

COMPARATIVE WOOD AND BARK ANATOMY OF STEM, ROOT AND XYLOPODIUM OF *JACARANDA ULEI* (BIGNONIACEAE)¹

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ABSTRACT

Jacaranda ulei is a common shrub from Cerrado that presents medicinal properties. Aerial stem is not resistant to the naturally recurrent fire of this ecosystem. The plants re-sprout via the xylopodium. This paper compares the anatomical structures of the wood and the bark of the root, the stem, and the xylopodium. A sample of five individuals of *Jacaranda ulei* was processed using usual techniques. In common, the wood is diffuse porous and the axial parenchyma is confluent and vasicentric, but there are clear differences among the root, the stem and the xylopodium. The bark is thin, with gradual transition seen between the conducting and the nonconducting phloem, and with groups of fibers and sclereids. In the stem, the fibers are arranged in bundles and the periderm presents hairs. In the subterranean organs, the sclerenchymatic tissue is arranged in concentric lines and secretory canals were seen. Such differences are probably related to the different functions of aerial and subterranean organs.

Key words: Bignoniaceae; Cerrado; drought; fire; *Jacaranda ulei*; resilience; savannah.

RESUMO

[Anatomia do lenho e casca do caule, raiz e xilopódio de *Jacaranda ulei* (Bignoniaceae)].

Jacaranda ulei é um arbusto comum do Cerrado e de propriedades medicinais. O caule aéreo não é resistente aos incêndios naturais recorrentes deste ecossistema. As plantas rebrotam via xilopódio. O presente trabalho compara as estruturas anatômicas do lenho e casca, da raiz, caule e xilopódio. Uma amostra de cinco indivíduos de *Jacaranda ulei* foram processados, usando-se técnicas usuais. Em comum, o lenho apresenta porosidade difusa e o parênquima axial é confluyente e vasicêntrico, mas existem diferenças nítidas entre a raiz, o caule e o xilopódio. A casca é delgada, com transição gradual entre os floemas funcional e não funcional, e com grupos de fibras e esclereidas. No caule, as fibras estão arranjadas em feixes e a periderme apresenta pêlos. Nos órgãos subterrâneos, o tecido esclerenquimático está arranjado em linhas concêntricas e são vistos canais secretores. Tais diferenças estão provavelmente relacionadas às diferentes funções dos órgãos aéreos e subterrâneos.

Palavras-chave: Bignoniaceae; Cerrado; fogo; *Jacaranda ulei*; resiliência; savana; seca.

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INTRODUCTION

The organography of the subterranean portions of plants has revealed a great diversity and complexity of structures (Appezato-da-Glória 2003; Appezato-da-Glória and Cury 2011), such as occurring in *Smilax goyazana*, which shows a subterranean caulinar system made of a rizophore that emits roots and many rhizomes that emits the aerial stems, which are culms (Palhares and Zaidan 2011). The types of subterranean organs tend to be more diverse in savannahs and other harsh ecosystems because under the soils there is a microclimate more stable and protected from the fire (Appezato-da-Glória 2003).

This way, the genus *Jacaranda* is of a particular interest: it includes 49 species of trees and shrubs, native from the Neotropical region. Several species have been introduced to Africa, Asia and Oceania and successfully cultivated, often as ornamental trees, and some of them eventually naturalized (Mostafa *et al.* 2014). While morphological observations of the arboreal species have shown simply root systems, some shrubby species have disclosed more complex subterranean systems, such as xylopodium and soboles: for instance, one individual of *Jacaranda decurrens* of more than one thousand years of life was identified, with a large and dense ramification of the soboles (Oliveira *et al.* 2003, Alves *et al.* 2013).

Jacaranda ulei Bureau & K. Schum. is a small sub-shrub from the Cerrado with a wide distribution in its various phytophysiognomies (Medeiros 2011), being frequently used in folk medicine for the treatment of pains, wounds, infections, and digestion problems (Gachet and Schühly 2009; Guarim Neto and Morais 2003; Nunes *et al.* 2003).

The subterranean system of *J. ulei* presents an axial taproot and a xylopodium, which can be recognised as a rigid fusiform thickened portion between the root and the stem. The xylopodium has a great ability to produce gems and to sprout, despite being very rigid. Unlike many other species of the Cerrado, the aerial stem is not fire-resistant, such that the survival and establishment of individuals depend on the re-sprouting abilities of the xylopodium (Silveira *et al.* 2013). With such differences in functions, it is expected that differences in structure will be seen. At the same time, the taxonomic groups tend to present similar structures: in the genus *Jacaranda*, the number of anther thecae is the basis for the division of the genus into two sections: Monolobos and Dilobos, and the wood anatomy of the stem corroborate such division (Santos and Miller 1997).

So, this work compares the anatomical structure of the wood and bark of the stem, the

xylopodium, and the taproot of the *Jacaranda ulei*.

METHODS

Five adult individuals out of the period of flowering/fruitification were sampled in areas of Cerrado *sensu strictu*, close to the Olympic Center of University of Brasilia (15°46'1" S e 47°51'17,6" W), whose vegetation underwent a phytosociological study by Assunção and Felfili (2004) and a floristic analysis by Zuany *et al.* (2007). Such sample size followed the recommendations of Eckblad (1991), as it gives data with a precision of about 85%. Voucher specimens were deposited at the Herbarium of University of Brasilia (UB), under the registers of UB06-Miranda, T.D., UB07-Miranda, T.D., UB08-Miranda, T.D., UB09-Miranda, T.D. e UB10-Miranda, T.D. The regions selected for anatomical transections were: the medial portion of the xylopodium; for the taproot, at 10cm below the insertion of the xylopodium; for the stem, the middle portion, that is, the portion between the soil and the first branches. The sections were obtained in fresh material in transversal, radial, and tangential sections with a sliding microtome, in an attempt to obtain the thinnest sections possible, which varied from 20 to 30 µm. The sectioned material were clarified, dehydrated, and stained with Alcian blue and safranin, according to Johansen (1940) and Kraus and Arduin (1997), and mounted in slides with acrylic resin as per Paiva *et al.* (2006). Fresh fragments were submitted to histochemical tests with lugol for detection of starch (Langeron, 1949), acidified phloroglucion for lignin (Foster, 1949), and Sudan IV for lipids (Jensen 1962). Fragments of 3 cm were also dissociated in Franklin's solution (Franklin 1946), for observation and description of the cell types. Photographs and scales were obtained with digital cameras and processed in computers. The nomenclature of wood followed the guidelines of the International Association of Wood Anatomists (IAWA 1989). The nomenclature of bark were as per Machado *et*

al. (2005) and Palhares *et al.* (2007a). The sample size of each parameter (see tables) was of $n = 50$ per individual, totalling 250 measurements. Statistical analysis followed the Student's t-test.

RESULTS

1. Xylopodium (figures 1 and 2)

In the middle portion of the organ, the wood presented distinct growth rings, marked in the inner wood by radially flattened and thick-walled fibers, and in the outer wood by marginal parenchyma bands.

The vessels were diffuse, solitary (59%), or in multiples of up to five elements. The perforation plate was simple and oblique. The inter-vessel pits were bordered, alternate, circular, with tangential diameter of $9,9 \mu\text{m}$. Appendices were present in almost all vessel elements, appearing in either only one, or both extremities. The fibers presented simple pits. Axial parenchyma was abundant, being mostly apotracheal, but also paratracheal vasicentric, and scanty. The bands of apotracheal axial parenchyma, with two to eight layers of cells, delimited the growth rings.

The rays were large, multiseriate, and non-storied, with one to seven cells wide and one or two cells in the ends. They were heterogenous, made up of procumbent cells in the central region, and rows of upright and square cells in the margins. The radial pits were simple with oblique pores. Histochemical tests showed starch grains in the axial and radial parenchyma cells.

The bark of the xylopodium was 0.2 to 4.0 mm thick. The phloem presented tangential bands of phloematic fibers, one to five cells wide, interleaved by solitary or grouped sclereids. Sclereids were frequent between the bands of fibers, placed mostly in the rays, showing thickened and lignified walls. In the outer part of the secondary phloem, the rays underwent dilatation.

The sieve elements were short. There were conducting and nonconducting sieve tubes

together, even in the portions at the sides of the dilated rays. The rays of inner phloem presented a length and width similar to the rays of wood, being heterogenous, made up of square and upright cells and, sometimes, procumbent cells. The axial parenchyma was abundant. Secretory channels were observed in the phloem and sometimes in the cortical zone.

The cortical zone was made of isodiametric cells, organised in tangential bands. The peridermis was made at least by four layers of cells: phelodermis, with one or two cells; phellogen, with two bands of tabular cells; and phellem, with one to three layers of cells. In the outer region of the bark there was a discrete rhytidome.

2. Root (figures 3, 4 and 5)

The primary structure of the root was diarch. The wood showed growth rings marked in the inner wood by radially flattened and thick-walled fibers and in the outer wood by marginal parenchyma bands. The vessels were diffuse. The majority (90%) was of solitary vessels, but there were multiple vessels (10%) of up to three cells. The vessel elements presented a simple perforation plate, horizontal to oblique. The inter-vessel pits were bordered, alternate, sometimes opposed, coalescent, circular, with a diameter of about $6.3 \mu\text{m}$. Tyloses were seen obliterating a vessel, either partially, or totally. Histochemical tests with Sudan IV revealed the lipidic nature of the tyloses.

The fibers presented simple pits with oblique pores. The axial parenchyma was scanty paratracheal vasicentric, but showing confluence when vessels grow close one to each other. Axial parenchyma was also seen forming marginal bands of one to four cells wide. The radial parenchyma was uniseriate (73%), biseriate (24%) or triseriate (3%), homogenous, and made of square cells. The vascular cambium was 1-5-seriate and made of tabular cells.

The bark was between 0.1 and 1.2 mm thick. The phloem showed tangential bands of fibers of 1-7 cells wide, together with 1-3 bands of

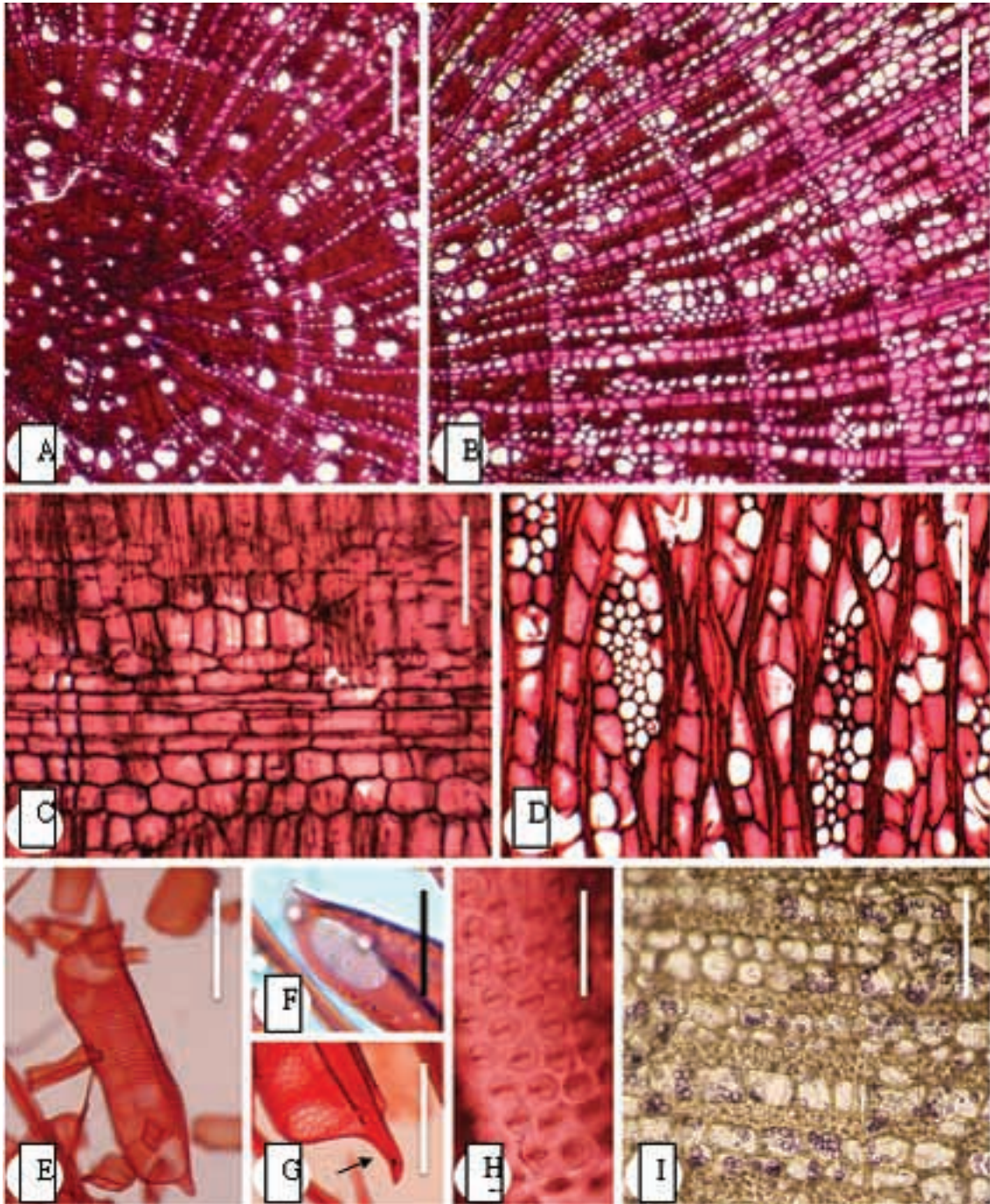


FIGURE 1 – Wood anatomy of xylopodium of *Jacaranda ulei*. A – Transversal section showing diffuse porous vessels. B – Transversal section showing confluent paratracheal axial parenchyma. C – Radial longitudinal section showing heterogeneous rays. D – Tangential longitudinal section showing radial parenchyma 1-6 seriate. E – Vessel element. F – Detail of the perforation plate. G – Dissociated vessel element with an appendix (arrow). H – Detail of bordered pits. I – Lugol test in transverse section showing starch in the parenchyma. Bars: 290 μm (A); 340 μm (B); 190 μm (C, D, G); 140 μm (E, F); 30 μm (H); 210 μm (I).

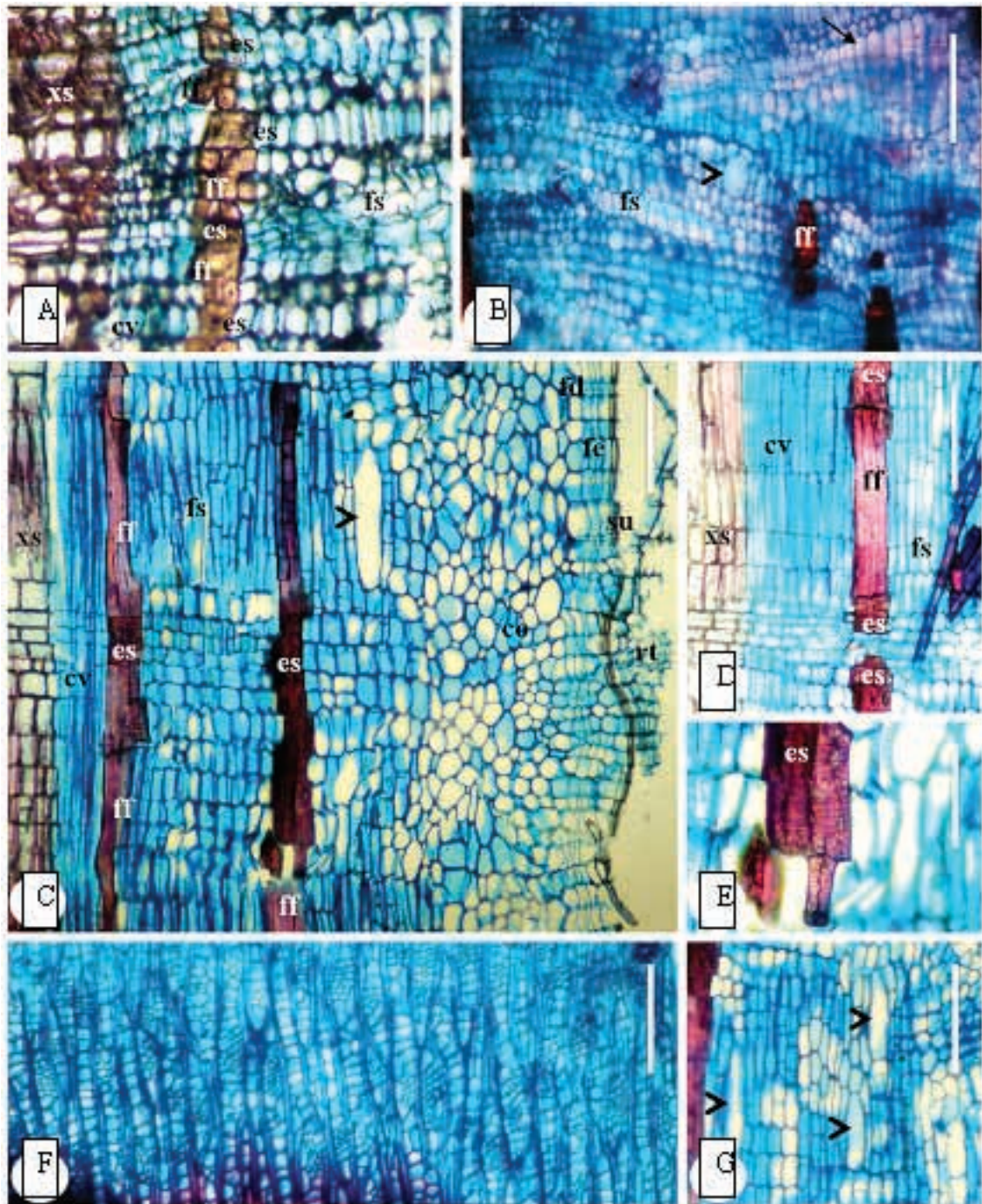


FIGURE 2 – Bark anatomy of xylopodium of *Jacaranda ulei* A – Transversal section showing bands of fibers and sclereids. B – Transversal section showing a secretory channel (arrowhead) in the phloem. Dilated rays (arrow) in the external portion of the phloem. C – Radial section showing phloem with heterogenous rays and secretory channel (arrowhead). D – Radial section showing sclereids in the rays. E – Detail of sclereid. F – Tangential section showing the phloem rays similar to wood rays. G – Detail of a secretory channel (arrowhead) in the phloem. co: cortex. cv: vascular cambium; es: sclereid; fd: phellodermis; fe: phellogen; ff: phloematic fibers; fs: secondary phloem; rt: rythidome; su: suber; xs: secondary xylem. Bars:130 μm (A); 150 μm (B); 100 μm (C); 140 μm (D, G); 60 μm (E); 290 μm (F).

sclereids. The fibers presented a thick wall that fills the cellular lumen. Sclereids were seen in the rays.

The sieve tubes and the companion cells were distributed in radial bands between the phloem rays. In the phloem, there were bands of fibers and sclereids.

The peridermis was made of 1-3 layers of isodiametric cells that form the phellogen; 2-3 layers of tabular cells that form the phellogen and there were also 1-4 layers of suberised square cells forming the suber. A seriated rhytidome was observed, with regions of detachment.

Histochemical tests using Sudan IV showed the presence of lipidic compounds diffusely in the wood: inside the vessels, in parenchymatic cells, and in the fibers. In the bark, lipids were evidenced in vascular cambium, in the phloematic fibers, in the sclereids, and in the peridermis. Tests using acid phloroglucinol showed lignin in the phloem fibers, in the sclereids, and in the tabular cells of the phellogen. Starch grains were seen in a small amount in the axial parenchyma of the wood and in a greater amount in the bark – especially in the companion cells of the sieve tubes and in the axial parenchyma.

3. Stem (figures 6, 7 and 8)

Although the sample included only adult plants, the stems showed to be young, as about 1/3 of the diameter was of primary xylem and pith. No growth rings could be distinguished. The vessels were diffuse, solitary (49%), and multiple (51%) of 2-6 cells (Table 5). The perforation plate was simple, with horizontal or oblique opening. The vessels presented bordered pits, alternate, coalescent, circular. There were appendices in the ends of vessel elements. The fibers showed small simple pits. The axial parenchyma was scanty, paratracheal, and vasicentric. The rays were uniseriate (70%), or biseriate (30%), homogenous, and made of square cells. The vascular cambium showed 2-3 layers of tabular cells.

The bark was thin. The phloem presented fibers of thickened walls, arranged in bundles of up to 13 cells. In the phloem, gelatinous fibers were present. The sieve tubes and companion cells were arranged in tangential bands and the presence of a nonconducting phloem was not clear. The phloematic rays showed a seriation similar to the wood. The cortex was made of tabular or rounded cells, with 5-10 tangential layers, with gelatinous fibers. The peridermis was made of 3-6 layers of cells. The phellogen was 1-2 seriate. The phellogen was made of 1-2 layers of tabular cells. The suber presented 1-3 layers of tabular, square, and rounded cells, with lignified walls. There were bands of sclereids in the peridermis, with 1-5 cell layers. Rhytidome was seen in some samples. There were simple tectonic hairs, unicellular, and with a sharp apex.

The histochemical tests with acidified phloroglucion showed lignin in some of the phloematic fibers, in the phellogen and in the sclereids of the peridermis. Lugol showed starch grains in the cortex. Sudan IV showed lipidic compounds in the bordering parenchyma between the pith and the secondary xylem, in the gelatinous fibers of the phloem and in some clusters in the internal layers of peridermis.

DISCUSSION

1.1 Comparison

The anatomical structure of wood was different among the stem, the root, and the xylopodium. The barks of the root and xylopodium were similar, but different from the stem.

Overall, the structure of the wood of each organ was typical of the family Bignoniaceae: diffuse porous, single and multiple vessels, simple perforation plate, and circular bordered pits. However, the arrangements of the wood anatomical aspects are very different.

Regarding vessels, the roots present the majority as solitary, while stem and xylopodium present 50% of solitary and 50% of multiple vessels. Vessels of both, root and xylopodium,

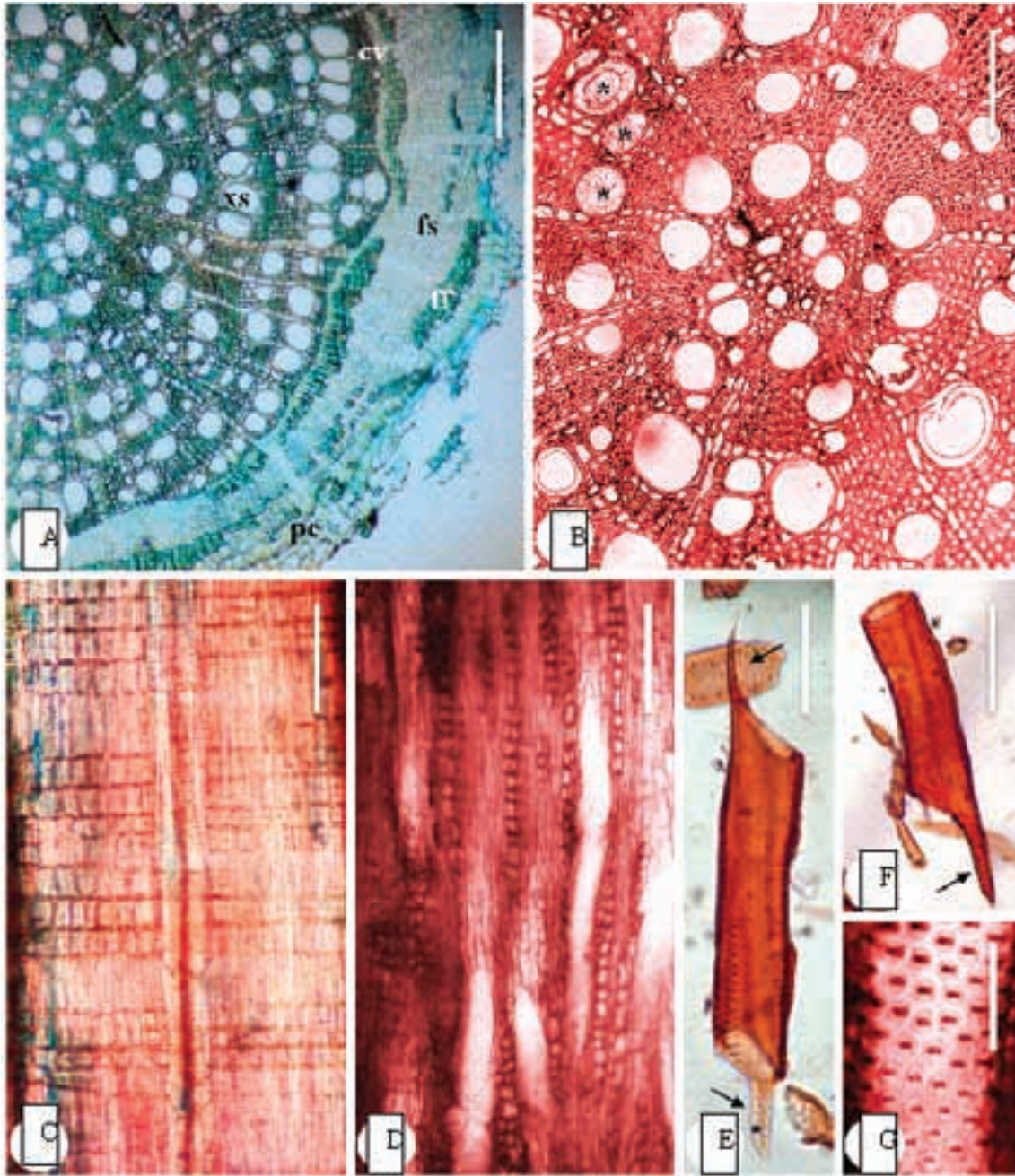


FIGURE 3 – Wood anatomy of taproot of *Jacaranda ulei*. A. general view. B – Transversal section, vessels with tyloses (*). C – Radial section showing heterogeneous rays. D – Tangential section showing uniseriate and biseriate rays. E – Dissociated material. Vessel element showing appendices (arrows) in both ends. F – Detail from appendix (arrow) in one of the ends of a vessel element. G – Details of the bordered pits of vessel elements. cv: vascular cambium. ff: phloematic fibers. fs: secondary phloem; pe: peridermis; xs: secondary xylem. Bars: 220 μ m (A); 150 μ m (B); 180 μ m (C, D); 90 μ m (E); 200 μ m (F); 20 μ m (G).

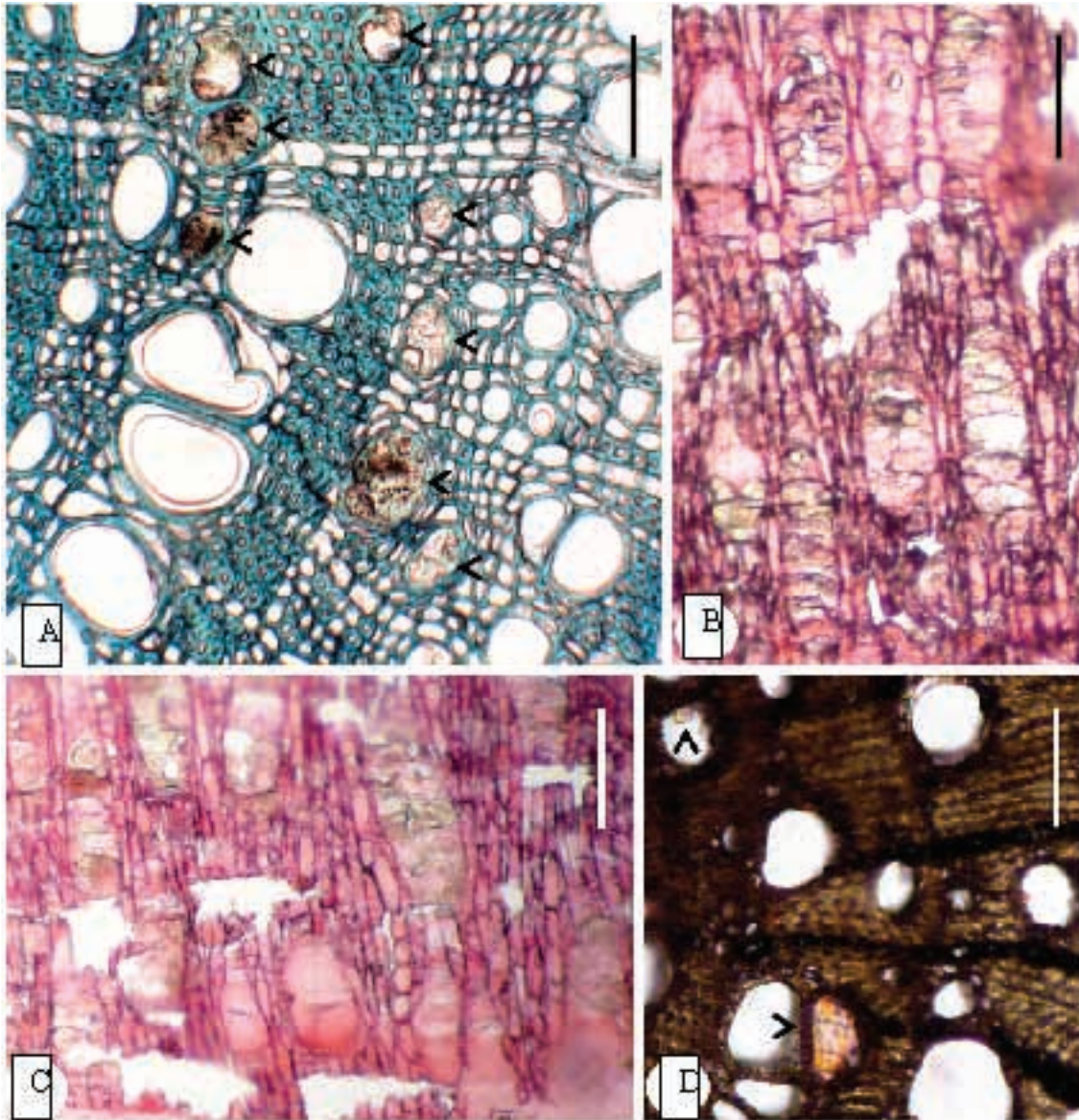


FIGURE 4 – Details of wood of taproot of *Jacaranda ulei*. A – Transversal section showing tyloses closing the lumen of vessels. B, C – Tangential section. Vessels filled up with tyloses. D – Sudan IV test in transversal section showing the lipidic nature of the tyloses. Bars: 120 μm (A); 90 μm (B); 100 μm (C); 110 μm (D).

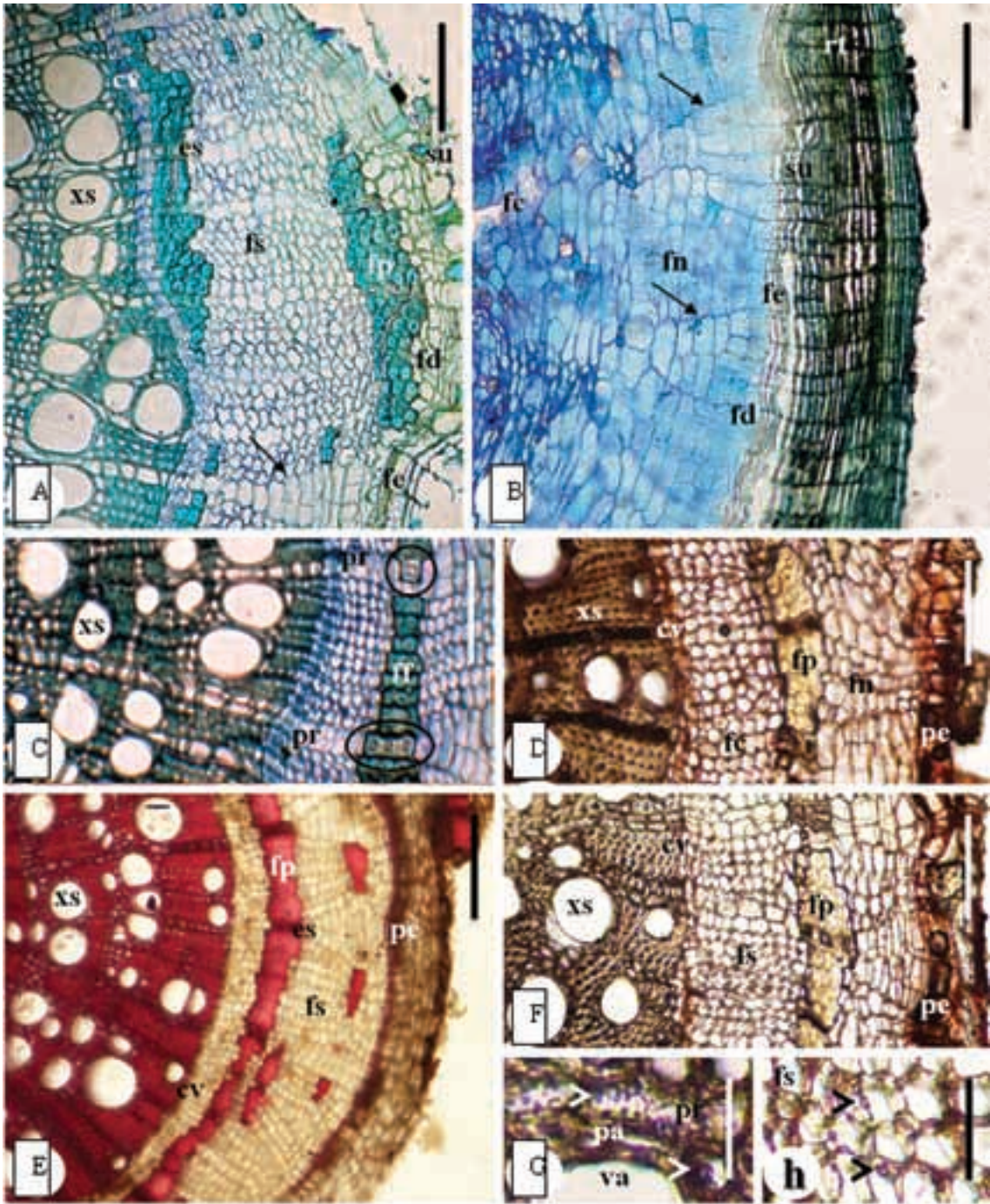


FIGURE 5 – Transversal section of bark and histochemical tests in taproot of *Jacaranda ulei*. A – General overview of bark, showing dilated rays (arrows). B – Presence of rhytidome and of dilated rays in the phloem. C - Sclereids seen in the bands of fibers. D – Sudan IV test showing lipids in the peridermis. E – Acidified phloroglucion test showing lignin in the phloematic fibers and sclereids. F, G, H – Lugol test showing starch grains (arrowhead) in parenchymatic cells of xylem and of phloem. Cv: vascular cambium; es: sclereid; fc: previous phloem; fd: phelodermis; fe: phellogen; ff: fibers of primary phloem; fn: collapsed phloem; fp: primary phloem; fs: secondary phloem; pa: axial parenchyma; pr: radial parenchyma; rt: rhytidome; su: suber; va: vessel; xs: secondary xylem. Bars: 140 μm (A, D); 150 μm (B); 180 μm (C); 120 μm (E); 130 μm (F); 30 μm (G, H).

TABLE 1. Parameters of wood and bark of root, stem, and xylopodium of *Jacaranda ulei*

Parameters	Mean \pm S			Min	Max
	Root	Xylopodium	Stem		
Wood					
Vessels					
Diameter (μm)	49,9 \pm 13,2 ^a	43,4 \pm 13,2 ^a	107,5 \pm 43,1 ^b	14,5	224,1
Diameter of lumen (μm)	36,3 \pm 10,7 ^a	36,7 \pm 12,4 ^a	88,3 \pm 38,0 ^b	10,8	188,7
Length (μm)	326,5 \pm 96,8 ^a	374,9 \pm 80,7 ^a	408,2 \pm 105,1 ^a	159,0	735,5
Number/mm ²	142,4 \pm 30,4 ^a	12,2 \pm 8,6 ^b	91,3 \pm 30,2 ^a	2,0	58,0
Diameter of pits (μm)	6,3 \pm 1,8 ^a	9,9 \pm 2,4 ^b	12,5 \pm 1,4 ^c	3,8	14,9
Length of vessel appendix (μm)	85,0 \pm 38,1 ^a	51,7 \pm 24,0 ^b	82,7 \pm 64,9 ^a	16,1	282,6
Fibers					
Diameter (μm)	15,0 \pm 3,9 ^a	14,0 \pm 4,6 ^a	14,8 \pm 3,4 ^a	6,9	27,5
Diameter of lumen (μm)	5,4 \pm 2,8 ^a	5,4 \pm 3,1 ^a	5,9 \pm 3,2 ^a	0,2	15,5
Length (μm)	560,5 \pm 117,3 ^a	789,6 \pm 186,0 ^b	637,2 \pm 196,4 ^a	308,9	1512,8
Wall thickness (μm)	4,8 \pm 1,5 ^a	4,3 \pm 1,4 ^a	4,4 \pm 1,0 ^a	2,1	8,7
Width (μm)	19,7 \pm 4,4 ^a	23,8 \pm 8,5 ^b	17,5 \pm 4,3 ^a	6,2	55,2
Rays					
Height (μm)	276,9 \pm 128,7 ^a	834,7 \pm 325,3 ^b	431,2 \pm 194,1 ^b	173,6	1599,5
Width (μm)	15,2 \pm 6,5 ^a	68,0 \pm 22,7 ^b	25,2 \pm 7,2 ^b	14,9	119,4
Number/mm ²	14,8 \pm 2,7 ^a	9,3 \pm 2,0 ^b	14,3 \pm 3,1 ^a	6,0	20,0
Phloem					
Sieve tubes					
Diameter (μm)	28,9 \pm 9,1 ^a	25,5 \pm 5,1 ^a	17,9 \pm 4,6 ^a	11,8	45,8
Length (μm)	465,0 \pm 105,7 ^a	249,5 \pm 76,4 ^b	293,9 \pm 119,8 ^b	143,6	679,4
Bark					
Thickness (mm)	0,5 \pm 0,3 ^a	1,0 \pm 0,9 ^b	0,5 \pm 0,2 ^a	0,2	4,3

Letters compare lines and different letters mean $P < 0,05$ at Student's t-test

TABLE 2. Proportion of solitary and multiple vessels in the wood of *Jacaranda ulei*

Vessels	Solitary	Double	Triple	Multiple of 4	Multiple of 5 or +
Xylopodium	59%	22%	9%	5%	5%
Root	90%	8%	2%	0	0
Stem	49%	20%	15%	12%	4%

present the same diameter, while the ones of the stem are larger. However, the density of vessels of root and stem is similar, and both are greater compared to the xylopodium.

The xylopodium of *Jacaranda ulei* is different from the stem and the root because it is densely fibrous, and the abundance of fibers is the anatomical expression of the macroscopic hardness of the organ. The amount of fibers is not only greater in the xylopodium, they also tend to be longer than the ones in the stem and the root.

Regarding the parenchymatic tissues, the xylopodium presents a greater amount of axial parenchyma compared to the root, and the root, greater than the stem. The axial parenchyma of the stem is common to the genus *Jacaranda*: scarce, vasicentric paratracheal, aliform, and sometimes, confluent. However, the axial parenchyma of the root and the xylopodium are not only more abundant than the stem, but also form apotracheal concentric bands, an aspect that is not salient to the genus.

The radial parenchyma of the stem and the root are similar, and mostly uniseriate and homogenous, which anatomically corroborates the classification of *J. ulei* in the section *Monolobos*. However, the xylopodium contrasts, as the radial parenchyma is biseriate and heterogenous, and has a greater height compared to the stem and the root, which could classify the species in the section *Dilobos*. Nevertheless, according to Pace *et al.* (2015), even being different among themselves, the anatomical pattern of the wood is typical of the tribe *Jacarandae*.

Regarding the bark, the overall structure is similar to other species from the genus *Jacaranda*: thin, with fibers in the phloem, and rhytidome, when present, is made of a few cell layers (Roth 1969). The structure of the bark is different between the stem and the subterranean system (xylopodium + taproot); in the subterranean system, the sclerenchyma of the phloem is organised in concentric layers, while in the stem the sclerenchyma they present in bundles. In the subterranean system, there is dilatation of the rays, which was not seen in the stem. The peridermis of stem and subterranean system present concentric layers of sclerenchymatic tissue and, in general, the cells present an abundance of lipids; however, the phelloderm of the stem shows trichomes, which were not seen in the subterranean system. Inversely, secretory channels in the bark were seen in the subterranean system, but were not perceived in the stem.

1.2) General considerations

The family Bignoniaceae comprises about 82 genera and 860 species of mostly lianas and herbs, but also trees, shrubs, and sub-shrubs (APGIII 2009; Olmstead *et al.* 2009; Machado and Romero 2014). Anatomical studies of wood and bark of species from the family Bignoniaceae have been carried out in a descriptive manner (Panizza 1967; Roth 1969; Trivedi *et al.* 1976; Mohiuddin 1995; Mauro *et al.* 2007; León 2007; Muñoz & Marchiori 2009), for taxonomical classification (Gasson and Dobbins 1991; Santos and Miller, 1997), for the

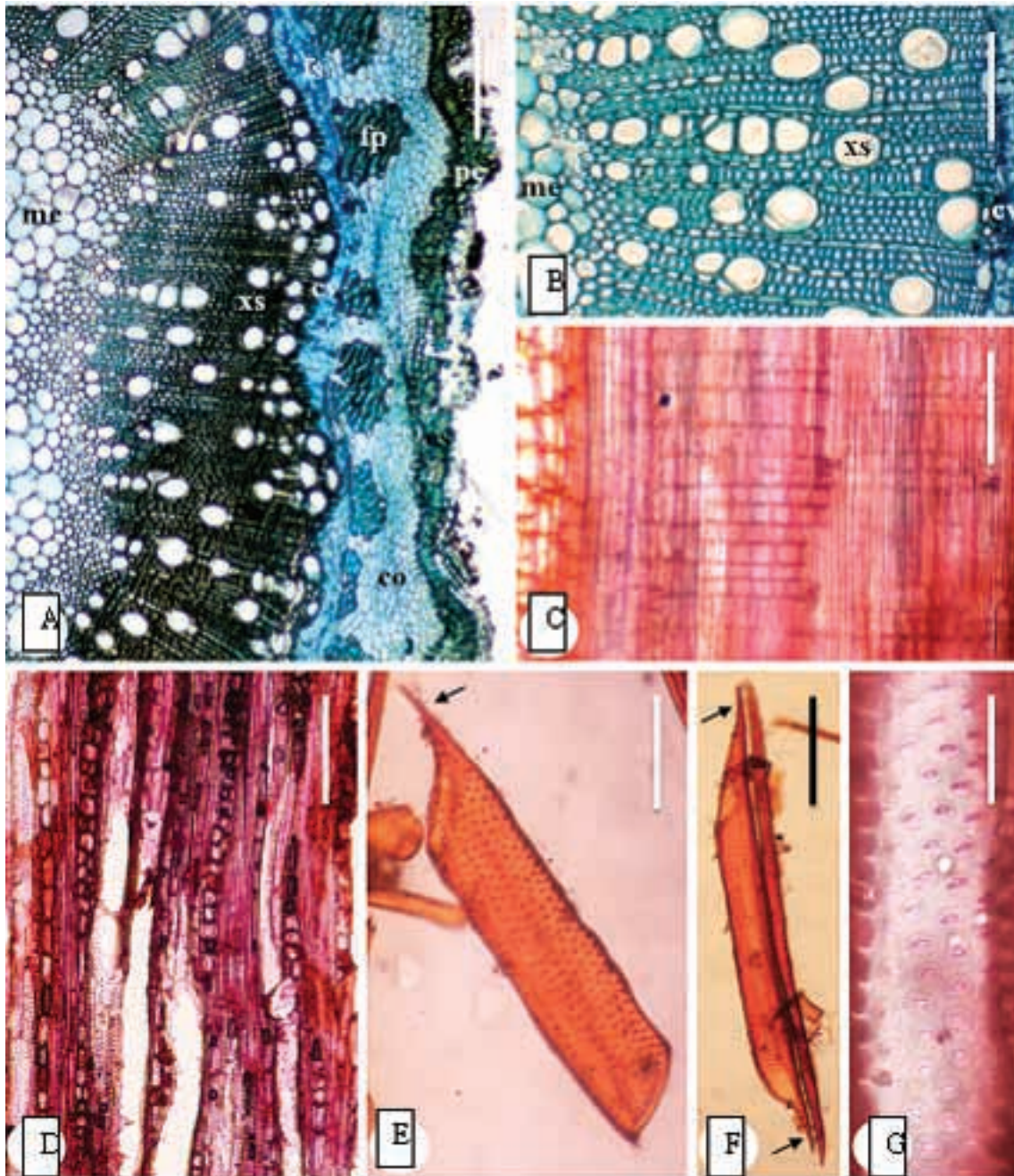


FIGURE 6 – Wood anatomy of stem of *Jacaranda ulei*. A – Transversal section showing an overview of wood and bark. B – Transversal section showing solitary and multiple vessels. C – Radial section showing homogenous rays. D – Tangential section showing uni- or biseriate rays. E – Vessel element presenting appendix. F – Dissociated material, showing in detail the appendix in both ends of a vessel element and a fiber. G – Details of the bordered pits of the vessels. co: cortex; cv: vascular cambium; fp: primary phloem; fs: secondary phloem; me: pith; xs: secondary xylem. Bars: 110 m (A); 150 μ m (B, C); 170 μ m (D); 70 μ m (E); 120 μ m (F); 30 μ m (G).

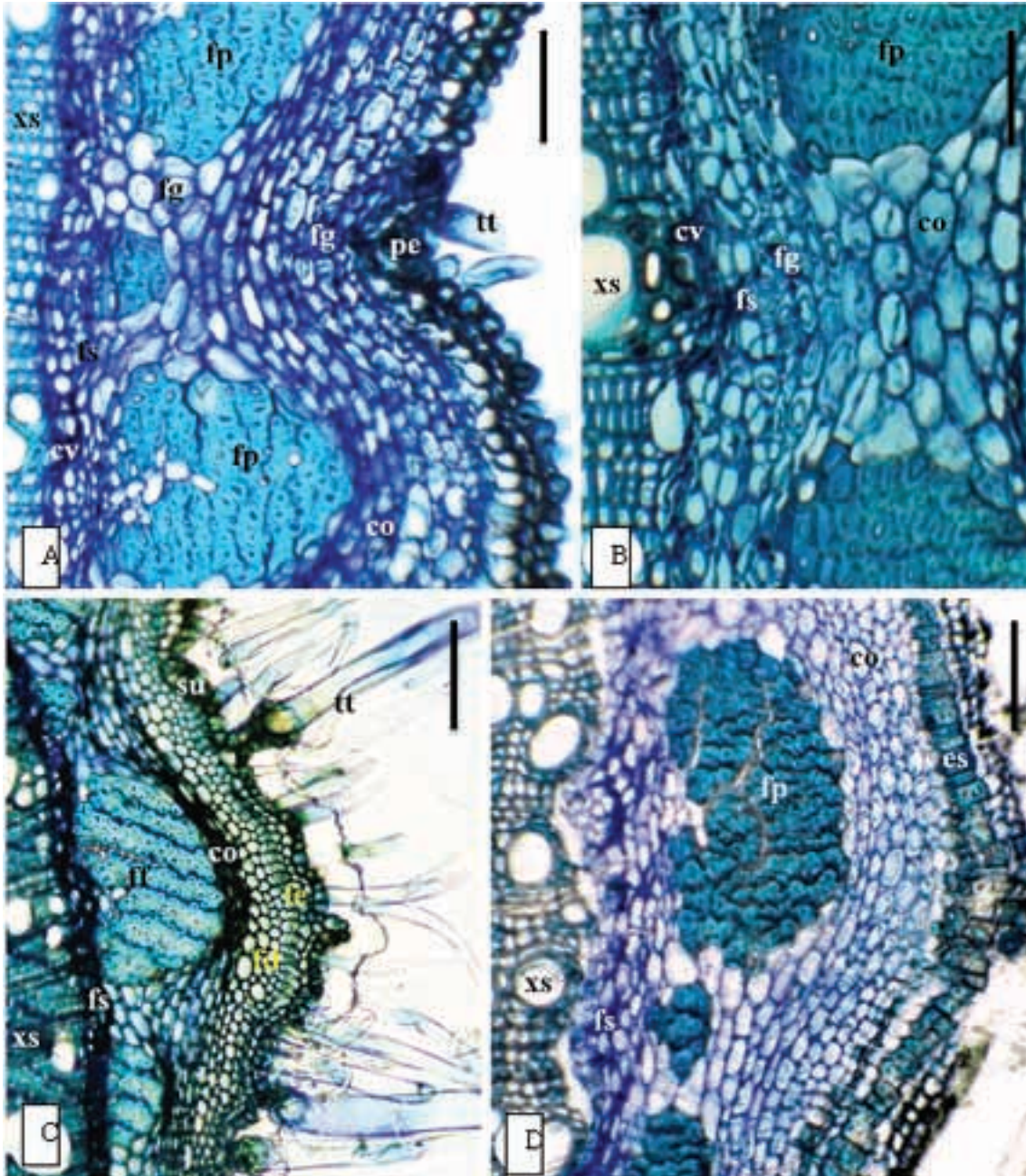


FIGURE 7 – Bark anatomy of stem of *Jacaranda ulei*. A – Cortical parenchyma arranged in tangential bands with gelatinous fibers. B – Detail of gelatinous fibers. C – Detail of peridermis, showing simple tector trichomes. D – Bands of sclereids in the peridermis. Co: cortex; cv: vascular cambium; es: sclereids; fd: phellodermis; fe: phellogen; ff: primary phloem fibers; fg: gelatinous fibers; fp: primary phloem; fs: secondary phloem; su: suber; tt: trichomes; xs: secondary xylem. Bars: 100 μ m (A, D); 70 μ m (b); 110 μ m (C).

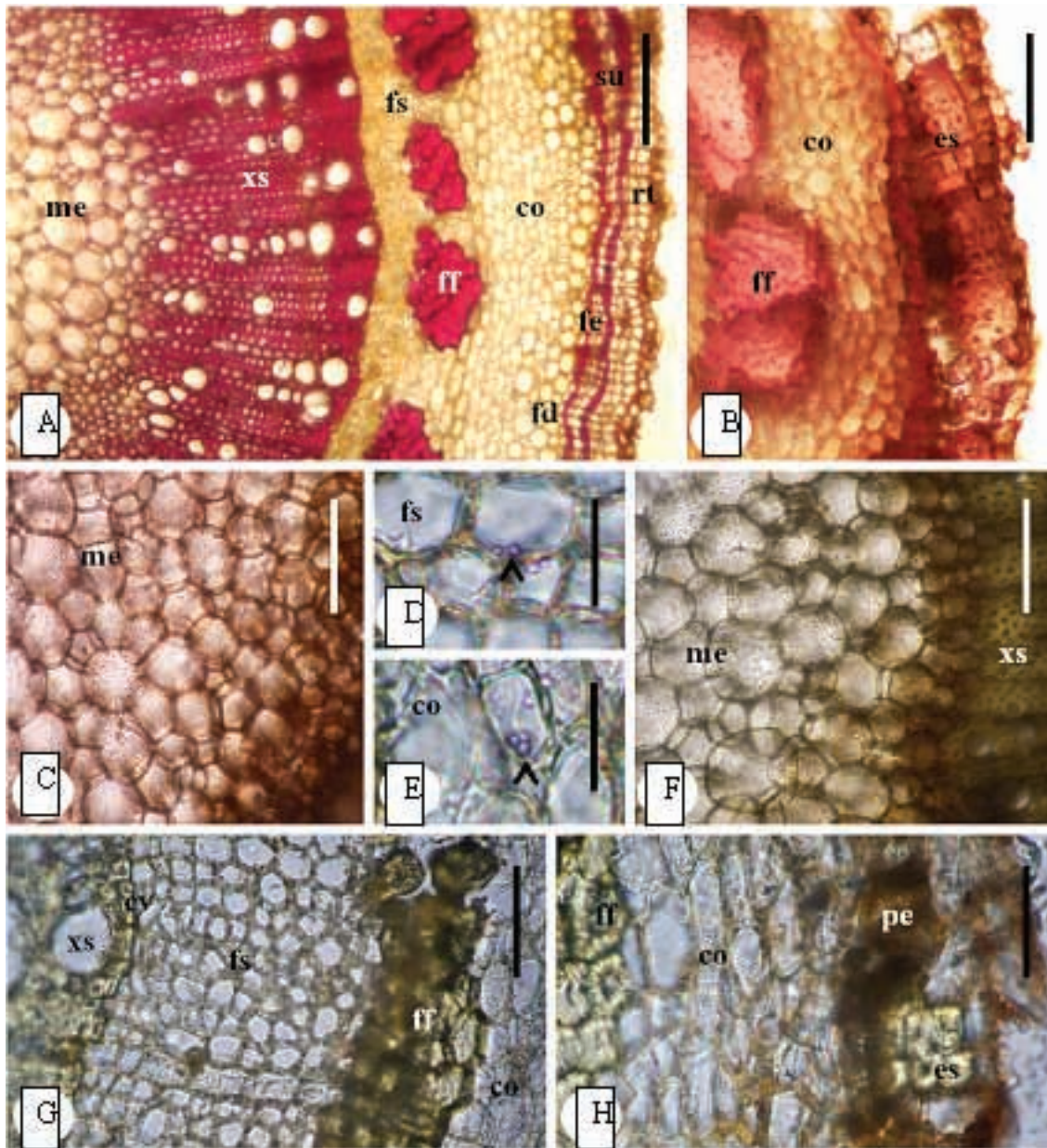


FIGURE 8 – Histochemical tests in stem of *Jacaranda ulei*. A – Acidified phloroglucinol showing lignin in the fibers from primary phloem. B – Acidified phloroglucinol showing sclerenchyma. C – lugol, not revealing starch in the pith. D, E – Lugol showing starch grains (arrowheads) in the parenchyma of phloem and in the cortex. F, G, H – Sudan IV, not revealing lipids in the pith and presence in phloematic fibers and in the peridermis. co: cortex; cv: vascular cambium; es: sclereids; fd: phellodermis; fe: phellogen; ff: phloematic fibers; fs: secondary phloem; me: pith; pe: peridermis; rt: rhytidome; su: suber; xs: secondary xylem. Bars: 120 μ m (A, C, F); 60 μ m (B); 40 μ m (D, E); 90 μ m (G, H).

comprehension of some ecophysiological aspects (Lima *et al.* 2010; Gerolamo and Angyalossy 2017), and also as part of a great phylogenetical analysis, sampling a considerable number of species (Pace and Angyalossy 2009, 2011, 2013; Pace *et al.* 2015a, 2015b). However, almost all those studies are based upon the anatomy of branches or stems, with only a few studies on root and/or subterranean system, such as the ones of Panizza (1967), Gabriele (1992) and Alves *et al.* (2013).

The definition of xylopodium first appeared in 1906, in the manuscripts of Lindman and Lofgren (1906), and it refers to a rigid, sclerified region in the transition between the stem and the taproot. Contrary to the common knowledge that gemmiferous organs are soft, the xylopodium shows a high ability of re-sprouting, and is more frequently observed in shrubs and sub-shrubs (Rizzini and Heringer 1962). Some species show xylopodium and can grow into trees, such as *Brosimum gaudichaudii* (Palhares *et al.* 2006). In this study, the middle portion of the xylopodium was taken as a standard, because the superior portions might have contained the lost stems, which could produce anatomical patterns even more complex and difficult to enable comparison.

The anatomical differences between the root and the shoot are related to physiological differences. Regarding water transport, the narrower vessels of the subterranean system are more constant regarding hydraulic flow, with fewer chances of embolism occurrence, while the wider vessels of the stem are related to a greater hydraulic conductivity (Hacke and Sperry 2001; Gerolamo and Angyalossy 2017). It was inverse to *Phlomis fruticosa* and other species from the Mediterranean climate, where the vessel diameter of the roots are double of the stem (Psaras and Sofroniou 2004) and also to some other Cerrado arboreal species as described by Longui *et al.* (2017). Regarding the parenchymatic tissue, Braun (1984), Hacke and Sperry (2001), and Luchi (2004), consider its function of water storage and ion

transportation to the vessels to be an ecological tendency of species with larger rays, found more frequently in environments regularly submitted to the hidric deficit, such as evidenced in the Cerrado. However, this was not the case of *J. ulei*; the rays seemed to be more related to a taxonomic pattern (section *Monolobos*) than to an ecophysiological trend.

The anatomic structure of the xylopodium corroborates the double function of the organ in being at the same time very hard, but with a great ability of sprouting. This is clear from the abundance of fibers as well as the abundance of parenchymatic tissues, since parenchyma and cambium are regions typically known to have ability of generating new shoots.

The anatomical differences between the wood of root and shoot are related to physiological differences as well as to the plant's strategies of survival (Patel 1965). Indeed, in *Styrax camporum*, there are conspicuous differences between its root and stem, in such a manner that the anatomical structure of the root suggests the root to be more specialised than the stem (Machado *et al.* 1997, 2005).

The bark presents several functions, some of them antagonising one against the other. The anatomy of the bark is related to the wood, especially regarding the density of rays, since the rays of the bark and the wood derive from the same cambial initials. Rosell *et al.* (2014) state that the density of wood and bark are related: the denser the wood, the denser the bark, and vice-versa. Additionally, the thickness of the bark is related to leaf size; the bigger the leaves, the thicker the bark, and vice-versa. Indeed, the thin bark of *J. ulei* corroborates this idea, as the leaves are small, and the branches are short.

According to Rosell *et al.* (2014), species with thicker barks are more frequent in savannahs, but even in those places, there are species with thin barks. This is typical of humid ecosystems, since the internal structure and thickness of the bark have more to do with physiological strategies than ecosystem trends.

Commonly, the anatomical structure of the

wood of the stem and the shoots is the same; however, in the bark, the older ones show anatomical differences compared to the newer ones. Therefore, the anatomic aspect of the stem of *J. ulei* suggests being significantly younger than the root, as evidenced by the great proportion of the pith in the stem diameter. Thus, the differences in the bark anatomy may be related mostly to the age of the bark, and hence, anatomical studies of plants known to be older and/or the apical regions of the root could elucidate such questions. Indeed, in *Brosimum gaudichaudii*, the thickness and anatomical structure of the bark of older stems and roots were similar; however, the bark of younger stems were not only thinner but also showed differences in the anatomical structure, especially with the presence of fibers in bundles (Palhares *et al.* 2006; Palhares *et al.* 2007a, Palhares *et al.* 2007b), as seen in *J. ulei*. In *Styrax camporum* (Machado *et al.* 2005), the bark of both, root, and shoot, were strongly different, including the type of sieve plate of the sieve tube elements.

As a conclusion, important anatomical differences were seen between aerial and subterranean organs. Most of the structures were in accordance to a general taxonomic pattern, but some details were out of what has been described for the genus. To the future, systematic studies should include anatomical observations of the subterranean organs, not only the aerial ones.

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