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Original Papers

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

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Abstract
Underground plant organs, usually the thickened ones, can be capable of producing buds that allow shoot regrowth when the aerial part of the plants is eliminated. 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 reserves. This study aimed to analyze and compare the anatomy of the roots of two Brazilian species, *Apeiba tibourbou* and *Pachira aquatica*, that present starch grains, buds and the ability to propagate vegetatively. Material of both species was analyzed *in loco*, collected and compared through anatomical analysis using standardized methods. Tests for carbohydrate detection were also applied. Anatomical analyses showed that the roots produced endogenous buds, originating from pericycle cells in *A. tibourbou* and from parenchyma rays in *P. aquatica*. Both species presented starch as carbohydrate reserve. The results demonstrated not only the high potential of differentiation and specialization of plant cells, but also the diverse reproductive strategies adopted by these species of the family Malvaceae, whether they are associated with the environment or not.
Key words: gemiferous roots, reserve carbohydrates, starch, underground systems, vegetative propagation.

Resumo
Órgãos subterrâneos das plantas, geralmente os mais espessados, podem produzir gemas que permitem novo crescimento de brotos quando sua parte aérea é eliminada. Alguns vegetais possuem raízes que produzem gemas, que podem ou não ser sistemas ramificados, mas que permitem o desenvolvimento vegetativo em ambientes desfavoráveis, devido à presença de carboidratos de reserva. Este estudo teve como objetivo analisar e comparar a estrutura anatômica das raízes gemíferas de duas espécies brasileiras, *Apeiba tibourbou* e *Pachira aquatica*, que apresentam grãos de amido e capacidade de propagação vegetativa. O material de ambas as espécies foi analisado in loco, coletado e métodos anatômicos padronizados foram utilizados para comparação das espécies. Também foram feitos testes para detecção de carboidratos. Análises anatômicas mostraram que essas raízes produzem gemas endógenas, originadas de células do periciclo em *A. tibourbou* e de raios do parênquima em *P. aquatica*. Ambas as espécies apresentaram amido como reserva de carboidratos. Os resultados demonstraram a diversidade não só em relação ao alto potencial de diferenciação e especialização das células vegetais, mas também em relação a estratégias reprodutivas adotadas por espécies da família Malvaceae, estejam elas associadas ao ambiente ou não.
Palavras-chave: raízes gemíferas, reserva de carboidratos, amido, sistemas subterrâneos, propagação vegetativa.

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Introduction

Thickened underground organs are structures generally with growth-forming potential that allow the growth and vegetative propagation of plants (Appezzato-da-Glória 2015). They generally occur in disturbed environments, playing an important role in the evolutionary ecology of the terrain (Gleason 1926; Grubb 1977; Grime 1979; Bellingham & Sparrow 2000; Alonso & Machado 2007; Pausas & Bond 2019). Among the subterranean organs capable of vegetative propagation, root buds are responsible for the sprouting of tree species in Brazilian forest areas (Appezzato-da-Glória 2015). Root sprouting consists in the ability to form adventitious buds on roots, as an important 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).

Malvaceae, a family of great economic importance, consists of about 200 genera and more than 4,000 species distributed throughout the tropics. In Brazil, members of this family are distributed among 81 genera and 866 species and can be found in all phytogeographic domains (Santos & José Neto 2017; Flora & Funga do Brasil 2023a, continuously updated). Some studies have investigated the morphological and anatomical structure and the taxonomic classification of Malvaceae species, but none the presence of gemiferous roots (Ibrahim 2018; Said *et al.* 2018; Erarslan & Koçyiğit 2019; Karakish *et al.* 2020; Das *et al.* 2021; Khasanah & Kusumarini 2021; Luna-Márquez *et al.* 2021; Silva *et al*. 2023; Weemstra *et al.* 2023). Regarding vegetative propagation in Malvaceae, there is only one record of the species *Bombax costatum* Pellegr. & Vuillet presenting roots capable of producing clones from the mother plant (Zéphirin *et al*. 2019), but no information about the anatomical features of the structure or regarding the origin of the buds is provided.

Known in Brazil as *pau-de-jangada*, *Apeiba tibourbou* Aubl is distributed from the North of Brazil to Minas Gerais and São Paulo and is also found in the *restinga* forests of Maranhão, in the riparian forests of the *Cerrado* in Midwest Brazil and in the Atlantic Forest (Lorenzi 1992; Girnos 1993; Paula *et al*. 1996; Barbosa *et al*. 2005; Colli-Silva 2023). This species 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 (Lorenzi 1992) and some references on the germination (Pacheco *et al*. 2007; Pacheco & Matos 2009; Guedes *et al*. 2013).

Regarding the structural characterization, the literature does not provide anatomical descriptions of any organ. 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.

Pachira aquatica Aublet, commonly known as “munguba”, “castanheira-do-maranhão”, “castanheira” and “cacau-selvagem”, is a tree native to Brazil, measuring 6–14 m in height and producing fresh chestnuts suitable for consumption (Lorenzi *et al*. 2006, Flora & Funga do Brasil 2023b, continuously updated). It is found from southern Mexico to northern South America, generally in marshy lands and riparian forests but easily adapting to different edaphic and climatic conditions. In Brazil the periodically flooded forests of the coast of Pará and Maranhão are its natural habitat (Peixoto & Escudeiro 2002; Paula *et al*. 1996). The species was introduced in urban afforestation in the second half of the 19th century by French landscape designer and botanist Glaziou during his visit to Brazil (Lorenzi 1992).

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

In view of the context described above, this work aimed to compare the anatomical structure of bud roots of *A. tibourbou* and *P. aquatica* to investigate which tissues are responsible for buds formation and development of clonal individuals and identify the storage sites of carbohydrate 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 (UFAL - 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 used as a garbage area. Currently, despite being a small forested area and not having the biodiversity of a natural forest, it presents a stable microclimate free of external influences, such as anthropic actions or ecological disturbance.

Individuals of *P. aquatica* were also found in the UFAL, scattered in several different places. Four specimens were analyzed.

In addition to the material collected for anatomical analysis, leaves and reproductive organs were collected for herborization and deposited in the Herbarium Professor Honório Monteiro (Museum of Natural History - Federal University of Alagoas - AL, BR) (MUFAL) 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 analysis, 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. aquatica* 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.

The samples for the anatomical analyses were taken to the Laboratory of Plant Anatomy and Morphology at the Institute of Biological and Health Sciences, UFAL. Fragments of several segments of the material were fixed in FAA 70 for 24 hours (Johansen 1940) and stored in 70% alcohol. For the anatomical analyses, hand-cut cross and longitudinal sections were prepared with the aid of razor blades, sections were clarified with sodium hypochlorite solution, stained with Astra blue and Safranin (Bukatsch 1972), and mounted on semi-permanent histological slides with 40% glycerin for analysis under an optical microscope. Tests were performed with lugol solution to detect the presence of reserve carbohydrates, in this case starch (Johansen 1940); total lipids were detected with Sudan black B and Sudan IV (Jensen 1962); mucilage with toluidine blue and phenolic compounds with ferric chlorid (Johansen 1940).

A photographic documentation was made with the aid of a Olympus AX 70 photomicroscope equipped with U-PHOTO photographic accessory (Olympus) and analyzed using the IMAGE PRO-PLUS software.

Results

During the *in loco* analyses, *A. tibourbou* showed a diffuse underground root system with extensive branching, with many buds and new stem branches up to 4 meters away from the mother plant (Fig. 1).

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. 2).

The anatomical analyses showed, in the secondary growth, a coating composed of a periderm with six to 11 layers of phellem (Fig. 2b) and, adjacent to the phelloderm, two to four layers of parenchyma cells (Fig. 2c). Internally to the parenchyma cells, secretory cavities with mucilage were observed, always located opposite the primary phloem (Fig. 2a-e).

The secondary phloem was wedge-shaped, with parenchyma rays that undergo intense dilatation towards the primary phloem (Fig. 2c) and the conducting elements of the secondary phloem are interspersed with sclerenchyma cells (Fig. 2e). 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 these elements (Fig. 2f). In the middle of the structure (Fig. 3), there was the remaining exarch primary xylem with centripetal maturation, some samples with four and others with five protoxylem poles (Fig. 3a-b).

The samples showed buds on the periphery of the organ (Fig. 3c-d), with traces contiguous with the center of the structure, following its growth in diameter (Fig. 3e) and presenting vessel elements (Fig. 3f). When analyzing the central region in greater detail (Fig. 4), 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. 4a-b). Many starch grains were observed on the secondary xylem in cells of axial and radial parenchyma (Fig. 4c-d).

In loco analysis of *P. aquatica* revealed that the studied samples also had vegetative propagation through roots, but unlike *A. tibourbou*, the roots did not form a diffuse underground system; they

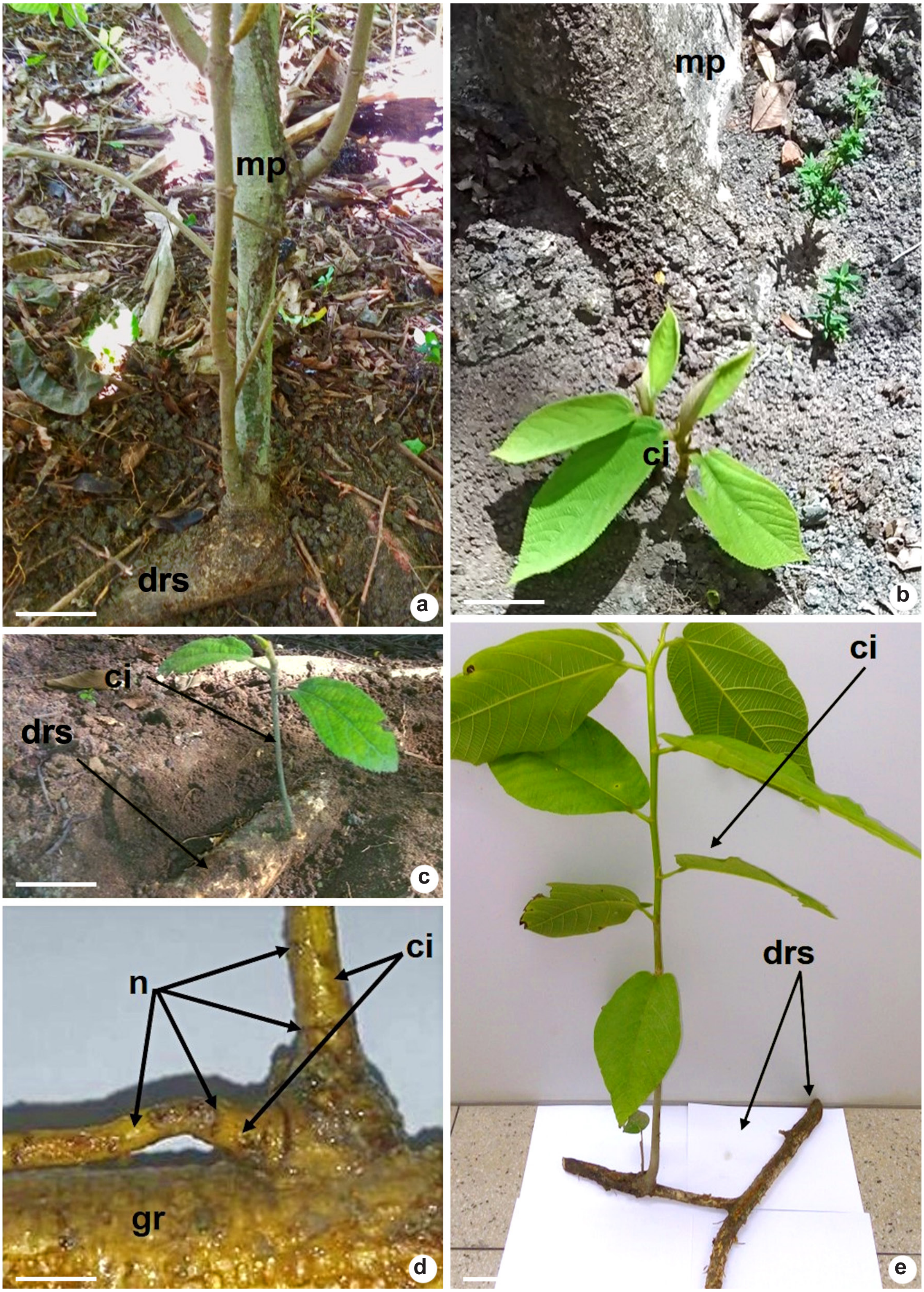

Figure 1 – a-e. *Apeiba tibourbou* – a-c. in the field at the *Arboretum* in UFAL – a. the mother plant; b. clonal individual in the soil next to the mother plant; c. clonal individual from the root; d-e. the samples collected in the laboratory – d. detail showing the structure; e. a complete clonal individual. ci = clonal individual; drs = diffuse root system; gr = gemiferous root; mp = mother plant; n = nodes. Bars: a = 1 m; b = 0,5 m; c = 20 cm; d = 1 cm; e = 0,5 cm.

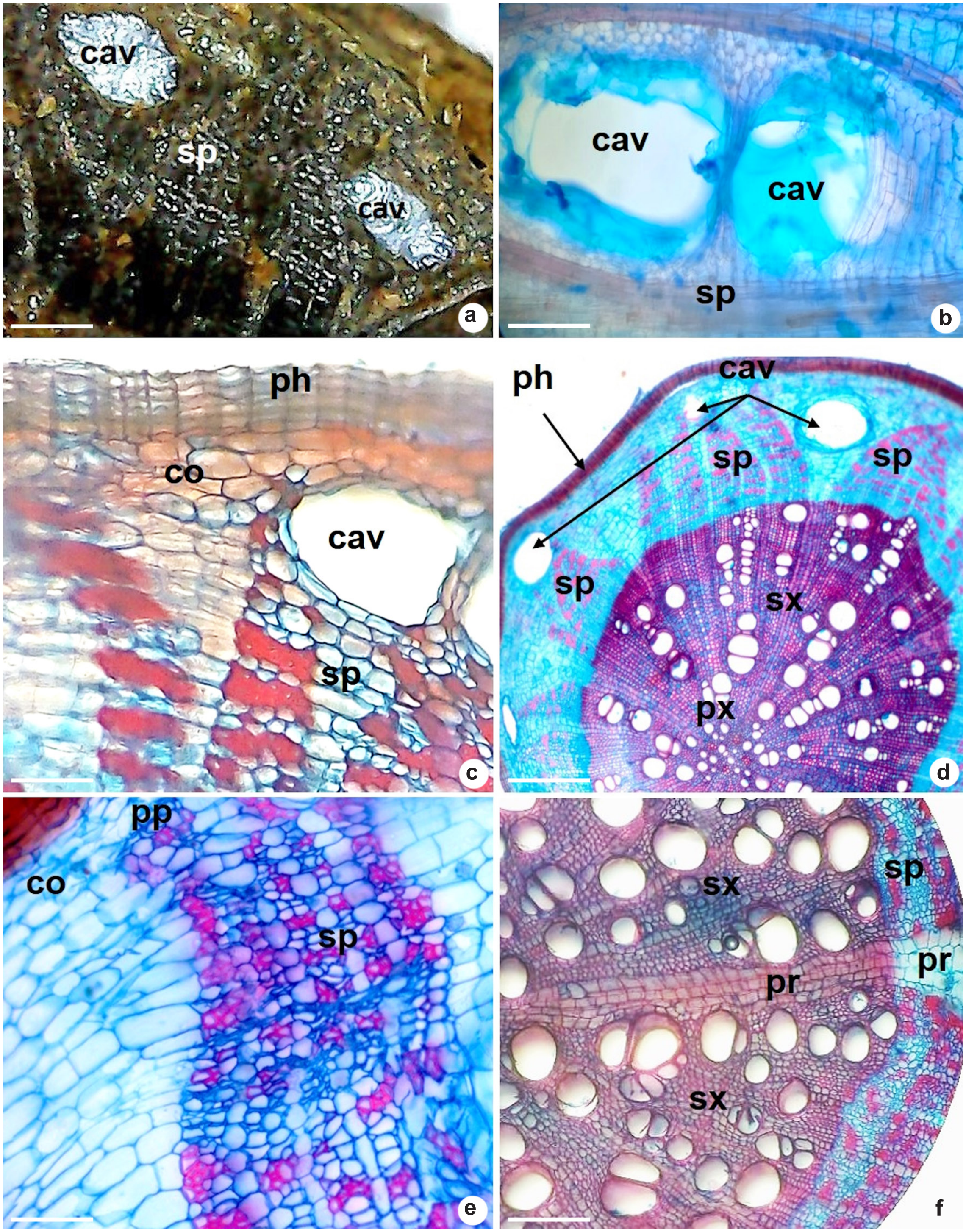

Figure 2 – a-f. *Apeiba tibourbou* (a,c-f. crossections of the gemiferous root; b. longitudinal section of the gemiferous root) – a. nature section showing cavities in the cortex; b. toluidine blue coloured section; c. sections showing cavities in the cortex; d. general anatomical structure of the root showing the cavities; e. secondary phloem; f. general anatomical structure of the root. cav = cavity; co = cortex; ph = phellem; pp = primary phloem; pr = parenchymal ray; px = primary xylem; sp = secondary phloem; sx = secondary xylem. Bars: a = 100 µm; b = 80 µm; c = 20 µm; d = 180 µm; e = 60 µm; f = 120 µm.

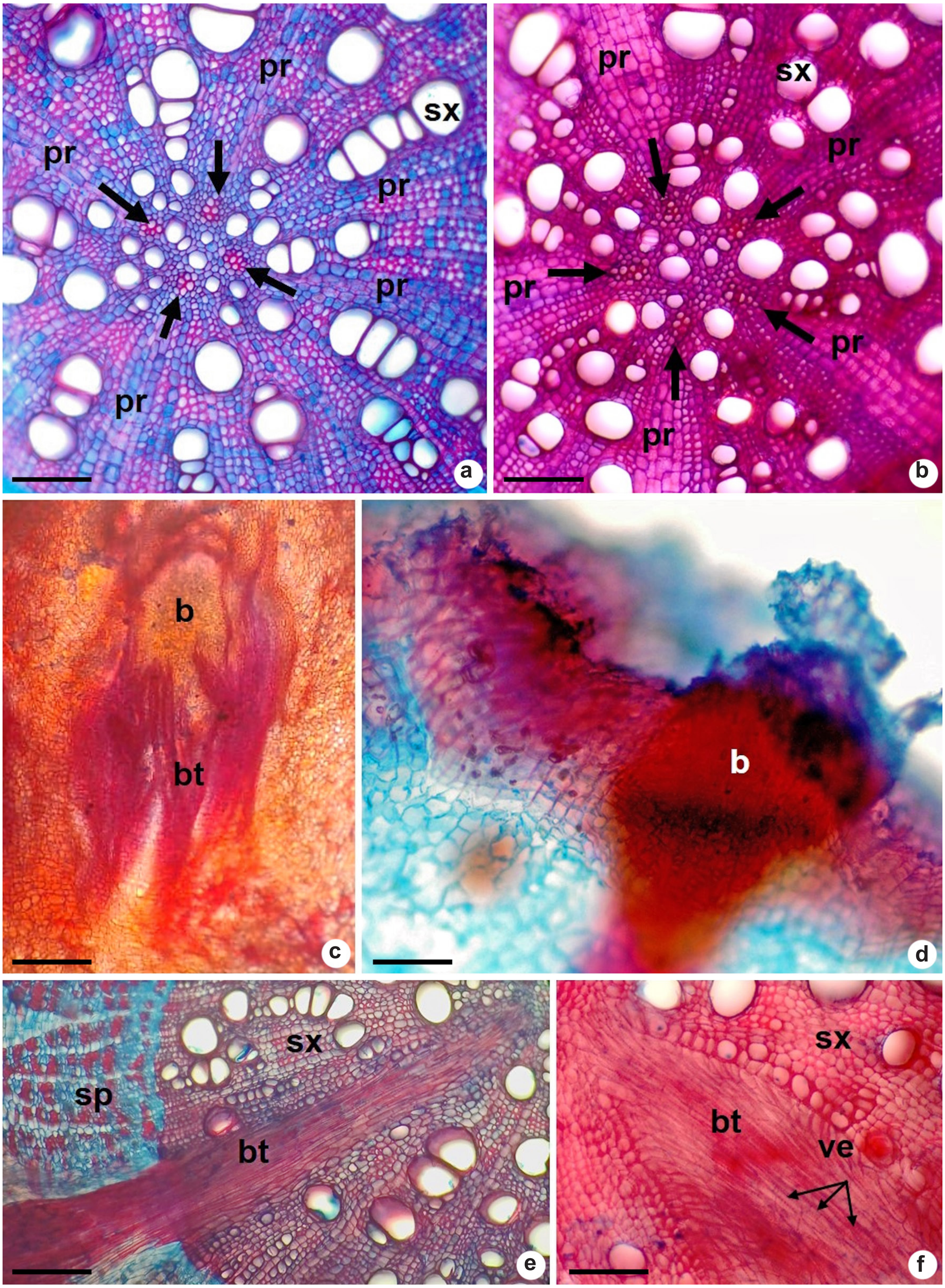

Figure 3 – a-f. *Apeiba tibourbou* crossections of the gemiferous root – a. root with four protoxylem poles; b. root with five protoxylem poles; c. bud in a longitudinal view with bud trace; d. bud at the periphery of the root; e. general anatomical structure of the root showing the bud trace; f. detail showing the vessel elements in the bud trace. b = bud; bt = bud trace; pp = pericycle; pr = parenchymal ray; sp = secondary phloem; sx = secondary xylem; ve = vessel element. arrows = poles of protoxylem. Bars: a, b, e, f = 120 μm; c = 180 μm; d = 200 μm.

led to the emergence of new individuals, through budding, only close to the mother plant (Fig. 5).

In roots with secondary structure, the anatomical analyses revealed a coating composed of periderm, with approximately seven layers of phellem, phellogen and phelloderm (Fig. 6a). Remaining 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. 6a). The secondary xylem was composed of thin rays, vessel elements, fibers and axial parenchyma cells (Fig. 6b). In the center of the organ, the primary xylem was exarch, with centripetal maturation and six protoxylem poles (Fig. 6c).

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. 6d-e), however, they were formed

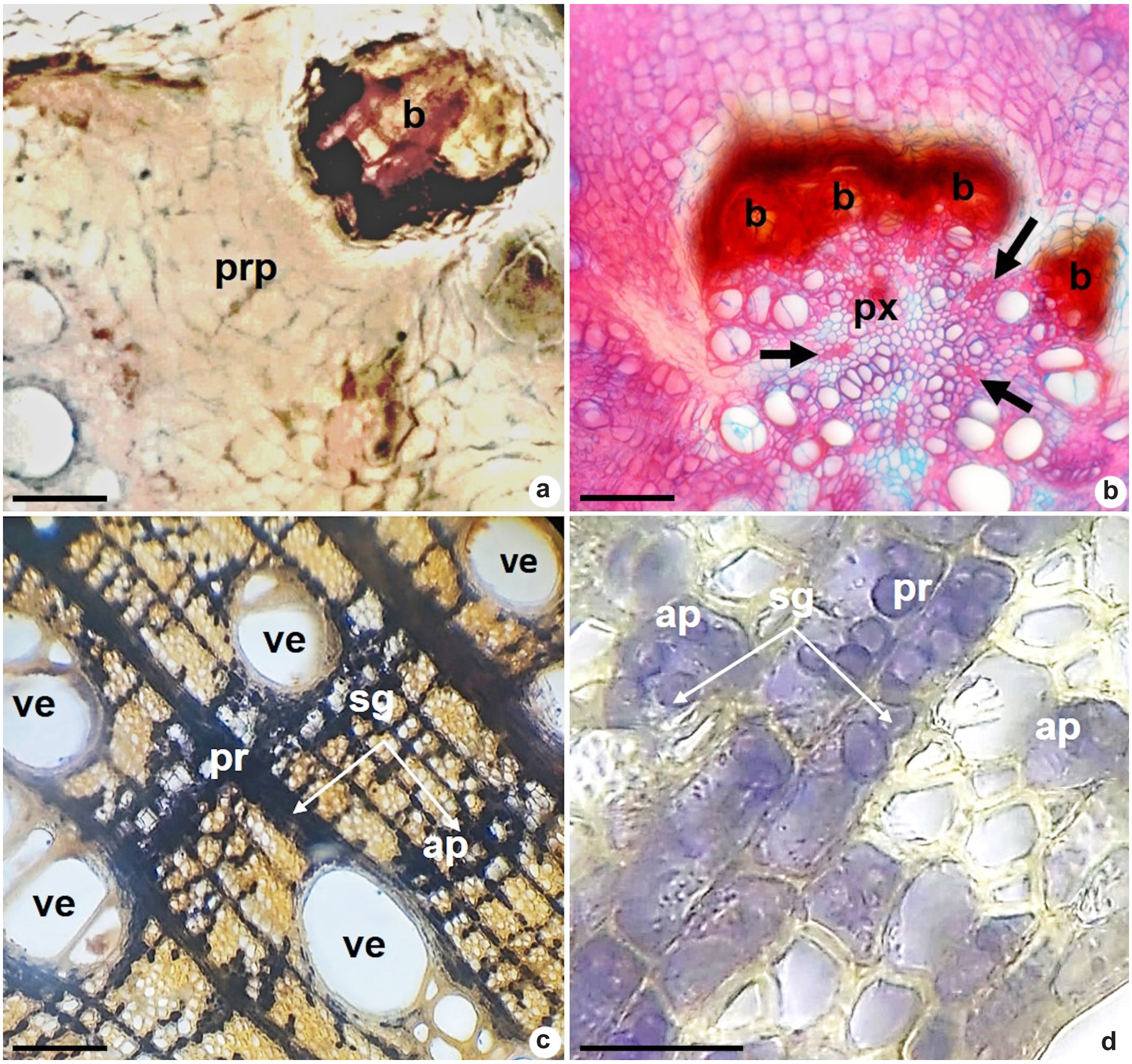

Figure 4 – a-d. *Apeiba tibourbou* – a-b. crossections of the gemiferous root showing the buds; c. lugol test showing dark areas with starch grains; d. natural section swowing starch grains in the parenchyma cells. ap = axial parenchyma; b = bud; pp = pericycle; prp = pericycle proliferatios; px = primary xylem; pr = parenchymal ray; sg = starch grain; sx = secondary xylem; ve = vessel element; dotted arrows = protoxylem poles; dotted arrows = divisions of the pericycle cells. Bars: a, c = 60 µm; b, d = 100 µm.

from divisions of parenchyma ray cells, opposite to the protoxylem poles (Fig. 6f). Starch grains were observed on the secondary xylem in cells of axial and radial parenchyma (Fig. 6g).

Discussion

The occurrence of diffuse bud systems in grassland plants, both in savannah environments and in other terrestrial habitats, is associated with the formation of root buds in disturbed environments, especially those under the action of fires. This is an effective regrowth mechanism following disturbances, including fires, since these below-ground buds are usually protected from fire (Rizzini & Heringer 1966; Pausas *et al*. 2018). This association, however, was not found in the present work because the sites from where the species analyzed come have never undergone fire episodes.

Rizzini & Heringer (1966) emphasized the need to analyze the structural nature of below-ground 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).

Buds can have an endogenous origins 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 endogenous buds, but originating from different cell lineages, namely, from the pericycle in the case of *A. tibourbou* and from parenchyma ray cells in the case of *P. aquatica*. The species *B. costatum* presents assexual reproduction through root buds with a concentration of fructose and soluble sugar responsible for the rooting of the new plant, however, the endogenous formation of shoots from the root buds has not been investigated (Zéphirin *et al*. 2019). In *Machaerium eriocarpum* Benth. and *Muellera nudiflora* (Burkart) M.J. Silva & A.M.G. Azevedo (two woody species of the family Fabaceae) additional buds were eventually observed, to result from normal plant branching as well as a response triggered by physiological or structural changes, promoting clonal growth (Silva *et al*. 2020) and leading to vegetative propagation.

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. Vegetative propagation also brings advantages in terms of the ability to “move” while maintaining a connection with the mother plant, ensuring the survival in environments where resources are scarce and/or irregulary distributed along the time and space. In this way, regrowth from subterranean bud organs is essential for the survival of the species (Rizzini 1966; Abrahamson 1980; Pitelka & Ashmun 1985; Alpert & Mooney 1986; Crawley 1997; Silvertown 2008). Some species with the ability to propagate vegetatively 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 in the present work. Germination tests conducted with the specimens used in the present study showed extremely low germination rates (unpublished data), 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 rates and vegetative propagation in plants that present these two forms of reproduction. Cury *et al*. (2010) observed such a relationship in species of Asteraceae in Cerrado, in the state of São Paulo. They found that a species that had the ability to propagate sexually had a germination rate up to 15 times greater than the species that reproduced vegetatively. This could indicate that the survival of species with low germination rates is enhanced by assexual reproduction, through the buds.

In woody perennial trees with starch reserves, as the plants analyzed in this study, this storage allows their survival during winter and 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 & van Cleve 1994).

It is also important to note that during winter, the starch stored in woody tissues is important 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 & van Cleve 1994; Witt & Sauter 1994).

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

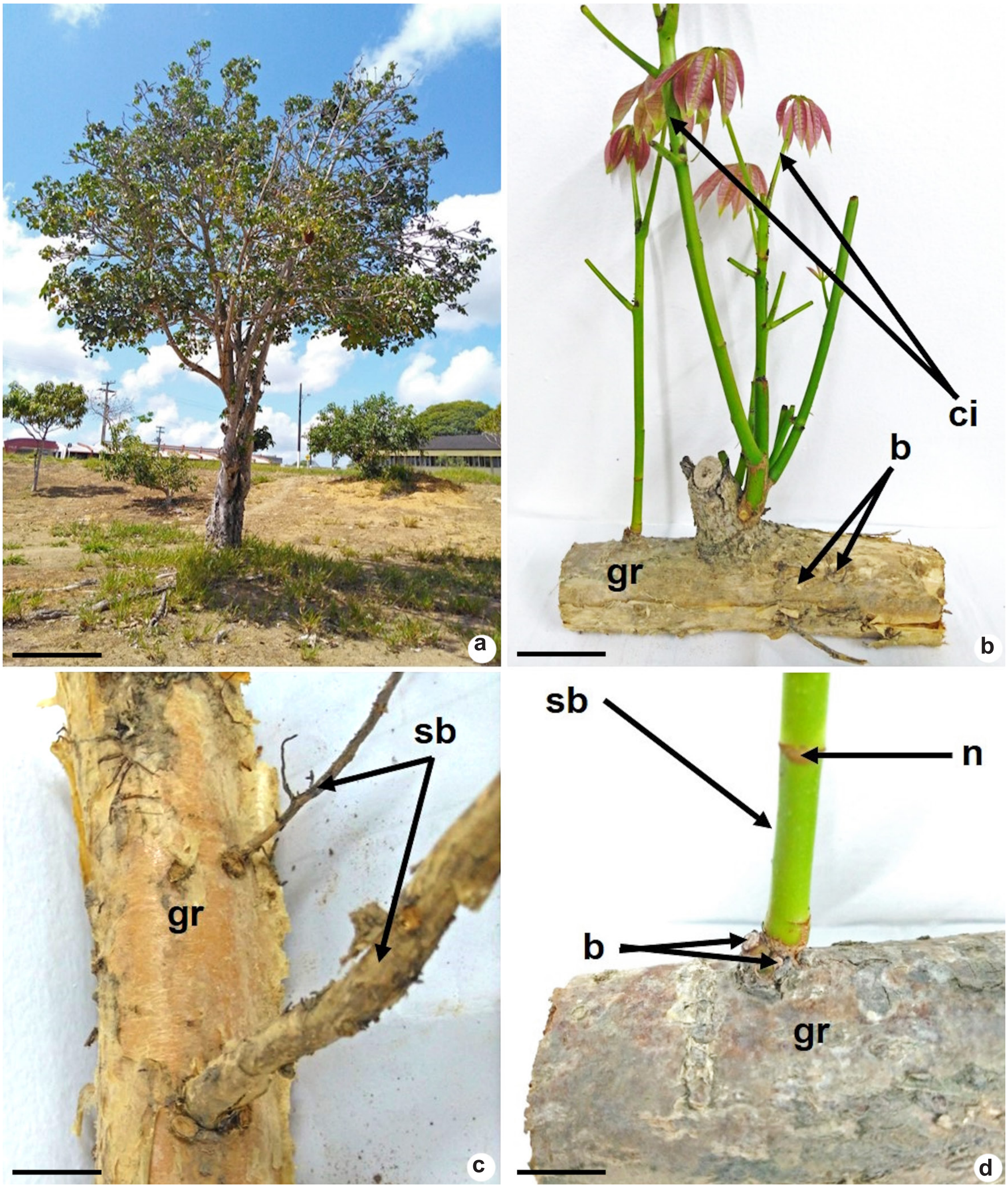

Figure 5 – a-d. *Pachira aquatica* in the field at the UFAL *campus* – b-d. details of the roots showing clonal individuals, buds and stem branches. b = bud; ci = clonal individual; gr = gemiferous root; n = nodes; sb = stem branches. Bars: a = 1 m; b = 2 cm; c = 1 cm; d = 0,5 cm.

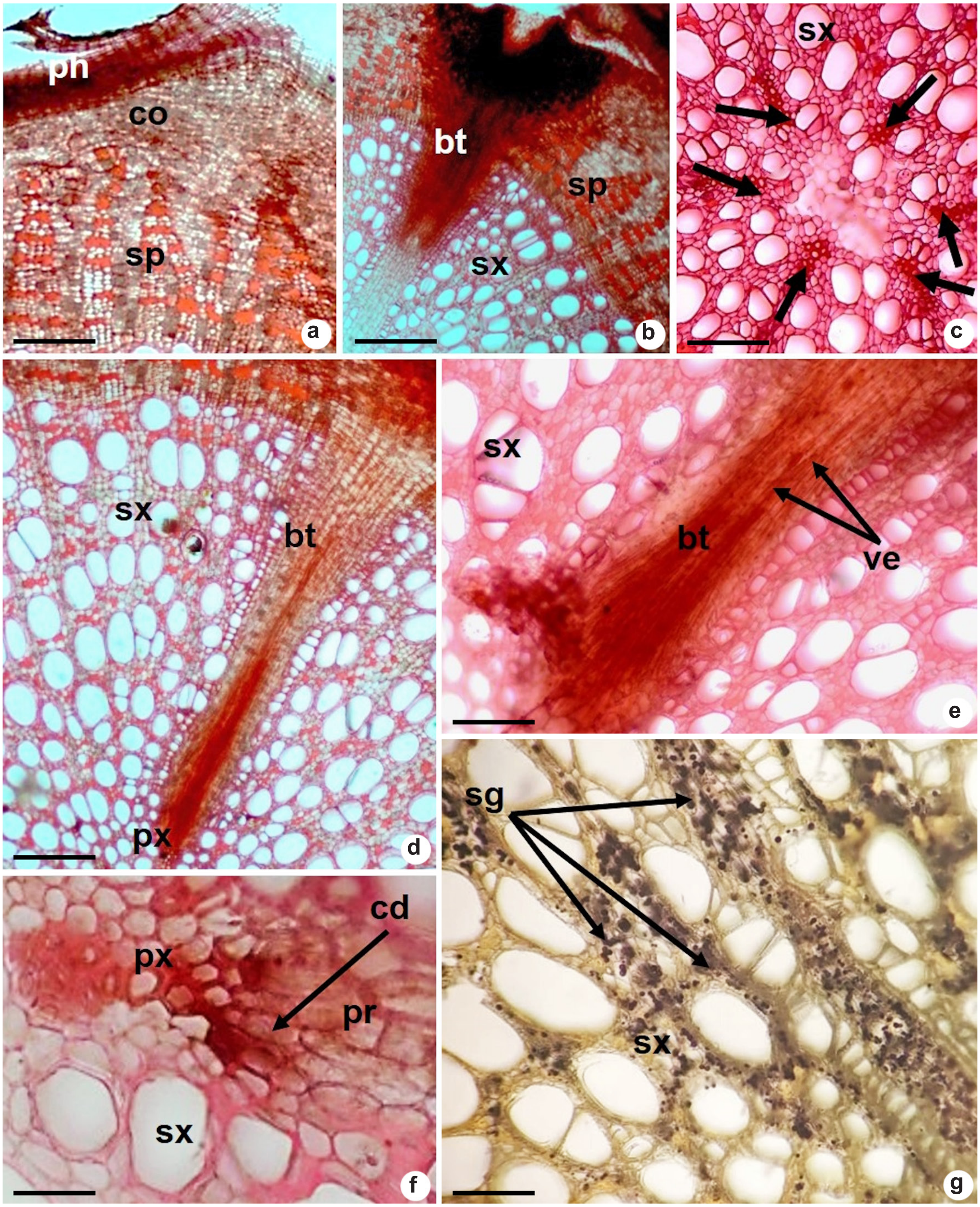

Figure 6 – a-g. *Pachira aquatica* crossections of the gemiferous root showing the general anatomical structure – a. periderm, cortex and secondary phloem; b. bud trace and secondary phloem and xylem; c. central of the root showing six protoxylem poles; d. secondary xylem around the secondary xylem; e. detail of the bud trace; f. cell division of the parenchyma ray; g. lugol test showing starch grains. 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 = poles of protoxylem. Bars: a, c, d = 180 µm; b = 200 µm; e = 120 µm; f, g = 60 µm.

as they are placed just opposite the phloem (Cury & Appezzato-da-Glória 2009).

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

Regarding the carbohydrate reserves in Malvaceae, in *Sida cordifolia* L. roots minute starch grains are frequent within the cortex and in the xylem parenchyma surrounding the vessels (Pramanick *et al*. 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 cortex, secondary phloem, phloem ray parenchyma, in xylem and in medullary rays (Navas *et al*. 2013). However, nothing has been reported about the relationship between the presence of starch and regrowth in the family Malvaceae.

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. As shown in literature this reserve allows plants not only to go through adverse conditions, but also develop new clonal individuals from the mother plant. This is the first report of gemiferous bud roots playing this role in the family Malvaceae. Further investigation is needed to establish whether this characteristic may be useful for phylogenetic studies or to improve the knowledge about this important function in plants.

Data availability statement

In accordance with Open Science communication practices, the authors inform that all data are available within the manuscript.

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