ISSN 0373-580 X
Bol. Soc. Argent. Bot. 48 (3-4): 435-442. 2013

Comparative wood anatomy of vegetative organs (stem and rhizome) of *Sophora linearifolia* (Sophoreae, Papilionoideae, Leguminosae)

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Summary: Wood anatomy of stem and rhizome of *Sophora linearifolia*, a rhizomatous plant endemic to centre Argentina, is described. Structural description of thin sections and macerations includes microphotographs of optical and scanning electron microscopy. Significant anatomical differences exist between secondary xylem of aerial orthotropic shoots and underground rhizome. Both organs have absent to indistinct growth ring boundaries, simple perforation plates, alternate and vestured intervessel pits and disjunctive parenchyma cell walls. However, stems have smaller vessels, longer fibres, partial storying (vessel elements and axial parenchyma) and narrower rays. Some anatomical characters of the rhizome suggest adaptations to its sinuous pattern of growth. The stem wood anatomy indicates a close relationship to *Sophora* sect. *Edwardsia.*

Key words: Secondary xylem, endemic, Fabaceae, Argentina.

Resumen: Anatomía comparada de órganos vegetativos (tallo y rizoma) de *Sophora linearifolia* (Sophoreae, Papilionoideae, Leguminosae). Se describe la anatomía de madera de *Sophora linearifolia*, una planta rizomatosa endémica del centro de Argentina. La descripción estructural de los cortes delgados y macerados incluye microfotografías de microscopio óptico y electrónico de barrido. Se observaron diferencias significativas entre el xilema secundario de los tallos aéreos ortótropos y los rizomas subterráneos. Ambos órganos poseen los anillos de crecimiento poco marcados a ausentes, placas de perforación simples, punteaduras intervasculares alternas y ornadas y pared de células parenquimáticas disyuntas. Sin embargo, los tallos poseen vasos más pequeños, fibras más largas, estratificación parcial (elementos de vaso y parénquima axial) y radios más angostos. Algunos caracteres anatómicos sugieren una adaptación del rizoma a un patrón de crecimiento sinuoso. La anatomía del tallo indica una relación cercana con *Sophora* sect. *Edwardsia*.

Palabras clave: Xilema secundario, endémico, Fabaceae, Argentina.

Introduction

Sophora L. is a legume genus distributed almost worldwide, with about 62 spp. of herbs, shrubs and trees (Yakovlev, 1967; Tsoon & Ma, 1981a, b; Heenan *et al.,* 2001; The Plant list, 2010). It includes two endemic species to Argentina (*Sophora linearifolia* Griseb. and *Sophora rhynchocarpa* Griseb.), as well as two endemic to continental Chile *Sophora cassioides* (Phil.) Sparre (=*Sophora macnabiana* (Graham) Skottsb.) and *Sophora macrocarpa* Sm. *Sophora linearifolia* is a shrub with aerial erect stems and underground rhizomes with adventitious roots (Tourn *et al.,* 2005) that inhabits San Luis and Córdoba provinces, in centre Argentina. This species was originally placed in *Sophora* sect. *Keyserlingia* by Yakovlev (1967) and later placed in sect. *Sophora* by Peña *et al.* (2000). Although some molecular analysis have been carried out including *Sophora* spp. (Hurr *et al.,* 1999; Mitchell & Heenan, 2002; Heenan *et al.,*

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2004; Boatwright & van Wyk, 2010), Argentinian species have never been included, so their exact taxonomic position based on molecular data has not been resolved yet.

Anatomy descriptions of different organs can be important in some disciplines as palaeobotany, dendrochronology and archaeology to distinguish among them (Bernabei & Bontadi, 2011). In addition, anatomy descriptions of rhizome secondary xylem are scarce. Stem wood anatomy of *S. linearifolia* has never been described in detail. Several aspects of its anatomy were only superficially mentioned by Cozzo & Cristiani (1950) and Cozzo (1948). Fujii *et al.* (1994) made the most complete wood anatomy study of *Sophora*, describing 13 species (of *Sophora sensu lato*) including several from South America. Cajas & Baeza (2000) briefly described the two insular Chilean species of *Sophora* (*S. fernandeziana* (Phil.) Skottsb. and *S. masafuerana* (Phil.) Skottsb.) and Wagemann (1948) described *S. cassioides* (as *Sophora tetraptera* Ait.) from continental Chile. Also Brown (1922), Cumbie & Mertz (1962) and Patel (1995) reported wood anatomy of this genus.

This contribution is a detailed secondary xylem anatomical study of erect aerial stem and underground rhizome. Comments on plant ecological adaptations in relation to the anatomy are made. Comparisons with other species of *Sophora* are carried out and systematic relationships based on stem anatomy are suggested.

Materials and Methods

Three stems from different plants and a rhizome from one of them were studied. Plants and slides are housed at the herbarium of the Museo Argentino de Ciencias Naturales. A new complete specimen with stem and rhizome and herbarium voucher (BA 92948) was collected for this study by some of the authors (RRP, HPB and MPS) at Huerta Grande locality, Punilla Department, Córdoba province, Argentina (31º 03’ S and 64º 29’ W). The other specimens (BAw 484 and BA 10590) were collected by Castellanos at San Alberto Department, Córdoba province, Argentina. Slides were made following standard techniques (O’Brien & McCully, 1981; D’Ambrogio de Argüeso, 1986) for wood anatomical description. Macerations were made following Boodle (1916) technique. The microscopic slides and macerations were observed at light microscopes (Leica DM2500) and small fragments were observed at SEM (Philips XL30) after being gold coated. Descriptions were made following the list of hardwood microscopic features (IAWA Committee, 1989). Measurements are given as the mean followed by the range between parentheses. Mean values of the stem are expressed as the weighted mean of the three observed specimens.

Results

Descriptions

Stem

Secondary stems have a diameter of up to 12 mm. Growth ring boundaries are indistinct to absent (Fig. 1 D). Porosity is diffuse to semi-ring. Vessel size and arrangement is different near the pith, vessels are smaller and more frequently clustered (Fig. 1 A). In the rest of the stem, vessels are solitary or in tangential pairs, short to long radial series (2 to more than 10) or clustered (normally up to 8 elements) often forming distinct tangential, diagonal and diagonal with tendency to dendritic patterns (Fig. 1 A-C). Perforation plates are simple and oblique, only observed in RLS (Fig. 1 F, 3 A). Intervessel pits are vestured, small, *ca.* 5-6 µm in vertical diameter and mainly alternate (Fig. 3 A-B). Vessel-ray pits are simple bordered, rounded, angular or horizontally elongated in shape (Fig. 1 I). Helical thickenings present in all vessels (Fig. 1 F, 4 A) are occasionally vestured. Vessels have a tangential diameter of 28 (10-58) µm and are *ca.* 195-229 vessels per mm^2. Vessel elements are 168 (110-220) µm in length. Vascular tracheids are present mixed with narrow vessel elements (Fig. 4 A). A size transition from vascular tracheids to large vessels is observed. Ground tissue fibres are non-septate, thin to thick-walled (Fig. 1 D) and 875 (590-1380) µm in length (Fig. 4 A). Axial parenchyma is scanty paratracheal to vasicentric (Fig. 1 A-C). Axial parenchyma cells are fusiform or ordered in two cells per parenchyma strand (Fig. 4 A) and densely pitted (Fig. 1 H). Occasionally locally chambered (up to 26 chambers) fibres with prismatic crystals are present (only observed in macerations) (Fig. 4 A). Rays are 2 to 6 -seriated, usually 3 to 4 (Fig. 1 E, G). They frequently reach more than 1 mm in height and are composed by procumbent, square and upright cells mixed through the ray

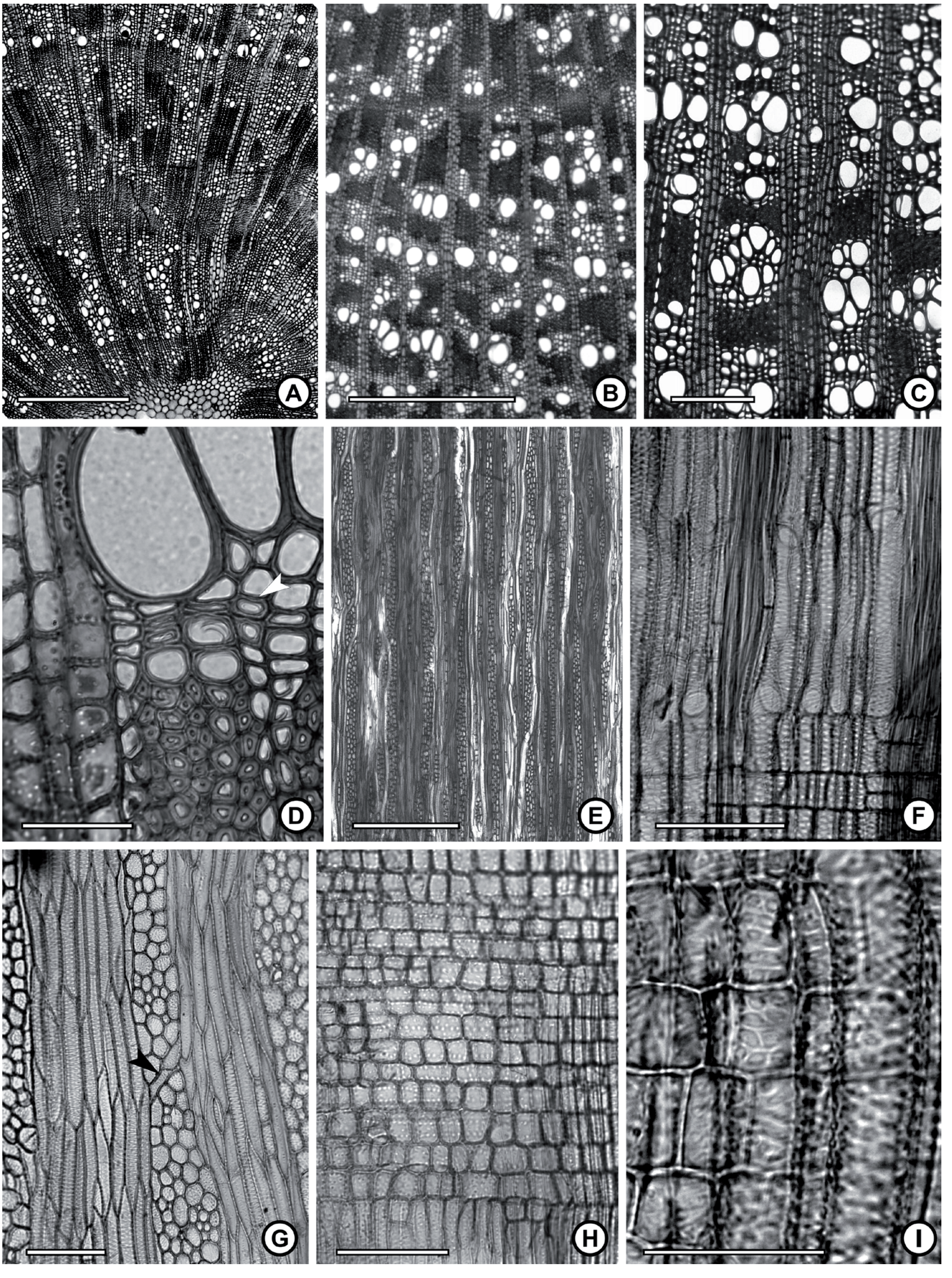

Fig. 1. Stem secondary xylem. **A:** Transverse section (TS) close to the pith. BA 10590. Bar = 500 µm. **B:** TS. BAw 484. Bar = 500 µm. **C:** TS. BA 92948. Bar = 200 µm. **D:** TS, indistinct growth-ring boundary (arrowhead). BA 92948. Bar = 50 µm. **E:** Tangential longitudinal section (TLS). BA 92948. Bar = 500 µm. **F:** Radial longitudinal section (RLS), simple perforation plates. BA 10590. Bar = 100 µm. **G:** TLS, partial storying of vessels, axial parenchyma, multiseriate rays and a vessel crossing a ray (perforated ray cell) (arrowhead). BA 10590. Bar = 100 µm. **H:** RLS, procumbent, square and upright densely pitted ray cells. BA 10590. Bar = 100 µm. **I:** RLS, angular to rounded ray-vessel pits. BA 10590. Bar = 50 µm.

(mostly upright cells) (Fig. 1 H). Ray frequency is 7-11, usually 8-9, rays per mm. Axial and radial parenchyma cell walls are rarely disjunctive (Fig. 4 A). Vessels crossing multiseriate rays (perforated ray cells) are frequently observed (Fig. 1 G). Narrow vessel elements and axial parenchyma are occasionally storied (Fig. 1 G).

Rhizome

Rhizome has adventitious roots of 1-2 mm in diameter. Pith was observed in early stage of rhizome development, but in mature rhizomes it was absent and the centre is occupied by vessels and fibres. Rhizome does not exhibit anomalous secondary growth and has a diameter of 15 mm. Growth ring boundaries are indistinct (Fig. 2 B). Porosity is diffuse. Vessels are mostly solitary or in tangential and radial pairs and occasionally in radial series of up to 4-5 vessels or clustered (Fig. 2 A-B). Perforation plates are simple and oblique, only observed in RLS (Fig. 2 E). Intervessel pits are vestured, small, *ca.* 6 µm in height and mainly alternate (Fig. 3 D). Vessel ray-pits are simple bordered and rounded, horizontally or

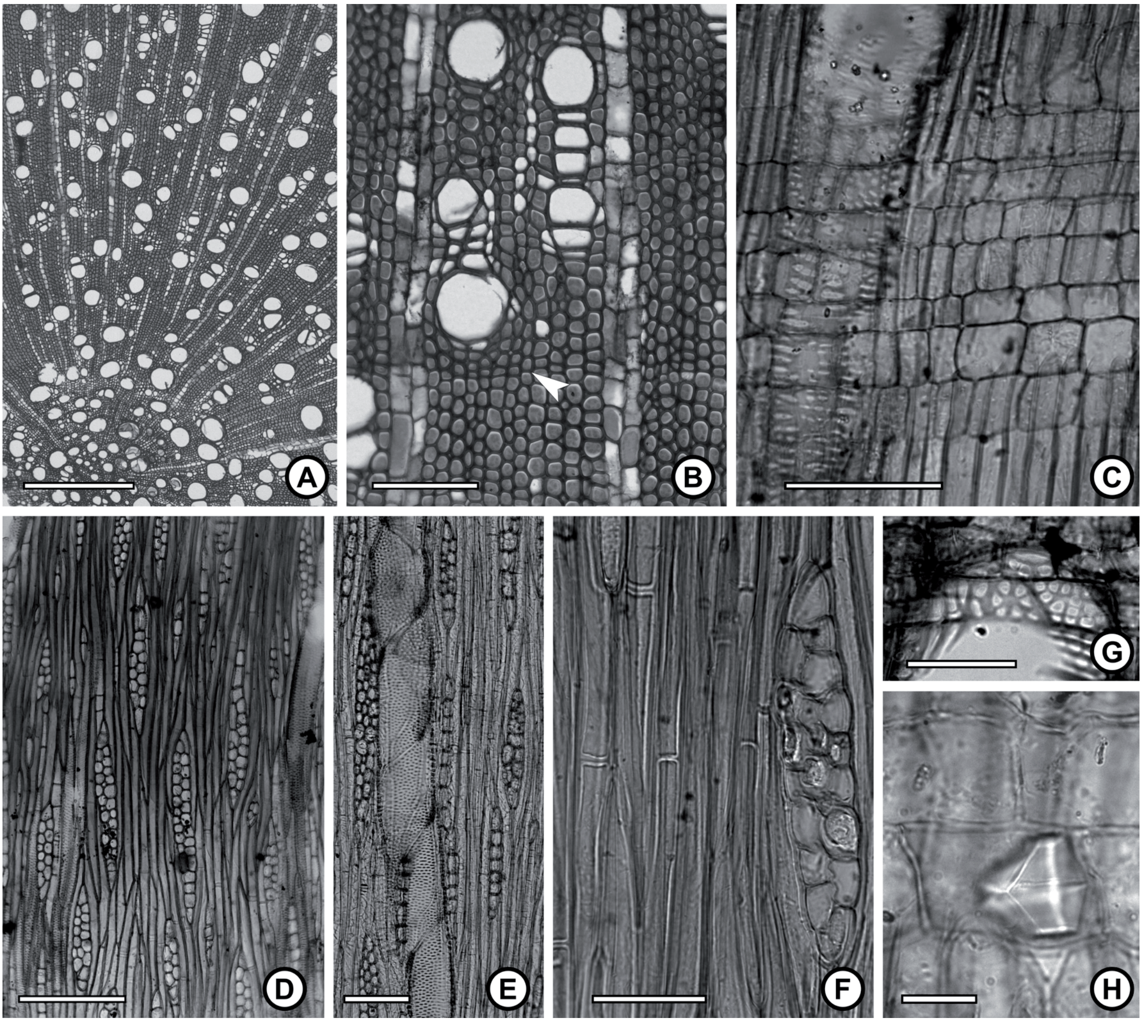

Fig. 2. Rhizome secondary xylem. BA 92948. **A:** TS including centre of the rhizome. Bar = 500 µm. **B:** TS, indistinct growth ring boundary (arrowhead). Bar = 100 µm. **C:** RLS, heterocellular rays and vessel-ray pitting. Bar = 100 µm. **D:** TLS. Bar = 200 µm. **E:** TLS. Bar = 100 µm. **F:** TLS, axial parenchyma and ray. Bar = 50 µm. **G:** RLS, vessel-ray pitting. Bar = 50 µm. **H:** RLS, crystal in a procumbent ray cell. Bar = 20 µm.

vertically elongated in shape (Fig. 2 C, G). Helical thickenings are present in all vessels (Fig. 4 B). Vessels have a tangential diameter of 63 (30-115) µm and are in a density of 64 (48-85) vessels per mm^2. Vessel elements are 247 (190-300) µm in length. Ground tissue fibres are septate (Fig. 4 B) very thin to thin walled (Fig. 2 B), simple or bordered pitted (fibretracheids) and 501 (320-720) µm in length (Fig. 4 B). Occasionally fibres exhibit an undulated contour and different extreme types (Fig. 4 B). Axial parenchyma is scanty paratracheal to vasicentric (Fig. 2 A, B). Axial parenchyma densely pitted cells are fusiform or ordered in two, 4 or more cells per parenchyma strand (Fig. 2 F, 4 B). Rays are 1 to 3 -seriated (Fig. 2 D, F) and in a frequency of 6 to 10, usually 7, rays per mm. Ray are composed of procumbent, square and upright cells mixed through the ray (Fig. 2 C). Rays cells appear densely pitted (Fig. 3 C). Axial and radial parenchyma cell walls are slightly disjunctive (Fig. 3 C, 4 B). Prismatic crystals are occasionally present in ray cells (Fig. 2 H).

Discussion

Stem and rhizome comparison

Stem and rhizome wood anatomy presents significant variation between them (Table 1). Vessels are smaller (mean 28 µm, rhizome mean 63 µm) and with a tendency to show dendritic patterns and clusterings in the stems and usually appear solitary or paired in the rhizome. In addition, fibres are longer (mean 875 µm, rhizome mean 501 µm), rays are wider and axial parenchyma is more abundant in the stems. Storying, absent in rhizomes; in stems is observed in small vessels and to a less degree in axial parenchyma. Shared characters between stems and rhizomes are: vestured pits, infrequent crystals (in different cell types) and a tendency to disjunctive ray and axial parenchyma cell walls.

These differences are probably related to their position in the plant. Due to its requirements, aerial stems are exposed to desiccation more than rhizomes. Vessel clustering is usually associated to xerophytic habits (Fahn & Cutler, 1992) and is present more frequently in stems than in rhizomes. Different vessel size suggests different mechanisms of water transport. Vascular tracheids, only found in stems, provide protection against the spread of embolism (Carlquist, 2001) and they are probably only necessary in orthotropic positions and possibly they would be not functional in the plagiotropic positions of the rhizomes. Shorter and undulated fibres with different endings present in rhizome could be an adaptation to its sinuous growth.

Note on rhizome wood anatomy

Rhizome wood anatomy descriptions are rare to find in the literature. For example, Carlquist (1981) described a rhizome of a semi-succulent perennial plant. Other studies report undetailed anatomical features or are focused on the primary growth of the rhizomes (*i.e.* McCulloch *et al.,* 1974; Carlquist, 1992; Rakotondrainibe & Deroin, 2006; Upton *et al.,* 2011).

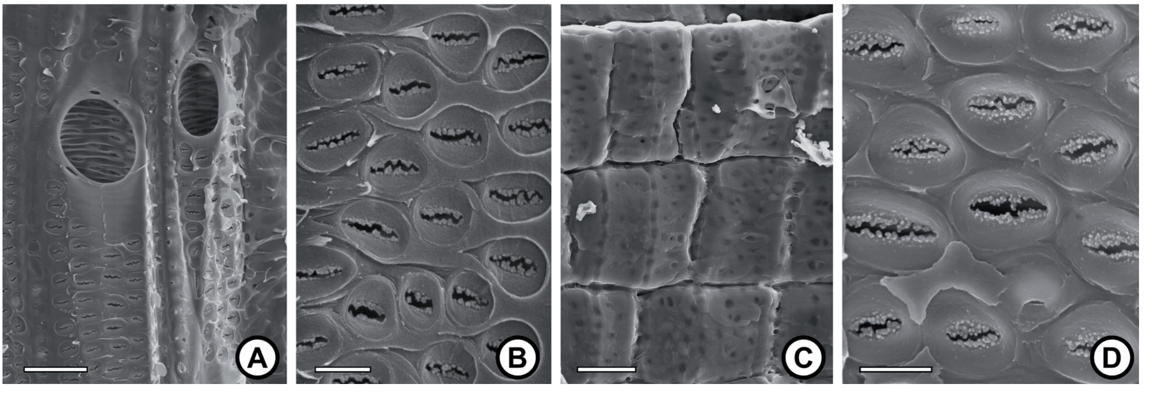

Fig. 3. SEM images of stem (A-B) and rhizome (C-D). BA 92948. **A:** simple perforation plates. Bar = 20 µm. **B:** vestured pits. Bar = 5 µm. **C:** densely pitted ray parenchyma. Bar = 20 µm. **D:** vestured pits. Bar = 5 µm.

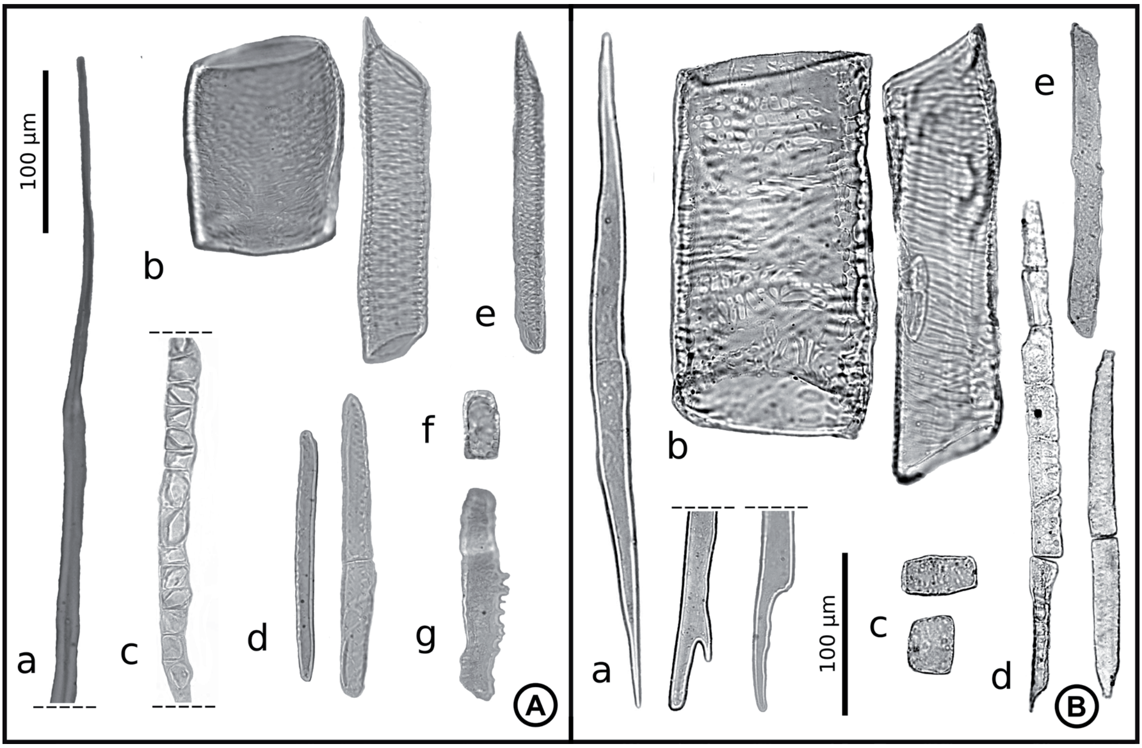

Fig. 4. Secondary xylem macerations. BA 92948. **A:** Stem, a, fibre portion, b, two vessel elements, c, crystalliferous fibre portion, d, axial parenchyma, fusiform and two-cell strand, e, vascular tracheid, f, ray parenchyma cell and g, disjunctive axial parenchyma cell wall. **B:** Rhizome, a, septate fibre and different fibre endings, b, two vessel elements, c, two ray parenchyma cells, d, axial parenchyma, 8-cell strand and two-cell strand and, e, fusiform axial parenchyma with slightly disjunctive cell walls.

Comparative stem wood anatomy

The following characters are shared among *S. linearifolia* and most species of *Sophora* sect. *Edwardsia*: growth ring boundaries indistinct to absent, helical thickenings in vessels, simple perforation plates, vestured pits, vascular tracheids, paratracheal axial parenchyma, multiseriate rays and disjunctive cell walls (Brown, 1922; Wagemann, 1948; Fuji *et al.,* 1994; Patel, 1995; Cajas & Baeza, 2000). Crystalliferous fibres, present in New Zealand species of *Sophora* (Patel, 1995), is a diagnostic character also observed in *S. linearifolia*. Although most species of *Sophora* from sect. *Edwardsia* exhibit tangential bands to dendritic vessel patterns (Fuji *et al.,* 1994), stems of *S. linearifolia* show a strong tendency to show dendritic patterns in the latewood and in the first growth rings. Storying is also present in all *Edwardsia* spp., and *S. linearifolia* stems show vessels and axial parenchyma somewhat storied. Rays of sect. *Edwardsia* are usually wider than *S. linearifolia* and in that section they are usually composed of procumbent cells (Brown, 1922; Wagemann, 1948; Cumbie & Mertz, 1962) or procumbent and upright cells (Patel, 1995) while in *S. linearifolia* are always heterocellular composed of procumbent, square and upright cells mixed through the ray. Abundant axial parenchyma, usually associated to warm climates (Fuji *et al.,* 1994), is less developed in *S. macrocarpa* and *S. linearifolia* than in other *Sophora* spp. These could be the result to the temperate climate where these plants growth.

Wood anatomy descriptions of *Sophora sensu stricto* species (excluding *Calia* Teran & Berland and *Styphnolobium* Schott) outside sect. *Edwardsia* are scarce (*e.g.* Cumbie & Mertz (1962) described *Sophora alopecuroides* L. and Fuji *et al.* (1994) described *Sophora mollis* (Royle) Baker). *Sophora tomentosa* L., apparently closely related to the

Table 1. Comparative table of stem and rhizome wood anatomy. Stem values and character states are based on the three studied samples. Values are expressed as the weighted mean followed by the range between parenthesis, or range of most common values followed by the range between parentheses.

	Growth ring boundaries	Vessels	Vessel tangential diameter [µm]	Vessel density [vessels per mm2]	Vessel element length [µm]	Axial parenchyma	Fibre lenght [µm]	Ray width [cells]	Rays per mm	Storying
Stems	Indistinct to absent	Solitary, pairs, short and long radial series and clustered	28 (10-58)	210 (195-229)	168 (110-220)	Scanty paratracheal to vasicentric	875 (590-1380)	3-4 (2-6)	8-9 (7-11)	Narrow vessels and axial aprenchyma occasionally
Rhizome	Indistinct	Solitary, pairs, short radial series	63 (30-115)	64 (48-85)	247 (190-300)	Scanty paratracheal to vasicentric	501 (320-720)	1-3 (1-3)	7 (6-10)	Not observed

sect. *Edwardsia* (Heenan *et al.,* 2004) lacks helical thickenings and has wider vessels (Fuji *et al.,* 1994). *S. nuttaliana* and *S. allopecuroides* exhibit vessels almost exclusively arranged in long radial series and very scarce axial parenchyma (Cumbie & Mertz, 1962). Moreover, these two species have similar ray width to *S. linearifolia* and their rays are exclusively composed of upright cells, while in *S. linearifolia* are heterocellular composed of procumbent, square and upright cells. Finally, in *S. mollis* all elements are non storied and vessels have similar ray width to *S. linearifolia* (Fuji *et al.,* 1994). *Sophora davidii* Kom. ex Pavol., is another species apparently very close to sect. *Edwardsia* (Pennington *et al.,* 2001; Wang *et al.,* 2006). Cozzo described for this species (as the junior synonym *Sophora viciifolia* Salisb.) tendency to dendritic patterns, helical thickenings and multiseriate rays similar to *S. linearifolia*. However, he described rays as homocellular but the description lacks more anatomical details about *S. davidii* wood anatomy. Overall wood structure of *S. davidii* also suggests a close relation to *S. linearifolia*.

Conclusions

The first complete detailed description of the wood anatomy, including stem and rhizome secondary xylem, of *S. linearifolia* is made.

Stems and rhizome have significant anatomical differences between them (Table 1). Vessel clustering and wider rays in stems seems to be related to xerophytic conditions, while shorter fibres and vessel elements of the rhizomes seems to be adaptations to its sinuous plagiotropic growth.

The stem wood anatomy suggests that *S. linearifolia* is related to sect. *Edwardsia*, and provides significant taxonomic information for this group, although wood structural descriptions of *Sophora* is still very incomplete (*e.g. Sophora rhynchocarpa* wood anatomical description has not been done).

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Recibido el 25 de septiembre de 2012, aceptado el 11 de marzo de 2013.