Comparative root anatomy and root bud development in two species of Malvaceae

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Abstract

Aims. Since underground plant organs, usually the thickened ones, are structures capable of producing buds that allow shoot regrowth when the aerial part of the plants is eliminated by human disturbances or fire episodes and some plants have roots that produce buds, which may or may not be branched systems, but which allow vegetative propagation in unfavorable environments, due the presence of carbohydrate of reserves tis study aimed to analyze the roots of two Brazilian species, *Apeiba tibourbou* and *Pachira aquatica*, which present starch grains, root buds and capacity to propagate vegetatively and to compare the anatomical structure of these gemiferous roots.

Methods. The material of both species was analyzed *in loco* environment, collected and anatomical standardized methods were used to compare the species. Also tests for carbohydrate detection were made.

Results. Anatomical analyses showed that these roots produce endogenous buds, originating from pericycle cells in *A. tibourbou* and from parenchyma rays in *P. aquatica*. Both species presented starch as carbohydrate reserve but with significance difference on the amount between them.

Conclusions. The results demonstrated the diversity not only in relation to the high potential of differentiation and specialization of plant cells, but also in relation to the reproductive strategies adopted by these species, whether they are associated with the environment or not.

Introduction

Thickened underground organs are usually structures with bud shoot-forming potential which allow the regrowth and vegetative propagation of plants. They usually occur in disturbed environments and have a stem, root or mixed nature (Appezzato-da-Glória 2015).

Disturbed environments involve ecological disturbances that can affect plant strategies, as well soil and climate playing a role in the evolutionary ecology of vegetation (Gleason 1926; Grubb 1977; Grime 1979; Bellingham and Sparrow 2000; Pausas and Bond 2018).

Among the subterranean organs capable of vegetative propagation, root buds are structures responsible for the sprouting of tree species in Brazilian forest areas and, according to Appezzato-da-Glória (1995), the first reports of root sprouting in these areas were those of Uhl (1982), Rodrigues et al. (1990), and Castellani and Stubblebine (1993).

Root sprouting has the ability to form adventitious buds on roots, as an importante form of clonal growth in a number of species, and serves as both a survival strategy and a means of spatial expansion, particularly in plants growing in severely and recurrently disturbed habitats (Bartušková 2021).

The largest survey of tropical species with root suckers was carried out in a remnant of Seasonal Semideciduous Forest in the cities of Campinas and Piracicaba (SP, Brazil) with Leguminosae species:

Bauhinia forficata Link, *Centrlobium tomentosum* Guill. ex Benth., *Inga laurina* Wild. and *Esenbeckia febrifuga* A. Juss. (Rutaceae) (Hayashi and Appezzato-da-Glória 2009).

In this study the authors have shown that in *Bauhinia forficata* adventitious buds, developed from meristemoids. In *Centrolobium tomentosum* buds developed near the vascular cambium and in *Esenbeckia febrifuga* buds originated from the callus in injured and non-injured areas of the cutting. *Inga laurina* had exogenous buds originated from meristemoids formed in the proliferated phloematic parenchyma.

It is importante to emphasize that gemiferous belowground organs wich resprout in favorable periods build up carbohydrate stores (Alonso and Machado 2007). Verdaguer and Ojeda (2005) associated the importance of the bud bank and the starch reserve being that the decrease of carbohydrates in underground organ after the sprouting period, was registered by Dietrich and Figueiredo-Ribeiro (1985). According to Hoffmann (1999), in Cerrado plants, there is a high investment in the accumulation of reserve carbohydrates in underground organs, which allows rapid replacement of tissues that were lost by the action of fire, thus contributing to their survival.

The species *Apeiba tibourbou* Aubl. is popularly known as "*pente de macaco*" or "*pau de jangada*". It is distributed from the North of Brazil to Minas Gerais and São Paulo, in the sandbank forests of Maranhão, in the riparian forests of the Cerrado in the Midwest of Brazil, and in the Atlantic Forest. It is a medium-sized tree easily recognized by its whitish leaves on the underside, and the presence of a tuft of stellate trichomes in the axils of the basal and lateral veins of the leaf blades. Its fruits are globose and flat, covered by thorns. It is a pioneer species and a good alternative for reforestation projects, also used in landscaping projects due to the beautiful fruits and flowers.

Apeiba tibourbou was widely used in the production of rafts in the mid-19th century, for its straight trunk and low-density wood, and it is now on the list of endangered species. The literature brings very little information about the structure of this plant, restricted to its external morphology. The presence of underground organs of vegetative propagation, as observed in individuals of *A. tibourbou* in the Arboretum of the Federal University of Alagoas (UFAL, AL - BR), has never been reported.

Regarding the structural characterization of *A. tibourbou*, the literature does not provide anatomical descriptions of any organ. However, the need for anatomical studies of its secondary xylem has already been mentioned by Lobão et al. (2008). These authors argued that such studies would provide support for the quality of the wood and consequent use in a sustainable manner, with different opportune possibilities of uses in the future, because the noblest wood species are already scarce in our forests. Due to its rapid growth, it can be used for the reforestation of degraded areas of permanent preservation (Colli-Silva 2020).

Most of the information available about the structure of *A. tibourbou* is related to external morphology (Lorenzi 1992; Lobão et al. 2008), and some references describe seed germination studies (Pacheco et al. 2004; Guedes et al. 2013).

Pachira aquatica Aublet, commonly known as “munguba”, “castanheira-do-maranhão”, “castanheira” and “cacau-selvagem”, is a tree native to Brazil, observed from southern Mexico to northern South America, generally found in marshy lands and riparian forests but easily adapting to different edaphic and climatic conditions (Peixoto and Escudeiro 2002; Paula et al. 1996). It has as natural habitat the periodically flooded forests of the coast of Pará and Maranhão, measures 6–14 m in height, and its fresh chestnuts are suitable for consumption, but they are usually roasted (Lorenzi et al. 2006). It is a fruit species that was introduced in urban afforestation in the second half of the 19th century by French landscape designer and botanist Glaziou during his stay in Brazil (Lorenzi 1992).

Similarly, to *A. tibourbou*, the literature provides little information about the structure and reproduction of *P. aquatica*, with better documentation of the anatomical structure of its secondary xylem (Hamad et al. 2017; Clair et al. 2019; Lehnebach et al. 2020).

For the Malvaceae family the presence of vegetative propagation by gemiferous roots was documented in the species *Bombax costatum* Pellegr. & Vuillet, however the work reports the effects of mother tree diameter and origin of cuttings (Zéphirin et al. 2019) and did not provide any information about the anatomical features of the structure, or regarding the origin of the buds.

In view of the context described above, this work aimed to compare the anatomical structure of gemiferous roots of *A. tibourbou* and *P. aquatica*, with the aim of investigating which tissues are responsible for the buds formation and development of new clonal individuals and also verifying the presence of carbohydrate reserves that provide energy for this process.

Materials And Methods

The individuals of *A. tibourbou* analyzed were found in the Arboretum of the Federal University of Alagoas (A. C. Simões Campus). In total, six specimens that presented underground vegetative propagation were analyzed.

The UFAL Arboretum is a natural forested area within the Federal University of Alagoas, which was reforested after being transformed into a garbage area. Currently, despite being a forest on a smaller scale and not having the biodiversity of a natural forest, it is a climate maintenance area and does not present any external influence, such as anthropic actions or ecological disturbance.

The individuals of *P. aquatica* were also found in the A. C. Simões Campus, scattered in several different places and four specimens were analyzed.

In addition to the material collected for anatomical analysis, leaves and reproductive organs were collected for herborization and deposit in the Herbarium Professor Honório Monteiro (Museum of Natural History - Federal University of Alagoas – AL, BR) (MUPAL) under the number 4676 (*P. aquatica*) and in the Herbarium MAC -Instituto do Meio Ambiente do Estado de Alagoas – AL, BR under the number 65690 (*A. tibourbou*).

For the analyses, the soil at the base of all tree individuals of the two species was removed to expose the most superficial underground part, in order to detect the points of insertion of the buds in the roots of the mother plant. In the case of *A. tibourbou*, the soil was removed throughout the whole extent of the branched organ. In the case of *P. aquatic* trees, soil removal was carried out only in the area of the base of the trees, since they did not present a diffuse system. When the underground part exposed, a visual analysis was carried out and a photographic record was made.

Fragments of several segments were collected and after that the material was fixed in FAA 70 for 24 hours (Johansen1940) and stored in 70% alcohol. For the anatomical analyses, hand-cut transverse and longitudinal sections were prepared with the aid of razor blades, stained with Astra blue and safranin (Kraus and Arduin 1997) and mounted on semi-permanent histological slides with 40% glycerin for analysis under an optical microscope. To detect the presence of reserve carbohydrates, in this case starch, it was performed tests with lugol solution (Johansen 1940).

Results

During the *in loco* analyses, it was possible to observe that *A. tibourbou* had a diffuse underground system with extensive branching, with many buds and new stem branches (Fig. 1,2) up to 4 meters away from the mother plant.

During the handling of the samples in the laboratory to separate them into smaller portions for storage, it was possible to observe a large amount of a viscous and transparent substance secreted through the peripheral part, which continued to be observed even after one year of sectioning the samples and of storage in 70% alcohol (Fig. 3A).

The anatomical analyses showed, in the secondary body, a coating composed of a periderm with six to 11 layers of phellem (Fig. 3B) and, adjacent to the phelloderm, two to four layers of parenchyma cells (Fig. 3C). Internally to the parenchyma cells, secretory spaces were observed, always located opposite the primary phloem (Fig. 3A-E).

The secondary phloem was wedge-shaped, with parenchyma rays that undergo intense dilatation towards the primary phloem (Fig. 3C) and the conducting elements of the secondary phloem are interspersed with sclerenchyma cells (Fig. 3E). Internal to the secondary phloem is the vascular cylinder with the cambium and xylem. The secondary xylem, adjacent to the cambium, is composed of broad rays and vessel elements, with fibers and parenchyma cells surrounding it (Fig. 3F). In the center of the structure, there was the exarch primary xylem with centrifugal maturation, some samples with four and others with five protoxylem poles (Fig. 4A, B).

The samples showed buds on the periphery of the organ (Fig. 4C, D), with traces contiguous with the center of the structure, following its growth in diameter (Fig. 4E) and presenting vessel elements (Fig. 4F). When analyzing the central region in greater detail it was observed that the origin of these buds was endogenous and their formation started from the proliferation of pericycle cells, between the protoxylem

poles (Fig. 5A, B). Many starch grains were observed on the secondary xylem in cells of axial and radial parenchyma (Fig. 5C, D).

In loco analysis of *P. aquatica* revealed that the studied samples also had vegetative propagation through the roots but, unlike *A. tibourbou*, the roots did not form a diffuse underground system; they led to the emergence of new individuals, through budding, only close to the mother plant (Fig. 6A-C).

In the secondary body, the anatomical analyses revealed a coating composed of periderm, with approximately seven layers of phellem (Fig. 7A). Cortex cells were observed internally to the periderm, distributed in approximately 10 layers. Obliterated primary phloem cells were visualized adjacent to these layers, followed by secondary phloem with cells arranged in a wedge shape resulting from the enlargement of the parenchyma rays between these cells (Fig. 7A). The secondary xylem was composed of thin rays, vessel elements, fibers and axial parenchyma cells (Fig. 7B). In the center of the organ, the primary xylem was exarch, with centrifugal maturation and six protoxylem poles (Fig. 7C).

As in *A tibourbou*, buds were also observed in the periphery of the organ, with traces contiguous with the center of the structure, following its growth in diameter (Fig. 7D, E), however, they were formed from divisions of parenchyma ray cells, opposite to the protoxylem poles (Fig. 7F). Starch grains were observed on the secondary xylem in cells of axial and radial parenchyma (Fig. 7G).

Discussion

The occurrence of clonal populations of tree species established by the process of bud formation in underground root systems in temperate climates is a topic already mentioned by Appezzato-da-Glória (2015), through the citation of several authors.

In Brazil, the occurrence of diffuse bud systems in grassland plants, both in savannah environments and in other terrestrial habitats, was first reported by Rizzini and Heringer (1966). In this work, the authors associated the formation of root buds with disturbed environments, mainly by the action of fire. This phenomenon was also reported by Pausas et al. (2018) as an effective regrowth mechanism in response to disturbances, including fires, since these below-ground buds are usually protected from fire by the ground. This association, however, was not found in the present work because the sites from where the species analyzed come have never undergone any fire episode in their history.

Rizzini and Heringer (1966) also emphasized the need to analyze the structural nature of these organs, since without an accurate anatomical analysis they could be confused with soboles, diffuse stem systems with the same characteristics of root buds as to thickness, depth and capacity of vegetative propagation (Appezzato-da-Glória 2015). Such analysis of underground structures has also been reported by other authors (Menezes et al. 1969; Figueiredo 1972; Paviani 1972).

Regarding the origin of the buds, it can be endogenous in the case of additional buds and exogenous in the case of reparative buds, with initial formation in different tissues (Appezzato-da-Glória 2015). In this

work, the two species analyzed presented buds of endogenous origin, originating in the pericycle in the case of *A. tibourbou* and in the parenchyma ray cells in the case of *P. aquatica*. The latter origin of the bud was not reported by Appezzato-da-Glória (2015).

Many secretory spaces opposite to the primary phloem were found in *A. tibourbou*. In the transverse and longitudinal planes, these spaces presented an irregular rounded shape. Thus, as these structures were not elongated spaces in the longitudinal plane, which would characterize them as secretory channels or ducts, they are secretory cavities (Col 1903; Cury and Apezzato-da-Glória 2009). The location of these cavities may indicate a protective function against herbivorous animals, as they are placed just opposite the phloem (Cury and Appezzato-da-Glória 2009).

In roots of *Santolina leucantha* Bertol. (Asteraceae, Anthemideae), the intense secretion of secondary metabolites from secretory spaces may have an important environmental role in preventing herbivory (Pagni and Masini 1999). Furthermore, secretory spaces close to the phloem may also have the function of transporting photoassimilates (Williams 1954).

In Bromeliaceae species, the number of protoxylem poles has been considered as a characteristic that allows grouping species into different genera and subfamilies (Silva and Scatena 2011). This constant pattern was also seen in *Pachyrhizus ahipa* (Wedd.) Parodi (Fabaceae). However, root samples of *A. tibourbou* presented sometimes four and other times five protoxylem poles. According to Eames and MacDaniels (1947), Esau (1965) and Fahn (1990), in most species, the number of protoxylem poles in the central cylinder of the root may vary between different plants or between different roots of the same plant.

Gabrielli (1992) verified, for *Pyrostegia venusta* (Ker) Miers (Bignoniaceae), a variation in the organization of the root stele, which can be triarch to heptarch. A similar situation was reported by Appezzato-da-Glória and Estelita (2000) for roots of *Mandevilla illustris* Woodson and *M. velutina* K. Schum (Apocynaceae), whose stele organization varies from triarch to hexarch.

Regarding the advantages of vegetative propagation, according to Silvertown (2008), clonal propagules are more likely to survive under extreme environmental conditions when compared to seedlings because, in the early stages of growth propagules are linked to the parental plant through the vascular system and they often have higher biomass than seedlings of similar age (Abrahamson 1980).

Vegetative propagation also brings advantages in terms of the ability to “move”, but still allowing the connection with the mother plant (Crawley 1997), ensuring the survival in environments where resources are scarce and/or distributed along the time and space (Pitelka and Ashmun 1985; Alpert and Mooney 1986).

In the Brazilian *Cerrado*, fires are relatively frequent events (Coutinho 1990). They can eliminate buds, flowers, fruits, seeds and seedlings, exerting a negative effect on the sexual reproduction of the affected species and favoring those capable of vegetative propagation (Hoffman 2020).

In this way, regrowth from subterranean bud organs is essential for the maintenance of the species and the environment (Rizzini 1965; Appezzato-da-Glória 2003). Some species with the ability to vegetative propagation can eventually also reproduce by sexual reproduction, through the germination of seeds.

For *A. tibourbou*, germination tests in various substrates and at different temperatures revealed a high germination rate, but specimens with vegetative propagation were not considered (Pacheco et al. 2007), as it was the case of the present work. Unpublished results of germination tests conducted with the specimens used in the present study showed extremely low germination rates, which may be an indication that the environment where the individuals develop interferes to some extent with their reproductive strategy.

There is a relationship between germination rate and vegetative propagation in plants that present these two forms of reproduction, as already analyzed in species of Asteraceae in the Cerrado of the state of São Paulo (Cury et al. 2010). The results of this study showed that the species that has the ability to propagate sexually had a germination rate up to 15 times greater than the species that reproduces vegetatively. This could mean that the survival of a species with a low germination rate or low germination rate is guaranteed by assexual reproduction.

Mello-de-Pinna et al. (2022) repoted that gemmiferous potential of the xylopodia associated to its tissue parenchyma, with nutrient reserve (starch), and tuberous roots, with wide storage xylematic parenchyma tissue, are important features in the regeneration of aerial organs after drought and fire occurrence in *Homalolepis* Turcz. (Simaroubaceae, Sapindales).

In woody perennial trees with starch reserves as we can observe in this study, this storage allow their survival during winter and for vegetative growth in the following spring. The woody tissues function essentially as vegetative storage tissues in which starch accumulates seasonally in well-defined amyloplasts in the ray parenchyma cells (Sauter and van Cleve 1994).

Also it is importante to note that during the winter this starch in woody tissues is importante for cold tolerance (Noronha et al. 2018) and during spring in poplar wood the starch is completely hydrolyzed at the time of bud burst (Sauter and van Cleve 1994; Witt and Sauter 1994).

In Cyperaceae starch concentrations increased in fire frequencies in all parts of the plant, as did carbohydrate concentrations. Some studies point out a relation between the increase in starch reserves and resprout, in fire-prone ecosystems (Pausas et al., 2018) or seasonal variations (Khanizadeh et al. 1989; Palacio et al.; 2007, 2008), defoliation (Atkinson et al., 2014), herbivory (Machado et al., 2013), frost (Stoller and Weber 1975) and also soil temperature changes (Dong et al. 2001).

Regarding the carbohydrates reserves in Malvaceae, in *Sida cordifolia* L. roots minute starch grains are frequent within cortex and in xylem parenchyma surrounding the vessels (Pramanick and Srivastava 2015). Coarse roots of *Kosteletzkya pentacarpos* L. enable perennial plants to store large quantities of sugars and starches as reserves (Halchak et al. 2011). In *S.rhombifolia* L. roots starch grains were found

in the córtex, secondary phloem, ray phloem parenchyma, in xylem and in medullary rays (Navas et al. 2013). However nothing was reported about the relationship between the presence of starch and regrowth for Malvaceae family.

Conclusion

Vegetative propagation organs, whether diffuse or not, provide the plants that have this ability with an extremely important reproductive strategy, whether linked to disturbed environments or not.

This study showed that the two species analyzed presented root buds, with a branched system in *A. tibourbou* but not in *P. aquatica*. However, the two species presented the ability of regrowth from the mother plants, for the survival of individuals.

The buds formed from the roots had different origins, which demonstrates the diversity found not only with respect to the high capacity for cell differentiation and specialization, which is notorious in plants, but also regarding the strategies adopted by each of them for reproduction, whether associated with the environment or not.

Starch was found in both species here studied. As shown in literature this reserve allows plants not only to go through adverse conditions, but enable the development of new clonal individuals from the mother plant. In Malvaceae family this is the first report of gemiferous bud roots that plays this role and new information are needed to establish if this characteristic may be useful for phylogenetical studies or to improve the knowledge about this important function of plants.

Declarations

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Authors' Contributions

CURY and SANTOS designed, performed and writed-up the experiment, CURY and SANTOS analyzed the data, and FERRO, BARBOSA and LIMA provided the guidance during all experiments. All authors have read and approved the manuscript.

Data Availability

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

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Figures

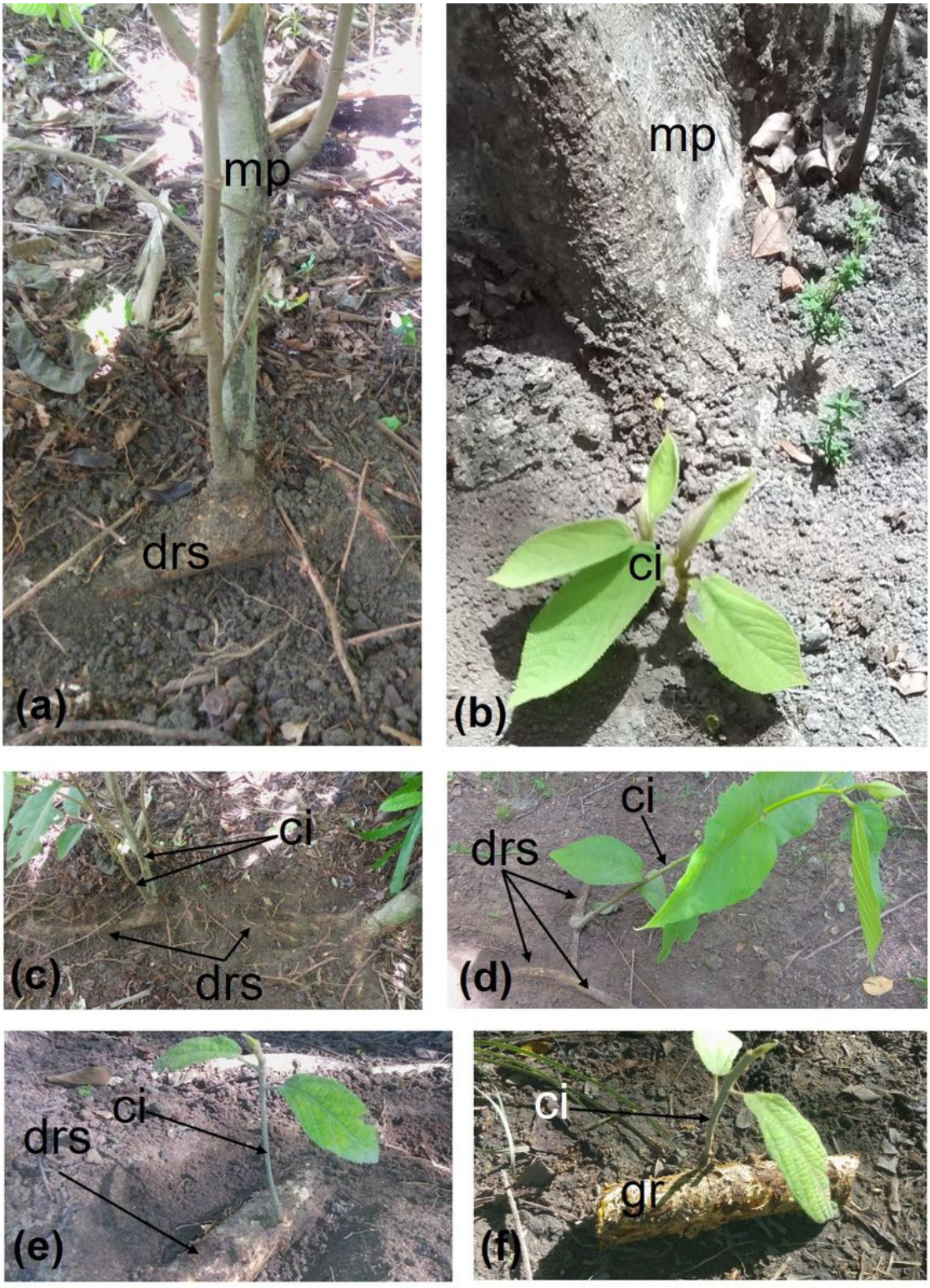

Figure 1

A. tibourbou in the field at the *Arboretum* in UFAL. ci = clonal individual; drs = diffuse root system; gr = gemiferous root; mp = mother plant.

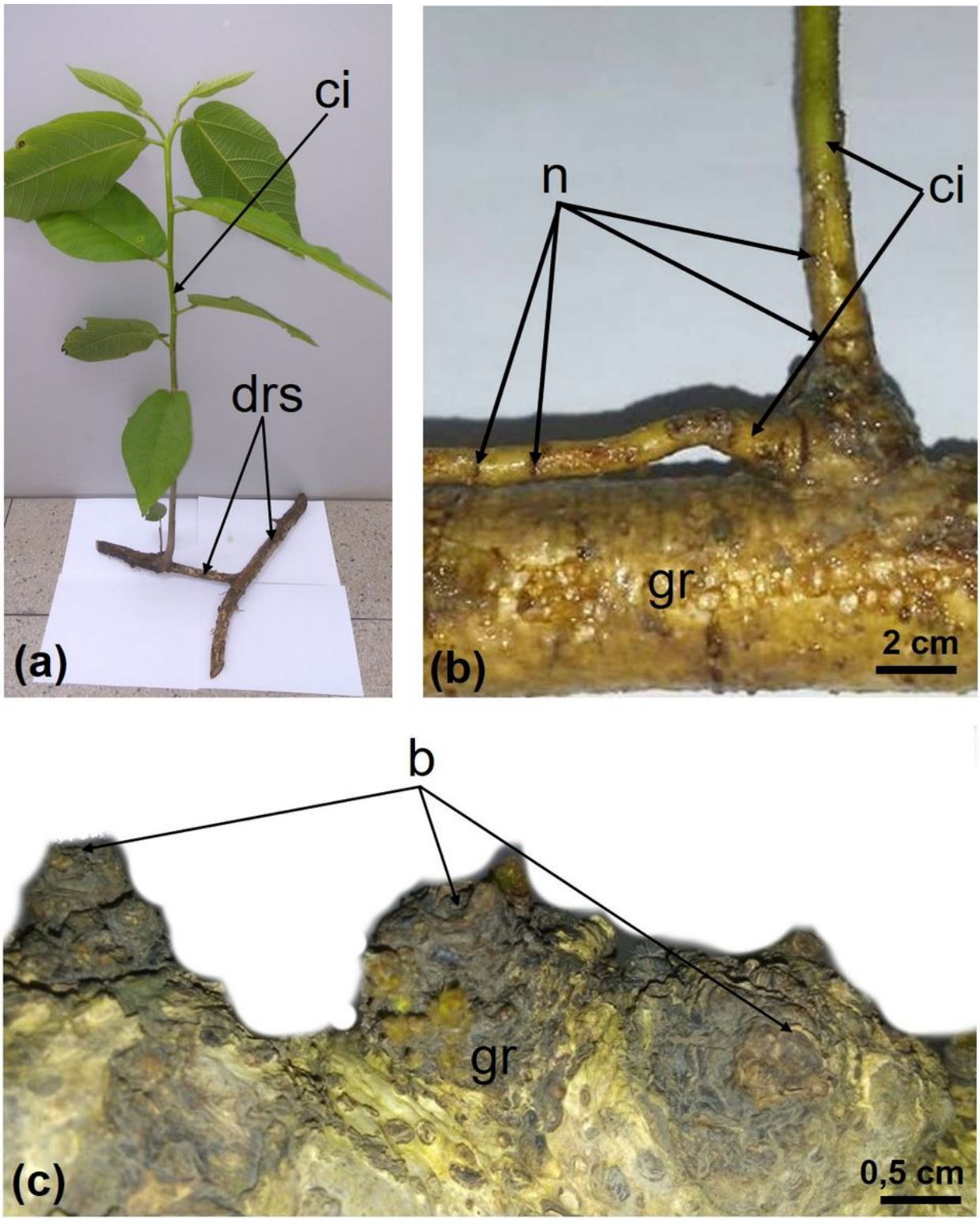

Figure 2

Samples of *A. tibourbou* in the laboratory after collection. b = bud; n = nodes.

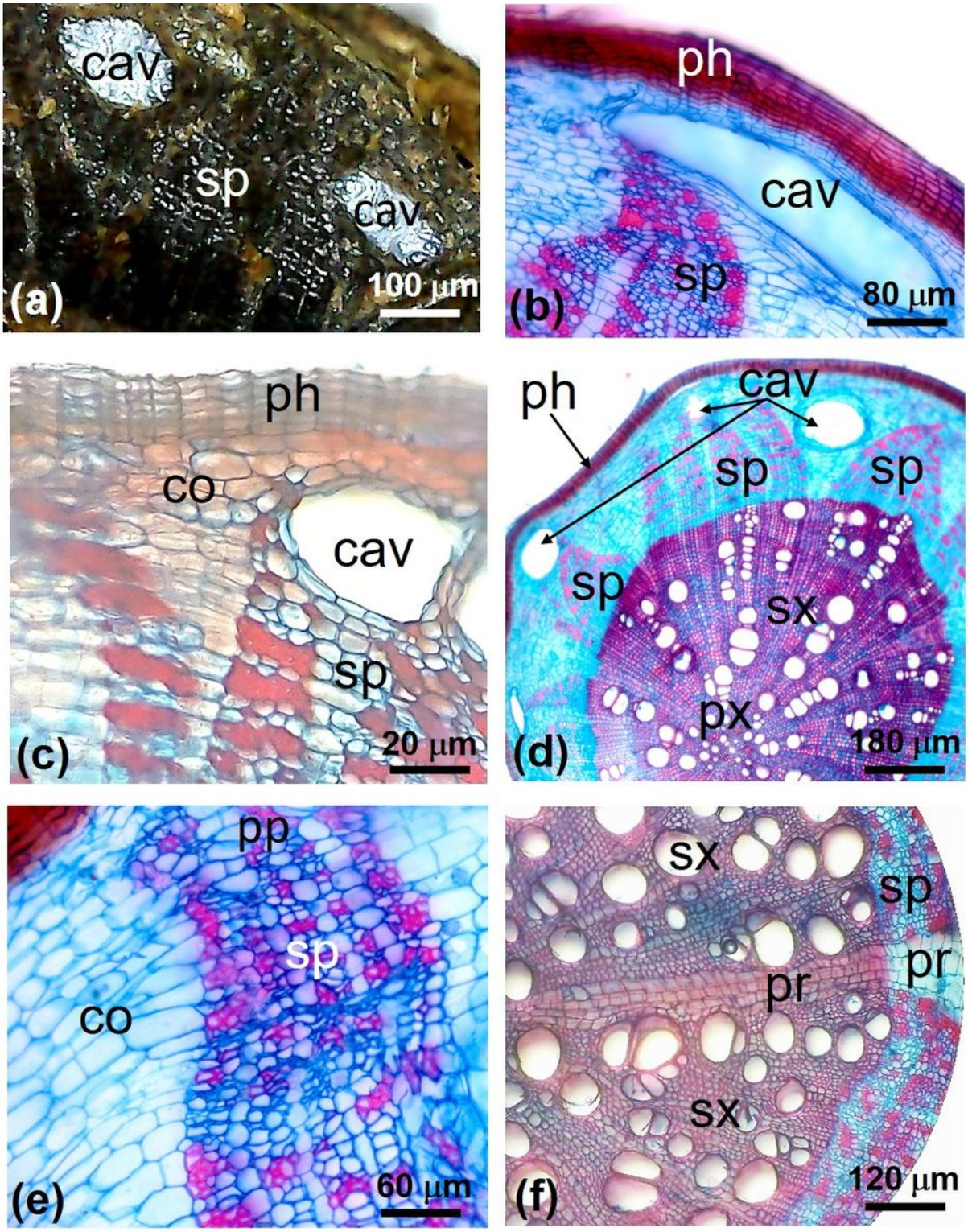

Figure 3

A. tibourbou crossections of the gemiferous root. cav = cavity; co = córtex; ph = phellem; pr = parenchymal ray; px = primary xylem; sp = secondary phloem; sx = secondary xylem.

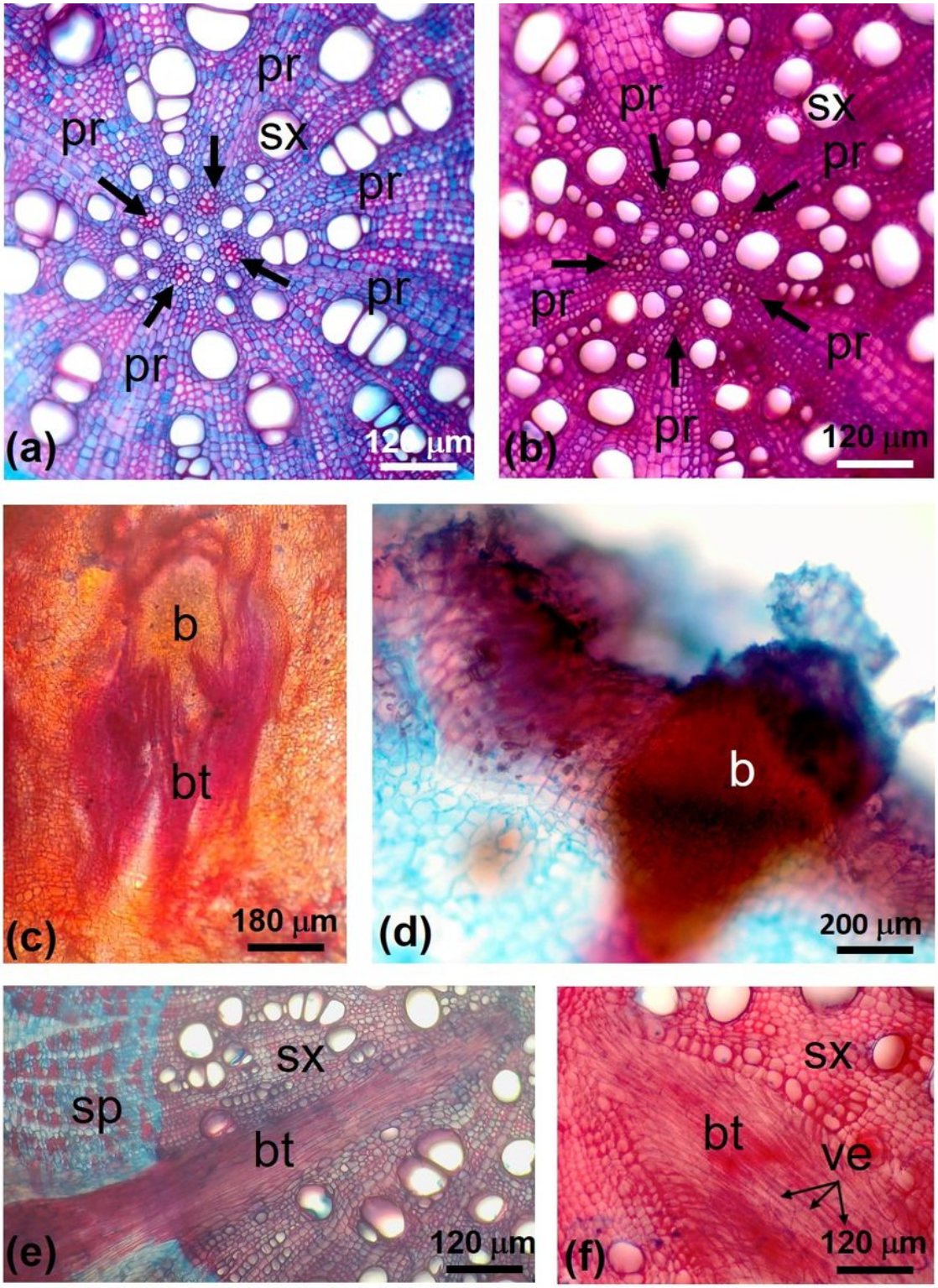

Figure 4

A. tibourbou crossections of the gemiferous root. b = bud; bt = bud trace; pp = pericycle; pr = parenchymal ray; sp = secondary phloem; sx = secondary xylem; ve = vessel element. arrows = protoxylem poles.

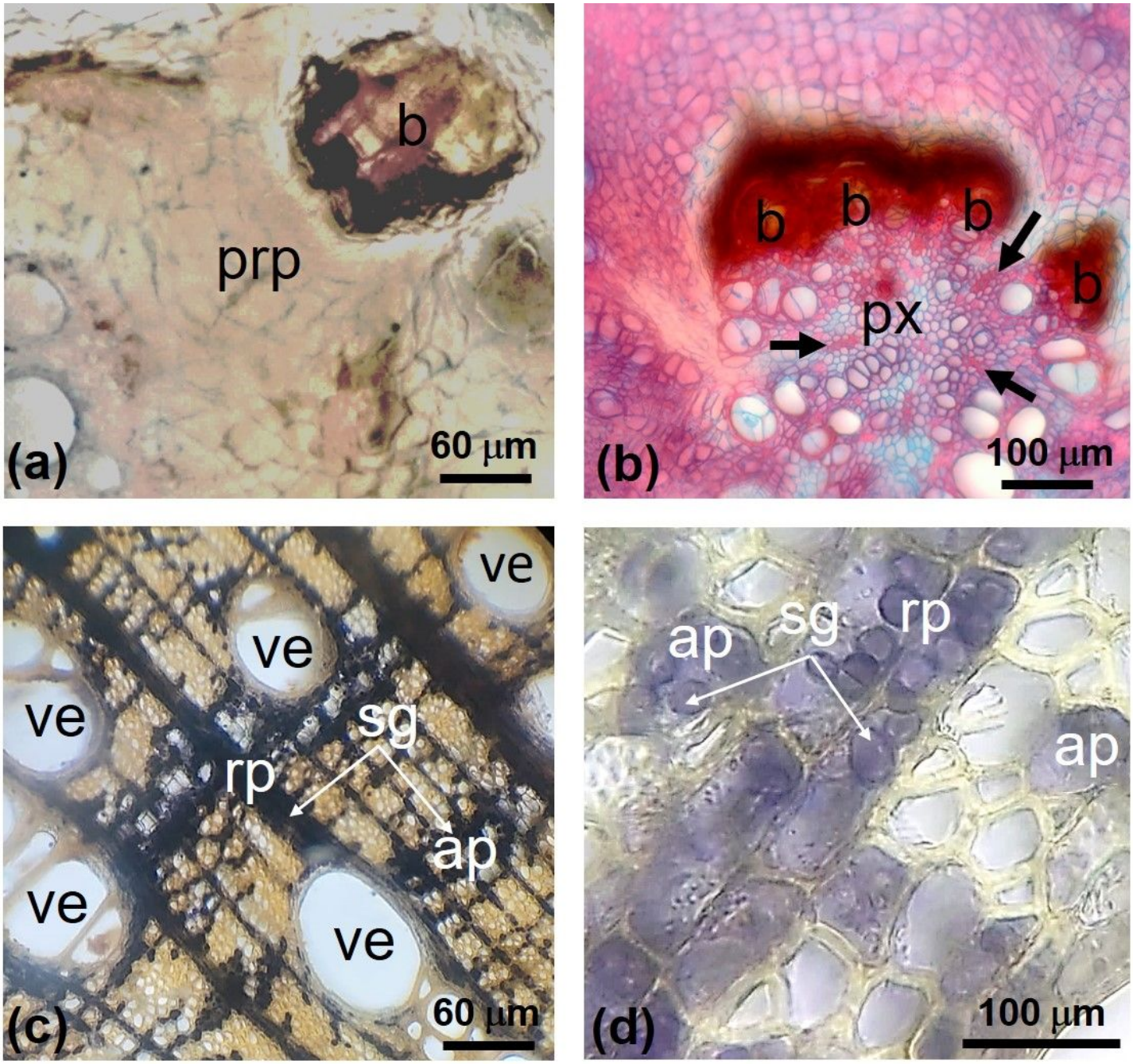

Figure 5

A. tibourbou crossections of the gemiferous root (A-D). *A. tibourbou* crossections of the stem (E,F). b = bud; co = córtex; p = pith; pp = pericycle; prp = pericycle proliferatios; px = primary xylem; sx = secondary xylem; sp secondary phloem; dotted arrows = protoxylem poles; dotted arrows = divisions of the pericycle cells.

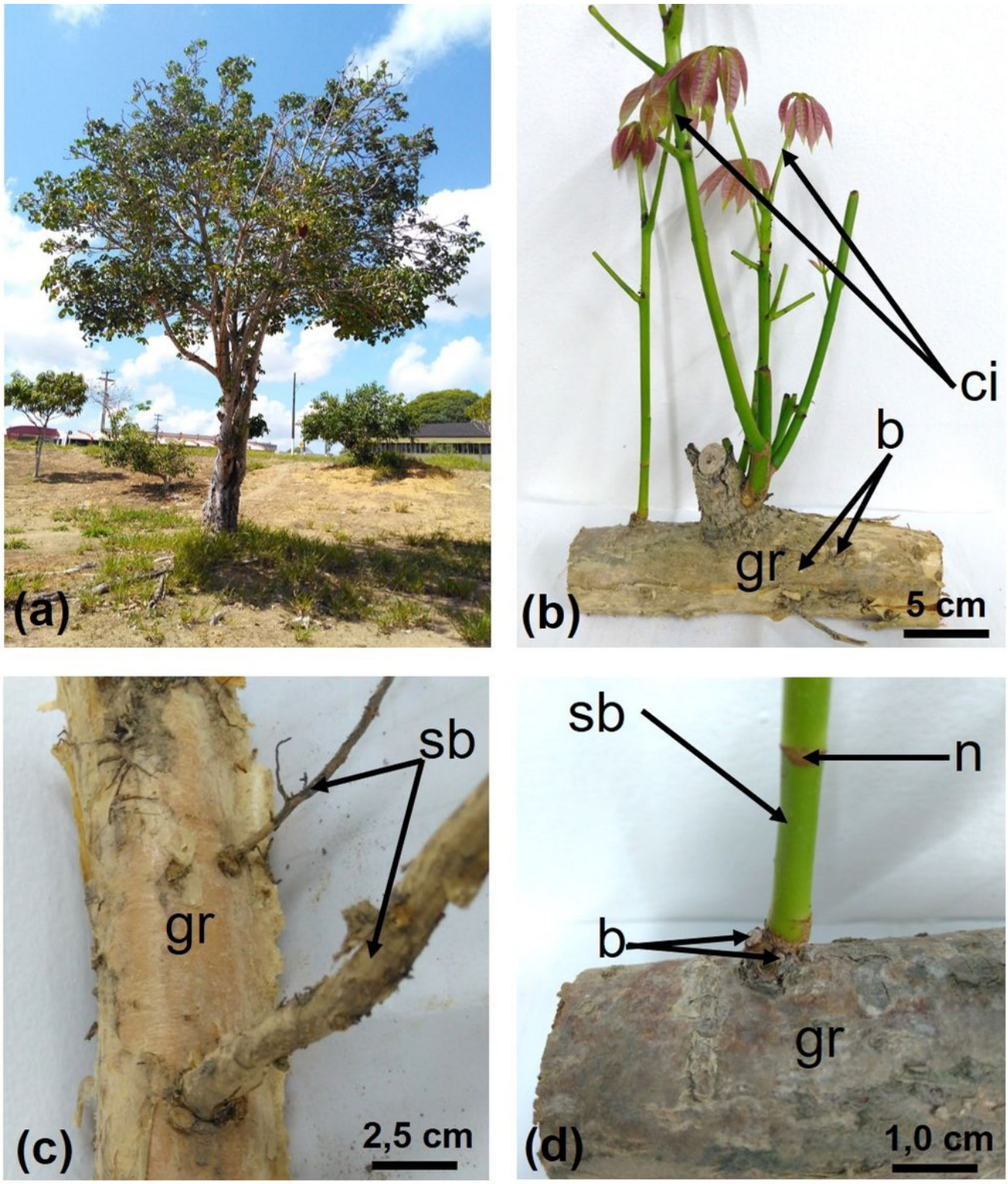

Figure 6

P. aquatica in the field at the UFAL *campus*. b = bud; ci = clonal individual; gr = gemiferous root; n = nodes; sb = stem branches.

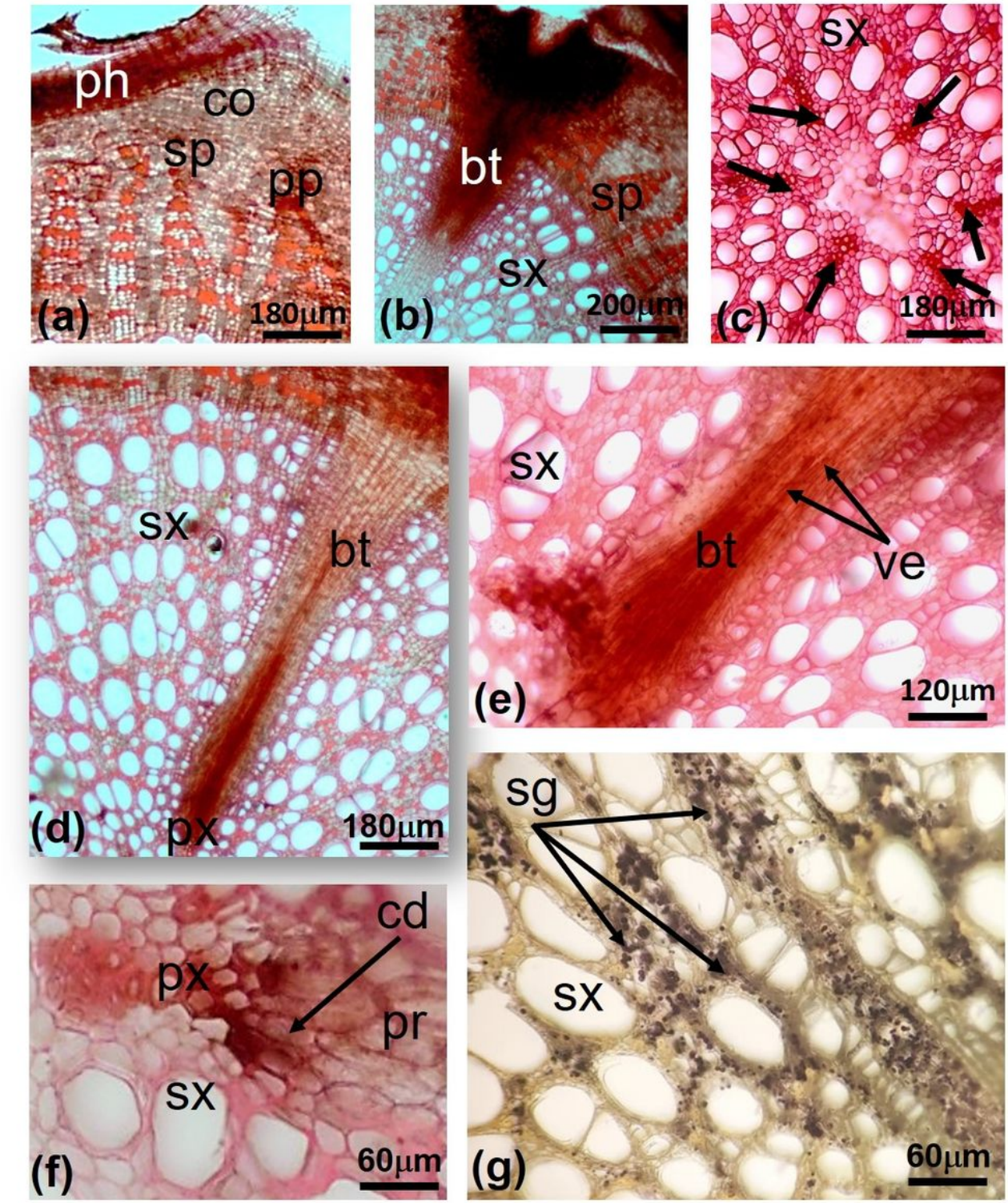

Figure 7

P. aquatica crossections of the gemiferous root. b = bud; bt = bud trace; cd = cell division; co = cortex; ph = phellem; pp = primary phloem; pr = parenchymal ray; px = primary xylem; sg = starch grains; sp = secondary phloem; sx = secondary xylem; ve = vessel element; arrows = protoxylem poles.