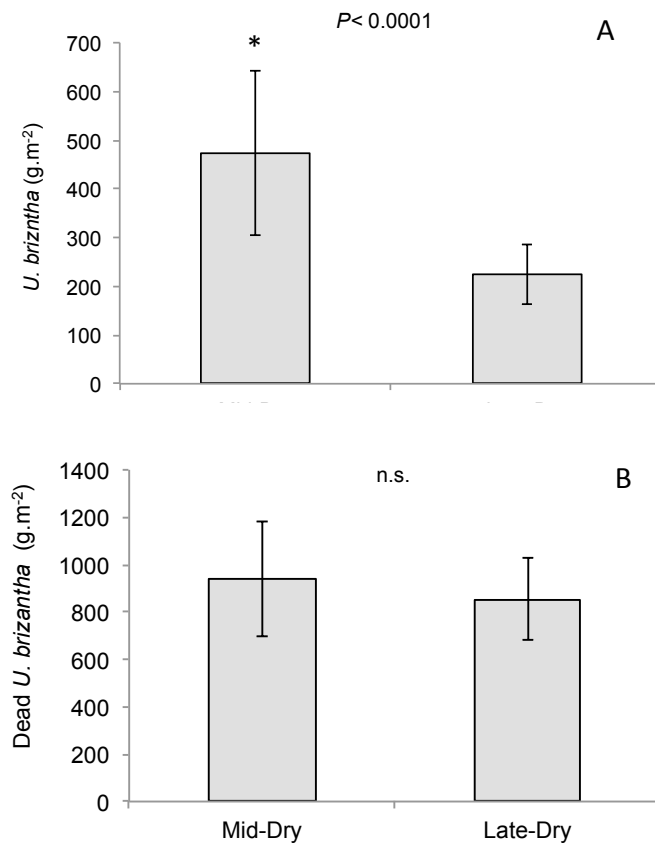


Figure 1. Biomass (% , mean $\pm$ standard error) of (A) live biomass of *U. brizantha* and (B) dead *Urochloa brizantha*, in invaded plots (IP) in Mid-Dry (MD) and Late-Dry (LD) fire treatments in invaded plots at the Serra do Tombador Nature Preserve (Central Brazil). Asterisk represents statistical differences ($P \leq 0.05$) between seasons.

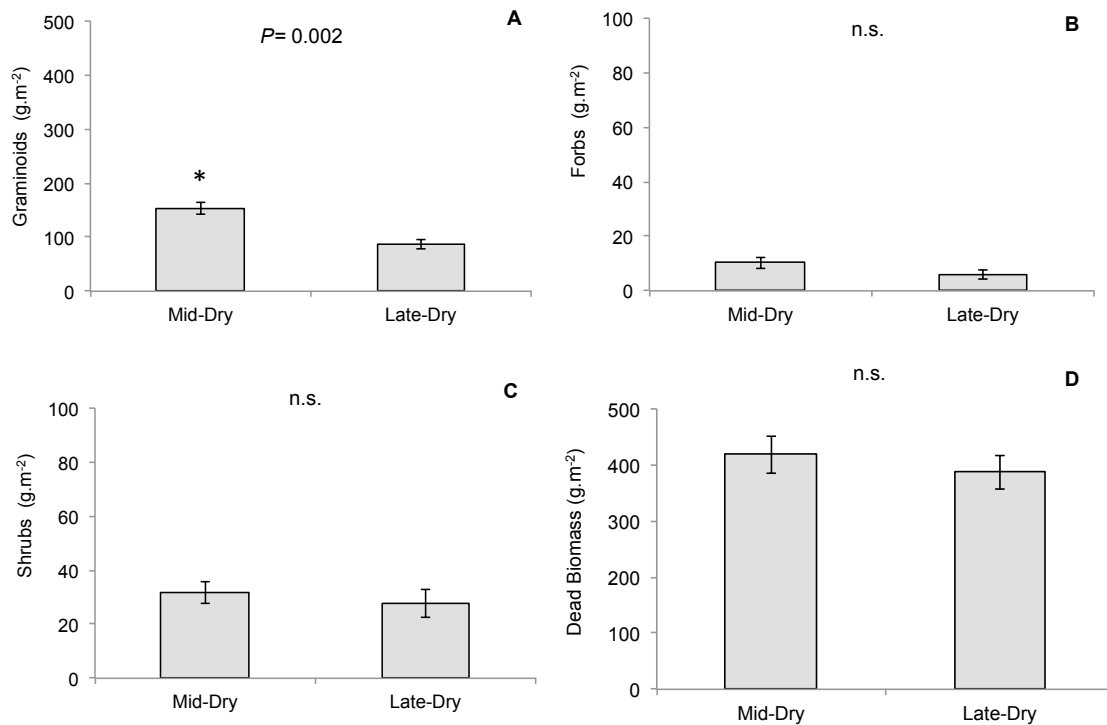


Figure 2. Biomass of graminoids (A), forbs (B), shrubs (C) and dead biomass (D) (% mean $\pm$ standard error) in non-invaded plots (NIP) in Mid-Dry (MD) and Late-Dry (LD) seasons at the Serra do Tombador Nature Preserve (Central Brazil). Asterisk represents statistical differences ($P \leq 0.05$) between seasons.

Effects of fire frequency on dead biomass, *U. brizantha* and native functional groups

In burned plots there was an increase in bare soil cover in both IP and NIP and in both seasons ($P \leq 0.05$, Table 2). Both Annual and Biennial treatments increased 70% of the cover of bare soil in IP during the Mid-Dry season and >45% in the Late-Dry. In NIP, both Annual and Biennial increased the cover of bare soil in almost 70% in both seasons (Table 2).

The cover of total dead biomass in IP was significantly reduced in both mid and late dry season ($P < 0.0001$, Table 2). In MD, independently of fire frequency, the cover of total dead biomass was 20% reduced, while in LD, it tended to decrease when compared to the Control in Annual (6%) and Biennial (18%) fire treatments ($P > 0.05$). The dead biomass in NIP varied from 50 to 70% and was not affected by any fire frequency in any season (MD – $P = 0.26$ and LD $P = 0.24$, Table 2). The biomass of live *U. brizantha* was neither reduced nor increased by any fire frequency in MD ($P = 0.49$, Table 2). However, when LD Biennial treatments were

applied, a significant reduction in the cover of *U. brizantha* could be observed compared to Annual and Control treatments ($P= 0.01$). At the beginning of the experiments (2012), there was no *U. brizantha* in the NIP. However, the invasive grass colonized those plots in the subsequent years, reaching $10\pm5\%$ of the vegetation cover in 2015 (Table 2). There was a significant increase of *U. brizantha* cover in Biennial treatments in Mid-Dry burns (60% , $P= 0.02$), but the same pattern was not observed in Late-Dry season ($P= 0.73$).

The cover of graminoids in the IPs was not affected by fire frequency in any fire season (MD – $P= 0.75$ and LD - $P= 0.59$), whilst in NIP, the Annual fires reduced the cover of graminoids in $15\pm15\%$ ($P= 0.001$). Biennial fires led to reductions of $30\pm5\%$ ($P= 0.001$, Table 2) in both seasons. While the cover of the cover of shrubs and forbs was not affected by fire frequency in any season in NIP ($P>0.05$, Table 2), the same pattern was not observed for IP: an increase in the cover of both shrubs and forbs was found in the Late-Dry Biennial compared to Control and Annual treatments ($P\leq0.05$, Table 2).

In general, the height of vegetation was not affected by fire frequency ($P> 0.05$), except for the shrubs, in NIP, which were taller in Annual Late-Dry season fires ($P= 0.03$).

In invaded plots, after the fire treatments, the dead biomass of *Urochloa brizantha* varied from 646 ± 124 to 1222.5 ± 151 g.m⁻². Differently from the total dead biomass cover data, fire treatments neither increased nor decreased the amount of dead biomass of *U. brizantha* in MD ($P= 0.59$). A different pattern was observed in LD: both Annual and Biennial fires were effective in reducing the dead biomass of *U. brizantha* in $> 40\%$ (Figure 3, $P< 0.0001$). However, live biomass of *U. brizantha* did not vary between plots with different fire frequencies in any season ($P>0.05$; Figure 3).

In invaded plots, the biomass of dead native species, live graminoids, shrubs, and forbs were not affected by any fire frequency in any season ($P>0.05$ – Figure 4 A). However, in non-invaded plots, the biomass of dead native species was reduced by fire (both frequency) only in MD ($P= 0.006$, Figure 4B). The live biomass of native species functional groups was not affected by fire frequencies in any season ($P>0.05$, Figure 4B).

Table 2. Bare soil, dead biomass and of the native functional groups cover - graminoids, shrubs and forbs - (% , mean $\pm$ standard error) at the seasons (Mid-Dry- MD and Late-Dry season-LD) and fire frequency treatments (Annual, Biennial, and Control) in the year 2015, at Serra do Tombador Nature Preserve (Central Brazil). Different letters represent differences among fire frequencies in each season, $P \leq 0.05$.

Invaded plots (IP)							
Season	Fire Frequency	Bare soil	Dead Biomass	<i>Urochloa brizantha</i>	Graminoids	Shrubs	Forbs
Mid-Dry	Annual	20 $\pm$ 5 ^a	60 $\pm$ 5 ^a	60 $\pm$ 9 ^a	15 $\pm$ 6 ^a	20 $\pm$ 6 ^a	2 $\pm$ 1 ^a
	Biennial	20 $\pm$ 4 ^a	60 $\pm$ 3 ^a	50 $\pm$ 7 ^a	20 $\pm$ 4 ^a	30 $\pm$ 2 ^a	2 $\pm$ 2 ^a
	Control	6 $\pm$ 3 ^b	75 $\pm$ 3 ^b	55 $\pm$ 6 ^a	20 $\pm$ 5 ^a	25 $\pm$ 3 ^a	2 $\pm$ 1 ^a
Late-Dry	Annual	15 $\pm$ 4 ^a	75 $\pm$ 6 ^a	33 $\pm$ 4 ^a	20 $\pm$ 5 ^a	38 $\pm$ 5 ^a	5 $\pm$ 1 ^a
	Biennial	25 $\pm$ 4 ^b	65 $\pm$ 6 ^a	26 $\pm$ 4 ^b	15 $\pm$ 10 ^a	40 $\pm$ 10 ^b	6 $\pm$ 2 ^b
	Control	8 $\pm$ 1 ^a	80 $\pm$ 2 ^b	44 $\pm$ 4 ^a	10 $\pm$ 3 ^a	23 $\pm$ 4 ^a	2 $\pm$ 1 ^a
Non-invaded plots (NIP)							
Mid-Dry	Annual	25 $\pm$ 4 ^a	50 $\pm$ 7 ^a	2 $\pm$ 1 ^a	55 $\pm$ 3 ^a	40 $\pm$ 4 ^a	10 $\pm$ 2 ^a
	Biennial	25 $\pm$ 2 ^a	50 $\pm$ 6 ^a	15 $\pm$ 8 ^b	45 $\pm$ 5 ^a	40 $\pm$ 2 ^a	10 $\pm$ 2 ^a
	Control	5 $\pm$ 2 ^b	60 $\pm$ 4 ^a	5 $\pm$ 3 ^a	65 $\pm$ 5 ^b	50 $\pm$ 5 ^a	10 $\pm$ 4 ^a
Late-Dry	Annual	20 $\pm$ 4 ^a	60 $\pm$ 5 ^a	2 $\pm$ 2 ^a	40 $\pm$ 5 ^a	40 $\pm$ 6 ^a	15 $\pm$ 5 ^a
	Biennial	25 $\pm$ 2 ^a	65 $\pm$ 1 ^a	5 $\pm$ 4 ^a	35 $\pm$ 2 ^a	45 $\pm$ 10 ^a	10 $\pm$ 3 ^a
	Control	10 $\pm$ 2 ^b	70 $\pm$ 3 ^a	5 $\pm$ 2 ^a	60 $\pm$ 6 ^b	45 $\pm$ 4 ^a	15 $\pm$ 6 ^a

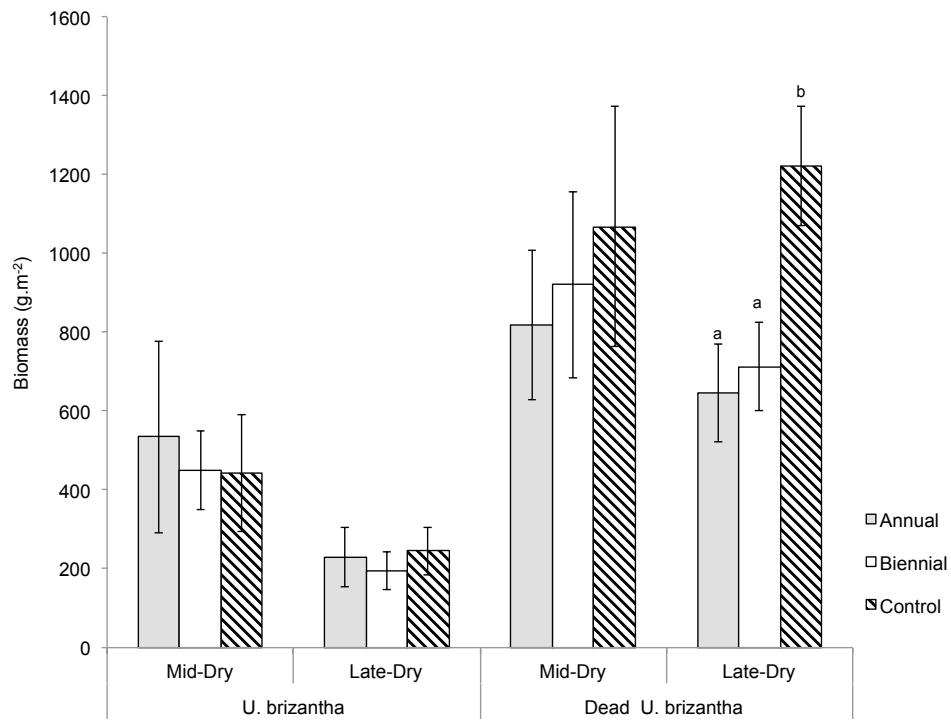


Figure 3. Live and dead biomass of *Urochloa brizantha* (g.m⁻², mean±standard error), in invaded plots (IP) in the Mid-Dry (MD) and Late-Dry (LD) fire treatments at different fire frequencies: Annual, Biennial and Control (no fire) at the Serra do Tombador Nature Preserve (Central Brazil). Different letters represent statistical differences ($P \leq 0.05$) between fire frequencies in each season.

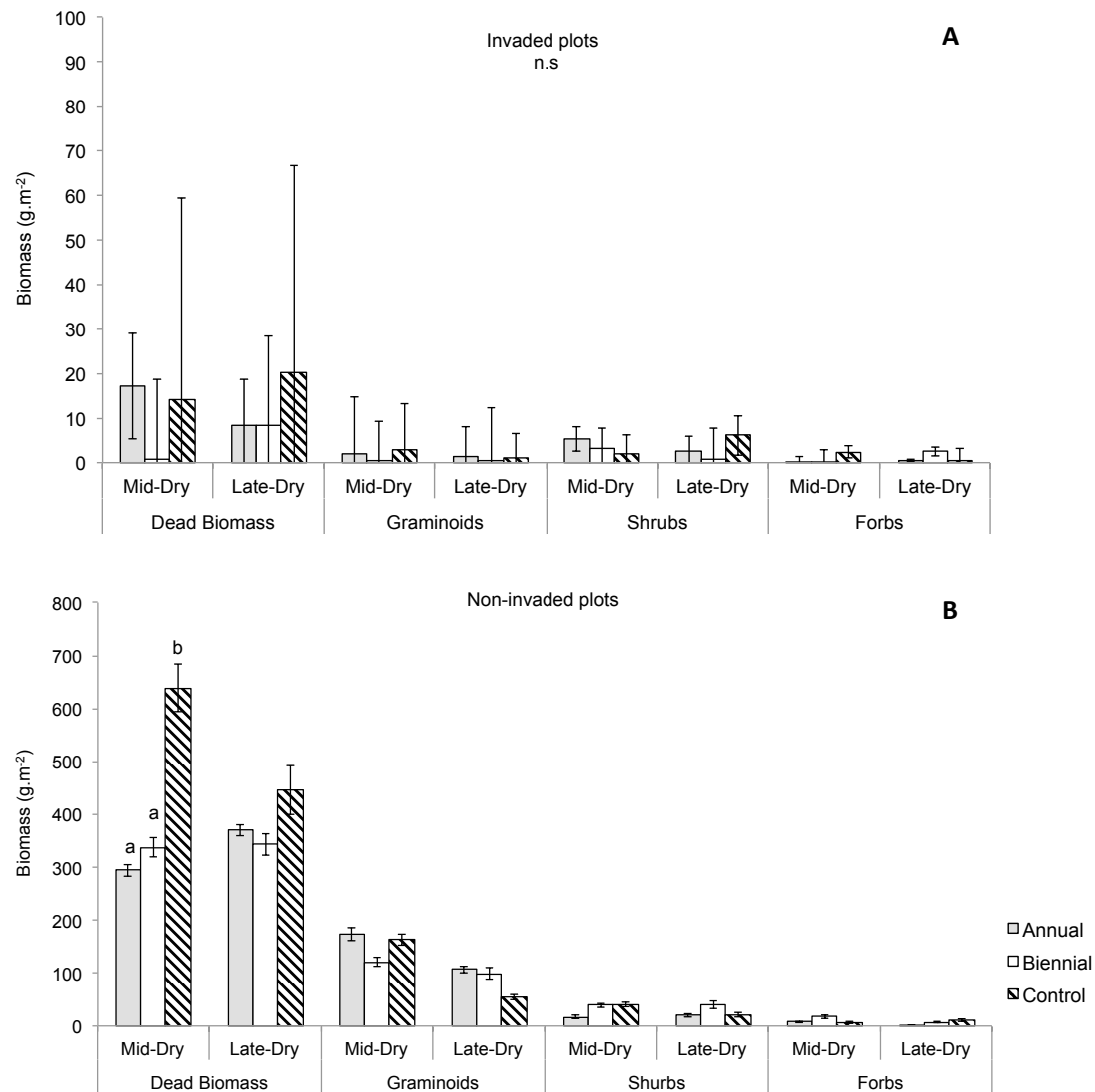


Figure 4. Biomass (g.m⁻², mean±standard error) of native groups in (A) invaded plots (IP) (B) and non-invaded plots (NIP): dead biomass, live graminoids, shrubs and forbs in the Mid-Dry (MD) and Late-Dry (LD) fire treatments at different fire frequencies: Annual, Biennial and Control (no fire), at the Serra do Tombador Nature Preserve (Central Brazil). Different letters represent statistical differences ($P \leq 0.05$) between fire frequencies in each season.

We found that both MD Annual and Biennial in non-invaded communities diverged from Control ones ($Pseudo-F= 4.5$; $P= 0.006$; Figure 5A, positive part of the graph), being the amount of native species dead biomass the major factor driving those differences. Still, MD fire frequencies did not influence the biomass compositional similarity in invaded plots ($Pseudo-F= 0.50$; $P= 0.73$; Figure 5A, negative part of the graph).

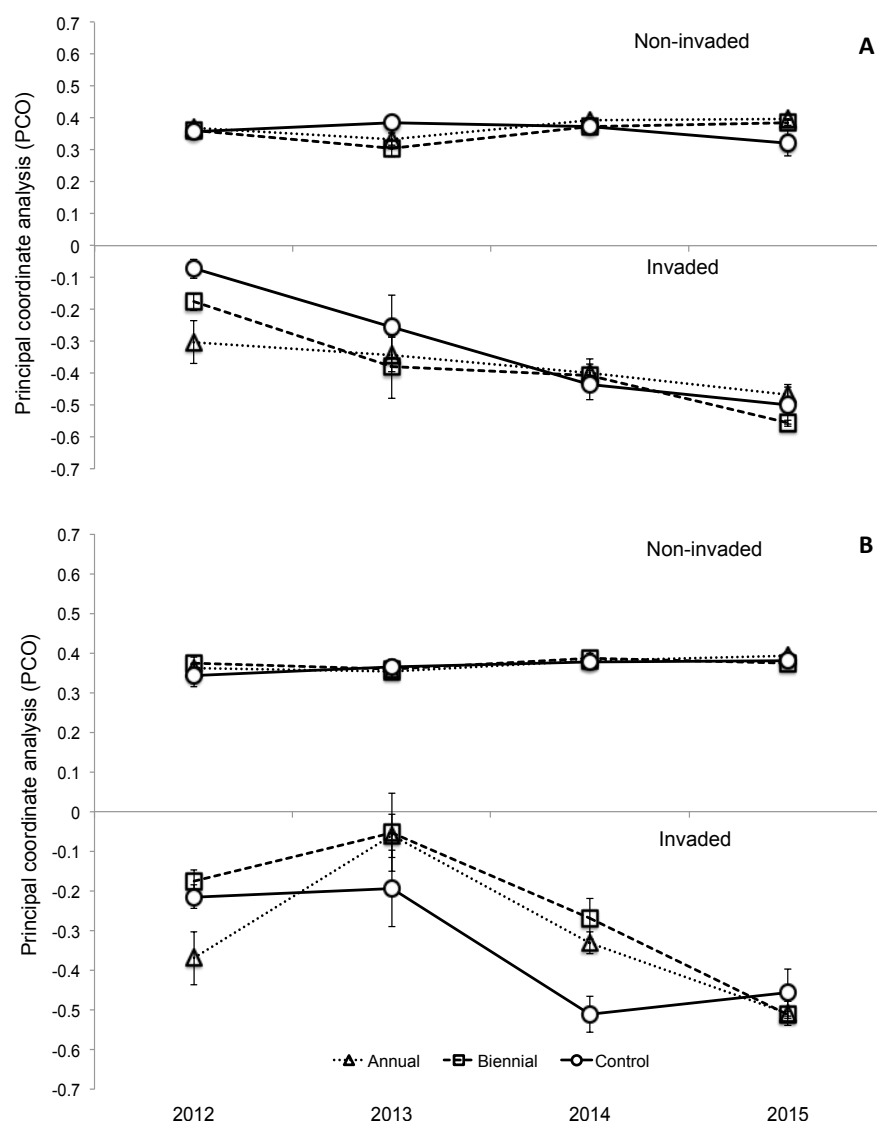


Figure 5. Principal coordinate analysis (PCO) from invaded and non-invaded plots burned in (A) Mid-Dry and (B) Late-Dry season at different fire frequencies: Annual, Biennial, and Control (not burned) along time in Serra do Tombador Nature Preserve (Central Brazil). The lines in the positive side of the graph are the non-

invaded plots (NIP) and the negative are the invaded plots (IP). Values are the average and T lines are the standard error.

On the other hand, we found the opposite pattern in the Late-Dry season: NIP were quite similar to the Control ones, independently of the fire frequency ($Pseudo-F=0.156$; $P=0.18$; Figure 6B, positive part of the graph), while the invaded plots differed between burned (Annual or Biennial) and Control plots ($Pseudo-F=5.25$; $P=0.005$; Figure 5B, negative part of the graph). The percentage of *U. brizantha* dead biomass was in this case, driving the compositional dissimilarity. Considering the cover data, invaded or non-invaded plots submitted to Annual or Biennial fires in MD and also those not burned (Control) were similar to each other (IP: $Pseudo-F=0.888$; $P=0.5$ and NIP: $Pseudo-F=1.78$; $P=0.11$). The same pattern was found to LD season (IP: $Pseudo-F=1.07$; $P=0.36$ and NIP: $Pseudo-F=1.19$; $P=0.35$).

Considering the interval from 2012 to 2015, fire frequencies (Annual and Biennial) increased the dissimilarity when compare to Control and influenced the biomass compositional turnover in invaded plots in both seasons (MD – $P=0.02$; LD – $P=0.005$; Figure 6A and B). For the invaded plots, turnover between wet and dry season was more evident in LD treatments, independently of the fire frequency, and usually by the increasing the biomass dissimilarity (Figure 6B; Table 3). In non-invaded plots, on the other hand, fire frequencies only affected the biomass compositional stability across time in the Mid-Dry season (MD: $P=0.005$; LD: $P=0.305$; Figure 6C and 6D). However, analyzing each interval separately, we can see that the effect of fire frequency on the dissimilarity changed through time, and it was more evident in intervals between wet and dry seasons (jan-jul and jan-oct; Figure 6; Table 3).

Table 3. One-way analysis of variance (ANOVA) results fire treatments (Annual, Biennial and Control) on compositional percentage of turnover in each time interval per season along time: 2012 = before starting the experiments; 2015 = after the end of experiments in the Serra do Tombador Nature Preserve (Central Brazil). Asterisk means significant difference of the treatments (Annual, Biennial and Control) in each intervals. ($P \leq 0.0$).

Intervals	Invaded	Non-invaded
	Mid-Dry	
jul12 - jul13	0.31	0.06
jul13 - jan14	0.09	0.90
jan14 - jul 14	0.006*	0.19
jul14 - jan15	<0.0001*	0.001*
jan15- jul 15	0.07	0.16
	Late-Dry	
oct12 - oct13	0.82	0.87
oct13 - jan14	0.015*	0.62
jan14 - oct14	0.015*	0.012*
oct14 - jan15	0.004*	0.06
jan15 - oct15	0.005*	0.77

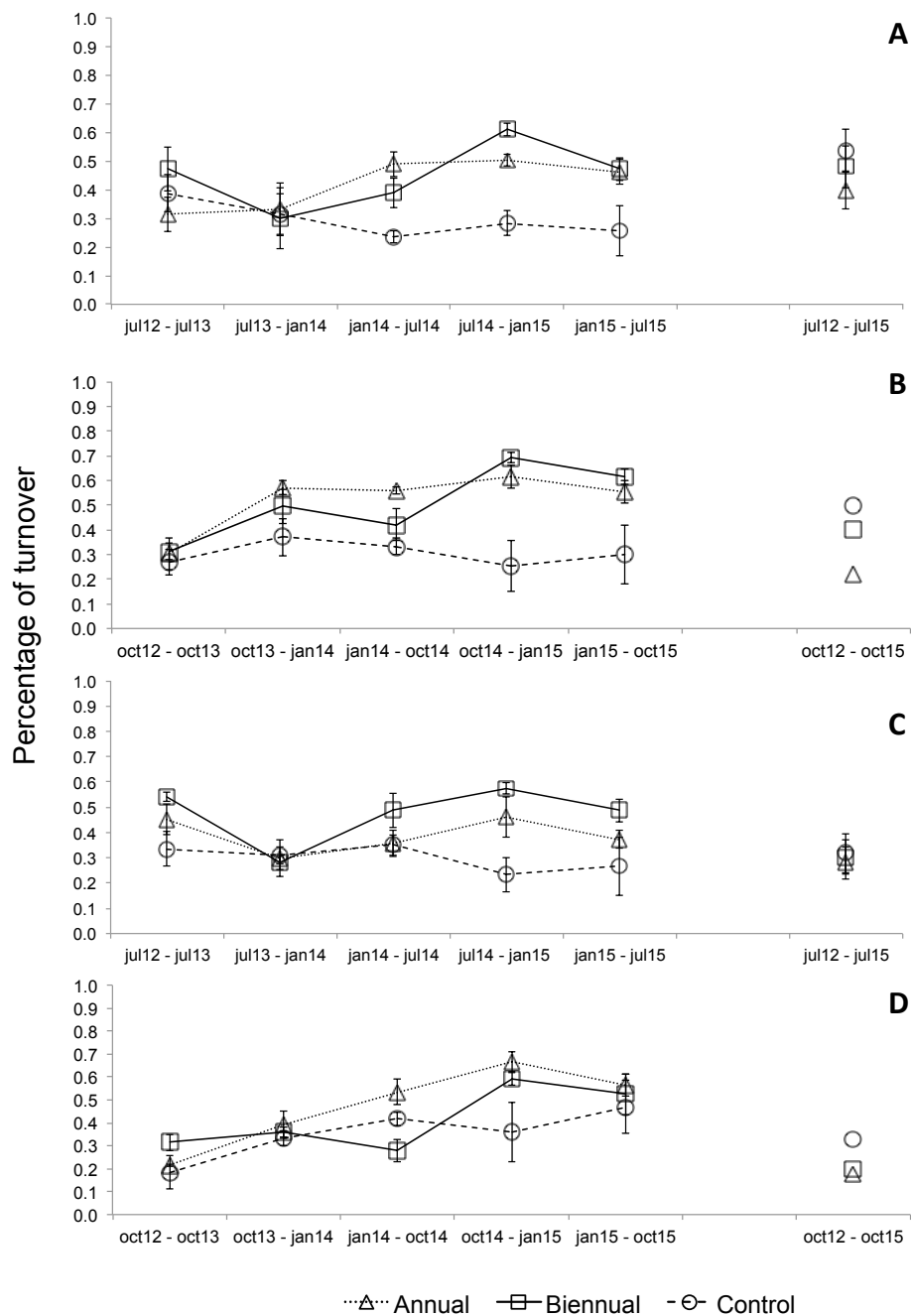


Figure 6. The effect of fire treatments on compositional percentage of turnover (dissimilarity; mean values and standard error) along time: 2012 = before starting the experiments; 2015 = after the end of experiments in the Serra do Tombador Nature Preserve (Central Brazil). Invaded communities (IP) in Mid-Dry (A) and Late-Dry season (B). Non-invaded communities (NIP) in Mid-Dry season (C) and Late-Dry season (D).

Effect of fire on reproductive traits of *Urochloa brizantha*

During the rainy season, the number of flowering culms varied from 0 culms.m⁻² (in the Control) to 6 culms.m⁻² (Biennial Late-Dry season fire). Biennial Late-Dry season fire plots had a higher number of flowering culms when compared to ALD and BMD ($P= 0.04$ - Figure 7A). On the other hand, we found a significant decrease in the number of flowering culms in ALD and BLD in the dry season ($P<0.0001$; Figure 7A). The number of dispersed spikelets plus spikelets with seeds varied from 7 to 33 spikelet.m⁻² and except for the BMD, all other treatments had higher number of dispersed culms when compared to the Control (Figure 9B). In the dry season, the number of flowering culms was also low (0 to 10 culms.m⁻²) in all treatments. However, The number of flowers per panicle did not differ between treatments ($P= 0.58$) and varied from 181±86 in the C to 192±7 flowers/panicle in BMD. Seeds of *U. brizantha* in the soil bank at the dry season varied from 1202±442 to 383±148 seeds.m⁻², however less than 5% of the seeds were intact (Table 4). We did not find any effect of the fire treatments on the soil seed bank ($P= 0.10$).

Table 4. Number of seeds of *Urochloa brizantha* (seeds.m⁻², mean±standard error) in the seed soil bank under the different fire regimes and the percentage of intact seeds (% ,mean±standard error) in Serra do Tombador Nature Preserve (Central Brazil).

	Total Seeds. m ⁻²	% Intact seeds
C	1023.3±658.0	3.6±2.5
AMD	1202.0±442.2	1.0±1.8
BMD	1054.1±376.9	2.6±2.8
ALD	716.6±296.1	3.5±4.1
BLD	383.3±148.7	3.2±9.5

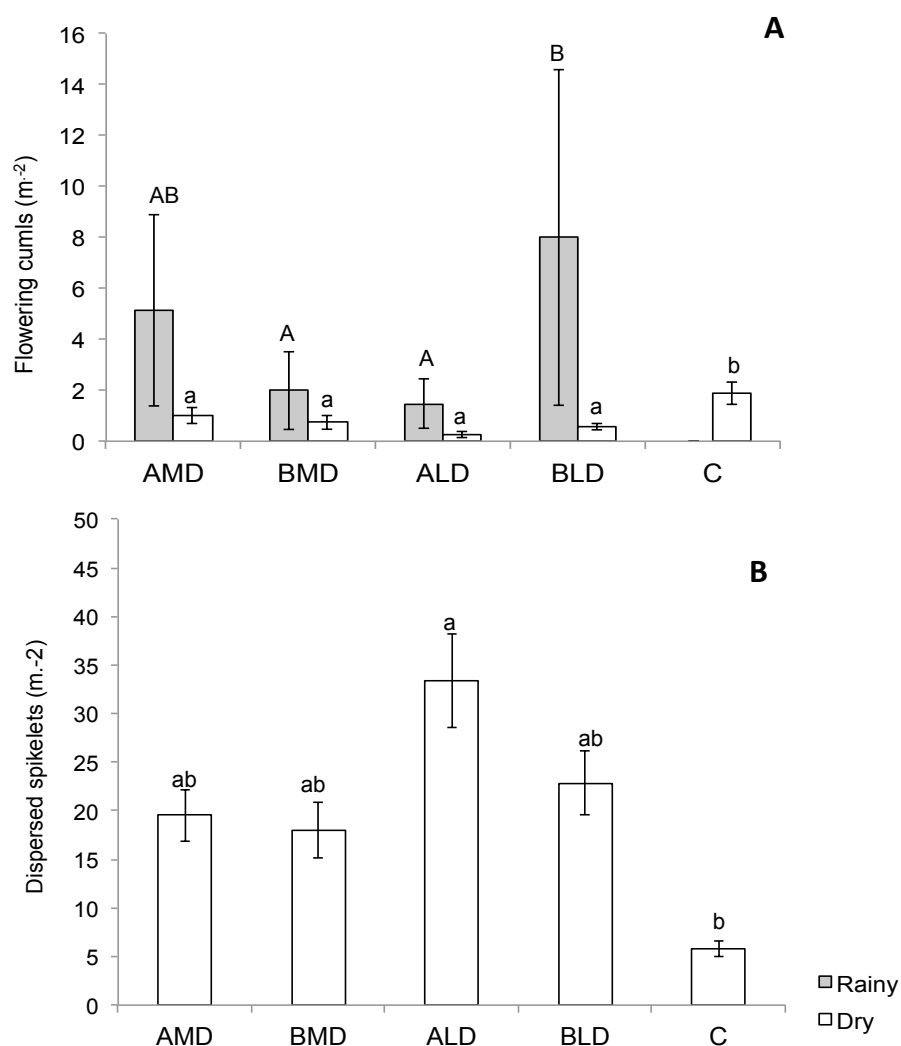


Figure 7. Number of reproductive culms (mean $\pm$ standard error) of *Urochloa brizantha* in the different fire regimes at the dry-season: (A) flowering culms and (B) dispersed culms at the Serra do Tombador Nature Preserve (Central Brazil). Different letters mean significant differences among treatments in Rainy season (capital letters) and in Dry-season (small letters) ($P \leq 0.05$).

Discussion

Natural fires have been present in the Cerrado for millions of years (Simon *et al.* 2009) but the ancient fire regime is unknown. Anthropogenic fires, on the other hand, have altered fire frequency and season (Ramos-Neto & Pivello 2000; Pivello 2011), bringing consequences for plant communities. Regarding the current problem of biological invasions in the Cerrado, it is essential to understand the responses of

plant communities – both native and invaded – to different fire regimes, in the search for scientific support for management decisions to protect the Cerrado biodiversity.

Our experiments showed that dead biomass, among the plant community components analyzed, was the most important factor in driving differences between burned (in different frequencies) and unburned areas, invaded and non-invaded communities and in both fire seasons. In general, LD fires, independently of their frequency, were more efficient to reduce the amount of dead biomass of *U. brizantha*, and the Mid-Dry season fires were also efficient in reducing the cover of dead *U. brizantha*. This is an important information, since the cover of dead *U. brizantha* is already higher in the Late-Dry than in the Mid-Dry season. Thus, by considerably reducing the amount of the invasive species dead biomass through Late-Dry prescribed burns (both Annual or Biennial) one could achieve: (1) fuel load Control and reduction of wildfire risk (Whelan 1995) and, (2) stimulation of the native species growth, since the accumulation of dead biomass over time decreases light availability and act as a physical barrier to native species establishment (Farrer & Goldberg 2009; Gaertner *et al.* 2014). The use of prescribed fires to prevent high intensity wildfires has become the most common use of fire in land management (Whelan 1995) and it enables the temporary change in the aboveground dominance (Pyke, Brooks & D'Antonio 2010) and could be useful to control the fuel accumulation of *U. brizantha*, since the amount dead biomass of *U. brizantha* it is directly related to higher intensity fires and high flames (Gorgone-Barbosa *et al.* 2015) and it is already known that the quantity of biomass is a key factor of plant-level flammability in grasses (Simpson *et al.* 2016).

Several studies display a positive-feedback between invasive species and fire (D'Antonio & Vitousek 1992; Brooks *et al.* 2004). African grasses introduced in the Americas, for example, both promote and are stimulated by fire, sometimes responding to fire positively than the native species (Williams & Baruch 2000). In our

experiments, Mid-Dry fires, both Annual and Biennial, neither reduced nor increased the live biomass and the cover of *U. brizantha* in the invaded plots, while Biennial fires in Late-Dry season reduced its cover in 40%. We cannot affirm that this treatment could help in controlling the invasive species, but we found some evidences that MD Biennial fires in the may facilitate new introductions of *U. brizantha* in the native communities and, as a consequence, stimulate the a positive feedback of this species with fire. The increase of invasive species cover and biomass related to fire frequency and intensity was also found in other studies. Wagner & Fraterrigo (2015), for example, found a positive feedback between intense fires and the annual grass *Microstegium vimeneum* that increased in biomass in burned sites. And, sites more frequently burned showed a higher cover of invasive annual grasses and forbs and lower native plants diversity when compared to sites less frequently burned in different ecosystems in California, US (Keeley & Brennan 2012). Nevertheless, in a West-African savanna, annual fires significantly reduced the population growth of the dominant native *Hyparrhenia diplandra* (Garnier & Dajoz 2001) and increased the native diversity. Thus the relationship between fire and dominance of native or invasive species may vary according to the species and their previously experienced fire regimes history.

The effect of fire can be different depending on the season, which is probably related to the phenology of the species. Prescribed burns during the growing season or just before flowering, for example, are usually more efficient to control invasive species since they are allocating resources aboveground to grow or to blossom (Lesica & Martin 2003; DiTomaso *et al.* 2006; Pivello 2006). In the study area, natives and invasive species start to allocate resources to resprout in the beginning of the rainy season, therefore, being more affected by LD fires (e.g. graminoids). The fire treatments we applied did not decrease the reproduction of *U. brizantha*, especially the Biennial Late-Dry burn, which tended to anticipate the flowering and dispersal of

U. brizantha seeds, which could be a rapid response to the disturbance. However, the number of intact seeds in the soil seed bank did not change between the treatments. During the rainy season in Cerrado, we can find higher amount of biomass (graminoids, forbs and shrubs) and soil nutrient concentration than in the dry-season (Oliveras *et al.* 2013), indicating that in the Late-Dry season plants are allocating nutrients for growth and reproduction and fire may cause further damage. Besides, the water soluble carbohydrates and starch amounts from above and below ground biomass of native and invasive species (*Melinis minutiflora*) in the Cerrado varied according to the time of the year and the site they are located (Souza *et al.* 2010). Thus it is important to identify the best time (season) to apply the prescribed burn in order to damage the invasive species and not the native ones.

Further, fire season also affected fire intensity in the invaded sites due the higher amount of dead biomass of *U. brizantha*, as showed by Gorgone-Barbosa *et al.* (2015): LD fires are hotter, with higher flames and 2-fold more intense than MD fires, which could directly or indirectly affect regeneration of invasive species. *U. brizantha* can resprout after fire from buds located in rhizomes near the soil surface, protected by leaf sheaths. For perennial herbaceous plants with underground organs, high fire intensity may produce lethal temperatures in soil and kill perennial buds that are near the soil surface, affecting negatively their post-fire regeneration (Pyke, Brooks & D'Antonio 2010). Havill *et al.* (2015), in a short grass prairie, demonstrated that hot fires could reduce the invasion by *Bothriochloa ischaemum*, by killing more meristemes when compare to the native species *Schizachyrium scoparium*.

Additionally, intense fires could also kill seeds and propagules of invasive species, and thus, a lower regeneration from the soils seed bank would occur (DiTomaso *et al.* 2006). Seeds *U. brizantha* die when submitted to 200°C, but can resist to 100°C (Gorgone-Barbosa *et al.* unpublished data). Since temperatures just below the soil surface (1-2 cm) during Cerrado fires are usually not higher than 55°C (Miranda *et al.*

1993) and fires are fast, once in the seed soil bank, seeds of *Urochloa brizantha* might resist the passage of fire and ensure seedlings establishment and the colonization of new sites. Moreover, fire can indirectly increase germination of this invasive species, since it increases the availability of open areas, which experience higher temperature fluctuation that is responsible for breaking dormancy and increase germination (Gorgone-Barbosa *et al.* 2016). Therefore, efforts to control adult individuals of the invader before reproduction is a good strategy to prevent new invasions.

Invasive and native species respond differently to manipulative experiments (Seabloom *et al.* 2015) and in our experiments, we found some opposite responses of the native functional groups compared to *U. brizantha*. The native community showed high resilience to fire, since forbs and shrubs were not affected by fire treatments. We found a significant decrease in the cover of graminoids in the fire frequencies in both season, but the amount of biomass was not affected. No differences between fire frequencies (Annual and Biennial) was observed for the native community composition and biomass turnover, although burned and Control plots diverged under MD fires, mostly due to the reduction of dead biomass. However, in invaded plots, Biennial fires in LD season enhanced forbs and shrubs, probably due to decrease in *U. brizantha*'s cover and as a consequence, increase in bare soil and lower competition with the invasive species, leading to new opportunities (e.g. more open space) for new colonization.

The most important issue related to the impact of invasive species is their abundance in the invaded community (Kumschick *et al.* 2014), thus interventions that prioritize the invasive species reduction and/or stimulate native species abundance should be applied to maintain the natural diversity. It is well known that disturbances (such as fire) deeply influence the performance of invasive against natives (Daehler 2003;

Fenesi *et al.* 2015), and a real challenge is to find a way to control the target plant with minimal impact on the native community.

Implications for managements

Different fire regimes (frequency and season) affected differently the invasive and the native species. The figure 8 summarizes the results we found for how fire regimes affect *Urochloa brizantha*. In a short-term study, the frequency of fire did not seem to be so important, since the major differences found were between burned and unburned plots. Mid-Dry fires can have a positive feedback with the invasive species and should be avoided. *Urochloa brizantha* is a high-impact invader (see definition in Gaertner *et al.* 2014) and probably fire alone cannot control it. However, Late-Dry fires could help in reducing fuel (dead biomass), and enhance some native groups. However, it is important to highlight that the Late-Dry fires are also more intense (Gorgone-Barbosa *et al.* 2015) and more dangerous (it is easy to escape and become a wildfire), therefore if applied, managers and the fire brigade should be aware of wind changes and set fire breaks to avoid fire to escape. The results we found is species-specific and and this should also be taken into account in management decisions, since other invasive species could respond differently to the same fire regimes.

The effectiveness of prescribed burns to control invasive species can be enhanced when in combination with other management actions (DiTomaso *et al.* 2006; Ellsworth, Litton & Leary 2015), and that should be the case for *Urochloa brizantha*. It is possible to combine prescribed burns with mechanical methods, such as clipping or the use of herbicides after fire. Therefore, our study using fire experiments brings new insights and knowledge to understand and predict the assembly of plant communities (invaded and non-invaded) and their post-fire regeneration to guide management strategies for conservation of the open areas in Cerrado.

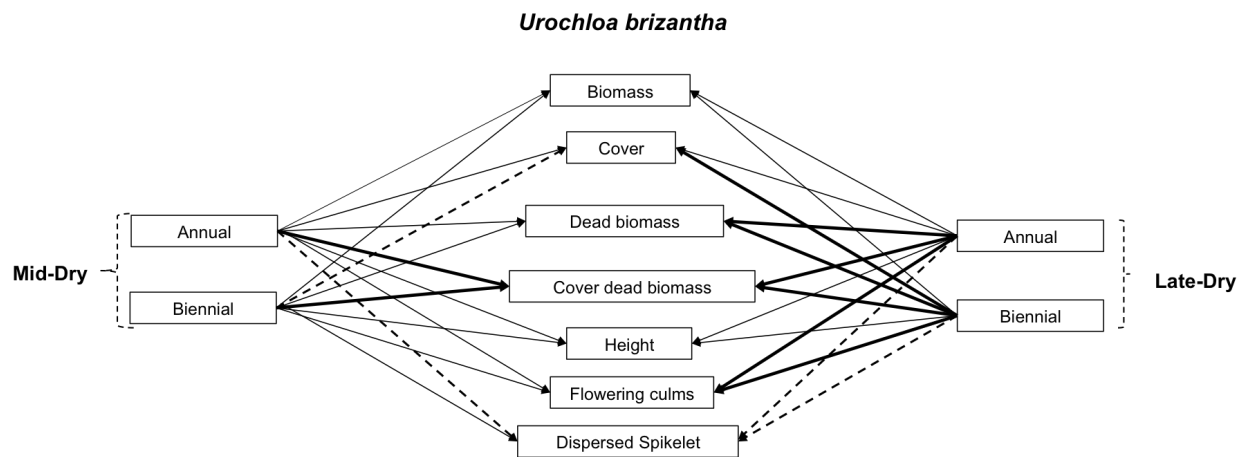


Figure 8. Principal effects of fire treatment on the invasive species, *Urochloa brizantha*, the black dark line arrows represent the decrease of the variable and the dash arrows represents the increase of the variable.

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Considerações Finais

Apesar da grande perda de área devido ao avanço da frente agrícola, as maiores ameaças atuais do Cerrado são as espécies invasoras e as queimadas não-controladas (Klink & Machado, 2005; Durigan et al. 2007). Como as espécies invasoras estão presentes em muitas as unidades de conservação de Cerrado (Pivello *et al.* 1999; Ziller & Dechoum 2013; Sampaio & Schmidt 2013) e, podem modificar o regime de fogo nesses ambientes, degradando ainda mais o ambiente, a compreensão dos processos de invasão, da relação de gramíneas africanas com o fogo e seus impactos na vegetação nativa, assim como a busca de alternativas eficientes para o manejo de invasoras e do fogo são necessárias.

No Brasil poucos estudos foram realizados verificando todo o processo de retroalimentação entre invasoras e fogo. Já conhecemos bem uma parte desse processo para a gramínea invasora *Melinis minutiflora*, que aumenta a intensidade e temperatura do fogo, além a altura das chamas (Kauffmann *et al.* 1994; Martins et al. 2004; Mistry and Berardi 2005; Martins 2006; Martins *et al.* 2011; Marinho 2013). No entanto, uma vez que a relação invasora-fogo é espécie-específica, e espécies do gênero *Urochloa* spp. são dominantes em diversas áreas de Cerrado, estudos que elucidassem tal processo para espécies de braquiária se fazia necessário. Assim, tomadores de decisão e gestores de unidades de conservação poderiam decidir por melhores estratégias para combater tais espécies, sendo que muitas vezes, tanto *Melinis minutiflora* quanto espécies de *Urochloa* spp aparecem na mesma unidade de conservação. Por essa razão, o objetivo principal desta tese foi elucidar o processo de retroalimentação (Figura 1) entre a invasora *Urochloa brizantha* e diferentes regimes de queimadas.

No primeiro capítulo, assim como esperado, verificamos que a gramínea invasora *Urochloa brizantha*, afeta o comportamento do fogo (e possivelmente seu regime a longo prazo). No entanto, a forma como a espécie modifica o comportamento do fogo é diferente de acordo com a estação do ano. Em queimas realizadas em julho, a presença de *U. brizantha* levou a uma diminuição da intensidade do fogo, mas essa intensidade é significativamente aumentada em queimas realizadas em outubro (final da estação seca - Figura 1). A intensidade do fogo nessas áreas está diretamente relacionada com a quantidade de *U. brizantha* morta (material combustível) e sua umidade. De maneira geral, queimas com a presença de *U. brizantha* nem sempre são mais intensas, mas são sempre mais quentes (maior severidade) e com maiores alturas de chama, que podem atingir as árvores, podendo levar a morte das mesmas e até mesmo, aumentar o risco de incêndios.

No segundo capítulo, com experimentos de laboratórios, verificamos que a germinação das sementes de *Urochloa* spp., uma vez presentes no banco de sementes do solo, não são afetadas pelo pico de temperatura durante a queima (50°C), mas parte da sua população de sementes têm sua dormência quebrada pela alternância de temperatura (10°C - 40°C), resultante da remoção da vegetação pelo distúrbio e conseqüente alterações no microclima. Desta forma, o fogo pode afetar indiretamente essas sementes, aumentando sua germinação (pela quebra da dormência), aumentando seu potencial invasor, ou seja, uma maior quantidade de plântulas, podendo levar a um maior sucesso de estabelecimento desta espécie. Esse é um mecanismo fundamental no processo de invasão biológica e dispersão destas espécies para novas áreas e que pode explicar, parcialmente, o sucesso dessas espécies invasoras, beneficiando-se de distúrbios nos ambientes invadidos. Entretanto, mais estudos realizados em campo são necessários para corroborar esta hipótese.

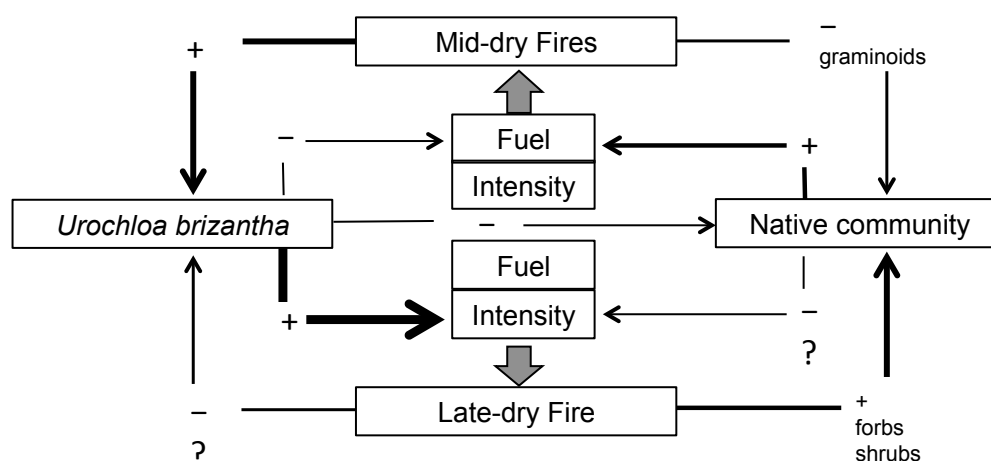


Figura 1. Representação do *feedback* entre a espécie invasora *Urochloa brizantha* e o fogo no Cerrado. Os sinais (-) significam relações negativas ou de diminuição e os (+) de relações positivas e aumento, enquanto (?) significam dúvidas quando ao processo ou uma potencial relação que ainda deve ser melhor estudada.

No terceiro capítulo, discutimos a capacidade de sementes de espécies invasoras (*Urochloa decubens*, *U. brizantha* e *Melinis minutiflora*) e nativas de resistirem e germinarem após choques de temperaturas de até 200°C (no laboratório). Assim como a invasora *M. minutiflora*, as espécies de gramíneas nativas testadas nesses experimentos, resistem (não há mudança na viabilidade das sementes ao término do experimento) e germinam igualmente ao controle após serem expostas a altas temperaturas. *U. decumbens* teve sua viabilidade diminuída quando submetida a 100°C, mas sua porcentagem de germinação se manteve a mesma em todos os tratamentos. Já *U. brizantha* teve sua viabilidade e germinação significativamente reduzida quando submetida à temperatura de 200°C. Embora a viabilidade de sementes de *Urochloa* spp. tenha diminuído com os choques de temperatura, uma porcentagem da população de sementes são capazes de sobreviver e germinar após fogo. Uma vez que as sementes sobrevivem, a

velocidade de germinação passa a ser um atributo chave para recolonização de novos ambientes. Nenhum dos tratamentos de choque de temperatura aplicados afetou o tempo médio de germinação de nenhuma das espécies, no entanto, verificamos que as espécies invasoras tendem a germinar muito mais rápido que as espécies nativas, o que atribui mais uma vantagem ao seu estabelecimento e expansão da invasão.

Finalmente, no último capítulo verificamos a resposta da invasora *Urochloa brizantha* e da vegetação nativa quando submetidas a diferentes regimes de queimas e como as comunidades invadidas e não-invadidas são modificadas pelo fogo. Os tratamentos com queimas controladas foram realizados de 2012 a 2014 e os dados aqui discutidos são referentes à 2015, quatro anos após a aplicação dos tratamentos. Tanto as comunidades com vegetação nativa quanto invadidas são bastante resilientes às queimadas e indiferentes à frequência da queima, pois as maiores diferenças encontradas foram entre parcelas queimadas x controle devido principalmente à quantidade de biomassa morta. Além disso, verificamos que a estação do ano também é um importante fator: queimadas no meio da estação seca (Julho) parecem favorecer o estabelecimento da invasora em áreas antes não ocupadas, revelando uma retroalimentação positiva (Figura 1). Isso pode ocorrer devido a menor intensidade do fogo e maior sobrevivência de sementes no solo, possibilitando novos recrutamentos. Já as queimadas no final da estação seca (Outubro), embora mais intensas, podem ser boas ferramentas para controle de material combustível, principalmente àquele formado por biomassa morta de *U. brizantha* e, ao mesmo tempo, favorecendo a recolonização de espaços antes invadidos por espécies nativas. No caso de áreas invadidas, as queimadas no final da estação seca podem trazer algum benefício da vegetação nativa. Entretanto, por serem queimadas mais intensas, devem ser bem planejadas e realizadas com muita cautela (por exemplo, no início da manhã ou final do dia, quando a umidade relativa

do ar é mais alta e a temperatura mais baixa) e com todas as medidas de segurança para evitar que o fogo se espalhe em áreas não desejadas e acidentes com as pessoas envolvidas nas queimas controladas.

O fogo pode ser uma importante ferramenta de manejo para a conservação da biodiversidade do Cerrado, e, por isso, experimentos de queimadas controladas, como os que foram realizados na Reserva Natural Serrado do Tombador, e que possibilitaram a realização desta tese, são de grande importância para fornecer dados que possam ser utilizados em modelos de risco de incêndio e nas tomadas de decisão sobre o manejo integrado do fogo e controle de invasoras em unidades de conservação que visam proteger o Cerrado. Tanto alterações nos parâmetros do fogo quanto na época e na frequência em que ocorrem as queimadas podem afetar a regeneração da vegetação nativa e das gramíneas invasoras.

Neste estudo de caso, queimadas controladas em um curto prazo mostraram que o fogo, independente da época ou frequência, por si só não controlaria a invasão de *U. brizantha*. No entanto, ele pode ser utilizado juntamente com outras ferramentas de manejo, como por exemplo controle mecânico (roçada) e dependendo do caso o uso de herbicidas. Além disso, ele também pode ser utilizado para a redução de material combustível e manutenção da diversidade das comunidades vegetais nativas. Portanto, os resultados desta tese visam auxiliar a tomada de decisões sobre onde, quando e como queimar a vegetação invadida e como estas queimas afetariam a vegetação nativa presente na área. O grande desafio no momento é conseguir conciliar o manejo do fogo com a presença das gramíneas invasoras, pois a maioria das unidades de conservação de Cerrado apresenta uma ou mais espécies invasoras, e muitas vezes elas podem responder diferentemente ao manejo de fogo aplicado. Portanto, estudos com experimentos em campo devem ser incentivados e realizados.

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