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

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA, EVOLUÇÃO E BIODIVERSIDADE

AVALIAÇÃO DOS ATRIBUTOS FUNCIONAIS RELACIONADOS AO FOGO, HERBIVORIA POR INSETOS E LUZ NO CERRADO

VAGNER AUGUSTO ZANZARINI

Rio Claro – SP
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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 Ecologia, Evolução e Biodiversidade.
Orientadora Profa. Assoc. Alessandra Fidelis
Coorientador Prof. Assoc. Davi R. Rossatto

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TÍTULO DA TESE: AVALIAÇÃO DOS ATRIBUTOS FUNCIONAIS RELACIONADOS AO FOGO, HERBIVORIA POR INSETOS E LUZ NO CERRADO

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RESUMO

Variáveis climáticas determinam o estabelecimento de florestas nas regiões tropicais; porém, nestas mesmas condições, podemos observar a ocorrência de ecossistemas abertos, como as savanas também. A vegetação savânica é principalmente determinada por distúrbios, como o fogo e a herbivoria, que atuam na remoção da biomassa, mantendo a vegetação aberta, mesmo em condições favoráveis ao estabelecimento de uma vegetação mais adensada. Sendo assim, uma seleção de atributos relacionados ao fogo e à presença dos herbívoros ocorre nas savanas. A herbivoria pode ser exercida tanto por grandes e médios mamíferos, como nas savanas africanas, quanto por insetos, como nas savanas australianas e sul-americanas, onde alguns estudos indicam que esse grupo também atua no consumo da biomassa, contribuindo para manter a vegetação. Uma vez que esses fatores mantém uma estrutura aberta na vegetação, diferentes incidências de luz atingem as comunidades herbáceas nesses mosaicos de savana e floresta, onde, nas áreas abertas mantidas por distúrbios, existe uma maior incidência de luz em comparação com as áreas fechadas mantidas por variáveis climáticas. Com isso, a seleção de atributos relacionados à alta ou baixa incidência de luz também ocorre nas comunidades savânicas e florestais. Além disso, as diferentes condições microclimáticas existentes diante de tais condições luz podem influenciar a abundância e os padrões de herbivoria por insetos. Enquanto nas áreas savânicas, a presença do fogo também pode afetar a dinâmica dos insetos no consumo da biomassa. Portanto, este trabalho tem como principal objetivo avaliar possíveis mudanças nos atributos funcionais das comunidades de plantas que compõem o estrato herbáceo (gramíneas, herbáceas e arbustos) em razão de alterações na ocorrência do fogo, padrões de herbivoria pelos insetos e disponibilidade de luz. Para isso, realizamos este estudo no Cerrado, onde mosaicos de florestas e savanas são encontrados. Especificamente, selecionamos áreas com diferentes frequências e anos desde o último fogo para realizarmos medições de atributos relacionados à inflamabilidade (quantidade de biomassa morta e teor de umidade da planta, temperatura máxima atingida e quantidade de biomassa consumida durante a queima e taxa de queima) e (i) investigar como mudanças em características do regime de fogo podem alterar a maneira como as savanas queimam. Também utilizamos áreas com altas e baixas frequências de fogo para mensurarmos atributos relacionados à herbivoria (dano foliar, concentração de taninos condensados e fenólicos totais) e (ii) investigar se o fogo pode influenciar a ação dos insetos no consumo de folhas, bem como se diferentes formas de crescimento (gramíneas, herbáceas e arbustos) possuem diferentes padrões de herbivoria. Por fim, utilizamos áreas de savanas abertas e adensadas e uma área florestal para (iii) avaliar se mudanças nos atributos relacionados ao fogo, a herbivoria por insetos e luz (dimensão foliar e pigmentos fotossintéticos) ocorrem. Como principais resultados, encontramos que a frequência de fogo e o ano desde a última queima influenciam a inflamabilidade de áreas savânicas, uma vez que a exclusão do fogo aumenta a quantidade de material combustível nas plantas, fazendo com que essas áreas queimem mais devagar e, consequentemente, apresentem um comportamento de fogo mais

intenso e severo, comprometendo a vegetação. A alta frequência de fogo também influencia positivamente a ação dos insetos, principalmente sobre as espécies de arbustos, as quais possuem folhas mais consumidas e, consequentemente, apresentam maiores concentrações de compostos de defesa. Concluindo, o fogo desempenha um papel crucial na determinação das savanas, influenciando os padrões de herbivoria nas áreas abertas, contribuindo para a abertura da vegetação, garantindo a chegada de luz e promovendo o estabelecimento de espécies adaptadas as altas concentrações de luz e também espécies graminóides que, ao mesmo tempo, influenciam a inflamabilidade do sistema. Enquanto nas áreas florestais, os padrões de herbivoria são maiores em relação às savanas, devido as condições de sombra no estrato herbáceo propiciada pelas lenhosas. Além disso, a baixa luminosidade faz com que atributos que otimizem a captação de luz sejam encontrados nas comunidades de plantas, indicando como este recurso pode influenciar as plantas neste tipo de vegetação. Portanto, entendemos que este estudo apresenta resultados inéditos a respeito de como esses fatores ambientais atuam sob as comunidades herbáceas e na manutenção das áreas savânicas, sendo o fogo o principal fator para a determinação dessa vegetação, garantindo sua funcionalidade e biodiversidade.

Palavras-chave: fogo, savana tropical, atributo, herbivoria por insetos, inflamabilidade, luz, Cerrado.

ABSTRACT

Climate variables determine the establishment of forests in tropical regions; however, under these same conditions, open ecosystems such as savannas also establish themselves. Savanna vegetation is primarily determined by disturbances, such as fire and herbivory, which consumes the biomass, keeping the vegetation open even under conditions favorable for woody vegetation. Thus, a selection of traits related to fire and the presence of herbivores occurs in savannas. Herbivory can be exerted by both large and medium mammals, as in African savannas, and by insects, as in Australian and South American savannas, where studies indicate that this group also consumes biomass, contributing to vegetation maintenance. Given that these disturbances maintain an open structure in the vegetation, different incidences of light reach herbaceous communities in the savannas and also in the forests, where in disturbance-driven environments, there is a higher incidence of light compared to closed areas maintained by climatic variables. Thus, the selection of traits related to high or low light incidence also occurs in savanna and forest communities, respectively. Moreover, the different microclimatic conditions existing under such light conditions can influence the abundance and patterns of herbivory by insects. While in the savannas, the presence of fire can also affect the dynamics of insects in biomass consumption. Therefore, this study aims to evaluate possible changes in the functional traits of herbaceous plant communities (grasses, forbs, and shrubs) due to changes in fire occurrence, insect herbivory patterns, and light availability. To do this, we conducted this study in the Cerrado, where forest and savanna mosaics are found. Specifically, we selected areas with different frequencies and years since the last fire to measure traits related to flammability (amount of dead biomass and plant moisture content, maximum temperature reached, amount of biomass consumed during burning, and burning rate) and (i) investigate how changes in fire regime characteristics influence the way savannas burn. We also used areas with high and low fire frequencies to measure herbivory-related traits (foliar damage, concentration of condensed tannins and total phenolics) and (ii) investigate if fire can influence insect leaf consumption, as well as if different growth forms (grasses, forbs, and shrubs) have different herbivory patterns. Finally, we used open and woody savanna areas and a forest area to (iii) assess whether changes in fire, insect herbivory, and light-related traits (leaf dimension and photosynthetic pigments) occur. As main results, we found that fire frequency and the year since the last fire influence the flammability of savanna areas, since fire exclusion increases the amount of dead biomass, especially in grasses, reducing the spread of fire consequently changing fire behavior, which can be more intense and severe, affecting the vegetation. Moreover, high fire frequency positively influences insect's herbivory, mainly on shrub species, which have more consumed leaves and, consequently, higher concentrations of defense compounds. Finally, we also observed that fire plays a crucial role in determining savannas, influencing herbivory patterns in open areas, contributing to vegetation openness, guaranteeing light incidences, and promoting the establishment of species adapted to high light concentrations and also grass species

that, at the same time, influence system's flammability. While in forest areas, herbivory patterns are higher compared to savannas, due to shading conditions in the herbaceous stratum provided by woody vegetation. Additionally, low light incidence leads to the selection of traits that optimizing light capture in plant communities, indicating how this resource can influence plants in this vegetation type. Therefore, we understand that this study brings new insights regarding how these environmental factors act on herbaceous communities and on the maintenance of savanna areas, and how fire is considered the main factor to determine savanna vegetation, contributing to the system's functionality and biodiversity.

Keywords: fire, tropical savanna, trait, herbivory by insects, flammability, light, Cerrado.

SUMÁRIO

1. INTRODUÇÃO GERAL

A distribuição dos diferentes tipos de vegetação pode ser explicada por variáveis do clima, como por exemplo, temperatura e precipitação (Whittaker 1975). Nas regiões tropicais, altas temperaturas e altos níveis de precipitação determinam a ocorrência de florestas, onde umidade, disponibilidade de luz e nutrientes são recursos que garantem o estabelecimento e crescimento de árvores (Whittaker 1975; Grime 1979). Dessa maneira, podemos dizer que muitos tipos de vegetação no mundo são controlados por recursos (*green world hypothesis;* Bond 2005). Porém, principalmente nas regiões tropicais, existem vegetações abertas ocorrendo em condições ideais para suportar o estabelecimento de florestas (Bond 2005; Bond 2019), como por exemplo as savanas tropicais, que ocupam aproximadamente 23 milhões de km^2 (Cole 1986). As savanas são ecossistemas determinados não apenas pelo clima, mas principalmente pela presença do fogo e de herbívoros, que são distúrbios atuando no consumo da biomassa e consequentemente, mantendo esta vegetação aberta (Bond 2005; Archibald et al. 2020). Desta forma, a distribuição das vegetações não é apenas determinada pelos recursos, mas também por consumidores da vegetação, como o fogo (*black world hypothesis*) e os herbívoros (*brown world hypothesis*) (Fig. 1; Bond 2005; Bond 2019).

Figura 1: Representação da teoria proposta por Bond 2005, onde vegetações não são apenas mantidas pelo clima (recursos), mas também por consumidores da vegetação (fogo e herbívoros). Adaptado de Bond 2005.

Savanas são caracterizadas por um regime de chuvas sazonal e um mosaico de ecossistemas abertos até mais adensados(Archibald et al. 2020; Cole 1986). Sendo assim, os ecossistemas savânicos são caracterizados pela presença de um estrato herbáceo contínuo, alternado com espécies lenhosas ocorrendo de maneira esparsa na paisagem ou, em algumas áreas, de maneira adensada (Bond 2008; Archibald et al. 2020). Tal relação de coexistência entre esses distintos estratos é mantida não apenas por fatores climáticos e edáficos, mas também por regimes de distúrbios (Bond 2008; Staver et al. 2011). O fogo, por exemplo, é considerado um importante distúrbio promovendo a abertura da vegetação (Bond 2005; Bond & Keeley 2005) e devido a sua presença, as regiões savânicas representam mais de 80% da área total queimada anualmente na superfície terrestre (Parr et al. 2014). Além do fogo, a presença de grandes e médios herbívoros também é considerada um importante distúrbio nessas áreas (Bond 2005; Archibald et al. 2020). Porém, atualmente, apenas nas savanas africanas podemos encontrar a presença massiva da megafauna herbívora, já que nas savanas australianas e sul-americanas (e.g. Cerrado), esses mamíferos foram extintos no final do Pleistoceno (10 mil anos atrás, (Barnosky et al. 2004; Owen-Smith 2013). No entanto, alguns estudos apontam que os insetos herbívoros também atuam na remoção da biomassa (Andersen & Lonsdale 1990; Costa et al. 2008). Todavia, estas quantidades de biomassa consumidas são consideradas baixas quando comparado a sistemas florestais, por exemplo (Costa et al. 2008). Portanto, nas savanas da Austrália e América do Sul, o fogo desempenha o papel principal no consumo da biomassa (Bond 2005; Bond 2019), ocorrendo há pelo menos 4 milhões de anos, como no Cerrado (Simon et al. 2009).

O fogo desempenha um papel crucial na estrutura e composição das savanas (Williams et al. 2003; Cochrane 2009), sendo o principal fator estruturador da vegetação em diversas regiões savânicas do mundo, como o Cerrado (Coutinho 1990; Simon et al. 2009). Este distúrbio consome a vegetação de forma irregular, com frequência e intensidade variável, constituindo assim um regime específico para uma determinada região (Archibald et al. 2013). Porém, de modo geral, as queimadas em ambientes savânicos são de superfície, consumindo rapidamente a vegetação, que apresenta um material combustível fino, e de moderada à baixa intensidade (Archibald et al. 2013). Assim, o regime de fogo é uma força seletiva sobre a vegetação, filtrando atributos de plantas capazes de persistirem no ambiente inflamável (Bond & Van Wilgen 1996; Keeley et al. 2011).

Dentre os principais atributos presentes nas plantas das savanas, estão os relacionados com a inflamabilidade do sistema (Fig. 2). A inflamabilidade trata-se de um conjunto de características responsáveis pela ignição, consumo e propagação das chamas no indivíduo (Pausas et al. 2017). Com isso, as gramíneas, que é o grupo mais abundante do estrato herbáceo das savanas (Bond 2008; Strömberg 2011), apresentam atributos inflamáveis como uma alta quantidade de biomassa morta presa à planta, baixo teor de umidade e arquitetura que permite melhor oxigenação durante a queima, garantindo uma rápida propagação do fogo no indivíduo e, consequentemente, na vegetação (Simpson et al. 2016; Cardoso et al. 2018; Archibald et al. 2019). Existem também espécies com baixa inflamabilidade compondo o estrato herbáceo, como herbáceas e arbustos. Estas formas de crescimento possuem baixas quantidades de biomassa morta e altos teores de umidade em comparação com as gramíneas (Zanzarini et al. 2022). Porém, mesmo sendo menos inflamáveis, tais grupos acabam sendo consumidos durante a passagem do fogo, visto que a eficiência da combustão no consumo da vegetação pode chegar até 90% em savanas (Rissi et al. 2017).

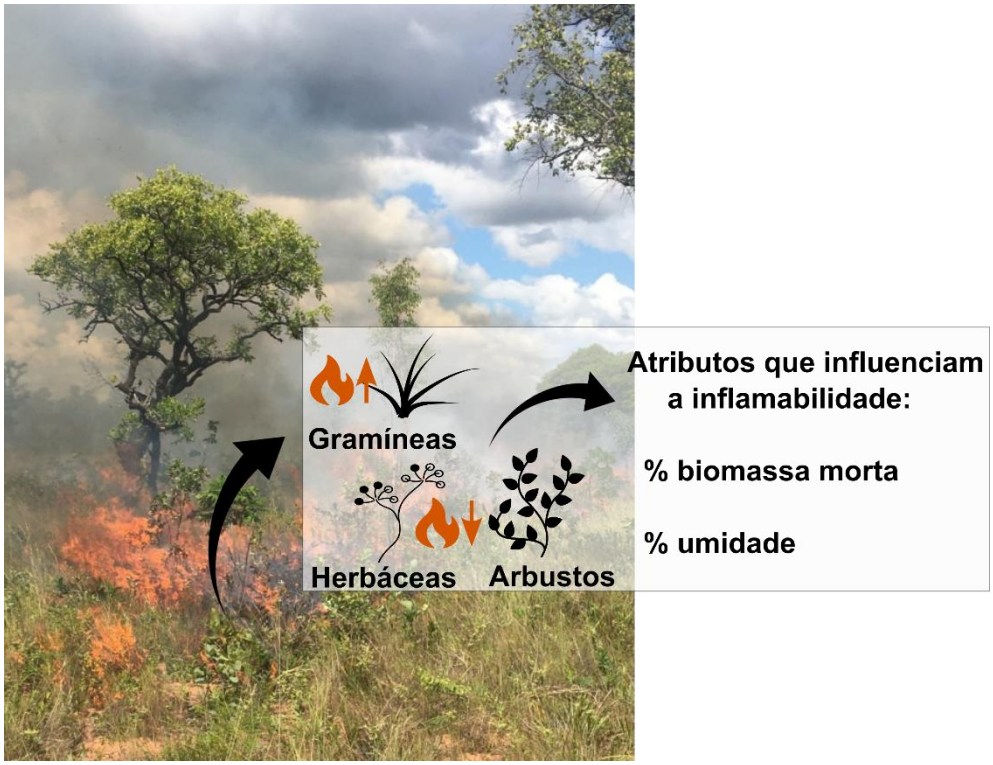

Figura 2: Atributos relacionados à inflamabilidade de áreas savânicas.

Apesar do papel dos insetos na remoção da biomassa de vegetações savânicas ser considerado baixo em relação ao fogo, é possível constatar que este grupo possui uma alta biodiversidade nas savanas tropicais (Fig. 3) (Massad 2023) e que este grupo pode ter um papel secundário na manutenção e determinação destes ecossistemas abertos. Além de ocorrerem nas savanas, os insetos também ocorrem com alta abundância e diversidade nas florestas (Novotny et al. 2006). Sendo assim, existem diferentes grupos de insetos herbívoros, os quais são responsáveis por se beneficiarem de diferentes partes da planta (Schowalter 2006). Dentre os mais comuns, podemos citar insetos mastigadores e sugadores (Schowalter 2006; de Araújo & Oliveira 2021), sendo os insetos mastigadores os principais responsáveis pelo consumo da biomassa vegetal (Andersen & Lonsdale 1990; Costa et al. 2008). Diversos atributos relacionados à presença dos insetos foram selecionados nas espécies vegetais, a fim de garantirem a sua persistência na comunidade vegetal (Schowalter 2006; Maron & Crone 2006).

Atributos físicos como a presença de tricomas e dureza foliar podem impedir o pouso, oviposição e mastigação dos insetos (Løe et al. 2007; War et al. 2012). Além disso, atributos químicos de defesa também são muito comuns nas plantas, como por exemplo a presença de taninos e compostos fenólicos, os quais podem ser induzidos pelas plantas durante a ação dos insetos (Wallace & Mansell 1976; Schowalter 2006; Barbehenn & Peter Constabel 2011). A presença de sílica em gramíneas também contribui para inibir a herbivoria foliar exercida pelos insetos, pois danos no aparato bucal e na digestibilidade podem ser causados (Hunt et al. 2008; Massey & Hartley 2009). Além disso, gramíneas apresentam menores quantidades de nutrientes nas folhas, não atraindo os insetos (Rossatto & Franco 2017). Já na floresta, maiores quantidades de nutrientes (e.g., nitrogênio) podem ser encontrados nas espécies de herbáceas e arbustos e, com isso, atrair os insetos (Rossatto & Franco 2017). Diante disso, podemos observar como diferentes atributos relacionados à presença dos insetos foram selecionados nas espécies vegetais, seja nos ecossistemas savânicos e/ou nos ecossistemas florestais.

Figura 3: Área de campo sujo no Cerrado e a presença de insetos herbívoros na vegetação.

Devido à presença desses distúrbios mantendo a abertura da vegetação principalmente pelo fogo, como nas savanas australianas e sul-americanas, a presença de alta intensidade de luz também se torna um importante fator, fazendo com que atributos relacionados aos altos

níveis de radiação sejam selecionados nas espécies vegetais de savanas (Fig. 4A) (Scholes & Archer 1997; Charles-Dominique et al. 2018). Enquanto isso, nos ecossistemas florestais, a cobertura do dossel propicia a formação de um ambiente sombreado, dificultando a chegada de luz, principalmente nas espécies do estrato herbáceo (Rossatto et al. 2018). Com isso, essas comunidades herbáceas requerem atributos que otimizem a captação da luz no ambiente sombreado (Fig. 4B). A presença de gramíneas C_4 altamente adaptadas às altas incidências de luz (e.g., folhas longas e estreitas) (Charles-Dominique et al. 2018; Pilon et al. 2020) e plantas com pigmentos fotossintetizantes que otimizam a absorção de luz (Rossatto et al. 2018), são encontradas nas comunidades das savanas. Espécies savânicas arbustivas também podem apresentar maiores concentrações de carotenoides em suas folhas, já que este pigmento auxilia na proteção contra o excesso de luz (Franco et al. 2007; Rossatto et al. 2018). Já nos ecossistemas florestais, a necessidade de capturar a luz difusa faz com que folhas largas e delgadas e o aumento na concentração de clorofila total sejam observados nas comunidades do estrato herbáceo, além de uma redução na abundância de gramíneas (Rossatto & Franco 2017; Rossatto et al. 2018; Pilon et al. 2020; Pinheiro et al. 2022). Sendo assim, variações na disponibilidade de luz podem influenciar na seleção de diferentes atributos e, consequentemente, na composição de espécies de savanas e florestas.

Figura 4: A) Sistema savânico e B) Sistema florestal ocorridos nas Reserva Natural Serra do Tombador, Cavalcante, Goiás.

A exclusão do fogo em áreas favoráveis ao estabelecimento de lenhosas, como solos profundos, arenosos e com alta disponibilidade de nutrientes, pode levar a uma substituição das espécies de savana por espécies florestais, ocasionando um adensamento lenhoso e, com o passar do tempo, uma mudança completa de estado (Pinheiro & Durigan 2009; Hoffmann et al. 2012; Rosan et al. 2019). Ao longo dessa mudança, reduções na inflamabilidade do sistema savânico são observadas, visto que gramíneas diminuem drasticamente sua abundância conforme as espécies lenhosas dominam o ambiente (Newberry et al. 2020; Pilon et al. 2020). Porém, em regiões onde as condições climáticas e edáficas não favorecem o crescimento de lenhosas, mudanças no estado da vegetação podem não ocorrer em razão da exclusão do fogo (Hoffmann et al. 2012; Veldman et al. 2015). Neste caso, o que ocorre é um aumento significativo nas quantidades de biomassa do estrato inflamável (gramíneas) (Rodrigues et al.

2021; Rodrigues & Fidelis 2022), podendo ocasionar eventos de fogo severos e intensos, que podem ser difíceis de controlar, colocando áreas adjacentes e sensíveis ao fogo em risco (Fidelis et al. 2018; Bowman et al. 2020).

Além disso, a presença do fogo nas savanas, além de contribuir para a abertura da vegetação, pode favorecer a presença de insetos (Kay et al. 2007; Lopes & Vasconcelos 2011; Ballarin et al. 2024). Áreas savânicas recém queimadas apresentam maiores quantidades de folhas consumidas pelos insetos em comparação a áreas excluídas do fogo (Lopes & Vasconcelos 2011). A presença do fogo também pode aumentar a disponibilidade de recursos para os insetos, visto que novas folhas são produzidas, contendo certos níveis nutricionais, atraindo os insetos (Fagundes et al. 2015). O fogo também pode promover relações mutualísticas inseto-plantas, visto que muitas espécies apresentam folhas com nectários extraflorais que atraem formigas que atuam como defensoras das plantas, por conta da ação dos insetos mastigadores (Delgado et al. 2017; Delgado et al. 2022; Porto et al. 2023). Assim sendo, entendemos que o fogo é um fator ecológico que beneficia não apenas a vegetação, mas também interações ecológicas entre a fauna herbívora das savanas.

Portanto, podemos esperar que em regiões onde savanas e florestas ocorrem, a frequência e variabilidade na ocorrência do fogo, insetos herbívoros e luz podem causar mudanças nos conjuntos de atributos das comunidades vegetais. Com isso, observar tais mudanças em uma escala de comunidade vegetal se faz necessária, a fim de salientar a importância de tais filtros na montagem de comunidades vegetais das savanas. Para isso, podemos investigar tais mudanças em comunidades herbáceas do Cerrado, considerado uma savana mésica, onde formações florestais e abertas coocorrem na paisagem (Coutinho 1982).

OBJETIVOS E ESTRUTURA DA TESE

Visto a importância de se entender sobre a ocorrência do fogo (black world hypothesis), da herbivoria por insetos (brown world hypothesis) e da presença ou ausência de luminosidade (green world hypothesis) na determinação dos ecossistemas savânicos, esta tese tem como principal objetivo avaliar possíveis mudanças nos atributos funcionais das plantas em razão de alterações na ocorrência desses três filtros ambientais. Para isso, utilizamos como modelo para este estudo o Cerrado, considerado a savana mais biodiversa do mundo. Assim, três objetivos específicos foram idealizados:

(i) Como a frequência e o tempo desde o último fogo pode alterar os atributos relacionados à inflamabilidade em áreas savânicas do Cerrado (Capítulo I – ***Fire frequency and time since last fire determine changes on flammability-related traits in tropical savannas)***;

(ii) Como a frequência de fogo e diferentes formas de crescimento podem alterar os atributos relacionados à herbivoria por insetos em áreas savânicas do Cerrado (Capítulo II – ***Fire frequency affects herbivory by insects in open savannas of the Cerrado);***

(iii) Como a frequência de fogo e diferentes formas de crescimento podem alterar os atributos relacionados à herbivoria por insetos em áreas savânicas do Cerrado (Capítulo II – ***Thinking beyond Africa savanas: fire determines savana-forest mosaics, while herbivory by insects plays a secondary role in the Cerrado;***

ÁREA DE ESTUDO E MÉTODOS GERAIS

Este estudo foi desenvolvido na uma Reserva Particular do Patrimônio Natural "Reserva Natural Serra do Tombador" (RNST, 13º 35'38''S, 47º 45'51''W, 8900 ha, 1118 m), localizada no município de Cavalcante, Goiás (Antonelli-Filho 2011); Fig. 5). Nesta Unidade de

Conservação é possível encontrar as diferentes fisionomias de Cerrado, que vão desde vegetações campestres, savânicas e florestais, sendo que a fisionomia de campo sujo é mais predominante na reserva (Antonelli-Filho 2011). Na RNST, a precipitação anual fica entre 1300 – 1500 mm, enquanto que a temperatura varia entre 15ºC – 36ºC (Antonelli-Filho 2011).

Figura 5: Visão geral da Unidade de Conservação onde foi realizado o estudo. Reserva Natural Serra do Tombador, Cavalcante, Goiás.

Para este estudo, selecionamos áreas de Cerrado com diferentes características em relação à frequência e tempo desde o último fogo e variações de luminosidade. Para os Capítulos I e II, selecionamos quatro áreas savânicas com variações de frequência e tempos desde o último fogo (Fig. 6). Duas áreas fazem parte de um experimento de fogo de longa duração, estabelecido na RNST em 2013, com diferentes frequências e épocas de queima (Rissi et al. 2017; Rodrigues et al. 2021). Essas duas áreas classificamos com alta frequência de fogo (11 e 9 eventos de queima nos últimos 21 anos), porém com tempos desde o último fogo distintos (2019 e 2011, respectivamente, Fig. 6A e 6B). As outras duas áreas selecionadas não fazem parte do experimento de longa duração, mas estão localizadas a uma distância de três quilômetros em linha reta do local do experimento. Essas áreas foram classificadas com baixa frequência de fogo (2 e 1 eventos de queima nos últimos 21 anos), sendo o último fogo em 2017

e 2001, respectivamente (Fig. 6C e 6D). Para o Capítulo I, realizamos coletas nas quatro áreas para responder as perguntas relacionadas. Para o Capítulo II, agrupamos as áreas de acordo com a alta e baixa frequência de fogo.

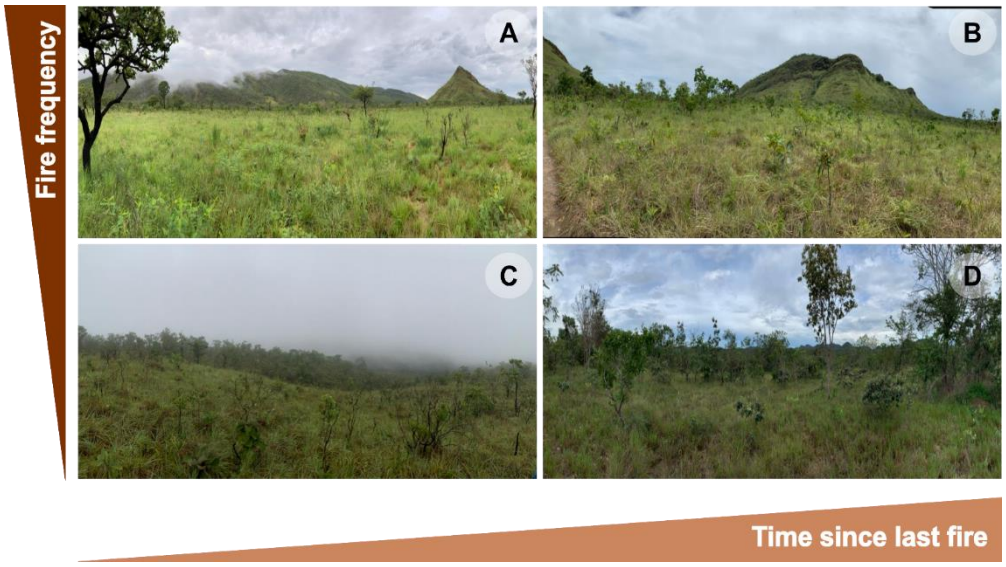

Figura 6: Áreas selecionadas para o desenvolvimento dos experimentos relacionados aos Capítulos I e II na Reserva Natural Serra do Tombador, Cavalcante, Goiás.

Já para o Capítulo III, selecionamos três áreas com diferentes frequências e históricos de fogo e diferentes níveis de luminosidade (Fig. 7; ver informações no cap. III). Assim, selecionamos uma área de savana aberta (*open savanna*), uma área de savana lenhosa (*woody savanna*) e uma área florestal (*forest*). A área de savana aberta é a mesma utilizada nos experimentos dos capítulos anteriores, pertencendo ao experimento de fogo. Já as outras duas áreas, encontram-se próximas uma da outra e próximas da área experimental.

Figura 7: Áreas selecionadas para o desenvolvimento do experimento relacionado ao Capítulo III, na Reserva Natural Serra do Tombador, Cavalcante, Goiás. A: Open savana; B; Woody savana; C:Forest.

Em cada uma das diferentes áreas selecionadas, subparcelas de 1x1m foram estabelecidas, para realização de um levantamento de espécies presentes no estrato herbáceo (graminóides, herbáceas e arbustos ≤1,5m), a fim de selecionarmos as espécies mais abundantes de cada uma das comunidades para a coleta de atributos (Fig. 8). Detalhes do delineamento experimental em cada uma das áreas estão presentes ao longo dos três capítulos. Para cada capítulo, um conjunto de atributos funcionais foi selecionado (Tab. 1) e cada um dos atributos foram mensurados a nível individual, seguindo seus respectivos protocolos de coleta e medição.

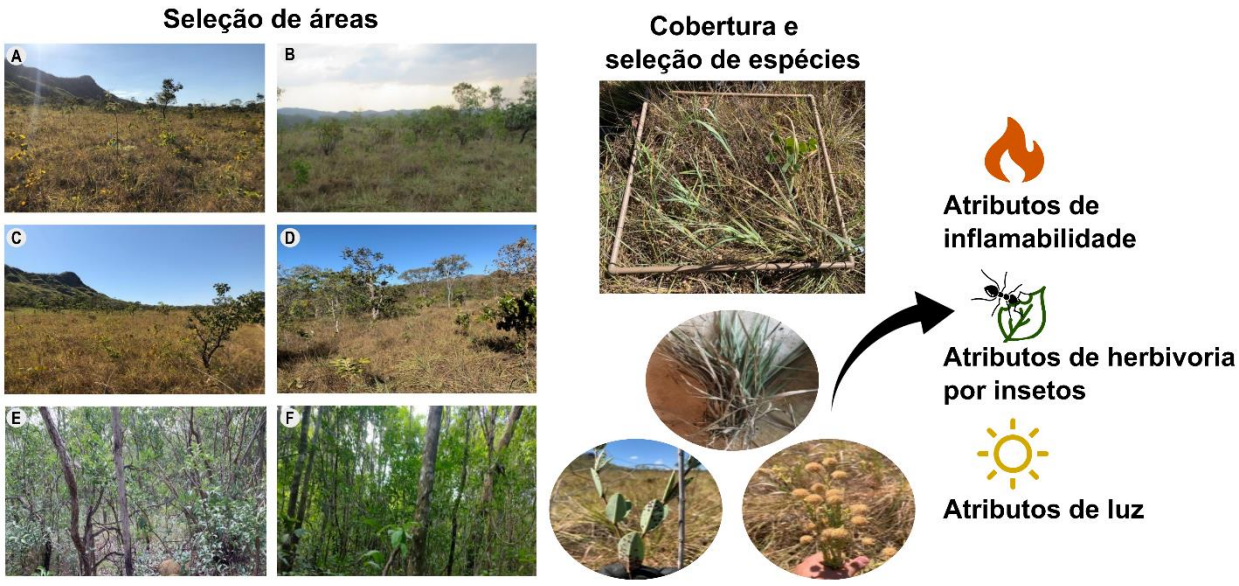

Figura 8: Representação do procedimento de seleção de áreas, amostragem de espécies e coleta de atributos na Reserva Natural Serra do Tombador, Cavalcante, Goiás. Para o capítulo I e II, utilizamos as áreas A, B, C e D e para o capítulo III, utilizamos as áreas A, E e F para a realização dos experimentos

e coletas de atributos. A: open savanna with high fire frequency (11 fires in the last 21 years), recently burned in 2019; B: open savanna with low fire frequency (2 fires in the last 21 years) burned in 2017; C: open savannas with high fire frequency (9 fires in the last 21 years) burned in 2011; D: open savannas with low fire frequency (1 fire in the last 21 years), occurred in 2001. E: woody savanna, mixed with trees and grasses, burned in 2017; F: forest (Cerradão), with no fire occurrence.

Tabela 1: Lista dos atributos funcionais relacionados ao fogo, herbivoria por insetos e luz e seus usos durante a elaboração de cada capítulo da tese. Atributos coletados em diferentes áreas de Cerrado na RNST e seguindo os devidos protocolos de coleta e medição.

	Capítulo		
Atributo	**I**	**Capítulo II**	**Capítulo III**
Atributos relacionados à inflamabilidade			
Teor de umidade da planta (%)	x		x
Quantidade de biomassa morta da planta (%)	x		x
Temperatura máxima atingida (ºC)	x		
Quantidade de biomassa consumida (%)	x		
Taxa de queima ($cm.s^{-1}$)	x		
Índice de inflamabilidade			x
Atributos relacionados à herbivoria por insetos			
Porcentagem de folha consumida (%)		x	x
Concentração de taninos condensados ($mg.g^{-1}$)		x	x
Concentração de fenólicos totais ($mg.g^{-1}$)		x	x
Atributos relacionados à luz			
Comprimento e largura foliar (cm)			x
Clorofila total ($\mu g.cm^{-2}$)			x
Razão clorofila a:b ($\mu g.cm^{-2}$)			x
Carotenoides ($\mu g.cm^{-2}$)			x

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2. CAPÍTULO I

Fire frequency and time since last fire determine changes on flammability-related traits in tropical savannas

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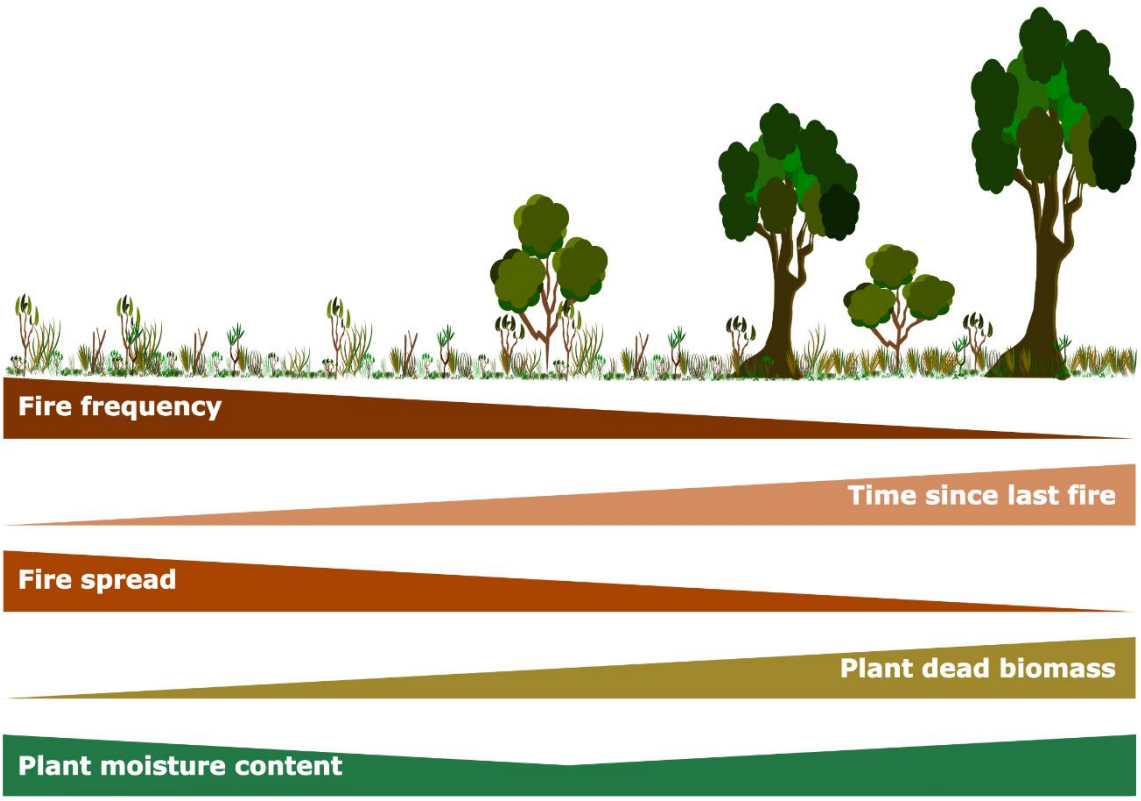
Abstract

In tropical savannas, the fire regime can vary in intensity, frequency, and extent, selecting for functional syndromes of flammability-related traits that influence the functional composition of plant communities, thereby affecting the way fire spreads across the landscape. Alterations in the fire regime of the savannas, such as fire frequency and time since last fire, can be responsible for changes in the flammability-related traits of species, thus affecting the fire behavior. Therefore, we aimed to investigate changes in flammability-related traits among four plant communities differing in fire frequency and time since last fire and among common grass species occurring in frequently burned and fire excluded areas. We selected four areas of savannas in the Cerrado with different fire frequencies (11, 7, 2, and 1 fire in the last 21 years) and time since the last fire (2019, 2011, 2017, and 2001, respectively). We selected the most abundant species and measured five flammability-related traits (biomass moisture content, dead biomass, maximum fire temperature, amount of burned biomass, and burn rate) on individuals of grasses, forbs, and shrubs of the four areas. Our results showed changes in flammability-related traits, and the area with frequent and recent fire occurrence differed to the area with last fire occurrence in 2001. These differences were observed especially due to the amounts of dead biomass, which influence the burn rate. In the area excluded from fire since 2001, plants burned slowly, due to high dead biomass accumulation mostly in grass species, while fire spreads more rapidly in plants from the frequently burned area. Such differences in the spread of fire could affect fire intensity and severity, modifying fire behavior. We conclude that the fire frequencies and the time since last fire contribute to changes in the flammability-related traits, affecting the burning process and fire behavior, thus impacting the system's flammability.

Keywords: flammability-related traits; fire frequency; time since last fire; fire regime; Cerrado; plant dead biomass, fire spread.

Graphical Abstract



Introduction

Fire-prone ecosystems exhibit distinct fire regimes worldwide that vary in terms of intensity, frequency, and extent (Archibald et al. 2013). In tropical savannas, fire regimes are diverse (Simpson et al. 2022), and fires can be intense and spread over large areas (e.g., Australian savannas; Archibald et al. 2013). In the savannas of Africa and South America, (e.g., Cerrado), fires occur in a mixture of large and small areas, with low or high intensity (Archibald et al. 2013). Fire regimes can act by selecting functional syndromes of fire-related traits, influencing the functional composition and diversification of plant communities, which in turn can affect the way that fire spreads across the landscape (Bond & Van Wilgen 1996; Keeley et al. 2011; Pausas & Bond 2022; Simpson et al. 2022). Furthermore, the way fire spreads and burns can be assessed through the measurement of flammability – which is characterized by a suite of individual plant traits that provide certain organs/tissues a capacity to burn and sustain fire under given environmental conditions (Pausas et al. 2017). Thus, studies investigating the relationships between fire regime and flammable components of the vegetation could help us predict fire behavior and even fire risk, contributing to improve future decisions on fire management techniques.

In tropical savannas, a diverse set of plant growth forms occur side by side (e.,g, trees, shrubs, forbs and grasses), but grasses are the plants which possess the most flammable plant tissues (Simpson et al. 2016; Zanzarini et al. 2022). In the Cerrado, fire normally consumes around 90% of the herbaceous layer biomass, particularly in open savannas (Rissi et al. 2017), because grasses are the major component of the fuel load (Coutinho 1982). This high combustion efficiency is associated with the presence of grass traits that allow them to burn easily and quickly (e.g., plant dead biomass amount, low plant moisture content, aerated and fine biomass, low leaf thickness and length, and high carbon:nitrogen ratio) (Hempson et al. 2019; Archibald et al. 2019; Zanzarini et al. 2022). Their high flammability contributes to

determining how plant parts start and sustain fire throughout the plant community, thus affecting fire behavior (Simpson et al. 2016; Pausas et al. 2017). In addition to grasses, it is also possible to find a high diversity of plants that are less flammable, such as forbs and shrubs (Zanzarini et al. 2022). These plants exhibit traits (e.g. high leaf water content, lower amount of dead biomass) that reduce their flammability (Zanzarini et al. 2022). Thus, the heterogeneous functional composition of the herbaceous layer in tropical savannas influences the spread of fire throughout the vegetation and its behavior (Bond & Van Wilgen 1996; Pausas & Keeley 2009), besides being an essential determinant of the fire regime (Simpson et al. 2022).

However, the fire regime of tropical savannas has been altered in the past years (Kelley et al. 2019; Bowman et al. 2020). Human activities and management decisions can respectively increase (Lasslop & Kloster 2017) or decrease fire events (Andela et al. 2017), due to land use around native areas and the zero-fire policies in flammable areas (Fidelis et al. 2018; Bowman et al. 2020). In the Cerrado, for example, the fire interval is between one to five years (Eiten 1972; Pivello 2011), but certain areas are experiencing longer periods without fire, thus affecting the fuel load and subsequent fire events (Pivello 2011; Fidelis et al. 2018). Alterations in fire frequency can significantly change the vegetation structure and composition of savannas, especially modifying grass traits, such as biomass amounts (Simpson et al. 2022; Rodrigues & Fidelis 2022). Across savanna-forest transitions, decreases in flammability are observed as the flammable grass layer is suppressed by tree cover (Newberry et al. 2020). Furthermore, savannas excluded from fire where climate and edaphic conditions favor tree establishment can transition from an open to a closed ecosystem (Abreu et al. 2017; Rosan et al. 2019), decreasing the flammability of the system (Hoffmann et al. 2012; Newberry et al. 2020). However, savannas occur along a varied range of environmental conditions, and even in the absence of fire, some savanna areas may not transition to a forest vegetation state, as soil conditions can limit tree growth, for example (Hoffmann et al. 2012; Veldman et al. 2015). In these situations,

biomass accumulation of the grass layer occurs over the years without fire (Fidelis et al. 2013; Rodrigues & Fidelis 2022), increasing fire risk and modifying fire intensity and spreading across the landscape (Zupo et al. 2022). Thus, changes in the flammable components of the vegetation can be investigated in savanna areas that are under different fire occurrences (e.g., fire frequency and year since last fire).

In this study, we aimed to evaluate how flammability-related traits change in areas of open savannas in the Cerrado that are under different fire frequencies and time since last fire. Therefore, we assessed individual plant moisture content, plant dead biomass amount, plant maximum temperature reached, burned biomass, and burn rate in herbaceous layer plant communities. Such traits were sampled in graminoids, forbs, and shrubs present in four areas with high (11 and 7 fires in the last 21 years) and low fire frequencies (2 and 1 fires in the last 21 years) and distinct time since the last fire (2001, 2011, 2017, 2019), respectively, to answer the following questions:

(a) Do flammability-related traits change according to fire frequency and time since last fire? We expect that areas with high fire frequency and recent time since last fire will exhibit plants burning more rapidly and being almost entirely consumed by fire, as these plants can exhibit aerated fuels (Simpson et al. 2016; Simpson et al. 2022). In areas excluded from fire, we expect to find plants taking more time to burn due to high amounts of biomass, especially in grasses, which will exhibit condensed and humid tussocks, decreasing the spread of fire.

(b) Will the dominant grasses in areas with different fire frequencies and time since last fire differ in their flammability-related traits? As grasses are the most flammable group in the herbaceous layer of open savannas (Zanzarini et al. 2022), we expect that the most dominant grasses of each area will exhibit differences in their flammability-related traits. We are expecting to find individuals with higher moisture content and more accumulated dead biomass in the fire-excluded area, while grasses in the frequently burned area will exhibit low amounts

of dead biomass and lower moisture content. Therefore, grasses in the fire-excluded area will burn slower, while grasses in the frequently and recently burned area will burn more rapidly.

Material and methods

Study site

The study was conducted at the Reserva Natural Serra do Tombador (RNST, 13º 35'38''S, 47º 45'51''W, 8900 ha, 118 m a.s.l), Central Brazil, in the savannas of the Cerrado. The climate in the region is tropical, with a marked dry season occurring between May to October. The mean annual rainfall is 1300-1500 mm and mean temperature is 20ºC - 25ºC (Antonelli-Filho 2011). These savannas are composed by a species-rich herbaceous layer, dominated by C_4 grasses, forbs, small shrubs with sparse trees (Coutinho 1982).

We selected four areas of open savannas at the RNST to sample species traits at the end of September/ 2021. These areas were subjected to different fire frequencies and time since last fire in the last 21 years (Fig. 1). Two areas are part of a long-term fire experiment established at the RNST in 2013, with different plots submitted to different fire treatments (season and frequency, Rissi et al. 2017; Rodrigues et al. 2021). We selected two areas subjected to high fire frequency (HF): one with 11 fires, being the last fire occurrence in 2019 (HF-Burned; Fig. 1A) and the other with seven fire occurrences, with the last fire occurring in 2011 (HF-Unburned; Fig. 1B). The other two areas are not part of the long-term fire experiment but are located close to the experimental area (three kilometers in a straight line) and have low fire frequency (LF): both suffered just two and one fires, respectively, in the last 21 years, with last fire occurrence in 2017 and 2001, respectively (LF-Burned; Fig. 1C and LF-Unburned; Fig.1D).

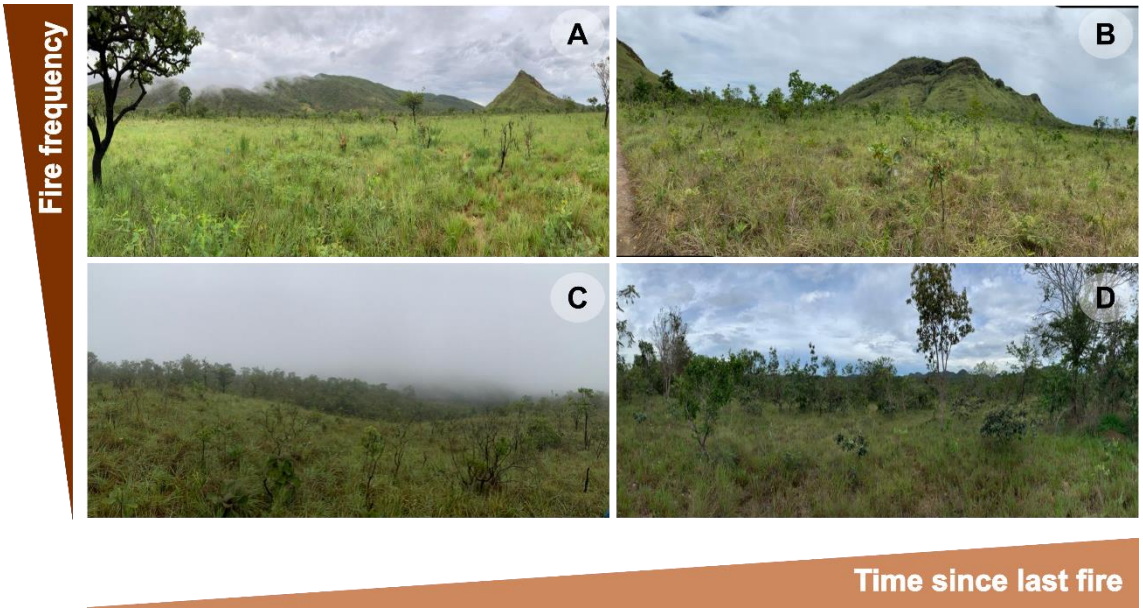


Figure 1: The four selected areas used to sample the flammability traits related to the species that represent 80% of total community abundance in each area. **HF-Burned:** High fire frequency, recently burned (burned in 2019); **HF-Unburned:** High fire frequency, fire-excluded (fire exclusion since 2011); **LF-Burned:** Low fire frequency, recently burned (burned in 2017); **LF-Unburned:** Low fire frequency, fire-excluded (fire exclusion since 2001). The areas are open savannas of Cerrado in Central Brazil.

Methods

Community composition and species selection

For each area, we randomly established 30 1x1m plots and visually estimated plant cover (%, according to Wikum & Shanholtzer 1978) of all species from the herbaceous layer (graminoids, forbs, and shrubs ≤1.5 m; Tab. SI1), during the dry season (September/2021). Afterwards, we selected the species that represented 80% of the entire community abundance in each area (following Magurran 2004), and measured flammability-related traits. We measured in total 10 individuals/species, considering five individuals/species for measuring plant traits in the laboratory (e.g., plant moisture content and plant dead biomass amount), the other five individuals were burned using an equipment to flammability components in the field, as described below. During the burn experiments, we measured the remaining traits (e.g., plant maximum temperature reached, burn rate, and burned biomass).

Trait measurements

We selected five flammability-related traits and measured them at the individual level to assess the differences in the flammability among the four areas. We sampled the traits at the dry season (ending of September/2021). We measured the total individual moisture content (%) and the percentage of attached dead biomass (%) in five individuals per species. To calculate moisture content, we obtained the fresh weight of the entire individual biomass in the field and the dry weight in the laboratory, drying the samples at 80 ºC for 48 hours. To obtain the percentage of dead biomass, we sorted the individual biomass in the lab, into live and dead biomass, and used the dry weight to calculate the percentage of dead material in relation to the total weight of each individual.

Afterward, we used another five individuals to assess plant traits through flammability experiments. We burned and measured the individuals, obtaining the plant maximum temperature (ºC), burned biomass (%), and the burn rate ($cm.s^{-1}$), following the methods described by Jaureguiberry et al. (2011). Using an equipment to measure flammability components in plant shoots (Jaureguiberry et al. 2011; Fig. SI 1), we burned each sample (entire individual) separately and during this process, we measured the three traits mentioned above. The plant maximum temperature (ºC) was obtained using an infra-red thermometer (Bosch 1000ºC) that was directed to the plant individual during the burn process, obtaining the maximum value of temperature reached during the burning process by the plant individual. The burned biomass (%) was visually estimated, determining the individual biomass percentage consumed by fire after the burning process. And the burn rate ($cm.s^{-1}$) was obtained after measuring the length of the burnt portion of the shoot (cm) and the time (s) of the burning process, dividing the length/time for each plant individual (Jaureguiberry et al. 2011).

Data analysis

To investigate how flammability-related traits differ among areas, we first calculated the Community Weighted Mean (CWM) matrix, which represents the abundance-weighted mean trait value for each 1x1m plot in the four areas (HF-Burned, HF-Unburned, LF-Burned, and LF-Unburned). The CWM matrix combines the species abundance data for each plot with the mean trait values (plant moisture content, plant dead biomass, plant maximum temperature, burned biomass, and burn rate) of each species (Kleyer et al. 2012). After, to explore how flammability-related traits (plant moisture content, plant dead biomass, plant maximum temperature, burned biomass, and burn rate) were associated with the sampling units (CWMs values) of each area, we performed a Principal Component Analysis (PCA) using Euclidean distance as resemblance measure. To assess whether there were significant differences of flammability-related traits among areas (plant moisture content, plant dead biomass, plant maximum temperature, burned biomass and burn rate), we conducted a permutational multivariate variance analysis (PERMANOVA), with 1000 permutations. Additionally, we performed pairwise post-hoc tests of HSD Tukey type, using the Bonferroni correction method, to compare the differences in flammability among the different areas.

We also explored the differences in each flammability-related traits (plant moisture content, plant dead biomass, plant maximum temperature, burned biomass, and burn rate) for all plant community within the studied areas (HF-Burned, HF-Unburned, LF-Burned, and LF-Unburned). To do this, we constructed Generalized Linear Mixed Models (GLMMs) with Gaussian distribution, using the CWMs matrix for each trait and considering the areas as a fixed factor and the plots as random factor. After, we conducted a *lsmeans* test (Tukey method) to compare the areas pairwise.

To answer if the most common grass species occurring in the frequently and recently burned area (HF-Burned) and in the fire-excluded area (LF-Unburned) have different

flammability-related traits, we selected the three most abundant (%) species for each area (HF-Burned: *Mesosetum ferrugineum* (29%), *Elionurus muticus* (14%), *and Trachypogon spicatus* (5%); LF-Unburned: *Mesosetum lolliforme* (40%), *Paspalum thrasyoides* (20%), *and Trachypogon spicatus* (8%). We constructed Generalized Linear Mixed Models (GLMMs) with Gaussian distribution and considered the areas as a fixed factor and the individuals as a random factor for each flammability-related trait (plant moisture content, plant dead biomass, plant maximum temperature, burned biomass, and burn rate). To compare the areas pairwise, we performed a *lsmeans* post-hoc test (Tukey method).

All analyses were conducted in the R environment (R Core Team 2018), using the packages *FD* (Laliberté et al. 2014), *Vegan* (Oksanen et al. 2018), *RVAdeMemoire* (Hervé 2022), *lme4* (Bates et al. 2015), and *lsmeans* (Lenth 2016).

Results

Changes in flammability-related traits were observed among the plant communities in the four study areas, based on CWMs matrix (plot by trait, PERMANOVA, $F= 27.05$; $p= 0.03$). The flammability-related traits of plants in the HF-Burned area were completely different from those in the LF-Unburned area ($p= 0.02$), and both areas had plants with different flammability-related traits when compared to the plants in the HF-Unburned and LF-Burned areas ($p < 0.05$). However, plants in the HF-Unburned and LF-Burned areas exhibited similar flammability-related traits ($p= 0.15$). These differences are illustrated in the first two axes of the PCA, which accounted for 70% of the total variation (Fig. 2). The HF-Burned area was separated from the other three areas, especially the LF-Unburned area (Fig. 2). Additionally, we also observed that the plants in the HF-Burned area were more associated with the burn rate, burning faster, while

plants in the LF-Unburned area were associated with the plant dead biomass amount, showing high amounts of dead biomass (Fig. 2).

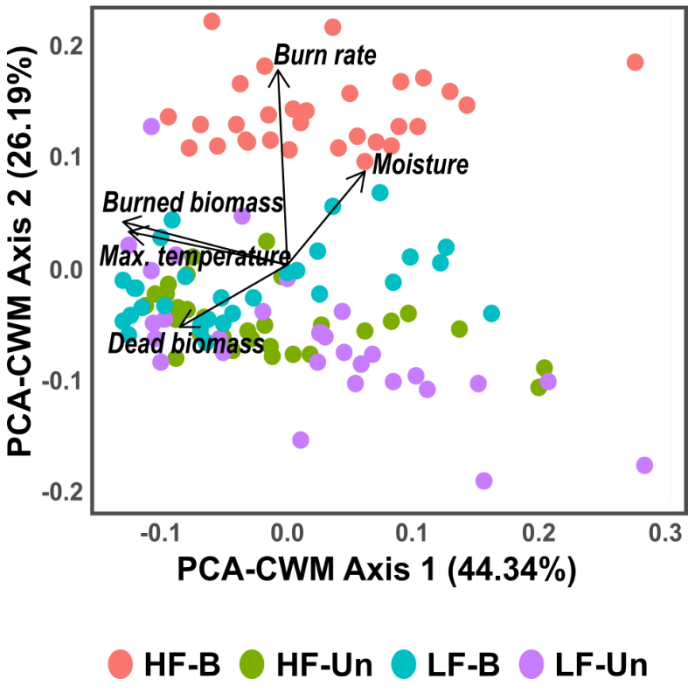


Figure 2: Principal Component Analysis (PCA) considering the CWMs matrix (plot by traits) of each area (**HF-Burned** with 11 fires and the last fire in 2019; **HF-Unburned** with nine fires and the last fire in 2011; **LF-Burned** with two fires and the last fire occurrence in 2017; **LF-Unburned** with one fire and last fire 2001) and the associated flammability-related traits (moisture content, dead biomass, maximum temperature, burned biomass, and burn rate) sampled in open savannas in Central Brazil. Each point represents the sampling unit in the CWM matrix (30 plots/area).

Plants in the HF-Unburned area exhibited the lowest moisture content among all studied areas (29.71±1.82%; $p<0.05$; Fig. 3A; Tab. SI2). Additionally, plants in the HF-Burned and LF-Unburned areas had similar moisture content between them, showing more than 30% of water in their biomass ($p= 0.91$; Fig. 3A; Tab. SI2). The LF-Unburned area showed plants with more than 80% of dead biomass (Fig. 3B; Tab. SI2). On the other hand, plants in the HF-Burned area exhibited 56% of dead biomass, being the lowest percentage among areas ($p< 0.05$; Fig. 3B; Tab. SI2).

Plants from all areas presented similar maximum temperature values, reaching temperatures of up to 650ºC (p= 0.07; Fig. 3C; Tab. SI2). There is no difference in burned plant biomass among areas, with more than 80% of the plant being consumed by fire in all areas (p= 0.17; Fig. 3D; Tab. SI2). However, plants in the HF-Burned area were consumed more rapidly by fire, with a burning at a rate of 1 $cm.s^{-1}$ (p< 0.0001; Fig. 3E; Tab. SI2). On the other hand, plants in the LF-Unburned area spent more time being consumed, burning slowly and at a rate of < 0.5 $cm.s^{-1}$, and differently from the other three areas (p< 0.05; Fig. 3E; Tab. SI2).

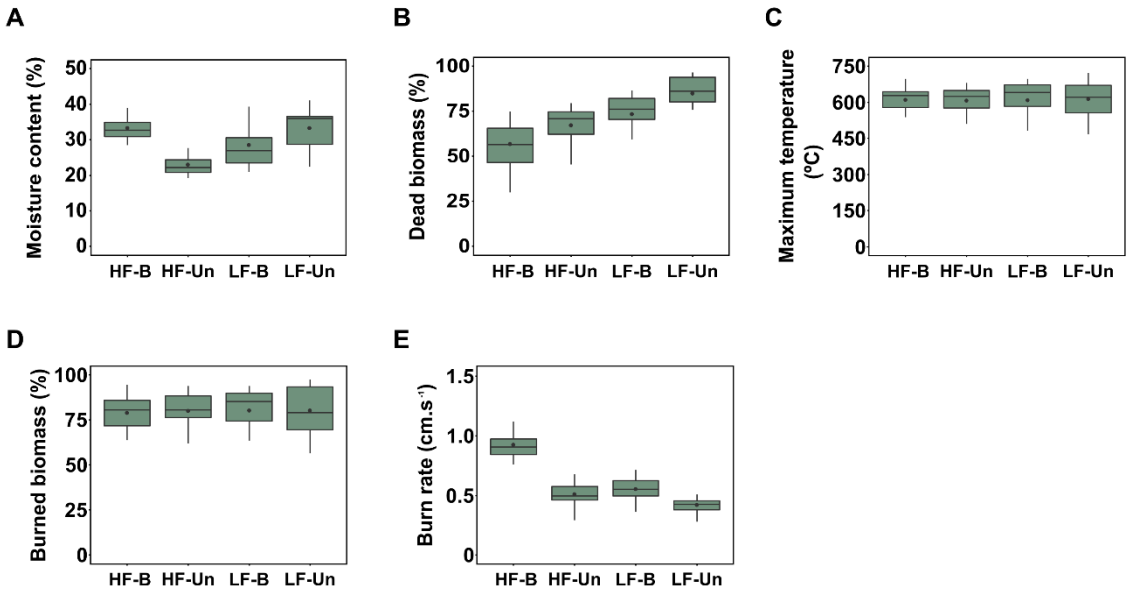


Figure 3: Flammability-related traits (**A-** moisture content, **B-** dead biomass, **C-** maximum temperature, **D-** burned biomass, and **E-** burn rate) measured in species from open savannas in Central Brazil in different areas: **HF-Burned** with 11 fires and the last fire in 2019; **HF-Unburned** with nine fires and the last fire in 2011; **LF-Burned** with two fires and the last fire occurrence in 2017; **LF-Unburned** with one fire and last fire 2001). Boxplots represent the median and the first and third quartiles.

When comparing the most common grasses occurring in the HF-Burned and LF-Unburned areas, we observed that grasses had similar moisture content (p= 0.27; Fig. 4A). However, grasses in the LF-Unburned exhibited higher amounts of dead biomass compared to the ones in the HF-Burned area (p= 0.05; Fig. 4B). Grasses also reached similar maximum temperatures in both areas (p= 0.5; Fig. 4C), but they had a higher percentage of their biomass

burned HF-burned (~95% of burned biomass) than grasses from the LF-Unburned area (~80% of burned biomass, p= 0.05; Fig. 4D). Finally, grasses burned faster (~1 $cm.s^{-1}$) in the HF-Burned, while in the LF-Unburned area they burned 70% slower (~0.3 $cm.s^{-1}$, p= 0.0002; Fig. 4E).

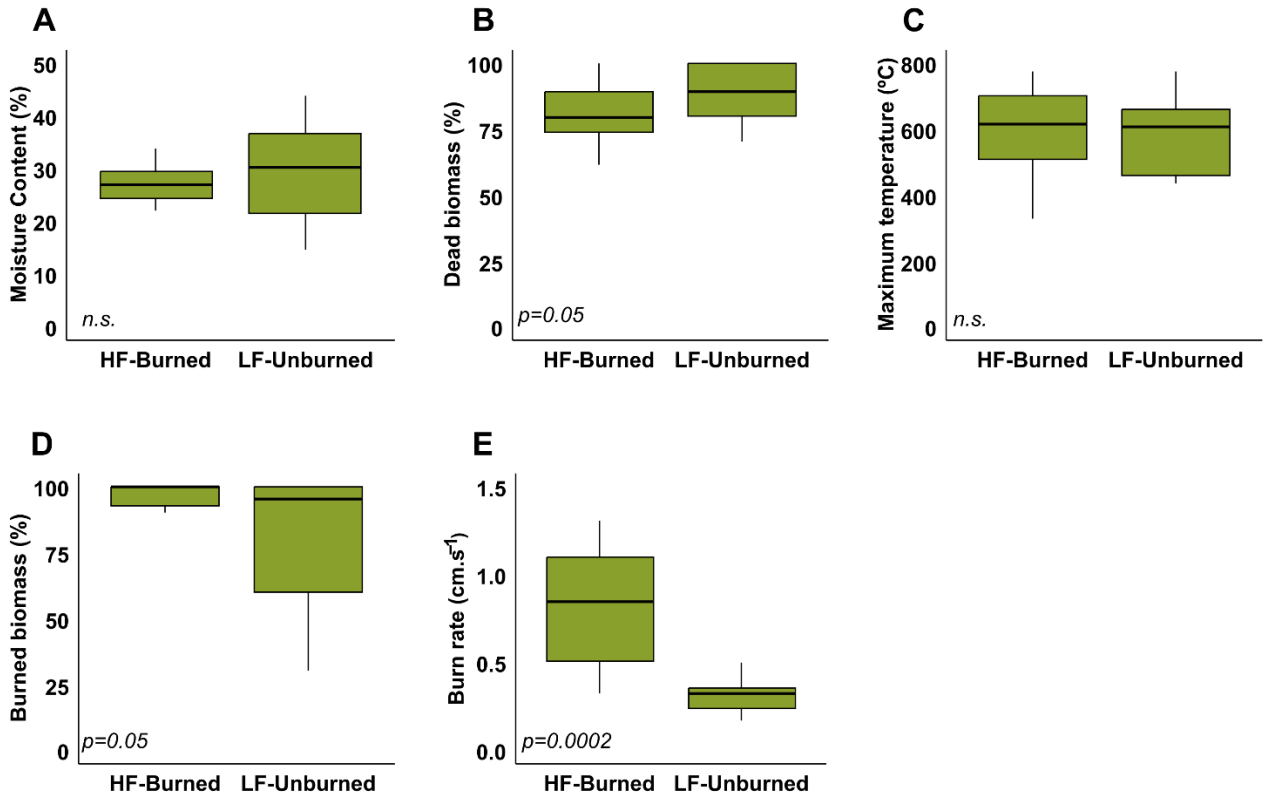


Figure 4: Flammability-related traits of the three most common grasses occurring in the HF-Burned area (*Mesosetum ferrugineum, Elionurus muticus, and Trachypogon spicatus*) and LF-Unburned area (*Mesosetum lolliforme, Paspalum thrasyoides, and Trachypogon spicatus*). (**A-** moisture content, **B-** dead biomass, **C-** maximum temperature, **D-** burned biomass, and **E-** burn rate) measured in different areas of open savannas in Central Brazil: **HF-Burned** with 11 fires and the last fire in 2019 and **LF-Unburned** with one fire and last fire 2001). Boxplots represent the median and the first and third quartiles.

Discussion

We showed in this study that fire frequency and time since last fire play a major role in how plant communities will burn in open savannas in the Cerrado. Flammability-related traits in these plant communities varied mostly in terms of dead biomass amount, especially between

the area with frequent and recent fire occurrence (HF-Burned) and the fire-excluded area (LF-Unburned). These plant traits significantly influence the burning process of plants (Simpson et al. 2016; Zanzarini et al. 2022), playing a major role of how the system will burn. In the HF-Burned area, the non-accumulated biomass of plants increased burn rate, while in the area excluded from fire for more than twenty years (LF-Unburned), the high amount of dead biomass of plants decreased burn rate. Furthermore, we found that the three most dominant grasses in the HF-Burned area exhibited individuals with low amounts of dead biomass compared to the three dominant grasses in the LF-Unburned area. These differences affected the burn rate and burned biomass, as grasses from HF-Burned were more rapidly and almost entirely consumed by fire, while the opposite was observed for grasses in the fire-excluded area. Thus, these flammability-related traits are responsible for influencing the way fire spreads through the herbaceous layer, affecting the system's flammability of open savannas under different fire frequencies and times since last fire.

The frequent occurrence of fire in savannas enhances the diversity of grasses, forbs, and shrubs (Rodrigues & Fidelis 2022) and controls the accumulation of dead biomass in the herbaceous layer (Zupo et al. 2022; Rodrigues & Fidelis 2022), which influences the fire spread. In the HF-Burned area, grasses composed 70% of the herbaceous layer, while shrubs and forbs covered 17%, 11% of the ground, respectively (Fig. SI2), influencing thus the distribution of flammability-related traits of the plant community (Zanzarini et al. 2022). As fire presence was frequent in the HF-Burned area, plants did not have time to accumulate large amounts of dead biomass, especially grasses, which contributed to higher burn rates. In this area, moisture content was over 30%, probably influenced by the presence of forbs and shrubs, which are more humid and less flammable than grasses (Zanzarini et al. 2022). Although the presence of forbs and shrubs could influence the burning process, grasses are still the main component of the

herbaceous layer and drive how the herbaceous layer burns, being more rapidly consumed by fire and thus, increasing the burn rate of the plant community.

On the other hand, the exclusion of fire for more than twenty years significantly promoted the accumulation of large amounts of dead biomass, mostly in grasses (> 80% of dead biomass). Grasses covered more than 97% of the ground (Fig. SI2), exhibiting individuals with large, condensed, and humid tussocks, leading to a decrease in the burn rate (Tab. SI2). The presence of condensed biomass in grass tussocks avoids oxygen circulation (Simpson et al. 2016; Archibald et al. 2019), resulting in fire spending a long time consuming plant individuals, as observed in our study. Furthermore, different plant architecture and biomass amount can also influence how grasses can start and sustain the fire, influencing the fire behavior (Zanzarini 2019). Thus, the amount of dead biomass, especially accumulated by grasses, influences how fire spreads in the herbaceous layer of open savannas, consequently affecting the fire regime, which is mostly dependent on grass trait diversity (Simpson et al. 2022).

The exclusion of fire can promote severe and high-intensity fires (Fidelis et al. 2018; Zupo et al. 2022), which is not the common fire behavior in savannas (Archibald et al. 2013; Rissi et al. 2017). These areas might be considered at risk for uncontrolled fires (Fidelis et al. 2018) and, if a fire occurs, the difficulty in controlling the flames can threaten areas that are fire-sensitive, such as gallery forests and other forest patches (Durigan & Ratter 2016; Fidelis 2020). These extreme fire events in savannas can negatively impact the regrowth of savanna trees and shrubs since the aboveground buds are affected (Chiminazzo et al. 2021). The long years without fire also reduces the diversity and the number of belowground bud-bearing structures, which can compromise the resilience of savannas (Bombo et al. 2022). Furthermore, some fire-excluded areas have already shifted from an open to a closed ecosystem (Abreu et al. 2017; Rosan et al. 2019). These changes caused by woody encroachment reduces the grass layer, and as a result, the system is not flammable anymore (Hoffmann et al. 2012; Newberry

et al. 2020). Thus, it is important to emphasize that the frequent presence of fire in the savannas is necessary to avoid the high accumulation of biomass, preventing uncontrolled fires and maintaining the vegetation structure suitable for herbaceous species.

Thus, assessing flammability-related traits of species can help us to understand and predict fire behavior in savannas (Archibald et al. 2018). Nevertheless, it is also important to investigate changes in the flammability-related traits of plant communities under different fire regimes and incorporate this information into fire models (Simpson et al. 2022). These contributions can elucidate the relationship between fire and vegetation in the context of climate change, enhancing the robustness of models predicting fire behavior across savanna landscapes (Simpson et al. 2022). In conclusion, we need to consider that fire frequency, along with the time since last fire, can influence the system flammability in savannas of the Cerrado. The accumulation of dead biomass creates condensed and humid material in the herbaceous layer, decreasing the spread of fire, thereby impacting fire behavior and the system flammability in areas excluded from fire.

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Support information

Supplementary material included in the end of this document.

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Support Information

Table SI 1: Species cover (%) for each of the four areas of savannas in Cerrado Central Brazil. HF-Burned: with 11 fires, last fire 2019; HF-Unburned: with 9 fires, last fire 2011; LF-Burned: with 2 fires, last fire 2017; LF-Unburned: with 1 fire, last fire 2001.

Growth form	Family	Species	HF-B	HF-Un	LF-B	LF-Un
	Poaceae	*Andropogon* sp.	2.73	0	1.68	0
	Poaceae	*Anthaenantia lanata* (Kunth) Benth	2.32	5.44	0	0
	Poaceae	*Aristida setifolia* Kunth	0	13.70	0	2.48
Grass	Poaceae	*Arthropogon villosus* Nees	0	0	0	2.52
	Poaceae	*Axonopus aureus* P. Beauv.	2.76	0	2.41	5.30
	Poaceae	*Elionurus muticus* (Spreng.) Kuntze	14.33	2.68	3.96	0
	Poaceae	*Mesosetum ferrugineum* (Trin.) Chase	29.14	31.31	31.30	14.02
	Poaceae	*Mesosetum loliiforme* (Hochst.) Chase	3.34	3.08	10.15	40.70
	Poaceae	*Oncorachis ramosa* (Zuloaga & Soderstr.) Morrone & Zuloaga	4.98	19.73	6.68	1.48
	Poaceae	*Paspalum gardnerianum* Nees	0	0	1.66	0
	Poaceae	*Paspalum pectinatum* Nees ex Trin.	5.05	5.55	0	0
	Poaceae	*Paspalum thrasyoides* (Trin.) S.Denham	0	0	0	20.58
	Poaceae	*Sporobolus cubensis* Hitchc.	0	0	0	2.22
	Poaceae	*Trachypogon spicatus* (L.f.) Kuntze	5.67	0	27.62	8.66
	Poaceae	*Trichanthecium cyanescens* (Nees ex Trin.) Zuloaga & Morrone	0	2.44	0	0

	Poaceae	*Trichanthecium* sp.	0	0	3.59	0
Total grass cover			**70.32**	**83.93**	**89.06**	**97.97**
	Asteraceae	*Ayapana amygdalina* (Lam.) R.M.King & H.Rob.	0	0	1.65	0
	Asteraceae	*Ichthyothere hirsuta* Gardner	1.53	0	0	0
Forb	Acanthaceae	*Ruellia nitens* (Nees) Wassh.	4.06	1.59	0	0
	Euphorbiaceae	*Croton gracilescens* Müll.Arg.	6.12	4.98	2.27	0
	Gentianaceae	*Calolisianthus speciosus* (Cham. & Schltdl.) Gilg	0	0	1.44	0
Total forb cover			**11.71**	**6.57**	**5.35**	**0**
	Fabaceae	*Bauhinia dumosa* Benth.	4.76	3.44	1.56	0
	Fabaceae	*Calliandra dysantha* Benth.	1.94	0	1.66	0
Shrub	Fabaceae	*Chamaecrista ochrosperma* (H.S.Irwin & Barneby)	3.08	0	0	0
	Fabaceae	*Mimosa pteridifolia* Benth.	8.18	6.06	0	0
	Moraceae	*Brosimum gaudichaudii* Trécul	0	0	0	2.03
	Vochysiaceae	*Vochysia pumila* Pohl	0	0	2.37	0
Total shrub cover			**17.96**	**9.5**	**5.59**	**2.03**

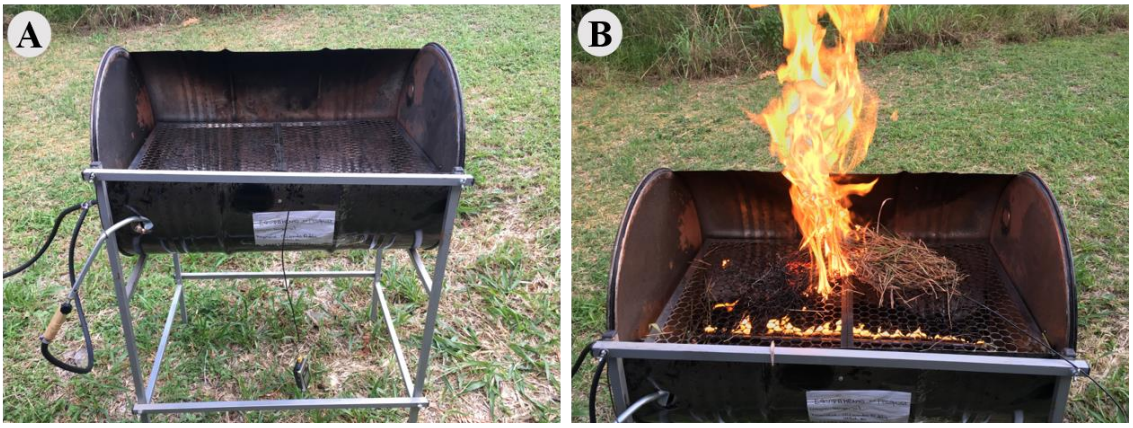

Figure SI 1: A) Equipment for flammability components measurements built based on *Jaureguiberry et al. 2011*. The device consisted of an 85 × 60 cm barrel cut in half and arranged horizontally on four long metal legs. The barrel was open at the front and closed at the back for wind protection. Samples were arranged on a grill and placed horizontally to be heated by a burner located beneath the grill. **B)** An equipment views during the flammability measurements.

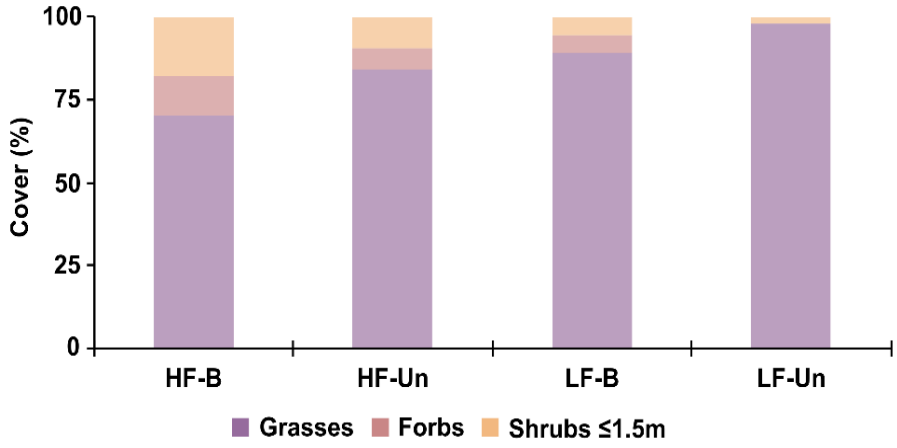

Figure SI 2: Cover (%) of grasses, forbs, and shrubs. Cover was visually estimated in 1x1m plots (30 plots/area) in open savannas in Central Brazil with different fire frequencies and time since last fire: **HF-Burned (HF-B)** with 11 fires and the last fire in 2019; **HF-Unburned (FH-Un)** with nine fires and the last fire in 2011; **LF-Burned (LF-B)** with two fires and the last fire occurrence in 2017; **LF-Unburned (LF-Un)** with one fire and last fire 2001

Table SI2: Mean±SE of moisture content, dead biomass, maximum temperature, burned biomass, and burn rate for each species sampled in areas with different fire frequencies and time since last fire: **HF-Burned** with 11 fires and the last fire in 2019; **HF-Unburned** with nine fires and the last fire in 2011; **LF-Burned** with two fires and the last fire occurrence in 2017; **LF-Unburned** with one fire and last fire 2001.

Area	Growth form	Family	Species	Moisture content (%)	Dead biomass (%)	Maximum temperature (ºC)	Burned biomass (%)	Burn rate ($cm.s^{-1}$)
HF-Burned	Grass	Poaceae	*Andropogon* sp.	20.83 ± 3.94	81.09 ± 1.95	651.5 ± 24.56	100 ± 0	1.38 ± 0.44
	Grass	Poaceae	*Anthaenantia lanata* (Kunth) Benth	33.08 ± 1.86	76.89 ± 1.48	653.04 ± 18.6	99 ± 1	2.33 ± 0.56
	Grass	Poaceae	*Axonopus aureus* P. Beauv.	35.81 ± 11.97	94.15 ± 3.19	611.13 ± 18.14	88.75 ± 9.66	1.14 ± 0.16
	Grass	Poaceae	*Elionurus muticus* (Spreng.) Kuntze	27.47 ± 2.43	74.78 ± 3.76	698.2 ± 43.93	94 ± 4.85	1.2 ± 0.33
	Grass	Poaceae	*Mesosetum ferrugineum* (Trin.) Chase	28.26 ± 1.5	74.32 ± 1.8	740.3 ± 23.13	100 ± 0	0.79 ± 0.16
	Grass	Poaceae	*Mesosetum loliiforme* (Hochst.) Chase	35.81 ± 11.97	86.99 ± 4.92	715.84 ± 19.47	98 ± 1.22	0.57 ± 0.11
	Grass	Poaceae	*Oncorachis ramosa* (Zuloaga & Soderstr.) Morrone & Zuloaga	27.61 ± 3	75.76 ± 4.02	696.84 ± 39.92	90 ± 7.58	1.27 ± 0.35
	Grass	Poaceae	*Paspalum pectinatum* Nees ex Trin.	32.11 ± 1.76	83.47 ± 1.8	553.74 ± 42.53	100 ± 0	1.42 ± 0.29
	Grass	Poaceae	*Trachypogon spicatus* (L.f.) Kuntze	22.34 ± 4.08	93 ± 2.09	430.22 ± 52.22	88 ± 5.83	1.04 ± 0.34
	Forb	Asteraceae	*Ichthyothere hirsuta* Gardner	58.85 ± 4.31	74.42 ± 6.46	346.22 ± 59.28	23.4 ± 17.01	0.53 ± 0.17
	Forb	Euphorbiaceae	*Croton gracilescens* Müll.Arg.	47.15 ± 2.62	0 ± 0	397.16 ± 32.6	33 ± 13	0.53 ± 0.07
	Shrub	Acanthaceae	*Ruellia nitens* (Nees) Wassh.	52.72 ± 2.7	0 ± 0	238.88 ± 138.09	14 ± 11.55	1.28 ± 0.77
	Shrub	Fabaceae	*Bauhinia dumosa* Benth.	57.46 ± 8.82	0 ± 0	611.13 ± 18.14	3.2 ± 1.93	0.19 ± 0.12
	Shrub	Fabaceae	*Calliandra dysantha* Benth.	36 ± 3.46	0 ± 0	170.1 ± 79.56	41 ± 13.08	0.42 ± 0.09
	Shrub	Fabaceae	*Chamaecrista ochrosperma* (H.S.Irwin & Barneby)	33.42 ± 2.58	0 ± 0	550.46 ± 109.12	59 ± 14	0.62 ± 0.19

	Shrub	Fabaceae	*Mimosa pteridifolia* Benth.	34.6 ± 2.69	0 ± 0	699.32 ± 47.86	64 ± 6.78	0.65 ± 0.17
			Total	**36.38 ± 1.67**	**50.38 ± 4.55**	**547.94 ± 23.91**	**68.2 ± 4.29**	**0.96 ± 0.09**
HF-Unburned	Grass	Poaceae	*Anthaenantia lanata* (Kunth) Benth	27.77 ± 3.22	83.83 ± 2.87	576.78 ± 42.75	93 ± 1.22	1.12 ± 0.15
	Grass	Poaceae	*Aristida setifolia* Kunth	19.38 ± 1.64	81.84 ± 3.65	709.56 ± 43.57	98 ± 2	0.44 ± 0.09
	Grass	Poaceae	*Elionurus muticus* (Spreng.) Kuntze	24.28 ± 3.16	75.08 ± 2.97	74.66 ± 74.66	99 ± 1	0.83 ± 0.13
	Grass	Poaceae	*Mesosetum ferrugineum* (Trin.) Chase	19.06 ± 1.93	79.09 ± 4.87	704.36 ± 27.31	93 ± 4.36	0.26 ± 0.02
	Grass	Poaceae	*Mesosetum loliiforme* (Hochst.) Chase	25.97 ± 3.11	89.29 ± 1.54	657.42 ± 51.55	96 ± 1.87	0.49 ± 0.09
	Grass	Poaceae	*Oncorachis ramosa* (Zuloaga & Soderstr.) Morrone & Zuloaga	13.7 ± 3.56	77.34 ± 1.86	739.72 ± 40.62	98 ± 1.22	0.8 ± 0.15
	Grass	Poaceae	*Paspalum pectinatum* Nees ex Trin.	23.69 ± 6.46	78.9 ± 2.18	467.3 ± 37.54	91 ± 4.58	0.91 ± 0.11
	Grass	Poaceae	*Trichanthecium cyanescens* (Nees ex Trin.) Zuloaga & Morrone	45.47 ± 6.45	92.42 ± 1.63	372.82 ± 46.25	13 ± 6.82	0.52 ± 0.03
	Forb	Euphorbiaceae	*Croton gracilescens* Müll.Arg.	33.39 ± 8.88	0 ± 0	130.38 ± 104.86	1.2 ± 0.97	0.24 ± 0.17
	Shrub	Acanthaceae	*Ruellia nitens* (Nees) Wassh.	41.3 ± 3.49	0 ± 0	91.22 ± 91.22	4 ± 4	0.11 ± 0.11
	Shrub	Fabaceae	*Bauhinia dumosa* Benth.	47.26 ± 0.88	0 ± 0	74.66 ± 74.66	0.2 ± 0.2	0.07 ± 0.07
	Shrub	Fabaceae	*Mimosa pteridifolia* Benth.	35.3 ± 6.15	0 ± 0	532 ± 43.99	36 ± 9.8	0.51 ± 0.11
			Total	**29.71 ± 1.82**	**54.82 ± 5.12**	**475.28 ± 34.63**	**60.2 ± 5.66**	**0.53 ± 0.05**
LF-Burned	Grass	Poaceae	*Aristida setifolia* Kunth	30.69 ± 6.4	84.83 ± 5.7	453.68 ± 70.55	77 ± 11.58	0.73 ± 0.14
	Grass	Poaceae	*Axonopus aureus* P. Beauv.	33.77 ± 3.63	98.31 ± 1.69	663.18 ± 19.05	88 ± 3.74	0.49 ± 0.06
	Grass	Poaceae	*Elionurus muticus* (Spreng.) Kuntze	27.34 ± 2.38	76.8 ± 2.84	741.62 ± 26.18	97 ± 1.22	1.04 ± 0.1
	Grass	Poaceae	*Mesosetum ferrugineum* (Trin.) Chase	24.13 ± 2.3	77.03 ± 1.98	717.96 ± 32.86	92 ± 3.74	0.33 ± 0.06
	Grass	Poaceae	*Mesosetum loliiforme* (Hochst.) Chase	39.67 ± 7.85	76.87 ± 6.83	691.26 ± 28.54	90 ± 0	0.5 ± 0.03

	Grass	Poaceae	*Oncorachis ramosa* (Zuloaga & Soderstr.) Morrone & Zuloaga	26.75 ± 4.81	70.11 ± 2.34	689.56 ± 19.5	81 ± 7.48	0.91 ± 0.26
	Grass	Poaceae	*Paspalum gardnerianum* Nees	42.46 ± 2.77	100 ± 0	436.06 ± 52.72	44 ± 11.22	0.92 ± 0.12
	Grass	Poaceae	*Trachypogon spicatus* (L.f.) Kuntze	13.62 ± 3.76	96.97 ± 1.08	647.66 ± 21.05	99 ± 1	0.79 ± 0.13
	Grass	Poaceae	*Trichanthecium* sp.	27.3 ± 4.25	95.26 ± 2.46	617.94 ± 35.03	88 ± 5.61	0.74 ± 0.16
	Forb	Asteraceae	*Ayapana amygdalina* (Lam.) R.M.King & H.Rob.	57.75 ± 1.86	6.2 ± 6.2	238.45 ± 90.01	8 ± 7.34	0.53 ± 0.22
	Forb	Euphorbiaceae	*Croton gracilescens* Müll.Arg.	54.2 ± 4.13	0 ± 0	196.86 ± 93.21	4.2 ± 2.37	0.21 ± 0.09
	Forb	Gentianaceae	*Calolisianthus speciosus* (Cham. & Schltdl.) Gilg	63.84 ± 1.17	0 ± 0	0 ± 0	0 ± 0	0 ± 0
	Shrub	Fabaceae	*Bauhinia dumosa* Benth.	48.52 ± 4.65	0 ± 0	237 ± 150.16	18 ± 13.56	0.17 ± 0.11
	Shrub	Fabaceae	*Calliandra dysantha* Benth.	51.54 ± 10.17	0 ± 0	321.6 ± 100.48	7.4 ± 3.56	0.52 ± 0.22
	Shrub	Vochysiaceae	*Vochysia pumila* Pohl	65.7 ± 4.49	0 ± 0	0 ± 0	0 ± 0	0 ± 0
			Total	**40.25 ± 2.16**	**52.78 ± 5.1**	**446.29 ± 33.61**	**53.51 ± 4.99**	**0.53 ± 0.05**
LF-Unburned	Grass	Poaceae	*Aristida longifolia Trin*	36.53 ± 8.62	38.11 ± 10.49	455.2 ± 88.72	72.2 ± 18.01	0.45 ± 0.07
	Grass	Poaceae	*Aristida setifolia* Kunth	42.48 ± 6.6	83.26 ± 5.3	178.22 ± 38.75	3.4 ± 0.98	0.93 ± 0.34
	Grass	Poaceae	*Arthropogon villosus* Nees	31.77 ± 2.59	76.21 ± 2.24	744.08 ± 25.13	90 ± 3.16	0.63 ± 0.1
	Grass	Poaceae	*Axonopus aureus* P. Beauv.	26.08 ± 4.25	95.09 ± 1.61	609.14 ± 33.19	73 ± 9.17	0.46 ± 0.07
	Grass	Poaceae	*Mesosetum ferrugineum* (Trin.) Chase	17.23 ± 2.2	73.25 ± 1.79	643.63 ± 16.42	98.33 ± 1.67	0.24 ± 0.06
	Grass	Poaceae	*Mesosetum loliiforme* (Hochst.) Chase	39.55 ± 6.13	87.64 ± 1.98	726.26 ± 29.16	94 ± 3.67	0.51 ± 0.08
	Grass	Poaceae	*Oncorachis ramosa* (Zuloaga & Soderstr.) Morrone & Zuloaga	21.74 ± 3.63	82.75 ± 3.87	708.56 ± 22.52	95 ± 3.87	0.63 ± 0.1
	Grass	Poaceae	*Paspalum thrasyoides* (Trin.) S.Denham	34.2 ± 1.21	100 ± 0	465.9 ± 18.11	98 ± 2	0.35 ± 0.04
	Grass	Poaceae	*Trachypogon spicatus* (L.f.) Kuntze	31.67 ± 4.9	86.32 ± 1.92	675.42 ± 34.24	52 ± 6.63	0.33 ± 0.05
	Shrub	Moraceae	*Brosimum gaudichaudii* Trécul	42.63 ± 2.19	0 ± 0	0 ± 0	0 ± 0	0 ± 0

Total	**33.02 ± 1.8**	**72.22 ± 4.48**	**515.52 ± 37.07**	**66.31 ± 5.65**	**0.46 ± 0.05**

3. CAPÍTULO II

Fire frequency affects herbivory by insects in open savannas of the Cerrado

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Abstract

Herbivory by insects influences biomass production across various biomes, including tropical savannas. However, different plant traits play a role in dealing with insect attacks, as structural or chemical defenses. In tropical savannas, fires are major disturbances that structure plant communities, and herbivory is also influenced by the occurrence of fire. Our study aimed to compare changes in herbivory traits (% leaf damage, condensed tannins, and total phenolics) between two fire frequencies (high and low) and among the most common growth forms in open savannas of the Cerrado – graminoids, forbs, and shrubs. Findings indicated that the two fire frequencies exhibited different herbivory patterns. In areas with high fire frequency, the preference of insects may be influenced by new leaf production and nutritional leaf content. Furthermore, plants in high fire frequency areas showed high concentrations of chemical compounds, which are important defenses against herbivorous insects. Among growth forms, shrub species exhibited the higher concentration of condensed tannins and total phenolics in comparison to graminoids and forbs. Graminoids did not have their leaves consumed, as such plants possess high concentrations of silica, which are indigestible for insects and affect their growth rates. In conclusion, the presence of fire influences the activity of herbivorous insects, and plants in areas with high fire frequency have high concentrations of chemical compounds, especially shrub species.

Keywords

Herbivory; Herbivorous insects; Open savannas; Herbaceous layer species; Fire; Tannins, Total phenolics; Leaf damage

Introduction

Herbivory consists in the act of animals consuming plant parts (Schowalter 2006), being an ecological interaction occurring in all tropical ecosystems (Mendes et al. 2020), affecting plant persistence (Schowalter 2006). Insects are known to be key herbivores, exerting significant pressure on primary production in many tropical ecosystems, including savannas (Andersen & Lonsdale 1990; Schowalter 2006). In tropical savannas, distinct functional groups of herbivorous insects (e.g., chewers, gall-formers, and sapsuckers) (Schowalter 2006) exert selective pressure on plants, which may possess traits conferring physical and chemical defenses against insects. These traits include the presence of trichomes, leaf toughness, or the investment on chemical compounds, which act as a repellent or affect the leaf palatability to insects (Wallace & Mansell 1976; War et al. 2012). The size and growth form of plants also influence the insects' attack, affecting insect's landing or mouthpart wear due to leaf conditions (Wallace & Mansell 1976; Robinson et al. 2023). Furthermore, the season of leaf production (Maron & Crone 2006) or the presence of disturbances (Spiller & Agrawal 2003), such as fire (Lopes & Vasconcelos 2011), can be ecological factors influencing herbivory by insects.

Fire is the main ecological factor shaping the vegetation in tropical savannas (Bond 2005; Bond & Keeley 2005), and in the Cerrado, fire occurs for more than four million years (Simon et al. 2009). Fire can affect the presence of insects (Schowalter 2006; Lopes & Vasconcelos 2011; Ballarin et al. 2024), which are the main herbivores in the Cerrado (Andersen & Lonsdale 1990; Costa et al. 2008). In recently burned areas, the abundance of insects can decline, but after a few months, the original abundance is recovered due to food availability (Fagundes et al. 2015; Anjos et al. 2016). Burned areas in the Cerrado usually show an increase in tree leaf damage by leaf chewers in contrast with unburned areas, due to the production of new and nutrient-rich leaves for insect consumption (Lopes & Vasconcelos 2011). The Cerrado holds an abundant community of insects (Marquis et al. 2001; Oliveira &

Marquis 2002) and different plant species possess defense mechanisms against them, which can be morphophysiological and/or chemical traits (War et al. 2012). These chemical defense mechanisms might be induced in areas with frequent fires due to the increase of susceptibility to insect attacks since new leaves are produced.

In recently burned areas, some plants increase the production of extrafloral nectaries (Oliveira & Freitas 2004), which are structures attracting ants (e.g., *Crematogaster* spp. and *Camponotus* spp.).These ants are responsible for repelling other herbivores (e.g., termites and caterpillars) that may be foraging on the new leaves produced (Delgado et al. 2022). However, not all plant species exhibit extrafloral nectaries that help to avoid leaf damage. Thus, secondary metabolites induced by insect's attack play an important role for the plant chemical defense against herbivory (Hanley et al. 2007). Tannins are the principal secondary metabolites produced by plants under insect attack, being deterrent or toxic for herbivores (Barbehenn & Peter Constabel 2011). Other phenolic compounds can affect the digestibility or palatability of plant parts, such as lignin, which contributes to increasing leaf toughness and decreasing leaf nutrition (War et al. 2012). However, despite knowing about the presence of these defenses, we still need to fill in gaps about the quantification of chemical defenses against insects (Massad 2023), especially in areas with different fire frequencies.

In the Cerrado, a diversity of species with different growth forms can be found (e.g. graminoids, forbs, and shrubs, (Coutinho 1978), which influence the herbivory by insects (Robinson et al. 2023). Moreover, fire affects the distribution of species among growth forms: a decrease in forb and small shrub diversity and the dominance of few grass species is observed (Rodrigues & Fidelis 2022), being grasses less attractive to insects (Massey & Hartley 2009). Graminoids typically experience low herbivore attacks compared to shrubs and trees: their narrow leaves tend to difficult the presence of insects and their oviposition on leaf surface (Brown & Lawton 1991). Furthermore, graminoids present high concentrations of silica in their

leaves, reducing digestibility (Massey et al. 2006). In comparison to forbs and shrubs, graminoids have lower concentrations of nitrogen, calcium, and magnesium, and thus, lower nutritional leaf content (Rossatto & Franco 2017). Therefore, changes in the plant community structure and composition under different fire frequencies could potentially influence insect's activity. However, few studies have addressed the effects of fire on plant-animal interactions (Ballarin et al. 2024), especially regarding species from the herbaceous layer.

Since fire and different plant groups affect both the presence and herbivory by insects in the Cerrado (Lopes & Vasconcelos 2011; Andrade et al. 2019), studies regarding herbivory patterns are necessary, especially focusing on plant traits that can be linked to herbivory. Thus, our study aimed to compare how herbivory traits related to insects – % leaf damage, condensed tannins, and total phenolics concentration – change in areas of open savannas with high and low fire frequency, and among the most dominant growth forms in the herbaceous layer of open savannas – graminoids, forbs, and shrubs. Thus, we addressed the following questions: (a) How does fire frequency affect the herbivory by insects in the herbaceous layer plants of open savannas in the Cerrado? We expect that leaves in areas with high fire frequency will be more consumed by insects, and, as an inducible mechanism, some species may exhibit high concentrations of chemical compounds in their leaves compared to plants in areas with low fire frequency. This is expected because insects can be attracted by the new and nutrient-rich leaf production. (b) Is there any difference in the herbivory by insects among the most common plant growth forms of the herbaceous layer in open savannas of the Cerrado? We expect that forbs and shrubs will have their leaves more consumed by insects compared to graminoids. Graminoids are poor in leaf nutrients and exhibit high silica content in comparison to forbs and shrubs. However, forbs and shrubs, being more attractive to insects, are likely to exhibit higher concentrations of chemical compounds as a defense mechanism.

Material and methods

Study site

The study was conducted at the Reserva Natural Serra do Tombador (RNST), located in Central Brazil (13º 35’38’’S, 47º 45’51’’W, 8900 ha, 118 m a.s.l) (Antonelli-Filho 2011). The main vegetation type in the reserve is open savannas, composed by a species-rich herbaceous layer, primarily covered by graminoid species, but also forbs and small shrubs (Coutinho 1982). At the RNST, precipitation varies between 1300 to 1500 mm/year). The climate is tropical, with a marked dry season occurring between May to October, and annual mean temperature range between 15ºC – 36ºC (Antonelli-Filho 2011).

In areas of open savannas at the RNST, we selected two areas with high (11 and 7 fires in the last 21 years – one fire event every 2.5 years approximately, which is the common fire return in open savannas, Pivello 2011; Fig. 1A) and two areas with low fire frequency (1 and 2 fire events in the last 21 years; Fig. 1B). The two areas with high fire frequencies (9 and 7 fires in the last 21 years) are part of a long-term fire experiment established in 2013 and are located close to each other (Rodrigues et al. 2021). The areas of low fire frequencies (2 and 1 fire in the last 21 years) are separated just by a road and are located close to the experimental area – three kilometers apart in a straight line. In each fire frequency areas (high and low), we randomly established 60 plots of 1x1m each (30 plots per area x 2 fire frequencies x 2 areas/fire frequency = 120 plots) for plant species surveys.

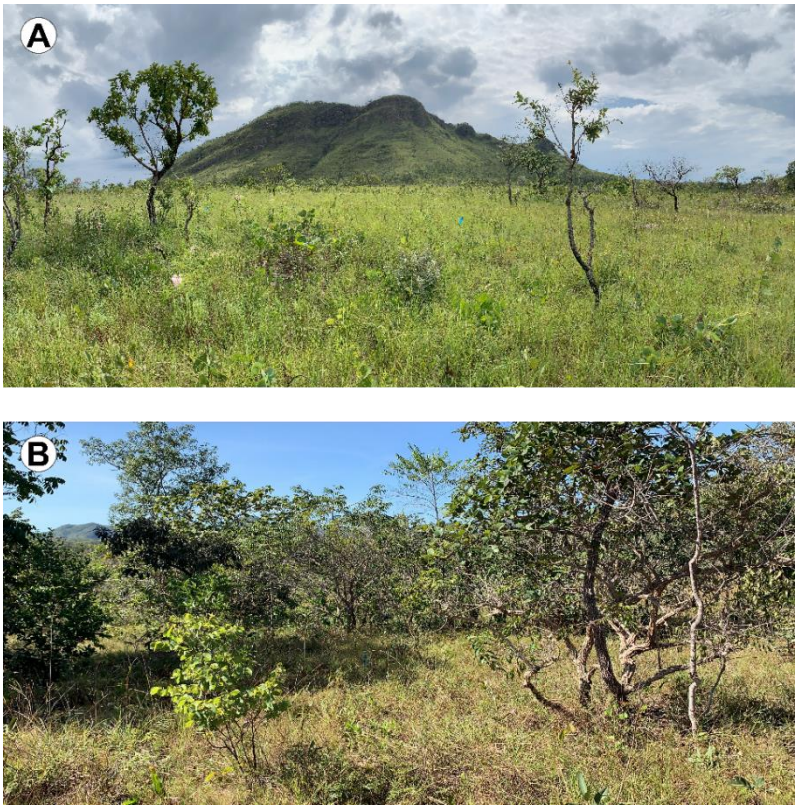

Figure 1: General view of the areas of open savannas with A- high and B- low fire frequency at the Reserva Natural Serra do Tombador, Central Brazil, where species were sampled.

Methods

Species selection

In each 1x1m plot, we visually estimated the cover of all species of graminoids, forbs, and shrubs ≤1.5m (%, Wikum & Shanholtzer 1978), during the rainy season (February/2022). To determine which species to include in the measurements of herbivory traits, we selected those representing 80% of the entire community abundance in each area (Magurran 2004). We collected three to five individuals per species to measure three herbivory traits related to herbivorous insects: leaf damage, condensed tannins, and total phenolics.

Herbivory traits

We accessed the three herbivory traits related to herbivorous insects and measured them at the leaf level for each plant individual collected during the rainy season (April/2022).

- *Leaf damage (%)*

For each individual we selected 10 leaves to measure the percentage of leaf damage by chewing insects. Individuals with less than 10 leaves, we measured all leaves. In the case of the individuals with more than ten leaves, ten leaves were randomly chosen to measure leaf damage. Using the free open source LeafByte mobile app (Getman-pickering et al. 2020), we scanned each leaf and then reconstructed the consumed portion by the insect. The app calculated the percentage lost by each leaf, obtaining the percentage removed by the chewing insects. We adapted the measurements from the Herbivory Variability Network Protocols (Pearse et al. 2020).

- *Condensed tannins ($mg.g^{-1}$)*

Condensed tannins concentrations were determined calorimetrically after the reaction with vanillin-HCl (Price et al. 1980). Since many of our plant species lacked enough expanded and healthy leaves, we opted to group individuals by species and select their most optimal leaves, obtaining an amount ranging from 4mg and 1g per species. All leaves underwent milling in liquid Nitrogen to extract the samples. Subsequently, after reacting with vanillin-HCl (8%), we assessed the condensed tannins concentrations for each species using a spectrophotometry in λ 500nm.

- Total phenolics *($mg.g^{-1}$)*

Using a spectrophotometer, we determined total phenolics after the reaction with Folin-Ciocalteu reagent (Wigley et al. 2020). We group individuals by species selecting their most optimal leaves to obtain an amount raging from 4mg to 1g per species. The leaves underwent milling in liquid Nitrogen to extract the samples. After, the reaction was combined with 1.5mL of distilled water, 0.1mL of Folin-Ciocalteu reagent and 0.2mL of sample extract. The spectrophotometric readings were taken at λ= 765nm.

Statistical Analysis

To investigate if fire frequency (high x low) influences the herbivory by insects, we first calculated the Community Weighted Mean (CWM) matrix, which represents the abundance-weighted mean trait value for each 1x1 plot in our two treatments (high and low fire frequency). The CWM matrix combines species abundance data for each plot with the mean trait values (% leaf damage, condensed tannins, and total phenolics) of each species (Kleyer et al. 2012; de Bello et al. 2021). Using the CWM matrix, we performed a Principal Component Analysis (PCA). We used the Euclidean distance as the resemblance measure to visually explore the data distribution according to each herbivory trait sampled in the species under the two fire frequencies. Subsequently, we conducted a PERMANOVA test with 1000 permutations to analyze if the three herbivory traits (% leaf damage, condensed tannins, and total phenolics) differed between the high and low fire frequency. Additionally, we also performed a pairwise test using the Bonferroni method to compare the differences in herbivory by insects between the two fire frequencies.

Furthermore, we separately explored the differences of each herbivory trait between the two fire frequencies. Using the CWM values for each trait, we constructed Generalized Linear Mixed Models (GLMMs). Fire frequency (high and low) was considered a fixed effect, and the plots were considered a random effect. For % leaf damage, we used the Tweedie family due to the presence of many zeros in the data. For condensed tannins and total phenolics, we used the Gaussian family, observing the normal data distribution.

To evaluate the herbivory by insects among the three growth forms (graminoids, forbs, and shrubs), we constructed GLMMs for each herbivory trait (leaf damage, condensed tannins, and total phenolics) using the observed data and independent of fire frequency and testing the interaction between fire frequency and growth forms. Growth forms and fire frequency were considered a fixed effect, and the individuals was considered a random effect. The Tweedie

family was used for leaf damage traits due to the presence of many zeros in the data, and Gamma family to condensed tannins and total phenolics, considering the normal data distribution. After, we conducted a *lsmeans* test (Tukey method) to compare the growth forms pairwise.

All analyses were performed in the R environment (R Core Team 2018), using the following packages: *tidyverse* (Wickham et al. 2019), *geoR* (Ribeiro Jr & Diggle 2001), *lme4* (Bates et al. 2015), *lsmeans* (Lenth 2016), *ggfortify* (Tang et al. 2016), *vegan* (Oksanen et al. 2018), *RVAdeMemoire* (Hervé 2022) and *glmmTMB* (Brooks et al. 2017).

Results

Considering the percentage of leaf damage, content of condensed tannins and total phenolics, we found that plants in communities under high fire frequency showed distinct herbivory patterns in relation to the ones under low fire frequency (PERMANOVA, F= 14.53; p= 0.001). These differences are illustrated in the PCA, where the first axis explained 79% and the second axis explained 14%, accounting for 94% of the total variation (Fig. 2). Content of condensed tannins, total phenolics, and % leaf damage were mostly associated with areas under high fire frequency (Fig. 2).

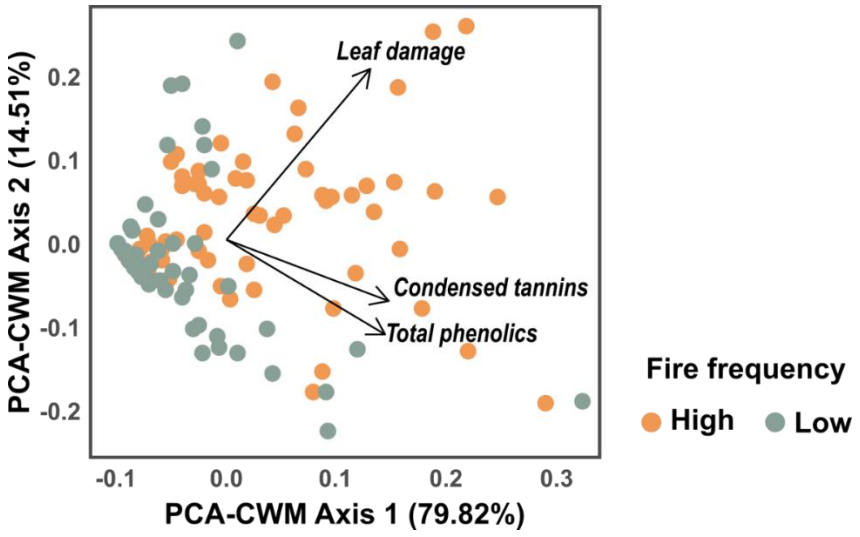

Figure 2: Principal Component Analysis (PCA) considering the three herbivory traits (% leaf damage, condensed tannins, and total phenolics), measured in plants occurring in areas with high and low fire

frequencies, located in open savannas of Central Brazil. Each point represents the sampling unit in the CWM matrix (plot by traits) according to the fire frequencies.

Plants in communities under high fire frequencies had their leaves more consumed by insects than plants in the areas with low fire frequencies (Fig. 3A). Furthermore, areas under high fire frequency showed plants with the higher condensed tannins (Fig. 3B) and total phenolics concentrations (Fig. 3C), compared with the plants presented in the low fire frequency areas.

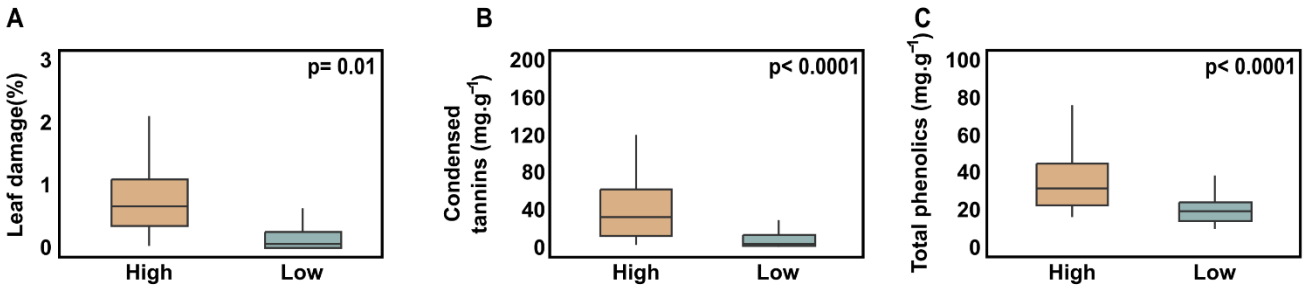

Figure 3: A- % Leaf damage, B- Condensed tannins, and C- Total phenolics concentrations, measured in leaves of plant species occurring in high and low fire frequency areas in open savannas of Central Brazil. Boxplots (median and first and third quartiles) represent the CWM values (plot by traits) according to the fire frequencies.

When comparing growth forms separately, fire and growth forms did not interact (p=0.99), We observed that graminoids, forbs, and shrubs suffered similar leaf damage by insects in their leaves, and all graminoids leaves did not present any percentage of leaf damage (Fig. 4A). Shrubs were the growth form with the highest concentrations of condensed tannins and total phenolics in their leaves, while forbs and graminoids showed similar compounds concentrations (Fig. 4B-C). Furthermore, shrubs presented a high variability in the concentrations of total phenolics, having species with less than 30 mg/g and species with more than 200 $mg.g^{-1}$ (Tab. SI1).

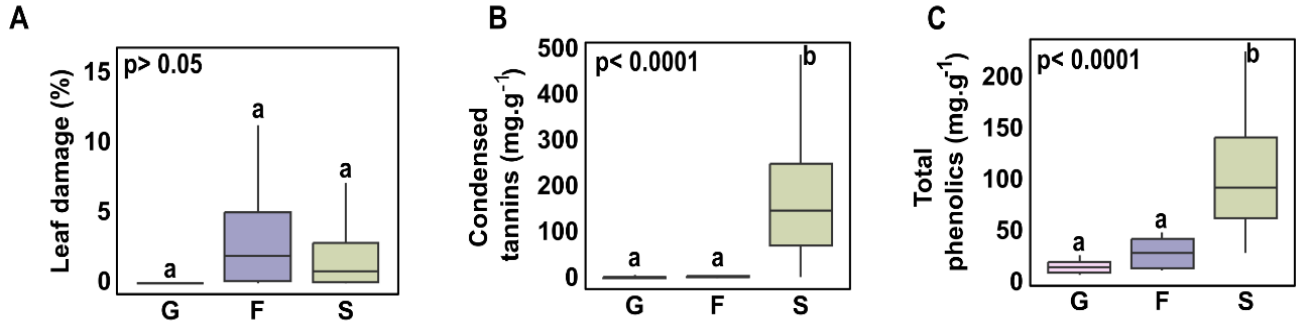

Figure 4: A- % Leaf damage, **B-** Condensed tannins, and **C-** Total phenolics concentrations, measured in leaves of graminoids (G), forbs (F), and shrubs (S) species, sampled in areas of open savannas in the Central Brazil. Boxplots represent the median and the first and third quartiles.

Discussion

We corroborated our hypothesis that fire frequency and different growth forms affect the herbivory by insects in the Cerrado. Increased leaf damage in plants in areas with high fire frequency were observed, and condensed tannins and total phenolics were produced, as a defense strategy. Additionally, we observed that shrub species exhibited the highest concentration of condensed tannins and total phenolics in their leaves compared to graminoids and forbs, suggesting that shrub leaves may be more attractive to herbivorous insects. Thus, we have presented initial findings regarding insect herbivory-related traits among plant communities in the herbaceous layer of open savannas in the Cerrado, showing how fire frequency and growth forms influence insect herbivory.

Fire leads to changes in resources availability, and alterations in its frequency can affect vegetation composition (Abreu et al. 2017; Rodrigues & Fidelis 2022) and biological interactions (Koltz et al. 2018). After fire, plants produce new and nutrient-rich leaves, increasing herbivore abundance and leaf damage in burned areas (Lopes & Vasconcelos 2011). However, as a defense strategy, plants may exhibit biotic and/or chemical mechanisms to avoid insect activity (Massad 2023). Some plants increase the production of extrafloral nectaries to reduce the insect herbivory, as a mutualist interaction (Delgado et al. 2022; Porto et al. 2023). Chemical compounds are produced by plants as an inducible strategy when insect herbivory

begins (Schowalter 2006; Barbehenn & Peter Constabel 2011; Krebs 2014). Total phenolics are abundant chemical defenses in Cerrado's plants, and their higher levels can result from soil nitrogen limitation (Massad 2023). Plant species in the Cerrado also exhibit high concentrations of condensed tannins (Barbehenn & Peter Constabel 2011; Massad 2023). Both compounds are also influenced by fire frequency because the new leaves produced in these areas synthetize compounds for protection, mostly against herbivores (Santacruz-García et al. 2019; Massad 2023). Therefore, plants in areas with frequent fires and under high pressure from insects exhibit high investments in these defense traits (Massad 2023), and thus, fire affects the interactions between insects and plants (Ballarin et al. 2024).

In the Cerrado, plants are nutrient-poor due to limited soils resources availability (Furley 1999; Pivello et al. 2010; Rossatto & Franco 2017), and investment in leaf production should be minimized by plants (Da Silva & Batalha 2011). Graminoids, for example, exhibit very low nitrogen concentration in their leaves, while shrubs and forbs exhibit higher and similar nitrogen concentration (Rossatto & Franco 2017). These differences in nutrient concentrations contribute to explaining why graminoids were not preferred by insects in our study. However, graminoids also exhibit high contents of silica in their leaves, which is a strategy to avoid insects. Silica increases leaf abrasiveness, causing mouthpart wear (Massey et al. 2006; Hunt et al. 2008; Reynolds et al. 2009), reducing insect growth rates and survival (Massey & Hartley 2009). Consequently, plants that seem more attractive to insects, such as shrubs and forbs, might invest in conservative traits to avoid herbivory, such as tough leaves with chemical defenses (Massad 2023). Since shrubs exhibited the highest concentrations of condensed tannins and total phenolics in our study, it could indicate that shrub species might attract more insects. Finally, we showed with our study that insects may play a secondary role as one of the savanna consumers (fire and herbivory, Bond 2005), since they are not successful in consuming and

controlling graminoids, which are the main component of the fuel load and the most flammable component of savannas (Simpson et al. 2016; Zanzarini et al. 2022).

Therefore, fire plays an important role influencing insect's activity and herbivory patterns. Its presence guarantees the biodiversity of Lepidoptera species – around 9000 species in the Cerrado (Abreu et al. 2017; Massad 2023). For example, *Atta laevegata* is one of the most generalist herbivores in the Cerrado, and their presence, along with other species, is essential to provide different ecosystem process, such as nutrient cycling (Costa et al. 2008; Abreu et al. 2017 p. 201; Massad 2023). In conclusion, our study contributes to the understanding of how insect herbivory is influenced by fire in open savannas of the Cerrado and how different growth forms in the herbaceous layer respond to herbivory pressures.

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Supplementary information

Table SI1: Mean±SE of leaf damage (%), condensed tannins (mg.g^{-1}), and total phenolics (mg.g^{-1}) for herbaceous layer species sampled in areas with high and low fire frequency located in open savannas of the Cerrado, in Central Brazil.

Occurrence	Growth form	Family	Species	% Leaf damage	Condensed tannins	Total phenolics
H	Graminoid	Poaceae	*Anthaenantia lanata* (Kunth) Benth	0±0	2.03±0.11	13.41±0.54
H		Poaceae	*Aristida setifolia* Kunth	0±0	23.41±1.33	15.68±0.51
L;H		Poaceae	*Axonopus aureus* P. Beauv.	0±0	3.22±0.48	24.36±4.83
L		Poaceae	*Paspalum thrasyoides* (Trin.) S.Denham	0±0	2.1±0.02	16.92±0.46
L;H		Poaceae	*Elionurus muticus* (Spreng.) Kuntze	0±0	7.86±0.83	22.45±1.6
L;H		Poaceae	*Mesosetum ferrugineum* (Trin.) Chase	0±0	3.27±0.1	20.45±0.82
L;H		Poaceae	*Mesosetum loliiforme* (Hochst.) Chase	0±0	2.48±0.35	9.96±0.3
L;H		Poaceae	*Oncorachis ramosa* (Zuloaga & Soderstr.) Morrone & Zuloaga	0±0	2.16±0.23	12.16±1.03
H		Poaceae	*Paspalum pectinatum* Nees ex Trin.	0±0	3.25±0.61	43.72±0.58
L		Cyperaceae	*Rhynchospora consanguinea* (Kunth) Boeckeler	0±0	1.83±0.03	11.74±0.12
L;H		Poaceae	*Trachypogon spicatus* (L.f.) Kuntze	0±0	2.73±0.11	9.68±0.15
H		Poaceae	*Trichanthecium cyanescens* (Nees ex Trin.) Zuloaga & Morrone	0±0	4.75±0.09	43.91±0.7
H	Forb	Asteraceae	*Aldama grandiflora* (Gardner) E.E.Schill. & Panero	2.54±1.74	5.66±0.09	42.23±0.69
L;H		Euphorbiaceae	*Croton gracilescens* Müll.Arg.	6.72±1.15	5.23±0.09	12.95±0.31
L		Lythraceae	*Cuphea spermacoce* A.St.-Hil.	0.54±0.29	5.48±0.05	105.83±1.67
H		Lamiaceae	*Gymneia chapadensis* Harley	1.59±0.94	3.25±0.02	33.54±0.47
L		Lamiaceae	*Hypenia* (Mart. ex Benth.) Harley	0.4±0.24	5.29±0.04	29.45±0.15
H		Lamiaceae	*Hyptis remota* Pohl ex Benth.	2.19±2.1	3.64±0.08	49.06±0.47
L		Velloziaceae	*Vellozia squamata* Pohl	0.09±0.03	1.47±0.05	16.74±0.09
H	Shrub	Annonaceae	*Annona tomentosa* R.E.Fr.	2.55±0.18	156±2.57	73.39±0.5
H		Malpighiaceae	*Heteropterys pannosa* Griseb.	4.83±2	293.65±0.73	142.09±1.45
H		Fabaceae	*Bauhinia dumosa* Benth.	4.9±1.29	169.42±17.8	78.78±7.27

H		Fabaceae	*Calliandra dysantha* Benth.	0.41±0.22	485.39±3.77	184.35±3
H		Fabaceae	*Chamaecrista claussenii* (Benth.) H.S.Irwin & Barneby	3.51±2.5	7.29±0.07	30.22±0.2
L		Lythraceae	*Diplusodon burchellii* Koehne	0.17±0.09	16.27±0.18	208±3.78
L		Lythraceae	*Diplusodon punctatus* Pohl	1.01±0.27	6.47±0.04	216.51±5.5
H		Fabaceae	*Eriosema congestum* Benth.	3.62±1.7	76.16±2.16	55.43±0.55
H		Fabaceae	*Harpalyce tombadorensis* São-Mateus et al.	5.11±0.97	169.59±8.62	153.19±4.96
H		Fabaceae	*Mimosa leiocephala* Benth.	0±0	114.95±1.13	63.27±0.25
L;H		Fabaceae	*Mimosa pteridifolia* Benth.	0±0	136.17±14.22	81.9±3.93
L		Myrtaceae	*Myrcia* sp.	0.75±0.6	197.56±2.66	90.4±0.62
L		Oxalidaceae	*Oxalis goyazensis* Turcz.	4.35±2.49	388.51±2.94	105.05±0.87
H		Acanthaceae	*Ruellia nitens* (Nees) Wassh.	0.61±0.17	5.52±0.68	48.07±4.58
L;H		Fabaceae	*Senna corifolia* (Benth.) H.S.Irwin & Barneby var. corifolia	1.03±0.85	343.61±10.31	111.73±1.22
L		Vochysiaceae	*Vochysia pumila* Pohl	2.74±1.87	355.58±6.64	143.32±0.58

4. CAPÍTULO III

Thinking beyond African savannas: fire determines savanna-forest mosaics, while herbivory by insects plays a secondary role in the Cerrado

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Abstract

Climate has been recognized as determining the distribution of vegetation types worldwide, and favorable conditions of temperature and precipitation can ensure the presence of forests in tropical regions. However, savannas are open ecosystems occurring under the same climate conditions that support forest, being thus maintained by fire and herbivory. These disturbances play a role in the functional composition of plant communities, besides maintaining the open structure and guarantee high light incidences in savannas, contrary to forest, where a closed structure created by trees decreases light availability. However, differently from African savannas, herbivory is mainly exerted by insects in the Cerrado, and their role is not well documented. Thus, we aimed to understand the determinants of savanna-forest mosaics in areas where climate supports both vegetation types. Thus, we used functional traits related to fire, herbivory by insects, and light of herbaceous layer species (graminoids, forbs, and shrubs) in the Cerrado. We selected areas of open savannas, woody savannas, and forest to measure different traits related to fire (flammability, plant dead biomass amount, and plant moisture content), herbivory by insects (% of leaf damage, condensed tannins, and total phenolics concentration) , and light (leaf length and width, total chlorophyll, a:b chlorophyll ratio, and carotenoids). As expected, fire-related traits decreased when grasses were suppressed by trees, decreasing the system's flammability, while light traits required to deal with diffuse light (e.g., leaf width) increased in the forest ecosystem. Herbivory patterns increased (% of damage) when suitable microclimate conditions for insects were created by trees and because plant leaves exhibited low chemical defenses against insects in the forest. In conclusion, fire plays a major role in savannas, while herbivory is not the major consumer in savannas, playing thus a secondary role.

Keywords: fire, herbivory by insects, light availability, savanna, flammability.

Introduction

Climate variables can determine the distribution of vegetation types globally (Whittaker 1975). Favorable temperature and high precipitation are suitable conditions for the occurrence of forest in the tropical regions, for example (Whittaker 1975). Moisture, light availability, and nutrients levels are resource variables responsible to ensure the establishment and growth of plants in forested areas (Whittaker 1975; Grime 1979). However, despite these conditions, there are also areas of open vegetation, such as savannas, occurring in the same climate conditions as those supporting forests (Bond 2005). In most situations, the occurrence of savannas is primarily influenced by fire and herbivory, which are consumer controllers of the vegetation (Bond 2005; Bond 2019). Thus, vegetation types are not only resource-controlled but also consumer-controlled, especially across the tropical region (Bond 2005), being described as disturbance-driven ecosystems (Buisson et al. 2018; Buisson et al. 2022).

Forest and savannas are considered stable states as even under small perturbations, both environments can return to the same state (Pausas & Bond 2020). In the case of savannas, both fire and herbivores consume large amounts of biomass, such as in African savannas, maintaining the open vegetation as a stable state (Bond 2005; Lehmann et al. 2014; Pausas & Bond 2020). In South American and Australian savannas, fire is known to be the main disturbance consuming and controlling the vegetation (Bowman et al. 2009; Simon et al. 2009), since mega herbivores were extinct in the Late Pleistocene (Barnosky et al. 2004; Owen-Smith 2013). However, some studies suggest that herbivory by insects also contributes to biomass consumption in savannas, since leafcutter ants can remove considerable amounts of biomass, for example (Andersen & Lonsdale 1990; Costa et al. 2008). Thus, understanding how the presence of fire and herbivores can contribute to determining forest-savanna mosaics is promising (Hoffmann et al. 2012). Moreover, investigating the functional responses of species in relation to these filters can be an interesting way to explore it (Hoffmann et al. 2012; Charles-

Dominique et al. 2015). However, there are few studies addressing this topic (see Charles-Dominique et al. 2015), especially regarding species from the herbaceous layer.

As fire and herbivores act in the consumption of biomass maintaining an open structure, high incidences of light are characteristic in savannas (Bond 2005; Bond 2019). In open ecosystems, herbaceous plants exhibit different traits related to high light incidences (Charles-Dominique et al. 2018; Rossatto et al. 2018), such as leaves with high photosynthetic rates, small leaf area, and high concentrations of photoprotective pigments (Rossatto et al. 2018). Furthermore, C_4 grasses are abundant in the herbaceous layer of savannas (Archibald et al. 2020; Cole 1986) and extremely sunlight dependent (Gibson 2009; Ratnam et al. 2011). On the other hand, when disturbance is excluded or changed and trees can establish (e.g., forest), a shaded environment with low light incidence has plants with functional traits related to the capture of diffuse light by plants in the herbaceous layer (Ratnam et al. 2011). In these conditions, large leaves with high chlorophyll concentrations are needed to increase light capture in the understory of forests (Valladares et al. 2002).

In savannas, the presence of grasses is essential for the occurrence of fire, which consequently keeps the vegetation open (D'Antonio & Vitousek 1992). Grasses produce large amounts of biomass, and during the dry season, their highly flammable biomass contributes to the fire spread (Bond & Van Wilgen 1996). On the other hand, forests eliminate C_4 grasses from the system mostly due to shading (Hoffmann et al. 2012; Charles-Dominique et al. 2018; Pilon et al. 2020), and maintains high moisture conditions in the herbaceous layer, decreasing flammability (Hoffmann et al. 2012). At the same time, in both vegetation types, the presence of insects can be positively influenced by fire in the savannas (Lopes & Vasconcelos 2011; Zanzarini in prep.) and also positively influenced by microclimate conditions created in the forests (Neves et al. 2010). After fire, the production of new and rich-nutrient leaves of shrubs increases insect's activity (Lopes & Vasconcelos 2011; Fagundes et al. 2015), and plants

require different traits to avoid herbivory (e.g., leaf trichomes, secondary compounds) (Schowalter 2006; Barbehenn & Peter Constabel 2011). However, grasses are unpalatable for insects, because they possess high silica content in their leaves (Massey & Hartley 2009). In forest, the nutrient availability and the moisture conditions can favor insect's activity and species of forbs and shrubs can be attractive to them (Neves et al. 2010).

Fire, herbivory and light availability cooccur and can be essential in determining the distribution of forest and savanna, but their relevance in filtering and assembling plant communities across these different vegetation types varies. In mesic savannas (e.g., Cerrado), where the climate is suitable for forests and a landscape mixed with open and closed vegetation can be found, frequent fires promote the vegetation openness (Staver et al. 2011; Hoffmann et al. 2012; Lehmann et al. 2014). Unlike Africa, where the presence of large mammals also determines the distribution of forest and savannas (Hempson et al. 2015), in the Cerrado large herbivores does not play this role (Barnosky et al. 2004). Therefore, it is important to investigate whether in the Cerrado, the presence of fire is essential to maintain vegetation structure, or if the presence of insects, which are the main herbivore group present in the Cerrado, is also acting as a potential consumer in the system. Furthermore, it is important to investigate how these herbivory patterns vary between these mixed vegetation types.

Thus, we aimed to investigate how traits related to light, fire, and herbivory by insects change across different vegetation types (from open savannas to forest), helping us to understand how these factors are contributing to determining the presence of savannas under a forest climate. Thus, we selected areas of open savanna (*campo sujo*), woody savanna (*cerrado sensu stricto*), and forest (*cerradão*) in the Cerrado, measuring functional traits in the herbaceous layer plants, to answer the following question: What are the determinants of savanna and forest in regions where climate supports forest? Since savannas are disturbance-driven, consumer-controlled and forests are climate-driven, resource-controlled (Bond 2005), we

predicted that savanna plant communities will exhibit functional traits related to fire such as high amounts of biomass, low moisture content, and high flammability. From open (savanna) to closed (forest) ecosystems, we expect to observe a decrease in the flammability, especially due to the reduction of grasses and their accumulated dead biomass. We expect that traits related to herbivory by insects can occur in plants present both in forest and savanna, as both fire and the suitable conditions of forest can benefit insect's communities. Finally, the functional traits related to optimize light capture will be required in areas with closed vegetation (forest and woody). Light is an important resource for plant growth, and herbaceous species need to exhibit acquisitive traits to capture diffuse light (e.g., leaf dimensions) and exhibit low photosynthetic capacity to deal with low irradiance (Rossatto et al. 2018; Pinheiro et al. 2022).

Material and methods

Study site

The study was conducted at the Reserva Natural Serra do Tombador (RNST, Cavalcante, Goiás) located in Central Brazil (13º 35'38''S, 47º 45'51''W, 8900 ha, 1118 m a.s.l) (Antonelli-Filho 2011). The reserve is situated in the Cerrado, which exhibits grasslands, savannas, and forest ecosystems (Coutinho 1990). Grasslands and savannas are mostly composed of graminoids, forbs, and small shrubs covering between 80% to 50% of the ground, while forest formations have trees as the main component, with just 35% of herbaceous species covering the ground (Coutinho 1976). Precipitation at the RNST is between 1300-1500 mm/year, with maximum levels occurring during the rainy season (October to May). Annual mean temperature ranges between 15ºC – 36ºC (Antonelli-Filho 2011).

Three areas were chosen at the RNST, differing in terms of fire frequency, year since the last fire and leaf area index (LAI), used as surrogate for light availability and canopy cover (Tab. 1). The first area is an **open savanna** (Fig. 1A) with a continuous C_4 grass-layer

(approximately 80% of grass covering the ground; Coutinho 1982) and sparse shrubs and trees. This area is part of a long-term fire experiment established in 2013, with areas being burned biennially in the late-dry season (Rissi et al. 2017). The second area is a **woody savanna** (Fig. 1B), exhibiting common Cerrado tree species (e.g., *Davilla elliptica, Hancornia speciosa, etc.)*, mixed with different herbaceous species and grasses covering around 50% of the ground (Coutinho 1982). The third area is a **forest** formation (Cerradão, Fig. 1C), with a closed canopy, without grass species occurring in the herbaceous layer (Coutinho 1982).

Fire frequency and year since last fire were obtained for each area with spatial images, mapping the fire occurrences since 2000, while LAI was obtained establishing a transect in each area and measuring the LAI at 15 points, maintaining an approximate five-meter distance between each point. LAI was obtained using a Plant Canopy Analyzer Equipment (LAI-2200), giving a value of the intercepted light by the plant leaves. The measurements were carried out after sunset or under homogeneous sky, considering the diffuse light, at a height of 1 m.

Table 1: Fire frequency (number of fires in the last 21 years), year since the last fire and leaf area index of the three selected areas at the Reserva Natural Serra do Tombador, Central Brazil.

Area	Fire frequency	Year since last fire	Leaf area index
Open savanna	11	2019	0.04
Woody savanna	2	2017	1.0
Forest	0	-	1.5

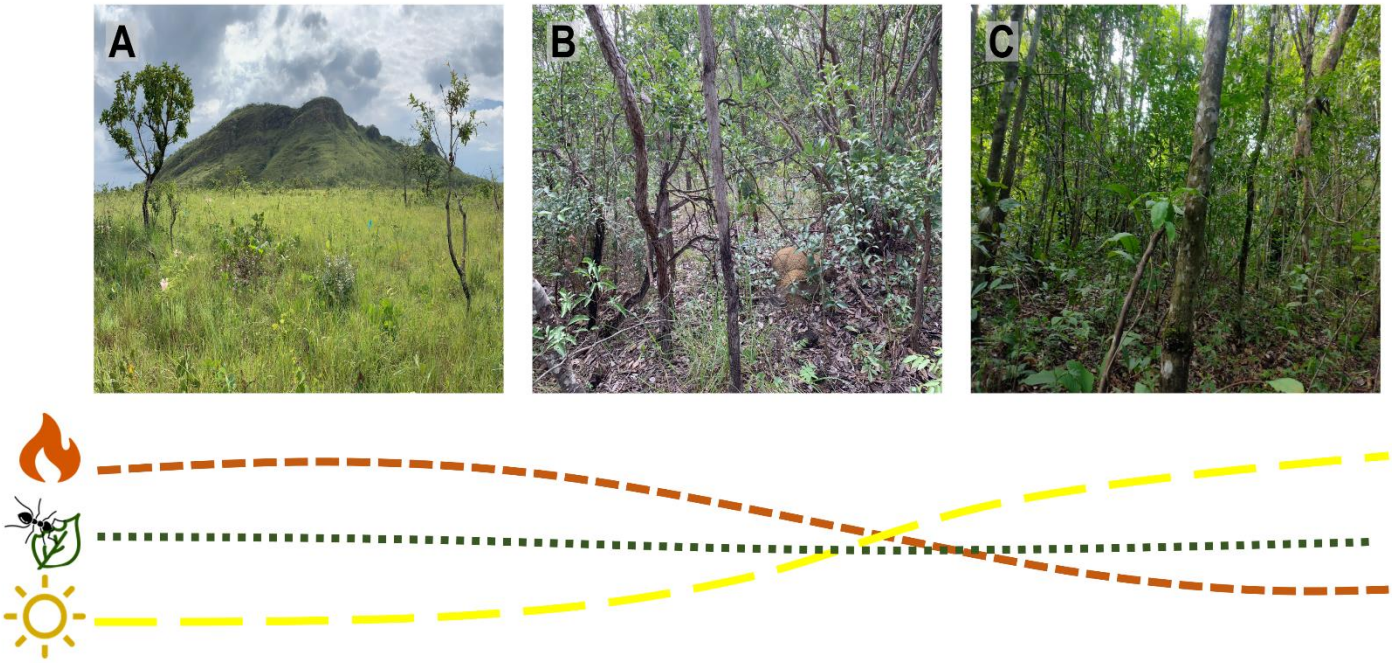

Figure 1: The three selected areas at the RNST, used to measure the light, fire, and herbivory traits. **A:** open savanna; **B:** woody savanna; **C:** forest.

Methods

In each area, we randomly established 1m^2 plots, with a minimum distance of five meters from each other. We sampled different numbers of plots, because we established an accumulation species curve to have sampling sufficiency: 30 plots in open savanna, 24 plots in woody savanna, and 20 in forest. In each plot, we visually estimated the plant cover of all species of graminoids, forbs, and shrubs ≤1.5m (%, Wikum & Shanholtzer 1978). Subsequently, we selected the species representing 80% of the entire plant community abundance in each area (Magurran 2004), and measured traits related to light, fire, and herbivory by insects in plant individuals for each selected species. For fire-related traits, we selected species and measured traits during the dry season (September to October/2021), because this is the season where fire occurs the most in the Cerrado (Coutinho 1990; Ramos-Neto & Pivello 2000) and the vegetation is more flammable (Zanzarini et al. 2022). For herbivory and light-related traits, we selected species and measured traits during the rainy

season (February to April/2022) since this is the growing season for most plants in the Cerrado (Furley 1999) and leaves are expanded for trait measurements.

Light-related traits

We sampled three individuals per species and collected four expanded leaves for each plant individual to assess the following traits related to light, as described below:

Leaf size: length and width (cm)

We collected and measured the leaf (surface area) length and width (Lebrija-Trejos et al. 2010) of three leaves per individual in the selected plants of each area. As leaves were collected in the field and trait measurements were taken in the laboratory, we rehydrated the leaves for 24h, to obtain an expanded leaf surface and measure leaf size after that.

Photosynthetic pigments

We determined the concentration of chlorophyll a, chlorophyll b, and total carotenoids by sampling 1cm² of leaf per individual (three individuals per species). The 1cm² was stored in 2mL amber-colored tubes containing DMF (N,N-dimethylformamide) (Porra et al. 1989) and kept in the dark at 4ºC for 48 hours. Afterward, the samples were analyzed in a spectrophotometer (Q898DRM) to determine the absorbance at wavelengths of 647, 664, and 480nm. The absorbance values were then used to calculate the concentrations of chlorophyll a, chlorophyll b and total carotenoids ($\mu g.cm^{-2}$) (Wellburn 1994). Finally, we used such values to obtain the total chlorophyll (sum of chlorophyll a and chlorophyll b) and the chlorophyll a:b ratio.

Fire-related traits

For fire-related traits, we selected five individuals per species encountered in the area haphazardly to determine flammability, and five individuals per species to assess dead biomass and moisture content. The description of each trait is provided below:

Flammability

To determine flammability, we used an equipment to measure shoot flammability in the field, which quantifies the flammability index of individual plants based on three parameters (Jaureguiberry et al. 2011). We determined the maximum temperature (MT, ºC) reached by the plant, burn rate (BR, $cm.s^{-1}$), and estimated the burned biomass (BB, %) of each plant individually. MT was obtained using an infra-red thermometer (Bosch 1000ºC) directed at the plant during the burn process. BR was calculated after measuring the length of the burnt portion of the shoot (cm) and the duration (s) of the burning process, dividing the cm/s. BB was visually estimated, determining the percentage of biomass consumed by fire. We used the values of these three components to calculate the flammability index, summing the scaled MT + BR + BB values, resulting in a value ranging between zero (no flammability) to three (maximum flammability) (Jaureguiberry et al. 2011).

Dead biomass (%)

Dead biomass was obtained by collecting plant individuals in the field and transporting them to the laboratory, where the live and dead material of each plant individual was separated and dried for 48 hours at 80ºC. This process yielded the live and dead dry weight (g). Subsequently, the percentage of dead biomass (%) was calculated for each plant individual.

Moisture content (%)

Moisture content was determined by obtaining the fresh weight (g) of each plant individual in the field. Subsequently, the plant individual was dried for 48 hours at 80ºC in the laboratory to obtain the dry weight (g), which was used to calculate the water content of each individual.

Herbivory-related traits

We accessed three traits related to herbivorous insects by measuring them at the leaf level for each plant individual. The description of each trait is provided bellow:

Leaf damage (%)

We sampled between three and five individuals per species and measured the percentage of leaf damage caused by chewer insects. For individuals with less than ten leaves, we determined the leaf damage for all leaves. For individuals with more than ten leaves, we randomly selected ten leaves to measure the leaf damage. We used an open source LeafByte mobile app (Getman-pickering et al. 2020) to scan each leaf and then reconstruct the consumed portion by the insect. Subsequently, the app calculated the percentage lost by each leaf, obtaining the percentage removed by chewing insects. Measurements of leaf damage were adapted from the Herbivory Variability Network (Pearse et al. 2020).

Total phenolics ($mg.g^{-1}$)

Total phenolics were obtained spectrophotometrically after the reaction with Folin-Ciocalteu reagent (Wigley et al. 2020), with modifications. As the majority of plant species lacked enough expanded and healthy leaves, we opted to group individuals by species and selected their most optimal leaves, obtaining an amount ranging from 4mg to 1g per species. All leaves underwent milling in liquid Nitrogen to extract the samples. The reaction was combined with 1.5mL of distilled water, 0.1mL of Folin-Ciocalteu reagent and 0.2mL of sample extract. After, spectrophotometric readings were taken at λ= 765nm.

Condensed tannins ($mg.g^{-1}$)

We obtained condensed tannin concentrations spectrophotometrically after the reaction with vanillin-HCl (Price et al. 1980). The same amounts of leaves to obtain total phenolics we used to obtain condensed tannins. After reacting with vanillin-HCl (8%), we determined the condensed tannin concentrations for each species using spectrophotometry at λ= 500nm.

Statistical analysis

To assess changes in light, fire, and herbivory-related traits among the three areas (open savanna, woody savanna, and forest), we first calculated a Community Weighted Mean (CWM) matrix for each trait in each area. The CWM provided the abundance-weighted mean trait value for each 1x1m plot of our three areas. The CWM matrix combines species abundance data for each plot with the mean trait values (leaf length, leaf width, total chlorophyll, chlorophyll *a:b* ratio, and total carotenoids, flammability, dead biomass, moisture content, leaf damage, total phenolics, and condensed tannins) of each species (Kleyer et al. 2012; de Bello et al. 2021). We used the CWM matrix values to perform a Principal Component Analysis (PCA), using the Euclidean distance as the resemblance measure to visually observe the distribution of data among the three areas. To investigate if light, fire, and herbivory-related traits differed among the three plant communities, we conducted a PERMANOVA test with 1000 permutations. Additionally, we performed a pairwise test using the Bonferroni method to compare the differences across the three plant communities.

To explore the trends of each trait among the three selected areas, we used the CWM values to construct Generalized Linear Mixed Models (GLMMs, *lmer* function), with Gaussian distribution, considering the areas as a fixed factor and the nested plots as a random factor. After, we performed a post hoc test (*lsmeans* function), to compare the factors pairwise.

The analyses were conducted using the R environment (R Core Team 2018), using the *lme4* package (Bates et al. 2015), *FD* package (Laliberté et al. 2014), *vegan* package (Oksanen et al. 2018), *RVAdeMemoire* package (Hervé 2022), and *lsmeans* package (Lenth 2016).

Results

Plant communities of open savanna, woody savanna, and forest exhibited differences in their functional traits related to light, fire, and herbivory by insects (PERMANOVA, F= 29.58;

p= 0.0009). Principal Component Analysis illustrated these differences, with the first two axes accounting for 64% of total variation (Fig. 2). Open savanna exhibited plants more associated chlorophyll *a:b* ratio, flammability, and dead biomass (Fig. 2). Woody savanna exhibited plants more associated with total chlorophyll, carotenoids, total phenolics, leaf length, and condensed tannins (Fig. 2). Forest plants exhibited more association with leaf width, moisture content, and % of leaf damage (Fig. 2)

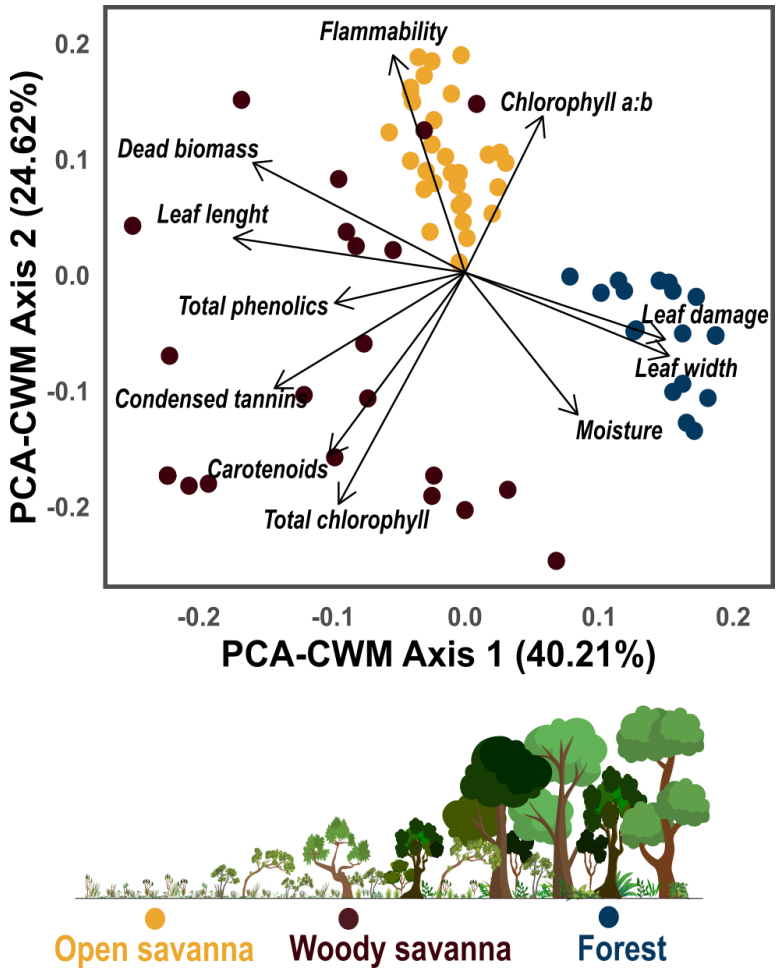

Figure 2: Principal Component Analysis (PCA) considering light (leaf length and width, *a:b* chlorophyll ratio – Cl a:b, total chlorophyll – Total Cl, and total carotenoids – Car), fire (flammability, dead biomass, and moisture content), and herbivory-related traits (% of leaf damage, condensed tannins, and total phenolics). Each trait was measured in plants sampled in open savanna, woody savanna, and forest, located in the Cerrado Central Brazil. Each point represents the sampling units in the CWM matrix (plot by traits), according to the different areas.

Open and woody savannas exhibited plants with longer leaves compared to forest ($p=0.0001$; Fig. 3A), while forest plants exhibited wider leaves ($p<0.05$; Fig. 3B). Total chlorophyll and carotenoids were higher in plants occurring in the woody savanna in comparison to open savanna and forest ($p<0.05$; Fig. 3C and 3D). Open savanna plants exhibited high chlorophyll *a:b* ratio in relation to woody savanna ($p<0.0001$; Fig. 2E), but the same ratio in relation to forest ($p=0.34$; Fig. 3E).

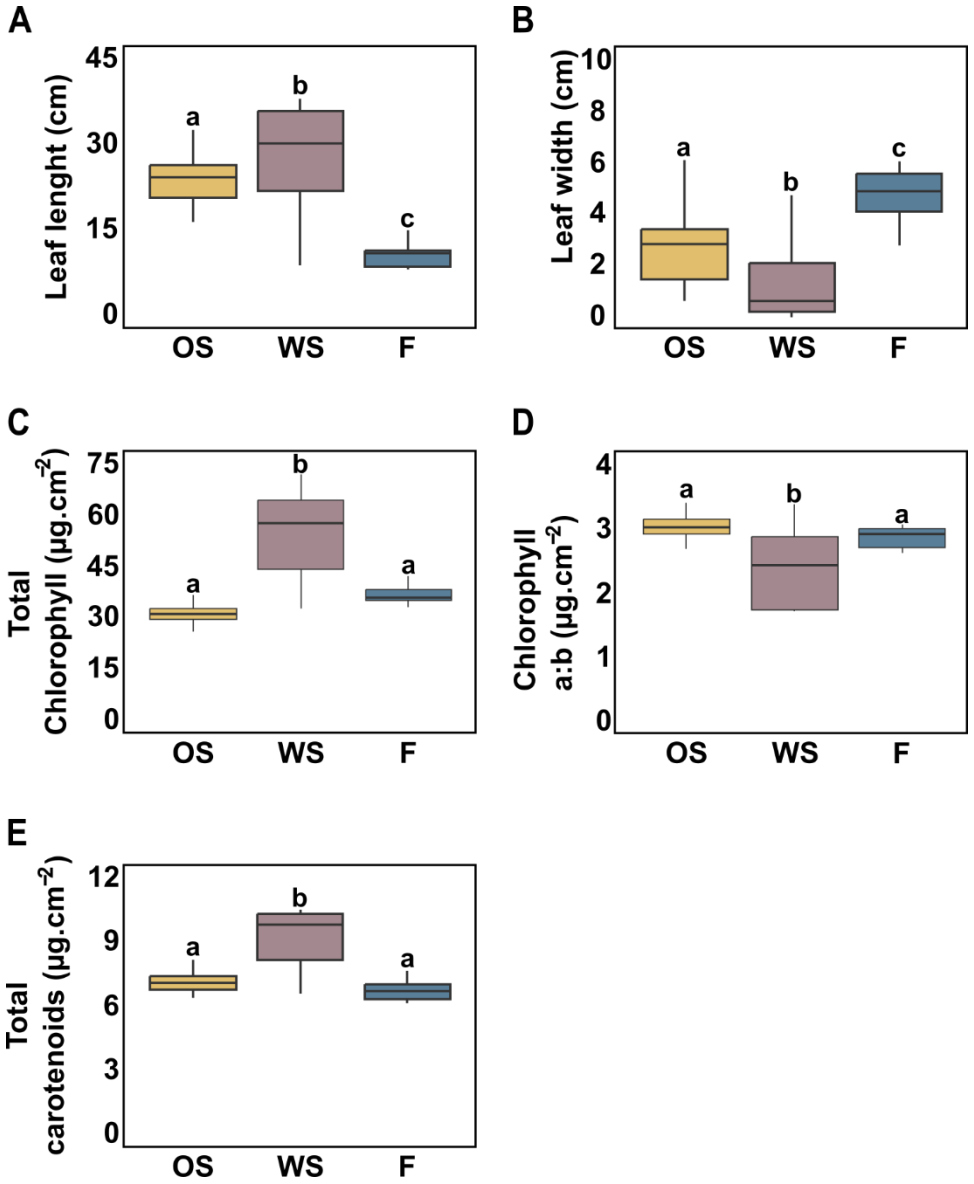

Figure 3: Light-related traits (A- leaf length, B- Leaf width, C- total chlorophyll, D- chlorophyll a:b, E- total carotenoids), sampled in plants of open savanna (OS), woody savanna (WS), and forest (F) located in the Cerrado Central Brazil. Boxplots (median and first and third quartile) represent the CWM values for each trait.

Plant flammability and dead biomass amount decreased from open savanna to forest (Fig. 4A e 4B). Plants exhibited similar amounts of dead biomass between open to woody savannas (p=0.3). Forest exhibited more humid plants in relation to both savanna areas (p=0.0003; Fig. 4C).

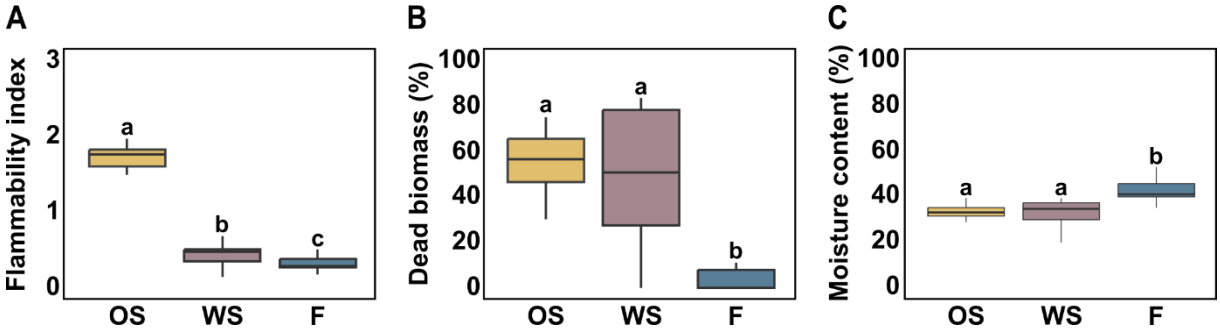

Figure 4: Fire-related traits (A- Flammability, B- Dead biomass, C- Moisture content), sampled in plants of open savanna (OS), woody savanna (WS), and forest (F) located in the Cerrado Central Brazil. Boxplots (median and first and third quartile) represent the CWM values for each trait.

In relation to herbivory patterns, we could observe that plants were more damaged in the forest when compared to the savanna areas (Fig. 5A). Condensed tannins and total phenolics exhibited higher concentrations in the woody savanna plants ($p<0.05$), while forest plants exhibited the lowest compounds concentration in relation to the savanna areas (Fig. 5B and 5C).

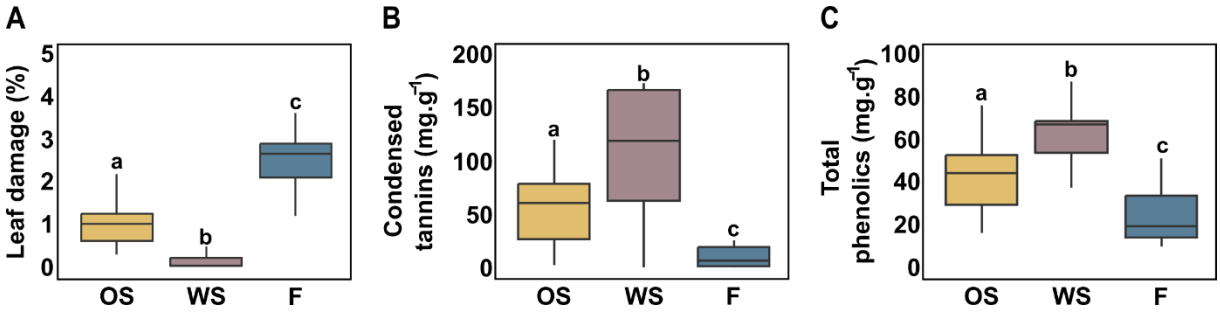

Figure 5: Herbivory-related traits (A- % of leaf damage, B- Condensed tannins, C- Total phenolics), sampled in plants of open savanna (OS), woody savanna (WS), and forest (F) located in the Cerrado Central Brazil. Boxplots (median and first and third quartile) represent the CWM values for each trait.

Discussion

Our study provides new insights into the key determinants of savanna and forest vegetation through the investigation of functional traits present in the herbaceous layer species.

As expected, fire- and light-related traits changed across our three studied areas. In open savannas, where fire frequency is high, plants exhibited high amounts of dead biomass, responsible for increasing flammability (Simpson et al. 2016; Zanzarini et al. 2022). When fire frequency is reduced in the savanna (like in the woody savanna), plants decrease their flammability and trees also occupies the ground. In woody savannas, almost 50% of the vegetation is composed by tree species (Coutinho 1982), creating a more shaded environment compared to open savannas. Due to that, plant communities exhibited traits to deal with the capture of light, such as total chlorophyll, to increase photosynthesis efficiency (Rossatto et al. 2018). In the forest, flammability is reduced, as grasses are not present in the system and consequently, fire cannot spread. In the shaded environment, plants exhibited low concentrations of photosynthetic pigments, but wider leaves were required to capture the diffuse light. Contrary to our expectations, herbivory patterns changed among the three areas. Leaf damage percentages increased in forest plants, while plants in the open savannas were less damaged by insects. Plants in the woody savannas exhibited the highest concentrations of condensed tannins and total phenolics, which are important chemical defenses against insects (Barbehenn & Peter Constabel 2011; War et al. 2012).

The presence of fire is essential to maintain the structure of savannas ((Bond 2019; Archibald et al. 2020), such as in the Cerrado, where fire is the disturbance capable of significantly consuming the vegetation (Coutinho 1982; Bond 2005). Fire favors the grass layer, which exhibits flammable traits allowing its spread while keeping the open structure suitable for sunlight-dependent species occurrence (Fig. 6, Charles-Dominique et al. 2018). Some grass species exhibit plant architecture suitable for the spread of fire, having aerated fuels, while others can exhibit sufficient biomass to sustain fire (Zanzarini 2019). In open savannas, grasses occupy more than 80% of the ground (Coutinho 1982), making the open areas highly flammable (Simpson et al. 2022; Zanzarini et al. 2022). When fire is excluded, light conditions change

because there is an increase in woody cover (Fig. 6, Abreu et al. 2017, Hoffmann et al. 2012). As a consequence, grasses are shaded, leading to a reduction in their abundance (Pilon et al. 2020) resulting in changes in flammability traits (Fig. 6). Thus, it is possible to observe shifts in the vegetation because species with flammable traits start to be replaced by species with shade-tolerant traits, creating a fire-sensitive environment (Fig. 6).

Plants in open savanna exhibited high leaf damage compared to woody savanna, probably because in open savannas the frequent presence of fire enhanced insect's activity (Kay et al. 2007; Lopes & Vasconcelos 2011). However, the savanna areas showed less leaf damage percentages compared to those in forest. The high abundance of grasses contributes to the lower percentages of leaf damage in the savannas (Fig. 6), because grasses are unattractive to insects, due to their high silica content and low nutrient concentrations (Massey et al. 2006; Reynolds et al. 2009; Rossatto & Franco 2017). However, when the abundance of grasses decreases as a result of fire-exclusion and increased shade conditions, herbivory patterns increase (Fig. 6). This is particularly observed in forests, where the herbaceous layer is dominated by forbs and shrubs with thinner and nutrient-rich leaves that are more attractive to insects (Neves et al. 2010). Furthermore, we also observed that in woody savanna, plant communities exhibited the highest concentrations of condensed tannins and total phenolics in comparison to open savanna and forest. In open savanna, the plant community is mainly composed of grasses, which is the growth form with the lowest contents of condensed tannins and total phenolics (Zanzarini et al., in prep.), and as a result, the plant community exhibits low compounds concentrations. In forest, on the other hand, forb and shrub species (the main components of the herbaceous layer) exhibited low concentrations of these compounds due to low light incidence (Mole et al. 1988). These compounds overflow secondary metabolites induced by light availability (Mole et al. 1988), and once in the forest light is reduced, the concentrations of condensed tannins and total

phenolics is also reduced. Thus, forest species do not exhibit these chemical defenses in their leaves, which may contribute to increase the leaf consumption in relation to open habitats.

Forests are fire-sensitive while savannas are fire-prone ecosystems and investigations about their determinants are necessary to better understand their distribution (Charles-Dominique et al. 2015; Bernardino et al. 2022), especially where both vegetation types can occur (e.g., Cerrado). The exclusion of fire in the Cerrado can lead to a woody encroachment, shifting the savanna state to a forest state (Abreu et al. 2017). Once this vegetation shift occurs, the savanna state may not return to its previous condition anymore, even in the return of fire (Pausas & Bond 2020; Buisson et al. 2022), as the propagules font, especially from belowground bud-bearing structures, are reduced or lost (Bombo et al. 2022), altering the system functionality and structure (Buisson et al. 2022). Different environmental factors filter different growth forms and plant functional responses in both vegetation types (Dantas et al. 2013; Charles-Dominique et al. 2015). Trees exclude C_4 grasses in forest, while the presence of grasses in open savannas reduces tree establishment by keeping the grass-fire cycle (D'Antonio & Vitousek 1992; Scholes & Archer 1997). Both trees and grasses influence ecosystem distribution and functioning in the tropics (Scholes & Archer 1997; Bond 2008), as trees create a shade and humid environment, inhibiting fire occurrence, while grasses act as fuel for fire spread (Fig. 6, Hoffmann et al. 2012). Moreover, in woody savannas, the mixed cover between trees and grasses still enables fire occurrence. However, the grass-layer is discontinuous in woody savanna (Coutinho 1982; Bond 2008), and the absence of fire promotes an accumulation of dead biomass in grass tussocks that are still present in the area. The high accumulation of biomass in grasses and the presence of shrubs increased the moisture content in this area, which are factors that may influence fire spread, reducing the flammability (Zanzarini et al. 2022). Fire exclusion could lead to changes in the vegetation structure, as trees

can dominate the space, contributing to the discontinuity of the grass-layer, leading to a decrease in the system's flammability (Fig. 6) (Hoffmann et al. 2012; Newberry et al. 2020).

Thus, fire is the major consumer in savannas, and it also influences plant-animal interactions. The herbaceous plant community of savannas is adapted to spread fire in the vegetation, which can benefit insects, as the regrowth of new and nutrient plants attract them. However, herbivory by insects would not play a major role as consumers in savannas. On the other hand, shade conditions in forests influence how plants deal with low light incidence, and positively influence insect's activity. This situation seems to increase herbivory patterns in forest vegetation compared to savanna vegetation. Furthermore, it is also important to note that while interactions are well studied in tree species, investigations regarding herbaceous plants in different vegetation types are lacking (Ballarin et al. 2024), and our study brings new insights about it.

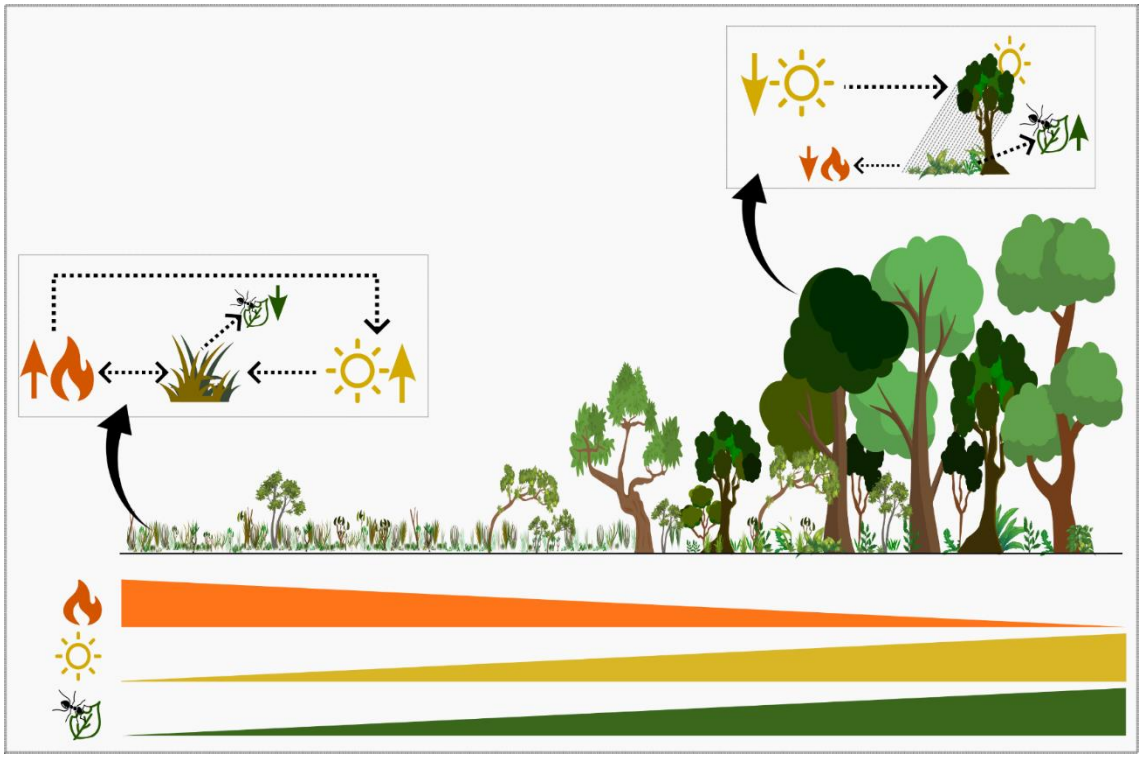

Figure 6: A scheme describing the main conclusions obtained in our study addressing the important determinants of savanna (fire as the major consumer, herbivory by insect playing a

secondary role) and forest vegetation (light is the major driver, also affecting insect herbivory) in areas where climate supports forest.

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Supplementary information

Table SI1: Pairwise comparisons and p values for each light-related trait among the three study areas: open savanna (OS), woody savanna (WS), and forest (F), located in the Cerrado Central Brazil.

Area	Carotenoids ($\mu g.cm^{-2}$)	Chlorophyll *a:b* ($\mu g.cm^{-2}$)	Leaf length (cm)	Leaf width (cm)	Total chlorophyll ($\mu g.cm^{-2}$)
OS - WS	<0.0001	<0.0001	0.02	0.03	<0.0001
OS - F	0.52	0.34	<0.0001	<0.0001	0.16
WS - F	<0.0001	0.001	<0.0001	<0.0001	<0.0001

Table SI2: Pairwise comparisons and p values for each fire-related trait among the three study: areas: open savanna (OS), woody savanna (WS), and forest (F), located in the Cerrado Central Brazil.

Area	Dead biomass (%)	Flammability	Moisture content (%)
OS - WS	0.3	<0.0001	0.96
OS - F	<0.0001	<0.0001	0.003
WS - F	<0.0001	0.05	0.003

Table SI3: Pairwise comparisons and p values for each herbivory-related trait among the three study areas: open savanna (OS), woody savanna (WS), and forest (F), located in the Cerrado Central Brazil.

Area	Leaf damage (%)	Total phenolics ($mg.g^{-1}$)	Condensed tannins ($mg.g^{-1}$)
OS - WS	0.005	0.0001	0.0001
OS - F	<0.0001	0.03	0.003
WS - F	<0.0001	<0.0001	<0.0001

Table SI4: Mean±SD of fire related traits (flammability index, dead biomass, and moisture content) of each species sampled in each area (open savanna, woody savanna, and forest), at the RNST, Cavalcante, Brazil.

		Open savanna			
Growth forms	**Family**	**Especies**	**Flammability index**	**Dead biomass (%)**	**Moisture content (%)**
Graminoid	Poaceae	*Anthaenantia lanata* (Kunth) Benth.	2.27 ± 0.13	76.89 ± 1.48	33.08 ± 1.86
Graminoid	Poaceae	*Axonopus aureus* P. Beauv.	1.86 ± 0.11	94.15 ± 3.19	33.81 ± 4.34
Shrub	Fabaceae	*Bauhinia dumosa* Benth.	0.28 ± 0.14	0 ± 0	57.46 ± 8.82
Shrub	Fabaceae	*Calliandra dysantha* Benth.	1.24 ± 0.15	0 ± 0	36 ± 3.46
Shrub	Fabaceae	*Chamaecrista ochrosperma* (H.S.Irwin & Barneby) H.S.Irwin & Barneby	1.38 ± 0.23	0 ± 0	33.42 ± 2.58
Forb	Euphorbiaceae	*Croton gracilescens* Müll.Arg.	0.92 ± 0.15	0 ± 0	47.15 ± 2.62
Graminoid	Poaceae	*Elionurus muticus* (Spreng.) Kuntze	2.03 ± 0.14	74.78 ± 3.76	27.47 ± 2.43
Graminoid	Poaceae	Sp.1	2.07 ± 0.09	81.09 ± 1.95	20.83 ± 3.94
Forb	Asteraceae	*Ichthyothere hirsuta* Gardner	0.76 ± 0.23	74.42 ± 6.46	58.85 ± 4.31
Graminoid	Poaceae	*Mesosetum ferrugineum* (Trin.) Chase	2.05 ± 0.05	74.32 ± 1.8	28.26 ± 1.5
Graminoid	Poaceae	*Mesosteum loliiforme* (Hochst.) Chase	1.95 ± 0.05	86.99 ± 4.92	35.81 ± 11.97
Shrub	Fabaceae	*Mimosa pteridifolia* Benth.	1.61 ± 0.12	0 ± 0	34.6 ± 2.69
Graminoid	Poaceae	*Oncorachis ramosa* (Zuloaga & Soderstr.) Morrone & Zuloaga	2 ± 0.16	75.76 ± 4.02	27.61 ± 3
		Total	**1.54 ± 0.07**	**50.38 ± 4.55**	**36.38 ± 1.66**

		Woody savanna			
Growth forms	**Family**	**Especies**	**Flammability index**	**Dead biomass (%)**	**Moisture content (%)**

Shrub	Annonaceae	*Annona sp.*	0 ± 0	2.81 ± 2.81	40.84 ± 3.36
Graminoid	Poaceae	*Anthaenantia* sp.	1.33 ± 0.34	73.25 ± 3.91	20.04 ± 2.38
Shrub		Sp. 2	0.17 ± 0.17	0 ± 0	42.76 ± 10.18
Graminoid	Poaceae	*Aristida longifolia* Trin.	0.55 ± 0.34	58.54 ± 8.3	31.07 ± 3.3
Graminoid	Poaceae	*Aristida* sp. 1	0.06 ± 0.06	86.2 ± 6.03	44.55 ± 4.36
Shrub	Fabaceae	*Bauhinia dumosa* Benth.	0.15 ± 0.15	0 ± 0	22.85 ± 2.77
Shrub	Fabaceae	*Calliandra dysantha* Benth.	0.52 ± 0.22	0 ± 0	24.55 ± 2.13
Graminoid	Cyperaceae	*Scleria secans* (L.) Urb.	0.43 ± 0.23	79.2 ± 2.64	16.68 ± 2.11
Graminoid	Poaceae	*Andropogon* sp.	1.89 ± 0.04	75.59 ± 2.06	30.31 ± 4.82
Graminoid	Poaceae	*Paspalum* sp.	1.79 ± 0.03	89.99 ± 4.44	18.42 ± 6.65
Shrub	Acanthaceae	*Ruellia nitens* (Nees) Wassh.	0 ± 0	0 ± 0	20.14 ± 5.25
Graminoid	Cyperaceae	*Rhynchospora consanguinea* (Kunth) Boeckeler	0.49 ± 0.32	80.28 ± 9.32	36.92 ± 5.44
		Total	**0.62 ± 0.1**	**46.26 ± 5.2**	**29.17 ± 1.82**

		Forest			
Growth forms	**Family**	**Especies**	**Flammability index**	**Dead biomass (%)**	**Moisture content (%)**
Graminoid	Cyperaceae	Sp. 3	0.83 ± 0.11	68.16 ± 11.42	48.5 ± 1.79
Graminoid	Poaceae	*Panicum sellowii* Nees	0.58 ± 0.05	16.06 ± 7.71	46.51 ± 3.44
Shrub		Sp. 4	0.31 ± 0.13	0 ± 0	57.93 ± 2.74
Shrub	Piperaceae	*Piper* sp. 1	0.39 ± 0.16	0 ± 0	58.62 ± 3.61
Forb	Piperaceae	*Piper* sp. 2	0.09 ± 0.09	0 ± 0	19.96 ± 7.71
Forb		Sp. 5	0.27 ± 0.27	0 ± 0	40.48 ± 5.4

	Total	**0.41 ± 0.07**	**14.04 ± 5.07**	**45.33 ± 2.95**

Table SI5: Mean±SD of herbivory related traits (% of leaf damage, condensed tannins, and total phenolics) of each species sampled in each area (open savanna, woody savanna, and forest), at the RNST, Cavalcante, Brazil.

		Open savanna			
Growth forms	**Family**	**Especies**	**Leaf damage (%)**	**Condensed tannins (mg.g^{-1})**	**Total phenolics (mg.g^{-1})**
Forb	Asteraceae	*Aldama grandiflora* (Gardner) E.E.Schill. & Panero	2.54 ± 1.74	5.66 ± 0.09	42.23 ± 0.69
Graminoid	Poaceae	*Anthaenantia lanata* (Kunth) Benth.	0 ± 0	1.80 ± 0.02	14.61 ± 0.06
Graminoid	Poaceae	*Aristida setifolia* Kunth	0 ± 0	26.3 ± 0.62	16.59 ± 0.13
Graminoid	Poaceae	*Axonopus aureus* P. Beauv.	0 ± 0	2.75 ± 0.02	16.52 ± 0.77
Forb	Malpyghiaceae	*Heteropterys pannosa* Griseb.	4.83 ± 2	293.65 ± 0.73	142.09 ± 1.45
Shrub	Fabaceae	*Bauhinia dumosa* Benth.	6.45 ± 1.73	209.12 ± 1.1	94.97 ± 1.47
Shrub	Fabaceae	*Calliandra dysantha* Benth.	0.41 ± 0.22	485.39 ± 3.77	184.35 ± 3
Forb	Euphorbiaceae	*Croton gracilescens* Müll.Arg.	2.4 ± 0.57	5.5 ± 0.06	13.08 ± 0.06
Graminoid	Poaceae	*Elionurus muticus* (Spreng.) Kuntze	0 ± 0	7.75 ± 0.17	27.09 ± 0.14
Forb	Lamiaceae	*Gymneia chapadensis* Harley	1.59 ± 0.94	3.25 ± 0.02	33.54 ± 0.47
Shrub	Fabaceae	*Harpalyce tombadorensis* São-Mateus et al.	3.91 ± 1.07	150.51 ± 0.66	142.26 ± 0.88
Forb	Lamiaceae	*Hyptis remota* Pohl ex Benth.	2.19 ± 2.10	3.64 ± 0.08	49.06 ± 0.47
Graminoid	Poaceae	*Mesosetum ferrugineum* (Trin.) Chase	0 ± 0	3.16± 0.08	21.08 ± 0.10
Graminoid	Poaceae	*Mesosteum loliiforme* (Hochst.) Chase	0 ± 0	2.3 ± 0.01	10.42 ± 0.16

Shrub	Fabaceae	*Mimosa leiocephala* Benth.	0 ± 0	114.95 ± 1.13	63.27 ± 0.25
Shrub	Fabaceae	*Mimosa pteridifolia* Benth.	0 ± 0	189.79 ± 0.72	89.14 ± 0.44
Graminoid	Poaceae	*Oncorachis ramosa* (Zuloaga & Soderstr.) Morrone & Zuloaga	0 ± 0	3.06 ± 0.04	16.14 ± 0.12
Graminoid	Poaceae	*Paspalum pectinatum* Nees ex Trin.	0 ± 0	4.61 ± 0.07	44.21 ± 1.19
Shrub	Acanthaceae	*Ruellia nitens* (Nees) Wassh.	0.81 ± 0.05	7.01 ± 0.24	58.29 ± 0.41
Shrub	Fabaceae	*Senna corifolia (*Benth.) H.S.Irwin & Barneby var. *corifolia*	1.36 ± 1.36	353.79 ± 2.29	110.67 ± 0.85
Graminoid	Poaceae	*Trachypogon spicatus* (L.f.) Kuntze	0 ± 0	2.36 ± 0.01	9.9 ± 0.07
		Total	**1.13 ± 0.27**	**89.35 ± 17.44**	**57.11 ± 6.34**

		Woody savanna			
Growth forms	**Family**	**Especies**	**Leaf damage (%)**	**Condensed tannins (mg.g^{-1})**	**Total phenolics (mg.g^{-1})**
Shrub	Annonaceae	*Annona* sp.	16.43 ± 1.71	NA	NA
Graminoid	Poaceae	*Anthaenantia* sp.	0 ± 0	NA	NA
Shrub		Sp. 2	2.08 ± 1.16	NA	NA
Graminoid	Poaceae	*Aristida longifolia* Trin.	0 ± 0	82.78 ± 40.51	64.09 ± 27.48
Graminoid	Poaceae	*Aristida* sp. 1	0 ± 0	16.12 ± 0.16	204.41 ± 2.03
Shrub	Fabaceae	*Bauhinia dumosa* Benth.	4.14 ± 1.59	156.0 ± 2.10	73.39 ± 0.41
Shrub	Malpyghiaceae	*Byrsonima* sp.	1.08 ± 0.7	4.4 ± 0.08	10.82 ± 0.03
Graminoid	Cyperaceae	*Scleria secans* (L.) Urb.	0 ± 0	1.84 ± 0.03	12.92 ± 0.14
Graminoid	Poaceae	*Andropogon* sp.	0 ± 0	2.54 ± 0.03	9.24 ± 0.1
Graminoid	Poaceae	*Paspalum* sp.	0 ± 0	265.57 ± 28.23	125.48 ± 15.75
Shrub	Acanthaceae	*Ruellia nitens* (Nees) Wassh.	0 ± 0	5.67 ± 2.40	30.59 ± 3.42

Graminoid	Cyperaceae	*Rhynchospora consanguinea* (Kunth) Boeckeler	0 ± 0	167.89 ± 162.34	68.98 ± 55.88
		Total	**1.97 ± 0.79**	**87.47 ± 28.32**	**66.71 ± 14.55**

		Forest			
Growth forms	**Family**	**Especies**	**Leaf damage (%)**	**Condensed tannins (mg.g^{-1})**	**Total phenolics (mg.g^{-1})**
Graminoid	Cyperaceae	Sp. 3	0.05 ± 0.05	44.41 ± 42.73	29.89 ± 21.49
Forb		Sp. 6	1.81 ± 1.75	1.58 ± 0.13	15.52 ± 1.13
Graminoid	Poaceae	*Panicum sellowii*	0 ± 0	1.49 ± 0.05	10.41 ± 0.03
Forb		Sp. 7	4.41 ± 0.4	1.85 ± 0.02	21.8 ± 10.74
Shrub		Sp. 4	1.19 ± 0.16	15.35 ± 4.7	8.36 ± 0.71
Shrub	Piperaceae	*Piper* sp. 1	2.24 ± 1.5	5.74 ± 0.05	42.29 ± 1.19
Shrub	Piperaceae	*Piper* sp. 3	1.01 ± 0.68	3.03 ± 1.23	23.76 ± 9.17
Shrub		Sp. 9	4.97 ± 2.4	52.91 ± 49.34	80.39 ± 31.81
Forb		Sp. 5	2.69 ± 2.18	2.3 ± 0.01	10.42 ± 0.16
Forb		Sp. 8	6.85 ± 4.22	NA	NA
		Total	**1.49 ± 0.35**	**11.22 ± 5.64**	**21.23 ± 3.5**

Table SI5: Mean±SD of light related traits (leaf length, leaf width, total chlorophyll, chlorophyll a:b ration, and carotenoids) of each species sampled in each area (open savanna, woody savanna, and forest), at the RNST, Cavalcante, Brazil.

		Open savanna					
Growth forms	**Family**	**Especies**	**Leaf lenght (cm)**	**Leaf width (cm)**	**Total Chlorophyll (µg.cm^{-2})**	**Chlorophyll a:b ratio (µg.cm^{-2})**	**Carotenoids (µg.cm^{-2})**
Forb	Asteraceae	*Aldama grandiflora* (Gardner) E.E.Schill. & Panero	12.80 ± 9.05	4.08 ± 2.88	41.21 ± 7.29	2.68 ± 0.28	9.16 ± 1.14
Forb	Malpyghiaceae	*Heteropterys pannosa* Griseb.	12.73 ± 9.0	4.63 ± 3.27	46.91 ± 7.2	3.47 ± 0.61	9.62 ± 1.01
Forb	Euphorbiaceae	*Croton gracilescens* Müll.Arg.	9 ± 0.12	1.53 ± 0.03	45.23 ± 7.24	3.02 ± 0.33	8.92 ± 1.01
Forb	Lamiaceae	*Gymneia chapadensis* Harley	6.37 ± 0.41	2.6 ± 0.1	29.07 ± 6.78	2.34 ± 0.2	7.76 ± 0.8
Forb	Lamiaceae	*Hyptis remota* Pohl ex Benth.	5.05 ± 3.57	2.71 ± 1.92	47.9 ± 3.18	2.5 ± 0.11	10.71 ± 0.37
Graminoid	Poaceae	*Anthaenantia lanata* (Kunth) Benth.	59.93 ± 5.26	0.33 ± 0.03	47.18 ± 8.5	3.83 ± 0.38	10.56 ± 1.29
Graminoid	Poaceae	*Aristida setifolia* Kunth	31.07 ± 2.78	0.2 ± 0	44.42 ± 5.71	1.2 ± 0.18	7.43 ± 0.73
Graminoid	Poaceae	*Axonopus aureus* P. Beauv.	10 ± 0.78	0.33 ± 0.03	16.32 ± 2.34	3.35 ± 1.39	4.48 ± 1.02
Graminoid	Poaceae	*Elionurus muticus* (Spreng.) Kuntze	51.73 ± 6.66	0.23 ± 0.03	25.26 ± 5.83	3.63 ± 0.35	5.65 ± 1.17
Graminoid	Poaceae	*Mesosetum ferrugineum* (Trin.) Chase	35.2 ± 1.27	0.3 ± 0	23.01 ± 1.75	3.58 ± 0.3	6.9 ± 0.21
Graminoid	Poaceae	*Mesosteum loliiforme* (Hochst.) Chase	7.17 ± 1	0.57 ± 0.07	25.65 ± 5.94	4.25 ± 0.29	5.74 ± 1.16
Graminoid	Poaceae	*Oncorachis ramosa* (Zuloaga & Soderstr.) Morrone & Zuloaga	43.67 ± 5.27	0.7 ± 0	26.26 ± 3.76	4.77 ± 0.17	6.68 ± 0.44
Graminoid	Poaceae	*Paspalum pectinatum* Nees ex Trin.	19.05 ± 2.65	0.35 ± 0.05	14.83 ± 2.15	3.33 ± 0.46	3.54 ± 0.72
Graminoid	Poaceae	*Trachypogon spicatus* (L.f.) Kuntze	29.17 ± 0.3	0.23 ± 0.03	29.46 ± 8.62	2.53 ± 0.96	5.98 ± 1.75
Shrub	Fabaceae	*Bauhinia dumosa* Benth.	11.53 ± 0.38	8.53 ± 0.43	54.43 ± 5.54	2.5 ± 0.09	10.84 ± 0.5
Shrub	Fabaceae	*Calliandra dysantha* Benth.	17.02 ± 12.03	16.75 ± 11.84	25.67 ± 10.45	2.59 ± 1	6.75 ± 1.08
Shrub	Fabaceae	*Harpalyce tombadorensis* São-Mateus et al.	14.55 ± 0.05	7.35 ± 0.35	53.84 ± 4.91	2.76 ± 0.35	11.87 ± 0.15

Shrub	Fabaceae	*Mimosa leiocephala* Benth.	14.88 ± 10.52	4.8 ± 3.39	23.47 ± 4.38	4.06 ± 0.8	4.52 ± 1.31
Shrub	Fabaceae	*Mimosa pteridifolia* Benth.	11.5 ± 1.08	7.47 ± 0.15	21.36 ± 9.84	2.43 ± 0.89	6.06 ± 0.79
Shrub	Acanthaceae	*Ruellia nitens* (Nees) Wassh.	6.13 ± 1.09	2.37 ± 0.43	40.43 ± 8.23	2.53 ± 0.34	6.95 ± 2.6
Shrub	Fabaceae	*Senna corifolia (*Benth.) H.S.Irwin & Barneby var. *corifolia*	13.8 ± 9.75	11.13 ± 7.87	69.1 ± 6.71	1.61 ± 0.3	10.37 ± 1.68
		Total	**21.04 ± 2.25**	**3.26 ± 0.55**	**36.26 ± 2.1**	**2.95 ± 0.15**	**7.66 ± 0.34**

		Woody savanna					
Growth forms	**Family**	**Especies**	**Leaf lenght (cm)**	**Leaf width (cm)**	**Total Chlorophyll (µg.cm^{-2})**	**Chlorophyll a:b ratio (µg.cm^{-2})**	**Carotenoids (µg.cm^{-2})**
Graminoid	Poaceae	*Anthaenantia* sp.	73.47 ± 4.73	0.33 ± 0.03	36.24 ± 7.95	3.6 ± 0.71	7.57 ± 1.28
Graminoid	Poaceae	*Aristida longifolia* Trin.	37.93 ± 2.66	0.23 ± 0.03	35.33 ± 13.11	3.26 ± 0.2	6.58 ± 2.4
Graminoid	Poaceae	*Aristida* sp. 1	22.17 ± 2.03	0.1 ± 0	55.91 ± 7.22	2.31 ± 0.25	9 ± 0.71
Graminoid	Cyperaceae	*Scleria secans* (L.) Urb.	25.27 ± 3.28	0.3 ± 0	33.65 ± 5.52	3.41 ± 0.2	7.61 ± 0.76
Graminoid	Poaceae	*Andropogon* sp.	42 ± 9.47	0.23 ± 0.07	26.04 ± 2.69	3.27 ± 0.13	6.53 ± 0.64
Graminoid	Poaceae	*Paspalum* sp.	30.07 ± 1.01	0.27 ± 0.03	34.74 ± 1.72	3.43 ± 0.08	7.38 ± 0.28
Graminoid	Cyperaceae	*Rhynchospora consanguinea* (Kunth) Boeckeler	36.97 ± 4.38	0.13 ± 0.03	72.24 ± 7.49	1.74 ± 0.37	10.35 ± 0.33
Shrub	Annonaceae	*Annona* sp.	9.07 ± 1.52	5.33 ± 1.28	44.7 ± 3.53	3.25 ± 0.06	9.99 ± 0.41
Shrub		Sp. 2	7.2 ± 0.64	3.23 ± 0.32	65.67 ± 1.55	2.06 ± 0.1	10.95 ± 0.26
Shrub	Fabaceae	*Bauhinia dumosa* Benth.	9.9 ± 0.95	9.87 ± 2.14	56.35 ± 7.4	2.73 ± 0.48	10.33 ± 0.36
Shrub	Malpyghiaceae	*Byrsonima* sp.	13.2 ± 0.72	6.97 ± 0.61	48.06 ± 5.25	2.9 ± 0.1	9.8 ± 0.81
Shrub	Acanthaceae	*Ruellia nitens* (Nees) Wassh.	5.87 ± 0.43	2.13 ± 0.18	65.71 ± 4.71	2.21 ± 0.41	10.69 ± 0.07

		Total	**26.08 ± 3.45**	**2.43 ± 0.59**	**47.19 ± 2.74**	**2.85 ± 0.12**	**8.82 ± 0.33**

		Forest					
Growth forms	**Family**	**Especies**	**Leaf lenght (cm)**	**Leaf width (cm)**	**Total Chlorophyll (µg.cm^{-2})**	**Chlorophyll a:b ratio (µg.cm^{-2})**	**Carotenoids (µg.cm^{-2})**
Forb		Sp. 6	25.13 ± 2.28	10.43 ± 1.01	42.49 ± 6.43	2.81 ± 0.27	7.74 ± 1.03
Forb		Sp. 7	14.47 ± 0.62	5 ± 0.2	28.8 ± 2.91	3.16 ± 0.15	5.37 ± 0.59
Forb	Piperaceae	*Piper* sp. 4	NA	NA	38.32 ± 1.93	2.87 ± 0.24	6.94 ± 0.42
Forb		Sp. 5	8.5 ± 1.92	6.03 ± 0.97	35.09 ± 2.4	2.69 ± 0.25	6.32 ± 0.25
Forb		Sp. 8	8.13 ± 0.73	4.7 ± 0.8	42.94 ± 1.21	2.62 ± 0.15	7.18 ± 0.12
Graminoid	Cyperaceae	Sp. 3	17.35 ± 0.85	2.1 ± 0	33.41 ± 3.25	3.24 ± 0.64	6.74 ± 0.08
Graminoid	Poaceae	*Panicum sellowii* Nees	8.1 ± 0.9	1.75 ± 0.05	39.91 ± 1.78	2.88 ± 0.18	7.15 ± 0.27
Shrub		Sp. 4	15.37 ± 2.38	4.07 ± 0.48	39.94 ± 4.73	2.9 ± 0.19	7.01 ± 0.71
Shrub	Piperaceae	*Piper* sp. 1	NA	NA	33.98 ± 6.87	3.08 ± 0.26	7.09 ± 1.04
Shrub	Piperaceae	*Piper* sp. 3	4.67 ± 0.52	1.87 ± 0.09	39.25 ± 1.34	3.07 ± 0.28	7.11 ± 0.24
Shrub		Sp. 9	12.3 ± 1.25	5.83 ± 0.73	54.35 ± 2.26	2.95 ± 0.29	8.88 ± 0.37
		Total	**12.66 ± 1.19**	**4.64 ± 0.51**	**39.10 ± 1.52**	**2.93 ± 0.07**	**7.06 ± 0.21**

5. CONSIDERAÇÕES FINAIS

Este estudo nos auxilia no entendimento sobre como o fogo desempenha um papel crucial na manutenção e distribuição das savanas, em especial no Cerrado. Obtivemos importantes e inéditas conclusões sobre como os atributos relacionados à inflamabilidade do sistema, à herbivoria por insetos e à incidência de luz podem ser alterados em diferentes comunidades do estrato herbáceo do Cerrado e como o fogo também influencia os padrões de herbivoria e disponibilidade de luz. A frequência e o tempo desde a última queima são variáveis do regime de fogo que influenciam a inflamabilidade da vegetação. A exclusão do fogo nesse sistema, promove um aumento na quantidade de biomassa morta no estrato herbáceo, principalmente em gramíneas. Esse grupo acumula sua biomassa ao longo dos anos sem fogo, criando um material úmido e condensado, dificultando a oxigenação durante a queima. Assim, a taxa de propagação do fogo nessas plantas diminui, fazendo com que as chamas permaneçam queimando o indivíduo por muito mais tempo. Diante disso, se áreas excluídas do fogo por longos anos acabam queimando, naturalmente ou acidentalmente, incêndios severos e de alta intensidade podem ser esperados devido ao acúmulo de material combustível mais inflamável, podendo comprometer inclusive estruturas de rebrote aéreo de muitas espécies arbustivas e até mesmo o entorno dessas áreas. Sendo assim, alterações no comportamento do fogo são ocasionadas devido a mudanças nos atributos relacionados à inflamabilidade, comprometendo a forma como as savanas queimam.

A frequência do fogo também influencia positivamente a ação dos insetos em savanas como o Cerrado. Em áreas frequentemente queimadas, observamos que as plantas possuem maiores porcentagens de dano foliar e maiores concentrações de compostos de defesa à herbivoria por insetos, em comparação com áreas excluídas do fogo. Isso ocorre devido a produção de novas folhas, algumas delas ricas em nutrientes, que acabam atraindo os insetos.

Além disso, observamos que dentre as principais formas de crescimento encontradas no estrato herbáceo de savanas, gramíneas não possuem suas folhas consumidas pelos insetos, devido à presença de sílica e baixas concentrações de nutrientes em suas folhas, tornando-as não palatáveis aos insetos. Por outro lado, arbustos são os mais consumidos pelos insetos devido à maior quantidade de nutrientes presentes em suas folhas. Porém, como estratégia de defesa, produzem maiores quantidades de compostos fenólicos e taninos. Diante disso, podemos observar como a presença do fogo afeta as diversas interações ecológicas entre os insetos e plantas, visto que áreas queimadas podem prover maiores quantidades de recursos e com isso favorecer a comunidade de insetos.

Por fim, concluímos este estudo investigando como os atributos relacionados à inflamabilidade, aos insetos herbívoros e a incidência de luz ocorrem num gradiente de vegetação de savana aberta para uma mais adensada, além de uma formação florestal, a fim de entender quais são os principais fatores atuando como consumidores principais das savanas. Diante disso, observamos como o fogo pode ser considerado o consumidor principal nas savanas, visto que as espécies do estrato herbáceo, principalmente as gramíneas, encontram-se adaptadas em promover a propagação do fogo na vegetação. Já nas formações florestais, a ausência desse grupo leva a uma diminuição da inflamabilidade do sistema, tornando estes ambientes sensíveis ao fogo. Além disso, ao contrário do que hipotetizamos, os padrões de herbivoria por insetos foram maiores na formação florestal, certamente devido às condições favoráveis de sombra, umidade e nutrientes ofertadas neste ambiente, favorecendo os insetos. Com isso, concluímos que a herbivoria exercida pelos insetos nas savanas possui um papel secundário no consumo da biomassa, até mesmo devido aos insetos não serem atraídos pelas gramíneas, que é o grupo que mais domina o estrato herbáceo dessas áreas. Quanto a isso, concluímos que o fogo é o principal distúrbio atuando no consumo da vegetação herbácea de savanas, mantendo-as em estado aberto e inflamável. Já em relação às diferentes condições de

luminosidade nessas três áreas, observamos como as espécies de áreas abertas estão adaptadas às altas concentrações de luz, com estratégias para uma melhor captação e otimização desse recurso. Isso inclui a presença de pigmentos fotossintéticos, bem como pigmentos que conferem proteção contra a radiação. Já no ambiente sombreado, o que observamos foi que as espécies do estrato herbáceo possuem atributos que auxiliam na captação da luz difusa, a fim de conseguirem otimizar este recurso, sendo desta forma a luz o principal fator nas florestas.

Em resumo, entendemos que o fogo tem um papel fundamental na estruturação e determinação das savanas através da análise dos atributos de plantas do estrato herbáceo. Além disso, o fogo atua na abertura da vegetação, garantindo a chegada de luz, estimulando o desenvolvimento das gramíneas que são o componente principal na propagação das chamas pela vegetação. Também salientamos como a frequente presença do fogo nas savanas afeta positivamente a herbivoria por insetos, sendo este o principal grupo de herbívoros removendo biomassa em savanas como o Cerrado. Por fim, devemos enfatizar que exclusão do fogo pode levar a mudanças na estrutura das savanas, comprometendo sua funcionalidade e biodiversidade.