

## Underground systems of Asteraceae species from the Brazilian Cerrado<sup>1</sup>

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APPEZZATO-DA-GLÓRIA, B., G. CURY, AND M.K.M. SOARES (Departamento de Ciências Biológicas, ESALQ, Universidade de São Paulo, 13418-900, Piracicaba, SP, Brazil), R. ROCHA (Universidade Estadual de Mato Grosso do Sul, 79804-970, Dourados, MS, Brazil), AND A. H. HAYASHI (Seção de Anatomia e Morfologia, Instituto de Botânica, 01061-970, São Paulo, SP, Brazil). *J. Torrey Bot. Soc.* 135: 103–113. 2008.—Underground systems of Asteraceae species from the Brazilian Cerrado. The aim of this study was to describe the underground systems structure, the origin of the shoot buds, and to identify the storage reserve of seven Asteraceae species in order to understand the adaptive strategies of these species in burned Cerrado areas and their higher frequency in the floristic surveys for herbaceous and undershrub layers of this biome. The subterranean systems types—diffuse underground system, rhizophore, tuberous roots, and xylopodium—varied among the studied species, but all of them have high shoot bud-forming potential. Fructans of the inulin type were detected as storage substances. The presence of these characteristics on the underground systems could explain the frequency of these species in the floristic surveys from the Brazilian Cerrado, in which fire and seasonal drought are frequent. It is possible that the belowground bud banks in the Cerrado biome are as important as demonstrated in North American prairies where fire is also frequent. However, in the Cerrado, as demonstrated here, there are types of underground systems other than rhizomes that are usually described in the prairie. Understanding the anatomical features of these plants is one of the steps to appropriate conservation management of these species in the Cerrado.

Key words: anatomy, Brazilian savannas, buds, roots, xylopodium.

Brazilian Cerrado is a mosaic of natural physiognomies varying from open fields (campos limpos), savanna fields (campos sujos, campos cerrados, and cerrados sensu stricto) and woodlands (cerradões) (Coutinho 1990). More than 71% of the live phytomass (aboveground biomass + root biomass) is belowground in the Brazilian Cerrado (Castro and Kauffman 1998). Total belowground biomass has been reported as 16.3 mg ha<sup>-1</sup> in campo limpo, 30.1 mg ha<sup>-1</sup> in campo sujo, 46.5 mg ha<sup>-1</sup> in cerrado aberto, and 52.9 mg ha<sup>-1</sup> in cerrado denso. This quantity of belowground biomass is similar to, or exceeds that, reported for many tropical dry and moist forests (Castro and Kauffman 1998).

Several herbaceous and undershrub species of the Cerrado biome have thickened underground systems (Rizzini and Heringer 1961, Hayashi and Appezzato-da-Glória 2005). These species usually enter dormancy at the end of autumn, with senescence and abscission of the aerial organs, and sprout in the following spring; flowering occurs subsequently followed by a period of vegetative growth in the summer (Figueiredo-Ribeiro et al. 1986). Pate et al. (1990) showed that a wide range of fire-resprouter species from Australia had high starch concentration and swollen organs belowground. In a number of Asteraceae species from the Cerrado, where prolonged drought, nutrient availability, and frequent fires have been pointed out as important factors on the survival and growth of plants in this biome (Ratter et al. 1997), fructans have been found to be the main reserve in underground organs (Figueiredo-Ribeiro et al. 1986). Fructans have an important role as reserve carbohydrates and are involved in a number of adaptive strategies in plants sub-

<sup>1</sup> This work was supported by Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP grant number 2000/06422-4).

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Received for publication October 30, 2007, and in revised form, December 10, 2007.

Table 1. Studied species, tribe, locality, and date of collection and accession number in UEC and ESA Herbaria, Brazil.

Species	Tribe	Locality of collection	Date of collection	Accession number
<i>Chromolaena squalida</i> (DC.) K&R	Eupatorieae	Mogi Guaçu	01/03/2001	UEC 118440
<i>Gyptis lanigera</i> (Hook. & Arn.) R.M.King & H.Rob.	Eupatorieae	Botucatu	18/03/2005	ESA 94509
<i>Pterocaulon angustifolium</i> DC.	Plucheeae	Botucatu	26/01/2005	ESA 88783
<i>Chresta sphaerocephala</i> DC.	Vernonieae	Botucatu	11/05/2005	ESA 94508
<i>Lessingianthus bardanoides</i> (Less.) H.Rob.	Vernonieae	Itirapina	29/01/2003	ESA 84369
<i>Lessingianthus glabratus</i> (Less.) H.Rob.	Vernonieae	Itirapina	24/01/2003	ESA 84368
<i>Orthopappus angustifolius</i> (Sw.) Gleason	Vernonieae	Itirapina	24/01/2005	ESA 88782

jected to drought or cold (Figueiredo-Ribeiro et al. 1991).

After the Leguminosae, Asteraceae has the most species represented in the Brazilian Cerrado (Mendonça et al. 1998). Almeida et al. (2005) studied eight Cerrado fragments in the State of São Paulo (Brazil) from 2000 to 2002 to produce an inventory of Asteraceae species. Their species list was then compared to 24 other Cerrado species list in the literature. The most frequent species are *Chresta sphaerocephala* DC., *Chromolaena squalida* (DC.) K&R, *Lessingianthus bardanoides* (Less.) H.Rob., *Orthopappus angustifolius* (Sw.) Gleason, and *Piptocarpha rotundifolia* Baker (Almeida et al. 2005). It is possible that this higher frequency is related to the presence of belowground buds in the Cerrado as demonstrated in species of North American prairies (Benson et al. 2004). However, in the Cerrado biome, there are types of underground systems other than rhizomes described from prairies. The terminology of these belowground structures is also different and it is presented here.

The objective of the present work was to describe the underground systems structure, the origin of shoot buds, and to identify the storage reserve of seven Asteraceae species, including those species mentioned above (except for *Piptocarpha rotundifolia*, which was already described by Achutti, 1978), in order to understand the adaptive strategies of these species in burned Cerrado areas and their higher frequency in those floristic surveys. The importance of this study is based on the fact that the belowground biomass in the Cerrado soils must be considered in global change studies, especially when analyzing the carbon cycle, since Cerrados are the ecosystem mostly affected by Brazilian agricultural expansion—losing an estimated 34,000 km<sup>2</sup> area

every year (Delitti et al. 2001). It is postulated that plants in the herbaceous and subshrub layers are probably more sensitive to anthropogenic disturbances than trees in Cerrados. Therefore, plants in those categories may be used as a parameter to assess the level of human intervention in Cerrado ecosystems (Filgueiras 2002).

**Materials and Methods.** Adult plant material of seven Asteraceae species were collected in natural populations from the campos sujos Brazilian Cerrado physiognomy of the State of São Paulo (Table 1).

For the anatomical study, underground systems of five adult plants were fixed in FAA 50 (formalin-acetic acid-alcohol) (Johansen 1940), dehydrated in a graded ethylic series and then infiltrated in glycol methacrylate resin. Serial sections (5–7 µm thick) were cut 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 then dehydrated in a graded ethylic series, and 50 and 100% butyl acetate, respectively. Permanent slides were mounted in synthetic resin.

To identify the fructans of the inulin type, samples of the subterranean systems were fixed in 70% ethanol and sectioned by freehand. Inulin crystals were visualised under polarized 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. Images were captured digitally through a Leica DMLB microscope with a video camera attached to a PC, using IM50 image analysis software.

Table 2. Presence of fructans as detected by histological tests in subterranean systems of seven selected species of Asteraceae from the Cerrado.

Species	Subterranean system type	Fructans*
<i>Chromolaena squalida</i> (DC.) K&R	xylopodium with adventitious roots	–
<i>Gyptis lanigera</i> (Hook. & Arn.) R.M.King & H.Rob.	Moniliform tuberous root	+
<i>Pterocaulon angustifolium</i> DC.	xylopodium with adventitious roots	+
<i>Chresta sphaerocephala</i> DC.	diffuse underground system	+
<i>Lessingianthus bardanoides</i> (Less.) H. Rob.	xylopodium with adventitious roots	+
<i>Lessingianthus glabratus</i> (Less.) H.Rob.	xylopodium with adventitious roots	+
<i>Orthopappus angustifolius</i> (Sw.) Gleason	rhizophore with adventitious roots	+

\* + and – signs indicate the presence or absence of fructans in roots, respectively.

**Results.** All studied Asteraceae species (Table 2) have subterranean systems (Figs. 1–5, 7, 9) which can vary among the species even in the same tribe.

Some of them have unusual underground systems and their terminology is different to what is applied in other ecosystems, such as diffuse underground systems, rhizophores, and xylopodium (Table 2).

*Chromolaena squalida* (Fig. 1), *Lessingianthus bardanoides* (Fig. 2), *L. glabratus* (Fig. 3), and *Pterocaulon angustifolium* (Fig. 9) have xylopodium that is situated superficially in the driest portion of the soil (Figs. 1–3, 9). The xylopodium is very lignified, it has high shoot bud-forming potential (Fig. 10) and its structure is complex due to self-grafting of the stems (Figs. 11–12) produced periodically. The xylopodium exhibit caulinar and radicular structure as verified in *Pterocaulon angustifolium* (Figs. 13–15) and *Chromolaena squalida*. There is an association between xylopodium and thickened roots in *Lessingianthus bardanoides* and *L. glabratus* (Figs. 2–3) and *Pterocaulon angustifolium* (Fig. 9). The thickened roots can have a great amount of fructans in *Lessingianthus bardanoides*, *L. glabratus*, and *P. angustifolium*, while the xylopodium does not exhibit any type of carbohydrate reserves. The thickened subterranean system of *Orthopappus angustifolius* is a rhizophore (Fig. 4). Rhizophores constitute an underground cauline system (Fig. 16) in plants that have bipolar cauline ramification system. *Gyptis lanigera* has moniliform tuberous root (Fig. 5) as underground organ. The cambial activity leads to the production of secondary vascular tissues with large amounts of parenchyma cells (Fig. 17). *Chresta sphaerocephala* has aerial stems (Fig. 6) produced by a diffuse underground system (Fig. 7) of radicular structure (Fig. 18). There are remaining carbonized bases of some branches

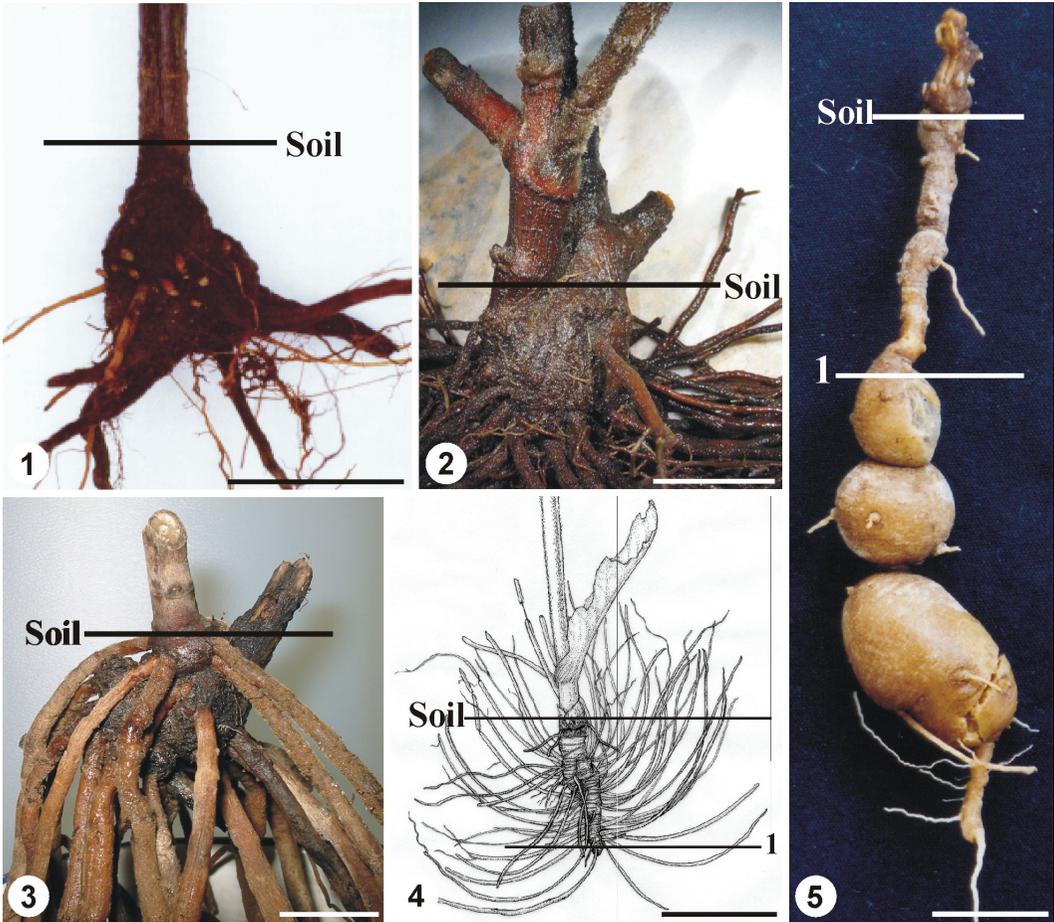
emitted in previous periods from the underground system (Fig. 8).

All the studied species form shoot buds in the thickened underground systems (Figs. 19–26). Two types of buds are found in *Chresta sphaerocephala* roots (Figs. 19–20). One of them is not connected with the vasculature of its parent roots (Fig. 19) while the other one produces bud traces in the secondary xylem (Fig. 20) indicating its origin at the beginning of the root development.

In tuberous roots, the adventitious buds of *Gyptis lanigera* originate close to the cambium (Fig. 21). In the xylopodium, they originate from the cambium (*Chromolaena squalida* and *Pterocaulon angustifolium*) (Fig. 22–23) or the pericycle (*Lessingianthus bardanoides*); in *Lessingianthus glabratus*, there are axillary buds (Fig. 24). In the *Orthopappus angustifolius* rhizophore, the axillary buds and the bud gap reaches the pith (Fig. 25).

All analyzed species accumulate fructans of the inulin type in the cortical parenchyma of lateral or adventitious roots (Fig. 26) produced by the subterranean systems, except for *Chromolaena squalida*.

**Discussion.** Xylopodium, as described in *Chromolaena squalida*, *Lessingianthus bardanoides*, *L. glabratus*, and *Pterocaulon angustifolium*, is one of the main types of subterranean systems found in geophytes from Brazilian open grasslands areas. Xylopodium was first described by Lindman (1900) for plants with woody subterranean systems whose aerial parts are herbaceous or very slightly woody and die back each year (or they frequently are burned off) leaving an underground woody system. The renewal buds can originate from the cambium (*Chromolaena squalida* and *Pterocaulon angustifolium*), from the pericycle (*Lessingianthus bardanoides*), from the parenchyma proliferation (Paviani

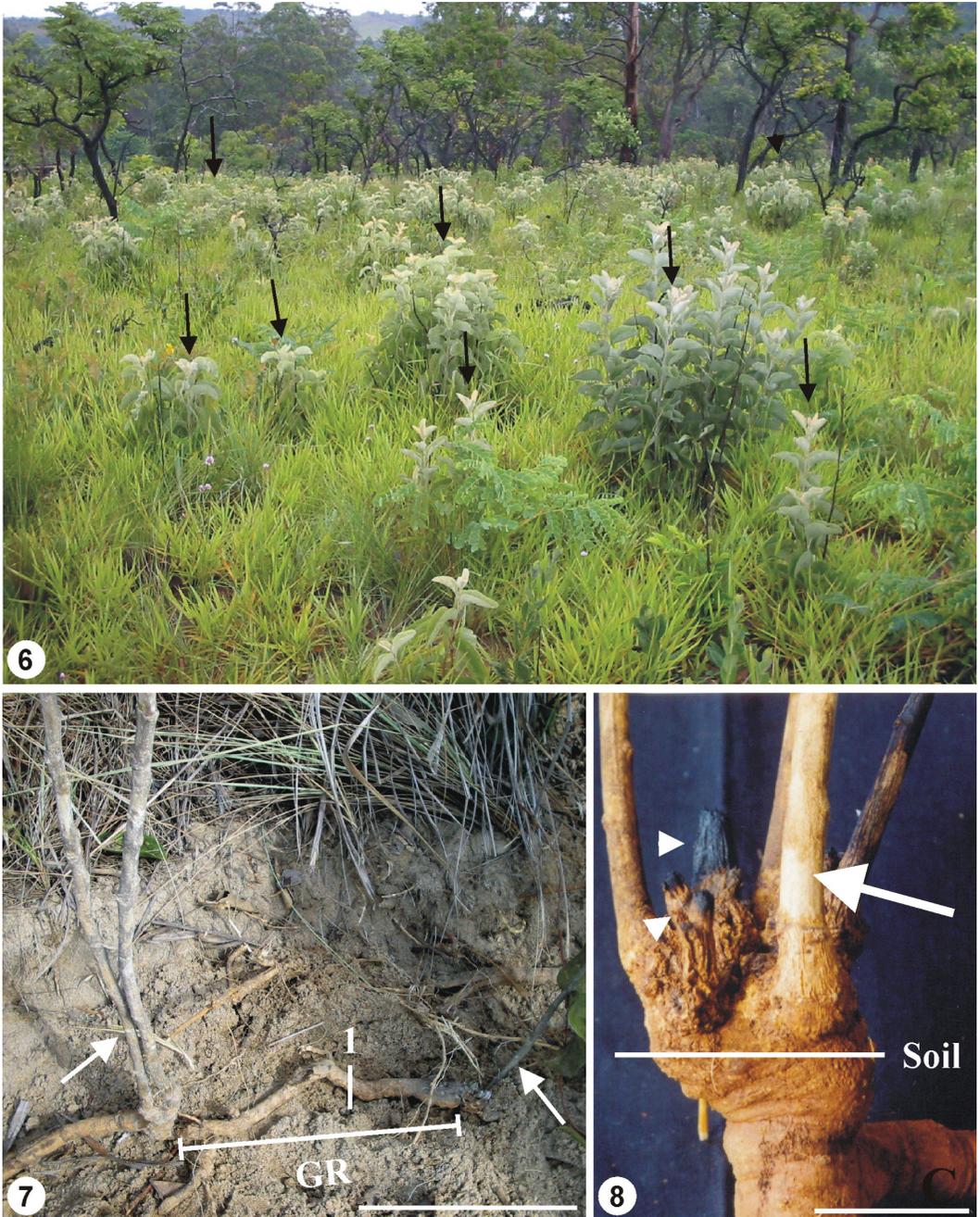


FIGS. 1–5. General view of the subterranean systems. 1. *Chromolaena squalida* (DC.) K&R. 2. *Lessingianthus bardanoides* (Less.) H. Rob. 3. *Lessingianthus glabratus* (Less.) H. Rob. 4. *Orthopappus angustifolius* (Sw.) Gleason. 5. *Gyptis lanigera* (Hook. & Arn.) R.M. King & H. Rob. Level 1 of Figs. 4 and 5 indicate the transections shown in Figs. 16 and 17. Scale bars = 5 cm (Fig. 1), 2 cm (Figs. 2, 3, 5), and 4 cm (Fig. 4).

1987, Hayashi and Appezzato-da-Glória 2007), or they are axillary buds (*Lessingianthus glabratus*). The xylopodium buds are just below the soil surface as a rule, but they are very irregularly placed and the general form of the aerial growth of branches varies considerably. These woody organs are different to those described as lignotubers by Kerr (1925). Unlike xylopodia, lignotubers arise from cotyledonary, and a few succeeding nodes on the primary seedling stems, or even from their accessory buds (Carr et al. 1982). They are storage organs with a supply of bark-suppressed buds (Kerr 1925) or epicormic strands (Burrows 2002). Xylopodium originates from the hypocotyl and exhibits caulinar and radicular structure (Paviani 1987) as verified

in *Vernonia grandiflora* (Hayashi and Appezzato-da-Glória 2007) and in our study in *Pterocaulon angustifolium* and *Chromolaena squalida*. Therefore, they differ from lignotubers in their origin, structure, and renewal buds origin.

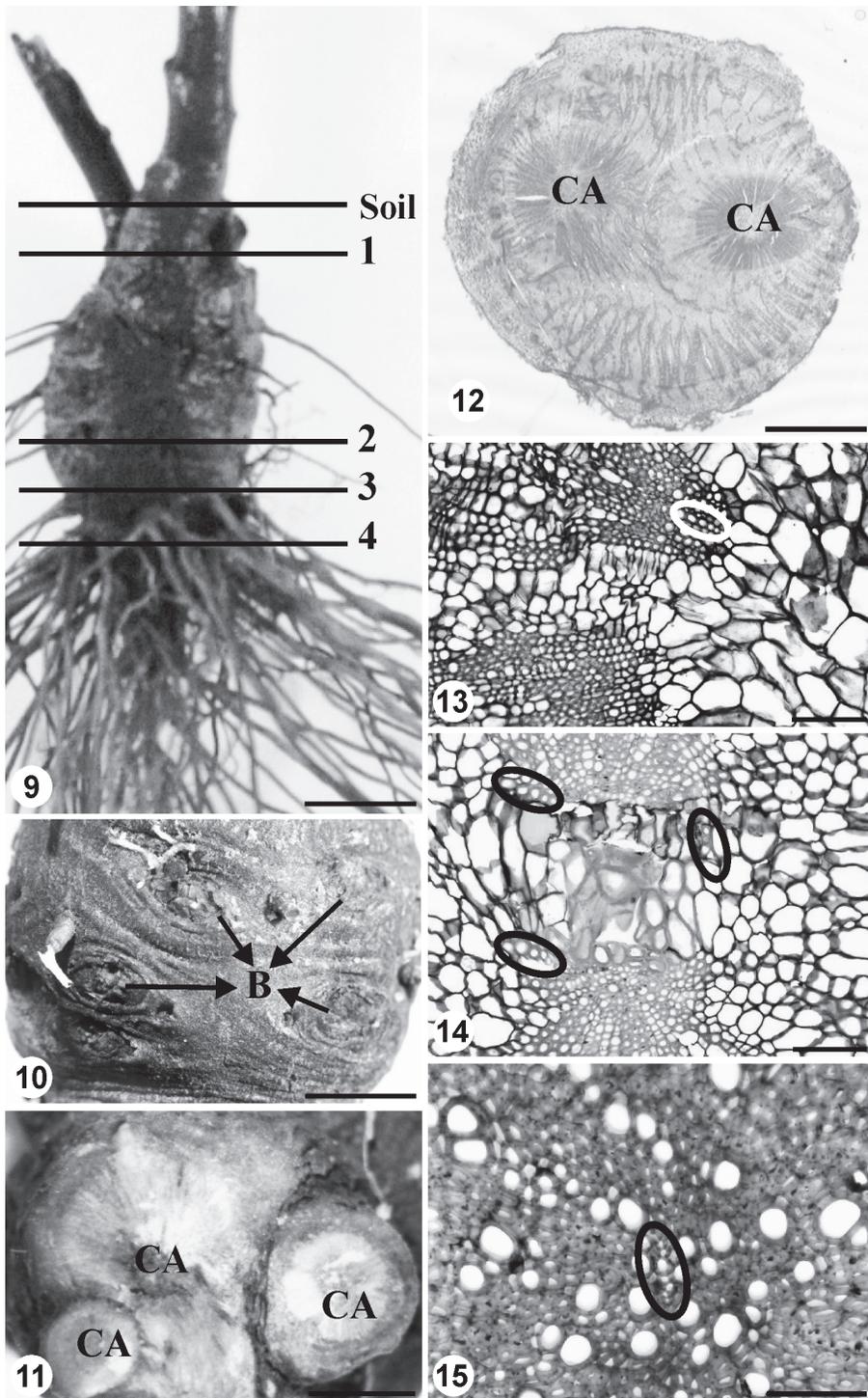
All studied xylopodia lose their aerial stems during the dry season (from May to September) and resprout during the rainy season (from October to April). Fire can burn the aerial stems causing new resprouting from the xylopodium. Rizzini and Heringer (1961, 1962) have already mentioned the shoot bud-forming potential of xylopodium and its function on plant survival under severe conditions of Cerrado (dry seasons associated with fire). The crucial role of the bud bank in



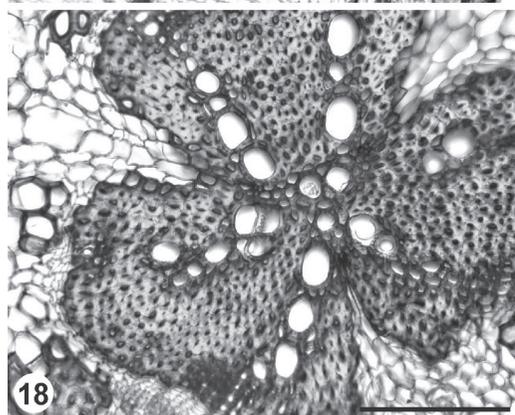
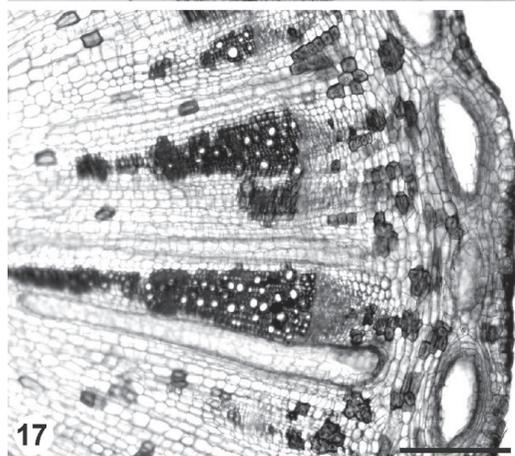
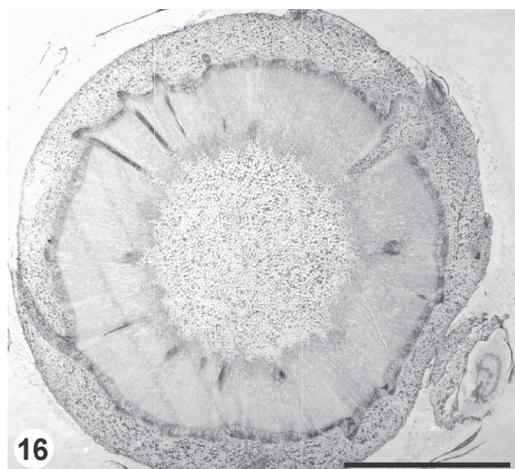
FIGS. 6–8. *Chresta sphaerocephala* DC. 6. Natural population of adult individuals (some of them arrowed). 7. Diffuse underground system constituted by gemmiferous roots (GR), which produces aerial stems (arrows). 8. Proximal portion of the underground system showing some aerial stems (arrow) and parts of carbonised branches (arrowheads). Level 1 of Fig. 7 indicates the transection shown in Fig. 18. Scale bars = 17 cm (Fig. 7) and 4 cm (Fig. 8).

regeneration after a fire disturbance event has been documented in numerous environments with fire-prone areas such as Australia, South Africa, the Mediterranean Basin, and Califor-

nia, where many woody plants cope with recurrent fire disturbance by resprouting from lignotubers (Klimesova and Klimes 2007). In general, the xylopodium is situated superfi-



FIGS. 9-15. *Pterocaulon angustifolium* DC. 9. General view of the xylopodium and its adventitious roots. Levels 1-4 indicate the transections shown in Figs. 12-15. 10. Shoot buds (B) on the globose portion of the xylopodium. 11. Frontal view of the natural self-grafting of the caulinar axis (CA). 12-15. Transections of the xylopodium showing the self-grafting of the caulinar axis (CA) and cauline, shoot-root transition region and radicular structures, respectively. Protoxylem poles are indicated in Figs. 13-15. Scale bars = 1 cm (Fig. 9), 3 cm (Figs. 10-12), 50  $\mu$ m (Figs. 13-14), and 60  $\mu$ m (Fig. 15).

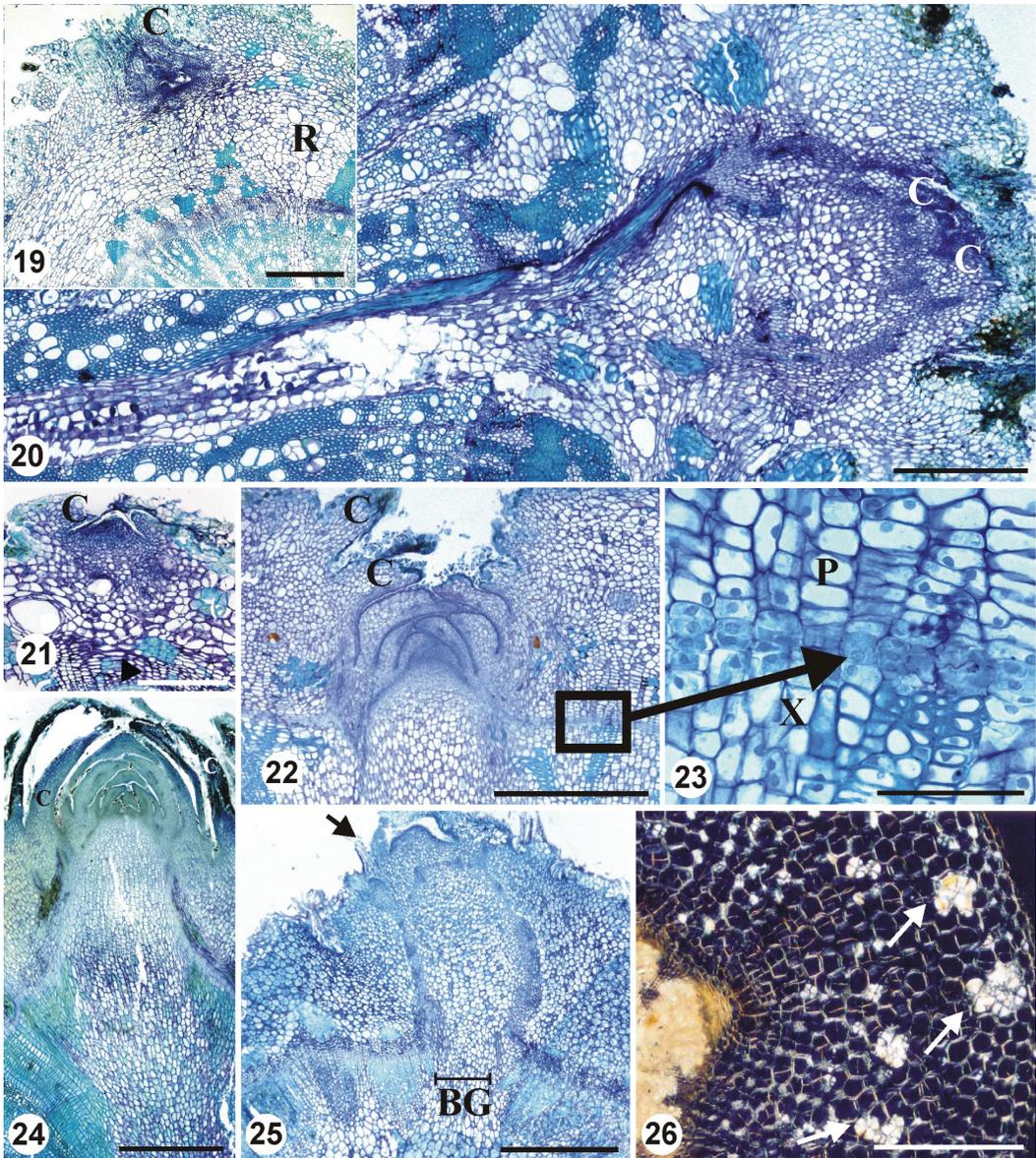


FIGS. 16–18. Transsections of the *Orthopappus angustifolius* (Sw.) Gleason rhizophore, *Gyptis lanigera* (Hook. & Arn.) R.M.King & H.Rob. moniliform tuberous root and *Chresta sphaerocephala* DC. gemmiferous roots with the sectioned regions shown in Figs. 4, 5, and 7. Scale bars = 3 mm (Fig. 16), 800  $\mu$ m (Fig. 17), and 200  $\mu$ m (Fig. 18).

cially in the driest portion of the soil, as verified in the present study and thus, it is important to store water and nutrients necessary for above-ground sprouting during the rainy season (Rizzini and Heringer 1961). The association between xylopodium and thickened roots, as verified in *Lessingianthus bardanoides*, *L. glabratus*, and *Pterocaulon angustifolium*, was already described in other Cerrado species such as *Mandevilla illustris* and *M. velutina* (Apocynaceae) by Appezzato-da-Glória and Estelita (2000), *Brosimum gaudichaudii* (Moraceae) by Palhares et al. (2007), and *Vernonia grandiflora* (Asteraceae) by Hayashi & Appezzato da Glória (2007). The thickened roots can have a great amount of starch (*Mandevilla* spp. and *B. gaudichaudii*) or fructans (*Lessingianthus bardanoides*, *L. glabratus*, and *P. angustifolium*), while the xylopodium does not exhibit any type of carbohydrate reserves. Although the xylopodium has not been considered a storage organ, Braga et al. (2006) have demonstrated that in *Ocimum nudicaule*, xylopodium varies in the content and molecular mass of cell wall pectins, as well as changes in their composition and structure. This may be related to storage function and extension growth; both required for the sprouting of new buds from the xylopodium.

Rhizophores, as verified in *Orthopappus angustifolius*, have already been described for Vernonieae tribe, more specifically for *Vernonia* spp. (Sajo and Menezes 1986a, 1986b, Hayashi and Appezzato-da-Glória 2005) and also for Heliantheae tribe (*Smallanthus sonchifolius* by Machado et al. 2004). The rhizophores of *Orthopappus angustifolius* accumulate fructans as carbohydrate reserves as verified in *Vernonia herbacea* (Vell.) Rusby (Dias-Tagliacozzo et al. 1999, Asega and Carvalho 2004). They are used at different phenological phases, mainly during sprouting, flowering, and fructification (Carvalho and Dietrich 1993).

The cambial activity leads to the production of secondary vascular tissues with large amounts of parenchyma cells in *Gyptis lanigera* moniliform tuberous root. However, *Vernonia oxylepis* and *V. brevifolia* (Asteraceae) showed the root thickening results from the pericycle proliferation (Vilhalva and Appezzato-da-Glória 2006, Hayashi and Appezzato-da-Glória 2007, respectively) and in *Smallanthus sonchifolius* (Asteraceae) from



FIGS. 19–26. Longitudinal sections of the adventitious buds in *Chresta sphaerocephala* DC. root. 19. Reparative bud is not connected with the vasculature of its parent root. 20. Additional bud with bud traces produced in the secondary xylem. 21. Longitudinal section of the adventitious bud of *Gyptis lanigera* (Hook. & Arn.) R.M.King & H.Rob. originated from the cambium (arrowhead). 22. Longitudinal section of the adventitious bud in *Pterocaulon angustifolium* DC. xylopodium. 23. Detail of the region indicated in Fig. 22 showing the cambium. 24. Axillary bud of the *Lessingianthus glabratus* (Less.) H. Rob. xylopodium. 25–26. *Orthopappus angustifolius* (Sw.) Gleason. 25. Longitudinal section of the axillary bud (arrow) of the rhizophore. 26. Distribution of spherocrystals of inulin (translucent bodies, some indicated by arrows) in parenchyma cells of reserve tissues in transection of root. BG = bud gap; C = cataphyll; P = secondary phloem; R = vascular ray; X = secondary xylem. Scale bars = 300  $\mu$ m (Fig. 19), 800  $\mu$ m (Figs. 20, 22, 25–26), 400  $\mu$ m (Fig. 21), 120  $\mu$ m (Fig. 23), and 1.2 mm (Fig. 24).

the divisions of the inner cortex (Machado et al. 2004).

Many Cerrado species, as *Chresta sphaerocephala*, show an unusual behavior. A single

individual plant can occupy an area of about 10 m in diameter (see Fig. 6). They have a complex, profusely-branched, and superficial subterranean system described by Rizzini and

Heringer (1966) as “diffuse underground systems.” Some of these diffuse underground systems are caulinar structures named ‘so-boles’, or radicular structures named ‘gemmiferous roots’ (Rizzini and Heringer 1966). They clearly have the capacity of vegetative reproduction. The plant sprouts in different directions, but all the shoots are interconnected belowground, forming an extensive, complex system. Colonies of *Annona pygmaea*, *Andira humilis*, *Pradosia brevipes*, and *Parinari obtusifolia*, among others, can reach several meters in diameter (Filgueiras 2002). A similar pattern can be seen for *Chresta sphaerocephala*, where the aerial stems can be as far as 100 cm apart and shows diffuse underground systems of radicular structure. Even though it is difficult to define an individual in Cerrado vegetation types, this phenomenon seems to be widespread and should be investigated since it is of crucial importance for population biology and community studies (Filgueiras 2002). According to Rizzini and Heringer (1966), these belowground systems were consequences of repeated destruction of the aerial biomass due to fire disturbance and also affected reproduction by seed and stimulated shoot bud-forming roots. The remaining carbonized base of some branches emitted in previous periods from the diffuse underground system of *Chresta sphaerocephala* confirms the interference of the fire in the sprouting process.

All the studied species form shoot buds in the thickened underground systems. The origin of the buds can vary among species according to the anatomical structure of the underground systems. Two types of buds were found in roots “additional” buds and “reparative” buds (Bosela and Ewers 1997, Hayashi et al. 2001). Additional buds form during the early growth of uninjured roots and they perennate by growing outwards in concert with the vascular cambium such that bud traces are produced in the secondary xylem as verified in *Chresta sphaerocephala*. Reparative buds form ‘de novo’ in response to senescence, injury, or to other types of disturbance and do not have bud traces produced in the secondary xylem as shown in *Chresta sphaerocephala*. The presence of additional buds other than reparative ones is a characteristic related to clonal spread (Bosela and Ewers 1997). Such a characteristic may explain why *C. sphaerocephala* is one of the most frequent species in different floristic surveys of the herbaceous

and undershrub layers (Almeida et al. 2005). In tuberous roots, the adventitious buds of *Gyptis lanigera* originate close to the cambium, while in *Vernonia oxylepis* (Asteraceae), the adventitious buds originate from the proliferated pericycle (Vilhalva and Appezzato-da-Glória 2006). In rhizophores of *Orthopappus angustifolius*, the axillary buds and the bud gap reaches the pith as previously described for rhizophores in *Vernonia* spp. (Sajo and Menezes 1986a, 1986b, Hayashi and Appezzato-da-Glória 2005) and in *Smalanthus sonchifolius* (Machado et al. 2004).

All analyzed species accumulate fructans of the inulin type in the cortical parenchyma of lateral or adventitious roots produced by the subterranean systems, except for *Chromolaena squalida*. In *Chresta sphaerocephala*, the fructans are also found in the vascular parenchyma. These carbohydrates may act as osmotic regulators due to their rapid polymerization and depolymerization (Figueiredo-Ribeiro et al. 1991). The variation in composition and content throughout the phenological phases suggest that this carbohydrate is also a reserve, which contributes to adaptive features in plants subjected to unfavorable environmental conditions (Carvalho and Dietrich 1993, Dias-Taglicozzo et al. 1999, 2004).

It is interesting to notice that the most frequent species listed in the inventory of Asteraceae species in eight Cerrado fragments in the State of São Paulo (Almeida et al. 2005) possess thickened subterranean systems that give rise to buds and store fructans. It is well known that belowground meristems and the density of established stems may regulate plant population abundance and productivity in tallgrass prairies (Benson et al. 2004). In fact, belowground biomass in the Cerrado showed significant seasonal variation, values being higher during the rainy season and lower during the dry period (Delitti et al. 2001). According to the authors, fire and soil depth also had significant effects on belowground biomass and must be taken into consideration in the studies of fire effects, land use changes, global carbon storage, and release capacity. Probably the reserve of belowground meristems maintained in the form of bud bank on subterranean systems—rhizophore, xylopodium, tuberous, and diffuse underground systems—is clearly important to the maintenance of species in this severely and repeatedly disturbed Cerrado biome. Understanding the

features of herbaceous plants is one of the steps to appropriate conservation management of these species in the Cerrado, which is being rapidly devastated.

### Literature Cited

- ACHUTTI, M. H. C. 1978. Aspectos morfológicos e anatômicos dos sistemas aéreo e subterrâneo e o óleo essencial das folhas de *Piptocarpha rotundifolia* (Less.) Baker (Compositae). PhD thesis. Instituto de Biociências—Universidade de São Paulo, São Paulo, SP.
- ALMEIDA, A. M., C. R. FONSECA, P. I. PRADO, M. ALMEIDA-NETO, S. DINIZ, U. KUBOTA, M. R. BRAUN, R. L. G. RAIMUNDO, L. A. ANJOS, T. G. MENDONÇA, S. M. FUTADA, AND T. M. LEWISOHN. 2005. Diversidade e ocorrência de Asteraceae em cerrados de São Paulo. *Biota Neotrop.* 5: 1–17.
- APPEZZATO-DA-GLÓRIA, B. AND M. E. M. ESTELITA. 2000. The developmental anatomy of the subterranean system in *Mandevilla illustris* (Vell.) Woodson and *M. velutina* (Mart. ex Stedelm.) Woodson (Apocynaceae). *Rev. Bras. Bot.* 23: 27–35.
- ASEGA, A. F. AND M. A. M. CARVALHO. 2004. Fructan metabolising enzymes in rhizophores of *Vernonia herbacea* upon excision of aerial organs. *Plant Physiol. Bioch.* 42: 313–319.
- BENSON, E. J., D. C. HARTNETT, AND K. H. MANN. 2004. Belowground bud banks and meristem limitation in tallgrass prairie plant populations. *Am. J. Bot.* 91: 416–421.
- BOSELA, M. J. AND F. W. EWERS. 1997. The mode of origin of root buds and root sprouts in the clonal tree *Sassafras albidum* (Lauraceae). *Am. J. Bot.* 84: 1466–1481.
- BRAGA, M. R., N. C. CARPITA, S. M. C. DIETRICH, AND R. C. L. FIGUEIREDO-RIBEIRO. 2006. Changes in pectins of the xylopodium of *Ocimum nudicaule* from dormancy to sprouting. *Braz. J. Plant Physiol.* 18: 325–331.
- BURROWS, G. E. 2002. Epicormic strand structure in *Angophora*, *Eucalyptus* and *Lophostemon* (Myrtaceae): Implications for fire resistance and recovery. *New Phytol.* 153: 111–131.
- CARR, D. J., S. G. M. CARR, AND R. JAHNKE. 1982. The eucalypt lignotuber: a position-dependent organ. *Ann. Bot.* 50: 481–489.
- CARVALHO, M. A. M. AND S. M. C. DIETRICH. 1993. Variation in fructan content in the underground organs of *Vernonia herbacea* (Vell.) Rusby at different phenological phases. *New Phytol.* 123: 735–740.
- CASTRO, E. A. DE AND J. B. KAUFFMAN. 1998. Ecosystem structure in the Brazilian Cerrado: a vegetation gradient of aboveground biomass, root mass and consumption by fire. *J. Trop. Ecol.* 14: 263–283.
- COUTINHO, L. M. 1990. Fire in the Ecology of the Brazilian Cerrado, p. 82–105. In J. G. Goldammer [ed.], *Fire in the tropical biota*. Springer-Verlag, Berlin, DE.
- DELITTI, W. B. C., J. G. PAUSAS, AND D. M. BURGER. 2001. Belowground biomass seasonal variation in two Neotropical savannahs (Brazilian Cerrados) with different fire histories. *Ann. For. Sci.* 58: 713–721.
- DIAS-TAGLIACCOZZO, G. M., R. C. L. FIGUEIREDO-RIBEIRO, M. A. M. CARVALHO, AND S. M. C. DIETRICH. 1999. Fructan variation in the rhizophores of *Vernonia herbacea* (Vell.) Rusby, as influenced by temperature. *Rev. Bras. Bot.* 22: 267–273.
- DIAS-TAGLIACCOZZO, G. M., N. M. ITAYA, M. A. M. CARVALHO, R. C. L. FIGUEIREDO-RIBEIRO, AND S. M. C. DIETRICH. 2004. Fructans and water suppression on intact and fragmented rhizophores of *Vernonia herbacea*. *Braz. Arch. Biol. Technol.* 47: 363–373.
- FIGUEIREDO-RIBEIRO, R. C. L., S. M. C. DIETRICH, E. P. CHU, M. A. M. CARVALHO, C. C. J. VIEIRA, AND T. T. GRAZIANO. 1986. Reserve carbohydrates in underground organs of native Brazilian plants. *Rev. Bras. Bot.* 9: 159–166.
- FIGUEIREDO-RIBEIRO, R. C. L., E. M. ISEJIMA, G. M. DIAS-TAGLIACCOZZO, M. A. M. CARVALHO, AND S. M. C. DIETRICH. 1991. The physiological significance of fructan accumulation in Asteraceae from the Cerrado. *Cienc. Cult.* 43: 443–446.
- FILGUEIRAS, T. S. 2002. Herbaceous Plant Communities, p. 121–139. In P. S. Oliveira and R. J. Marquis [eds.], *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna*. Columbia University Press, New York, NY.
- HAYASHI, A. H., A. S. PENHA, R. R. RODRIGUES, AND B. APPEZZATO-DA-GLÓRIA. 2001. Anatomical studies of shoot bud-forming roots of Brazilian tree species. *Aust. J. Bot.* 49: 745–751.
- HAYASHI, A. H. AND B. APPEZZATO-DA-GLÓRIA. 2005. The origin and anatomy of rhizophores in *Vernonia herbacea* and *V. platensis* (Asteraceae) from the Brazilian Cerrado. *Aust. J. Bot.* 53: 273–279.
- HAYASHI, A. H. AND B. APPEZZATO-DA-GLÓRIA. 2007. Anatomy of the underground system in *Vernonia grandiflora* Less. and *V. brevifolia* Less. (Asteraceae). *Braz. Arch. Biol. Technol.* 50: 979–988.
- JOHANSEN, D. A. 1940. *Plant Microtechnique*. McGraw-Hill Book Company, New York, NY. 523 p.
- KERR, L. R. 1925. The lignotubers of *Eucalyptus* seedlings. *Proc. R. Soc. Vic.* 37: 79–97.
- KLIMEŠOVÁ, J. AND L. KLIMEŠ. 2007. Bud banks and their role in vegetative regeneration – A literature review and proposal for simple classification and assessment. *Perspect. Plant Ecol. Evol. Syst.* 8: 115–129.
- LINDMAN, C. A. M. 1900. *Vegetationen i Rio Grande do Sul (Sydbrasilien)*. Nordin & Josephson, Stockholm. 239 p.
- MACHADO, S. R., D. M. T. OLIVEIRA, M. R. DIP, AND N. L. MENEZES. 2004. Morfoanatomia do sistema subterrâneo de *Smallanthus sonchifolius* (Poepp. & Endl.) H. Robinson (Asteraceae). *Rev. Bras. Bot.* 27: 115–123.
- MENDONÇA, R. C., J. M. FELFILI, B. M. T. WALTER, M. C. SILVA JÚNIOR, A. V. REZENDE, T. S. FILGUEIRAS, AND P. E. NOGUEIRA. 1998. Flora vascular do Cerrado, p. 289–257. In S. M. Sano and S. P. Almeida [eds.], *Cerrado: ambiente e flora*. EMBRAPA-CPAC Planaltina, GO.

- PALHARES, D., J. E. PAULA, L. A. R. PEREIRA, AND C. E. S. SILVEIRA. 2007. Comparative wood anatomy of stem, root and xylopodium of *Brosimum gaudichaudii* (Moraceae). IAWA J. 28: 83–94.
- PATE, J. S., R. H. FROEND, B. J. BOWEN, A. HANSEN, AND J. KUO. 1990. Seedling growth and storage characteristics of seeder and resprouter species of Mediterranean-type ecosystems of S. W. Australia. Ann. Bot. 65: 585–601.
- PAVIANI, T. I. 1987. Anatomia do desenvolvimento do xilopódio de *Brasilia sickii* G.M.Barroso. Estágio inicial. Ciênc. Cult. 39: 399–405.
- RATTER, J. A., J. F. RIBEIRO, AND S. BRIDGEWATER. 1997. The Brazilian cerrado vegetation and threats to its biodiversity. Ann. Bot. 80: 223–230.
- RIZZINI, C. T. AND E. P. HERINGER. 1961. Underground organs of plants from some southern Brazilian savannas, with special reference to the xylopodium. Phytol. 17: 105–124.
- RIZZINI, C. T. AND E. P. HERINGER. 1962. Studies on the underground organs of trees and shrubs from some southern Brazilian savannas. An. Acad. Bras. Ciênc. 34: 235–247.
- RIZZINI, C. T. AND E. P. HERINGER. 1966. Estudo sobre os sistemas subterrâneos difusos de plantas campestres. An. Acad. Bras. Ciênc. 38: 85–112.
- SAJO, M. G. AND N. L. MENEZES. 1986a. Anatomia do rizôforo de espécies de *Vernonia* Scrib. (Compositae) da Serra do Cipó, MG. Rev. Bras. Biol. 46: 189–196.
- SAJO, M. G. AND N. L. MENEZES. 1986b. Origem e crescimento do rizôforo em espécies de *Vernonia* Scrib. (Compositae), da Serra do Cipó, MG. Rev. Bras. Biol. 46: 197–202.
- SAKAI, W. S. 1973. Simple method for differential staining of paraffin embedded plant material using toluidine blue O. Stain Technol. 48: 247–249.
- VILHALVA, D. A. A. AND B. APPEZZATO-DA-GLÓRIA. 2006. Morfoanatomia da raiz tuberosa de *Vernonia oxylepis* Sch. Bip. in Mart. ex Baker – Asteraceae. Acta Bot. Bras. 20: 591–598.