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Anatomy of vegetative organs and seed histochemistry of *Physalis peruviana* L.

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Abstract

Physalis peruviana L. (Solanaceae) is a plant species whose fruits can be classified as fine fruits, which is similar to other species such as blueberry, raspberry, cherry, blackberry and pitaya. The consumption of this fruit remains limited due to cost, which remains high due to limited production, crop management, intensive labor requirements and the associated transport and storage requirements. Studies that investigate the anatomy of vegetative organs may be important from an agronomic point of view because they provide information on anatomical structures and may be applied to cultivation practices. The objectives of the present study were to evaluate the type of reserve that occurs in seeds and anatomically characterize vegetative organs of *Physalis peruviana* L. (physalis). Histochemical tests and anatomical characterization were performed on the vegetative organs such as root, stem and leaf. Cross-sections (apical, middle and basal) of the seeds were examined using histochemical tests with specific dyes and reagents. Leaves and stems were used to examine the anatomy of the vegetative organs. Physalis seeds showed the presence of lipid reserves. The exposure of physalis to the east-west axis promoted thickening of the leaf midrib and blade and promoted the development of secondary xylem and phloem in the stem. Thus, the leaves on this axis appeared to show traits that favor greater radiation tolerance, which is a trait typical of sun leaves. The root of physalis has a uniseriate epidermis with the exodermis just below the epidermis.

Keywords: Fruticulture; greenhouse; lipid reserve; physalis; solanaceae.
Abbreviations: ANOVA_analysis of variance; CV_coefficient of variation; cut_cuticle; D_stomatal density; ead_adaxial epidermis; eab_abaxial epidermis; ED_equatorial diameter; had_hypodermis; PD_polar diameter; pf_fundamental parenchyma; ph_phloem; pp_palisade parenchyma; ps_spongy parenchyma; st_stomata; tric_trichome; x_xylem.

Introduction

The *Physalis* genus includes approximately 90 species with a pantropical distribution occurring from southern North America to South America with centers of diversity in Mexico, the United States and Central America (Hunziker, 2001). Some species of the *Physalis* genus have been cultivated for their importance in human nutrition (Silva and Agra, 2005). *Physalis peruviana* L. (Solanaceae) is a plant species whose fruits can be classified as fine fruits, which is similar to other species such as blueberry, raspberry, cherry, blackberry and pitaya. The consumption of this fruit remains limited due to cost, which remains high due to limited production, crop management, intensive labor requirements and the associated transport and storage requirements. According to Velasquez et al. (2007), the cultivation of the *Physalis peruviana* fruit is a potential agricultural alternative crop with good prospects for commercialization in Brazilian and international markets due to the high nutritional/pharmaceutical content and the possibility to cultivate the *Physalis peruviana* L. (physalis) fruit as an organic crop. The cultivation of physalis remains limited due to the lack of knowledge regarding crop management practices, the heavy manpower requirements and demanding logistics between harvest and market. The high price of this crop restricts its consumption to a niche market of people with higher purchasing power, although prices tend to decrease at peak harvest, which makes the fruit more accessible to a wider range of consumers (Muniz et al., 2011). Although the genus *Physalis* contain more than one hundred species, is a less explored genre, making anatomical studies on this are preliminary, recent and almost nonexistent. To date the work involved studies conducted in pharmacobotany (Silva and Agra, 2005), morphology and seed development seminal post (Souza et al., 2010), Anatomy of the formation and growth of the fruit (Mazorra et al., 2006) multiplication *in vitro* (Rodrigues et al., 2013b), phenological characterization and productivity (Rodrigues et al., 2013a), harvest time (Rodrigues et al., 2012). Information regarding the anatomy of the vegetative organs of physalis can be useful from an agricultural perspective especially with regard to standardized cultivation practices. The objectives of the present study are to investigate the type of storage that occurs in the seeds of physalis and to anatomically characterize the vegetative organs.

Results

The results of the histochemical tests are shown below (Fig. 1). The presence of lipids can be observed in the seeds of

Table 1. Cross-sections of physalis leaf blades (µm) from different regions of the plant. ead = adaxial epidermis; eab = abaxial epidermis; had = adaxial hypodermis; hab: abaxial hypodermis; pp: palisade parenchyma; ps: spongy parenchyma; CV: coefficient of variation.

Region	Ead	eab	had	hab	pp	ps
North	9.54 a	8.54 a	25.71 a	23.72 a	60.32 b	110.75 a
South	8.50 a	7.29 a	21.19 a	21.82 a	60.05 b	92.26 b
East	9.31 a	9.62 a	26.53 a	23.67 a	79.78 a	123.57 a
West	8.98 a	8.30 a	24.39 a	22.93 a	62.91 b	114.43 a
CV (%)	19.27	24.25	19.50	22.71	9.68	11.15

Variable means followed by different letters differ significantly as determined by the Scott-Knott test with 5% error probability.

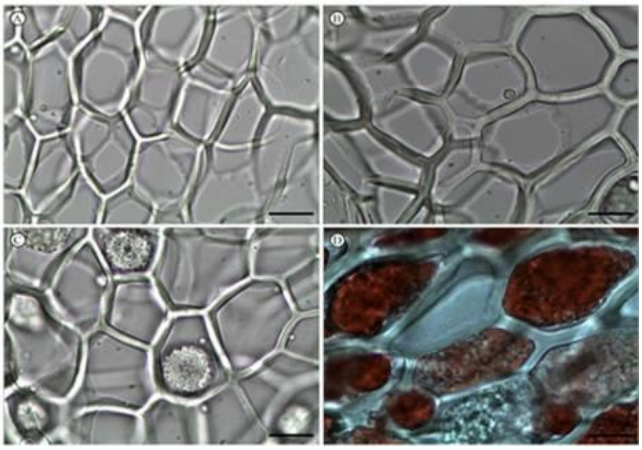

Fig 1. Representation of histochemical tests of storage tissue cross-sections in the seeds of physalis using different specific dyes. A) Coomassie blue (negative), B) iron III chloride (negative) C) Lugol's dye (negative), D) Sudan IV (positive). Scale bar = 20 µm.

Physalis peruviana L. (physalis) based on the positive reaction upon Sudan IV staining in different sections of the seed (apical, median and basal). The staining pattern of the reagents used in this study was similar in the three regions where a large amount of lipids was observed in the cells. Tests for the presence of protein, starch and phenolic compounds were negative for all regions tested. The leaves of physalis have dorsiventral mesophyll with a palisade layer immediately beneath the adaxial epidermis and spongy parenchyma immediately beneath the palisade layer (Fig. 2). However, the palisade and spongy parenchyma showed significant differences between regions (Table 1). The thickest (79.78 µm) palisade parenchyma was found in leaves from the east-facing section of physalis, whereas the thinnest spongy parenchyma was found in the south-facing section. Cross section of the midrib region of the leaf (Fig. 3) revealed a uniseriate epidermis with angular collenchyma just below the epidermis and a vascular system composed of xylem on the adaxial side and phloem on the abaxial side. There is a quantity of fundamental parenchyma below the collenchyma and around the vascular system. The midrib is thicker in leaves from the east-west axis when compared with leaves from the north- and south-facing sections (Fig. 3). The anomocytic stomata of physalis (Fig. 4.A) were distributed randomly in the leaves; however, they were limited to the abaxial surface, which suggests that physalis leaves are hypostomatic. The stomata were located above the epidermis (Fig. 5). The average stomatal frequency (number per mm²) was 56, 77, 59 and 60 in leaves from the north-, south-, east- and west-facing regions, respectively (Table 2). There were significant differences in stomatal density and ED (Table 2). A higher density occurred in the south-facing regions of physalis, which was 37.5% higher when compared with the other leaf positions. There was no significant difference between the polar and equatorial diameters across the positions analyzed (Table 2). There were significant differences in stomatal density and ED (Table 2). A higher density occurred in the south-facing regions of physalis, which was 37.5% higher when compared with the other leaf positions. There was no significant difference between the polar and equatorial diameters across the positions analyzed (Table 2). Physalis is a species with numerous trichomes present in the stem and leaves. Uniseriate and multiseriate trichomes occurred in the leaves on both the adaxial and abaxial epidermal surface (Fig. 6). The stem of physalis (Fig. 7) displayed a uniseriate epidermis covered by a cuticle with trichomes present. Internally to the epidermis lies the cortex, which presents three to four layers of collenchymal cells and cortical parenchyma with flattened cells arising during the early development of the secondary vascular tissues. The vascular system consists of open collateral bundles, which delimit a typical eustele stem with vascular bundles arranged in a circular fashion surrounding the cortex formed of medullary parenchyma with large isodiametric cells. The vascular system in the sampled region was in the early stages of secondary vascular tissue development, which is formed with an outer phloem layer and an innermost xylem produced by the vascular cambium formed by a layer of cells. In the branches facing the east, secondary xylem and phloem were formed in quantities well above those found in the stems from the other regions (Fig. 7). Uniseriate and multiseriate trichomes were observed on the epidermis of the stem.

Discussion

The results of this work for histochemical tests on seeds, although qualitative, corroborate Picoli et al. (2013) who found the same pattern of reserves in *Solanum granulosum-leprosum* species, ie, lipid drops over the proteins, carbohydrates, alkaloids and phenols. According to Gagliardi

Table 2. Characteristics of abaxial stomata in physalis leaves from different regions of the plant. D: density of stomata, PD: Polar Diameter and ED: Equatorial diameter.

Region	D (stomata/mm^2)	PD (µm)	ED (µm)	PD/ED
North	56 b	32.71 a	18.72 b	1.63 a
South	77 a	31.72 a	22.94 a	1.38 a
East	59 b	34.81 a	24.66 a	1.42 a
West	60 b	32.52 a	22.16 a	1.47 a
CV (%)	15.61	8.62	17.20	15.14

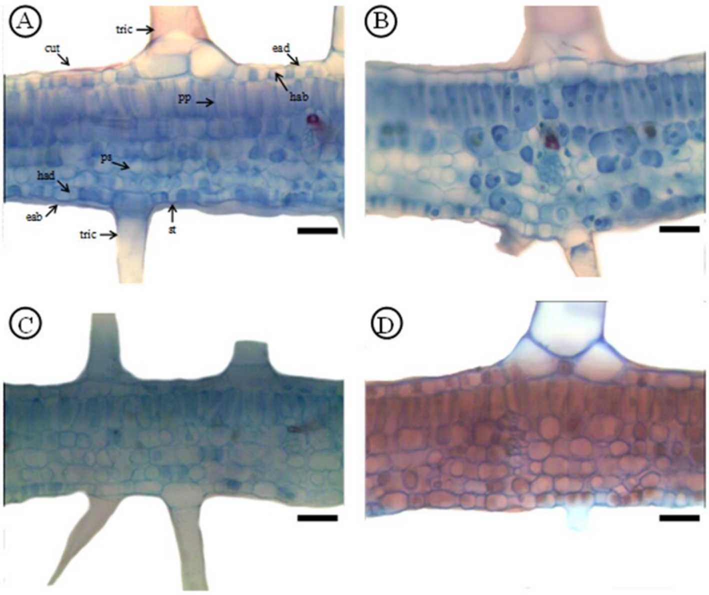

Fig 2. Cross-sections of physalis leaf blades from different regions of the plant. A) North, B) East, C) South and D) West. Labels: tric = trichome; cut =cuticle; ead = adaxial epidermis, pp = palisade parenchyma, ps = spongy parenchyma; eab = abaxial epidermis; st = stomata; had = hypodermis. Scale bar = 40 µm.

and Marcos-Filho (2011) oil seeds should be stored with lower degree of moisture compared to the starchy origin, because major changes during the decay are attributed to the enzyme, hydrolysis peroxidation and autoxidation, which are manifest in moderate elevation of humidity and temperature. According Santos et al. (2004) in studies with several species of Solanaceae, it was found that the esterase is an enzyme involved in the hydrolysis of esters, being directly linked to the metabolism of lipids and membranes of the degenerative process, and possibly because of this, the seeds tomato in general should be stored at an average 8.3% moisture (Panobianco and Marcos-Filho, 2001) due to the lipid content of reserves. The detection of primary reserves as of lipid origin on seed physalis it is important because until now no one knows the standards for storage of the seed lot, with respect to moisture and temperature, but the results of this work show an indication for further research storage and quality of the seed lot of physalis. Leaves from physalis facing the south were thinner when compared with leaves from the other cardinal regions, and the leaves facing the east-west axis had more differentiated tissues and greater blade thickness. The greater the thickness of the mesophyll or the number of chlorenchymal layers, the greater the efficiency of photosynthesis. However, excessive exposure to radiation can lead to photoinhibition and photooxidation damage of the photosynthetic apparatus (Araujo et al., 2009). Thus, the leaves located on the east-west axis appear to have characteristics that favor tolerance of a larger amount of radiation, which is typical of sun leaves containing more mesophyll, more trichomes and more developed chlorenchyma (Castro et al., 2009). These findings show the anatomical plasticity of physalis leaves, and these organs can be adjusted to optimize the capture of radiation and photosynthesis. There was no significant difference in the thickness of the adaxial epidermis, abaxial epidermis, adaxial hypodermis or abaxial hypodermis in leaves from the different regions of the physalis. As found in the leaf blade, the increased thickness of midrib is due to these leaves receiving more light, which increases their development. The enhanced development of the midrib enables increased development of the vascular tissue, which is consistent with the observed increased amounts of xylem and phloem. Increased vascular development can provide greater water conveyance capacity and photosynthetic assimilates allowing greater utilization of nutrients and energy by the leaves along the east-west axis. The collenchyma is responsible for sustaining young plant organs and may be present in the upper and lower limits of the organ. The collenchyma can also form collenchymal rings depending on the species (Castro et al., 2009). The presence of collenchyma is important for the maintenance of leaf structure and enables leaves to receive adequate radiation. The stomata are important structures for vegetative production because they represent the gateway for the flow of photosynthetic gases, a process related to plant productivity. Different plant species vary in the number, frequency, size, shape and distribution of stomata, which in turn influences their photosynthetic capacity. Even in the same plant, the stomatal arrangement can differ between leaves depending on their shape and the position of the leaves in the canopy (Silva et al., 2005). Silva

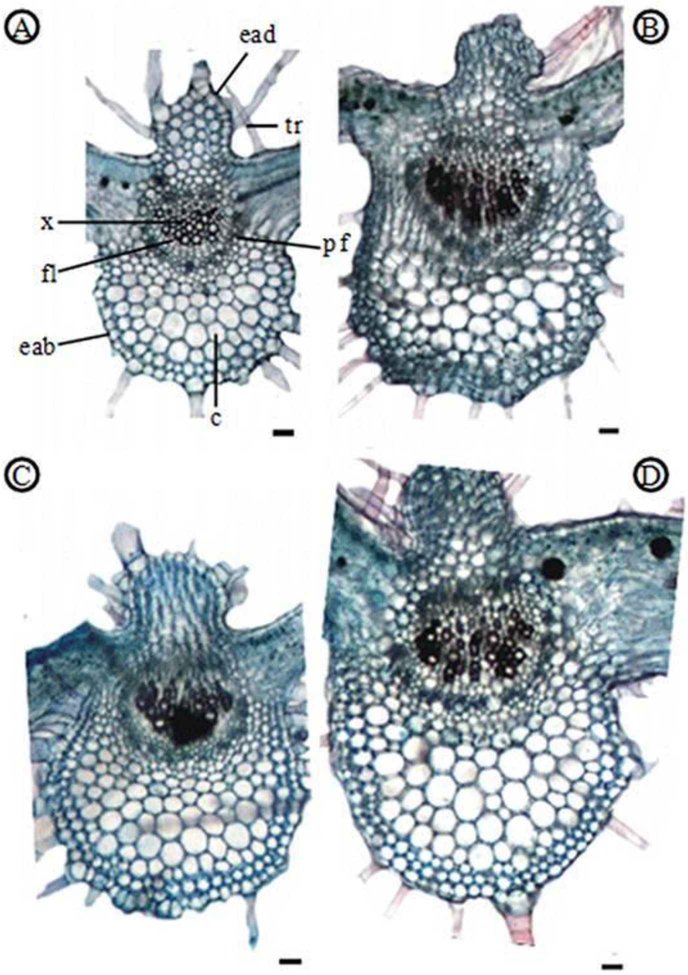

Fig 3. Cross-sections of physalis leaf midribs from different regions of the plant. A) North, B) East, C) South and D) West. Labels: tric = trichome; x = xylem, ph = phloem, pf = fundamental parenchyma. Scale bar = 50 µm.

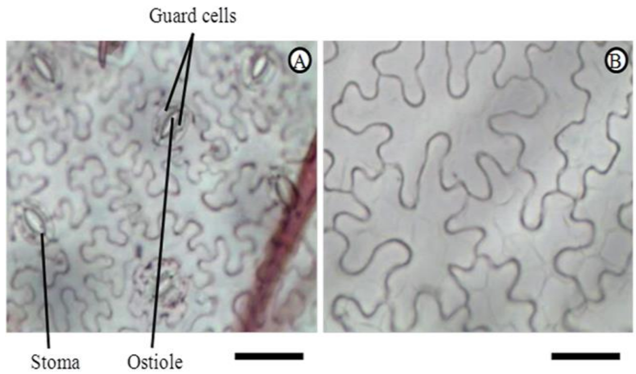

Fig 4. Paradermic leaf sections from physalis. A) Abaxial side and B) Adaxial side. Scale bar = 50 µm.

and Agra (2005) performed a comparative pharmacological/botanical study of *Nicandra physalodes* and *Physalis angulata* and found that the leaf blade of *Physalis angulata* was amphistomatic, and the stomata were anisocytic and sporadically anomocytic on both sides occurring in greater numbers on the abaxial side. This fact is important because it enables the localization of the stomata to aid in the correct identification of *Physalis peruviana* and *Physalis angulata*, which suggests that the type and distribution of stomata have taxonomic value. The polar diameter (PD) and equatorial diameter (ED) are related to stomata functionality by the ratio of PD to ED, and a higher PD/ED ratio indicates greater stomatal function (Castro et al., 2009). According to Khan et al. (2002), the elliptical shape is a characteristic of functional stomata, whereas a rounded shape is often associated with abnormal stomata. According to Rocha (2007), the larger the PD/ED ratio, the more ellipsoid is the stoma, which can result in increased functionality. However, the functionality of the stomata of physalis remained unchanged in the different leaf positions on the same plant, suggesting that all stomata harbor a similar functional capacity for capturing CO_2 and using CO_2 in photosynthesis.

The north-south axis typically receives less radiation than the east-west axis due to the movement of the sun throughout the day. The stomata of physalis were protrusive being more exposed to changes in the boundary layer, which can lead to excessive transpiration. The leaves of physalis show clear mesomorphic characteristics and do not appear to tolerate drought stress conditions well, which is most likely because the stomata are responsible for most of the transpiration in plants (Castro et al., 2009). Thus, the development of higher stomatal densities in leaves of the south-facing region results in reduced transpiration due to the lower radiation intensity in this region. The other regions showed lower stomatal densities, as they receive more radiation than the South-facing regions. Trichomes present in Physalis prevent excessive transpiration providing a barrier against wind that can decrease the relative humidity at the leaf surface. Trichomes also protect against excessive water accumulation on the leaf surface (Castro et al., 2009). Similarly to the cuticle and stomata, the trichomes also develop differently according to the environmental conditions in which the plants grow (Silva et al., 2005). The development of structures with a greater ability to transport water, nutrients and photosynthetic assimilates can provide greater functionality to the plant stem. As noted, the east-west orientation favored a more rapid development of secondary vascular tissues and may allow greater support and transport through the stem. Thus, the east-west orientation may therefore be better suited for cultivation purposes. Additionally, the stem is responsible for transporting water and minerals from the roots to the leaves via xylem and substances produced in the leaves via the phloem to other parts of the plant (Castro et al., 2009). The root is a relatively simple structure compared to the stem and serves several functions including anchoring the plant to the ground, absorption of water and nutrients, storage and transport (Apezzato-da-Glória and Hayashi, 2009). The root of physalis (Fig. 8) has a uniseriate epidermis with the exodermis just below the epidermis forming a layer of cells that may act as an apoplastic barrier to the flow of water and ions (Hartung et al., 2002). We also observed an endoderm, which is an apoplastic barrier formed by the thickening of primary cell walls from the most internal portion of the cortex of the primary roots, which results in a ring of cells surrounding the vascular system. The endoderm may also protect the pericycle and transport substances from damage caused by adverse environmental factors such as the presence of heavy metals and salinity (Castro et al., 2009). The cortical parenchyma was characterized by the presence of several layers of isodiametric cells with thin primary walls and small intercellular spaces, which were mostly of the meatus type (Fig. 8).

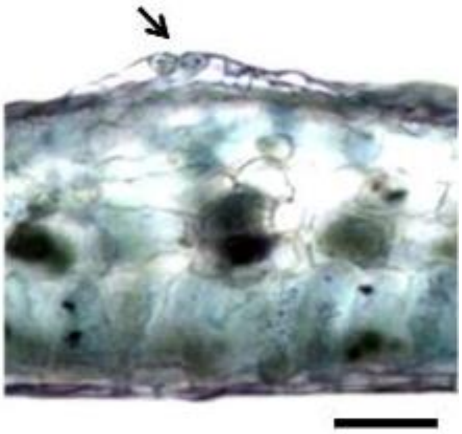

Fig 5. Cross-section of a physalis leaf. The arrow indicates a stoma located above the epidermal cells. Scale bar = 20 µm.

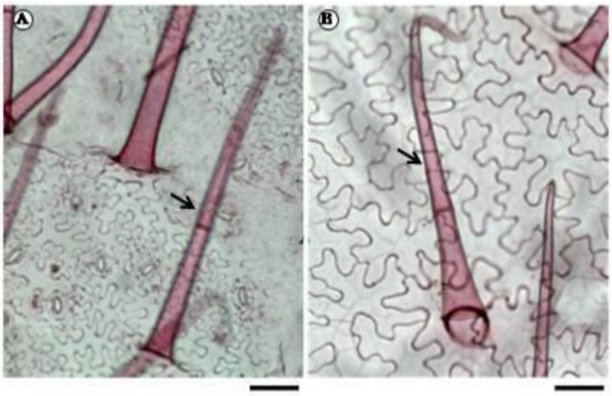

Fig 6. Paradermic leaf sections of physalis. A) abaxial surface, B) adaxial surface, the arrows indicate trichomes. Scale bar = 50 µm.

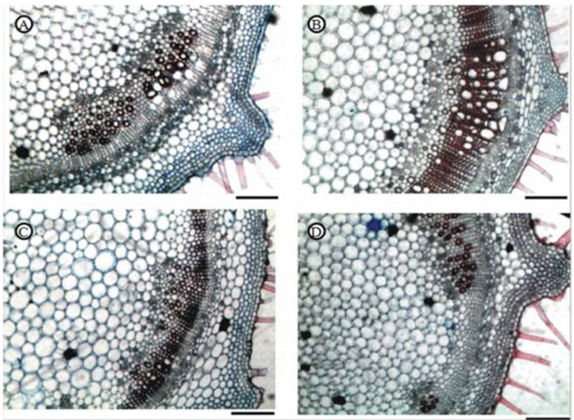

Fig 7. Cross-sections of physalis stems from different regions of the plant. A) North, B) East, C) South and D) West. Scale bar = 100 µm.

Materials and Methods

Plant materials

The fruits, leaves, stems and roots of *Physalis peruviana* L. (physalis) grown in a greenhouse at Lavras Federal University in Minas Gerais State in Brazil were harvested at physiological maturity. Subsequently, the fruits were transported to the Tissue Culture Laboratory of the

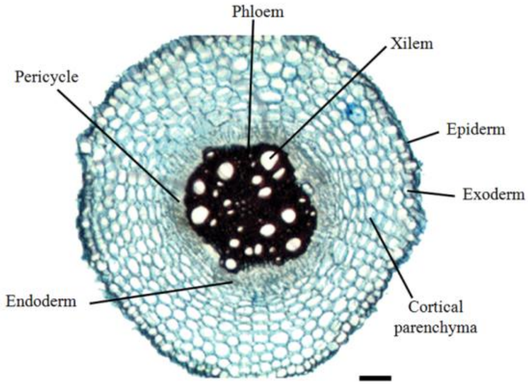

Fig 8. Cross-section of a physalis root. Scale bar = 100 µm.

Department of Agriculture at Lavras Federal University ("Laboratório de Cultura de Tecidos do Departamento de Agricultura/ Universidade Federal de Lavras" - DAG/UFLA) where they were pulped to remove the seeds.

Histochemical tests

Histochemical tests of seeds and anatomical characterization of vegetative organs were conducted in the Laboratory of Plant Anatomy in the Department of Biology of Lavras Federal University ("Laboratório de Anatomia Vegetal, do Departamento de Biologia da UFLA"). For the histochemical tests, seed cross-sections were taken from the apical, median and basal regions, with the chalazal region considered as basal. Sections were made using a table microtome (model LPC) to determine the type of storage and the presence of phenolic compounds using the following specific dyes: Coomassie Blue to detect proteins, iron III chloride to detect phenolic compounds, Lugol's dye to detect starch and Sudan IV to detect lipid substances following methods previously described by Kraus and Arduin (1997). The sections were mounted in 50% glycerin on a slide with cover slip according to the semi-permanent slide preparation methodology previously described (Johansen, 1940). An optical microscope (Olympus CX41) coupled with a digital camera was used to obtain photomicrographs.

Anatomical analysis

To examine the anatomy of the vegetative organs, the first two fully expanded leaves and 5-cm-long fragments of orthotropic stems were collected. These materials were fixed and stored in 70% ethanol until analysis, which took place in the Laboratory of Plant Anatomy at the Department of Biology (UFLA). Leaves and stems used in the anatomical analyses were collected from regions corresponding to the four cardinal points of the plant as grown in the greenhouse (DAG/ UFLA), and pilifera zone segments were used to study the roots. The cross-sections were obtained from the median region of the leaves using a table microtome. The sections were immediately clarified in sodium hypochlorite solution (50%), washed in distilled water and stained with Safrablau solution (1% safranin and 0.1% astra blue) and mounted on slides with 50% glycerin (Melo et al., 2007). Paradermic sections were obtained from the adaxial and abaxial epidermis of the median leaf region using a steel blade. Subsequently, the sections were clarified in sodium hypochlorite solution (50%) and rinsed in distilled water and stained with safranin 1% (Melo et al., 2007), and then slides were mounted with 50% glycerin. The stomatal density (D), polar diameter (PD), equatorial diameter (ED) and PD/ED ratio were obtained from ten measurements for each parameter considered. Photomicrographs were taken using a Canon PowerShot A620 digital camera attached to the Ken-A-Vision TT18 microscope. The anatomical analyses were performed using the Software ImageTool 3.0 of UTHSCSA.

Statistical analysis

Data from paradermic sections (D, PD, ED and PD/ED) were subjected to analysis of variance (ANOVA) and the Scott-Knott test using a 5% probability cutoff using the statistical program Sisvar (Ferreira, 2011).

Conclusions

The seeds of *Physalis peruviana* L. (physalis) harbor lipid reserves, the leaves and stems have numerous uniseriate and multiseriate trichomes, and the structure of these organs was typical of the Solanaceae family with mesomorphous and hypostomatous leaves and a eustele stem. The exposure of physalis in the east-west axis promotes the thickening of the leaf midrib and blade and the development of secondary xylem and phloem in the stem, which are characteristics that may help to improve the growth and development of this species. The root of physalis has a uniseriate epidermis with the exodermis just below the epidermis.

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