RESSALVA

Atendendo solicitação da autora, o texto completo desta dissertação será disponibilizado somente a partir de 19/01/2023.

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

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

VEGETATIVE MORPHOANATOMICAL TRAITS OF FABACEAE FROM OPEN SAVANNA ‘CAMPO SUJO’

ALICE SOUZA LEAL

Rio Claro – SP
2021

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

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

VEGETATIVE MORPHOANATOMICAL TRAITS OF FABACEAE FROM OPEN SAVANNA ‘CAMPO SUJO’

ALICE SOUZA LEAL

Orientadora: Aline Redondo Martins

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

Rio Claro – SP
2021

L435v

Leal, Alice Souza
Vegetative morphoanatomical traits of Fabaceae from open savanna 'campo sujo' / Alice Souza Leal. -- Rio Claro, 2021
86 p. : il., tabs., fotos

Dissertação (mestrado) - Universidade Estadual Paulista (Unesp), Instituto de Biociências, Rio Claro
Orientadora: Aline Redondo Martins

1. Cerrado. 2. Functional traits. 3. Fabaceae. 4. Fire ecology. 5. Belowground systems. I. Título.

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

Essa ficha não pode ser modificada.

unesp UNIVERSIDADE ESTADUAL PAULISTA

Câmpus de Rio Claro

CERTIFICADO DE APROVAÇÃO

TÍTULO DA DISSERTAÇÃO: VEGETATIVE MORPHOANATOMICAL ATTRIBUTES OF FABACEAE FROM CERRADO

AUTORA: ALICE SOUZA LEAL

ORIENTADORA: ALINE REDONDO MARTINS

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

Aline R. Martins

Profa. Dra. ALINE REDONDO MARTINS (Participaçao Virtual)
Departamento de Biologia e Zootecnia / Faculdade de Engenharia de Ilha Solteira - UNESP

Graziela Cury Guapo

Profª Drª GRAZIELA CURY GUAPO (Participaçao Virtual)
Universidade Federal de Alagoas, Instituto de Ciências Biológicas e da Saúde

Davi R. Rossatto

Prof. Dr. DAVI RODRIGO ROSSATTO (Participaçao Virtual)
Departamento de Biologia Aplicada a Agropecuária / UNESP - Faculdade de Ciências Agrárias e Veterinárias de Jaboticabal - SP

Rio Claro, 19 de janeiro de 2021

Título alterado para:
VEGETATIVE MORPHOANATOMICAL TRAITS OF FABACEAE FROM OPEN SAVANNA 'CAMPO SUJO'

Dedico este trabalho à minha família

AGRADECIMENTOS

Ao universo por sempre me proporcionar aprendizados maravilhosos, e me permitir seguir meu caminho ajudando as pessoas e trabalhando em prol da natureza.

Agradeço a Dra. Aline Redondo Martins e Dra. Alessandra Fidelis por terem me dado oportunidade de realizar este projeto. A Dra. Alessandra, muito obrigada pelas leituras, excelentes contribuições e direcionamento dos meus estudos.

Agradeço à minha orientadora Dra. Aline Martins pelo suporte no laboratório, leituras e direcionamento. Agradeço o apoio e incentivo, e por sempre estar disposta a responder qualquer dúvida. Agradeço a atenção, preocupação e cuidado em relação à pesquisa e também assuntos pessoais. A nossa convivência sem dúvidas me agregou extremamente no âmbito profissional e pessoal, fico muito feliz e lisonjeada em tê-la como minha orientadora e parceira em pesquisas.

Agradeço aos Professores Dr. José Delgadillo Rodriguez, Dr. Walnir Gomes Ferreira Junior, Dr. Wellington Marota Barbosa, Dr. José Antônio Dias Garcia, Dra. Lêda Gonçalves Fernandes do IFSULDEMINAS - campus Machado e UABC - México, pelo apoio e incentivo em minha caminhada acadêmica, vocês sempre serão uma grande influência para mim. Em especial, agradeço aos professores Dr. José Delgadillo Rodriguez e Me. Yoni Rubio, professores da UABC-México, e Dr. Walnir do IFSULDEMINAS que me guiaram diretamente também nessa etapa do Mestrado. Ao meu amigo Yoni, obrigada pelas aulas de Inglês e nossas conversas agradáveis. E finalmente ao meu querido Professor José Delgadillo pela amizade, que mesmo distante sempre está presente em minha vida.

A Família Jorge Luiz Rezende Leal (Pai), Benilda Maria de Souza Leal (Mãe), Bernadete da Conceição de Souza Pereira (Madrinha), Hélio Laje (Melhor amigo) obrigada pelo incentivo, amizade, apoio incondicional e conselhos. Obrigada por sempre me ajudarem a me tornar uma pessoa melhor.

Aos grandes amigos Giselle Schwab, Matheus Martins obrigada por me acolherem no seu lar, pelo cuidado e apoio todas as vezes que precisei ir para Rio Claro. Gi muito obrigada pelo carinho, me sinto muito honrada de ter encontrado vocês pelo caminho. Vinícius Moreira Barbosa, e Gislaine Moreira meus amigos de longa data, obrigada por tudo, estaremos sempre juntos. Joana Pattini, obrigada pelo apoio, cuidado e amizade. Frederico Albuquerque obrigada pela parceria, apoio e incentivo.

Aos colegas do LEMAV- Ilha Solteira pela grande ajuda no desenvolvimento da pesquisa, e aos colegas do LEVEG- Rio Claro pela ajuda na coleta das espécies. Em especial a Eloisa e Talita pela disponibilização de alguns materiais necessários para a conclusão da pesquisa. Aos colegas que me ajudaram diretamente no Laboratório, Júlia Marrega (Luna), Marilaine Leite, Bruno Cozin, Thalissa Cagnin e Beatriz Shenaide vocês foram fundamentais para a realização desse projeto, muito obrigada pela ajuda. Agradeço também a Juliana Teixeira e Viviane por terem me hospedado em seus lares nos meus primeiros meses do Mestrado.

Ao Prof. Luciano Alves dos Anjos pelo auxílio com as fotografias para as análises morfológicas.

Agradeço ao departamento de Biologia e Zootecnia pela solicitude em relação a burocracias, em especial Meiri e Junior.

A seção técnica de Pós-graduação da UNESP Rio Claro, e o Programa de pós-graduação em Biologia Vegetal também pela solicitude e apoio.

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

Processo n° 2015/06743-0, Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP).

RESUMO

Contexto e objetivo: O fogo é um distúrbio essencial para a ecologia de vários ecossistemas no mundo, tais como o Cerrado. O Cerrado do Brasil Central caracteriza-se como uma savana mésica, com clima marcado por uma longa estação seca. Plantas que vivem nesses ambientes necessitam de atributos de sobrevivência para lidar com filtros ambientais característicos desses ambientes, como o fogo, a seca e a herbivoria. Tais atributos estão presentes em órgãos aéreos e subterrâneos. Algumas plantas, por exemplo, possuem características xeromórficas ou mesomórficas em seus órgãos aéreos. Além disso, muitas espécies da família Fabaceae tem capacidade de rebrotar depois do fogo, pois possuem órgãos subterrâneos com capacidade de acumular recursos que podem ser realocados para a regeneração de suas partes aéreas, demonstrando adaptação ao fogo. Com isso, esse estudo teve como objetivo avaliar e descrever características morfoanatômicas e funcionais de órgãos vegetativos de oito Fabaceae do campo sujo.

Métodos: Foram coletadas três plantas adultas inteiras de cada espécie para análise morfoanatômica, histoquímica e ultra estrutural de caules, folhas e órgãos subterrâneos.

Resultados principais: De acordo com as análises morfoanatômicas dos órgãos aéreos, foram encontradas características mesomórficas e xeromórficas. Tais características tem a função de proteção contra as altas temperaturas do fogo, herbivoria e também evitam a perda de água. Além disso, muitas plantas apresentaram nectários extraflorais, os quais viabilizam relações mutualísticas das plantas com insetos**.** Os órgãos subterrâneos analisados foram classificados como raízes tuberosas e xilopódios. Todos os xilopódios apresentaram gemas visíveis em sua porção superior e estavam associados a raízes tuberosas. Além disso, em algumas espécies, essas raízes tuberosas foram classificadas também como raízes gemíferas. A combinação de raízes gemíferas com xilopódio confere a tais espécies vantagem de persistência, pois estas plantas tem a capacidade de rebrotar através do xilopódio, bem como podem propagar-se lateralmente por crescimento clonal através de raízes gemíferas. Além disso, todos os xilopódios apresentaram grandes quantidades de tecido lignificado, compostos de defesa contra herbívoros (compostos fenólicos e substâncias lipídicas), e substâncias de reserva (amido).

Conclusões: É interessante relatar que espécies de Fabaceae rebrotadoras têm diversas características morfológicas e anatômicas importantes em órgãos vegetativos aéreos e subterrâneos. Estas características permitem que essas espécies sobrevivam aos distúrbios ambientais nesses tipos de ecossistemas. Além disso, essas espécies podem armazenar reservas, rebrotar, e propagar-se lateralmente. O que proporciona a persistência das mesmas nesses tipos de ecossistemas e sua alta longevidade.

Palavras-chave: Xilopódio, ecologia do fogo, rebrotamento, crescimento clonal, Fabaceae

ABSTRACT

Background and Aim: Fire is an essential disturbance for the ecology of several ecosystems in the world, such as the Cerrado. The Cerrado of Central Brazil is a mesic savanna with a long dry season. Thus, plants living in these environments need survival traits to support fire, drought, and herbivory. Thus, these plants can show persistence traits in below and aboveground organs. For example, Cerrado plants can have xeromorphic or mesomorphic traits in their aboveground portion and are characterized by its post-fire regeneration, because of its high bud protection. Several species of the Fabaceae family have the capacity to resprout after fire due to the presence of bud-bearing underground structures, as well as their capacity to rapidly allocate resources for the formation of new aboveground shoots, showing to be adapted to fire. Therefore, the aim of this study was to evaluate and describe the morphoanatomical functional structures of above and belowground vegetative organs of eight Fabaceae from Cerrado.

Methods: It was collected three entire adult plants of each species for the morphoanatomical, histochemical and ultra-structural analysis of stem, leaves and belowground organs.

Key results: To the analyses of the aboveground portion, we found xeromorphic and mesomorphic traits, with the function of protecting against fires heat temperature, herbivory, and avoid water loss, as well as extrafloral nectary's related to mutualistic relation. Regarding the belowground portion, we found two types of organs: tuberous roots and xylopodia. All xylopodia presented visible buds on the upper portion of the organs and associated tuberous roots. To some species these roots were also root suckers. These plants had a persistence advantage because they can resprout by xylopodium and had clonal growth through root suckers. Besides this, all xylopodia were composed of a great amount of lignified tissues, defense against herbivory (phenolic compounds and lipidic substances), and storage substances (starch).

Conclusions: It is interesting to relate that resprouting species have several important morphological and anatomical traits from above to belowground vegetative organs, that enable these species to resist the mean environmental filters. Additionally, these species can store reserves, resprouting, and propagate laterally, which enable their persistence in this environment, and provide it high longevity.

Key words: Xylopodium, fire ecology, resprouting, clonal growth, Fabaceae

SUMÁRIO

GENERAL INTRODUCTION

Cerrado is a seasonally dry savanna vegetation and it is considered one of the richest savanna vegetations in the world (Eiten 1994). It is an extensive ecosystem in South America located in Brazil (Eiten 1972), and it is globally recognized as a biodiversity hotspot (Myers *et al.* 2000). It is characterized by a mosaic of open fields to woodlands, which are defined by resource availability and disturbances (Sarmiento 1983, 1984; Lenthall *et al.* 1999; Oliveira-Filho, A.T.; Ratter 2002; Franco *et al.* 2014). An example is the Cerrado of central Brazil (Lenthall *et al.* 1999), which among other types of physiognomies includes “campo sujo” (a type of open savanna). This Cerrado vegetation type is characterized by a continuous herbaceous layer dominated by grass with some herbs and sub-shrubs as well as a few woody layers with scattered shrubs and trees (Eiten 1972).

The climate of the Cerrado is tropical characterized by a well-defined dry season from May to September and a long period of water restriction during which fire is frequent (Hoffmann *et al.* 2009). Additionally, savannas from Central Brazil are considered mesic savannas (Franco *et al.* 2014), because they are characterized by an average annual rainfall greater than 1,000 mm (Myers *et al.* 2000).

Savannas are fire-prone ecosystems in which fire has modified the vegetation for millions of years (Simon *et al.* 2009; Simon and Pennington 2012) determining survival traits of the species (Coutinho 1990) and great part of Cerrado vegetation such as savannas and grasslands are fire prone (Miranda *et al.* 2002). Besides fire, the Cerrado vegetation is submitted to the dry season that is characterized by water scarcity, which is a determinant period in the life cycle of these plants (Franco 2002). Water scarcity affects plants in the acquisition/assimilation of carbon (C), nutrients (Franco *et al.* 2005) and the defense against insect herbivory (Mcdowell *et al.* 2013). Besides this, one of the most important effects of water restriction is the death by hydraulic failure (Mcdowell *et al.* 2013).

Characterized as a vegetation fire-prone and a seasonally dry environment (Warming and Ferri 1973), Cerrado plants have many adaptive strategies to survive and persist under disturbances (fire and herbivory) and changes in environmental conditions (water and nutrients availability) (Franco *et al.* 2014), it depends of the vegetations phygsionomy (Coutinho 1990). Besides that, Cerrado plants with different growth forms have survival and persistence strategies related to aboveground organs (Rossatto *et al.* 2015) as well as belowground organs (Appezzato-da-Glória 2015). A set of strategies in these plants improve the survival under environmental instabilities and enable the plants species richness with high longevity (Dayaram *et al.* 2020).

In regard to the aboveground portion, some Cerrado plants lose their leaves during the winter dry season and this characteristic is common in herbs (Filgueiras 2002). These plants have a short lifespan and need to develop their aerial portion with low cost, high efficiency, and quickly (Rossatto et al, 2015). On the other hand, other Cerrado plants that maintain the aerial portion (Warming and Ferri 1973), have long leaf lifespans and need to develop an efficient aerial portion to survive the dry season and in some cases even fire (Warming and Ferri 1973; Wright *et al.* 2004). Thus, Cerrado species can developed from mesomorphic traits, related to short lifespan (Rossatto *et al.* 2015), and xeromorphic traits, related to long leaf lifespan, which improve the capacity of these plants to survive through drought and fire events (Warming and Ferri 1973).

Besides this, many traits related to leaf hydric economy can be also related to other abiotic and biotic factors. Traits with multiples functions can protect the plant against sunlight exposition, water loss, and herbivory. Some examples are well-developed cuticle (Read and Sanson 2003), glandular trichomes (Ambrósio *et al.* 2008), and tectors trichomes (Gonzáles *et al.* 2008). On the other hand, Cerrado plants also have extra floral nectaries, which are organs responsible to maintain mutualistic relations with insects (Del-Claro *et al.* 2016).

Regarding the belowground portion, many Cerrado species have belowground organs with a great capacity to produce buds and nutrients storage (Appezzato-da-Glória 2015) which enables faster aerial portion regeneration through resprouting (Whelan 1995; Clarke *et al.* 2013; Pausas *et al.* 2018). The resprouting ability after disturbances such as fire and drought (Zeppel *et al.* 2015), is frequently found in fire-prone ecosystems (Pausas *et al.* 2018)**.** Resprouting depends on several plants' traits, mainly the degree of protection and grouping of the viable bud bank, as well as storage reserves in these organs (Klimešová and Klimeš 2007; Clarke *et al.* 2013).

Xylopodium is an underground organ that is common in South America, especially among Fabaceae and Asteraceae (Pausas *et al*. 2018), and it is commonly found in the Cerrado (Rizzini and Heringer 1961; Appezzato-da-Glória 2015), located close to the soil surface (Appezzato-da-Glória 2015). It is characterized to have woody and hard consistence constituted by lignified tissues, commonly associated with tuberous roots containing storage parenchyma (Rizzini and Heringer 1961). There are buds located on the upper portion of the xylopodium that originates from the cambium and can be axillary or adventitious (Appezzato-da-Glória 2015). Additionally, the xylopodia does not have a specific storage parenchyma tissue (Appezzato-da-Glória and Estelita 2000) but the presence of storage is only related to the axial and radial parenchyma of the xylopodium secondary xylem (Paviani 1987) that can often storage starch or fructans (Appezzato-da-Glória 2015; Pausas *et al*. 2018).

Plants with resprouting ability can regenerate better after fire, recovering the pre-disturbances biomass much faster (Kelley *et al.* 2014). Thus, these plants are often dominants in climates with a high variation of fire and water availability (Clarke *et al.* 2013; Zeppel *et al.* 2015). Additionally, some resprouters plants have a competitive advantage since at the early stage of growth in which they already have resprouting ability (Vesk 2006).

The Fabaceae is one of the most important families of the Cerrado (Almeida *et al.* 2014; LPWG 2017), notably in the '*campo sujo*' open savanna studies (Tannus and Assis 2004; Munhoz and Felfili 2006). Additionally, it is also considered the third biggest family in terms of species richness worldwide (LPWG 2017).

This family is recognized to have a set of morphological and physiological adaptive traits to different environmental conditions, which enable ecological and evolutionary success (Rundel 1989). For example, water economy, nitrogen fixation, mycorrhizal associations, and morphologic traits from leaves to root architecture (Rundel 1989). This family is also characterized by having fire adapted belowground organs (Appezzato-Da-Glória *et al.* 2008; Simon and Pennington 2012). Thus, resprouting is often found in herbaceous and woody species of Fabaceae (Hayashi *et al.* 2001; Kennard *et al.* 2002). Fabaceae family has extraordinary evolutive importance, highlighting Cerrado species that often have belowground storage organs (Simon et al. 2009). Therefore, the presence of storage underground organs, with a greater capacity to produce buds, enabling the faster aerial biomass regenerations, summed a set of persistence traits shows the importance to study and understand the persistence and regeneration traits of Fabaceae in open savanna. Thus, the aim of this study was to describe and identify the functional traits of the above and belowground portions of eight Cerrado legume plants.

Thus, it was analyzed vegetative organs (leaf, stem, and belowground system) of Fabaceae species, in order to identify functional traits responsible for the persistence of these species in '*campo sujo*' open savanna vegetation. The final text was divided into two chapters: (1) Aboveground morphoanatomical traits and functional significance in Fabaceae from Cerrado (2) Belowground systems of Fabaceae species from the Cerrado

REFERENCES

Almeida RF, Fagg CW, De Oliveira MC, Munhoz CBR, De Lima AS, De Oliveira LSB. **2014**. Mudanças florísticas e estruturais no cerrado sensu stricto ao longo de 27 anos (1985-2012) na Fazenda Água Limpa, Brasília, DF. *Rodriguesia* **65**: 1–19.
Ambrósio SR, Oki Y, Heleno VCG, *et al.* 2008. Constituents of glandular trichomes of Tithonia diversifolia: Relationships to herbivory and antifeedant activity. *Phytochemistry* **69**: 2052–2060.
Appezzato-da-Glória B. 2015. *Morphology of plant underground systems*. Belo Horizonte: 3i Editora.
Appezzato-da-Glória Beatriz. **2015**. Morphology of plant underground systems. *Belo Horizonte: 3i Editora*.
Appezzato-da-Glória B, Estelita MEM. **2000**. The developmental anatomy of the subterranean system in Mandevilla illustris (Vell.) Woodson and M. velutina (Mart. ex Stadelm.) Woodson (Apocynaceae). *Revista Brasileira de Botânica* **23**: 27–35.
Appezzato-Da-Glória B, Hayashi AH, Cury G, Soares MKM, Rocha R. **2008**. Occurrence of secretory structures in underground systems of seven Asteraceae species. *Botanical Journal of the Linnean Society* **157**: 789–796.
Clarke PJ, Lawes MJ, Midgley JJ, *et al.* 2013. Resprouting as a key functional trait: How buds, protection and resources drive persistence after fire. *New Phytologist* **197**: 19–35.
Coutinho LM. **1990**. Fire in the ecology of the Brazilian Cerrado In: *Fire in the tropical biota*. Berlin, Germany: Springer-Verlag, 82–105.
Dayaram A, Witkowski ETF, Raimondo DC, Bamford MK. **2020**. Carbon-14 dating when there's no ring on it: Age of four Pondoland grassland geoxyles and lessons learned. *South African Journal of Botany* **132**: 415–422.
Del-Claro K, Rico-Gray V, Torezan-Silingardi HM, *et al.* 2016. Loss and gains in ant–plant interactions mediated by extrafloral nectar: fidelity, cheats, and lies. *Insectes Sociaux* **63**: 207–221.
Eamus D. **1999**. Ecophysiological traits of deciduous and evergreen woody species in the seasonally dry tropics. *Trends in Ecology and Evolution* **14**: 11–16.
Eiten G. **1972**. The Cerrado vegetation of Brazil. *The Botanical Review* **38**: 201–341.
Franco AC. **2002**. Ecophysiology of Woody Plants In: *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna*.178–197.
Franco AC, Bustamante M, Caldas LS, *et al.* 2005. Leaf functional traits of Neotropical savanna trees in relation to seasonal water deficit. *Trees - Structure and Function* **19**: 326–335.
Franco AC, Rossatto DR, de Carvalho Ramos Silva L, da Silva Ferreira C. **2014**. Cerrado vegetation and global change: the role of functional types, resource availability and disturbance in regulating plant community responses to rising CO2 levels and climate warming. *Theoretical and Experimental Plant Physiology* **26**: 19–38.
Fundação Grupo Boticário (2011) *Plano de Manejo da Reserva Natural Serra do Tombador.* Supervisor: G.A. Gatti. Curitiba, Brazil http://www.fundacaogrupoboticario.org.br
Gonzáles WL, Negritto MA, Suárez LH, Gianoli E. **2008**. Induction of glandular and non-glandular trichomes by damage in leaves of Madia sativa under contrasting water regimes. *Acta Oecologica* **33**: 128–132.
Hayashi AH, Penha AS, Rodrigues RR, Appezzato-da-Glória B. **2001**. Anatomical studies of shoot bud-forming roots of Brazilian tree species. *Australian Journal of Botany* **49**: 745–751.
Hoffmann WA, Adasme R, Haridasan M, *et al.* 2009. Tree topkill, not mortality, governs the dynamics of savanna-forest boundaries under frequent fire in central Brazil. *Ecology* **90**: 1326–1337.
Kelley DI, Harrison SP, And, Prentice IC. **2014**. Improved simulation of fire-vegetation interactions in the Land surface Processes and eXchanges dynamic global vegetation model (LPX-Mv1). *Geoscientific Model Development Discussions* **7**: 931–1000.
Kennard DK, Gould K, Putz FE, Fredericksen TS, Morales F. **2002**. Effect of disturbance intensity on regeneration mechanisms in a tropical dry forest. *Forest Ecology and Management* **162**: 197–208.
Klimešová J, Klimeš L. **2007**. Bud banks and their role in vegetative regeneration - A literature review and proposal for simple classification and assessment. *Perspectives in Plant Ecology, Evolution and Systematics* **8**: 115–129.
Lenthall JC, Bridgewater S, And, Furley PA. **1999**. A phytogeographic analysis of the woody elements of New World savannas. *Edinburgh Journal of Botany* **56**: 293–305.
LPWG TLPWG. **2017**. A new subfamily classification of the leguminosae based on a taxonomically comprehensive phylogeny. *Taxon* **66**: 44–77.
Mcdowell NG, Fisher RA, Xu C, *et al.* 2013. Evaluating theories of drought-induced vegetation mortality using a multimodel-experiment framework. *New Phytologist* **200**: 304–321.
Miranda HS, Bustamante MMC, And, Miranda AC. **2002**. The fire fator In: Oliveira, P. S., Marquis RJ, ed. *The*

Cerrados of Brazil:Ecology and Natural History of a Neotropical Savanna. New York: Columbia University, 51–68.
De Moraes MG, De Carvalho MAM, Franco AC, Pollock CJ, Figueiredo-Ribeiro RDCL. **2016**. Fire and Drought: Soluble Carbohydrate Storage and Survival Mechanisms in Herbaceous Plants from the Cerrado. *BioScience* **66**: 107–117.
Munhoz CBR, Felfili JM. **2006**. Fitossociologia do estrato herbáceoo-subarbustivo de uma área de campo sujo no Distrito Federal, Brasil. *Acta Botanica Brasilica* **20**: 671–685.
Myers Pn, Mittermeier RA, Mittermeier CG, Fonseca GAB da, And, Kent J. **2000**. Biodiversity hotspots for conservation priorities. *Nature* **403**: 853–858.
Oliveira-Filho, A.T.; Ratter JA. **2002**. Vegetation physiognomies and woody flora of the Cerrado Biome In: Oliveira PS MR, ed. *The Cerrados of Brazil:Ecology and Natural History of a Neotropical Savanna*. Columbia University, 91–120.
Pausas JG, Lamont BB, Paula S, Appezzato-da-Glória B, Fidelis A. **2018**. Unearthing belowground bud banks in fire-prone ecosystems. *New Phytologist* **217**: 1435–1448.
Paviani TI. **1987**. Anatomia do desenvolvimento do xilopódio de Brasilia sickii G.M. Barroso. *Estágio inicial. Cienc Cult* **39**: 399–405.
Read J, Sanson GD. **2003**. Characterizing sclerophylly : the mechanical properties of a diverse range of leaf types. **160**: 81–99.
Rizzini CT, Heringer EP. **1961**. Underground organs of plants from some southern Brazilian savannas, with special reference to the xylopodium. *Phyton* **17**: 105–124.
Rossatto D, Kolb R, Franco A. **2015**. Leaf anatomy is associated with the type of growth form in Neotropical savanna plants. *Botany* **93**: 1-12.
Rundel PW. **1989**. Ecological success in relation to plant form and function in the woody legumes. *Monographs in Systematic Botany from the Missouri Botanical Garden* **29**: 377–398.
Sarmiento G. **1983**. The savannas of Tropical America In: Oxford, ed. *Ecosystems of the world 13: tropical savannas*. Amsterdan, New York: Elsevier Scientific Publishing Company, 245–288.
Sarmiento G. **1984**. The Ecology of Neotropical Savannas. *Cambridge, Harvard University Press.*
Simon MF, Grether R, De Queiroz LP, Skemae C, Pennington RT, Hughes CE. **2009**. Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. *Proceedings of the National Academy of Sciences of the United States of America* **106**: 20359–20364.
Simon MF, Pennington T. **2012**. Evidence for adaptation to fire regimes in the tropical savannas of the Brazilian Cerrado. *International Journal of Plant Sciences* **173**: 711–723.
Tannus JLS, Assis MA. **2004**. Composição de espécies vasculares de campo sujo e campo úmido em área de cerrado, Itirapina — SP, Brasil. *Brazilian Journal of Botany* **27**: 489–506.
Vesk PA. **2006**. Plant size and resprouting ability: Trading tolerance and avoidance of damage? *Journal of Ecology* **94**: 1027–1034.
Warming E, Ferri MG. **1973**. *Lagoa Santa e a vegetação de cerrados brasileiros*. Belo Horizonte. Itatiaia.
Westoby M, Wright IJ. **2006**. Land-plant ecology on the basis of functional traits. *Trends in Ecology and Evolution* **21**: 261–268.
Whelan RJ. **1995**. *The ecology of fire*. Cambridge university press.
Wright IJ, Reich PB, Westoby M, *et al.* 2004. The worldwide leaf economics spectrum. *Nature* **428**: 821–827.
Zeppel MJB, Harrison SP, Adams HD, *et al.* 2015. Drought and resprouting plants. *New Phytologist* **206**: 583–589.

FINAL CONCLUSION

The present study demonstrated that resprouting species have several important morphological and anatomical traits that enable these species to resist drought, fire and pathogens. These plants live in a mesic savanna and cope with a long dry season, variable fire events, exposure to sunlight and frost, and are subject to pathogens at any time of year on the above and belowground plant organs. Faced with these environmental challenges, plants have a set of functional traits that are used as coping mechanisms.

In regard to the aboveground portion, the legume species presented two main persistence strategies: *Mimosa gracilis* plants that lose the aerial part in the dry season presented a mesomorphic traits in the leaves and stem and plants that did not lose the aerial part in the dry season had a set of xeromorphic traits. All plants had traits related to protection against herbivores. One interesting point was that often the same traits play multiple roles in the plant in order to protect against environmental conditions and disturbances and they are the key of survival of these plants in these environments.

In regard to belowground portion, these species can resprout after fire using belowground storage organs such as xylopodia, and taproots (root crown region). Additionally, these plants have the intrinsic resprouting capacity also as seedlings. The xylopodium has important morphological and anatomical traits that enable plants persistence after a fire such as well-developed phellem (thick bark), secondary growth, highly lignified tissues and starch storage in the xylopodium parenchyma.

Besides this, all plants have associated tuberous roots and some are root suckers. These roots store a high amount of starch in the parenchyma cells. Additionally, the plants of this study have protection against pathogens, through protective compounds such as phenolic compounds and lipidic substances.

Some studied species that had xylopodium as underground storage organs, also had xeromorphyc traits in their aerial portion. These plants did not lose their aerial organs during the dry season but lost the completely after fire. Because of this, they did not show strategies against fire in the aerial portion; however, their regeneration is in general still efficient and faster after fire. *Mimosa gracilis* also had xylopodium and is the only herbaceous species analyzed in the present study. This species loses its aerial organs in the dry season and under fire events. In this case, the plant had mesomorphic traits in their aboveground vegetative organs, responsible to the fast regeneration, between drought and fire events. Additionally, the xylopodium besides resprouting could be associated with root suckers with lateral spread capacity.

On the other hand, plants with tuberous root that resprout by basal region (probably transition zone), have a greater chance to protect their aerial organs against fire heat, because it showed developed phellem and stipules that protected the meristems (apical meristem and cambium) and other tissues that could protect against fire damage. All of the traits showed persistence strategies enable the high longevity of plants, and show the strong influence of these plants in the ecosystems to maintain their populations.