



Anastomosing laticifer in the primary and secondary structures of *Calotropis procera* (Aiton) W.T.Aiton (Apocynaceae) stems

Brenda Martins Cotta Salomé¹ · Ariadna Freitas Santos¹ · Leonardo Monteiro Ribeiro¹ ·
Islaine Franciely Pinheiro de Azevedo¹ · Maria Olívia Mercadante-Simões¹

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Abstract

An in-depth understanding of the development and distribution of laticifer (latex secretory structure) will be important for the production of both rubber and medicines and will support studies on plant adaptations to their environments. We characterize here and describe the ontogenesis of the laticifer system in *Calotropis procera* (Apocynaceae), an invasive shrub species in arid landscapes. Anatomical and histochemical evaluations of the primary and secondary structures of the stem were carried out on a monthly basis during a full year, with ultrastructural evaluations of laticifer on the stem apex during the rainy season. In the primary structure, laticifer differentiate early from procambium and ground meristem cells of the cortex and medulla and become concentrated adjacent to the external and internal phloem of the bicollateral bundles. In the secondary structure, laticifer differentiates from fusiform derivative cells of the phloem close to the sieve-tube elements. The laticifer is of the articulated, anastomosing, branched type, and it originates from precursor cells that lose the transversal and longitudinal walls by dissolution. Latex is a mixture of terpenes, alkaloids, flavonoids, mucilage, and proteins. The apical meristem and vascular cambium where the laticifer system begins its development are active throughout the year, including during the dry season. The vascular cambium produces phloem with laticifer precursor cells during the rainy season, with high temperatures and long days. The ability of *C. procera* to grow under water deficit conditions and produce laticifer throughout the year contribute to its wide distribution in arid environments.

Keywords Cambial activity · Fusiform phloem derivative cells · Latex · Articulated branched laticifer. Meristem

Introduction

Latex is an emulsion formed by compounds produced by plant primary and secondary metabolism (Lopes et al. 2009; Ramos et al. 2019). It acts to prevent infections by microorganisms as well as herbivory and also aids in wound sealing—thus contributing to the adaptive success of plants (Agrawal and Konno 2009; Habib and Ismail 2021). Latex has historical importance in terms of rubber production as well as significant medicinal value (Al-Snafi 2015; Cavalcante et al. 2020, Naidoo et al. 2020). Laticifers are specialized tubular structures that occur in numerous plant organs

and secrete latex (Teixeira et al. 2020). They generally originate in the procambium and the ground meristem of the cortex and medulla of the shoot apex (Gonçalves et al. 2018, Pirolla-Souza et al. 2019) and usually from phloem-derived cells from the vascular cambium in the secondary structure of the stem (Gonçalves et al. 2018; Souza et al. 2021). Studies on the development and distribution of laticifers will be important for improving latex production and will contribute to the expansion of our knowledge concerning plant adaptations to different environments.

The Apocynaceae family comprises many latex-producing species, and the anastomosing structural type of laticifer is reported to be predominant in the group (Gama et al. 2017; Pirolla-Souza et al. 2019). Laticifers of this type are formed by rows of cells whose terminal and lateral walls are absorbed, forming elongated and branching ducts (Gonçalves et al. 2018; Souza et al. 2021). Ontogenetic studies that allow a complete definition of the anastomosis processes through dissolution of adjacent cell walls are required for

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✉ Maria Olívia Mercadante-Simões
omercadante@hotmail.com

¹ Departamento de Biologia Geral, Universidade Estadual de Montes Claros, Montes Claros 39401-089, Brasil

the correct definition of their structural type (Gama et al. 2017; Gonçalves et al. 2018; Teixeira et al. 2020; Souza et al. 2021).

Laticifer differentiation in the secondary phloem is controlled by the cambium activity, which, in turn, is controlled by climatic conditions (Marcati et al. 2016; Almeida et al. 2019; Souza et al. 2021). Seasons are well-defined in the Brazilian Cerrado (neotropical savanna), one being dry and cold and the other rainy and hot (Alvares et al. 2014). Studies of the formation times of the laticifers of species that occur in dry environments can contribute to the sustainable harvesting of economically valuable latex (Souza et al. 2021).

Calotropis procera (Aiton) W.T.Aiton (Apocynaceae) is an erect subshrub capable of growing and fruiting throughout the year (Almeida et al. 2019) native to the desert regions of Africa and Asia (Hassan et al. 2015). The species was originally introduced into Brazil for ornamental purposes but soon became invasive, as it is well-adapted to semiarid environments (Oliveira et al. 2009; Frosi et al. 2012; Sobrinho et al. 2013). *Calotropis procera* has medicinal value; can be used to obtain fibers, biofuels, and nanoparticles; and is employed in phytoremediation projects (Kaur et al. 2021). The plant is rich in nutrients, which makes it a promising source of animal feed (Costa et al. 2009; Hassan et al. 2015), and produces an abundant white latex with medicinal uses (Freitas et al. 2011; Al-Snafi 2015; Cavalcante et al. 2020).

Considering the naturalization of *C. procera*, its potential economic use and wide distribution in semiarid regions of Brazil, we sought to describe laticifer ontogenesis and characterize their development in the stems of that species by addressing the following questions: (1) What is the distribution pattern of the laticifer system? (2) What is its structural type? (3) What is the composition of the latex? (4) How does climatic seasonality influence laticifer development?

Materials and methods

Climate data and plant material

The climate of the study region is tropical savanna with a dry season (type Aw, according to the Köppen classification; Köppen 1936), which is characterized by strong climatic seasonality with well-defined seasons, being hot/rainy in the austral spring/summer, and cold/dry in autumn/winter (Alvares et al. 2014). The average annual rainfall at the study site is 1086 mm, and the average annual temperature 24 °C (National Institute and Meteorology of Brazil (INMET) <https://portal.inmet.gov.br/>). The highest precipitation rate (between March 2020 and February 2021) occurred in March, the highest temperature in October, and the longest day length in December (Fig. 1a–b).

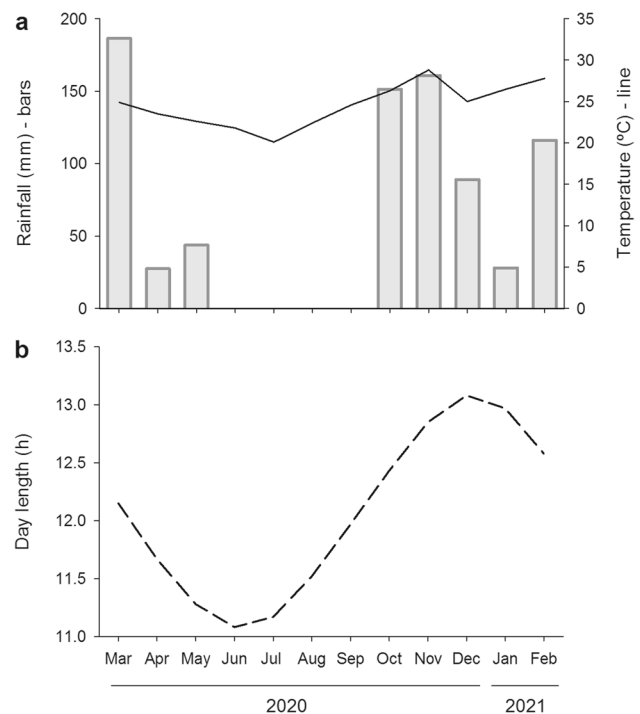


Fig. 1 Climate data (from Montes Claros, Minas Gerais State, Brazil). National Institute of Meteorology of Brazil – INMET (<https://portal.inmet.gov.br/>)

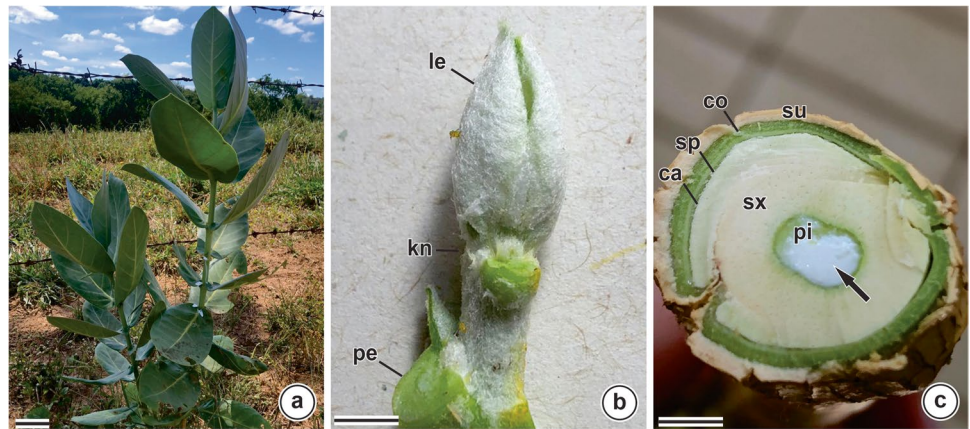
Plant material was obtained from 5 adult individuals occurring in a natural population in the Cerrado region of the municipality of Montes Claros, Minas Gerais State, Brazil (Fig. 2a). Samples were collected on a monthly basis between March 2020 and February 2021 and consisted of shoot apices approximately 3 mm long (Fig. 2b) as well as fragments of the basal region of stem (approximately 4 cm in diameter) containing tissues external to the vascular cambium (Fig. 2c).

Structural analyses and histochemistry

The samples were fixed in Karnovsky's solution (Karnovsky 1965), under vacuum (560 mm Hg) for 24 h, dehydrated in an increasing ethanol series (Jensen 1962), embedded in glycol-methacrylate resin (Leica Microsystem Inc., Heidenberg, Germany), and sectioned using a rotary microtome (Atako, Tokyo, Japan). Transverse and longitudinal Sects. (5 µm thick) were stained with toluidine blue pH 4.7 (modified from O'Brien et al. 1964) and mounted on permanent slides using acrylic resin (Itacril, Itaquaquecetuba, Brazil).

Histochemical tests were performed to detect: terpenes using dimethyl-para-phenylenediamine hydrochloride (David and Carde 1964); alkaloids using Lugol's reagent (Jensen 1962); phenolic compounds using toluidine blue, pH 4.7 (modified from O'Brien et al. 1964); flavonoids using

Fig. 2 Adult individual of *Calotropis procera* (Apocynaceae): **a** Panoramic view of a wild population in the Brazilian Cerrado region. **b** Stem apex. **c** Basal region of a transversally sectioned stem. *c* vascular cambium, *co* cortex, *kn* leaf node, *le* leaf, *pe* petiole, *pi* pith, *sp* secondary phloem, *su* cork, *sx* secondary xylem, *arrow* latex. Scale bars: **a** = 10 cm; **b** = 1 μ m; **c** = 500 μ m



p-dimethyl amino cinnamaldehyde (Feucht et al. 1986); acidic polysaccharides using toluidine blue, pH 4.7 (modified from O'Brien et al. 1964) and ruthenium red (Johansen 1940); and proteins using Xylidine-Ponceau (Vidal 1970). Photographic documentation was performed using an Axio Cam ICC3 digital camera coupled to an A1 Lab optical microscope (Zeiss, Oberkochen, Germany), under white and ultraviolet light with 505–530 nm filters.

Ultrastructural analyses

Ultrastructural analyses were performed on samples of the stem apical meristem undergoing vegetative growth (collected in November 2020, when rainfall, temperature, and day length values were high). Those samples were fixed in Karnovsky's solution (Karnovsky 1965) under vacuum (560 mm Hg) for 3 min, post-fixed with 1% osmium tetroxide (0.1 M phosphate buffer, pH 7.2), dehydrated in an increasing acetone series, and infiltrated with Araldite resin (Leica Microsystems, Heidelberg, Germany). Ultrathin Sects. (50 nm thick) were obtained using a UC6 ultramicrotome (Leica Microsystems, Heidelberg, Germany), counterstained in a saturated solution of uranyl acetate and lead citrate (Roland 1978), and examined using a CM 100 transmission electron microscope (Philips/ FEI Corporation, Eindhoven, The Netherlands) at 80 kV.

Results

Distribution, ontogenesis, and histochemistry

In the primary structure of the plant body, the laticifer system is distributed in the cortex and medulla, concentrated close to the phloem and including in regions between the outer and inner phloem strands of the bicollateral bundles (Fig. 3a–f). Laticifer development starts early in the promeristem of the shoot apex. The apex has well-defined

nodes and internodes, and colleters in the axilla of the leaf primordia. Laticifers are not observed within the colleters (Fig. 4a). Laticifer system differentiate from the ground meristem of the cortex and medulla being thick, longitudinally elongated, and branched (Fig. 4a–d, 5a–b). Laticifers have only a thin cytoplasm compressed against the cell walls, with latex accumulated in a voluminous central vacuole (Fig. 5c–d). Their structural type is the branched anastomosing, originating from the partial dissolution of the transverse and lateral walls of the precursor cells (Fig. 6a–d).

During ontogenesis of the laticiferous ducts, the precursor cells have a voluminous nucleus and nucleolus and a dense cytoplasm rich in organelles responsible for the synthesis of latex components (Fig. 7a–b). Anastomosis processes begin early, and the walls dissolve centrifugally in regions crossed by numerous plasmodesmata (Fig. 7a–d). The partial collapse of the cytoplasm gives rise to membrane recycling vacuoles and organelle residues, which integrate into the latex (Fig. 8a–b). Latex accumulates in a voluminous central vacuole, with only a thin peripheral layer of cytoplasm compressed against the cell wall (Fig. 8c–d, Fig. 5c–d).

In the secondary structure of the developing stem, a thick cork, the absence of a phelloderm, and the presence of cortex containing laticifer are observed (Fig. 9a–b). Laticifer system is distributed in the secondary phloem among the axial parenchymal elements associated with sieve tube elements and companion cells (Fig. 9b–d). The rays are uni- or biseriate, with cells containing crystals, without the recorded occurrence of laticifer (Fig. 9d). During the ontogenesis of the laticifer, increases in both their lengths and calibers are observed due to the dissolution of the transverse and longitudinal walls of the fusiform cambium derivatives, leading to the formation of the anastomosing laticifer (Fig. 10a–d).

Histochemical tests evidenced that the latex is an emulsion containing lipophilic and hydrophilic compounds from

Fig. 3 Distribution of laticifer system in the primary structure of the stem of *Calotropis procera* (Apocynaceae). **a–c, e–f** Cross-sections. **d** Longitudinal section. **a–e** Laticifer present in the cortex and pith and between the external and internal phloem bands, concentrated close to the phloem. *ca* vascular cambium; *co* cortex, *fi* gelatinous fibers; *ip* inner phloem; *op* outer phloem; *pi* medulla; *px* primary xylem; *sx* secondary xylem; *tr* trichomes; *vc* vascular cylinder; *arrow* laticifer. Scale bars: **a–b, d–f** 50 μ m; **c** = 200 μ m

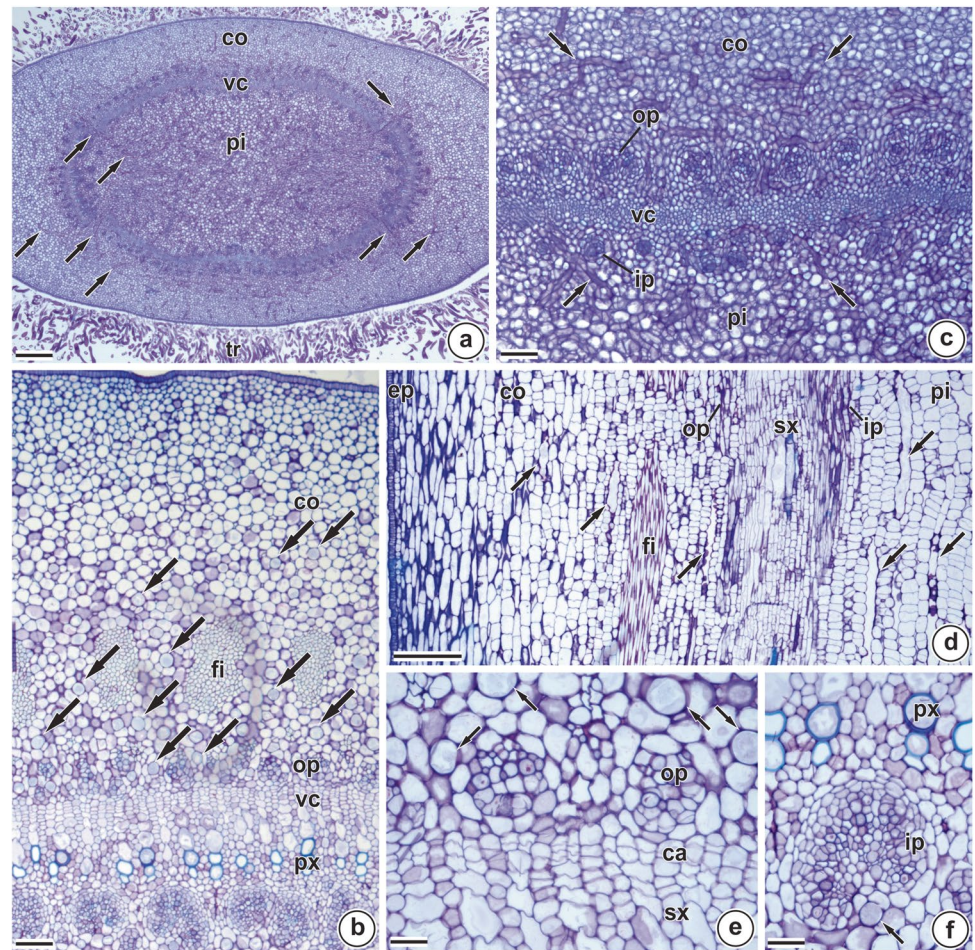


Fig. 4 Laticifer development in the stem apex of *Calotropis procera* (Apocynaceae). Longitudinal sections. **a** Early development in the promeristem. Well-defined nodes and internodes and colleters devoid of laticifer located in the axils of leaf primordia. **b–c** Laticifer differentiating from the ground meristem of the cortex and medulla. **d** Large caliber, longitudinally elongated and branched laticifer. *am* apical meristem, *cl* collater, *co* cortex, *fp* leaf primordium, *in* internode, *kn* node, *pc* procambium, *pi* medulla, *arrow* laticifers, *arrowhead* ramifications. Scale bars: **a** = 10 μ m; **b, d** = 25 μ m; **c** = 50 μ m

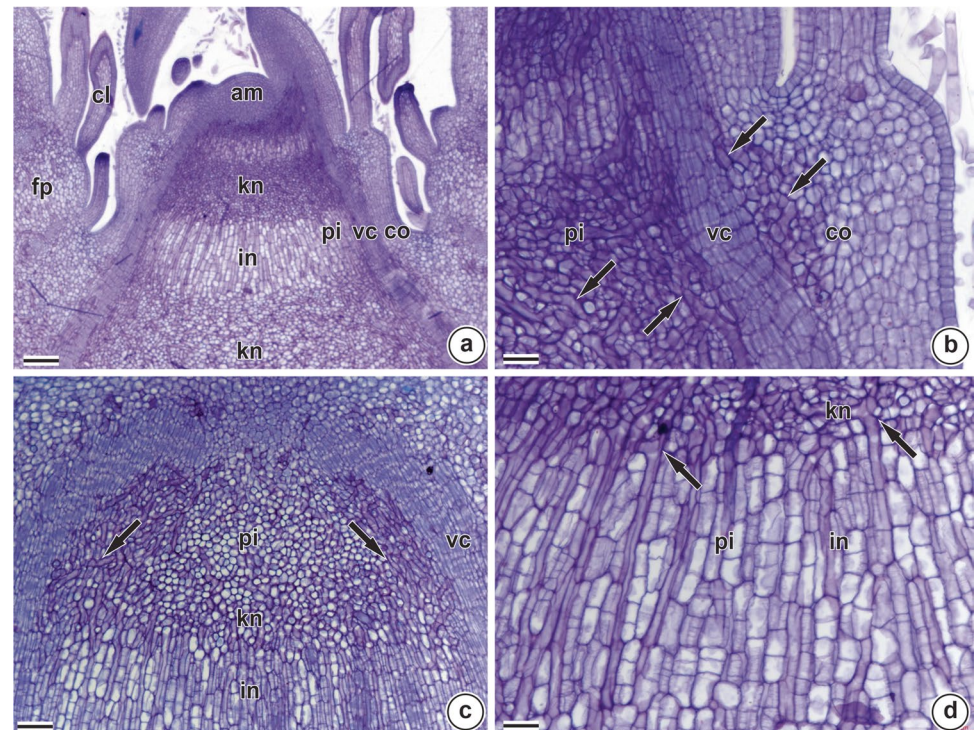


Fig. 5 Latex in laticifer in the primary structure of the stem of *Calotropis procera* (Apocynaceae). **a** Longitudinal section. **b–d** Cross-sections. **a–b** Elongated and branched laticifer in the regions of the cortex and medulla. **c–d** Thin cytoplasm, compressed against the cell wall, and latex accumulated in a voluminous central vacuole. *co* cortex, *cy* cytoplasm, *ep* epidermis, *fi* fibers, *pc* procambium, *pi* medulla, *vs* vascular system, *cw* cell wall, *arrows* laticifer, *arrowhead* latex. Scale bars: **a** = 50 μ m; **b** = 100 μ m; **c–d** = 10 μ m

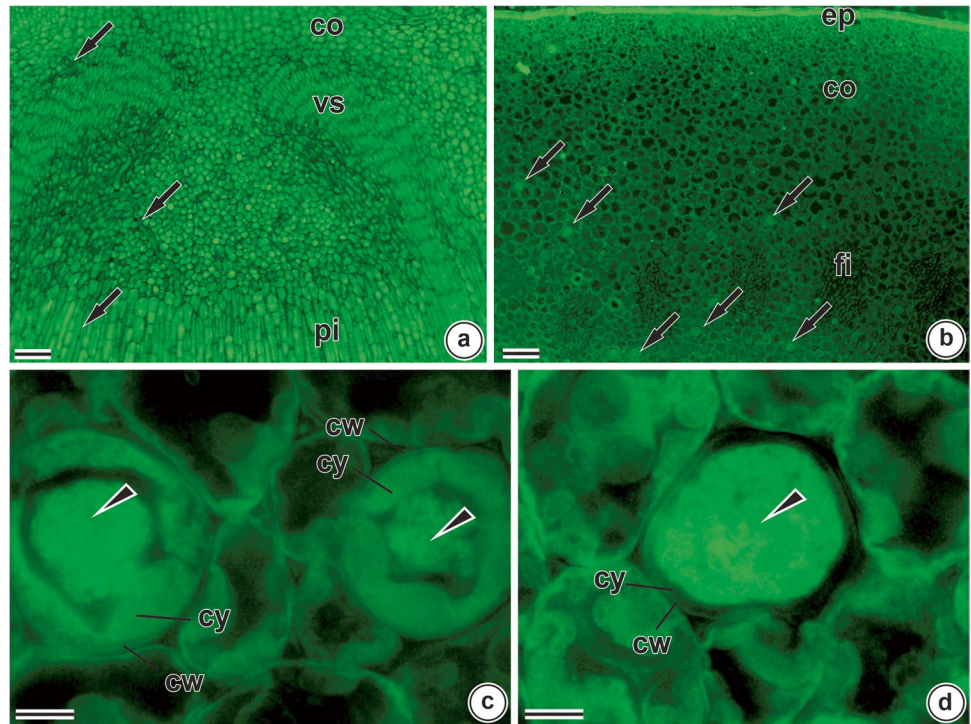
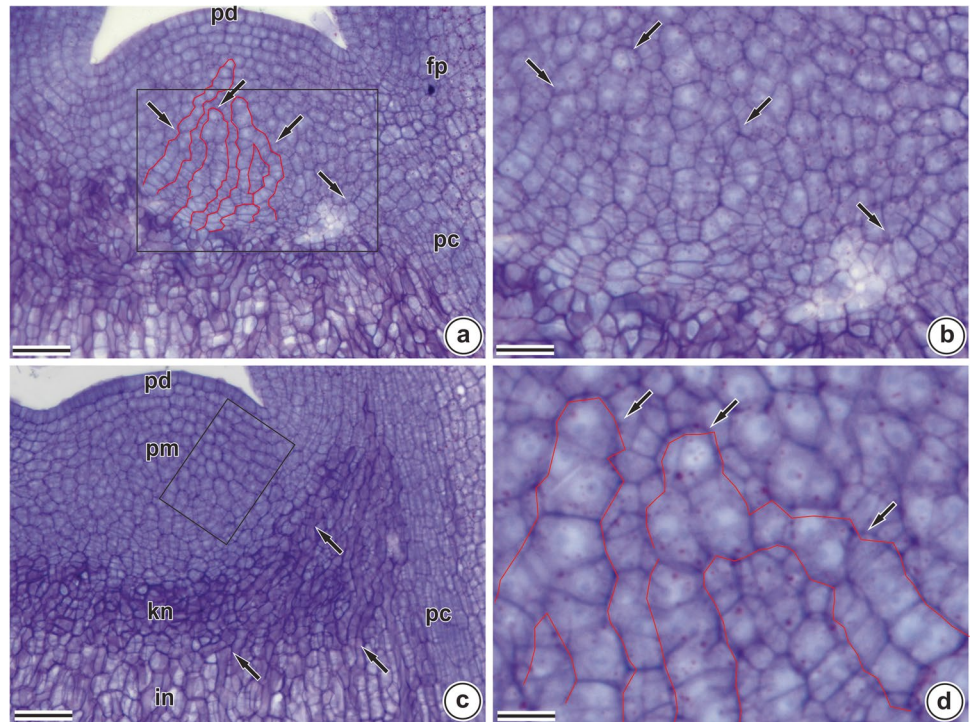


Fig. 6 Anastomosing laticifers at the shoot apex of *Calotropis procera* (Apocynaceae). Longitudinal sections. **a–d** Branched anastomosing structural type, originated through the partial dissolution of the transverse and lateral walls of precursor cells (arrowheads). Boxes in **a** and **c** correspond to figures **b** and **d**. *fp* leaf primordium, *in* internode, *kn* node, *pc* procambium, *pd* protoderm, *pm* promeristem, *arrows* laticifer precursor cells. Scale bars: **a**, **c** = 40 μ m; **b** = 20 μ m; **d** = 10 μ m



secondary and primary metabolism. The main classes of compounds recorded were terpenes (Fig. 11a–b), alkaloids (Fig. 11c–d), flavonoids (Fig. 11e–f), mucilage (Fig. 11g–h), and proteins (Fig. 11i–j).

Climatic seasonality

Cambial activity remains uninterrupted throughout the year. Phloem is produced when rainfall, temperature, and

Fig. 7 Laticifer ontogenesis—**anastomosis**—in the primary structure of the stem of *Calotropis procera* (Apocynaceae). **a–d** Anastomosis from precursor cells. Voluminous nucleus and nucleolus. Cytoplasm rich in organelles responsible for latex synthesis. Numerous plasmodesmata associated with the centrifugal dissolution of the walls. Box in **b** corresponds to **c**. *cy* collapsed cytoplasm, *cw* cell wall, *dc* dense cytoplasm, *mi* mitochondria, *nc* nucleolus, *nu* nucleus, *pl* plastid, *lp* laticifer precursor cell, *pe* peripheral cytoplasm, *rv* recycling vacuole, *arrowhead* plasmodesmata, *arrow* anastomosis. Scale bars: **a, d** = 3 μ ; **c** = 500 nm; **d** = 2 μ m

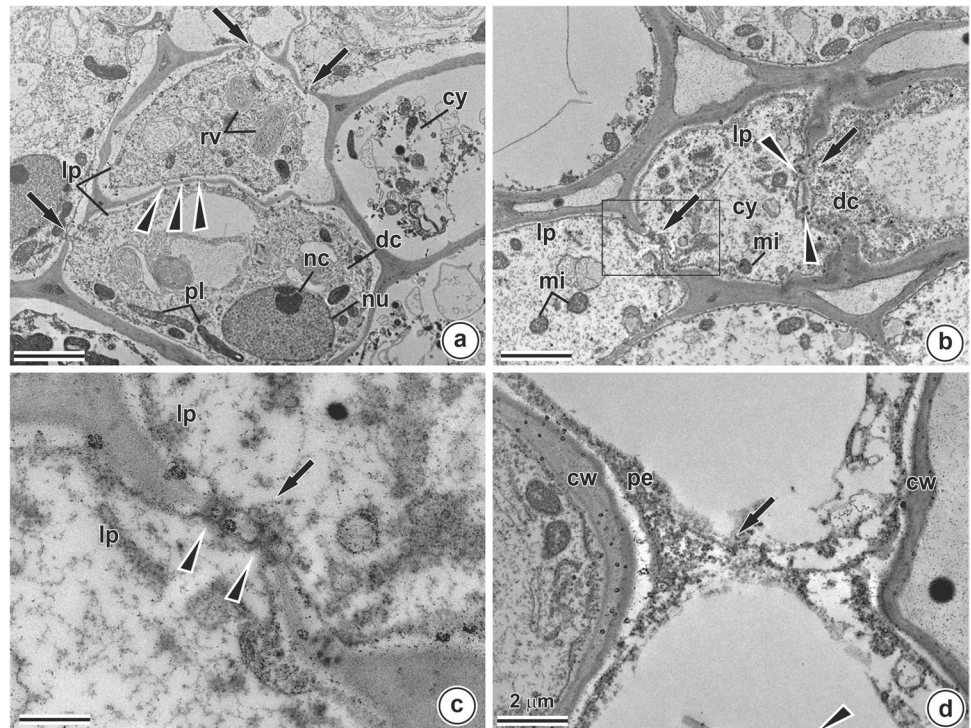
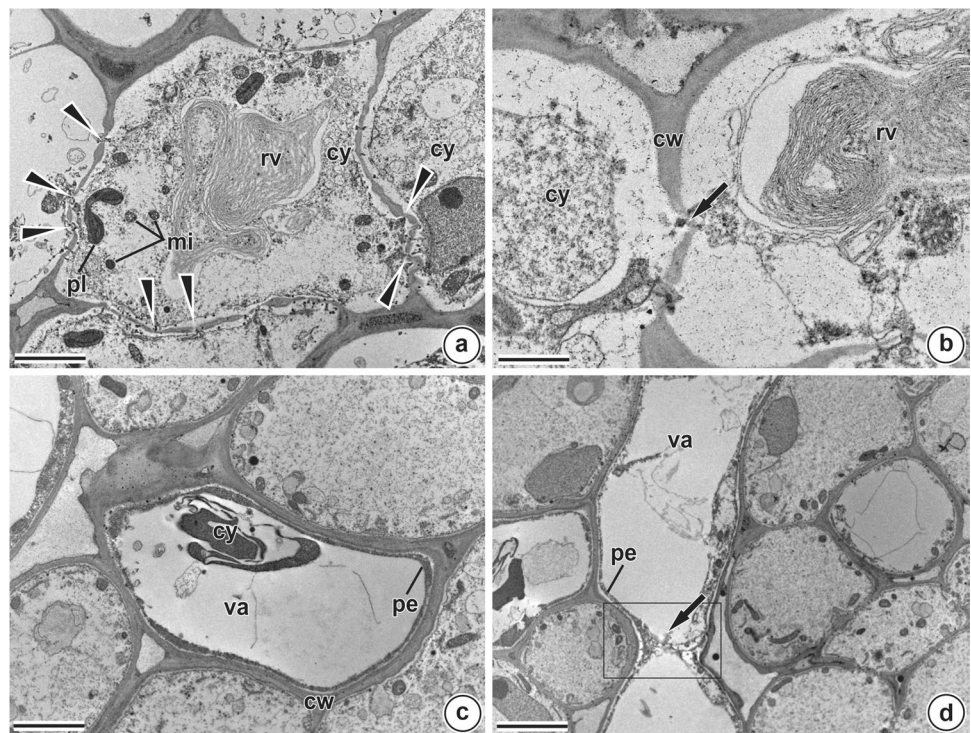


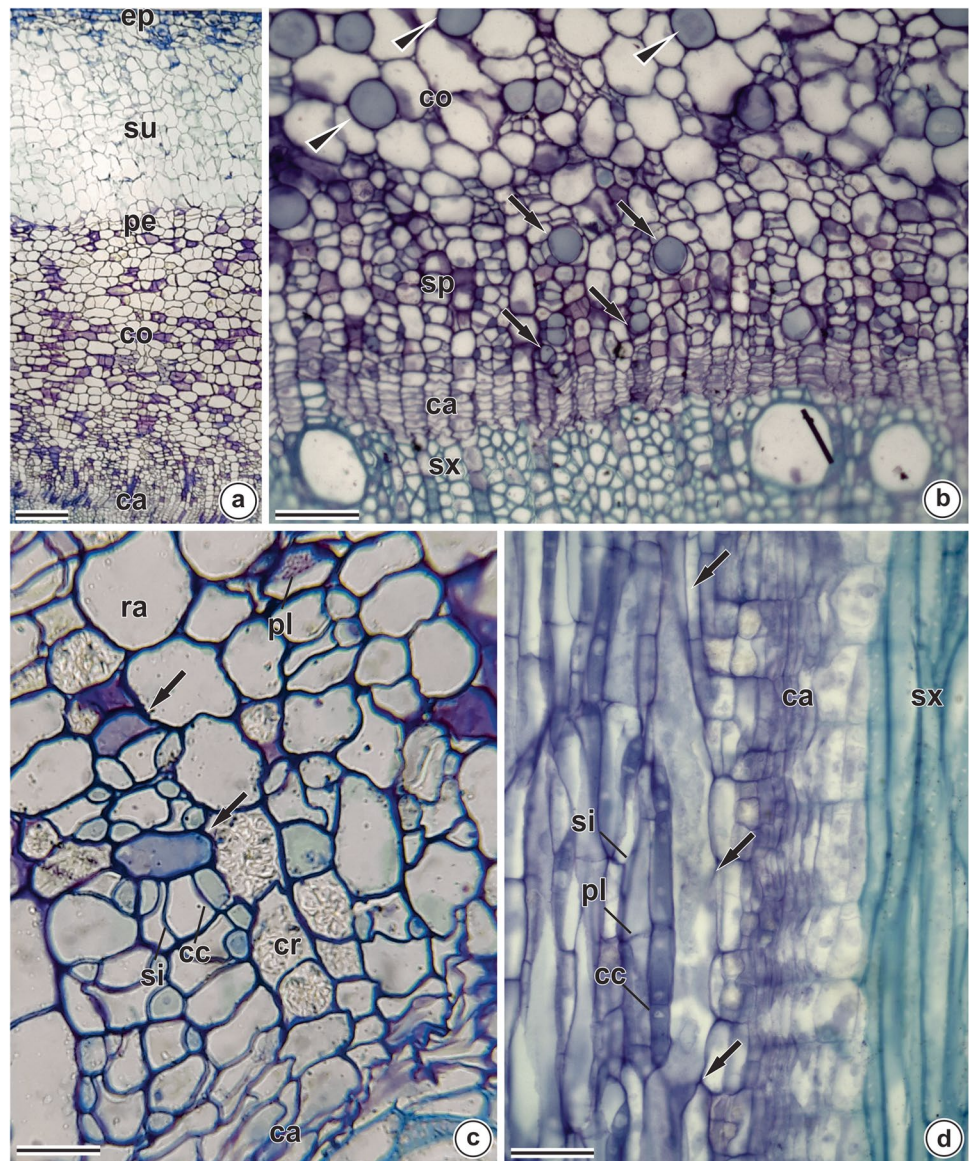
Fig. 8 Laticifer ontogenesis—**cytoplasm collapse**—in the primary structure of the stem of *Calotropis procera* (Apocynaceae). **a–b** Collapse of part of the cytoplasm integrated into the latex. **c–d** Latex accumulated in the central vacuole and a thin peripheral layer of cytoplasm compressed against the cell wall. *cy* collapsed cytoplasm, *cw* cell wall, *lp* laticifer precursor cell, *pe* peripheral cytoplasm, *pl* plastid, *rv* membrane recycling vacuole, *va* central vacuole, plasmodesmata *arrowhead*, anastomosis *arrow*. Box in **d** corresponds to Fig. 6d. Scale bars: **a–b** = 1 μ m; **c** = 3 μ m; **d** = 5 μ m



photoperiod are all increasing (between October and March) during the rainy season, and laticifers develop during that period (Fig. 12a–d). Xylem production occurs in the months

when these climatic parameters are decreasing (between the months of April and September) during the dry season (Fig. 12e–f), and no laticifers are observed in the xylem.

Fig. 9 Distribution of laticifer in the secondary structure of the stem of *Calotropis procera* (Apocynaceae). **a–c** Cross-sections. **d** Longitudinal section. **a–b** Stem section showing thick cork, absence of a phelloderm and cortex containing laticifer. **c** Phloem containing laticifer between the axial parenchymatic elements and associated with sieve tube elements. Uni- or biseriate rays containing crystals and without laticifer. **d** Laticifer associated with sieve tube elements and companion cells. *ca* vascular cambium, *cc* companion cell, *co* cortex, *cr* crystals, *ep* epidermis, *pl* sieve plate, *ra* ray, *si* sieve tube element, *sp* secondary phloem, *su* cork, *sx* secondary xylem, *arrow* laticifer in the secondary structure, *arrowhead* laticifer in the primary structure. Scale bars: **a–b** = 100 μ m; **c** = 50 μ m; **d** = 40 μ m



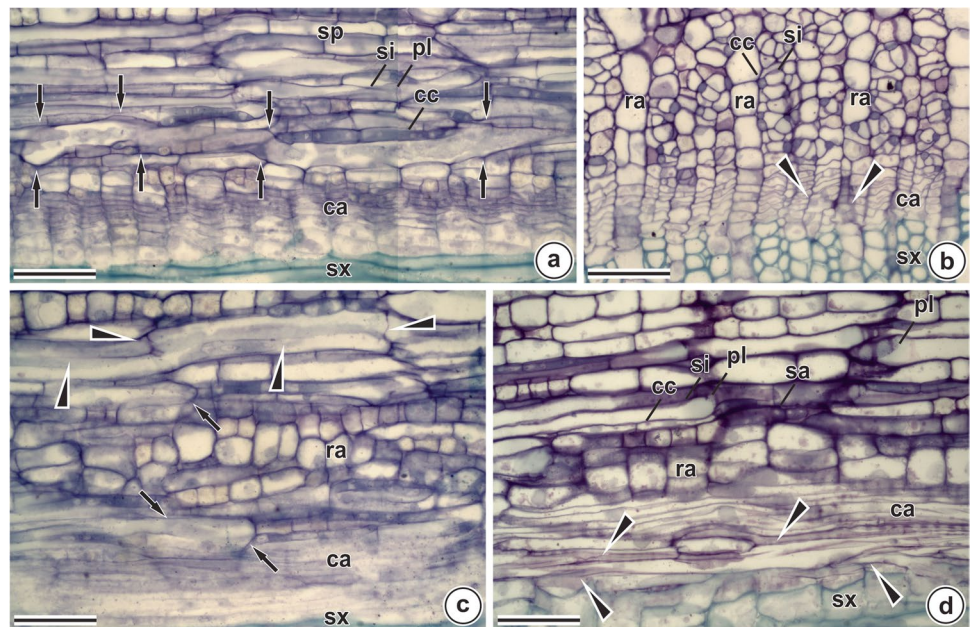
Discussion

Laticifer distribution in primary and secondary structures of the plant body

In *C. procera* the presence of laticifer is recorded in the cortex, pith, and between the outer and inner phloem strands of the bicollateral bundles of the stems. In *Allamanda blanchetii* (Gama et al. 2017), laticifer was recorded in the cortex and medulla and in the inner primary phloem. Pro-cambial origins were recorded in *Tabernaemontana catharinensis* (Canaveze and Machado 2016), and *Vallis solanaceae* (Gondaliya and Rajput 2016). These differences in origin of the laticifer could constitute a taxonomic marker for groups of closely related species. However careful evaluations starting at

the beginning of their development are necessary in order to correctly delimit laticifer distributions in the stem primary structure, in light of their close association with the phloem when they originate in the ground meristem. The occurrence of laticifers within colleters has not been observed in *C. procera*, but was reported in both *Mandevilla illustris* (Apezzato-Da-Glória and Estelita 2000) and *A. cathartica* (Thomas and Dave 1989). Colleters are secretory structures found in the axils of expanding leaves whose secretions are capable of protecting the leaf primordia and apical meristem against dehydration, herbivores, and pathogens (Mercadante-Simões and Paiva 2013). The presence of laticifer in primary stem tissues is related to the protection of the shoot apex against biotic components of the environment (as observed in the rubber tree *Hevea brasiliensis* [Euphorbiaceae]) (Tan et al. 2017).

Fig. 10 Ontogenesis of laticifer—*anastomosis*—in the secondary structure of the stem of *Calotropis procera* (Apocynaceae). Longitudinal sections (**a**, **c–d**) and transversal section (**b**). Increase in the lengths and calibers of the laticifer through the dissolution of the transverse and longitudinal walls of fusiform cambial derivatives. *ca* vascular cambium, *cc* companion cell, *pl* sieve plate, secondary phloem *sp*, *ra* ray, *si* sieve tube element, *sx* secondary xylem, *arrow* laticifer, *arrowhead* anastomosis. Scale bars: a–d = 50 μ m



Laticifer originating from cambial fusiform derivatives cells, recorded in *C. procera*, was likewise observed in the stems of *V. solanaceae* (Gondaliya and Rajput 2016) and *Tabernaemontana catharinensis* (Canaveze and Machado 2016), as well as in the roots of *M. atrovioleacea* (Lopes et al. 2009), and we point out that there are few studies on the presence of laticifer in the secondary body of Apocynaceae plants. The axial distribution of laticifers in secondary phloem gives rise to specific organizational patterns in relation to other cellular elements of that tissue. Laticifer of *H. speciosa* are randomly distributed throughout the phloem (Souza et al. 2021), but organized in axial concentric layers in the rubber tree *H. brasiliensis* (Tan et al. 2017; Nicole et al. 1991); in *Swartzia* (Fabaceae), they are positioned in groups of tangential bands (Oliveira et al. 2021a, b). Laticifers may also be present in the rays, as in *V. solanaceae* (Gondaliya and Rajput 2016). The radial parenchyma behaves as a repair system in case of any interruptions of axial flow caused by biotic or abiotic factors (Prado and Demarco 2018). Laticifer has also been observed in the inner intra-xylem secondary phloem, originating from the bidirectional activity of the inner cambium of the bicollateral bundles (Gondaliya and Rajput 2016). The association of the laticifer with the phloem provides plant sap for the intense biosynthetic demands of these secretory structures for latex synthesis (Prado and Demarco 2018).

Structural type

The laticifer present in the cortex, pith, and secondary phloem of *C. procera* is of the anastomosing type.

Transverse anastomosis (the fusion of longitudinally adjacent cells) results in the elongation of the laticifer, and the fusion of laterally adjacent cells gives rise to ramifications in the primary structure (Gonçalves et al. 2018). In the secondary structure, the fusion of laterally adjacent cells increases the caliber of the laticifer (Souza et al. 2021). The structural type of laticifer can often constitute taxonomic characters (Ramos et al. 2019; Pirolla-Souza et al. 2019; Leme et al. 2020; Medina et al. 2021; Teixeira et al. 2020). However, different types of laticifer can be observed in the same species (Teixeira et al. 2020). The structural type already described must be treated with care, as those classifications must be based on ontogenetic studies (Lopes et al. 2009; Gama et al. 2017; Gonçalves et al. 2018; Teixeira et al. 2020; Souza et al. 2021).

An anastomosing structural type appears to be the most frequent in most Apocynaceae species and in the most of the families studied until now. The laticifers of that group are formed by the rapid and early dissolution of the cell walls of stem apical meristem precursors through the centrifugal dissolution of the cell walls and the formation of a central lytic vacuole that contains part of the cytoplasm as well as previously synthesized latex, as described for *H. speciosa* (Gonçalves et al. 2018; Souza et al. 2021), *A. blanchetii* (Gama et al. 2017), and *Rhabdadenia* (Prolla-Souza et al. 2019). Transverse and longitudinal anastomosis of the fusiform cambial derivatives (the precursors of the laticifer) was observed in *H. speciosa* (Souza et al. 2021) and is very similar to that described here for *C. procera*.

Fig. 11 Chemical compounds in *Calotropis procera* (Apocynaceae) latex. Transversal (**a**, **d–g**, **i–j**) longitudinal sections (**b–c**, **h**). **a–b** Terpenes (stained purple with dimethyl-para-phenylenediamine hydrochloride). **c–d** Alkaloids (stained brown with Lugol's reagent). **e** Phenolic compounds (stained blue with toluidine). **f** Flavonoids (stained red with *p*-dimethyl amino cinnamaldehyde). **g–h** Mucilage (stained pink with toluidine blue pH 4.7). **i–j** Protein (stained red with Xylidine-Ponceau). *ca* vascular cambium, *co* cortex, *fi* gelatinous fibers, *pl* sieve plate, *pi* pith, *si* sieve plate element, *sp* secondary phloem, *sx* secondary xylem, *vs* vascular cylinder, *arrow* laticifers in the secondary phloem, *arrowhead* laticifers in the cortex. Scale bars: **a**, **c**, **g** = 200 μ m; **b**, **d**, **f** = 50 μ m; **e**, **h** = 100 μ m

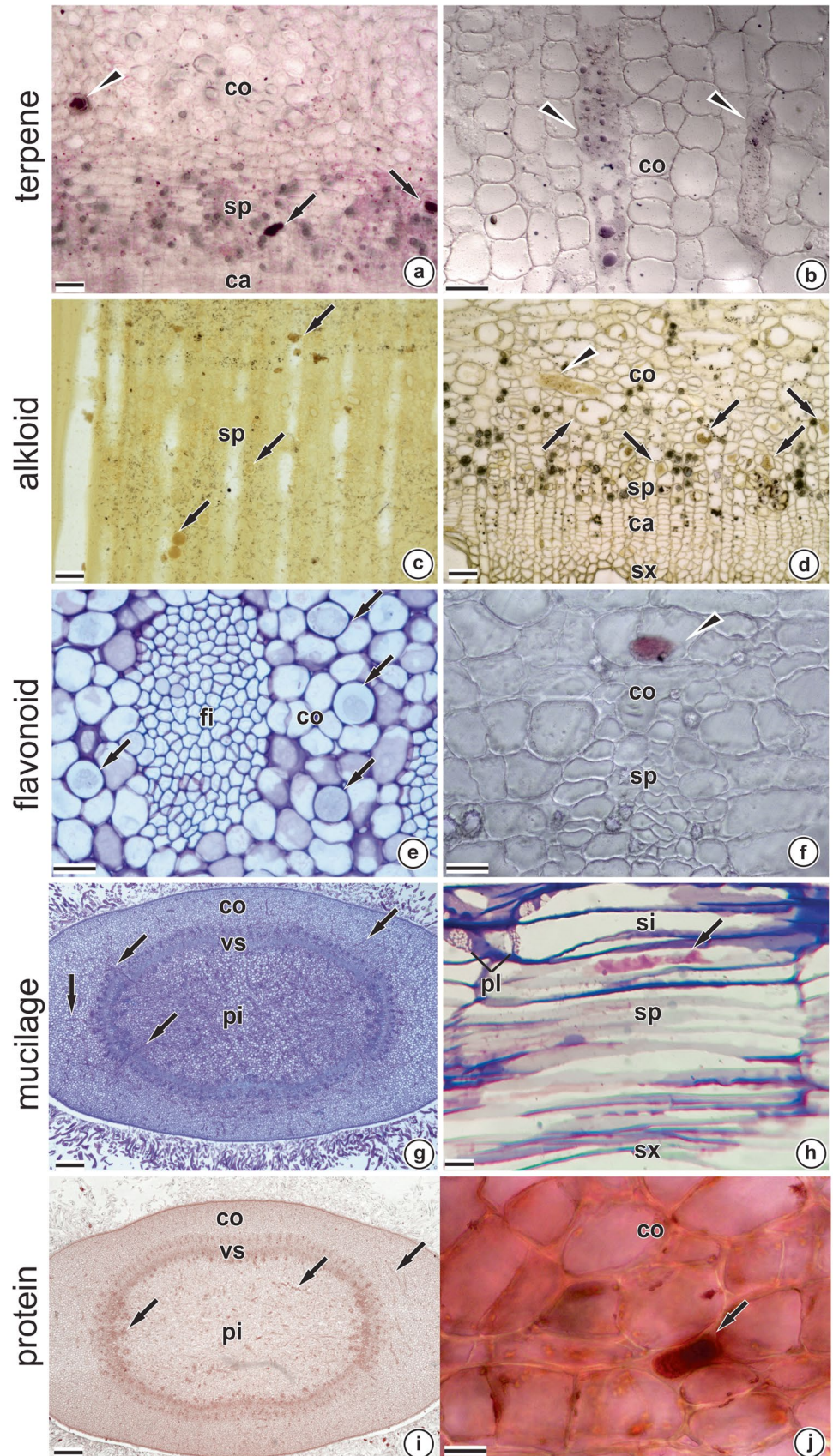
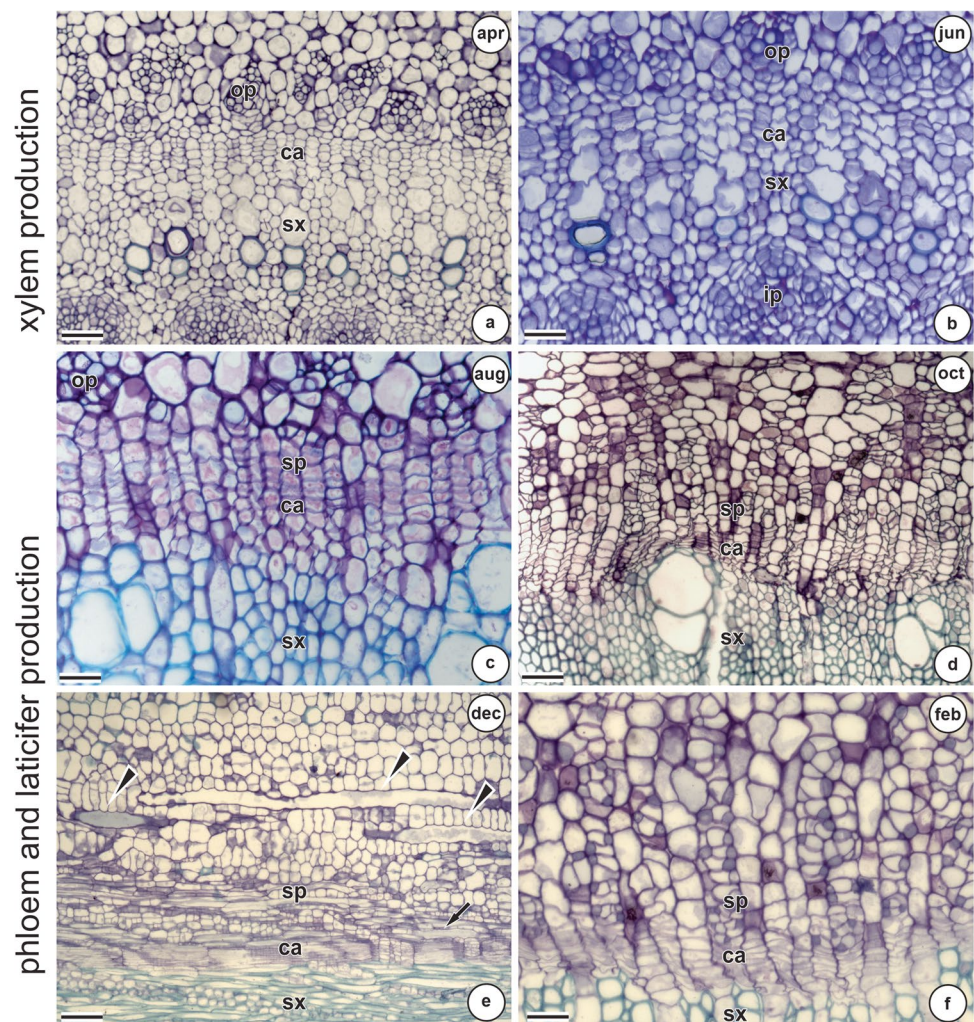


Fig. 12 Cambial activity and the ontogenesis of laticifer in secondary phloem in the stem of *Calotropis procera* (Apocynaceae) as a function of climatic seasonality. **a–d, f** Transversal sections. **e** Longitudinal sections. **a–d** Cambial activity directed toward the production of phloem from October to March, when rainfall, temperature, and day length are all increasing. **e–f** Cambial activity directed toward the production of xylem between April and September, when rainfall, temperature, and day length are decreasing, and no laticifer is observed. *ca* cambium, *ip* inner phloem, *op* external primary phloem, *sp* secondary phloem, *sx* secondary xylem. Scale bars: **a–f** = 50 μ m



Latex composition and laticifer development

The economic potential of latex is well known, especially in terms of the production of morphine from the poppy *Papaver somniferum* (Papaveraceae) (Labanca et al. 2018) and natural rubber from *H. brasiliensis* trees (Habib and Ismail 2021). Our results indicate that the latex of *C. procera* is composed of a mixture of terpenes, alkaloids, flavonoids, mucilage, and proteins. Earlier studies evidenced that the chemical constituents of *C. procera* latex like steroids, glycosides, flavonoids, alkaloids, and saponins offer promise for the development of new therapeutic drugs in light of their high effectiveness and low LD50 (Al-Snafi 2015; Kaur et al. 2021). Antitumor (Viana et al. 2017), antimicrobial (Tavares et al. 2021), and antiparasitic (Cavalcante et al. 2020) properties of fractions of *C. procera* latex have been reported. The latex is also associated with ecological functions of plant protection against herbivory (Agrawal and Konno 2009; Ramos et al. 2019) and controlling phytopathogens (Freitas et al. 2011, 2020; Kaur et al. 2021).

Calotropis procera is an evergreen species that grows throughout the year (Almeida et al. 2019) and continually produces latex in laticifer that develop in the apical meristem. While its cambial activity remains uninterrupted, it produces phloem and laticifer only during the rainy and hot spring/summer season. *C. procera* has ecophysiological attributes that allow positive water use dynamics, which has resulted in its becoming an invasive species in the semiarid regions of Brazil (Oliveira et al. 2009; Frosi et al. 2012; Sobrinho et al. 2013). The native species in those environments demonstrated distinct behavioral from *C. procera*, evidencing a period of vascular cambium dormancy—but reactivation in response to increasing day length, temperature, and rainfall during the rainy/cold season (Marcati et al. 2016; Souza et al. 2021). In the Cerrado, most species show vegetative growth in the transition from the dry to the rainy season, demonstrating an adaptation to maximize the use of water and nutrients (Novaes et al. 2020; Oliveira et al. 2021a, b; Pereira et al. 2022). The distinct behavior of *C. procera* from the other species of the Cerrado

can be useful for defining strategies for the commercial exploitation of *C. procera* latex.

Conclusion

The laticifer present in the primary structure of *C. procera* stems originates from the procambium and ground meristem of the cortex and medulla and differentiates from the phloem fusiform derivative cells in secondary stem structures. Careful evaluations starting at the beginning of their development are necessary in order to correctly delimit laticifer distributions in the stem primary structure, in light of their close association with the phloem when they originate in the ground meristem. The structural type of laticifer (in both primary and secondary stem structures) is the anastomosing, and it increases in lengths and calibers and ramifies through the dissolution of the transversal and longitudinal walls of the precursor cells. The ontogeny of laticifers in the secondary phloem, derived from cambial activity, has been little studied, however, constituting a gap in our knowledge concerning laticifer. The latex from *C. procera* is related to its deterrent actions against herbivores and pathogens and can provide raw materials for the production of useful drugs. The synthesis is uninterrupted in the apical meristem and occurs only in the wet/hot season in the secondary phloem. The vegetative growth, without a resting phase in the dry/cold season, typical of cerrado plants, gives *C. procera* some advantages in terms of obtaining latex for commercial purposes.

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Author contribution MO Mercadante-Simões conceived and designed the research and performed the ultrastructural analyses. LM Ribeiro analyzed the quantitative data. BMCS and AFS performed the anatomical, histochemical, morphometric, and micromorphometric analyses. IFPA performed the field work. All authors contributed to writing the text.

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Declarations

Conflict of interests The authors declare no competing interests.

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