



Comparative wood anatomy of *Ficus cestrifolia* (Moraceae) in two distinct soil conditions

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Abstract

Wood anatomical traits respond to environmental variables and among them, soil has a direct impact on secondary xylem. This study compares the wood anatomy of two populations of *Ficus cestrifolia* occurring in two lowland formations of Southern Brazil (MAQ and SJS) with similar climate but different soil conditions. Wood samples were collected at breast height and prepared according to standard wood anatomy techniques. Soil samples were collected and subjected to a nutrient analysis. Wood was described quali and quantitatively. The qualitative wood anatomical features of both populations were similar. Some quantitative differences were observed. In MAQ area, the levels of macro- and micronutrients were higher than in SJS. Its population presented higher vessel frequency, thicker-walled fibers, and lower vulnerability index. SJS's population had longer fibers, wider rays and a higher ray frequency, and higher vulnerability index. This suite of characters indicates that the MAQ population has a safer and more efficient xylem structure for water conduction. Under the influence of similar climate and soil type, differences regarding wood anatomical traits found between the two populations of *Ficus cestrifolia* can thus be regarded as an ecological response to the micro-environmental soils nutrients composition.

Key words: Atlantic Forest, Brazilian coastal lowland, secondary xylem plasticity, soil nutrients.

Resumo

O lenho responde às variáveis ambientais e o solo tem um impacto direto no xilema secundário. Este estudo compara a anatomia de duas populações de *Ficus cestrifolia* (Moraceae) de terras baixas no Sul do Brasil (MAQ e SJS), em duas áreas com climas semelhantes, mas diferentes condições nutricionais dos solos. As amostras de lenho foram coletadas a altura do peito e preparadas segundo técnicas usuais de anatomia da madeira para descrição qualitativa e quantitativa. Amostras de solo foram coletadas e submetidas a análise de nutrientes. As médias foram comparadas utilizando-se o teste t em ambiente R. Foram calculados o índice de vulnerabilidade para ambas as populações. As características qualitativas foram semelhantes entre as duas populações. MAQ apresentou os maiores níveis de macro e micronutrientes no solo, e a população apresentou os maiores valores para frequência dos vasos, espessura da parede das fibras e menor índice de vulnerabilidade, enquanto que a de SJS apresentou fibras mais longas, raios mais largos e uma frequência maior de raios, além de um maior índice de vulnerabilidade. Estas características indicam que a população de MAQ possui uma estrutura do xilema mais segura e eficiente para a condução de água. Sob a influência de clima e tipo de solo semelhantes, as diferenças com relação às características do lenho entre as populações podem ser consideradas uma resposta ecológica ao conteúdo nutricional dos solos.

Palavras-chave: Mata Atlântica, formação de terras baixas, plasticidade do xilema secundário, nutrientes do solo.

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Introduction

Genus *Ficus* L. comprises ca. 750 species distributed worldwide, mainly in the tropics and subtropics (Corner 1965). Out of its ca. 120 neotropical species (Berg 1991), 64 have been reported in Brazil (Berg & Villavicencio 2004), 23 of which grow in Atlantic Forest formations (BFG 2015).

Ficus cestrifolia Schott *ex* Spreng. occurs from the northern state of Pará to the southern state of Rio Grande do Sul (Backes & Irgang 2004), protected by law (Melo Júnior *et al.* 2007). It is commonly found on alluvial plain soils in lowlands and rarely above 100 m a.s.l. (Marchiori 1997; Carauta & Diaz 2002). Since the anatomical studies of *F. cestrifolia* are restricted to leaves (Mello-Filho & Neves 1989), wood anatomical information is scarce.

Wood structure, which plays an important functional role in water transport, mechanical support, and water and nutrients storage, is affected by several environmental factors (Baas *et al.* 2004). Several ecological studies have demonstrated that many wood anatomical traits present a strong relation with climate conditions (Baas 1982; Baas *et al.* 1983; Alves & Angyalossy-Alfonso 2000; Carlquist 2001; Hacke & Sperry 2001; Fichtler & Worbes 2012).

Since it determines fertility, soil nutrient composition is a limiting factor for plant growth (Henriques & Marcelis 2000), especially nitrogen, phosphorus and potassium (Aerts & Chapin III 2000). Nutrient availability in soils affects the development of different strategies of resource allocation in plants, leading to variations in certain morphological attributes, and may constrain plant organs to resorb nutrients (Lü *et al.* 2012). Although most studies focus on the nutritional status of leaves, stems and roots also play important roles in the absorption, transport, and storage of nutrients (He *et al.* 2015). For instance, soil fertilization affects both the structure and chemical composition of stem wood (Kostiainen *et al.* 2004), affecting the plant's hydraulic architecture (Bucci *et al.* 2006; Faustino *et al.* 2013), increasing plant growth, photosynthesis and transpiration (Goldstein *et al.* 2013).

Section Americanae, which *F. cestrifolia* belongs, is represented by hemipiphyte species. It is demonstrated that individuals undergo water stress at the epiphytic phase (Holbrook & Putz 1996). Indeed, water is important to determine

abundance and diversity of fig trees in seasonal environment (Coelho *et al.* 2014). Particularly in hemiephytic species, adventitious roots can grow superficially several meters on the ground, allowing the individual tree to forage water and nutrients at hectare-scale area (Silman & Krisel 2006). Thus, vulnerability index can express the risk of cavitation that Americanae fig tree species are potentially subjected to undergo.

Therefore, the present study compares the wood anatomy of two populations in a functional perspective considering the soil characteristics of two lowland areas of Atlantic Forest in Southern Brazil. Our hypothesis is that the wood structure of the population growing in soils richer in nutrients present features that enhance its hydraulic and load bearing capacity.

Methods

Study areas and soil analysis

Samples were collected in two areas in Southern Brazil: Maquiné city (MAQ), Rio Grande do Sul state, and São João do Sul city (SJS), Santa Catarina state (Fig. 1). The areas are characterized with lowland vegetation in coastal plains (Brack 2006), partially or completely flooded during summer by intense rainfall, forming temporary ponds of poor drainage (Klein 1980). Soil samples were collected for analysis 15 cm below ground level close to each studied individual accordingly to Embrapa methods (Embrapa 2013), homogenized in order to obtain a composed sample for each population, processed at Brazilian Agricultural Research Corporation - EMBRAPA, for quantifying macro and micronutrients concentration, Ph, organic matter and base saturation. Geographical coordinates and climate data of the two study areas are shown in Table 1, obtained from Climate-Data (2015).

Sampling, wood anatomy and statistical analysis

We sampled ten trees from Maquiné municipality (13–15 m height and 150–420 cm diameter at breast height) and ten trees from São João do Sul municipality (7–12 m height and 73–124 cm diameter at breast height). All wood samples were collected at breast height from the sapwood portions with the aid of a hammer and chisel. Wood sections were prepared according to standard techniques used in wood anatomy (Johansen 1940). Slides were deposited in the reference wood and slide collection of the Universidade da Região de Joinville (JOIw).

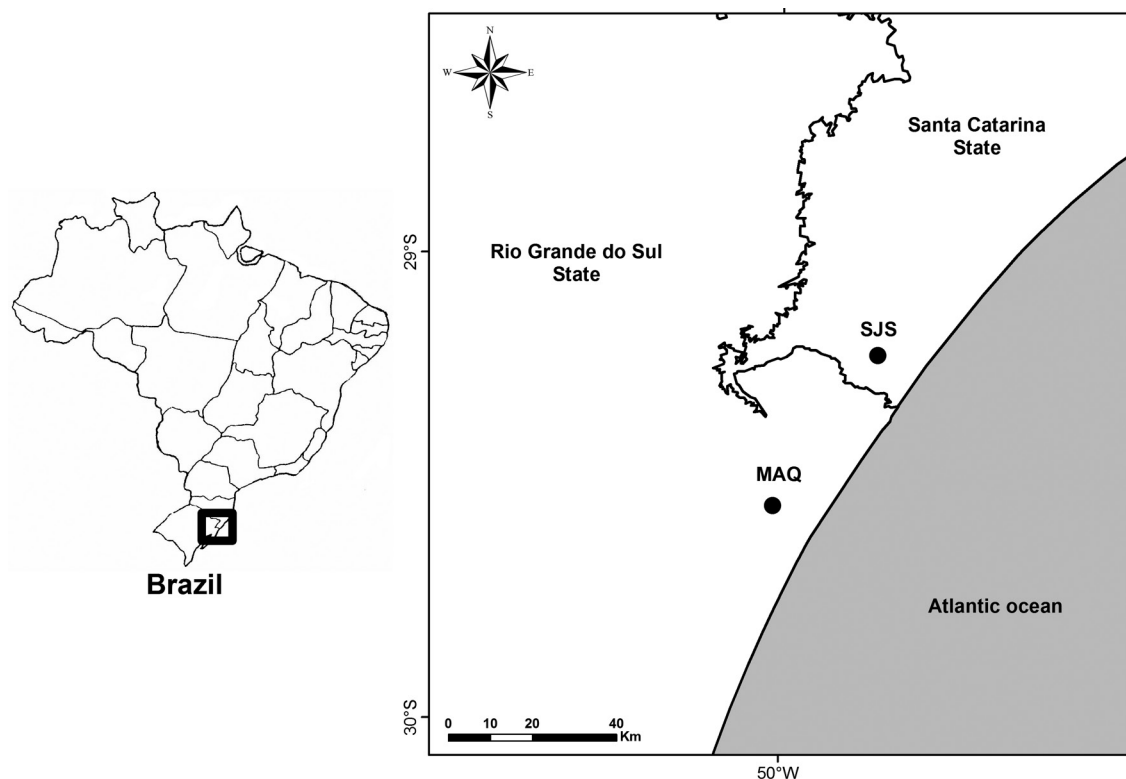


Figure 1 – Location of study areas of *Ficus cestrifolia* (Moraceae) populations. MAQ = Maquiné, RS; SJS = São João do Sul, SC.

Table 1 – Geographical coordinates and environmental data of Maquiné (MAQ) and São João do Sul (SJS) study areas.

	Areas	
	MAQ	SJS
Altitude (m)	12	15
Latitude (S)	29°32'30.1"	29°13'3.3"
Longitude (W)	50°1'0.9"	49°45'43.1"
Distance of ocean (km)	11.5	10.5
Climatic type (Köppen classification)*	Cfa (hot summer, no dry season)	Cfa (hot summer, no dry season)
Mean precipitation (mm)*	1503	1398
Mean minimum temperature (°C)*	14.7	15.2
Mean maximum temperature (°C)*	23.4	23.5
Mean relative humidity (%) [#]	78.3	82.0
Soil type [#]	Neosol	Neosol

Data sources and year: * = Climate-data 2015; [#] = IBGE 2015.

Small fragments of wood were dissociated using Franklin's method (Franklin 1945), stained with alcoholic safranin and mounted in synthetic resin. Anatomical description and measurements were based on the recommendations of the IAWA Committee (1989). Quantitative data are based on 25 measures for each trait. For each population, we calculated the vulnerability index VI (D/F , D = vessel diameter and F = vessel frequency, Carlquist 1977).

Mean and standard deviation were calculated for each wood quantitative trait. After checking the normal distribution of data, means were compared using *t*-test for two independent samples (Zar 1999) in software R (Crawley 2007).

Results

Comparative soil analysis of the two study sites

The chemical soil analysis showed that both areas present a very acid soil (Tab. 2). At MAQ, a higher level of the following macronutrients phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg) were found when compared to SJS. The greatest variation was observed regarding levels of K at MAQ, where values were 40 times higher than for SJS. The same trend was obtained for micronutrientes zinc (Zn), aluminium (Al), copper (Cu), manganese (Mn) and iron (Fe). Cations exchange capacity (CEC) had a great disparity between the study areas, higher at MAQ. The levels of organic matter (OM) found at MAQ were also higher. Although the higher values for macro and micronutrientes were found at MAQ, base saturation (V) showed that both soils are eutrophic.

Wood description of *Ficus cestrifolia* and comparison between Maquiné and São João do Sul populations

Both populations are characterized by the following anatomical traits (Figs. 2 and 3): growth rings indistinct or absent. Vessels diffuse, solitary (55,55%), in radial multiples of 2–14 (37,05%) and few in clusters (7,41%); tyloses common; perforation plates simple; intervessel pits alternate, oval to polygonal; large $\geq 10 \mu\text{m}$; vessel-axial parenchyma and vessel-ray pits with reduced borders and irregular shape (Fig. 2d). Fibres with simple to minutely bordered pits; thin to thick-walled. Axial parenchyma in bands composed of more than three cells wide; strands of 4–8 cells.

Rays 1–4 seriate; 9–28 cells tall; heterocellular, with body cells procumbent and one row of upright and/or square marginal cells; ranging from 4 to 12 rays/mm. Prismatic crystals present in chambered axial and radial parenchyma cells. Quantitative traits are presented in Table 3.

Higher vessel frequency was observed at MAQ, although the tangential diameter and vessel length were similar between populations. Longer fibres were found at SJS, while thicker walls were present at MAQ. Wider rays with a higher frequency were found at SJS, however with similar height than those at MAQ. A higher risk of cavitation, given by the Vulnerability Index, occurred at SJS (Tab. 3).

Discussion

The wood anatomy of the studied species is similar to other *Ficus* species described in the literature, especially regarding large vessel diameter and abundant axial parenchyma (Détienne & Jacquet 1983; Koek-Noorman *et al.* 1984). The presence of axial parenchyma bands more than three cell wide is a common feature in other species occurring in Southern Brazil's Atlantic Forest, as *Ficus eximia* Schott (Inside Wood 2004).

Wood qualitative traits did not vary much among populations, corroborating other similar comparative studies in Atlantic Forest areas (Marcati *et al.* 2001; Bosio *et al.* 2010; Marques *et al.* 2012; Carvalho 2013). Yet variations in the mean values of some quantitative traits according to the area show the different strategies observed in the wood. We can assume they reveal the plastic responses of secondary xylem to soil attributes, since climate is quite similar in our two study areas.

Both populations present similar vessel diameter means, but MAQ population has a higher vessel frequency. Studies show that an increase in soil fertilization results in vessel frequency raise (Lima *et al.* 2010). There is an interaction between water and nutrient uptake affecting tree physiology in processes such as photosynthesis, thus increasing transpiration and affecting wood hydraulics (Phillips *et al.* 2001).

Besides, woods with larger vessels and lower frequency reflect a trade-off between efficiency and safety, considered a pattern in wet and hot environments (Alves & Angyalossy-Alfonso 2000; Carlquist 2001; Barros *et al.* 2006). Higher vessel frequency is associated with higher conductivity. Besides, the lower vulnerability index (VI) value in MAQ population means that it is more resistant

Table 2 – Comparison of soils' chemical composition of Maquiné (MAQ) and São João do Sul (SJS) study areas.

	Areas	
	MAQ	SJS
pH	3.8	4.0
P (mg/dm ³)	14.4	4.9
K (mmolc/dm ³)	40	10
Ca (mmolc/dm ³)	4.1	0.3
Mg (mmolc/dm ³)	1.2	0.1
Zn (mg/dm ³)	2.5	0.0
Cu (mg/dm ³)	2.2	0.0
Mn (mg/dm ³)	12.1	0.7
Fe (mg/dm ³)	36.0	5.1
Al (cmolc/dm ³)	2.8	1.0
H + Al (mmolc/dm ³)	19.40	2.46
CEC (mmolc/dm ³)	67.5	13.86
BS	24.58	14.75
V (%)	95.56	51.03
OM (g/dm ³)	2.2	0.6

to cavitation than that of SJS population (Carlquist 1977). A higher number of vessels increases redundancy. Some authors point out a positive relation between VI and higher vessel frequency (Lens *et al.* 2011). VI expresses the potential risk of embolism and cavitation formation, which affects the hydraulic conductivity of xylem (Carlquist 2001). Loss of conductivity entails lower water flow to leaves, thus impacting photosynthetic production and, consequently, tree growth (Tyree 2003). Goldstein *et al.* (2013) showed that the higher the nutrient availability, the higher the resistance to cavitation due to the fact that plants operate at more negative water potentials.

The presence of thicker-walled fibers in MAQ population can also be correlated to higher vessel frequency, increasing xylem safety. A matrix of thicker-walled fibers surrounding vessel elements helps supporting them under negative pressures and improves wood strength (Lens *et al.* 2011).

On the other hand, wider rays are observed in SJS population, which may be a consequence of

poorer soils, as demonstrated by Goulart & Marcati (2008), and reveal a conservative strategy towards nutrient allocation in this condition. Besides, the role of parenchyma in embolism repair is suggested by many authors (Tyree *et al.* 1999; Brodersen & McElrone 2013; Zheng & Martinez-Cabrera 2013) and we can hypothesize that considering that the SJS population is more prone to cavitation than MAQ population, these larger rays might play a role on safety.

The chemical composition of soils is considered a determining factor in the plant ability to allocate essential growth nutrients (Hodge 2006). Acid soils are common in tropical environments, where generally high precipitation and temperature enhance weathering processes and favor soil aging (Ronquim 2010). Organic matter thus increases because of lower reduction rates (Silva 1990), which improves nutrient absorption through root development (Bonilha *et al.* 2013). Characterized by the amounts of basic cations and cations exchange capacity (CEC), soil

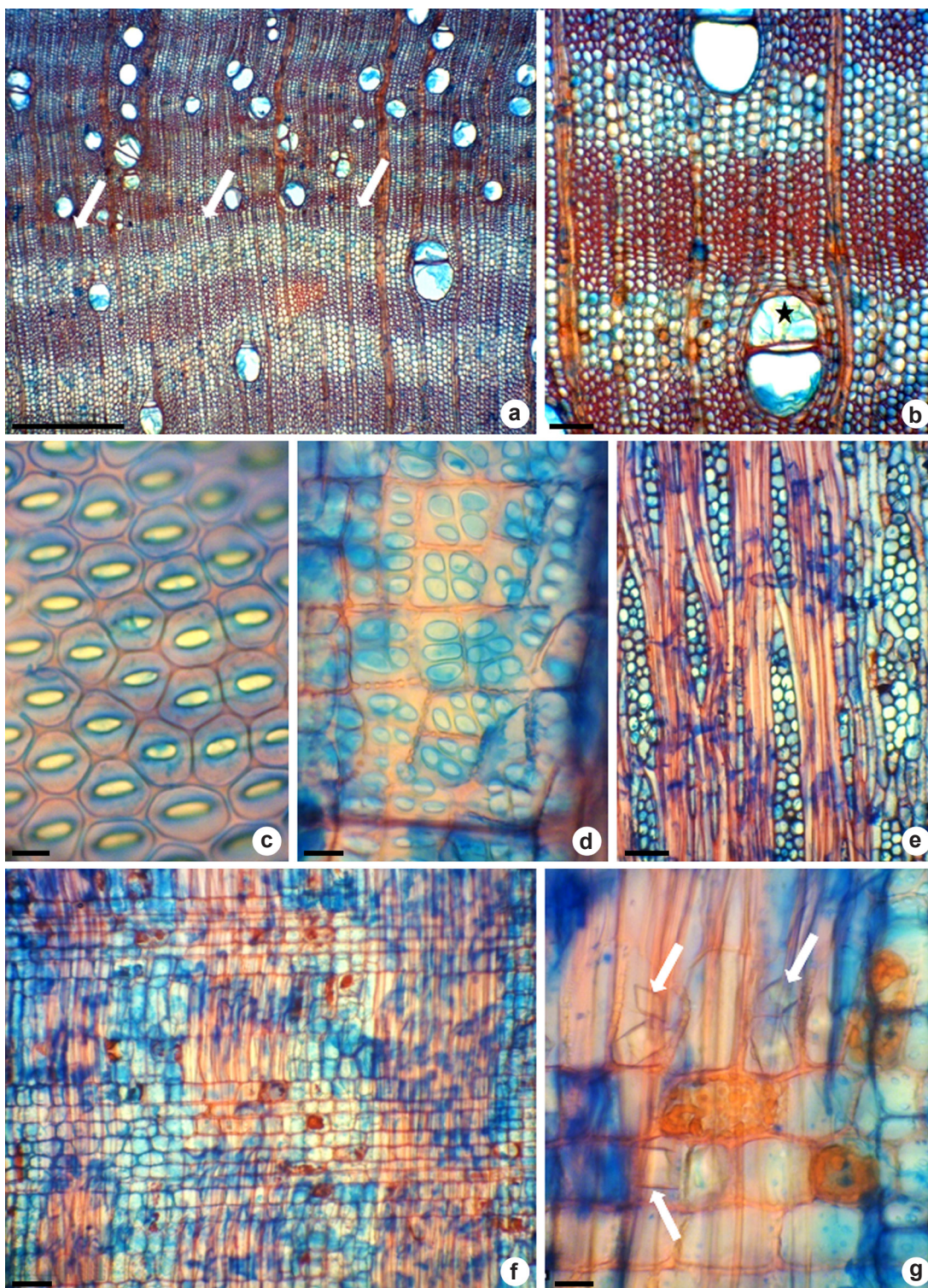


Figure 2 – a-g. General wood traits of *Ficus cestrifolia* (Moraceae) – a. TS, axial parenchyma in bands composed of more than tree cells wide (arrow); b. TS, tyloses (black star); c. TLS, alternate polygonal and oval pitting; d. RLS, vessel-rays pits with reduced borders; e. TLS, rays 1-4 seriate; f. RLS, heterocellular rays; g. RLS, prismatic crystal in parenchyma (arrow). (RLS = radial longitudinal section; TLS = tangential longitudinal section; TS = transversal section). Scale bars: a = 200 μ m; b-f = 100 μ m; c = 10 μ m; d,e,g = 20 μ m.

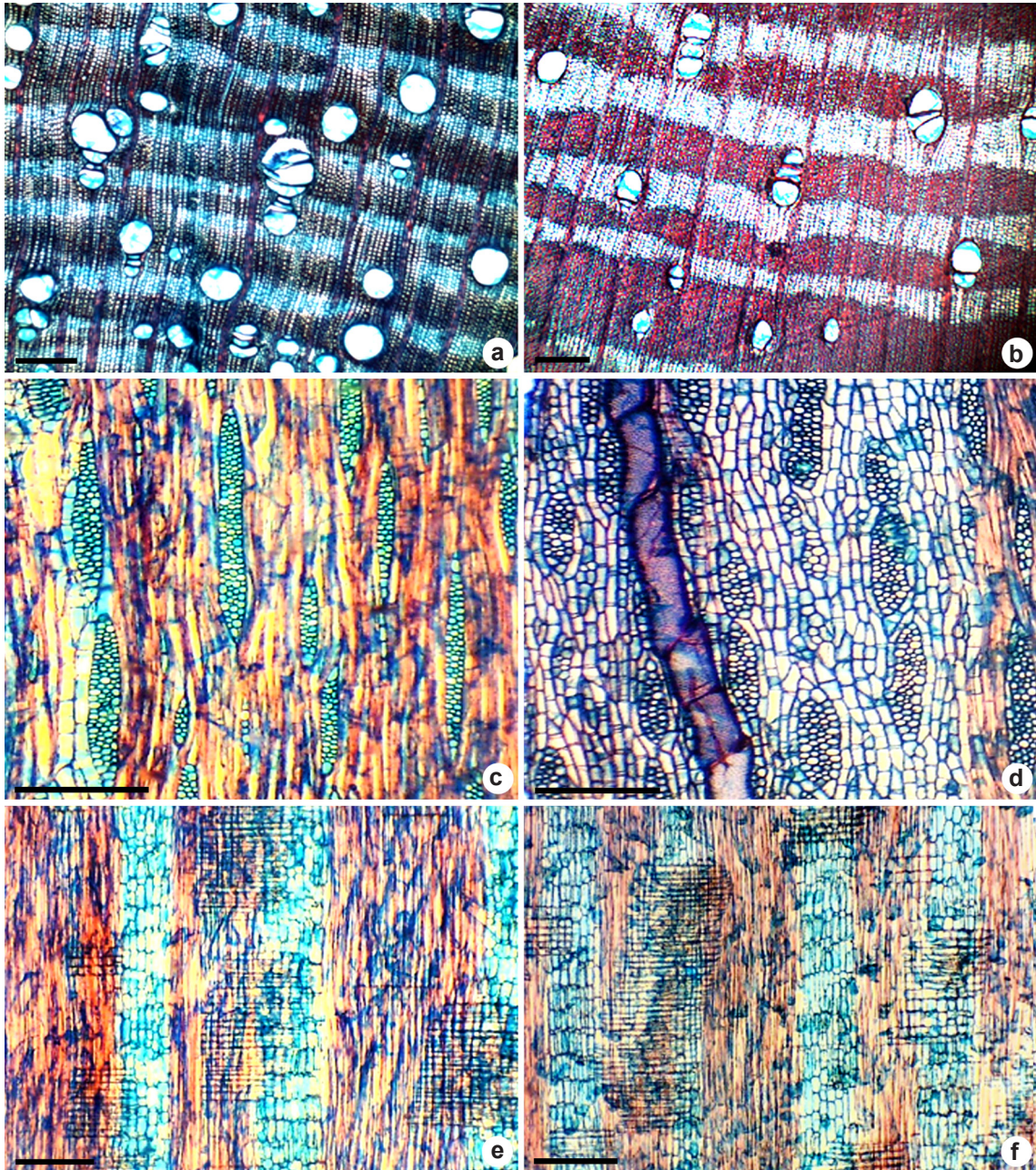


Figure 3 – a-f. Comparative wood anatomy of *Ficus cestrifolia* (Moraceae) occurring in Maquiné, RS (a,c,e) and SJS, SC (b,d,f) – a,b. TS, vessel frequency and tangential vessel diameter; c-f. ray – c,d. TLS; e,f. RLS. Scale bars: 100 μ m.

fertility is considered crucial to plant development and biomass production (Phillips *et al.* 2001; Ronquim 2010; Goldstein *et al.* 2013). In the two populations of *F. cestrifolia* studied here, the largest trees (Tab. 1) were found on the most fertile soil (MAQ) (Tab. 2), which contains the highest amounts of most of macro and micronutrients evaluated when compared to SJS soil.

Although under the influence of similar climate and soil type, these two populations are subject to different edaphic conditions, since more resources are available to MAQ than SJS trees. Soil nutrients availability will affect carbon allocation and hence hydraulic architecture. The MAQ population has less vulnerable wood, with a higher vessel frequency and thicker-

Table 3 – Mean values and standard deviations (in parentheses) of wood anatomical traits of *Ficus cestrifolia* (Moraceae). Different letters on the same line indicate statistically significance difference between Maquiné (MAQ) and São João do Sul (SJS) populations (n = 10 for each area).

Trait	Areas		p value
	MAQ	SJS	
Plant height	14.4 (0.73) ^a	9.72 (2.29) ^b	0.002
Stem diameter	219.68 (15.90) ^a	96.56 (16.39) ^b	0.0001
Fiber length (µm)	1123.2 (42.61) ^b	1253.6 (51.47) ^a	0.00004
Fiber wall thickness (µm)	1.8 (0.32) ^a	1.5 (0.25) ^b	0.00002
Ray height (µm)	15.7 (5.02) ^a	15.2 (4.83) ^a	0.59
Ray width (µm)	2.9 (0.10) ^b	3.3 (0.08) ^a	0.05
Ray frequency (n°.mm ⁻¹)	5.2 (0.22) ^b	6.5 (0.31) ^a	0.0002
Vessel frequency (n°.mm ⁻²)	8.8 (1.57) ^a	4.8 (1.61) ^b	0.00001
Vessel diameter (µm)	154.8 (15.09) ^a	152.6 (15.49) ^a	0.48
Vessel element length (µm)	276.9 (31.62) ^a	276.3 (29.34) ^a	0.92
Vulnerability index (D/F)	17.7	32.1	

walled fibers than that of SJS, indicating both a higher efficiency and safety in conduction. The populations of *Ficus cestrifolia* employ distinct wood anatomical strategies, in which secondary xylem functional attributes vary and can be regarded as ecological responses to different soil composition.

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