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

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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

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CHAPTER 1

ABOVEGROUND MORPHOANATOMICAL TRAITS AND FUNCTIONAL SIGNIFICANCE IN FABACEAE FROM TROPICAL OPEN SAVANNAS

ABOVEGROUND MORPHOANATOMICAL TRAITS AND FUNCTIONAL SIGNIFICANCE IN FABACEAE FROM TROPICAL OPEN SAVANNAS

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Abstract

Background and Aim: Savannas are fire-prone seasonal ecosystems that are determined by environmental filters such as fire, herbivory, water availability, which change the dynamics in these environments. The Cerrado vegetation of Central Brazil is a mesic savanna in which the plants can have from mesomorphic to xeromorphic traits that enable plant persistence. Therefore, this study aimed to describe the morphoanatomy of the above-ground vegetative organs of Fabaceae species and identify the persistence traits related to the main environmental filters in the Cerrado (fire, drought, and herbivory).

Methods: We performed morphoanatomical and structural analysis of belowground organs using four techniques: (1) Samples included in historesin were sectioned on a rotatory microtome (2) Fresh samples were sectioned on sliding microtome (3) Fresh samples were free-hand sectioned (4) The structural analysis of the leaf samples were performed on Scanning Electron Microscope. (5) To leaf blade analysis was performed paradermical analysis.

Key results: According to morphoanatomical analyses of stem and leaves, it was possible to identify two functional groups, such as plants with xeromorphic traits, and plants with mesomorphic traits. These traits protect the plants against sunlight exposition, water deficit, and insect herbivory.

Conclusions: Resprouting species of this study also has several important morphological and anatomical traits that enable these species to resist drought, fire, and pathogen attack. Both of the functional groups found in this study have traits related to protection against herbivory. Besides, sometimes alone trait had the function of protecting the plants against multiple environmental factors. Additionally, the morphoanatomical found traits can be used to subsidize taxonomic studies and help phylogenetic studies.

Key words: Fabaceae, Xeromorphy, Mesomorphy, Leaf, Stem, Functional traits

Introduction

Savannas are mainly seasonal, and plants present in these ecosystems accompany the weather changes during the year (Sarmiento 1983, 1984). These ecosystems are ruled by resource availability (e.g. water, nutrients, soil fertility), and disturbance regimes (fire and herbivory) (Sankaran *et al.* 2004, 2005). Thus, fire disturbance coupled with a drought period, soil, and herbivory can change dynamics and plant function during the year in these fire-prone ecosystems (Sarmiento 1984; Pivello and Coutinho 1996; Hoffmann 1999; Miranda *et al.* 2002; Oliveira and Freitas 2004; Smit *et al.* 2010; Lopes and Vasconcelos 2011; Alves-Silva and Del-Claro 2013, 2014; Franco *et al.* 2014; Ruggiero *et al*. 2002).

In Brazil, Cerrado is a savanna vegetation mosaic, ranging from open fields to woodlands, which is also determined by resources availability and disturbances (Franco *et al.* 2014). Additionally, it is highly threatened and globally recognized as a biodiversity hotspot (Myers *et al.* 2000; Strassburg *et al.* 2017). The climate of the Cerrado is characterized by a well-defined dry season, from May to September, with a long period of water restriction, in which the fire is frequent (Hoffmann *et al.* 2009). Additionally, savannas from Central Brazil are considered a mesic savanna (Franco *et al.* 2014), because it is characterized by an average annual rainfall > 1,000 mm (Myers *et al.* 2000).

Among the vegetation types of Cerrado mosaic, that range from open fields to woodlands, without forest formations, are fire prone vegetations (Coutinho 1990). Therefore, fire has an important role in the evolutionary history of the Cerrado, selecting survival traits in the species (Simon & Pennington 2012). One of those traits is the adaptation to fire (Coutinho 1990; Pivello 2011), due to the high degree of bud protection (Coutinho 1990; Miranda *et al.* 2013). These traits enable the recovery of the aerial biomass through resprouting in the rain season, which was lost in the dry season by fire (Filgueiras 2002). Additionally, some plants also can resprout in the dry season, in 15 days after fire damage (Fidelis *et al*. 2019). Thus, it is important to mention that there are two strategies of resprouters from fire-prone environments: storage underground organs which protect belowground buds and storage for resprouting (Clarke *et al.* 2013; Appezzato-da-Glória 2015), and containing bark thickness by aerial bud protection (Simon *et al.* 2009; Clarke *et al.* 2013; Charles-dominique *et al.* 2015)**.** Thus, these traits enable fast resprout after fire which is one of the most important adaptations for plant persistence (Bellingham and Sparrow 2000; Bond and Midgley 2003; Clarke *et al.* 2013).

Moreover, dry season is a stressful period in the life cycle of the Cerrado vegetation and it is characterized by low water availability (Franco 2002). In this context, the water can be a limiting factor in plant survival, affecting its metabolism, as well as its structure and its composition (Skoss 1955; Griffiths and Parry 2002; Osakabe *et al.* 2014). This directly affects the acquisition and assimilation of carbon (C) and nutrients (Franco *et al.* 2005), which can cause mortality by hydraulic failure, carbon suppression, and failure to defense against biotic attack (Mcdowell *et al.* 2013).

Plants that grow in seasonally dry environments, with high light intensity and nutrition deficit exhibit a set of strategies to persist (Franco 2002). Drought tolerant plants have the capacity of staying alive until they virtually do not have any water absorption by roots (Levitt 1956). These plants have morphoanatomic and physiologic adaptations in the entire plant which reduce the loss of water, increase water capture, storage, and translocation (Fahn and Cutler 1992; Franco *et al.* 2005), which is commonly associated to anatomical variances. In this context, leaves are the vegetative organs that have the highest ecological plasticity, and this characteristic improves the ability to resist environmental changes (Dickison 2000; Sultan 2000, 2003; Valladares *et al.* 2000).

Variations in the morphological, anatomical and physiological features of leaves developed at different growth stages in the plants have been reported for many species (Dickison 2000; Bieras and Sajo 2009) and related especially to environmental variation such as the amount of sun exposure, water availability and edaphic conditions (Givnish 1984; Feng *et al.* 2019). For example, fully sun-exposed leaves were denser and thicker due to a development in the length of the palisade parenchyma cells and a high stomatal and trichome density and frequency, under high light conditions (Marques *et al.* 2000; Rossatto and Kolb 2010).

Traits related to adaptations to dry seasons found in aerial organs are the control of stomatal conductance by leaves, limiting water loss (Franco *et al.* 2005), water storage and sclerenchymatic tissues, and thick cuticle in leaves (Rossatto *et al.* 2015). Traits commonly found in stems of Cerrado plants are bark properties involved with storage and water loss prevention (Loram-Lourenço *et al.* 2020). Some stems also have storage tissues (Rojas-Jiménez *et al.* 2007; Scholz *et al.* 2007), thick cuticle and trichomes (Fahn and Cutler 1992) which are involved in water balance. Indeed, in the underground portion, some plants have storage belowground organs which enable them to regenerate by resprouting even after drought (Zeppel *et al.* 2015).

Plants living in seasonal dry environments need to be able to survive in post-fire drought and herbivory to persist (Lpez-soria and Castell 1992). Cerrado species have xeromorphic features, that were selected in the course of evolution to improve the capability of these plants to persist through drought, and fire events (Warming and Ferri 1973) and herbivory (Haworth and McElwain 2008). Many xeromorphic characteristics are commonly found in Cerrado plants, such as epidermis with thick cuticle coated with epicuticular wax (Bieras and Sajo 2009), and the photosynthetic organs which are commonly covered by trichomes (Fahn and Cutler 1992). Additionally, the stomata in these plants are commonly limited to the inferior surface (Bieras and Sajo 2009); palisade parenchyma related to both leaf surfaces (Donato *et al.* 2018); sclerified cells in the mesophyll and around the vascular bundles, and a developed midrib (Bieras and Sajo 2009).

Physiological and morphological plant traits have a functional variation that influences their growth and survival (Violle *et al.* 2007). These traits are related to the “economic spectrum”, in which some plants have long leaf life times, and to resist drought season. On the other hand, other plants have quick regeneration, with high leaf nutrients concentration, short leaf lifetimes, and low dry-mass per leaf area. These traits enable high rates of photosynthesis, respiration and carbon sequestration (Wright *et al.* 2004).

In the Cerrado vegetation, herbs commonly lost the aerial biomass during the dry season, that revert through underground organ once a year (Filgueiras 2002). Thus, herbs tend to have a low lifespan and to produce aboveground biomass with low cost and rapidly (Westoby and Wright 2006). To these features, leaves of herbs exhibited mesomorphic traits such as larger leaves, with little or no sclerenchyma (Rossatto *et al.* 2015; Guerra and Scremin-Dias 2018).

Fabaceae is widespread known as the third most important plant family worldwide (LPWG 2013). This plant family has large distribution and abundance mainly in the neotropical region (Seigler 2004). Regarding the savannas, in the Cerrado Fabaceae is one of the richest families (BFG 2015). This success is explained by several traits that provide efficient persistence responses to different environments, providing ecological and evolutionary success (Rundel 1989). For example, the *Mimosa* genus, have morphological adaptations to extreme environmental conditions such as drought, high altitude, cold, and fire (Marcelo F. Simon *et al.* 2009). They can be morphological adaptations (e.g., from leaves to root architecture) and physiological (e.g., solar tracking, water relations, nitrogen fixation, and mycorrhizal associations) (Rundel 1989). Fabaceae certainly present remarkable anatomy traits linked to ecological functions. Therefore, this study aimed to identify persistence functional traits in aboveground vegetative organs of Fabaceae species. Those functional traits are related to the main environmental filters in open savanna (fire, drought and herbivory).

Material and Methods

Study site

The species were collected from Reserva Natural Serra do Tombador - RNST. The RNST is set in 47°45'; 47°51' W and 13°35'; 13°38' S, 8900 ha, 560-1118 m a.s.l, located in the Central region of Brazil. The climate of RNST is seasonal, marked by a long dry season from May to September in which the total precipitation is < 60 mm, as well as a wet season from October to April in which the annual precipitation varies from 1300 to 1500 mm. Additionally, the average annual temperature ranges from 22 to 25 °C. Minimal temperature <15 °C and maximum > 36 °C (Fundação Grupo Boticário, 2011).

The vegetation from RNST is composed of different Cerrado physiognomies, such as '*campo limpo'*, '*campo sujo'*, '*cerrado rupestre'*, '*cerrado sensu stricto'*, '*veredas'*, besides '*florestas de vale* '(AER 2009). The species were collected in Open savanna "*campo sujo"* that is a sparse savanna vegetation physiognomy of Cerrado, with a rare wood coverage (Eiten 1994)**.** This vegetation type is composed of dominant herbaceous stratum with a great grass predominance, besides the presence of sparse shrubs, subshrubs, and trees (Coutinho 1978).

Plant collection

Eight of the dominant resprouter species in the area (Zupo et al., 2020) were selected next to plots related to fire experiments from RNST. Non reproductive whole adult plants (3 individuals / species) of the eight Fabaceae species (Table1) were collected with a garden spade. Adult plants were identified through the belowground great development of the size and volume. All collected species were taken to the laboratory in which were separated the subterranean and aerial portions with garden shears. Organs of both portions were fixed separately on a plastic bottle with FAA 70 (Johansen 1940). The volume ranged from 500 ml to 1L to aerial portion and for the subterranean portion varied to 500 ml to 5l depending on the organ size.

The subterranean portion was separated for another study (Leal et al., *in prep*-Chapter 2). Regarding the aerial portion, stems and leaves were stored on the same bottle. Then, after 48 hours, the aerial portion immersed in FAA 70, were dehydrated in an ethylic series until 70 % alcohol concentration

Table 1. Adult species collected in Reserva Natural Serra do Tombador, GO, Brazil. The species was registered in HRCB herbaria, Rio Claro, Brazil.

Species	**Growth form**	**Vegetation type**	**Date of collection**	**Accession number**
Bauhinia dumosa Benth.	shrub	Open savanna	9/5/2014	63501
Chamaecrista claussenii (Benth.) H.S.Irwin & Barneby	shrub	Open savanna	10/10/2015	65891
Harpalyce tombadorensis São-Mateus, L.P.Queiroz & D.B.O.S.Cardoso	shrub	Open savanna	2/4/2015	64365
Mimosa kalunga M.F. Simon & C.E. Hughes	shrub	Open savanna	10/10/2013	63932
Mimosa sp nova	shrub	Open savanna	9/2/2014	63775
Mimosa leiocephala Benth.	shrub	Open savanna	9/5/2014	63793
Mimosa gracilis Benth.	forb	Open savanna	9/5/2014	63794
Senna corifolia (Benth.) H.S.Irwin & Barneby	shrub	Open savanna	9/5/2014	63900

Leaf and stem morphology

Morphologic analyses were carried out with the support of scientific illustration, photographs of plants in the field, and fresh samples observations in a stereomicroscope. The results' analyses were based on papers related to legume descriptions and classifications (Da Fonseca Vaz and Tozzi 2003; Dantas and Da Silva 2013; Pascal *et al.* 2000; São-Mateus *et al.* 2019; Irwin, H. S. & Barneby 1982; Borges 2014; Romagnolo 2019) as well as, classic books of plant morphology (Bell & Bryan 2008; Schweingruber & Börner).

Leaf and stem anatomy

Subsequently, stem fresh samples were cross-sectioned (approximately 5 cm), the stem was sectioned in their internodes, without damage and pathogens. Stem portions with visually higher diameter were selected in order to facilitate the sectioning. A minimum of two samples per individual, to each of the three individuals of each species, were separated. Additionally, a minimum of five leaves were separated, these leaves were fully expanded and had no herbivory or pathogens. For fresh samples, the middle fragment with the midrib was separated.

Therefore, both organs were performed cross sections (10-20 µm thick) on a sliding microtome. Additionally, leaves were sectioned through free-hand sections. The sections resulting by the both techniques to leaves and stems were clarified with 30% sodium hypochlorite solution and stained with 1% Safranin and Alcian blue in 3 % acetic acid (Burger, L.M.; Richter, 1991 - Modified). The sections were subsequently dehydrated in an ethylic alcohol, and butyl acetate, respectively. Permanent slides were mounted with synthetic resin "Entellan".

Additionally, a minimum of two samples of the stem (approximately 0,5 cm, portions with lower diameter) and leaves (same samples separation than fresh leaves) both samples were dehydrated in a graded ethylic series until 100% alcohol and subsequently infiltrated in Hydroxy-ethyl-Methacrylate resin (Leica Historesin). Cross sections (6-10 µm thick) were performed on a rotatory microtome (Leica SM2000R) and stained with toluidine blue (Sakai 1973). Permanent slides were mounted with synthetic resin "Entellan".

To leaf blade analyses, one leaf of each individual (3 individuals/species) were separated, these leaves were fully expanded and without herbivory or pathogen. The middle fragment with the midrib were separated. All leaves samples after dehydration were dried in the critical point with the model of Leica- CPD 300 equipment, fixed of aluminum bracket with double-sided tape of carbon and metallized with a gold layer of 5 nm to 1.5 nm in the Quorum model - Q 150TE equipment. After metallization, the samples were taken to the Scanning Electron Microscope Zeiss EVO / LS15 to make the electron micrographs, as with printed scales directly in electron micrographs. This step was carried out at the Electron Microscopy Laboratory at the Department of Physics and Chemistry - Unesp Ilha Solteira.

Additionally, leaf blade analysis also was carried out with fresh leaves (one leaf per individual), paradermical sections were performed and subsequently clarified with 30% sodium hypochlorite solution and stained with Iodine green, and Safranin (Johansen 1940; Sass 1951), as well as fresh leaves paradermical impressions in slides (Segatto et al. 2004).

For trichome classification and description was used the terminology by Payne (1978) and Santos-Silva *et al.,* (2013). Besides, was carried out sections image capture of mounted slides, and to image edition was used CorelDraw Graphics Suite editor.

Group classification and traits functionalities

Two groups were created to describe the leaf anatomy, in which the only herb species with mesomorphic traits was separated from the shrub species with xeromorphic traits. Additionally, to describe the stem anatomy, the species were grouped into two groups: (1) stem with secondary growth and well-developed phellem, and (2) species in the early stages of secondary growth. Groups were created to describe the stem and leaf anatomy in order to facilitate the understanding of traits and their related functionalities for these plants. To discuss the results, two general groups were formed. For general group separation, the first criterion was (evergreen and deciduous plants), and then these plants were divided into shedding and perennial species. The perennial species were sub grouped according to the stem growth system (monopodial and sympodial growth).

A literature survey was performed in order to identify the ecological functions of the anatomical and morphological traits founded (Table 2). This revision was based on classic literature and some papers.

Results

Leaf and stem morphology

Bauhinia dumosa (Fig. 1A) has a coriaceous compound leaf that exhibits alternate phyllotaxy and is petiolate. The leaf is bilobed with palmate venation as well as has a low prominent midrib, secondary, and tertiary lateral vein. The stipules are linear. Additionally, the branches have extrafloral nectaries (EFNs). Regarding the leaf blade, it exhibits glabrous on the adaxial face and pilosum on the abaxial face. The stem is cylindric with sternal bark thin and rough. The epidermis is striate, color dark grey reddish and covered by a layer of trichomes.

Chamaecrista claussenii (Fig. 1B) has a coriaceous compound leaf that exhibits alternate phyllotaxy and is petiolate. The leaflets have an oval shape with a rounded apex and base, and the venation is characterized by a brochidodromous pattern. The leaflets have prominent veins on both faces and the plant presents EFNs. The leaf blade is glabrous on both faces. The stem is cylindric with thin sternal bark and rough. It is flexible, color green on the apex and dark grey reddish on the base.

Harpalyce tombadoriensis (Fig. 1C) has a coriaceous imparipinnate compound leaf that exhibits alternate phyllotaxy and is petiolate. The leaflets have an elliptic shape with rounded base, apex strongly attenuate-apiculate, with pulvinules. The leaflets have prominent midrib on lower surface with leaf venation brochidodromous. The adaxial surface was glabrous, and abaxial was pilosum, globose-peltate glands only on the lower surface and distributed throughout the blade. Persistent shorter linear stipule. Stem branches slightly sulcate, color ferruginous-tomentose with short erect trichomes.

Senna corifolia (Fig. 1D) has a coriaceous compound leaf that exhibits alternate phyllotaxy and is petiolate. The leaves are paripinnate, and the leaflets are ovate-oblong; the venation was classified as cladodromous. The petiole includes pulvinus, and pulvinule was present in the petiolule. The leaflets have prominent veins on both faces. Additionally, the stipules are coriaceous and reniform. Additionally, EFNs were found between all pairs of leaflets (in the petiole or the rachis) and the leaflets are glabrous on both faces. The stem is cylindric and flexible and it has sympodial growth. The sternal bark is thin and rough and the color in the apex is green and the base is grey.

All *Mimosa* species (Fig. 1E, F, G, H) have coriaceous compound leaves with long petioles. The leaves are long and multijugate (have several pairs of leaflets). Stipules are present in this genus, and the plants have lanate indumentum in the branches and petioles. Regarding the leaf blade, it can exhibit glabrous or pilosum.

Mimosa kalunga and *Mimosa sp. nova* have leaves congested in the apex (Figure 1-E-H). The leaflets have an oblong shape, and the leaflets of all pinnae are inserted alternate along pinna-rachis, except the *Mimosa sp. nova* (Fig. 1E) that exhibits spiral opposite phyllotaxy. *Mimosa gracilis* (Fig. 1F) is the only of the all four *Mimosa* species of this study in which the leaflets and branches are glabrous.

Regarding the stem, *Mimosa gracilis* is non-cylindrical and has lateral projections (Fig.8-C), sympodial growth and the color is light brown. *Mimosa kalunga*, *Mimosa sp. nova* the stem has monopodial growth, with leaves closer in the apical meristem. The stem form is cylindric, flexible, the sternal bark is thick, rough, scamiform and with color dark grey reddish. *Mimosa leiocephala* the stem has sympodial growth, is cylindric, flexible, the sternal bark is thin and rough. The stem apical meristem is reddish green and covered by a layer of trichome and the base is grey.

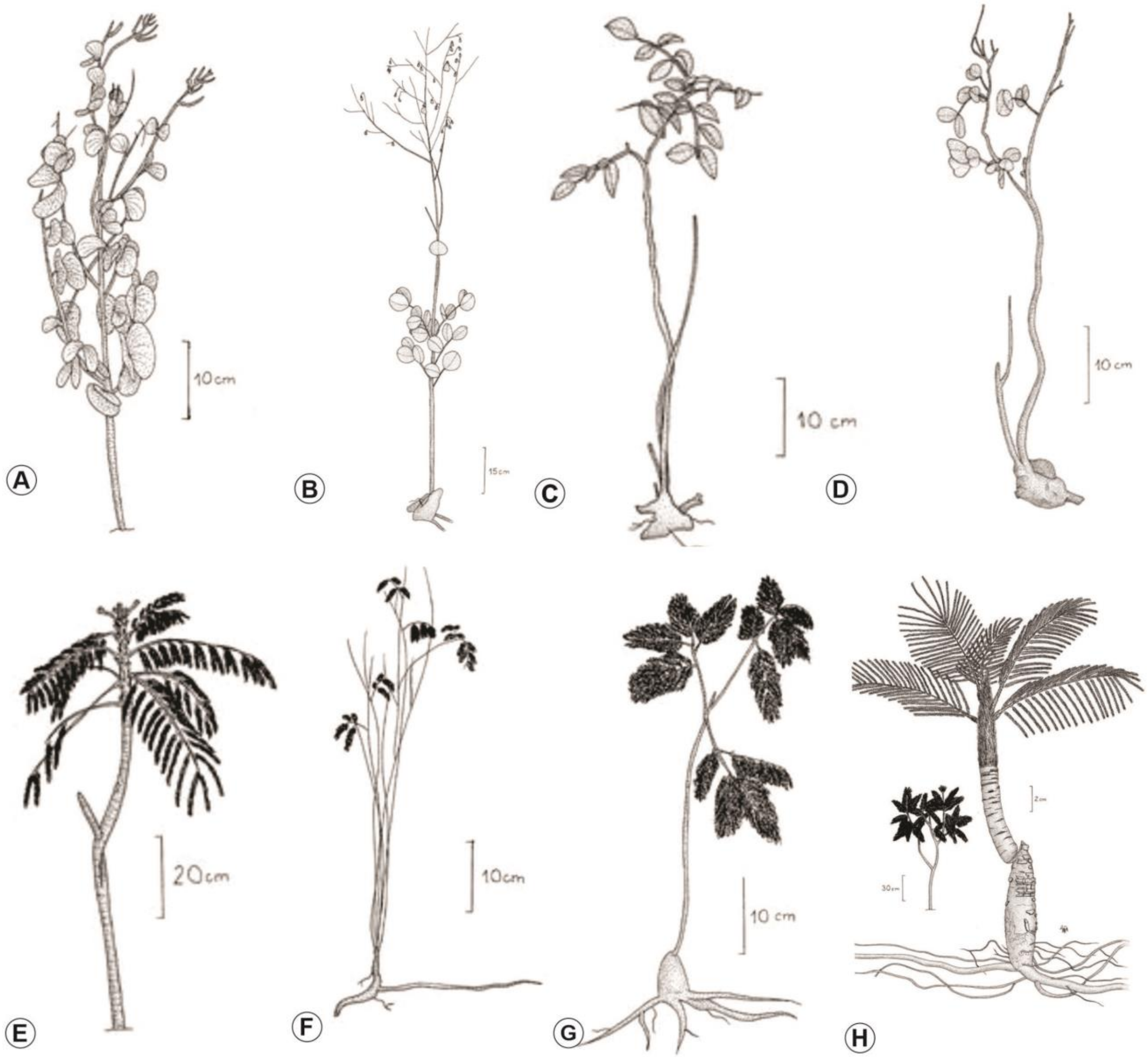

Figure 1. Aerial portion illustration **A-** *Bauhinia dumosa*; **B-** *Chamaecrista claussenii*; **C-** *Harpalyce tombadorensis*; **D-** *Senna corifolia*; **E-** *Mimosa sp. nova*; **F-** *Mimosa gracilis*; **G-** *Mimosa leiocephala*; **H-** *Mimosa kalunga.*

Leaf anatomy and ultrastructure

All species had one epidermal layer, and the epidermal cells had isodiametrical, squared and rectangular shape, to proportional size on both faces of the leaf blade (Fig. 2F). And then, the internal anticlinal cell walls were sinuous in all species, while the external periclinal walls varied from smooth (Fig. 2 B, G, J; 3 F, G, L) to papillose (Fig. 3 B, G, J). The epidermis was covered by a well-developed cuticle (Fig. 2 A, E, H, L, M; 3 D, L, N).

Dorsiventral mesophyll was found in all species (Fig. 2; 3), with exception of *Chamaecrista claussenii* that had heterogeneous isobilateral mesophyll (Fig. 3E, F). This mesophyll had spongy parenchyma in the center, and palisade parenchyma occupied the two faces of the leaf, in higher proportion.

Besides the common traits identified in the two above paragraphs, it was possible to divide the species into two groups:

(1) The first group comprised *Mimosa gracilis* species (Table 2). In this species no type of trichome could be detected, however the cuticle presented a thick layer of scale wax type on both faces (Fig. 2 H). The adaxial palisade parenchyma occupied more area than abaxial spongy parenchyma which had cells with an isodiametric shape. This species presented collateral vascular bundles with accessory bundles in low amounts, reduced size, and fewer sclerenchymatic cells than other studied species (Fig. 2 G). This species exhibited amphistomatic leaflets (Fig. 2 G; Fig. 4 C), and the stomates could be classified as paracitic. The palisade parenchyma had one layer, and the spongy parenchyma had three layers. The distribution of leaf vascular bundles is composed by one middle wider vascular bundle and around nine smaller along the blade.

(2) The second group comprised *Bauhinia dumosa*, *Chamaecrista claussenii*, *Harpalyce tombadorensis*, *Senna corifolia*, *Mimosa sp. nova*, *Mimosa kalunga* and *Mimosa leiocephala species* (Table 2). These species presented their adaxial palisade parenchyma with elongated cells juxtaposed arranged, which occupied more area than abaxial spongy parenchyma, which presented cells with an isodiametric shape. All species presented a high amount of sclereids in the vascular bundles, and only *Bauhinia dumosa* presented sclereids scattered in their mesophyll. The number of layers of both palisade and spongy parenchyma which defined the limits of wide intercellular spaces varied within species (Fig. 2-3). In the spongy parenchyma, there were different amounts of cell layers with various shapes loosely arranged (Fig. 2-3).

All these seven species had collateral vascular bundles with different amounts of accessory bundles (Fig. 2 F, J, M). These vascular bundles were surrounded by fiber caps orientated to the phloem directions; however, in *Harpalyce tombadorensis* it is directed by phloem and xylem. The number and size of vascular bundles varied in the species (Fig. 2; 3).

Thus, the parenchyma layers and vascular bundles varied among the species, such as in *Mimosa sp. nova* the palisade parenchyma had two layers, and the spongy parenchyma had four layers. There were three higher vascular bundles and, around five smaller along the blade; in *Mimosa kalunga* the palisade parenchyma had one layer, and the spongy parenchyma had five layers. There were approximately two higher vascular bundles and eight smaller along the blade; in *Mimosa leiocephala* the palisade parenchyma had two layers, and the spongy parenchyma had three layers. There were around two higher vascular bundles and eight smaller along the blade; in *Bauhinia dumosa* the palisade parenchyma had four layers, and the spongy parenchyma had two layers. There were approximately 1one higher vascular bundle and six smaller along the blade; in *Chamaecrista claussenii* the palisade parenchyma had two layers, and the spongy parenchyma had five layers. There were approximately one higher vascular bundle, and six smaller along the blade; in *Harpalyce tombadorensis* the palisade parenchyma had two layers, and the spongy parenchyma had four layers. There were approximately one higher vascular bundle, and four smaller along the blade; in *Senna corifolia* the palisade parenchyma had two layers, and the spongy parenchyma had four layers. There were approximately one higher vascular bundle, and six smaller along the blade.

The epiderm of some leaves also presented other important traits, such as stomata and trichomes. Stomata were present in all species and occurred at the same level as the other epidermal cells, which exhibited amphistomatic leaflets (Fig. 2 A, F, J; Fig. 4; Fig. 5 A, B, C, E, J, L), except *Harpalyce tombadorensis* that had hypostomatic leaves (Fig. 3 G, Fig. 5 G, H). Additionally, all species had larger substomatal chambers.

For five of the eight analyzed species – *Mimosa kalunga*, *Mimosa leiocephala*, *Mimosa sp. nova*, *Harpalyce tombadorensis*, and *Bauhinia dumosa* trichomes and stomates could be detected by an electron microscope. Stomates were classified as parasitic (Fig. 4 and 5), and trichomes could be grouped into two main types, tector and glandular. Variation in the density and size of trichome produced differences in the epiderm which could be sparse (Fig. 6. A, G) or in large amounts (Fig. 6 K; 7 C, K).

Tector trichomes were unbranched, commonly known as a unicellular simple trichome. The shape of these trichomes were acute at the apex and slender (Fig. 6A, H, K; 7 E). The glandular trichomes were sessile (e.g. Fig. 3 I, k- *Harpalyce tombadorensis;* Fig. *3B- Bauhinia dumosa*) or stalked (e.g. Fig. 2 N -*Mimosa leiocephala,* Fig. 6 A *Mimosa sp. nova*). In both forms, the head was multicellular. Sessile trichomes had a short-immersed stalk in the epidermis. In the glandular sessile trichomes the stalks were uniseriate. The cells of the head were mostly larger in size than the stalk cells. The glandular head projected from the epidermis in the form of a lens (*Harpalyce tomadorensis* Fig. 3 I) or clavate heads (*Bauhinia dumosa* Fig 3B), which were classified as cavitate secretory trichome (Marinho *et al.* 2016). In the stalked glandular trichomes the stalk was uniseriate. These trichomes had globose heads supported by stalks.

The glandular trichomes in *Bauhinia dumosa* could be classified as cavitate secretory trichomes that had short stalk that was connected to a secretory clavate head. In *Bauhinia dumosa*, on the adaxial face, there weren't trichomes (Fig. 6 B). However, tector and glandular trichomes occurred simultaneously on the abaxial face, including in the midrib.

On both faces, the epidermis of *Bauhinia dumosa* was covered by a cuticle and a wax layer. Also, on both faces, the leaflets had cell papillae (Fig. 3 B, C; 7 A, C). Thus, that characterized a papillous epidermis. Also, on the adaxial face, there were from five to seven stomata grouped enclosures for papillae cells which recovered the secondary to the quaternary vein (Fig. 7 A). On both faces of the leaf, there was scattered stomata. The midrib region was recovered by papillate cells.

There were neither trichomes nor stomata on the adaxial face of *Harpalyce tombadorensis*, but a layer of wax could be observed. However, on the abaxial face, there were tector and glandular trichomes simultaneously (Fig. 3 G, H, I, J, K; Fig. 7 k)**.** Also, the midrib had scattered tector trichomes. On the adaxial face, there were stomates scattered in low amounts, however, on the abaxial face there was no stomate. The leaflets had cell papillae on both faces**.**

In *Mimosa leiocephala*, *Mimosa sp. nova* and *Mimosa kalunga* tector simple trichome occurred in the leaflets blade on both faces. However, only *Mimosa leiocephala* and *Mimosa sp. nova* had a stalked glandular trichome with mostly globose multicellular heads, in the edge. Regarding the cuticle at the species in *Mimosa sp nova***,** *Mimosa kalunga*, and *Mimosa leiocephala*, which were commonly smooth (Fig. 2), and the stomata could be detected on both faces of the leaf.

However, *Mimosa gracilis*, *Senna corifolia*, *Chamaecrista claussenii* (Fig. 6 C-E; Fig. 7 F-H, M-O) in the adult stage did not present any type of trichomes. The cuticle, in contrast to the other analyzed species, exhibited a thick scale of wax on both faces of the leaf for these species.

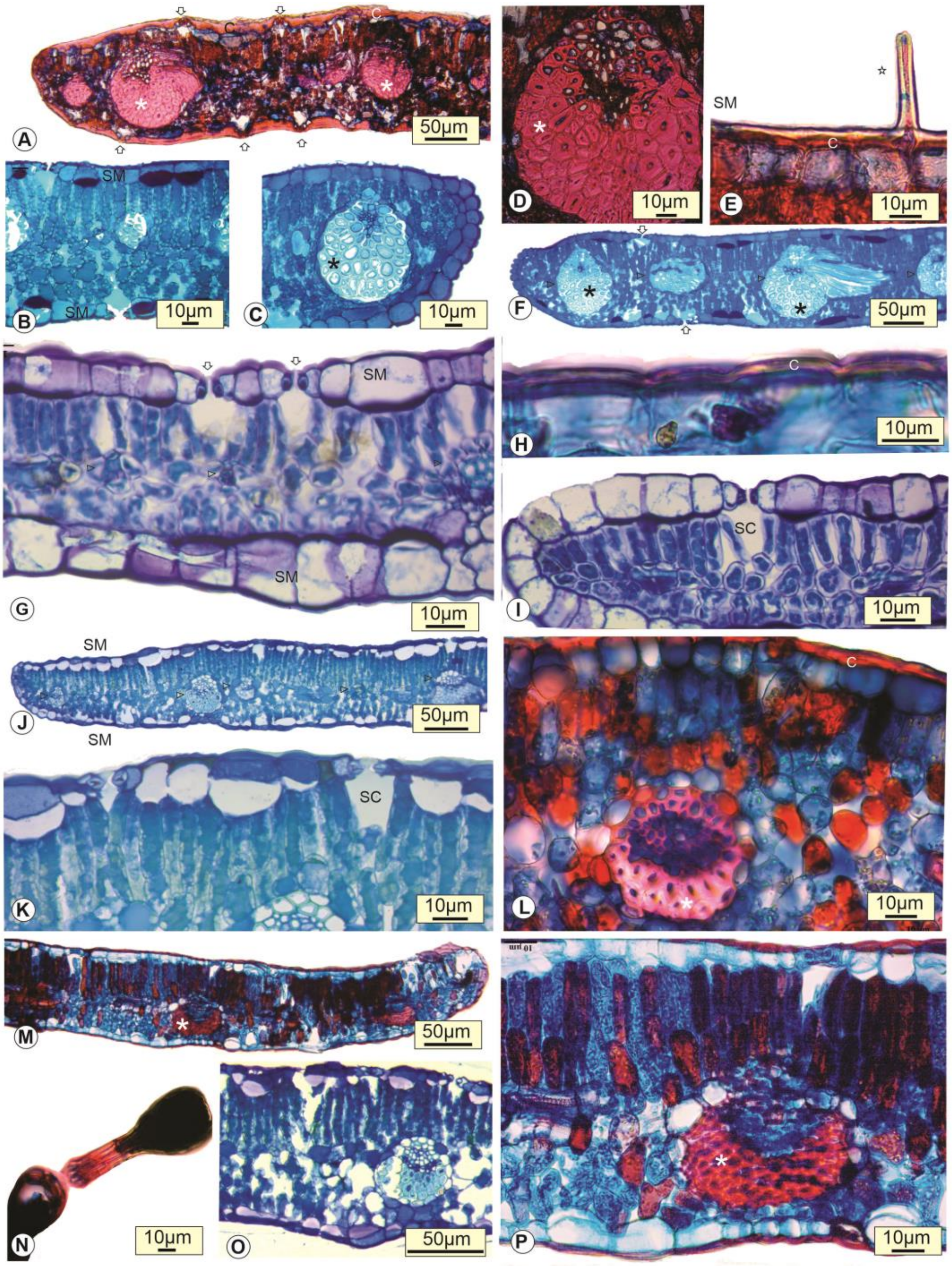

Figure 2- Leaf anatomy- A-F. *Mimosa sp. nova;* A, F General leaf vision; B. Metabolic secondary content and external periclinal walls smooth on both faces C , D. Vascular bundles with high amount of sclereids E. Tector trichome and cuticle detail G-I. *Mimosa gracilis*, G. vascular bundles, stomate, and external periclinal walls smooth on both faces H. Cuticle detail, I- Big substomatal chamber; J-L *Mimosa kalunga* J- General leaf vision, external periclinal walls smooth on both faces , K. Big stomatal chambers and stomates, L. Cuticle and mesophyll detail M-P *Mimosa leiocephala* M. General leaf vision, N. Glandular trichome O- Metabolic secondary content, external periclinal walls smooth on both faces P. Detail of vascular bundle and cuticle. Stomatal chamber (SC), smooth epidermis (SM), stomates (arrows), cuticle (C), tector trichome (☆), glandular trichome (★), sclereids (*), vascular bundles (arrows head).

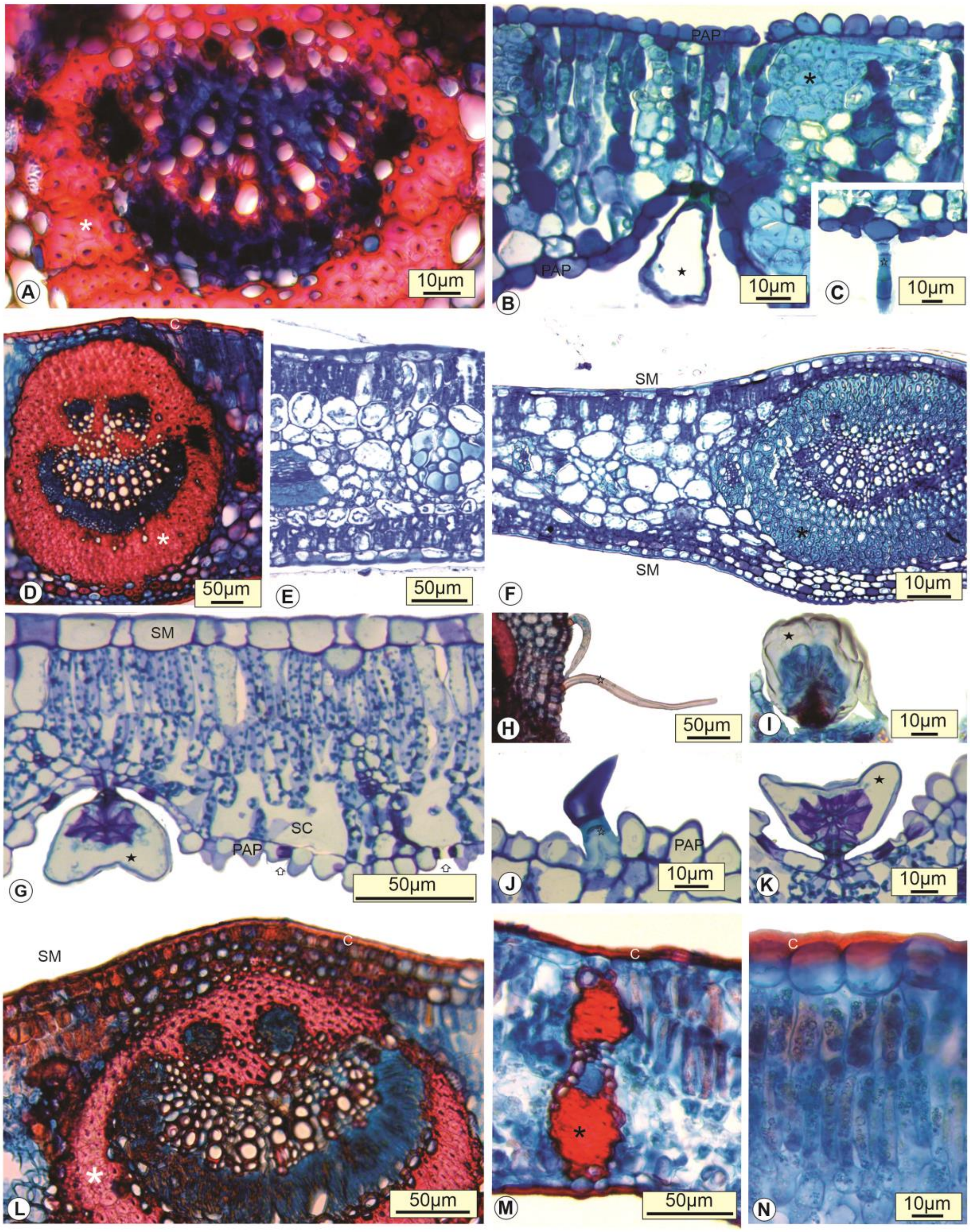

Figure 3. Leaf anatomy -A-C. *Bauhinia dumosa* A- Vascular bundle detail B, C. Glandular trichomes and epidermis with external periclinal walls papilosae on both faces D-F. *Chamaecrista claussennii* D. Vascular bundles detail E,F. Heterogeneous isobilateral mesophyll, epidermis with external periclinal walls smooth on both faces G-K *Harpalyce tombadorensis* G- Mesophyll detail, big substomatal chambers, external periclinal walls smooth on adaxial face and papilosae on abaxial face, H, J Tector trichome, I,K Glandular trichome L- *Senna corifolia L.* Vascular bundle detail, external periclinal walls smooth on both faces. Stomatal chamber (SC), smooth epidermis (SM), stomates (arrows), cuticle (C), tector trichome (☆), glandular trichome (★), sclereids (*), vascular bundles (arrows head).

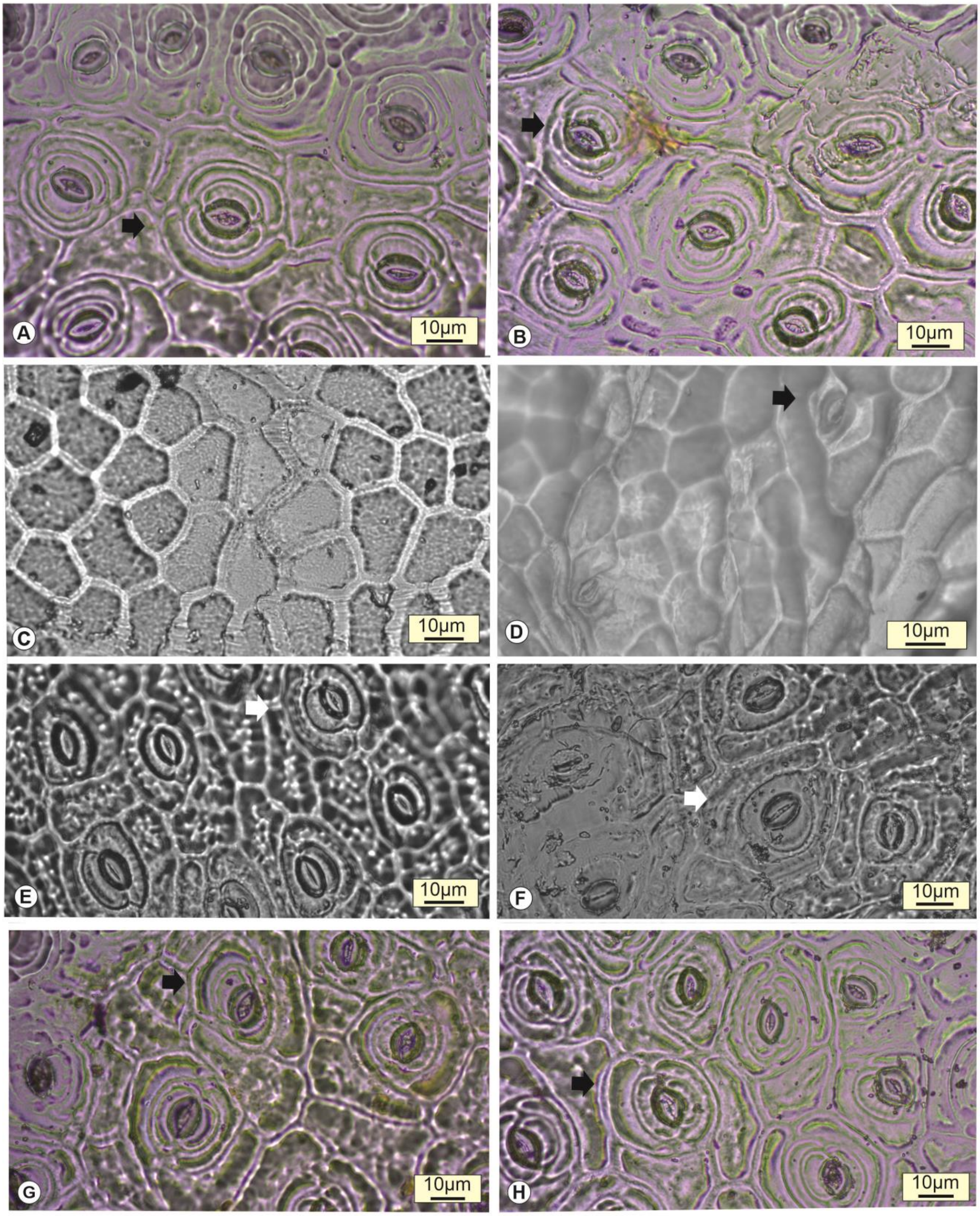

Figure 4 - Impression of leaves epidermis **A-B** *Mimosa sp. nova*- **A** Adaxial face, **B** Abaxial face; **C-D** *Mimosa gracilis* **C** Adaxial face, **D** Abaxial face; **E-F** *Mimosa kalunga* **E-** Adaxial, **F-** Abaxial face; **G-H** *Mimosa leiocephala* **G-** Adaxial face, **H-** Abaxial face. Stomates (arrows).

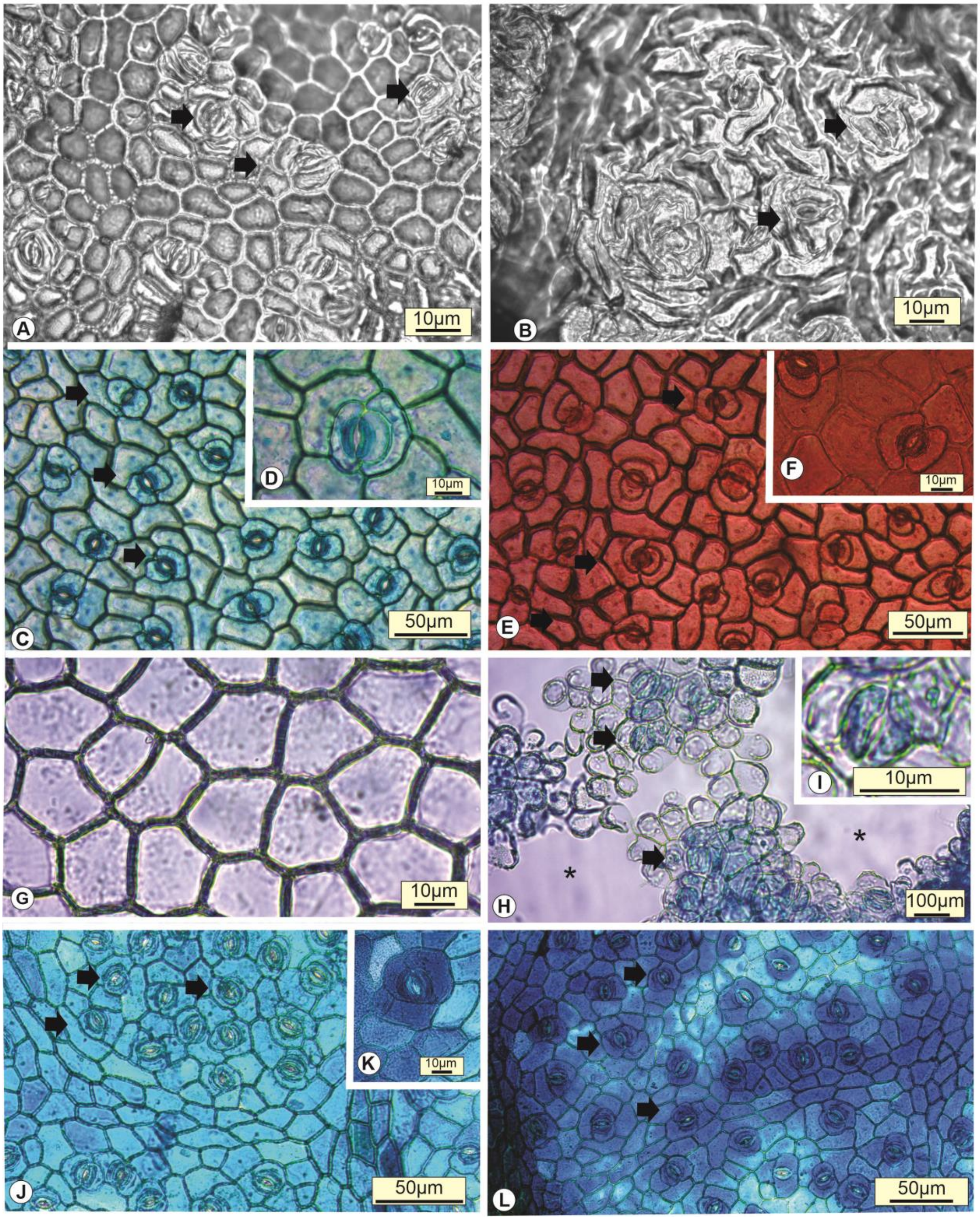

Figure 5- Leaf blade Paradermical sections **A-B** *Bauhinia dumosa*- **A** Adaxial face, **B** Abaxial face; **C-F** *Chamaecrista claussenii* **C-D** Adaxial face, **E-F** Abaxial face; **G-H** *Harpalyce tombadorensis* **G** Adaxial face, **H** Abaxial face; **I-K** *Senna corifolia* **I-J** Adaxial face, **K** Abaxial face. Glandular trichomes gap (*), stomates (arrows).

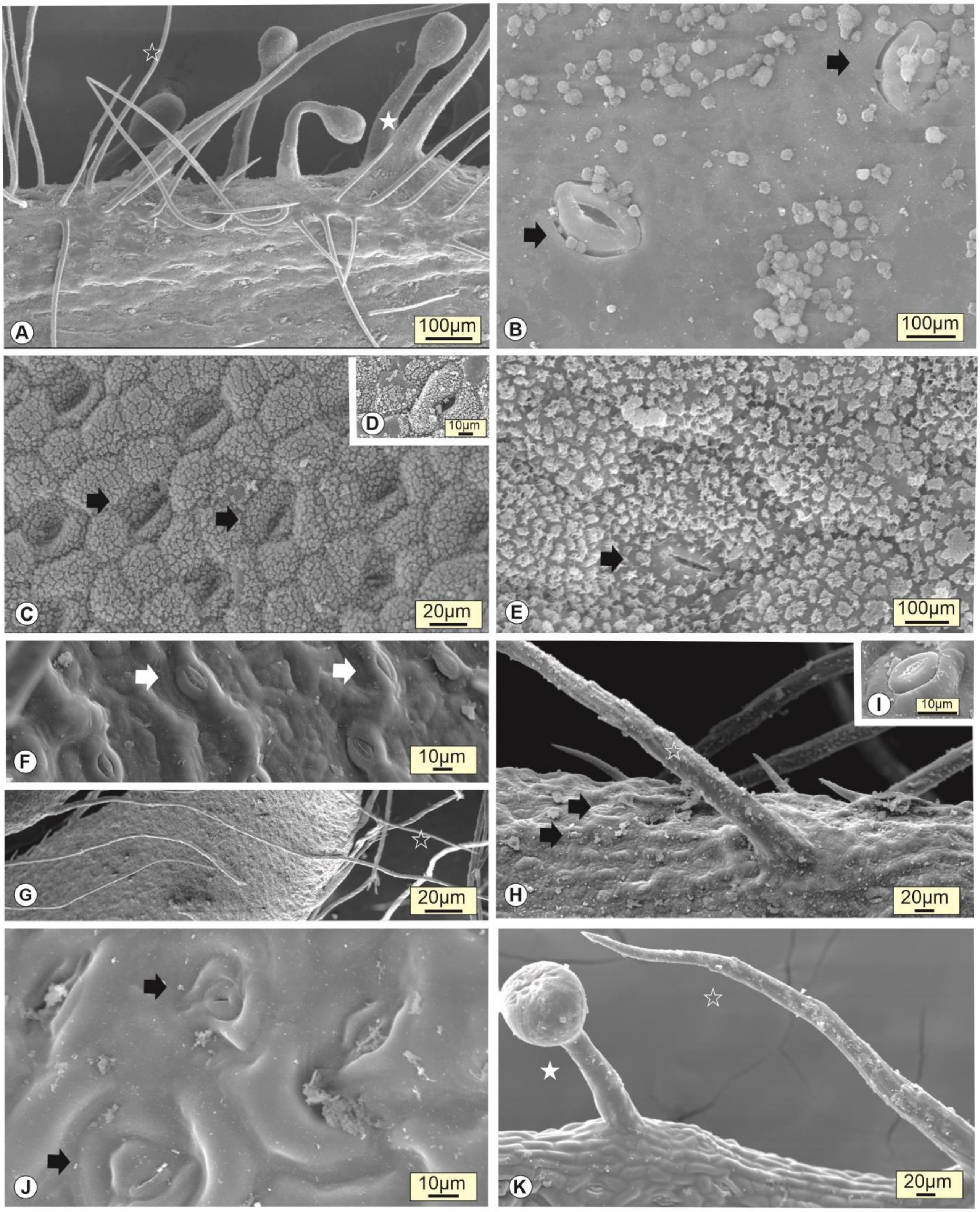

Figure 6- Elentromicrography of leaves epidermis **A-B** *Mimosa sp. nova*- **A-** Adaxial face, **B-** Abaxial face; **C-E-** *Mimosa gracilis*, **C-D -** Adaxial face **E-** Abaxial face; **F-I-** *Mimosa kalunga*, **F-G-** Adaxial face, **H-I-** Abaxial face; **J-K-** *Mimosa leiocephala* **J-** Adaxial face, **K-** Abaxial face. Tector trichome (☆), glandular trichome (★), stomates (arrows).

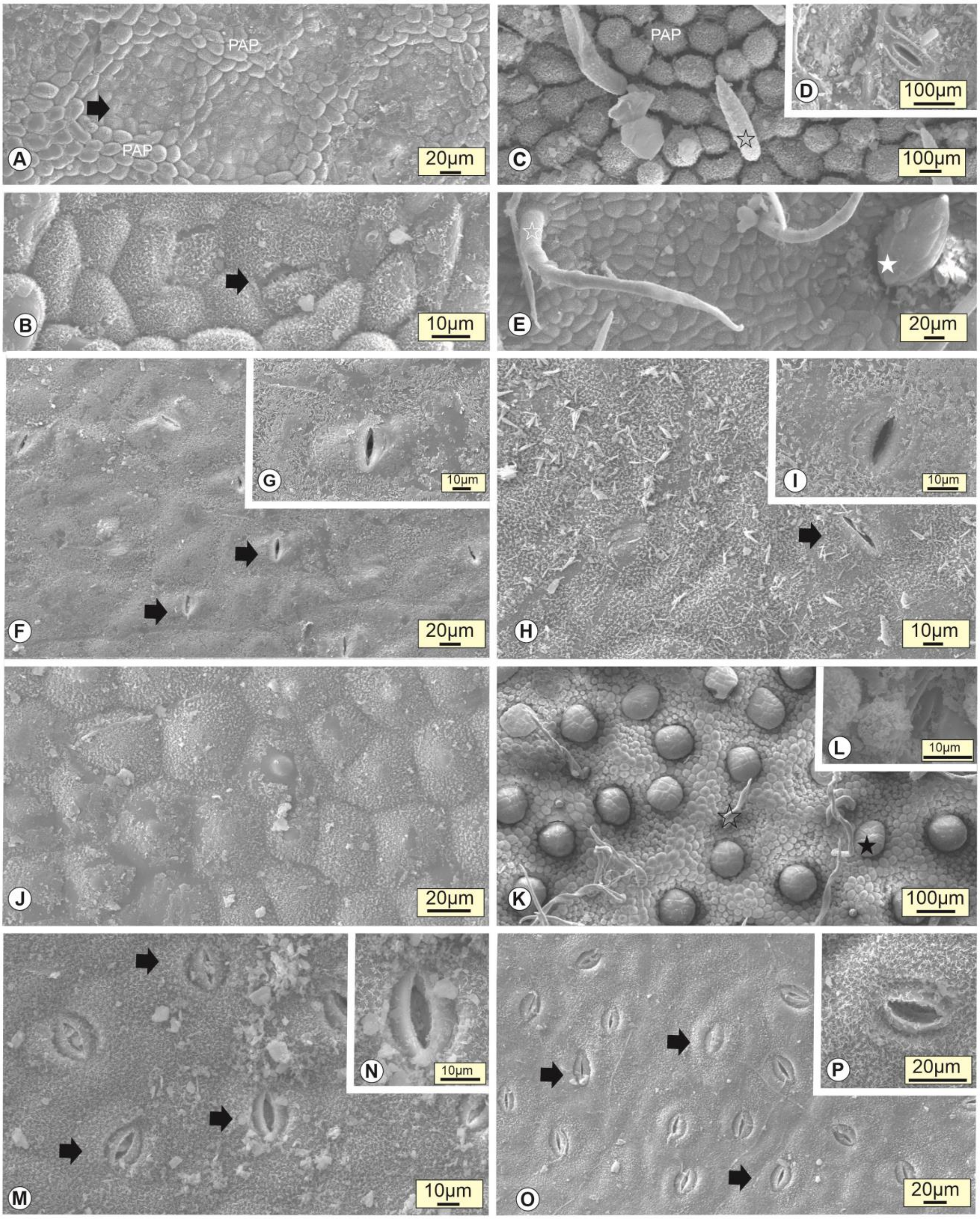

Figure - 7. Eletronmicrography of leaves epidermis **A-E** *Bauhinia dumosa*- **A-B** Adaxial face, **C-E** Abaxial face; **F-I** *Chamacrista claussenii* **F-G** Adaxial face, **H-I** Abaxial face; **J-L** *Harpalyce tombadorensis* **J** Adaxial face **K-L** Abaxial face; **M-P** *Senna corifolia* **M, N** Adaxial face **O, P** Abaxial face. Tector trichome (☆), glandular trichome (★), stomates (arrows), papillose epidermis (PAP).

*A*natomy of the stem

According to anatomical analyses of stem traits (Table 2), the plants could be divided into two groups:

(1) In the first group, *Mimosa kalunga* and *M. sp. nova* had secondary growth with a well-developed phellem (Fig. 8 A). The cortex was absent and the secondary phloem had a high amount of fibers scattered among the sieve tube elements and parenchyma cells. Thus, these fibers form a transversal ring in both species. Additionally, *Mimosa sp nova* had old sieve tube elements with large diameter in degeneration stage closer to the periderm (Fig. 8 A). The xylem contained vessel elements isolated or grouped in various amounts. Both species presented the xylem with an endarch maturation pattern (centrifugal development of xylem), and by a wide central pith, it confirmed the stem origin.

(2) The second group comprised *Bauhinia dumosa*, *Chamaecrista claussenii*, *Harpalyce tombadorensis*, *Senna corifolia*, *Mimosa gracilis* and *Mimosa leiocephala.* Their aerial stem presented in the early stages of secondary growth. In the cross section, the organ exhibited the transition stage for secondary growth. The primary growth was demonstrated by epiderm that was covered by a thick cuticle and the presence of a cortex. Indeed, the secondary growth was shown by the vascular system with secondary xylem and phloem, which was organized as a continuous cylinder. Another clear example of the transition growth was in *Chamaecrista claussenii* species in which the epiderm was present and it was possible to observe the periderm at the beginning of their formation (Fig. 9 C).

Some species exhibited epidermal outgrowth such as the *Harpalyce tombadorensis* (Fig. 9 E) *and Bauhinia dumosa* which had tector trichomes, *Senna corifolia and Mimosa gracilis* (Fig. 8C) which had rare stomates. All six species presented the primary xylem with an endarch maturation pattern (centrifugal development of xylem), and by a wide central pith, it confirmed the stem origin.

In all six species, the cortex presented parenchymatic and sclerenchymatic portions. The inner portion of the cortex had a thick fiber ring surrounding the vascular cylinder (e.g., Fig. 9 F). The number of cortical parenchyma layers varied among the species such as *Bauhinia dumosa* with five layers, *Chamaecrista claussenii* with seven layers, *Harpalyce tombadorensis* with six layers, *Senna corifolia* with seven layers, *Mimosa gracilis* with five layers, and *Mimosa leiocephala* with eight layers.

However, different from other analyzed species, *Harpalyce tombadorensis* had a structure similar to a hypoderm, which was identified through the presence of one or two layers with larger cells than other cortical cells (Fig. 9 E, F). Additionally, in all six species, the secondary phloem was smaller than the secondary xylem, and their structure could vary among the species. The xylem was formed by highly lignified fibers. Moreover, their vessel elements were single or grouped in the analyzed tissue.

The phloem was parenchymatic, and there were no fibers in *Mimosa leiocephala*, *Senna corifolia*, *Bauhinia dumosa*, *Mimosa gracilis* and *Harpalyce tombadorensis*. However, in *Chamaecrista claussenii* the secondary phloem portion had a small number of sclerenchymatic cells, sparse in the parenchyma tissue (Fig. 9C). In all six species, the xylem had its axial parenchyma exhibiting diffuse or aggregate formation, with the exception of the *Senna corifolia* which had the continuous ring strip. The radial parenchyma was uniseriate in *Bauhinia dumosa,* and is from one to two seriate in the remaining species. In *Mimosa leiocephala* and *Chamaecrista claussenii* species, the xylem exhibited their inner and external portions with a concave shape.

Mimosa gracilis species presented non-cylindric stem form, with lateral projections, stomates; well-developed cuticle; and star-shaped pith. The vascular bundles were involved in the external area for a strongly sclerenchymatic area of the cortex.

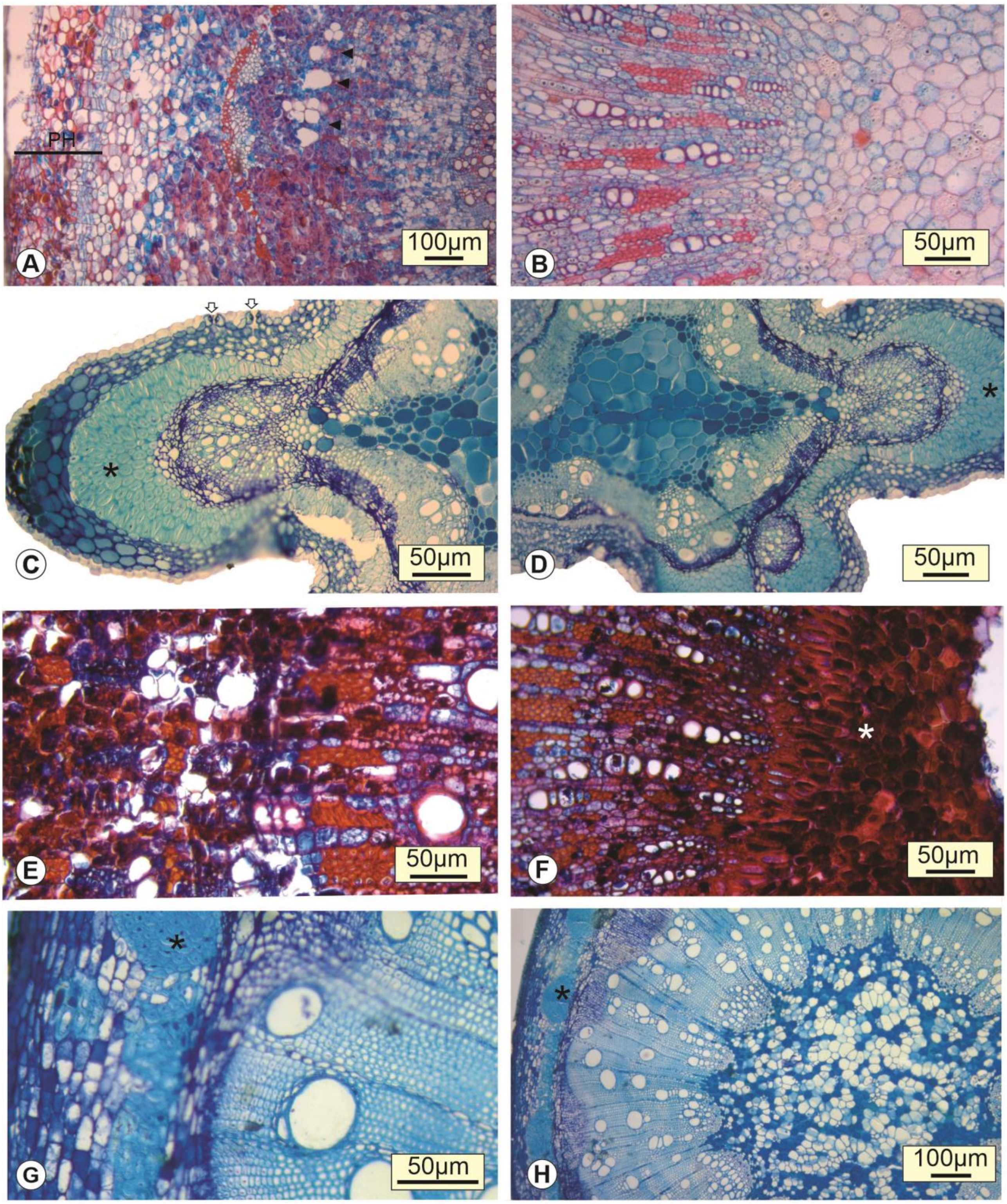

Figure 8- Cross sections of legume stems. A-B. *Mimosa sp. nova A*- Phloem with a large sieve tube elements B- Pith and secondary xylem C-D. *Mimosa gracilis* C- Vascular cylinder with a thick layer of sclereids D- Other vascular bundles formation E-F *Mimosa kalunga* F- Sclerenchymatic pith G-H *Mimosa leiocephala* H- Star shaped pith. Sieve tube elements (arrow head), phellem (PH), sclereids (*), stomates (arrows).

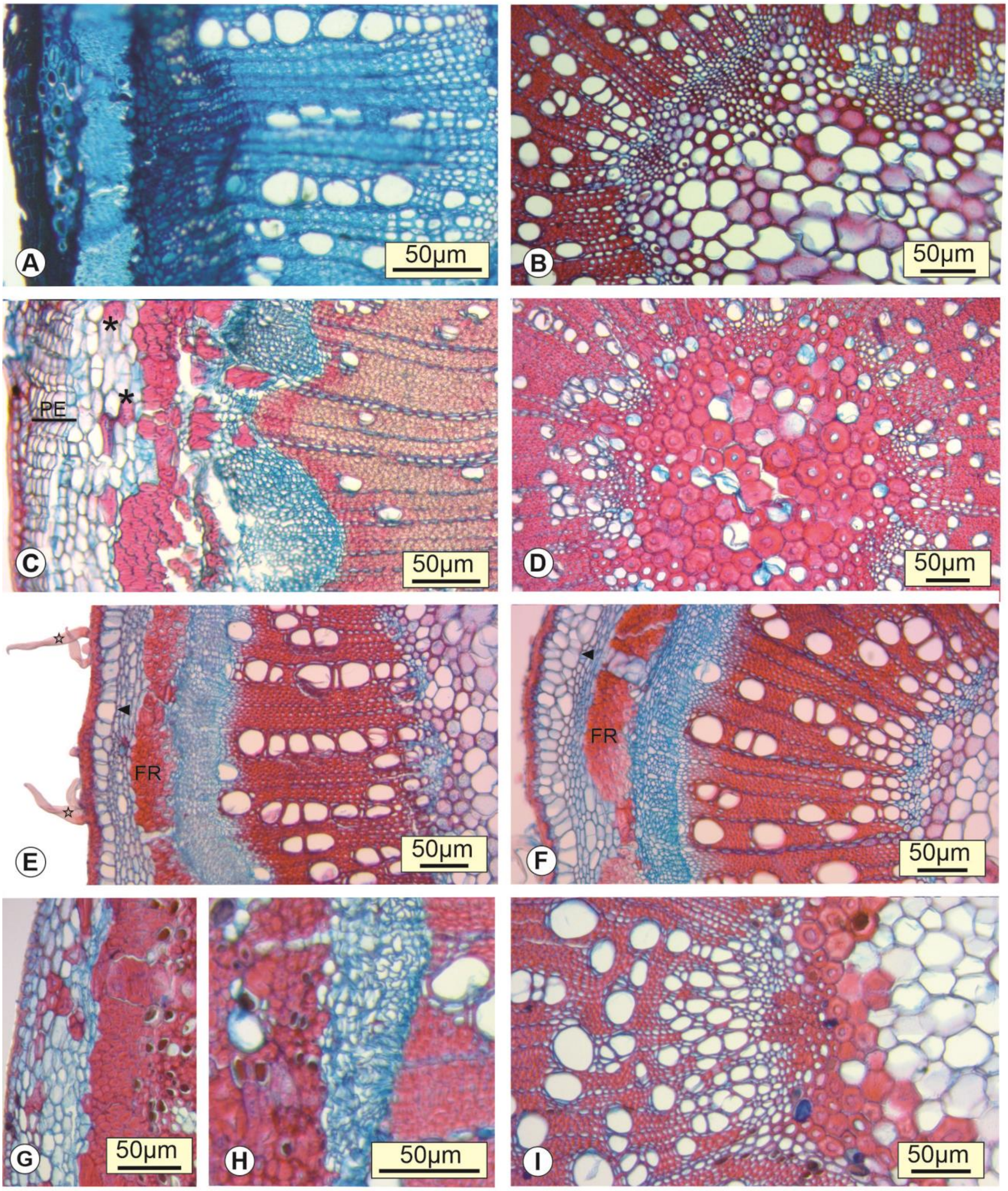

Figure 9- Cross sections of legume stems A-B. *Bauhinia dumosa*. C-D. *Chamaecrista claussenii*. D- Sclerenchymatic pith. E-F *Harpalyce tombadorensis*. E- Tector trichomes and thick cuticle detail. G-H-I *Senna corifolia*. I- Sclerenchymatic pith. Similar to a hypoderm (arrow head), phellem (PH), sclereids (*), stomates (arrows), periderm in formation (PE), fiber ring (FR), tector trichomes (☆).

Table 2- Morphological and anatomical traits of Fabaceae species.

Species	Organs	Morphological and ultrastructural traits	Anatomical traits
Mimosa sp. nova *Mimosa kalunga*	Stem	-Thick sternal bark -Monopodial growth -Trichomes	-well-developed phellem -Cortex absent -phloem with high amount of fibers -phloem with large sieve tube elements - Sclerenchymatic pith (*M. kalunga*)
	Leaf	-Coriaceous consistence -Leaves congested in the apse - Leaflets have an oblong shape -Trichomes	- Unstratified epidermis with well- developed cuticle -Anticlinal cell walls are sinuous -External periclinal walls smooth on both faces of leaf - Dorsiventral mesophyll - Collateral vascular bundles **(**These bundles were surrounded by a high amounts of fiber caps oriented to the phloem directions) - Paracitic stomata at the same level that other epidermal cells (larger substomatal chambers) - Amphistomatic leaves - Tector simple trichomes in both faces and *M. sp nova* had glandular trichomes in the margin
Mimosa leiocephala	Stem	-Thin sternal bark - Trichomes	-Early stages of secondary growth -Epiderm with well-developed cuticle -Cortex visible, with parenchymatic and sclerenchymatic portion -Vascular bundles with secondary xylem and phloem -Non-secretory trichomes -Secondary phloem was smaller than the secondary xylem -The phloem is parenchymatic - Tector trichomes
	Leaf	-Coriaceous consistence - Trichomes	-Unstratified epidermis with well- developed cuticle -Anticlinal cell walls are sinuous -External periclinal walls papilosae on both faces of leaf - Dorsiventral mesophyll - Collateral vascular bundles (These bundles were surrounded by a high amounts of fiber caps oriented to the phloem directions) - Paracitic stomata at the same level that other epidermal cells (larger substomatal chambers) - Amphistomatic leaves - Tector simple trichomes in the both faces, and glandular trichomes in the margin
Harpalyce tombadorensis	Stem	-Thin sternal bark - slightly sulcate shape - Trichomes	Early stages of secondary growth -Epiderm with well-developed cuticle -Hipoderm -Cortex visible, with parenchymatic and sclerenchymatic portion -Vascular bundles with secondary xylem and phloem -Non-secretory trichomes -Secondary phloem was smaller than the secondary xylem -The phloem is parenchymatic - Tector trichomes
	Leaf	-Coriaceous consistence -Inclined leaves -Elliptic shape -Pulvinules -Persistent shorter linear stipule -Adaxial surface is glabrous -Abaxial surface is pilosum -Trichomes	-Unstratified epidermis with well-developed cuticle -Anticlinal cell walls are sinuous -External periclinal walls smooth on adaxial face and papilosae on abaxial face -Dorsiventral mesophyll - Collateral vascular bundles **(**These bundles were surrounded by a high amount of fiber caps oriented to the phloem and xylem directions) -Paracitic stomata at the same level that other epidermal cells (larger substomatal chambers) -hypostomatic leaves - Tector and glandular trichomes in the abaxial face and midrib.
Bauhinia dumosa	Stem	-Thin sternal bark - Trichomes -EFNs	-Early stages of secondary growth -Epiderm with well-developed cuticle -Cortex visible, with parenchymatic and sclerenchymatic portion -Vascular bundles with secondary xylem and phloem -Non-secretory trichomes -Secondary phloem was smaller than the secondary xylem -The phloem is surrounded by a continuous ring of fibers - Tector trichomes

Bauhinia dumosa	Leaf	-Coriaceous consistence -Inclined leaves -Bilobed (rounded shape) - Pilosum on the abaxial face -Glabrous on the adaxial face - Stipules	-Unstratified epidermis with well- developed cuticle -Anticlinal cell walls are sinuous -External periclinal walls papilosae on both faces of leaf - Dorsiventral mesophyll - Collateral vascular bundles (These bundles were surrounded by a high amounts of fiber caps oriented to the phloem directions) - Paracitic stomata at the same level that other epidermal cells (larger substomatal chambers) - Amphistomatic leaves - Tector and glandular trichomes in the abaxial face and midrib.
Chamaecrista claussenii	Stem	-Thin sternal bark - Cylindric - Trichomes -EFNs	-Early stages of secondary growth -Epiderm with well-developed cuticle -Cortex visible, with parenchymatic and sclerenchymatic portion -Vascular bundles with secondary xylem and phloem -Non-secretory trichomes - The secondary phloem with sparce sclerenchyma cells -Secondary phloem was smaller than the secondary xylem -The phloem is surrounded by a continuous ring of fibers - Sclerenchymatic pith
	Leaf	-Coriaceous consistence -Inclined leaves - Oval shape -leaf blade is glabrous on both faces -stipules are early deciduous	-Unstratified epidermis with well- developed cuticle -Anticlinal cell walls are sinuous -External periclinal walls smooth on both faces -Heterogeneous isobilateral mesophyll - Collateral vascular bundles (These bundles were surrounded by a high amount of fiber caps oriented to the phloem directions) -Paracitic stomata at the same level that other epidermal cells (larger substomatal chambers) -Amphistomatic leaves - Non- type of trichome
Senna corifolia	Stem	-Thin sternal bark -Cylindric -EFNs -Sympodial growth	-Early stages of secondary growth -Epiderm with well-developed cuticle -Cortex visible, with parenchymatic and sclerenchymatic portion -Vascular bundles with secondary xylem and phloem -Non-secretory trichomes -Secondary phloem was smaller than the secondary xylem -The phloem is parenchymatic -Stomate -Sclerenchymatic pith
	Leaf	-Coriaceous consistence -Inclined leaves - Leaflets ovate-oblong shape -Pulvinus and pulvinule - Stipule -Glabrous on both faces	- Unstratified epidermis with well- developed cuticle -Anticlinal cell walls are sinuous -External periclinal walls smooth on both faces -Dorsiventral mesophyll - Collateral vascular bundles (These bundles were surrounded by a high amounts of fiber caps oriented to the phloem directions) -Stomata at the same level that other epidermal cells (larger substomatal chambers) -Amphistomatic leaflets - Non type of trichome
Mimosa gracilis	Stem	-Thin sternal bark - Non-cylindrical and had lateral projection - Glabrous	--Early stages of secondary growth -Epiderm with well-developed cuticle -Cortex visible, with parenchymatic and sclerenchymatic portion -Vascular bundles with secondary xylem and phloem -Non-secretory trichomes -Secondary phloem was smaller than the secondary xylem -The phloem is parenchymatic -Stomate
	Leaf	-Coriaceous consistence -Glabrous on both faces - Stipules	- Unstratified epidermis with well- developed cuticle -Epidermal cells have more diameter that mesophylls cells -Anticlinal cell walls are sinuous -External periclinal walls smooth on both faces -Dorsiventral mesophyll -Collateral vascular bundles with accessory bundles in low amounts, reduced size, and a few sclerenchymatic cells - Paracitic stomata at the same level that other epidermal cells (larger substomatal chambers) -Amphistomatic leaflets - Non type of trichome

Discussion

According to morphoanatomical analyses of stem and leaves, it was possible to identify two functional groups that were comprised by:

(1) The first group comprised resprouting species according to Zupo, (2020), an exception was *Mimosa sp. nova* species that did not have information about its vegetative propagation. All species maintained their aerial parts during the dry season (field observations), which was subdivided into other two subgroups:

  (a) The first subgroup comprised *Mimosa kalunga* and *Mimosa sp. nova* species, that had a stem in the secondary growth stage, with a well-developed phellem. Their leaves had a set of characteristics related to sunlight exposition, insect herbivory, and drought tolerance. Some of these traits included a thick cuticle, a high amount of sclerenchymatic tissue in the vascular bundles and compact palisade parenchyma with juxtaposed cells (Table 2, 3).

  (b) The second subgroup comprised the species *Bauhinia dumosa*, *Chamaecrista claussenii*, *Harpalyce tombadorensis*, *Senna corifolia*, and *Mimosa leiocephala* species. Plants in which the stem showed early stages of secondary growth and presented a set of traits to prevent water loss, insect herbivory as well as related to drought tolerance and sunlight exposition such as well-developed cuticle, periderm formation, trichomes, stomates, and a high amount of sclerenchymatic tissues (Table 2, 3). Their leaves had a set of traits related to sunlight exposition, insect herbivory, and drought tolerance. These included well-developed cuticle, a high amount of sclerenchymatic tissue distributed in the mesophyll and on the vascular bundles, as well as compact palisade parenchyma with juxtaposed cells (Table 2, 3).

These plant groups had many xeromorphic traits involving all the survival and protection functions: protect the plants against sunlight exposition, water deficit, and insect herbivory.

(2) The second group was comprised only by *Mimosa gracilis*, the only herbaceous species of this study, which is a resprouting species according to Zupo, (2020), and lost its aerial parts during the dry season (field observations). Thus, these species needed strategies to rapidly and efficiently grow aerial portion between the fire and drought events, which was during the wet season. These traits provide the species more probability of reaching the

> reproduction stage. The stem of the *Mimosa gracilis* was very different compared to other studied species in a number of traits such as non-cylindric stem form, with lateral projections; stomates; cuticle; star-shaped pith, and the vascular bundles were involved in the external area for a strongly sclerenchymatic area of the cortex. This thick layer of sclerenchyma cells has the main function as a protective barrier, which probably protects the vessels against pathogens**.** Their leaves presented a high amount of photosynthetic tissue, stomates, and well-developed cuticle. Other interesting traits presented in their leaves were very short leaflets**,** less sclerenchymatic tissue and less developed vascular system in comparison to other *Mimosa* species. Some of these traits were considered mesomorphic (Rossatto *et al.* 2015).

Mimosa kalunga resprouted after fire by the buds located in the base region according to Zupo, (2020). Additionally, these plants potentially had stem fire protection, which was shown for the presence of traits such as a thick bark, a sympodial growth, stipules persistence and leaves congested in the apex. These traits protected the buds against tissue damage by fire**.** These traits were registered to be related to fire protection by Simon et al. (2009), who identified thick shoots and leaves clustered at their apex, with persistent stipules to protect the apical meristem from fire damage.

Well-developed bark was shown by the studied species, that was a xeromorphic trait being a first barrier against fire damage because the bark worked as the thermal insulation of plant tissues against high fire temperatures (Gignoux *et al.* 1997; Sonsin *et al.* 2012)**.** The wood (stem) xeromorphic traits were evidenced by numerous relatively narrow grouped vessels**.** Another characteristic was that in xerophytes, the axial parenchyma could have the function of the conductive system (Carlquist 2015). Thus, the xylem and phloem were interconnected through the parenchyma developing the hydraulic networks (Sack *et al.* 2016). Moreover, *Mimosa sp. nova* had phloem with large sieve tube elements, these tubes increased the diameter, with storage function. As far as these sieve tube elements were closer to the periderm, along the growing process, they degenerate and can have the function of air conduction to cool the tissues under high temperature**.**

The plants of the second subgroup resprouted after fire (Zupo *et al*. 2020), however, the aerial part persisted during the dry season. For aerial portion persistence, the plants had xeromorphic traits. These traits played a set of ecological functions that enabled plant survival in different year seasons, and under a set of environmental filters.

The stem of these species presented in the early stage of secondary growth. Thus, these plants invested in secondary tissues to protect against water loss, and against herbivory damage. Indeed, these plants did not have the capacity to aerial part persistence during fire events.

Due to morphological and anatomical analyses of the leaves, the presence of the thick cuticle, sclerenchymatic tissues, and coriaceous consistency allowed the leaves to be identified as sclerophylls. Some Cerrado leaves showed these traits such as, a well-developed cuticle and epicuticular wax, sclerified cells, palisade parenchyma, a well-developed vascular system (Bieras and Sajo 2009). Sclerophyllous leaves were commonly found in seasonally dry environments, as in the Mediterranean. It is evidenced that these leaves had remarkable plasticity which enabled the high photosynthetic efficiency and was also considered a xeromorphic trait (Flexas *et al.* 2001). The coriaceous or hard leaf consistence permitted an advantageous adaptive trait against water loss, excessive luminosity and herbivory (Turner 1994).

All second subgroup studied species presented a well-developed cuticle (with exception of *Bauhinia dumosa*, that had papillose epidermis on both faces) and the epicuticular wax, which were classified as a xeromorphic trait (Fahn and Cutler 1992). The cuticle was constituted of lipidic substances such as wax and cutin and worked to reduce the loss of water in the leaf internal tissues to the atmosphere through to the process of transpiration (Burghardt and Riederer 2009), and also optimized the use of water (Riederer and Schreiber 2001; Simioni *et al.* 2017). The presence of the thick cuticle was in direct relation with plants living in environments that had a high incidence of light and had a considerable water deficit, dry environments (Fahn and Cutler 1992; Guerra and Scremin-Dias 2018). Indeed, the studied plants that live in an environment with a long dry season didn’t lose the aerial part along that period. Because of this, the well- developed cuticle was an important ecological trait to the studied plants. Other important functions of the cuticle were protection against the high incidence of light (Müller and Riederer 2005**)**, and against pathogens (Read and Sanson 2003), which offered protection along the year.

All species of this study had the mesophyll formed by palisade parenchyma that was well developed and little developed spongy parenchyma. In savanna environments, to be constantly exposed in the sunlight, plants present evident photosynthetic tissue. Therefore, savanna plants have poorly developed spongy parenchyma but a well-developed palisade parenchyma which is typically found in leaves exposed to high light intensity (Amorim *et al.* 2012; Simioni *et al.* 2017). Besides, palisade parenchyma with large, elongated perpendicular and united cells also contributes to forming a protective barrier against the loss of water (Dengler 2002).

Besides having compact leaves and well-developed palisade parenchyma, the studied plants had sclerenchymatic cells in the vascular bundles, and in the case of *Bauhinia dumosa* they were scattered in the mesophyll. These combined traits provided the leaves with a certain degree of protection against some types of damage (Kummerow 1973; Stephanou and Manetas 1997) during a long dry season. It was possible because the sclereids may also aid in water transport through the palisade parenchyma (Brodribb *et al.* 2010). Additionally, *Bauhinia dumosa* species had papillose epidermis on both leaf faces in which the function is unknown. However, the set of traits present in the species are very related to xeromorphy.

Some other interesting characteristics presented in the studied species that remind xeromorphic, was the alternate spiral phyllotaxis that could reduce the excess of solar radiation, thus preventing against photoinhibition (Valladares and Pearcy 1998; Ishida *et al.* 2001). Another trait was vertically inclined leaves that also minimized the direct sun exposition (Lausi and Nimis 1986)**.**

Most of the studied plants presented amphistomatic leaves. This is a common feature in plants of xeric habitats (Fahn and Cutler 1992). This stomatic distribution increases the photosynthesis rates, because the presence of stomata on both faces of the leaf can shorten the distance of carbon diffusion within the mesophyll cells. It also increases the leaf conductance to CO2 and allows leaves to be thick (Jordan *et al.* 2014). Amphistomatic leaves are present in Asteraceae and Amaranthaceae species living in open areas, where the luminosity is also high (Garibotti Lusa *et al.* 2014; Lusa *et al.* 2018).

Besides, in some plants, especially in the glabrous leaves, there is a high number of stomates in the blades. Thus, it has been reported that the stomatal density is proportionally related to the light intensity (Abrams *et al.* 1992; Cao 2000). The presence of a high amount of stomates increases the water supply on the epidermal surface. Thereby, the water and solute are not diffusing into the atmosphere (Struwig *et al.* 2011).

For this study, it was important to show the presence or absence of an indumentum for the selected species. In addition, it could be used as a diagnostic character (Santos-Silva *et al.* 2013; Silveira *et al.* 2019). Before analyzing the eight species by using the electronic microscope (EM), five species showed a visible indumentum.

Non-glandular trichomes is the important adaptation of Cerrado plants. Besides of many functions, such as: the reflection of the sun light, reduction of leaf temperature and the loss of water, reduction of humidity of the leaf surface, that promotes the photosynthetic rate, hampering the growth of pathogens, and acting as a mechanical barrier against herbivory. In addiction the density of trichomes can vary in response to environmental conditions, and in tending to be higher in environments with high luminosity and low water availability (dry seasonal environments) (Rossatto and Kolb 2010).

Glandular trichomes together with other glandular structures are the primary site of biosynthesis and storage of the secondary metabolites (Fahn 1979). These structures can be occur in leaves, stems, and even parts of flowers, depending on the species (Bell and Bryan 2008). Glandular trichomes in leaves, to cope the function of protect against herbivores (Fahn 1979; Ambrósio *et al.* 2008)**.**

The second group composed by *Mimosa gracilis* species, through the storage underground organ, this plant probably resprouts after drought and fire. And these herbaceous plants need to grow fast to achieve a reproductive size among fire and drought event. Their aerial part is destroyed by fire, because not possess the thick bark necessary to insulate tissues against drought damage (Hoffmann 1996).

To grow fast, these plants need to produce more economic and efficient new leaves and stems, in terms of water lost and herbivory defense. *Mimosa gracilis* leaves have scant sclerenchymatic cells in the mesophyll than in vascular bundles, and not have a well prominent cuticle. These traits were found in grasses and herbs and were classified as mesomorphic traits (Rossatto *et al.* 2015).

Table 3- Ecological functions of Fabaceae traits.

Leaves Traits	Ecological functions
-Inclinate leaves	-To avoid the direct incidence of sunlight in the leaf blade (Lausi and Nimis 1986)
-Alternate spiral phyllotaxis	-To reduce the excess of solar radiation (Valladares and Pearcy 1998; Ishida *et al.* 2001)
-Tick bark	-Protection against fire damage (Simon and Pennington 2012)
-Sclerenchymatic pith	- Protection against herbivory
-Stipule at the stem apse	-Protection against fire damage (Simon and Pennington 2012).
-EFNs	-Protection against herbivory through mutualistic ant-plant interactions (Del-Claro *et al.* 2016).
-Sclereids in leaf, and stem	-In leaves, aid in water transport through the palisade parenchyma (Heide-Jorgensen 1990). Improve the light distribution through the chlorophyllin tissue, and can influence the photosynthetic light-use efficiency (Karabourniotis 1998). Moreover, protect the plant tissues by increasing the resistance and hardiness (Turner 1994), prevent the cells from collapse when lost water.
-Smaller and isodiametric cells	-Leaves with smaller cells are mechanically stronger, because these cells have higher surface/volume ratios, and cell wall elasticity (Kaiser 1982; Terashima *et al.* 2001).
-Well-developed cuticle	-Protect against UV-B radiation, and resulting in efficient water conservation (Turner 1994; Riederer and Schreiber 2001)
-Epicuticular waxes	-Protection against water lost by transpiration, and insect herbivory (Oliveira *et al.* 2003)
-Hipoderms or multiple epidermis	-Avoid the water lost, and protect the leaf against sunlight radiation (Dickison 2000)
-Amphitomatic leaves	-Increasing the leaf conductance to CO2, reduce the transpiration and water lost (MOTT *et al.* 1982; Turner 1994; Rotondi *et al.* 2003; Jordan *et al.* 2014)
-Tector trichomes	-Reflection of the sunlight, reduce the leaf temperature and the loss of the stomata water vapor to the atmosphere (Fahn and Cutler 1992; Rossatto and Kolb 2010).
-Phloem with large sieve tube elements	-These tubes have storage function, and when increases the diameter, the tube suffers a degeneration and can have the function to conduction air to cool the tissues under high temperature.
-Large substomatal chambers	-Reduction of water loss (Pickard 1981, 1982)

Conclusions

Resprouting species of this study also have several important morphological traits that enable these species to resist drought, fire, and pathogen. Some of the most important traits found for these species were the coriaceous consistency, inclined leaves and well-developed cuticle present in all analyzed species. In the stem and leaves, some species present trichomes, which are an important feature of drought, fire resistance, and protection against herbivores. Additionally, extrafloral nectaries were found in some species, this structure is responsible for the mutualist ant-plant relations which also protect the plant against herbivores.

The only herbaceous species (*Mimosa gracilis*) that lost the aerial part in the dry season, showed mesomorphic traits in the leaves and stem. On the other hand, all of the remaining species (shrubs) that did not lose the aerial part in the dry season had a set of xeromorphic traits. However, these two functional groups have traits related to protection against pathogen. Therefore, sometimes a simple trait enables plant protection against multiple environmental factors. This can be observed, for instance, in the away trichomes protect plants against herbivory, loss of water by leaves, and even avoid apical meristem fire damage.

Besides the anatomic and morphologic traits that are strongly related to essential ecologic functions, these traits can help taxonomic and phylogenetic studies. Thus, basic morphological characteristics were identified and served the only purpose of diagnosing these species. Morphological traits along with accurate anatomic and structural analysis, mainly related to leaves, showed a detailed review of the species traits.

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CHAPTER 2

BELOWGROUND SYSTEMS OF FABACEAE SPECIES FROM TROPICAL OPEN SAVANNAS

BELOWGROUND SYSTEMS OF FABACEAE SPECIES FROM TROPICAL OPEN SAVANNAS

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- **Background and Aim.** The woody vegetation of the Cerrado is characterized by its post-fire regeneration, because of its high bud protection. Several species, as Fabaceae family, can resprout after the 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, this study evaluated the morphoanatomical structure of the belowground organ, buds and their storage**.**
- **Methods.** It was evaluated the morphoanatomy as well the histochemical test to belowground organs of 8 species of legumes collected in open savannas from Central Brazil**.**
- **Key Results.** After the morphoanatomical analysis, two species presented a taproot tuber and the six remaining species were formed by xylopodium. All xylopodia presented buds on the upper portion of the organs. These organs were composed by a great amount of lignified tissues, defense (phenolic compounds and lipidic substances), and storage (starch) substances. All xylopodia presented associated tuberous roots, and in two species these roots were also root suckers.
- **Conclusions.** The xylopodia has important morphological and anatomical persistence traits. Besides the strong capacity of these plants to resprout and/or their associated root suckers to propagate laterally, the plants of this study have protection against pathogens, through the defense compounds. The functions of these traits are essentials for the understanding of the great capacity of legume survival in fire-prone ecosystems.
- **Key words:** Cerrado, Fabaceae, belowground organ, xylopodium, tuberous root, root sucker, taproot, fire ecology

Introduction

Fire is an essential factor for the ecology of several ecosystems in the world, due to the fact that it is an ecological and evolutionary agent responsible for maintaining biodiversity in flammable ecosystems (Whelan 1995; Bond and Keeley 2005; Hardesty *et al.* 2005). Since millions of years, the fire has been an environmental driver, which models the savanna ecosystems (Simon *et al.* 2009; Simon and Pennington 2012).

Considering fire-prone environments, vegetation structure defines the savanna that encompasses a landscape mosaic of grasslands, scattered trees, and closed woodlands that vary in proportion depending on the spatial and temporal aspects (Scholes and Archer 1997; Wiegand *et al.* 2005). Thus, specifically the tropical savannas are characterized by a discontinuous stratum of woody species and a continuous C4 herbaceous layer that can support disturbance (Lloyd *et al.* 2008; Ratnam *et al.* 2011).

The most important savannas in the world are located in regions of Australia, Africa and South America (Trollope 1982; Coutinho 1990; Sarmiento 1996; Morgan 1999; Simon *et al.* 2009). The second most extensive ecosystems in South America is the Cerrado located in Brazil (Eiten 1972)**.** It encompasses a mosaic of vegetation from grasslands, savannas and closed or open forests (Lenthall *et al.* 1999; Oliveira-Filho, A.T.; Ratter 2002). Among the savanna vegetation, the Cerrado represents the richest savanna worldwide (De Moraes *et al.* 2016). Therefore, the Cerrado of Central Brazil (Lenthall *et al.* 1999), is a mesic savanna that encompass different vegetation types, such as open savanna '*campo sujo*' (Franco et al., 2014).

Besides high floristic richness, Cerrado plants have many adaptive strategies to overcome the hostile environmental conditions imposed by the dry season, poor nutrition of the soils, and a fire-prone environment (De Moraes *et al.* 2016). Furthermore, as far as within the Cerrado is concerned, all this vegetation can be affected by other events such as drought (Furley 1999). However, fire causes the biggest loss of aerial biomass, making it easier to kill buds and poorly insulated meristems than other environmental drivers (Lamont *et al.* 2004; Chalwell and Ladd 2005; Pausas *et al.* 2016). These factors demonstrate the importance of fire in savanna vegetation (Solbrig 1996; Lehmann *et al.* 2014). Thus, plants that live in fire-prone environments have traits related to plant persistence and regeneration after fire (Paula *et al.* 2009), yet fire is not the only associated disturbance in the plant life cycle. The influence of fire, as a consequence, increases plant fitness (De Moraes *et al.* 2016).

Resprouting trait is considered to be a determinant functional trait to the plant persistence in fire prone environment (Clarke *et al.* 2012)**.** The savanna vegetation of the Cerrado is characterized by its post-fire regeneration related to its high bud protection (Coutinho 1990; Miranda *et al.* 2013). Thus, the ability to resprout is related to many traits of the plants such as the degree of bud protection and the viable bud bank (Klimešová and Klimeš 2007). A bud bank is the total amount of buds considering the plants whole body, which can be potentially used for vegetative regeneration. New shoots can be formed after the partial or total removal of aboveground biomass caused by extreme climatic factors, such as drought or fire (Harper 1977; Klimešová and Klimeš 2007; Appezzato-da-Glória and Cury 2011).

The location of the bud bank is also determinant for the resprouting ability **(**Vesk and Westoby 2004; Clarke *et al.* 2013; Charles-dominique *et al.* 2015)**.** Thus, the buds can be aerial, basal and belowground (Lawes and Clarke 2011; Clarke *et al.* 2013). These buds can be protected in different ways: in the case of aerial buds, being protected by bark, or the tissues that involve them (Charles-Dominique *et al.* 2015). Additionally, the plant height and fast growth so that the buds can avoid the fire line, and avoid the stress (Bond 2008). While belowground buds have twice the protection by soil layer and by other plant traits such as bark, leaf sheaths and scale leaves (Clarke *et al.* 2013).

Another important trait which can also enable the resprouting is the amount of storage reserves (Clarke *et al.* 2013). This way, the stored carbohydrates allow the plant to resprout from the protected buds reestablishing the aerial biomass (Schutz *et al.* 2009; Appezzato-da-Glória and Cury 2011; De Moraes *et al.* 2016; Silva and Rossatto 2019).

In the fire-prone ecosystems, some plants can resprout by using the belowground organs that already had buds. These organs enable the survival and recovery of the aerial biomass after a fire (Pausas *et al.* 2018). Therefore, the ability of resprouting quickly after fire (Zaloumis and Bond 2011) and the allocation of biomass to belowground organs (Coutinho 1990; Miranda *et al.* 2002), are some traits of Cerrado plants which guarantee them a persistence advantage (Coutinho 1990; Miranda *et al.* 2002)**.** Essentially, the belowground organs that store reserves are directly related to efficient regeneration (Appezzato-da-Glória and Cury 2011; De Moraes *et al.* 2016).

There is a variety of belowground organs present in the plants on savannas worldwide (Pausas *et al.* 2018). In the Cerrado plants, different types of belowground organs can be found, such as tuberous roots; soboles; root suckers; rhizophore and xylopodium (Tansley

1946; Hoffmann 2000; Appezzato-da-Glória 2003; Hayashi and Appezzato-da-Glória 2005, 2007; Appezzato-Da-Glória *et al.* 2008; Hayashi and Appezzato-da-Glória 2009; Appezzato-da-Glória and Cury 2011; Alves *et al.* 2013; Appezzato-da-Glória 2015; Burrows 2016). In regard to the xylopodium, this is one of the most common belowground organs found in fire prone ecosystems. Also, xylopodia are commonly found in Asteraceae and Fabaceae families, and occur mostly in small shrubs and forbs (Pausas *et al.* 2018). Additionally, these organs were first identified in the Brazilian grasslands (Warming 1893; Lindman 1900).

The Fabaceae is one of the most important families of the Cerrado (Almeida *et al.* 2014; LPWG 2017), and their distribution on these phytogeographic domains is very broad (Strassburg *et al.* 2017). Additionally, in the global context, Fabaceae is considered the third family with the biggest richness of species (LPWG 2017).

Besides of the richness, Fabaceae family is characterized for having fire adapted belowground organs (Appezzato-Da-Glória *et al.* 2008; Simon and Pennington 2012). Thus, resprouting is a frequent trait in several herbaceous and woody species of the Fabaceae (Hayashi *et al.* 2001; Kennard *et al.* 2002).

Therefore, in other studies, it was suggested that the studied species resprouted from belowground systems (Zupo *et al.* 2020). And then, the morphoanatomy of these organs as well as the description and observation of bud is interesting to show where do come from these resprouts. So, this study aimed to evaluate the morphology and anatomy of the buds present in belowground organs of the eight Fabaceae species. Hence, to identify the types of the organs and their stored reserves, in order to understand the persistence features, which enable the high survival of these plants.

Materials and methods

Study site

The species were collected from Reserva Natural Serra do Tombador - RNST. The RNST is set in 47°45'; 47°51' W and 13°35'; 13°38' S, 8900 ha, 560-1118 m a.s.l, located in the Central region of Brazil. The RNST has 8.900 ha of the area and currently represents the largest RPPN of the Cerrado in Brazil. The climate is tropical with average annual precipitation of the 1300-1500 mm and the average maximum temperatures vary from 26 to 36°C and minimum from 8 to 14°C (Fundação Grupo Boticário 2011). The prevailing soils in the area are latosol red/yellow, with a large quantity of aluminum and it is not considered fertile (AER 2009). The vegetation from RNST is composed of different Cerrado physiognomies, such as '*campo limpo'*, '*campo sujo'*, '*cerrado rupestre'*, '*cerrado sensu stricto'*, '*veredas'*, besides '*florestas de vale* '(AER 2009).

The species were collected in an open savanna 'campo sujo' that is a very grassy savannah physiognomy of Cerrado in which trees and schrubs are few and far between (Archibold 2012; Eyre 2017). These plant life forms reach a height of more than 2 or 3 meters (Cole 1960). Thus, this savanna is characterized by a continuous herbaceous layer dominated by grass with some herbs and sub-shrubs and few woody layers with scattered shrubs and trees (Eiten 1972).

Study species and sampling

Eight of the dominant resprouter species in the area (Zupo *et al*. 2020) were selected next to fire plot experiments from RNST. Non reproductive whole adult plants (3 individuals / species) of the eight Fabaceae species were collected (Table 1). All collected specimens were taken to the laboratory in which were separated the subterranean and aerial part with a garden shears. Both organs of each portion were fixed separately in FAA 70 (Johansen 1940). Then, after 48 hours, they were placed to alcohol 70 % in a plastic bottle with a volume from 500 ml to 1L to aerial portion and to the subterranean portion varied to 500 ml to 5l depending on the structure size.

The aerial portion was separated into another study (Leal *et al*. *in prep*-Chapter 1). Anatomical analyses were performed in belowground organs of eight species in triplicate. The samples were separated following the technique by Coradin & Muñiz (1991): the organs were chopped in some portions that varied from 3X3 cm (*Mimosa gracilis*) and 5X5 cm to another seven species. To samples separation, were selected areas that containing buds and was sectioned in a manner to show transversal axis. The following steps were carried out (minimum two samples per steps) , and can be visually on the illustrations of the figures 3 to 6: Step 1: The central area in which growing the aerial stem were separated (number 1 that indicate the sectioned points); Step 2: was chosen a region below the central region to continue the analyses of the specialized underground organ (number 2 that indicate the the point of section); Step 3: was chosen some points on the associated structures (probably roots, but in some cases that was not observed in the study species, can be a stem), the portions had variable diameters and the sections varied from 0,5 cm to 5 cm.

Separated samples of the step 3, that presented smaller diameter and 0,5 cm were dehydrated in a graded ethylic series and infiltrated in Hydroxy-ethyl-Methacrylate resin (Leica Historesin). Serial sections (6-10 µm thick) were performed on a rotary microtome (Leica SM2000R) and stained with toluidine blue (Sakai 1973).

Samples of the step 1 and 2 were treated in a 10% ethylenediamine solution (Carlquist 1982). They were subsequently boiled in distillate water + glycerine (1:1) until the plant tissue softening for the sectioning point. Serial sections (20-40 µm thick) were performed on sliding microtome. The sections were clarified with 30% sodium hypochlorite solution and stained with 1% Safranin and Alcian blue in 3 % acetic acid (Burger, L.M.; Richter, 1991 - Modified). The sections were subsequently dehydrated in an ethylic alcohol, and butyl acetate, respectively. Permanent slides were mounted with synthetic resin “Entellan”.

The histochemical tests were performed in fresh sections obtained on sliding microtome for central and associated structures, were used Sudan IV and Sudan Black B (Jensen 1962) to detect the lipidic substances; Lugol to starch (Berlyn, G.P. & Mikdche 1976); Ferric Chloride to phenolic compounds (Johansen 1940); Red Ruthenium to pectic substances (Johansen 1940). Some slides were evaluated in water as a control.

Photomicrographs were obtained with a camera (AxioCam ERCS) to a microscope (Zeiss Primo Star) and the images were analyzed and the belowground system was classified following Appezzato da Gloria 2015 and Pausas *et al*., 2018.

Group classification and ecological functions

To identify the type, functionalities, and to describe the belowground organs, were created two groups. The first criterion to the separation was the morphological aspect, in which the first group encompassed plants that presented visually noncomplex belowground system, that was similar to a simple taproot, with vertical growth. And then, the second group encompassed plants with a complex belowground system. This group was divided into two subgroups, in which the first subgroup encompassed belowground systems with globose form, and the second subgroup encompassed belowground systems with horizontal orientation without defined form, and have lateral propagation. The second criterion was the anatomical aspect, that formed the same two groups, in which was identified three distinct belowground systems.

A literature revision was performed in order to identify the ecological functions of the anatomical and morphological traits founded (Table 2). This revision was following classic literature and some papers.

Table 1. Adult species collected in Reserva Natural Serra do Tombador, GO, Brazil. The species was registered in HRCB herbaria, Rio Claro, Brazil.

Species	**Growth form**	**Vegetation type**	**Date of collection**	**Accession number**
Bauhinia dumosa Benth.	shrub	Open savanna	9/5/2014	63501
Chamaecrista claussenii (Benth.) H.S.Irwin & Barneby	shrub	Open savanna	10/10/2015	65891
Harpalyce tombadorensis São-Mateus, L.P.Queiroz & D.B.O.S.Cardoso	shrub	Open savanna	2/4/2015	64365
Mimosa kalunga M.F. Simon & C.E. Hughes	shrub	Open savanna	10/10/2013	63932
Mimosa sp nova	shrub	Open savanna	9/2/2014	63775
Mimosa leiocephala Benth.	shrub	Open savanna	9/5/2014	63793
Mimosa gracilis Benth.	forb	Open savanna	9/5/2014	63794
Senna corifolia (Benth.) H.S.Irwin & Barneby	shrub	Open savanna	9/5/2014	63900

Results

Morphology

It was possible to organize the eight species into three groups according to the morphology of their belowground organs: The first group comprised *Mimosa sp nova* and *Mimosa kalunga* (Fig.3 A, H). Species presented a thickened belowground system characterized by a fusiform, highly lignified and tuberized axis. The belowground organ presented a vertical growth. The bark of the belowground systems was scaly, becoming peeling. All the radicular systems were formed by an axial and lateral root. The only aerial stem was formed near the surface of the soil. In the transition zone (root crown) presented itself thick (Fig. 3 A, H), however, there were no found visible buds.

The second group includes the species *Mimosa leiocephala* (Fig. 4 A) and *Senna corifolia* (Fig. 6 A) with tuberized and globose belowground system. The organ showed a uniform connected bark. The radicular system showed thin roots, with low tuberization and from one to four thin aerial branches were connected to the belowground system.

In the third group *Harpalyce tombadoriensis* (Fig. 4 G), *Chamaecrista claussenii* (Fig. 6 F), *Bauhinia dumosa, Mimosa gracilis* (Fig. 5 A; F) presented thickened belowground system with, horizontal growth. The belowground organ was protected by a strong, uniformly connected bark. Also, from two to three aerial stem branches were connected to the belowground organs. The radicular system presented low tuberized roots.

The species of the third group (*Bauhinia dumosa* and *Mimosa gracilis* and *Harpalyce tombadorensis*) and the species of the first group (*Mimosa leiocephala*) presented the large horizontal extension of the belowground system, and had shoots originating in these horizontal structures (Fig. 1).

Besides the characteristics in the paragraphs above, the species belonging of the second and third groups (*Mimosa leiocephala, Senna corifolia, Bauhinia dumosa, Mimosa gracilis, Harpalyce tombadoriensis,* and *Chamaecrista claussenii*) were formed by a strong woody structure.

Furthermore, the morphology analyses evidenced which the buds occupied approximately all the extension of the upper portion of the belowground organs (Fig. 2; 4 A, G; 5 A, F; 6 A, F), and some buds could be found scattered from the organ. These buds were protected by scale leaves and the thick bark (Fig. 2).

Figure 1- A-F- Plants in the field - photography showing shoots and root suckers. A- *Mimosa gracilis*- xylopodium with root suckers; B- *Mimosa kalunga* - resprouts of the basal region*;* C- *Bauhinia dumosa* - xylopodium with root suckers*;* D- *Mimosa leiocephala* - belowground resprouts; E, F- *Harpalyce tombadorensis*, E- Xylopodium with root suckers, F- Xylopodium detail.

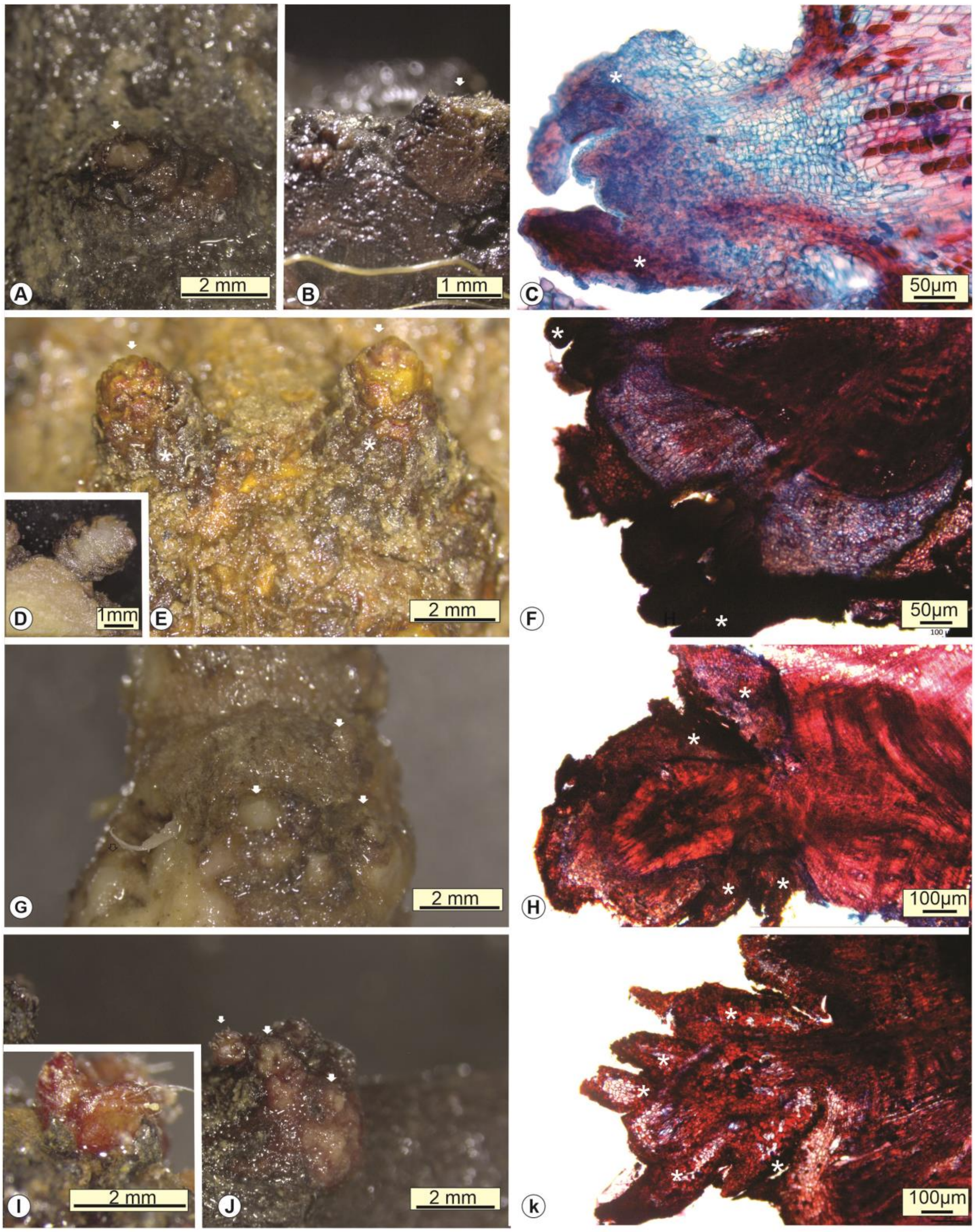

Figure 2- Photography and anatomical sections of the xylopodia buds' A- *Bauhinia dumosa* B- *Chamaecrista claussenii* C- *Senna corifolia* D- F- *Harpalyce tombadorensis G-H Mimosa gracilis I-K Mimosa leiocephala*. Buds (arrows), bud scale leaves (*).

Anatomy

According to anatomical analyses based on Appezzato da Gloria 2015 and Pausas *et al*. 2018, two species (*Mimosa sp. nova* and *Mimosa kalunga*) presented a primary tuber root (taproot tuber) as a belowground storage organ. And the six remaining species were formed by xylopodium (Table 3).

In both species (*Mimosa sp. nova* and *Mimosa kalunga*) the taproot tuber presented root anatomy. The roots showed a well-developed periderm, and the cortex was almost absent. The vascular system was constituted by secondary phloem, vascular cambium, and secondary xylem. In *Mimosa sp. nova* the phloem contained small fiber group scattered among the sieve tube elements and parenchyma cells (Fig. 3E). *Mimosa kalunga* showed multistratified phloem (Fig. 3K**).** In both xylem and phloem tissue there was a high amount of parenchymatic cells.

These organs are mainly single storage structure; nevertheless, the transition zone (root crown) was thick, swollen and it was continuous to the primary tuber root (taproot tuber). Additionally, the transition zone had stem anatomy (Fig. 3D) as a well developed phellem (Fig. 3B) and the buds were not found in the anatomy either.

Regarding to the xylopodia, it had secondary growth and thus was covered with periderm. The vascular cylinder was constituted by secondary phloem, vascular cambium, and secondary xylem. Both the vascular tissues were highly lignified. Additionally, the upper region of these belowground organs was formed by a natural self-grafting bases of stems axes (Fig. 4 M; 5 C, J; 6 I, J). Along the region between two grafted stems sclerenchymatous and parenchymatous tissues were observed filling the xylopodium from the center until the bark. Also, there were portions where the wood xylem tissue was oblique to the transverse plane of the section.

In species *Harpalyce tombadoriensis* (Fig. 4 K, L), *Senna corifolia* and *Chamaecrista claussenii* (Fig. 6 D, I) there were parenchymatic and sclerenchymatic cortex. The phloem contained a small fiber group scattered between the sieve tube elements and parenchymatic cells. In the species *Mimosa leiocephala* and *Bauhinia dumosa* (Fig. 4 B; 5 B) the cortex was absent, and the phloem was multistratified. Besides, in *Mimosa gracilis* (Fig. 5 I) the cortex was absent and the inner portion of the phloem had a fiber cap. All species had phloem with uni or multiseriate parenchyma rays continuous from the xylem to the phloem.

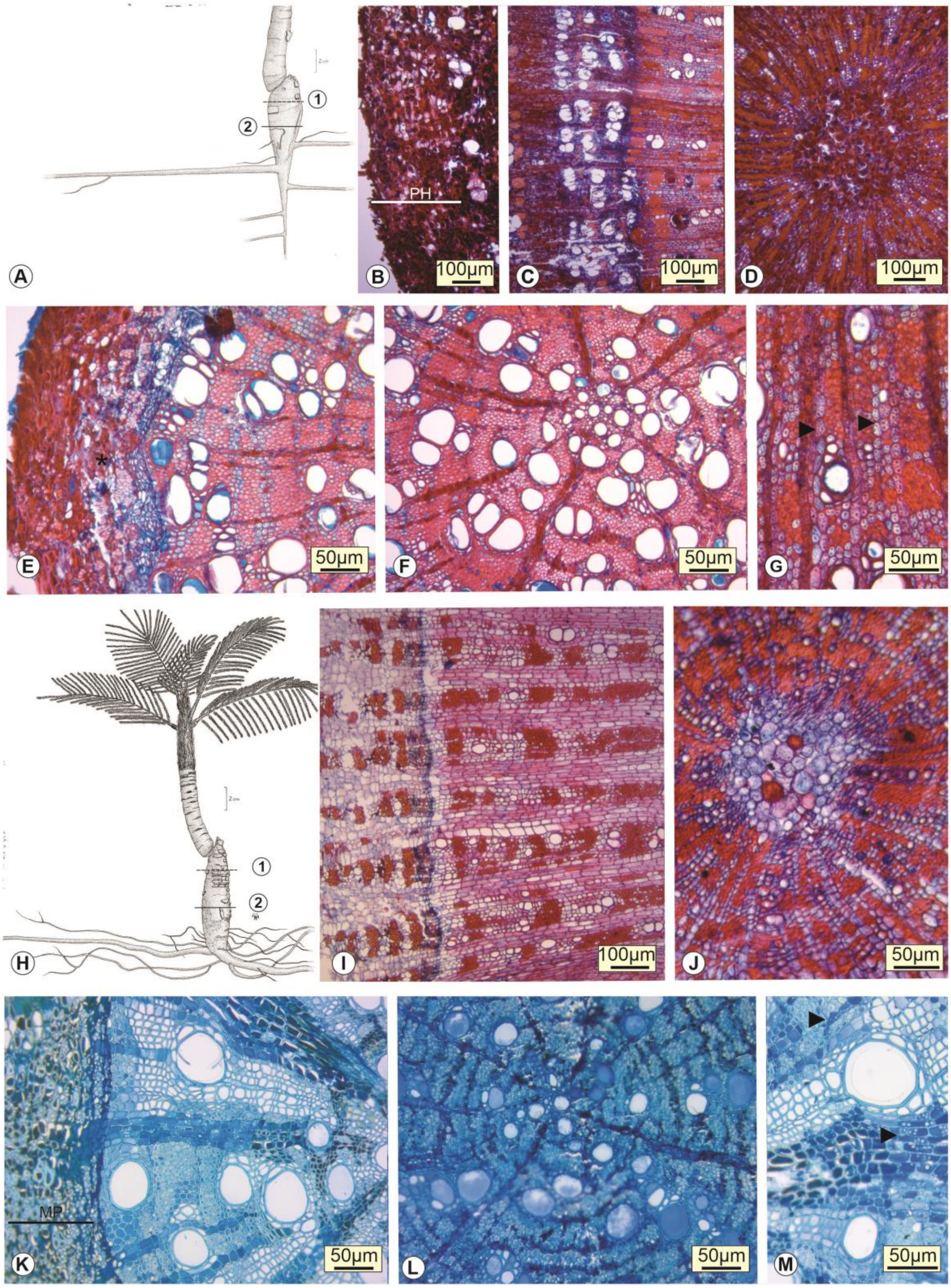

Figure 3- Cross sections of roots and stems A-G Transections of *Mimosa* sp nova A- Entire plant illustration**.** B-D- Stem. E-G Tuberous root (E) Vascular System (F) Polyarch root (G) Starch in the axial and radial parenchyma of the xylem (arrows) H -M - Transections of *Mimosa kalunga* H- Entire plant illustration. I-J- Stem K-M Tuberous root (k) Vascular System (L) Polyarch root (M) Starch in the axial and radial parenchyma of the xylem (arrows). (1)- Transition zone/root crown (2) root. Fiber group (*), multistratified phloem (MP), starch (arrow head).

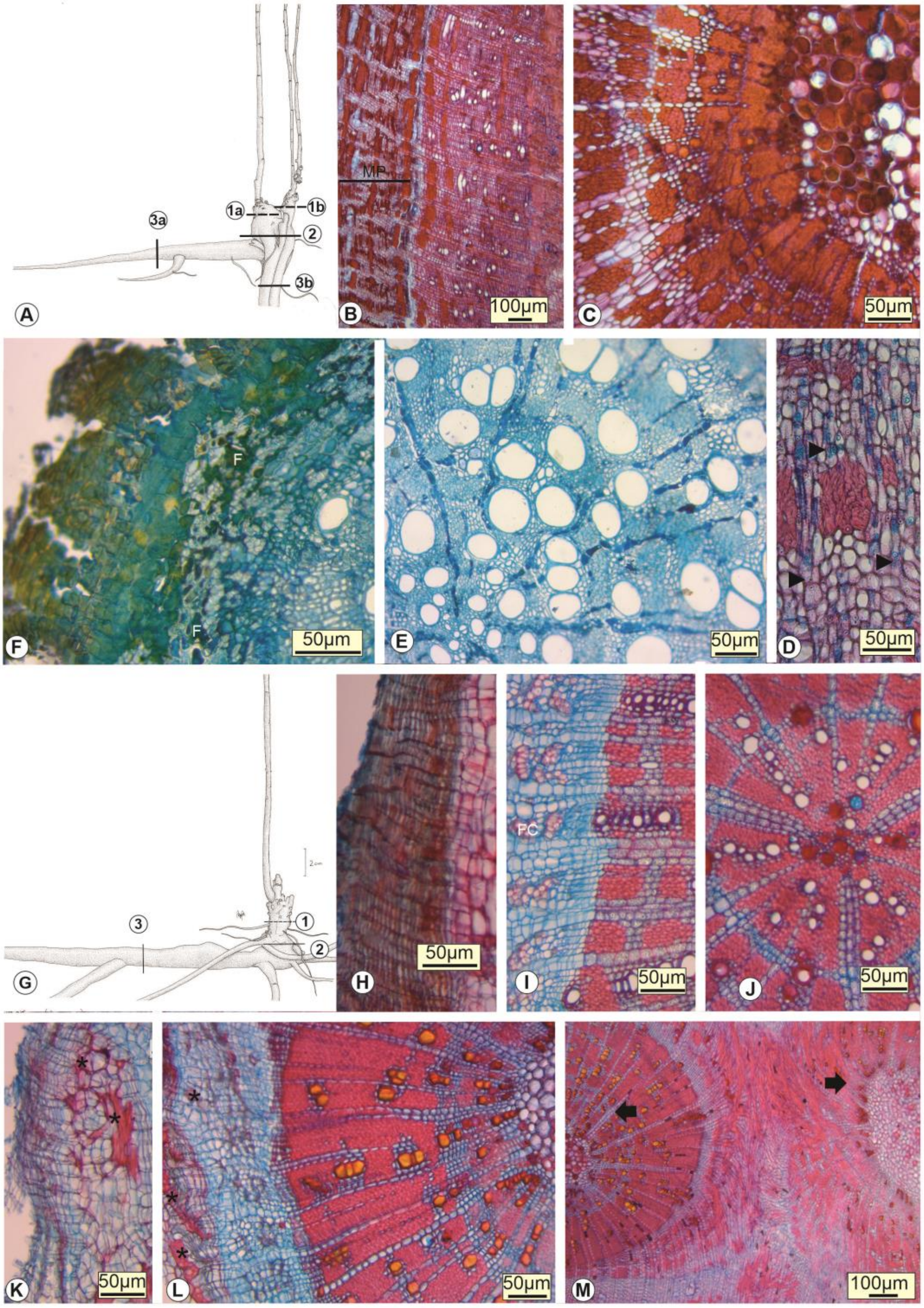

Figure 4- Cross sections of roots and xylopodia A-E Transections of *Mimosa leiocephala.* A- Entire plant illustration. B-D Xylopodium. (B) –Vascular system with multistratified phloem; (C)- Idioblasts and fibers with phenolic compounds (D) Starch in the axial and radial parenchyma of the xylem. E-F Root (E)- Polyarch root (F)- Periderms layers G-M Transections of *Harpalyce tombadorensis*. G-Entire plant illustration. H-J Root (H) Periderms layers (J) Polyarch root K-M Xylopodium. K-Periderms layers and phloem with a small fiber groups (L) Vascular system (M) Natural self-grafted stems (arrows). (1) Bud region - see figure 5, (2) Xylopodium, (3) Root. Starch grains (arrow head), sclerenchyma (*), multistratified phloem (MP), fibers (F).

After xylem analysis, the following species *Mimosa leiocephala, Harpalyce tombadoriensis, Bauhinia dumosa* and *Mimosa gracilis* presented stem anatomy (Fig. 4 C, M; 5 C); demonstrated by the endarch maturation pattern (centrifugal development of xylem), and by a wide central pith. However, in *Senna corifolia* and *Chamaecrista claussenii* because of the high lignification, and the complex tissue growth (Fig. 6), it was not possible to determine the anatomical origin of the organs making it necessary to analyze the ontogenesis.

The xylopodium of *Mimosa leiocephala*, *Harpalyce tombadoriensis* (Fig. 4)*, Senna corifolia*, *Chamaecrista claussenii* (Fig. 6), *Bauhinia dumosa* and *Mimosa gracilis* (Fig. 5), had associated axial tuberous roots, with different tuberization degrees. However, in *Bauhinia dumosa, Mimosa gracilis, Harpalyce tombadorensis* and *Mimosa leiocephala* (Fig. 1) the primary tuber root was associated to lateral root suckers. All roots presented secondary growth, well developed periderm, and low developed phelloderm.

Xylopodia associated to tuberous roots analyses demonstrated that in some roots *Harpalyce tombadoriensis* (Fig. 4 I), *Senna corifolia* and *Chamaecrista claussenii* (Fig. 6. B, G) the secondary phloem presented a small group of fiber scattered between the sieve tube elements and parenchyma cells. In *Bauhinia dumosa* the phloem was multstratified (Fig 5. D). However, *Mimosa leiocephala* (Fig 4.F) and *Mimosa gracilis* (Fig. 5 G) had parenchymatic phloem with scattered fibers. In all species, the protoxylem was polyarchy and had centripetal maturation (exarch xylem). The xylem is formed by highly lignified fibers. Moreover, their vessel elements were single or grouped in the analyzed tissue.

Buds were perfectly found in the anatomic analysis, as well as their protector scale leaves. The buds originated from the phloem region and were located approximately at the same level of xylopodium thick bark. Buds also had a great amount of fibers in all their structure (Fig. 2).

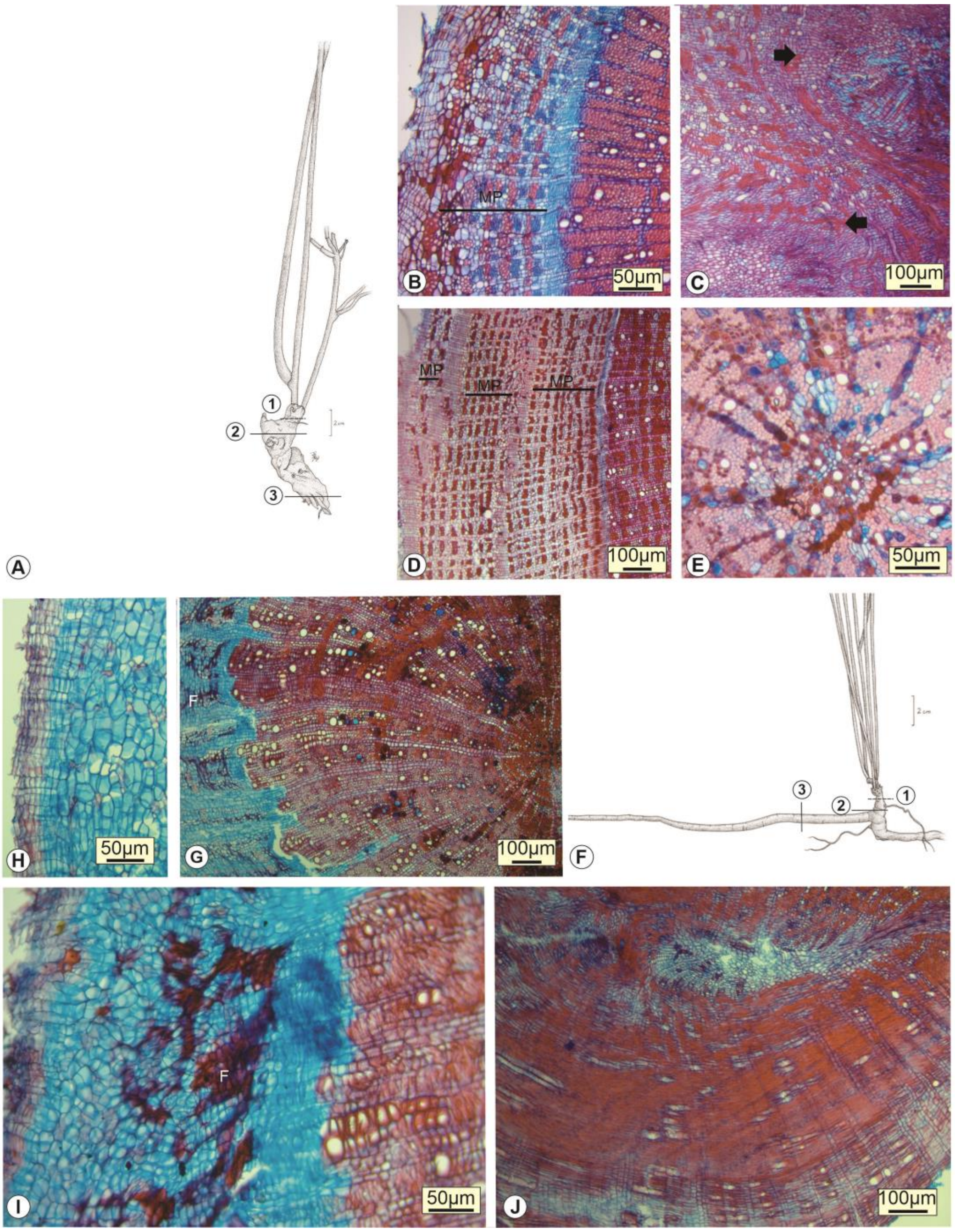

Figure 5- Cross sections of roots and xylopodia. A-E Transections of *Bauhinia dumosa* A- Entire plant illustration. B-C Xylopodium (B) Periderms layers (C) Natural self-grafted stems (arrows) D-E. Root. (D) Many meristematic strips forming interspersed periderms and multistratified phloem (E) Polyarch root F-J Transections of *Mimosa gracilis***.** F- Entire plant illustration. G-H - Root. (G) Polyarch root. (H) Periderms layers I-J Xylopodium (I) Periderms layers, phloem with a small fiber group (J) Stem-like structure. (1)- Bud region - see figure 5, (2) Xylopodium, (3) Root. Multistratified phloem (MP), fibers (F).

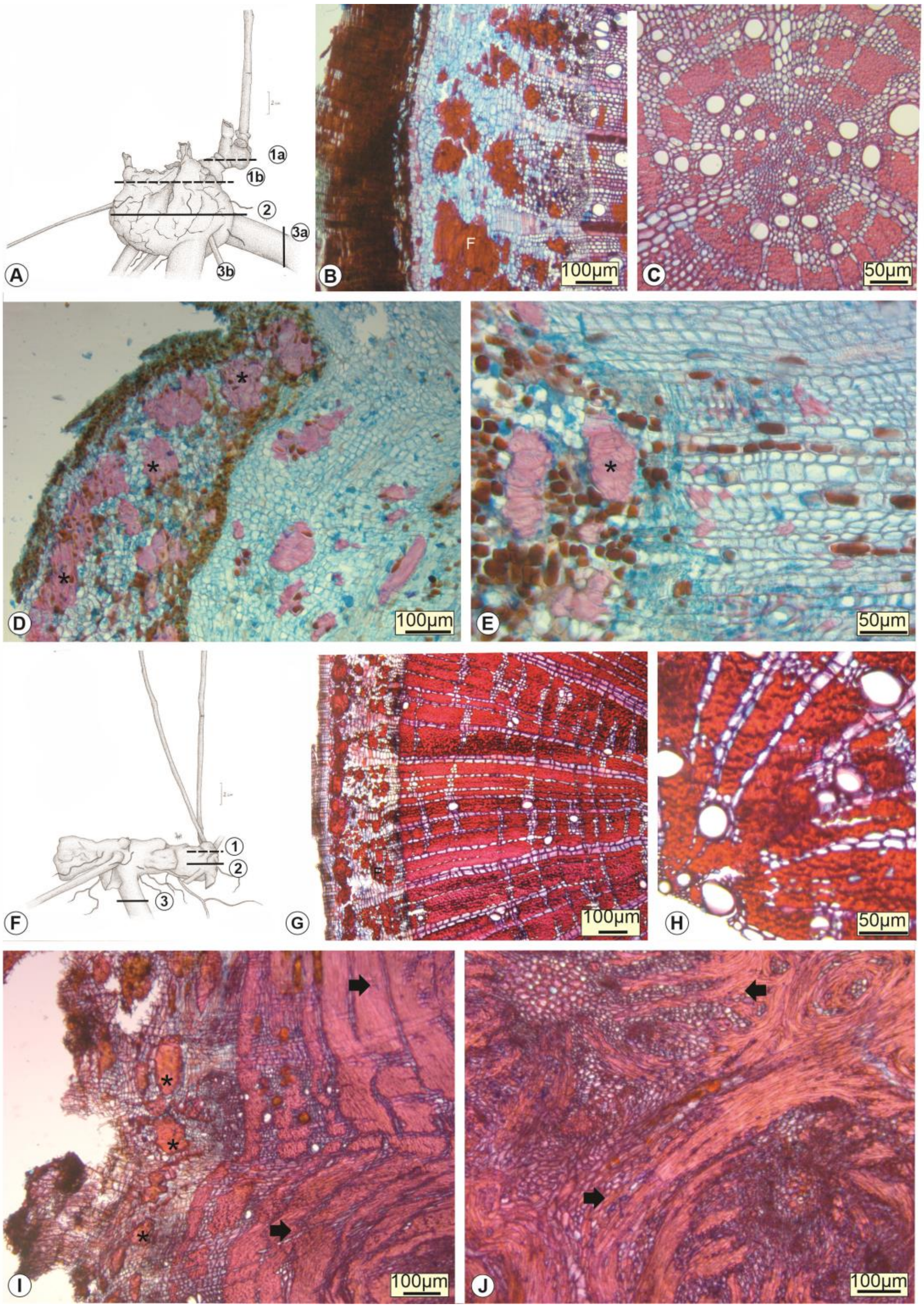

Figure 6- Cross sections of roots and xylopodia A-E Transections of *Senna corifolia* A- Entire plant illustration**.** B-C Root. (B) Periderms layers and phloem with a small fiber group. (C) Polyarch root. D-E Xylopodium**.** (D) Phloem with a small fiber group (E) Phenolic compounds in the parenchyma cells F-J Transections of *Chamaecrista claussenii* F- Entire plant illustration. G-H Root (G) Periderms layers and phloem with small fiber group (H) I-J Xylopodium**.** (I) Phloem with a small fiber groups, and natural self-grafted stems (arrows) (J) Natural self-grafted stem (arrows). (1)- Bud region - see figure 5; (2) Xylopodium; (3) Root. Fibers (F), sclerenchyma (*).

The histochemical tests showed that all the eight plants had abundance of reserve (starch) and defense substances (phenolic compounds). Also, these tests revealed as well as some species presented other defense substances (lipidic substances) that were less abundant (Table 2).

Table 2 - Histochemical test of xylopodia and roots of the studied species - (-) non found compounds.

Species	Organs	Starch(reserve)	Phenolic compounds(defense)	Lipidic substances(defense)
Bauhinia dumosa	**Xylopodium**	Xylem (radial and axial parenchyma)	Xylem (radial and axial parenchyma); phloem(parenchyma); pith; periderm	-
	Root	Xylem (radial and axial parenchyma); phloem(parenchyma)	Xylem (radial and axial parenchyma); phloem (parenchyma)	Phloem(fibers)
Harpalyce brasiliana	**Xylopodium**	Xylem (radial and axial parenchyma)	Parenchymatic rays near the pith	Pith
	Root	Xylem (radial and axial parenchyma); phloem(parenchyma)	Some vessel elements	Periderm
Mimosa gracilis	**Xylopodium**	Xylem (radial and axial parenchyma)	Pith	Periderm
	Root	Xylem (radial and axial parenchyma); phloem(parenchyma)	-	Xylem (radial and axial parenchyma); phloem(parenchyma); periderm
Mimosa leiocephala	**Xylopodium**	phloem(parenchyma)	Xylem (radial and axial parenchyma); pith	Xylem (radial and axial parenchyma); phloem(parenchyma)
	Root	Xylem (radial and axial parenchyma); phloem(parenchyma)	Xylem (radial and axial parenchyma)	Xylem (vessel elements)
Mimosa sp nova	**Root**	Xylem (radial and axial parenchyma)	Xylem (radial and axial parenchyma); phloem(parenchyma); periderm	phloem(parenchyma); periderm
Mimosa kalunga	**Root**	Xilema (Parênquima radial e axial) Floema(parênquima)	Xilema (Parênquima radial e axial)	Periderm
Senna corifolia	**Xylopodium**	Xylem (radial and axial parenchyma)	Xylem (radial and axial parenchyma); phloem(parenchyma)	Phloem(fibers)
	Root	Xylem (radial and axial parenchyma)	Xylem (radial and axial parenchyma)	-
Chamaecrista claussenii	**Xylopodium**	Xylem (radial and axial parenchyma)	Xylem (radial and axial parenchyma)	-
	Root	Xylem (radial and axial parenchyma)	Xylem (radial and axial parenchyma)	Phloem (idioblasts with lipids) Periderm

In regards to species with taproots (Table 2), these organs had idioblasts with defense substances (phenolic compound) among phloematic parenchyma cells. Additionally, other defense substances (lipidic substances) were also found in the phloematic parenchyma in the *Mimosa sp. nova* species and reserve substance (starch) in *Mimosa kalunga.* In both species, the xylem's radial and axial parenchyma cells stored starch (Fig. 3 G, M) and phenolic compounds. Therefore, both plants had reserve and defense substances in the xylem. Additionally, both species exhibited defense substances in the periderm. *Mimosa sp. nova* presented two types of substances (Lipidic substances, and phenolic compounds) and *Mimosa kalunga* exhibited only phenolic compounds.

The histochemical tests showed that xylopodium and the associated tuberous roots had an abundance of phenolic compounds and starch. Also, these tests revealed that some species presented lipidic substances. Starch and phenolic compounds can be stored simultaneously by the xylematic parenchyma in most of species. These substances can also be stored by phloematic parenchyma, and/or the pith. Some species also presented phenolic compounds in the vessel elements. The lipidic substances could be stored by the periderm, xylematic parenchyma, phloematic fibers, phloematic parenchyma, and / or the pith depending on the species and the organ (Table 2).

Discussion

According to the morphoanatomical analysis, the plants belowground organs were classified: two species presented a taproot tuber (Fig. 3; Table 3); six remaining species presented xylopodium (Fig. 4,5,6; Table 3).

Nevertheless, each type of organ and their respective association have a respective function. Consequently, these functions affect the ecologic dynamics of the ecosystem. In regard to the plants with taproots, although these roots don't have buds, they do store reserves in order to support their metabolism. These organs also presented substances that protected against pathogens, which were responsible for maintaining the integrity of the tissue during the entire life cycle of these plants. Additionally, their reserves also serve to maintain the aerial bud bank. The basal resprouting in *Mimosa kalunga* was already registered by (Zupo 2020).

In the taproot the reserves and defense compounds were found in the parenchymatic tissue of the xylem, phloem and cortex. Then, in species with a low cortex/xylem ratio, the xylem presented a parenchyma tissue specialized in storage (Burrows 2016), which is observed in *Mimosa kalunga* that exhibited few vessels with large diameter, and a high amount of parenchyma. It is also present in *Mimosa sp. nova*, however, the parenchyma exhibited a smaller proportion. So, *Mimosa kalunga* and *Mimosa sp. nova* species presented taproot tuber as a belowground storage organ. Therefore, they are characterized as possessing tuberous roots which were swollen structures for the storage of nutritional reserves (Appezzato-da-Glória 2015), named taproot tuber (Pausas *et al.* 2018).

These species also presented a thick root crown region, however, as previously mentioned, the buds were not found in the present study. Additionally, *Mimosa kalunga* were able to resprout after the fire from basal portion (Field observations, Fig. 1 D). Thus, *Mimosa kalunga* was classified as resprouter and heat-tolerant by Zupo, (2020). Despite the buds were not observed in this study, this plant sprout of the base (probably transition zone) at the early stage of development (Leal *et al. in prep*.), besides, the stem characteristic probably protected the aerial buds, through the well-developed phellem already mentioned in the transition zone. Resprouting from the transition zone (root crown) is the most common survival strategy in plants living in fire prone environments; and these plants commonly store starch in the roots when resprouting (Pausas *et al.* 2018). Thus, an example of this wood is Fabaceae species from Chaco vegetation that produce buds below the ground located on the root or root crown region, and the stored reserve of carbohydrate is starch (da Silva *et al.* 2020).

Regarding the species that contained xylopodium, their great resprout potential was characterized by a group of traits which enable the development of a viable bud bank. These characteristics encompass a resistance structure from their external morphology to their anatomy.

These traits also enable the classification of these belowground organs because present features which are typically found in xylopodium, mainly: wood tissue; situated superficially in the soil; high potential for bud formation, and the buds are located mainly in the upper portion of the organ; they have only xylematic parenchyma by reserve; and they are associated with thickened and thin roots. Additionally, they have a complex structure forming the natural self-grafting, and have a complex anatomy having either stem or root anatomy or both (Rachid 1947; Rizzini and Heringer 1961; Paviani 1978; Appezzato-da-Glória and Estelita 2000; Milanez and Moraes-Dallaqua 2003; Alonso and Machado 2007; Appezzato-da-Glória *et al.* 2008; Cury and Appezzato-da-Glória 2009; Appezzato-da-Glória and Cury 2011), and it is commonly found in many genera of Asteraceae and Fabaceae (Pausas *et al.* 2018).

Additionally, the definition xylopodium was primarily described by Lindman (1900) as being a wood belowground system responsible for sprouting after fire, this way reestablishing the aerial parts. Also, it is common in grasslands of the southern part of Brazil and the Cerrado Biome. Regarding the origin, the xylopodia are originated from the hypocotyl and sometimes from the main root (Rizzini and Heringer 1961; Appezzato-da-Glória and Estelita 2000; Appezzato-da-Glória *et al.* 2008)**.**

The xylopodium was composed by a great amount of lignified tissues. That evidences the great capability of resistance of these plants, which is found from the thick bark to the exclerenchymatic tissue among the grafted stems. These lignified tissues protect the parenchyma at the same location which also has phenolic compounds.

All xylopodia in this study were constituted by natural self-grafting bases of stem axes. This characteristic is frequently found in xylopodium (Paviani 1987). Self-grafting is formed in xylopodium when during the life cycle, aerial biomass is damaged by some disturbance such as fire or drought. Thus, the aerial stems are formed due to the repeated sprout, through protected buds below ground (Jeník 1994).

It was observed, along the self-grafting region, obliquely-orientated xylem and parenchymatic xylopodium tissue. The obliquely-orientated xylem was detailed by Palhares et al. (2007). This formation is explained by the radial development of the shoot, for sprouting subsequently (Appezzato-da-Glória and Estelita 2000). In studies about xylopodium ontogeny, it was pointed that the new shoots possibly developed in the parenchymatic tissues or the vascular cambium (Appezzato-da-Glória 2003). Thus, the parenchyma tissue can have the capacity to differentiate in new shoots (Paviani 1987; Appezzato-da-Glória and Estelita 2000). Therefore the natural graft increases the complexity of the organ and maintains the bud bank (Appezzato-da-Glória and Cury 2011).

Because of the strong lignification and robustness presented in *Senna corifolia* and *Chamaecrista claussenii* species, it was not possible to determine the anatomical origins. According to Paviani (1977) the xylopodia structure in *Brasilia sickii* has stem and root anatomical structure, growing in more than one axis of symmetry. This is also caused by the formation of the natural self-grafting (Paviani 1977). Additionally, lignified structure and transitional aspects between stem and root are a typical characteristic of the xylopodia

(Rizzini and Heringer 1961; Rizzini, C. T. & Heringer 1962; Paviani 1977, 1978, 1987). As already mentioned, it is necessary to analyze the ontogenesis of the xylopodium for confirmation of the anatomical origins.

The woody and lignification of the xylopodium is also evidence of the high longevity of these species. Radiocarbon dating techniques to estimate the ages of geoxylic plants have been carried out with a focus on xylopodia, but did not show conclusive ages (Dayaram *et al.* 2020). However, these analyses confirmed that these plants were medium- to long-lived, and showed that they can have ages up to 50 years. This study also opened up new paths for future and more accurate analyses (Dayaram *et al.* 2020). Additionally, plants with high longevity give a long-term ecological service that help with their in populations' persistence and regeneration.

According to Fidelis et al. (2014), a tendency to find a high amount of xylopodium and tuberous roots and sometimes both together in the same structure, has been observed in the areas where frequent fires have occurred, specifically burned grasslands. Rizzini and Heringer (1961) described that xylopodium is an organ with dry and hard consistence constituted by woody tissues, commonly associated with tuberous roots characterized by storage parenchyma. The present study verified the same association (tuberous roots + xylopodium), in which starch is stored in the xylematic parenchyma in xylopodia, and in all parenchymatic tissues in their associated roots.

The presence of starch in the xylopodium is only related to the axial and radial parenchyma of the xylem (Rizzini and Heringer 1961; Paviani 1987), not being described the typical storage parenchyma tissue (Appezzato-da-Glória and Estelita 2000).

The association of the tuberous roots with the xylopodium is probably related to the wood consistence and the bud presence from xylopodium. Thus, the sprout after the fire depends on energy (starch), which is stored mainly by tuberous roots. In contrast, the xylopodium is characterized as a non-storage organ (Rizzini and Heringer 1961; Hayashi and Appezzato-da-Glória 2007; Appezzato-da-Glória *et al.* 2008).

The associated root tuber has the function of supplying the xylopodium with the carbohydrate reserve needed to resprout and maintain the bud bank. Despite the fact that the majority of plants with xylopodium had associated root tuber, only two plants had xylopodium associated tuberous roots that were root suckers. Field observation found clonal propagation in these species (*Bauhinia dumosa, Mimosa gracilis, Harpalyce tombadorensis and Mimosa leiocephala*) (Fig. 1). Anatomical analysis identified the root structure and confirmed that these structures have the ability to resprout through to the root suckers. Furthermore, the presence of the xylopodium in *Bauhinia dumosa* was already register, as well as the presence of the clonal growth. However, in contrast with the present study, it had not been performed the anatomy analysis for confirming the type of the organ and the origin of the clonal growth (da Fonseca Vaz *et al.* 2003).

Some species are able to sprout from roots since the stem was damaged due to the high intensity of the fire (Lacey and Johnston 1990; Castellani and Stubblebine 1993). The roots suckers in *Bauhinia* were already related by Hayashi et al, (2001) in the evaluation of the Atlantic Forest species. According to Hayashi; Appezzato-da-Glória (2009), Pagano and Leitão-Filho (1987), Rodrigues et al. (2004) many Fabaceae species present the root suckers, including *Bauhinia forficate.* Additionally, the formation of the buds in roots was already registered in Asteraceae species (Vilhalva and Appezzato-da-Glória 2006; Appezzato-da-Glória et al. 2008).

Thus, the great advantage of these plants is their strong capacity to resprout due to their resistant xylopodium and their viable bud bank. These plants also have the capacity to spread laterally (through root suckers). Therefore, with their lateral propagation and their high capacity to resprouting, these plants will probably be more resilient after the fire.

These plant species presented starch as a carbohydrate of the reserve, while some plants presented two types of defense substances, such as lipidic substances and phenolic compounds. This refers to plants that presented xylopodium with associated tuberous roots as well as associated root suckers.

All xylopodia analyzed contained phenolic compounds, as found in other studies by (Appezzato-da-Glória and Cury 2011; Ferraro and Scremin-dias 2017). Phenolic compounds in the tissues is associated with the protection against external biotic and abiotic agents (Hutzler *et al.* 1998). Some species can produce and accumulate large amounts of defense substances (Canton *et al.* 2002), such as phenolic compounds (Palhares *et al.* 2007).

Table 3- Review of traits and assigned functions. The number overwritten on traits refer to the corresponding ecological functions.

Species	Organs	Morphological traits	Anatomical traits	Ecological function	Histochemical test and function
Mimosa sp nova ***Mimosa kalunga***	**Taproot**	-Fusiform thickened - Vertical growth - Bark was scaly - Only aerial stem near the soil surface - Transition zone was itself thick - Lateral roots	- Root anatomy - Secondary growth - Well- developed periderm **(1)** - Cortex absent - Xylem and phloem with a high amount of parenchymatic cells **(2)** - Transition zone was itself thick, with stem anatomy **(3)**	**(1)** Protections against fire and herbivory damage **(2)** The parenchyma is specialized in the storage of water and nutritional reserves (B. Appezzato-da-Glória 2015; Burrows 2016) to give the energy to resprouting **(3)** This zone protects the buds to post-fire resprouting	**Starch**: Reserve carbohydrate, that the plants storage for resprouting **Phenolic compounds and Lipidic substances**: Protected stem, Xylopodium, and roots against insect herbivory.
Senna corifolia ***Mimosa leiocephala***	**Xylopodium**	- Tuberized and globose - Uniform connected bark - From one to four aerial branches - Buds in the upper portion -	- Secondary growth; -Buds located at the same level the bark, protected by scale leaves, and had a great amount of fibers **(1.1)**; - Well- developed periderm **(2)**; - Highly lignified vascular tissues **(3)**; - Upper region with natural self-grafting bases of stems axes **(4)**; - Parenchymatous tissues from the center until the bark **(5)**; - *S. corifolia* and *C. claussenii* was not possible to determine the anatomical origin **(6)**; - The remaining species had stem anatomy **(7)**; - Lateral root suckers associated with the Xylopodium of *B. dumosa, M. gracilis, and M. leiocephala, Harpalice tombadorensis* **(8)***;*	**(1)** and **(1.1)** The bud bank of these species was well – developed. Was located in the soil line, and was protected by bark, scale leaves and fibers. These traits protect the buds against fire and herbivory damage; **(2)** Protect the buds and tissue damage; **(3)** Tissues protection against fire and herbivory damage; **(4)**, **(5)** The self-grafted stem shows that these plants already resprouting many times, and the parenchymatic tissues between the grafted stems show the high potential of bud production because the parenchyma have dedifferentiation ability; **(6)**, **(7)** These plants have high longevity, and after a determined amount of time the lignification increase, and the self-grafted stem are merged, turned impossible to determine the origin. The plants as stem anatomy origin probably are very early that these species before cited;	
	Root	-Roots, with low tuberization	- Roots with secondary growth; - Well developed periderm in roots **(9)**	**(8)** The clonal propagation associated with xylopodium already mentioned by Rizzinii, 1961, and can strongly increase the survival and persistence of these plants. **(9)** Protection against pathogen attack and water lost.	
Harpalyce tombadorensis ***Chamaecrista claussenii*** ***Mimosa gracilis*** ***Bauhinia dumosa***	**Xylopodium**	-Horizontal growth; - Uniform connected bark; - Buds in the upper portion **(1)**			
	Root	- Low tuberized root			

Conclusions

The xylopodium has an important persistence strategy, in which its morphological and anatomical traits enable plants to persist after a fire. Thus, besides the strong capacity of these plants to resprout and/or their associated root suckers to propagate laterally, the plants of this study have protection against pathogens, through the protective compounds such as phenolic compounds and lipidic substances. In some plants, the protection begins in the bark and can continue until the pith, protecting the entire organ.

According to Coutinho, (2002) this belowground organ is considered as an organ of resistance to severe conditions of the Cerrado, such as drought and fire. This happens because the xylopodia have a lignified structure with potential of bud formation (Rizzini and Heringer 1961). The resprout capacity after fire is commonly seen in Cerrado species (Simon *et al.* 2009; Simon and Pennington 2012) mainly due to xylopodia (Rizzini and Heringer 1961; Rizzini and Heringer 1962; Appezzato-da-Glória *et al.* 2008; Pausas *et al.* 2018), guaranteeing the persistence of plant populations in the area after disturbance events (Appezzato-da-Glória, 2015).

Consequently, the understanding of xylopodia traits and their functions, provides better insights about population and community dynamics. Therefore, xylopodium and its associated tuberous roots present two kinds of cooperative defense compounds with a great amount of storage. It enables the formation of a viable bud bank, in which in spite of the presence of defense compounds, the buds are still protected by bark and scale leaves. Furthermore, some xylopodia presented associated root suckers which enabled the vegetative propagation of these species, having more chances of survival before and after fire. Enabling the persistence of these plants in the ecosystems.

Some plants were classified as xylopodium based on a great amount of morphoanatomical traits similar to those required to name these organs, even though an ontogenetic analyses needs to be carried out for better identification (Appezzato-da-Glória, 2015). However, the present study did a through morphoanatomical analyses that did enable this classification. In addition, grouping traits based on similarities can help other ecologic studies to identify these structures. Regarding the xylopodia associated with root suckers, the clonal growth was already mentioned in (Rizzini and Heringer 1961; Pausas *et al.* 2018), as an important competitive advantage in which the same plants have lateral spread and resprouting in their respective organs.

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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.