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Morpho-anatomical features of underground systems in six Asteraceae species from the Brazilian Cerrado

BEATRIZ APPEZZATO-DA-GLÓRIA[1] **and GRAZIELA CURY**[2]

[1]Departamento de Ciências Biológicas, Escola Superior de Agricultura 'Luiz de Queiroz',
Universidade de São Paulo, Caixa Postal 09, 13418-900 Piracicaba, SP, Brasil
[2]Departamento de Botânica, Instituto de Biociências, Universidade de São Paulo,
Rua do Matão, 277, Cidade Universitária, Butantã, 05508-090 São Paulo, SP, Brasil

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ABSTRACT

In the Brazilian Cerrado (neotropical savanna), the development of bud-bearing underground systems as adaptive structures to fire and dry periods can comprise an important source of buds for this ecosystem, as already demonstrated in the Brazilian *Campos* grasslands and North American prairies. Asteraceae species from both woody and herbaceous strata have subterranean organs that accumulate carbohydrates, reinforcing the adaptive strategy of these plants to different environmental conditions. This study aims to analyse the morpho-anatomy of underground systems of six species of Asteraceae (*Mikania cordifolia* L.f. Willd., *Mikania sessilifolia* DC, *Trixis nobilis* (Vell.) Katinas, *Pterocaulon alopecuroides* (Lam.) DC., *Vernonia elegans* Gardner and *Vernonia megapotamica* Spreng.), to describe these structures and to verify the occurrence and origin of shoot buds, and to analyse the presence of reserve substances. Individuals sampled in Cerrado areas in São Paulo State showed thick underground bud-bearing organs, with adventitious or lateral roots and presence of fructans. Xylopodium was found in all studied species, except for *Trixis nobilis*, which had stem tuber. The presence of fructans as reserve, and the capacity of structures in the formation of buds indicate the potential of herbaceous species of Asteraceae in forming a viable bud bank for vegetation regeneration in the Brazilian Cerrado.

Key words: anatomy, buds, Compositae, fructans, stem tuber, xylopodium.

INTRODUCTION

The Cerrado vegetation is composed of a mosaic with different physiognomies due to distinct factors, such as deep and well drained soils that are acidic and with high aluminium content, seasonality, with dry periods of 3-4 months, and fire (Coutinho 1982). Species from the herbaceous strata are dominant in open physiognomies ("campos", grasslands). Plants have seasonal growth: the aboveground biomass dies during autumn, and these species persist as thick underground systems (Filgueiras 2002). During spring and the beginning of rainy season, individuals rapidly resprout and flower using the reserves stored in the underground structures. Alonso and Machado (2007) and Appezzato-da-Glória et al. (2008a) suggested that bud-bearing underground systems could contribute to the formation of a belowground bud bank in the Cerrado. Bud bank was first described by Harper (1977), and its concept was expanded by Klimesova and Klimes (2007). It comprises all buds from plants, which can be potentially used for vegetative regeneration by the formation of new shoots after the partial or total removal of aboveground parts caused by extreme climatic factors as drought or fire. Recently, the importance of underground systems of the bud bank for the regeneration of vegetation after disturbance and on the maintenance of plant populations were de-

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Correspondence to: Beatriz Appezzato-da-Glória
E-mail: bagloria@esalq.usp.br

scribed by some authors for the subtropical grasslands in Southern Brazil ("Campos grasslands" by Fidelis 2008) and the North American prairies (Benson et al. 2004, Dalgleish 2007).

Among the different types of underground systems found in the Cerrado, some can be classified as xylopodium (Hayashi and Appezzato-da-Glória 2007, Appezzato-da-Glória et al. 2008a), tuberous roots, stemlike or radicular difuse system (Alonso and Machado 2007) and rhizophores (Hayashi and Appezzato-da-Glória 2005). The presence of such organs can influence the population dynamics of plant species, since they are able to produce new shoots after the removal of aboveground biomass. According to Kauffman et al. (1994), fire can stimulate the formation of new shoots from buds located in underground organs in the Cerrado, being thus an important trait for plant persistence after disturbance events (Soares et al. 2006). Recurrent fires can favour especially species with higher capacity of resprouting. After fires, there is an increase in number of species resprouting from buds located in underground organs after the death of aboveground biomass, confirming thus the importance of such bud-bearing organs (Medeiros and Miranda 2008, Fidelis 2008).

Verdaguer and Ojeda (2005) associated the importance of the bud bank and the carbohydrate reserves. Reserves of carbohydrates decreased in underground organs during the resprouting phase, as observed by Carvalho and Dietrich (1993) and Portes and Carvalho (2006). According to Hoffmann (1999), in woody species of Cerrado, plants invest in carbohydrates accumulation in underground storage organs, which allow them to rapidly recover after biomass loss caused by fire and assuring, thus, their survival.

Asteraceae plays an important role on the herbaceous and woody vegetation of Cerrado (Almeida et al. 2005). Several species have thick underground structures with storage reserves, mostly fructans, and a high capacity of bud formation (Tertuliano and Figueiredo-Ribeiro 1993). Fructans are not only sources of carbon, but they also play an important role for plants in environments with water restriction due to their rapid polymerization and depolymerization reactions involved in osmoregulation processes (Nelson and Spollen 1987, Pontis 1989, Hendry 1993, Figueiredo-Ribeiro 1993, Talbott and Zeiger 1998, Orthen 2001).

Therefore, this study aims to analyse the underground systems of six species of Asteraceae (*Mikania cordifolia* L.f. Willd., *Mikania sessilifolia* DC, *Trixis nobilis* (Vell.) Katinas, *Pterocaulon alopecuroides* (Lam.) DC., *Vernonia elegans* Gardner and *Vernonia megapotamica* Spreng.) describing their different structural types, verifying the occurrence and origin of shoot buds and, finally, analyzing the presence of reserve substances.

MATERIALS AND METHODS

The species of this study (*Mikania cordifolia*, *Mikania sessilifolia*, *Trixis nobilis*, *Pterocaulon alopecuroides*, *Vernonia elegans* and *Vernonia megapotamica*) were selected from surveys in the state of São Paulo (Tertuliano and Figueiredo-Ribeiro 1993, Katinas 1996, Almeida et al. 2005, Ishara et al. 2008), and the criteria of selection was analyzing species of the same genera (in the case of *Mikania* and *Vernonia*) and among different genera (*Mikania*, *Pterocaulon*, *Vernonia* and *Trixis*), and compare the subterranean systems types among them. Adult individuals were collected in natural populations in areas of Cerrado located in Botucatu (22°53″S, 8°29″W) and Itirapina (22°13″S, 47°54″W), São Paulo State, Brazil, where Asteraceae is well represented. The vouchers of the specimens (88792, 88791, 92159, 88790, 88787 and 88789, respectively) are deposited in the ESA Herbarium, Brazil.

For the anatomical study, underground systems of three adult plants were fixed in FAA 50 (1 part formaldehyde: 1 part glacial acetic acid: 18 parts 50% ethanol, v/v) for 48 h (Johansen 1940), dehydrated in a graded ethylic series and infiltrated in glycol methacrylate resin (Leica Historesin-Leica^{TM} – Wetzlar, Germany). Serial sections (5-7μm thick) were performed on a rotary microtome and stained with toluidine blue O (Sakai 1973). Freehand cross-sections were also cut and stained with astra blue and basic fuchsin and, subsequently, dehydrated in a graded ethylic series, and 50 and 100% butyl acetate, respectively. Permanent slides were embedded in synthetic resin. The presence of phenolic compounds was investigated in sections from fresh or plastic resin-embedded samples using ferric trichloride (Johansen 1940).

TABLE I
Subterranean type, shoot bud origin and presence of fructans in subterranean systems of six selected species of Asteraceae from the Cerrado. Negative signs indicate the absence of fructans.

Species	Subterranean system type	Shoot bud origin	Fructans	
			Subterranean system	Root
Mikania cordifolia	Xylopodium and adventitious roots	Cambium	—	Xylem parenchyma ray
Mikania sessilifolia	Xylopodium and adventitious roots	Cambium	—	Cortical parenchyma
Trixis nobilis	Stem tuber and adventitious roots	Axillary	Cortical parenchyma	Medullary and cortical parenchyma
Pterocaulon alopecuroides	Xylopodium and lateral roots	Cambium	Cortical parenchyma	—
Vernonia elegans	Xylopodium and adventitious roots	Cambium	—	Cortical parenchyma
Vernonia megapotamica	Xylopodium and adventitious roots	Axillary	—	Medullary and cortical parenchyma

To identify the fructans of the inulin-type, samples of subterranean structures were fixed in 70% ethanol and sectioned by freehand. Inulin crystals were visualised under polarised light, and the presence of these crystals was confirmed by a treatment with thymol-sulphuric acid reagent (Johansen 1940).

Photomicrographs were taken with a Nikon Labophot microscope or a Nikon SMZ-2T stereomicroscope. The images were digitally captured with a Leica DMLB microscope (Leica^{TM} – Wetzlar, Germany) by using a video camera plugged to a computer utilising the IM50 (Leica^{TM} – Wetzlar, Germany) software for image analysis.

RESULTS

All studied species (Fig. 1a-h) had thickened and bud-bearing underground systems (Table I), with or without thickened roots. Additionally, all species accumulated fructans of inulin-type in the parenchyma of adventitious roots (Fig. 2a), except for *Trixis nobilis*, which also showed fructan accumulation in the thickened underground structure, and *Pterocaulon alopecuroides*, which accumulates only in the thickened underground structure (Table I).

Based on our anatomical study, we classified *T. nobilis* as a stem tuber (Fig. 1e), and the thickened woody axis of underground systems of *M. cordifolia*, *M. sessilifolia*, *P. alopecuroides*, *V. elegans* and *V. megapotamica* as a xylopodium (Fig. 1b-d, 1f-h).

The size and shape of xylopodia varied among species (Fig. 1), but a common feature is the self-grafting of the stems basis formed in different development periods (Fig. 2b, 3a, b). Buds could be found spread all over the structure, protected by cataphylls (Fig. 2c), or they were concentrated in the median part of the organ in *Pterocaulon alopecuroides*. Buds originating from the cambium of xylopodia could be observed in *M. cordifolia*, *M. sessilifolia*, *P. alopecuroides* and *V. elegans* (Fig. 3d, e). Buds located at the upper portion of the stem tuber of *Trixis nobilis* and on the xylopodium of *Vernonia megapotamica* were axillaries (Fig. 3a, c).

The xylopodia of *M. cordifolia*, *M. sessilifolia*, *V. elegans* and *V. megapotamica* were of stem-like origin, which was confirmed by the centrifugal development of the primary xylem (Fig. 3f). The xylopodium of *Pterocaulon alopecuroides*, on the other hand, was a radicular structure (Fig. 3g).

In all xylopodia analysed, the 2-4 cortical parenchyma cell layers containing phenolic compounds functioned as a protective tissue (Fig. 4a). The cover tissue of stem tuber of *Trixis nobilis* consisted of epidermis

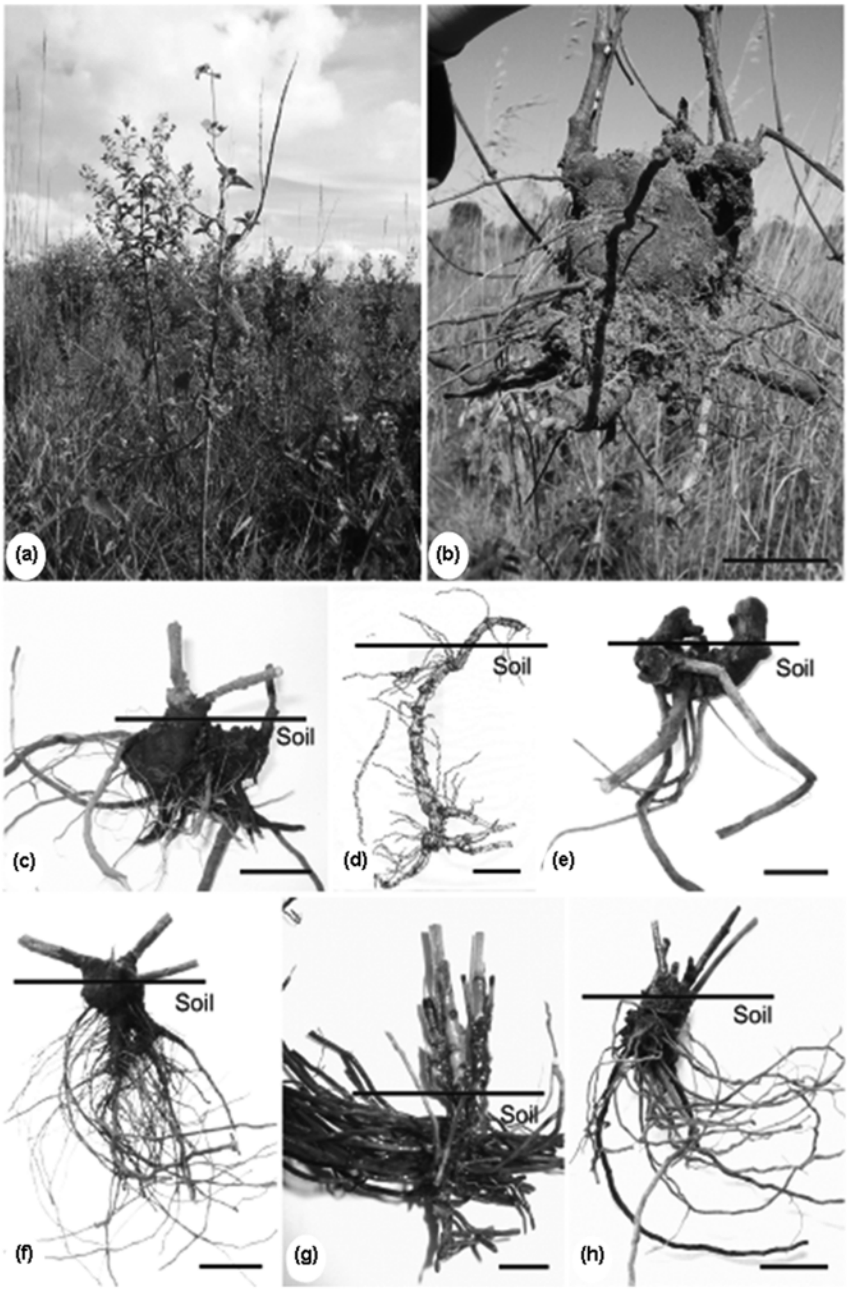

Fig. 1 – Adult plant of *Mikania cordifolia* L.f. Willd. in its natural habitat (a). General view of the subterranean systems (b-h). *M. cordifolia* (b-c). *Mikania sessilifolia* DC (d). *Trixis nobilis* (Vell.) Katinas (e). *Pterocaulon alopecuroides* (Lam.) DC (f). *Vernonia megapotamica* Spreng (g). *Vernonia elegans* Gardner (h). Bars = 5 cm (b); 3 cm; (c); 7 cm (d); 2.5 cm (e, f); 1 cm (g); 2 cm (h).

with stomata and trichomes (Fig. 4b). Brachisclereids in the cortex could be observed in all the studie species. In *Vernonia elegans* and *V. megapotamica*, prismatic crystals were found in the brachisclereids (Fig. 4c). The underground stem-like axis of *Trixis nobilis* showed cortical vascular bundles (Fig. 4d).

Mikania cordifolia, the only liana species (Fig. 1a), had a xylopodium with vascular cylinder characterised by the formation of successive layers of secondary phloem, cambium and secondary xylem, with abundant conjunctive tissue (Fig. 5a, c). *Mikania sessilifolia* and the other studied species, which are plants with erect

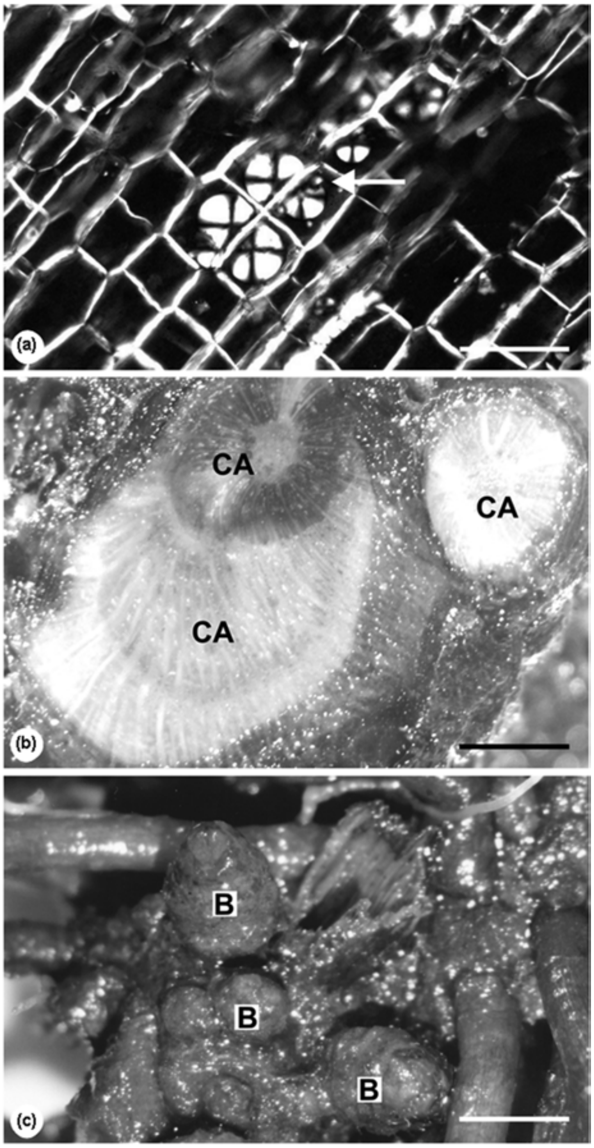

Fig. 2 – *Vernonia megapotamica* Spreng. Distribution of spherocrystals of inulin (arrow) in parenchyma cells of reserve tissues in the transection of a root (a). Frontal view of the natural self-grafting of the stem-like axis (CA) of xylopodium (b). Shoot buds (B) of the xylopodium (c). Bars = 100 μm (a); 2.7 mm (b, c).

habitus, showed vascular cylinders with secondary phloem, cambium and secondary xylem (Fig. 5b).

DISCUSSION

The presence of thickened and bud-bearing underground systems, distributed superficially in the driest portion of the soil in the Cerrado, verified in all studied species, indicates their importance in storing water and nutrients needed for aboveground sprouting during the rainy season (Rizzini and Heringer 1961, Appezzato-da-Glória et al. 2008a). In the Cerrado species, the importance of fructan reserves in underground structures, as verified in the studied species, is mostly related to regeneration processes of aboveground biomass, flowering and plant resistance against water loss (Figueiredo-Ribeiro 1993, Portes and Carvalho 2006, Itaya et al. 2007). Dias-Tagliacozzo et al. (2004) demonstrated that the resistance of *Vernonia herbacea* (Vell.) Rusby (Asteraceae) to water deficit is regarded to alterations

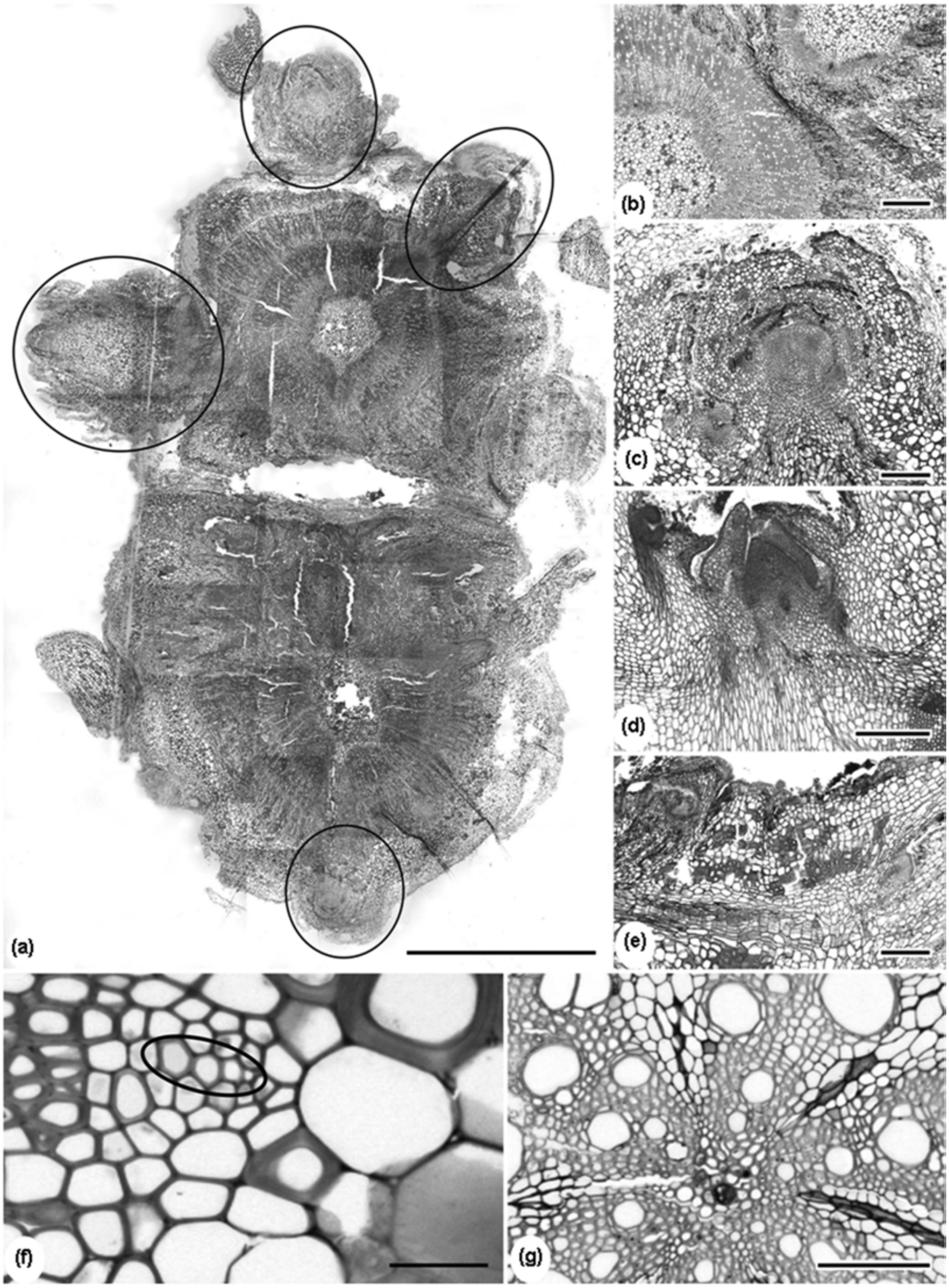

Fig. 3 – Transections of the xylopodium of *Vernonia megapotamica* Spreng (a-c). Four axillary buds are indicated by circles (a). Natural self-grafting of the stem-like axis (b). Detail of the axillary bud (c). Transections of the xylopodia showing adventitious buds originated from the cambium (d-e). *Pterocaulon alopecuroides* (Lam.) DC (d). *Mikania cordifolia* L.f. Willd (e). Centrifugal maturation of the protoxylem pole (indicated) in *Mikania sessilifolia* DC (f). Transection of the xylopodia of *P. alopecuroides* with metaxylem elements in the center of the organ (g). Bars = 3 mm (a); 400 μm (b,c); 300 μm (d); 200 μm (e); 50 μm (f, g).

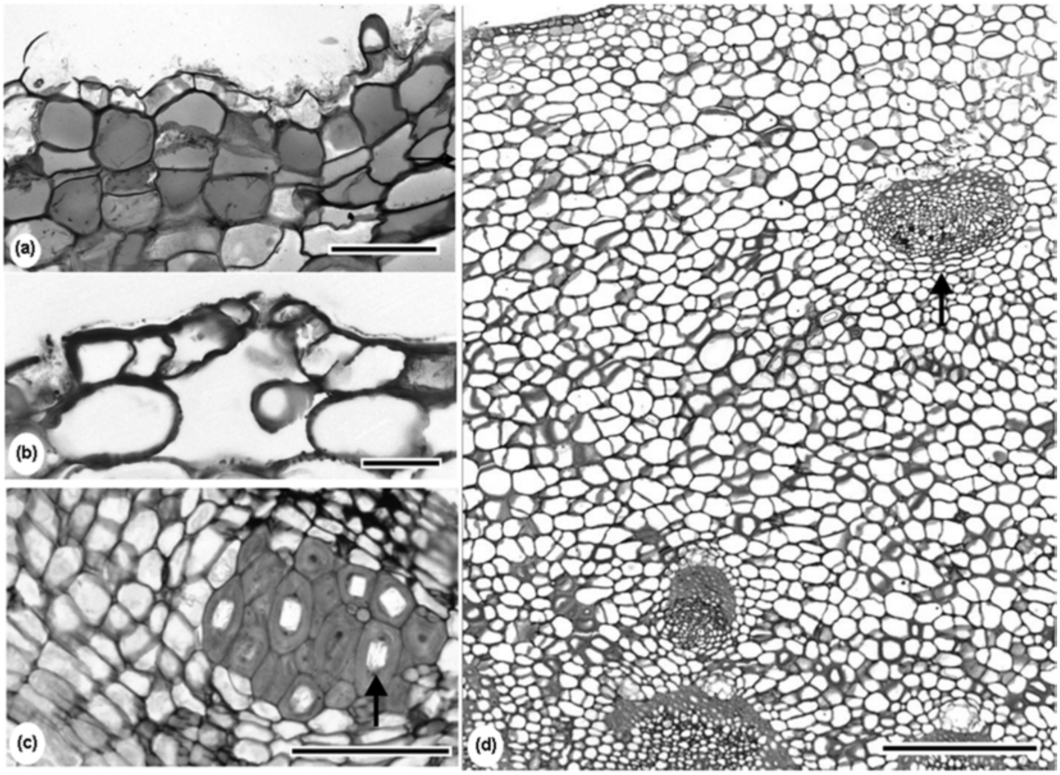

Fig. 4 – Stem tuber of *Trixis nobilis* (Vell.) Katinas with protective tissue constituted by cortical parenchyma cell layers containing phenolic compounds (a) and epidermis with stoma (b). Brachisclereids with prismatic crystals (arrow) in the *Vernonia elegans* Gardner xylopodium (c). Cortical vascular bundle (arrow) of the *T. nobilis* stem tuber (d). Bars = 100μm (a, c); 50 μm (b); 400 μm (d).

in the metabolism of fructans, which favoured the water retention in the rhizophores. In experiments carried out with *Viguiera discolor* Baker (Asteraceae), Isejima et al. (1991) pointed out that flowering induced individuals to produce a higher content of fructans in tuberous roots than in control plants. Carvalho and Dietrich (1993) also verified that *Vernonia herbacea*, during the vegetative and dormant phases, achieved the highest levels of fructan concentration in underground organs. On the other hand, during the flowering and sprouting phases, the levels of fructan decreased (Figueiredo-Ribeiro et al. 1991).

Xylopodium, as described here for most species, is a common underground organ, being found in more than 90 genera in some Brazilian Biomes (Appezzato-da-Glória et al. 2008a). This structure was described by Lindman (1900) for an underground system that is very common in grasslands of the southern part of Brazil and in the Cerrado Biome, and found more often in plants in areas under frequent influence of fires than in excluded ones (Fidelis 2008). According to Rizzini (1965), it is a perennial thickened woody organ with numerous buds and high resprout capacity, formed from tuberisation of the hypocotyl or the root-stem transition region and of the proximal portion of the main root. Its structure, ontogenesis and ecological function do not found correspondence with previously subterranean structures described in the international literature, but this term is already accepted by Botanists from other countries who had the opportunity to study Brazilian vegetation, and some Brazilian authors have already employed the term in other studies (Alonso and Machado 2007, Appezzato-da-Glória et al. 2008a, Cury and Appezzato-da-Glória 2009). The variation of the xylopodium size and shape verified in the present study was already mentioned by Appezzato-da-Glória et al. (2008a) for Asteraceae species of the Cerrado. Xylopodium buds of cambial origin, as observed in *M. cordifolia*, *M. sessilifolia*,

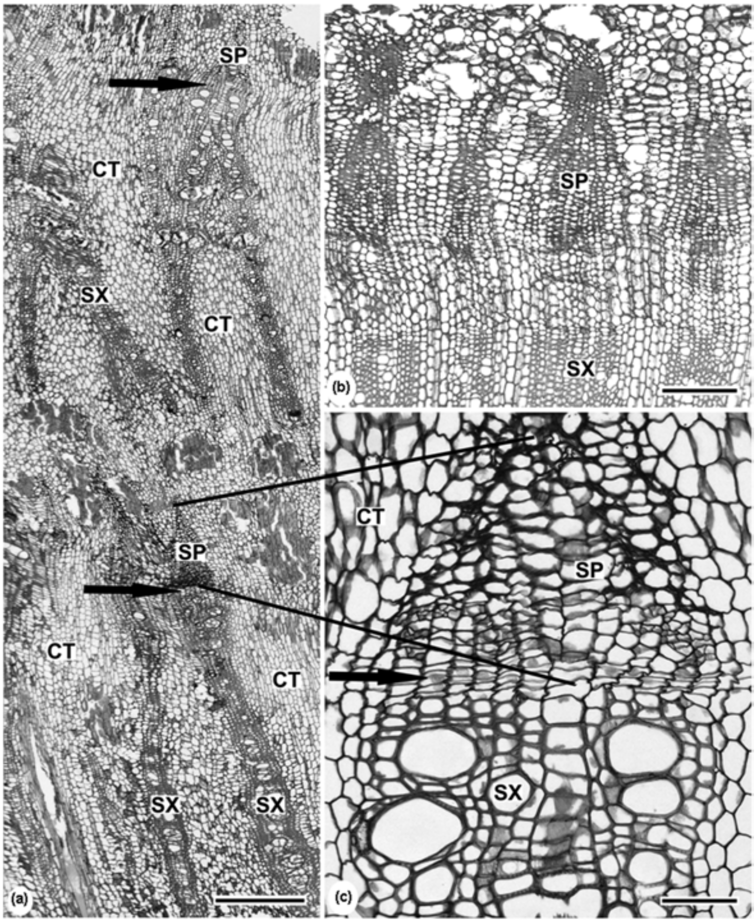

Fig. 5 – Transections of the xylopodium of *Mikania cordifolia* L.f (a, c). Willd. and *Mikania sessilifolia* DC (b). Vascular cylinder with successive layers of secondary phloem (SP), cambium (arrows) and secondary xylem (SX), with abundant conjunctive tissue (CT) (a). Vascular cylinder with secondary phloem (SP), cambium and secondary xylem (SX) (b). Detail of the figure (a) (c). Bars = 400 μm (a,b); 100 μm (c).

P. alopecuroides and *V. elegans*, was also reported by Vilhalva and Appezzato-da-Glória (2006) and Appezzato-da-Glória et al. (2008a). Plants with the presence of xylopodia showed seasonal growth and, besides the loss of aboveground biomass during the dry season or destruction caused by e.g. fire, the bases of aboveground shoots and their buds persisted. Therefore, at the upper portion of the xylopodia, stems formed in different development periods naturally graft; moreover, in this portion, buds are axillary like in *Vernonia megapotamica*. The production of stems periodically leading to the formation of a self-grafting structure on the bases of the stem axes is a common feature for xylopodia (Paviani 1987). This phenomenon increases the complexity of this organ and the number of available buds for sprouting. Therefore, xylopodia play an important role on the survival and regeneration of the Cerrado species, bearing several viable buds for plant resprouting after disturbance events.

The anatomical structure of xylopodia can be radicular, stem-like or both, depending on the analysed species (Appezzato-da-Glória et al. 2008a). The stem-like origin of xylopodium, as described in *M. cordifolia*, *M. sessilifolia*, *V. elegans* and *V. mepapotamica*, has already been observed for some other species, such as *Isostigma megapotamicum* (Spreng.) Sherff (Asteraceae) (Vilhalva and Appezzato-da-Glória 2006); radicular origin, as described in *Pterocaulon alopecuroides*, was observed for *Clitoria guyanensis* (Aubl.) Benth (Leguminosae) (Rizzini and Heringer 1961). The protective tissue, constituted by parenchyma cells filled with phenolic compounds, found in all xylopodia analysed, was also described in rhizomes of *Rhaponticum carthamoides* (Asteraceae) by Lotocka and Geszprych (2004). The presence of phenols in these layers is related to the protection against external biotic and abiotic agents (Hutzler et al. 1998). The covering tissue of stem tuber of *Trixis nobilis* consisted of epidermis with stomata and trichomes. Such traits were also described for rhizophores of *Smilax quinquenervia* Vell. (Smilacaceae) by Andreata and Menezes (1999), *Vernonia herbacea* and *V. platensis* (Hayashi and Appezzato-da-Glória 2005), and *Orthoppapus angustifolius* (Appezzato-da-Glória et al. 2008b). As already proposed by Andreata and Menezes (1999), the presence of stomata and trichomes, including secretory trichomes (Appezzato-da-Glória et al. 2008b) in underground stem-like systems, suggests the evolution of these stems from an aerial ancestral structure.

Brachysclereids present in the cortex of all studies species regards the sclerophylly common in the Cerrado plants (Rizzini 1997).

Cortical vascular bundles in the underground stem-like axis of *Trixis nobilis* (analysed in this study) and *Ianthoppapus corymbosus* (Melo-de-Pinna and Menezes 2002) confirm the observations from Metcalfe and Chalk (1950) about the occurrence of this kind of vascular tissues in Asteraceae and the tribe Mutisieae.

The anomalous secondary thickening verified in *Mikania cordifolia* has already been described by Solereder (1908) and Metcalfe and Chalk (1950) for other liana stems of *Mikania*. It can be considered as another structural trait from aerial systems, which has been conserved in underground organs. Adamson (1934) described the lignified shoots of small shrubs of different genera of Inulaea and the cambium of pericyclic origin, producing phloem and xylem. The author suggested that this kind of anomalous secondary growth should have developed from plants with herbaceous growth form. On the other hand, *Mikania sessilifolia*, with erect habitus, showed vascular cylinders with secondary phloem, cambium and secondary xylem.

As a conclusion, the formation of aerial shoots from buds located in underground structures associated to the accumulation of fructans reinforces the importance of a viable belowground bud bank for the persistence of forb and subshrub species in grassland physiognomies of the Brazilian Cerrado. It is important to point out the importance of bud-bearing structures in ecosystems under fire influence, such as the rhizomes in tallgrass prairies (Benson et al. 2004), lignotubers in Australia, South Africa and California (Klimesova and Klimes 2007), and the presence of different underground structures (e.g. xylopodia and rhizophores) in the Brazilian *Campos* grasslands (Fidelis 2008), since they contain the buds and reserve substances needed for vegetation regeneration.

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RESUMO

No Cerrado brasileiro (savana neotropical), o desenvolvimento de sistemas subterrâneos que produzem gemas, como estruturas adaptativas contra o fogo e períodos de seca, pode compreender um importante suprimento de gemas para esse ecossistema, como já demonstrado nos campos brasileiros e nas pradarias norte-americanas. Espécies de Asteraceae tanto do estrato lenhoso, quanto do herbáceo têm órgãos que acumulam carboidratos, reforçando a estratégia adaptativa dessas plantas a diferentes condições ambientais. Este estudo tem o objetivo de analisar a morfo-anatomia de sistemas subterrâneos de seis espécies de Asteraceae (*Mikania cordifolia* L.f. Willd., *Mikania sessilifolia* DC, *Trixis nobilis* (Vell.) Katinas, *Pterocaulon alopecuroides* (Lam.) DC., *Vernonia elegans* Gardner e *Vernonia megapotamica* Spreng.), para descrever essas estruturas e verificar a ocorrência e origem de gemas caulinares, e analisar a presença de substâncias de reserva. Indivíduos amostrados em áreas de Cerrado no Estado de São Paulo apresentaram órgãos subterrâneos espessados produtores de gemas, com raízes adventícias ou laterais e presença de frutanos. Em todas as espécies estudadas foi constatada a presença de xilopódio, com exceção de *Trixis nobilis*, a qual apresentou caule tuberoso. A presença de frutanos como reserva e a capacidade de estruturas na formação de gemas indicam o potencial de espécies herbáceas de Asteraceae em formar um banco de gemas viável para regeneração da vegetação no Cerrado brasileiro.

Palavras-chave: anatomia, gemas, Compositae, frutanos, caule tuberoso, xilopódio.

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