IAWA Journal, Vol. 27 (4), 2006: 341–376

TENSION WOOD AND OPPOSITE WOOD IN 21 TROPICAL RAIN FOREST SPECIES
2. Comparison of some anatomical and ultrastructural criteria

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SUMMARY

The anatomy of tension wood and opposite wood was compared in 21 tropical rain forest trees from 21 species belonging to 18 families from French Guyana. Wood specimens were taken from the upper and lower sides of naturally tilted trees. Measurement of the growth stress level ensured that the two samples were taken from wood tissues in a different mechanical state: highly tensile-stressed wood on the upper side, called tension wood and normally tensile-stressed wood on the lower side, called opposite wood. Quantitative parameters relating to fibres and vessels were measured on transverse sections of both tension and opposite wood to check if certain criteria can easily discriminate the two kinds of wood. We observed a decrease in the frequency of vessels in the tension wood in all the trees studied. Other criteria concerning shape and surface area of the vessels, fibre diameter or cell wall thickness did not reveal any general trend. At the ultrastructural level, we observed that the microfibril angle in the tension wood sample was lower than in opposite wood in all the trees except one (*Licania membranacea*).

Key words: Tension wood, opposite wood, tropical rain forest, vessels, wood anatomy, wood fibre.

INTRODUCTION

The study of the anatomy of tropical woody species in South America is a rich and dynamic science. Up till now it has been predominantly directed towards anatomical descriptions for the purpose of classification, identification and phylogeny reconstruction (Loueretro & Freitas da Sylva 1968; Détienne & Jacquet 1983; Miller & Détienne 2001).

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Accordingly the best anatomical criteria are considered those that do not vary much within the species. For example, pit size of vessel members or ray seriation are key criteria for identification (IAWA Committee 1989). Less reliable parameters for identification are those which vary considerably within species such as frequency or diameter of the vessels. These criteria can vary naturally between individuals depending on the environment or genome. They also vary during the life of the individual tree, depending on age (between juvenile and adult wood) or, as is the subject of our study, in the case of the formation of reaction wood.

This article follows a previous article (Clair *et al.* 2006) which discussed the presence of the gelatinous layer in the same trees. It showed that a gelatinous layer (G-layer) is present in less than half of the 21 studied trees. However, besides morphological differences within fibres, tension wood is always the cause of strong growth tension stresses and is accompanied by distinct physical and mechanical properties, in particular longitudinal shrinkage and axial rigidity (Baillères *et al.* 1995; Grzeskowiak *et al.* 1996; Clair *et al.* 2003a; Clair *et al.* 2003b).

This paper addresses the differences which exist between tension and opposite wood, and attempts to identify some common criteria other than the occurrence of G-fibres, linked to the marked differences between properties that are usually observed in tension wood. As our main aim was to study the diversity of structures occurring in tension wood among species, we chose to maximize the number of species studied, rather than repeating measures within given species. As such, this study will serve as the starting point for further research addressing intraspecific variability for anatomical features.

Equivalent studies have been carried out on species from temperate zones, such as poplar (Jourez *et al.* 2001), and some of the criteria used in our study are the same. This work also aims to complete data banks on the anatomical structure of tension wood, especially for tropical species, by comparison with opposite wood. Presentation of anatomical plates of tension and opposite wood samples enables the demonstration of the wide variability of the specific structural characteristics encountered from one species to another. These plates also enable the direct observation of structural modifications that can occur between two kinds of wood inside the same tree.

MATERIAL AND METHODS

Material and sampling

The material and sampling methods are identical to those described by Clair *et al.* (2006). Twenty-one species in the tropical rain forest distributed in 18 families (see Table 1) were selected.

Anatomical measurements

Sectioning, staining and image acquisition

Anatomical sections (15 µm thickness) were cut on a microtome and stained with Azure II that stains lignified tissues light blue and highly cellulosic tissues dark blue. This staining method provides satisfactory contrast for image analysis (Clair *et al.* 2003b). Sections were observed with a light microscope and pictures were taken with a digital camera (720 × 576 pixels).

Table 1. List of trees studied.

N°	Family	*Genus species*
1	Annonaceae	*Guatteria schomburgkiana* Martius
2	Annonaceae	*Oxandra asbeckii* (Pulle) R.E. Fries
3	Apocynaceae	*Lacmellea aculeata (*Ducke) Monachino
4	Burseraceae	*Protium opacum* Swart subsp. *rabelianum*
5	Chrysobalanaceae	*Licania membranacea* Sagot
6	Clusiaceae	*Symphonia globulifera* L.f.
7	Flacourtiaceae	*Casearia javitensis* H.B.K.
8	Goupiaceae	*Goupia glabra* Aublet
9	Hugoniaceae	*Hebepetalum humiriifolium* (Planchon) Benth.
10	Icacinaceae	*Dendrobangia boliviana* Rusby
11	Lauraceae	*Ocotea indirectinervia* C.K. Allen
12	Lecythidaceae	*Eschweilera sagotiana* Miers
13	Lecythidaceae	*Lecythis poiteaui* O.C. Berg
14	Meliaceae	*Trichilia schomburgkii* C.DC.
15	Mimosaceae	*Inga marginata* Willd.
16	Myrtaceae	*Myrcia decorticans* DC.
17	Papilionaceae	*Ormosia bolivarensis* (Rudd) Stirton
18	Papilionaceae	*Ormosia coutinhoi* Ducke
19	Rhizophoraceae	*Cassipourea guianensis* Aublet
20	Sapindaceae	*Cupania scrobiculata* L.C. Rich.
21	Sapindaceae	*Talisia simaboides* Kramer

The number of vessels was counted on the microscope at a magnification of ×25. Anatomical attributes of vessels and fibres were measured in pictures taken with respectively ×100 and ×500 magnifications.

Quantitative anatomical criteria and image analysis

- Vessel frequency (VF): measured for each section on 10 windows of 1.6 mm^2 with ×25 magnification (on sections with a smaller surface area, measurements were made on a smaller area). Frequency is expressed in mm^{-2}.
- Radial (VRD), tangential (VTD) and average (VD) diameters of the lumens of the isolated vessels (expressed in μm).
- Vessel surface area (VS) (isolated vessels only) (expressed in μm^2).
- Vessel shape index (VSI), calculated from isolated vessels using the formula:
  $$(VRD–VTD) / VRD \times 100$$
  For each section vessel diameters were measured on all entire vessels observed on 30 pictures of 0.3 mm^2 taken at ×100 magnification.
- The index of vessel grouping (VGI), recommended by IAWA (1989):
  VGI: total number of vessels / number of groups

An isolated vessel was considered as a group, an index equal to 1 indicates that there were only isolated vessels. The higher the index the more the vessels were grouped. The number of groups was measured using the same procedure as for vessel frequency.

- Fibre radial (FRD), tangential (FTD) and average (FD) diameter (expressed in µm).
- Fibre lumen radial (FLRD), tangential (FLTD) and average diameter (FLD) (expressed in µm).
  The fibre diameter was estimated as the average diameter of two to three adjacent fibres. The diameter of the lumens of fibres used for measurements was measured individually. The “very small fibres” visible on the sections were not taken into account because they corresponded to the ends of the fibres (Détienne & Jacquet 1989).
- Fibre wall radial (FWRT), tangential (FWTT) and average (FWT) thickness was calculated for each cell by the difference between fibre diameter and lumen diameter in a given direction (double wall) (expressed in µm).
- Relative fibre wall radial (ReFWRT), tangential (ReFWTT) and average (ReFWT) thickness was calculated for each cell by the ratio of the double wall thickness to the fibre diameter in a given direction.
- Relative amount of each tissue on a transverse plane, i.e. fibre area (FA), gelatinous fibre area (GFA), axial parenchyma area (APA), vessel area (VA) and ray parenchyma area (RA). These areas were measured on 20 pictures of 0.3 mm^2 taken at ×100 magnification for both tension and opposite wood in each tree.

Measurements of all the anatomical parameters were made with the image analysis software Optimas v. 6.5.

Microfibril angle measurement

Microfibril angle (MFA) was estimated using the X-ray diffraction method which allows rapid scanning of the average MFA for the entire specimen studied (Barnett 2004).

An X-ray diffractometer (SHIMAZU, XD-D1) was used to measure the average microfibrillar angle (Cave 1966; Yamamoto *et al.* 1993). A point-focused X-ray beam (Cu-Kα X-ray, beam diameter 1 mm) was applied to tangential sections, 1 mm thick × 15 mm long. An X-ray diffraction apparatus with a symmetrical transmission mode was used. The speed of rotation of the sample support was 6 degrees per minute, Bragg’s angle was 22.4° and we used a 2 mm divergence slit and a 0.6 mm receiving slit. Parameter T defined by Cave (Cave 1966) was obtained from the diffraction intensity around the (200) arc. The average microfibrillar angle (MFA) was calculated using the formula (Yamamoto *et al.* 1993):

$$\mathrm{MFA} = 1.575 \times 10^{-3}\,T^3 - 1.431 \times 10^{-1}\,T^2 + 4.693\,T - 36.19$$

As this calibration was made for species other than those we studied, we can consider the result from this experiment as an MFA indicator. Therefore, even if the result is not the absolute average MFA of the specimen, it still allows us to make a comparison between two specimens from the same tree.

Statistical analysis

Variability within individuals

Within each tree, anatomical parameters of tension and opposite wood were compared to highlight significant differences between these two types of wood. We used the bilateral Student test to account for the significance of these results.

In a preliminary analysis we checked whether data distribution followed a normal distribution using *Kurtosis* and *Skewness* tests (*Kurtosis* and *Skewness* both ranging between -2 and 2). Results of Student tests are presented only for data that allowed its calculation (normality criteria). Application of the F test informed on the equality of the variances (with 5% threshold) in order to use the appropriate Student test.

Variability between individuals

For each parameter, after checking that the difference in averages (tension wood–opposite wood) followed a normal distribution, the average obtained in tension wood was compared with the average in opposite wood by a paired Student test. For each criterion and for all trees this gave the significance of the difference between TW and OW.

Comparison of radial–tangential directions

For each parameter based on measurements in radial and tangential directions (fibre diameters, cell wall thickness, vessel diameters, *etc.*), the values were compared by a Student test (using the same procedure as for analysis of the variability within individuals) to evaluate on the one hand the significance of a separate treatment of these values, and on the other hand to highlight differences in shape (ovality) between tension and opposite wood.

RESULTS AND DISCUSSION

To simplify the interpretation in the rest of the discussion, we refer hereafter to each tree sampled by its species name. We note, however, that the points discussed are attributed to the individual studied rather than an intrinsic property of the species, as intraspecific variability for these properties remains to be studied.

Anatomical observations

Anatomical sections of the 21 species are presented in Figures 1 to 21. For each tree, tension wood is compared to opposite wood using four magnifications (×25, ×100, ×200 and ×500). For the species displaying fibres with a G-layer, the pictures do not attempt to present the characteristic of these fibres but only show the general appearance of tension wood. Details of fibres with a G-layer are presented and discussed in Clair *et al.* (2006).

Comparison of anatomical parameters

Before presenting and discussing results concerning each anatomical criterion, we will consider the differences between measurements in radial and tangential directions.

(text continued on page 367)

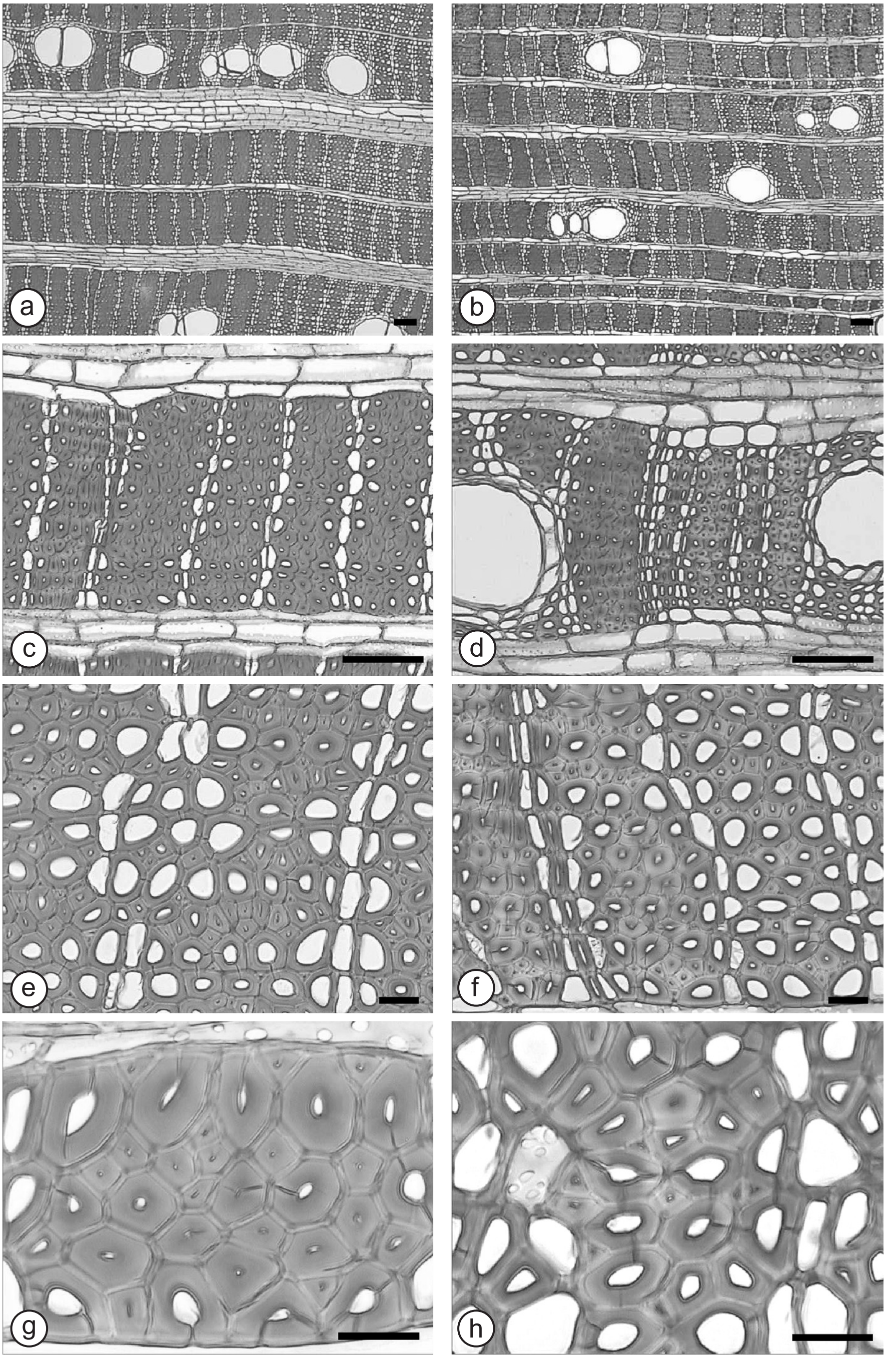


Fig. 1. Comparison of transverse sections of tension wood (a, c, e, g) and opposite wood (b, d, f, h) of *Guatteria* aff. *schomburgkiana* (Annonaceae). — Scale bars of a–d = 100 µm, of e–h = 25 µm.

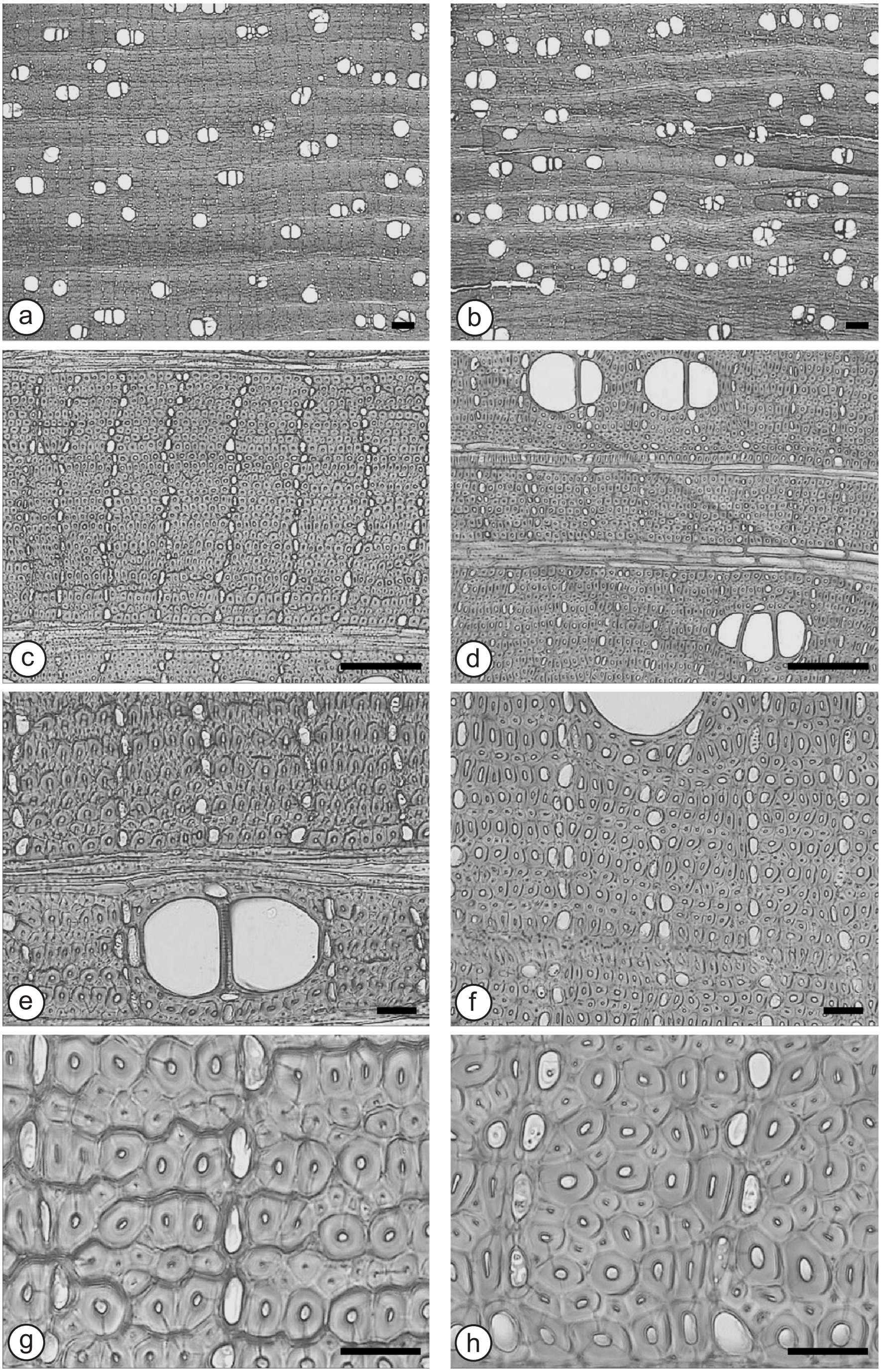


Fig. 2. Comparison of transverse sections of tension wood (a, c, e, g) and opposite wood (b, d, f, h) of *Oxandra asbeckii* (Annonaceae). — Scale bars of a–d = 100 µm, of e–h = 25 µm.

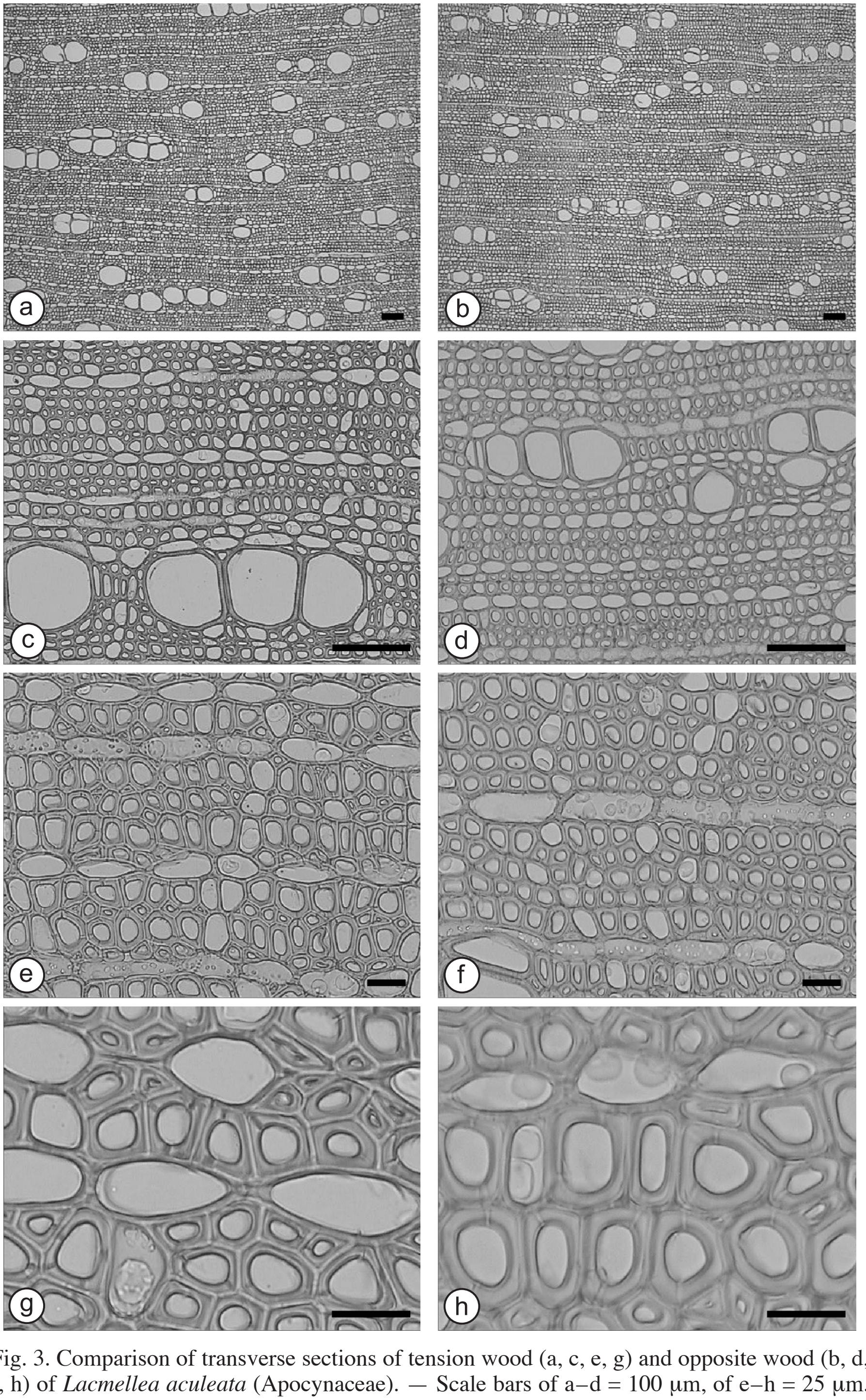


Fig. 3. Comparison of transverse sections of tension wood (a, c, e, g) and opposite wood (b, d, f, h) of *Lacmellea aculeata* (Apocynaceae). — Scale bars of a–d = 100 μm, of e–h = 25 μm.

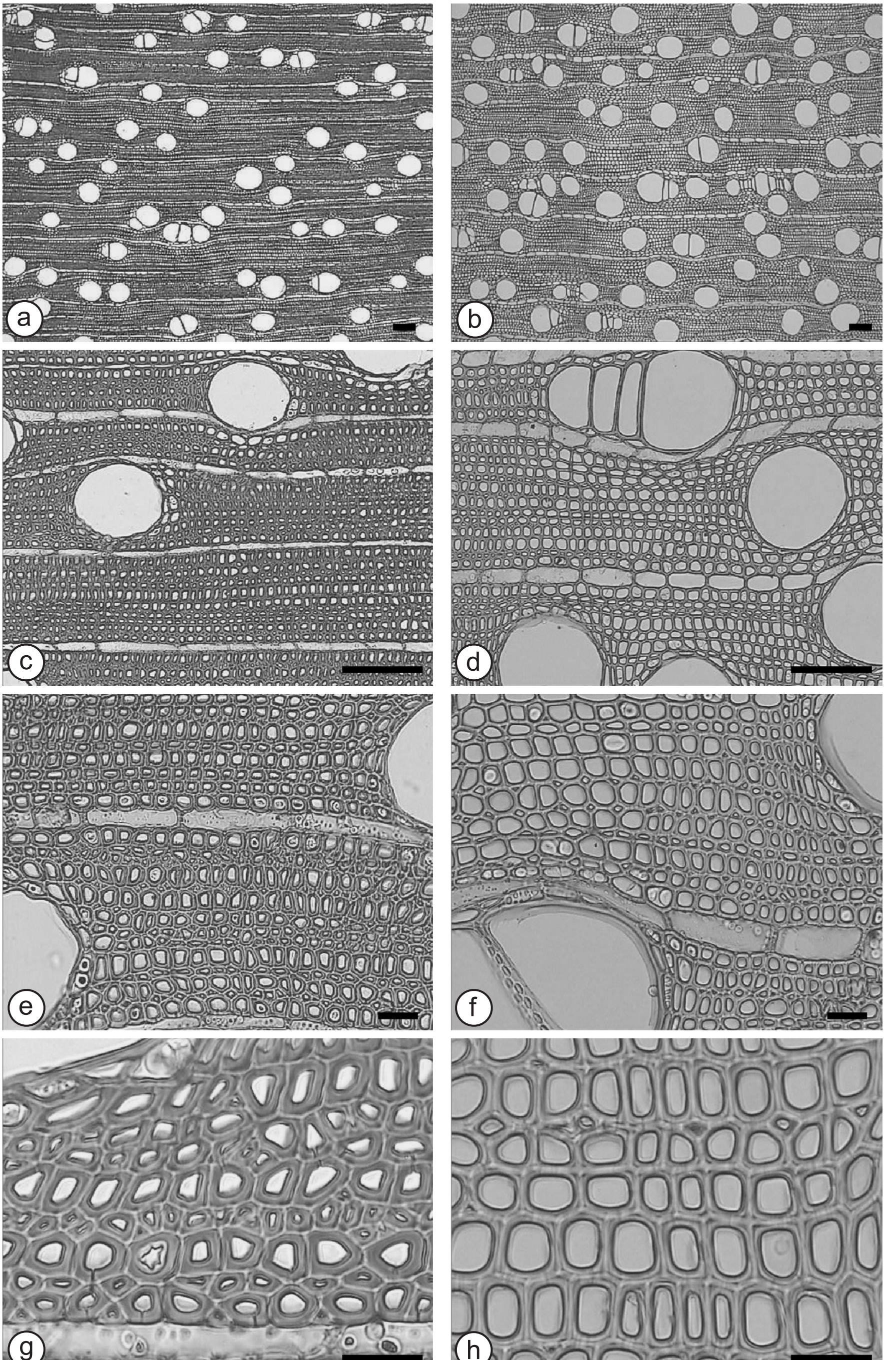


Fig. 4. Comparison of transverse sections of tension wood (a, c, e, g) and opposite wood (b, d, f, h) of *Protium opacum* (Burseraceae). — Scale bars of a–d = 100 μm, of e–h = 25 μm.

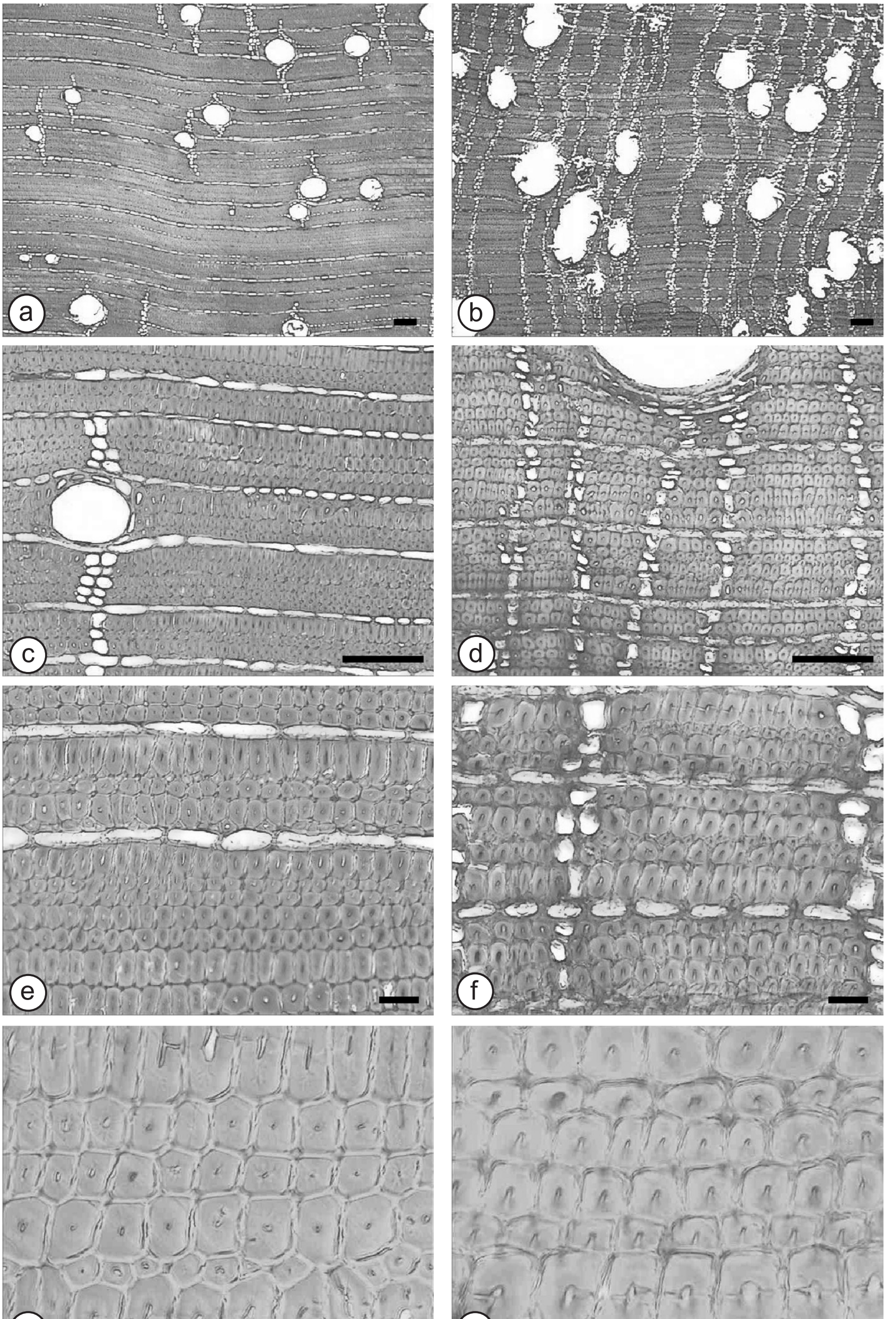


Fig. 5. Comparison of transverse sections of tension wood (a, c, e, g) and opposite wood (b, d, f, h) of *Licania membranacea* (Chrysobalanaceae). — Scale bars of a–d = 100 μm, of e–h = 25 μm.

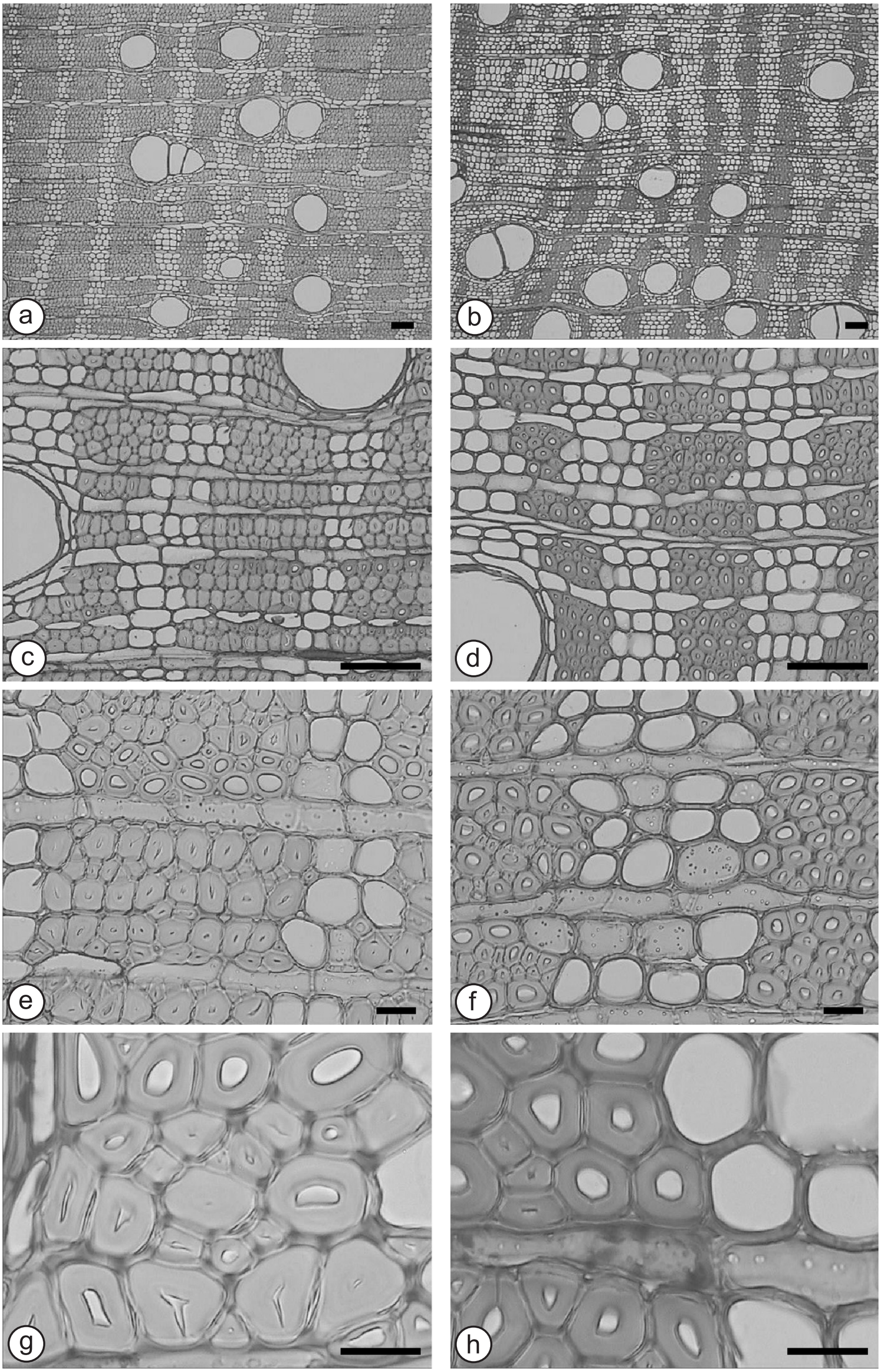


Fig. 6. Comparison of transverse sections of tension wood (a, c, e, g) and opposite wood (b, d, f, h) of *Symphonia globulifera* (Clusiaceae). — Scale bars of a–d = 100 µm, of e–h = 25 µm.

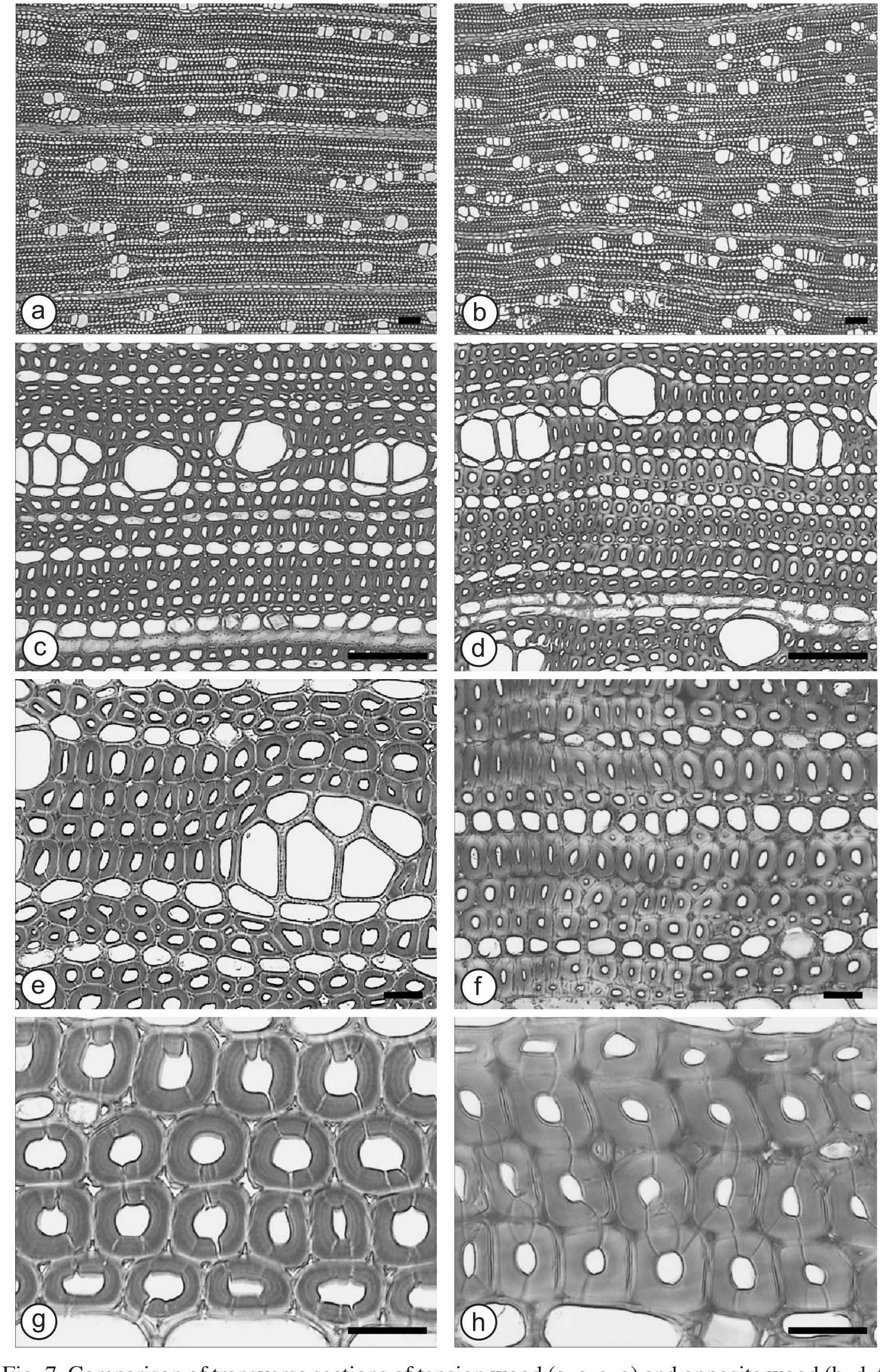


Fig. 7. Comparison of transverse sections of tension wood (a, c, e, g) and opposite wood (b, d, f, h) of *Casearia javitensis* (Flacourtiaceae). — Scale bars of a–d = 100 µm, of e–h = 25 µm.

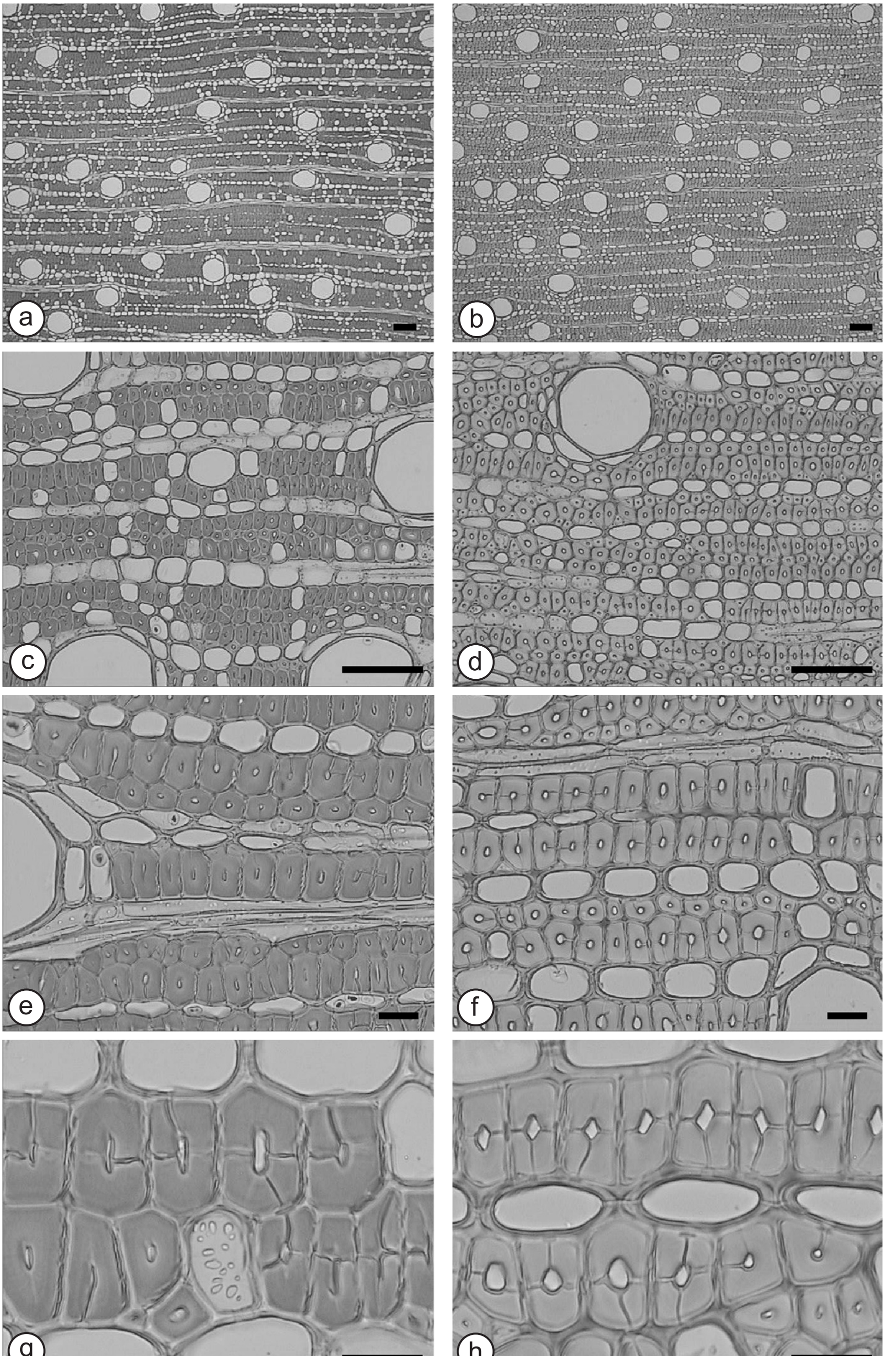


Fig. 8. Comparison of transverse sections of tension wood (a, c, e, g) and opposite wood (b, d, f, h) of *Goupia glabra* (Goupiaceae). — Scale bars of a–d = 100 μm, of e–h = 25 μm.

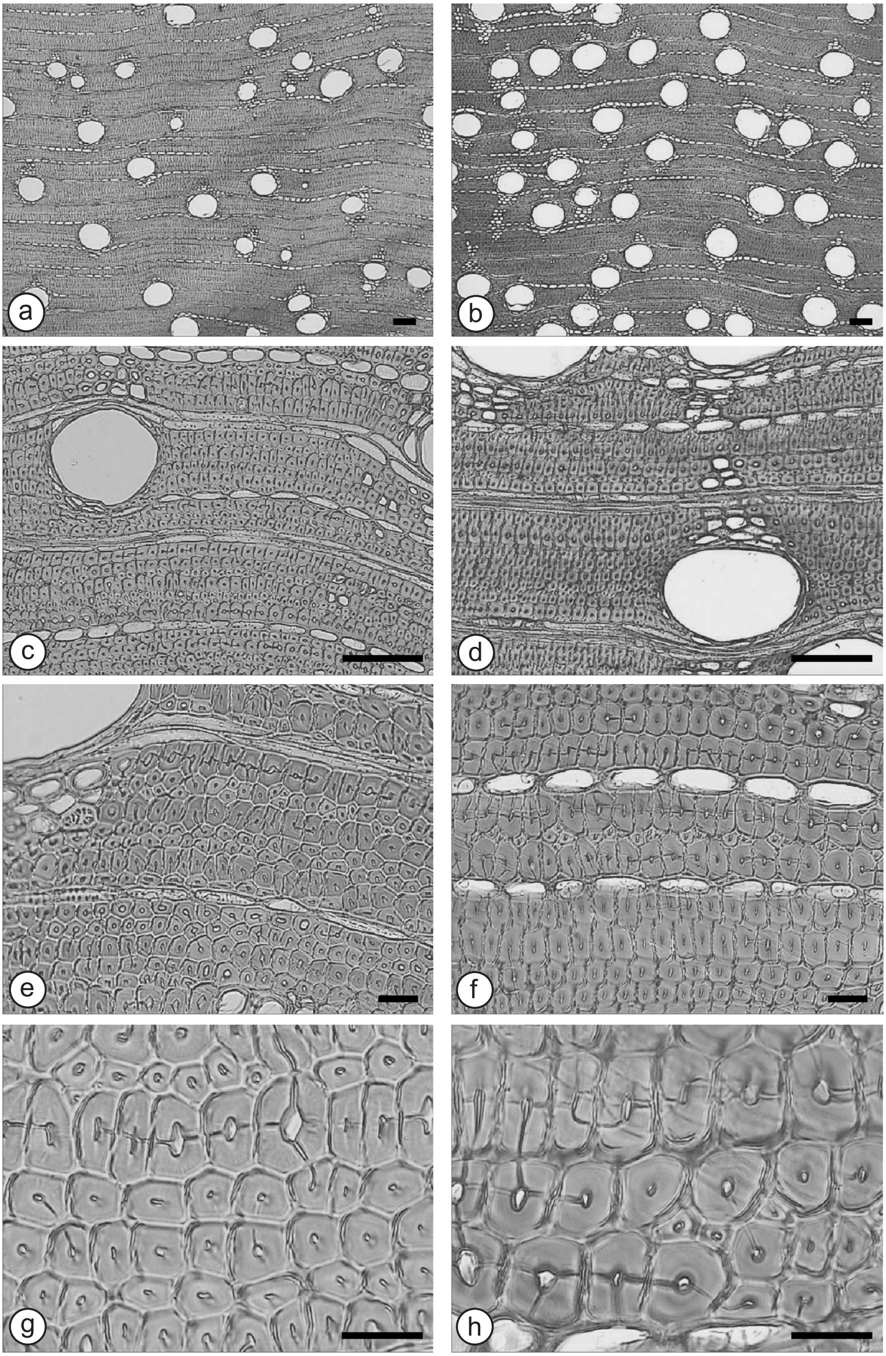


Fig. 9. Comparison of transverse sections of tension wood (a, c, e, g) and opposite wood (b, d, f, h) of *Hebepetalum humiriifolium* (Hugoniaceae). — Scale bars of a–d = 100 µm, of e–h = 25 µm.

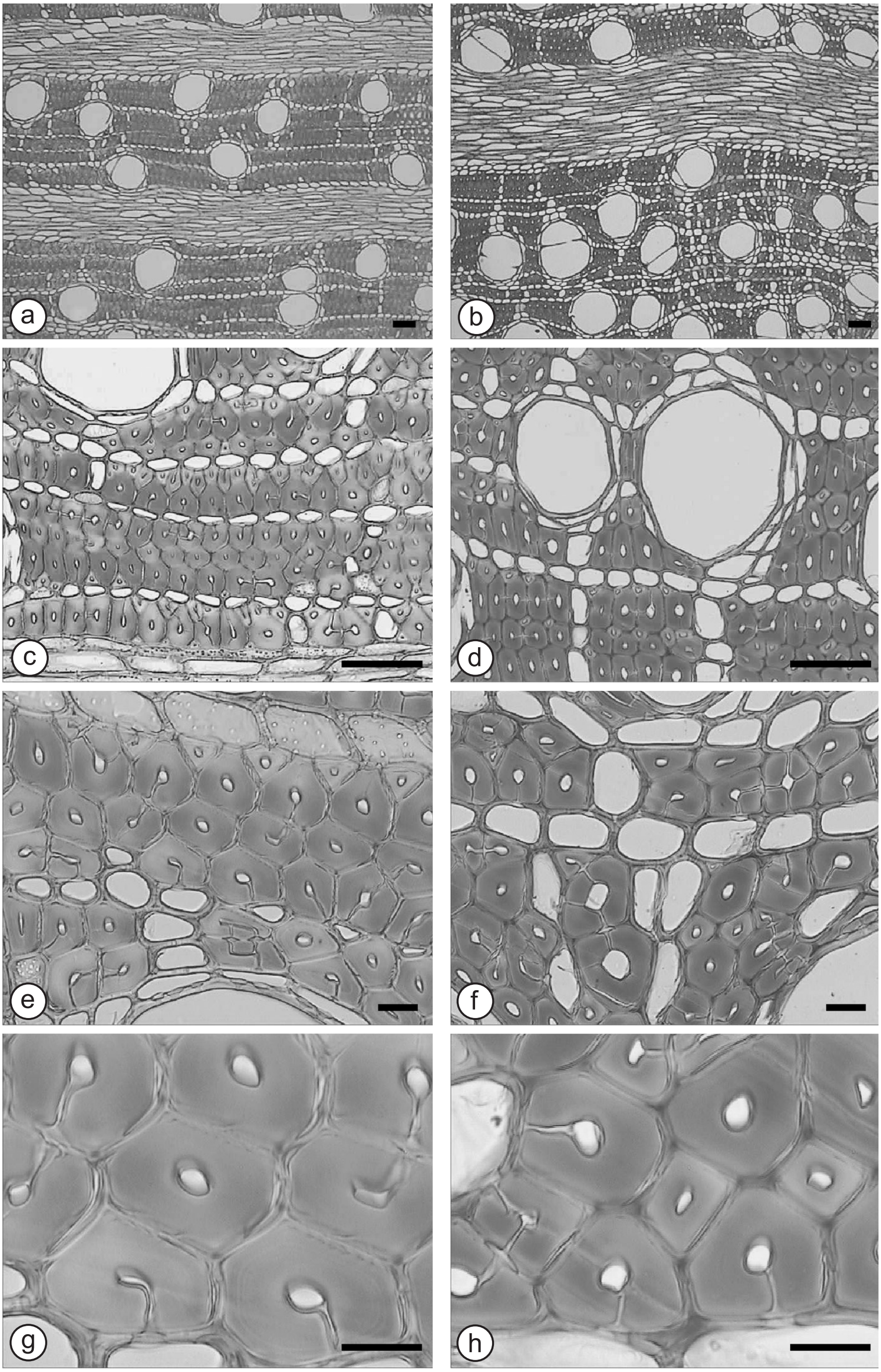


Fig. 10. Comparison of transverse sections of tension wood (a, c, e, g) and opposite wood (b, d, f, h) of *Dendrobangia boliviana* (Icacinaceae). — Scale bars of a–d = 100 µm, of e–h = 25 µm.

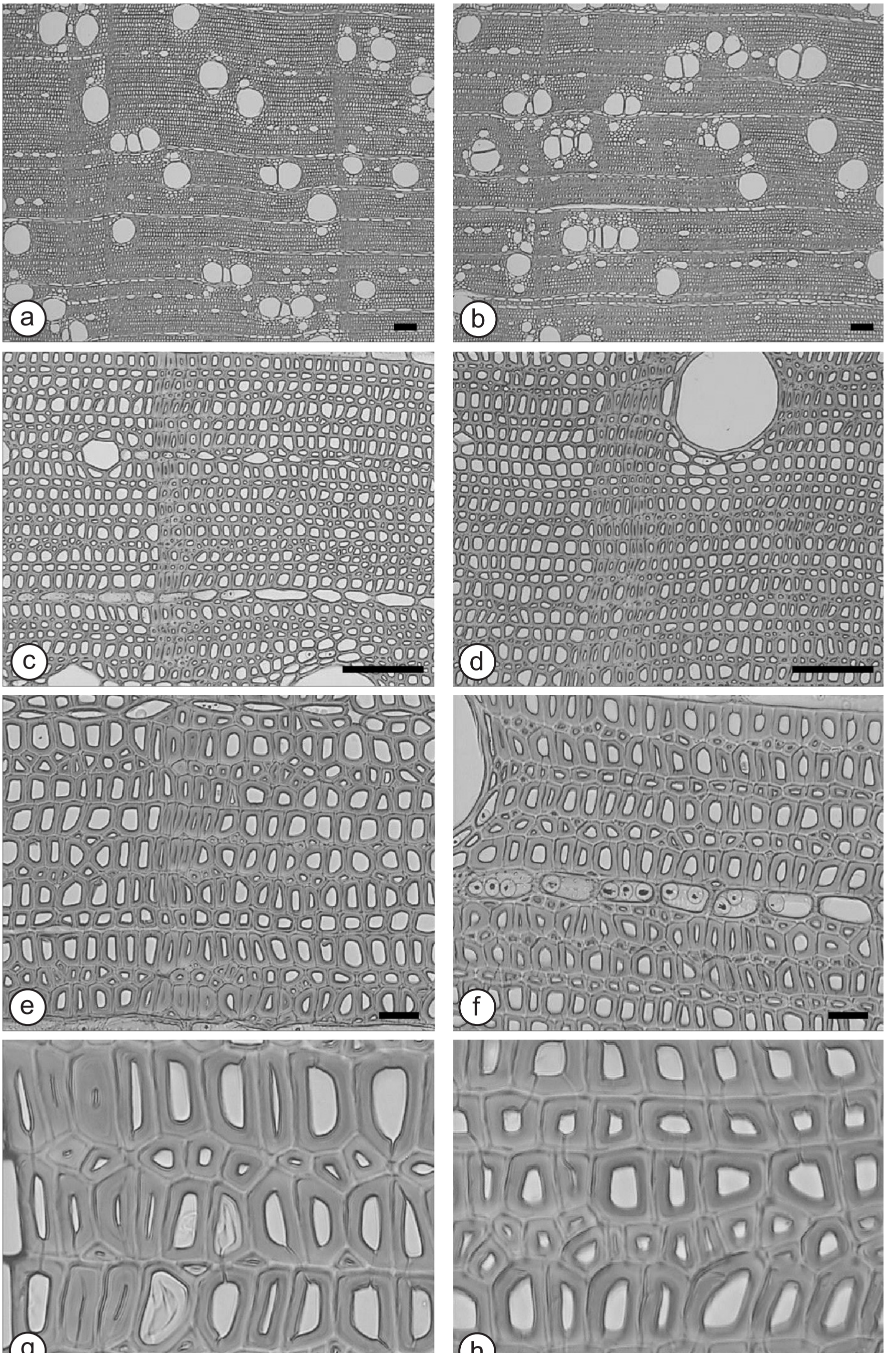


Fig. 11. Comparison of transverse sections of tension wood (a, c, e, g) and opposite wood (b, d, f, h) of *Ocotea indirectinervia* (Lauraceae). — Scale bars of a–d = 100 µm, of e–h = 25 µm.

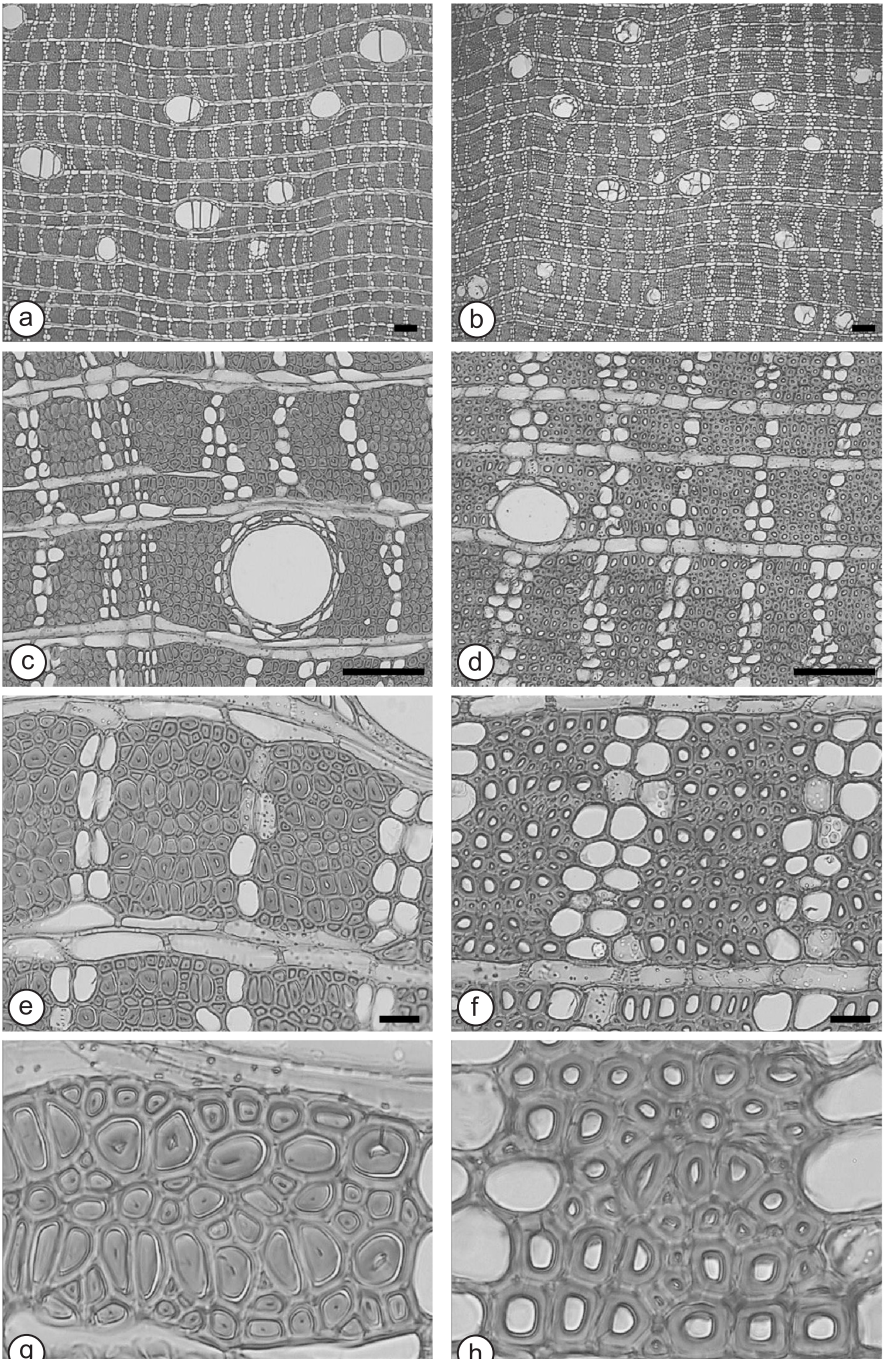


Fig. 12. Comparison of transverse sections of tension wood (a, c, e, g) and opposite wood (b, d, f, h) of *Eschweilera sagotiana* (Lecythidaceae). — Scale bars of a–d = 100 μm, of e–h = 25 μm.

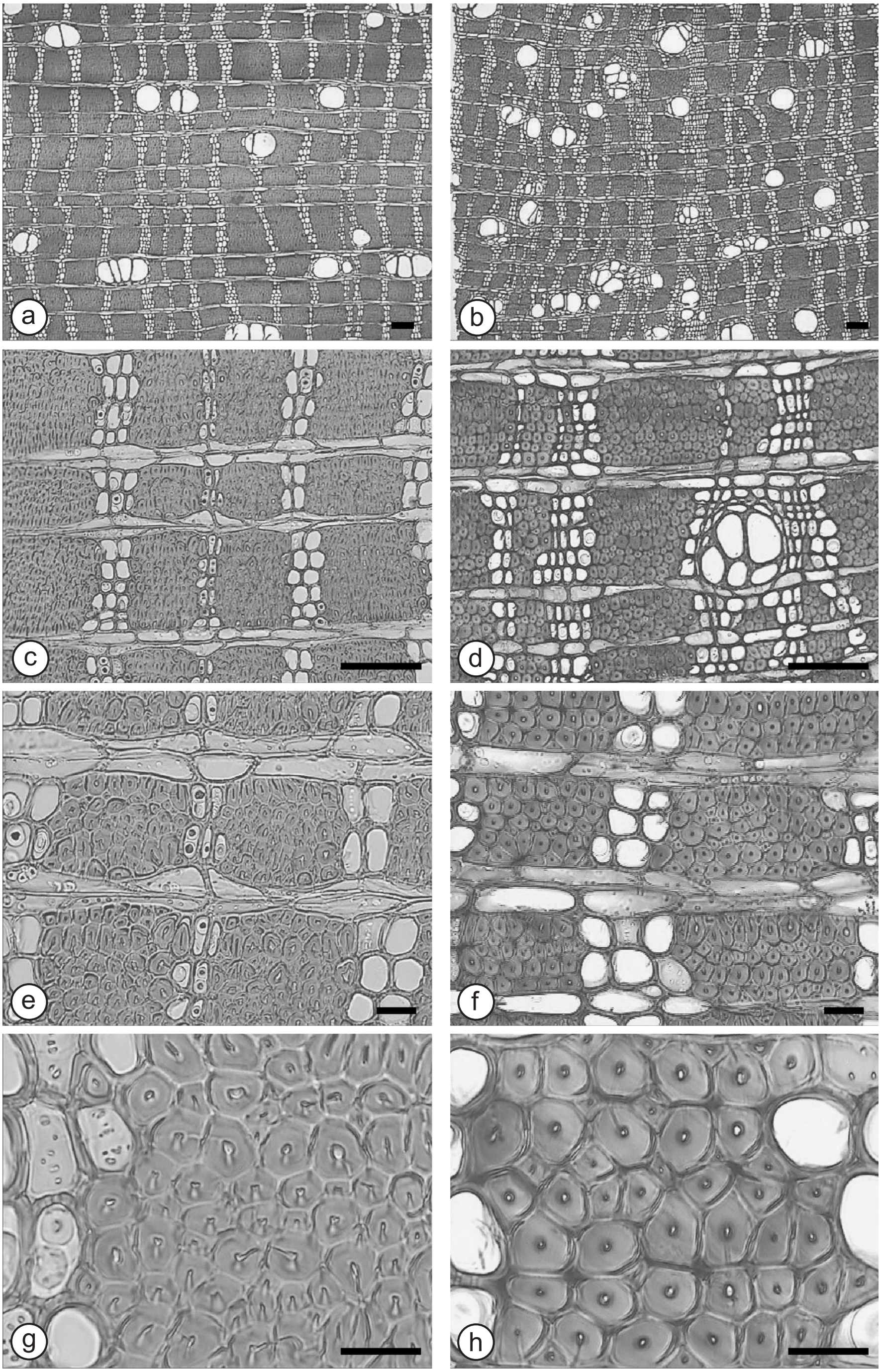


Fig. 13. Comparison of transverse sections of tension wood (a, c, e, g) and opposite wood (b, d, f, h) of *Lecythis poiteaui* (Lecythidaceae). — Scale bars of a–d = 100 μm, of e–h = 25 μm.

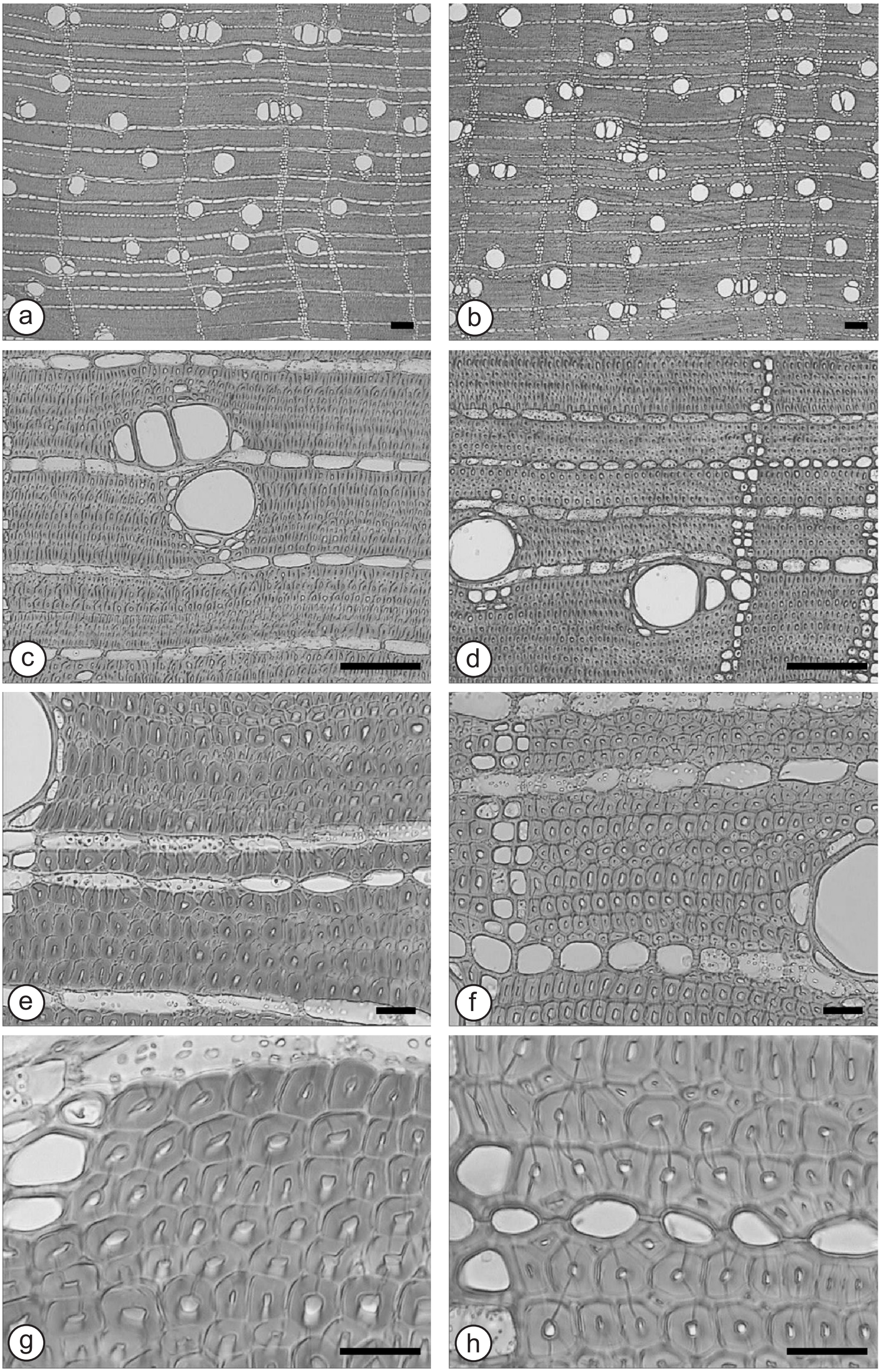


Fig. 14. Comparison of transverse sections of tension wood (a, c, e, g) and opposite wood (b, d, f, h) of *Trichilia schomburgkii* (Meliaceae). — Scale bars of a–d = 100 μm, of e–h = 25 μm.

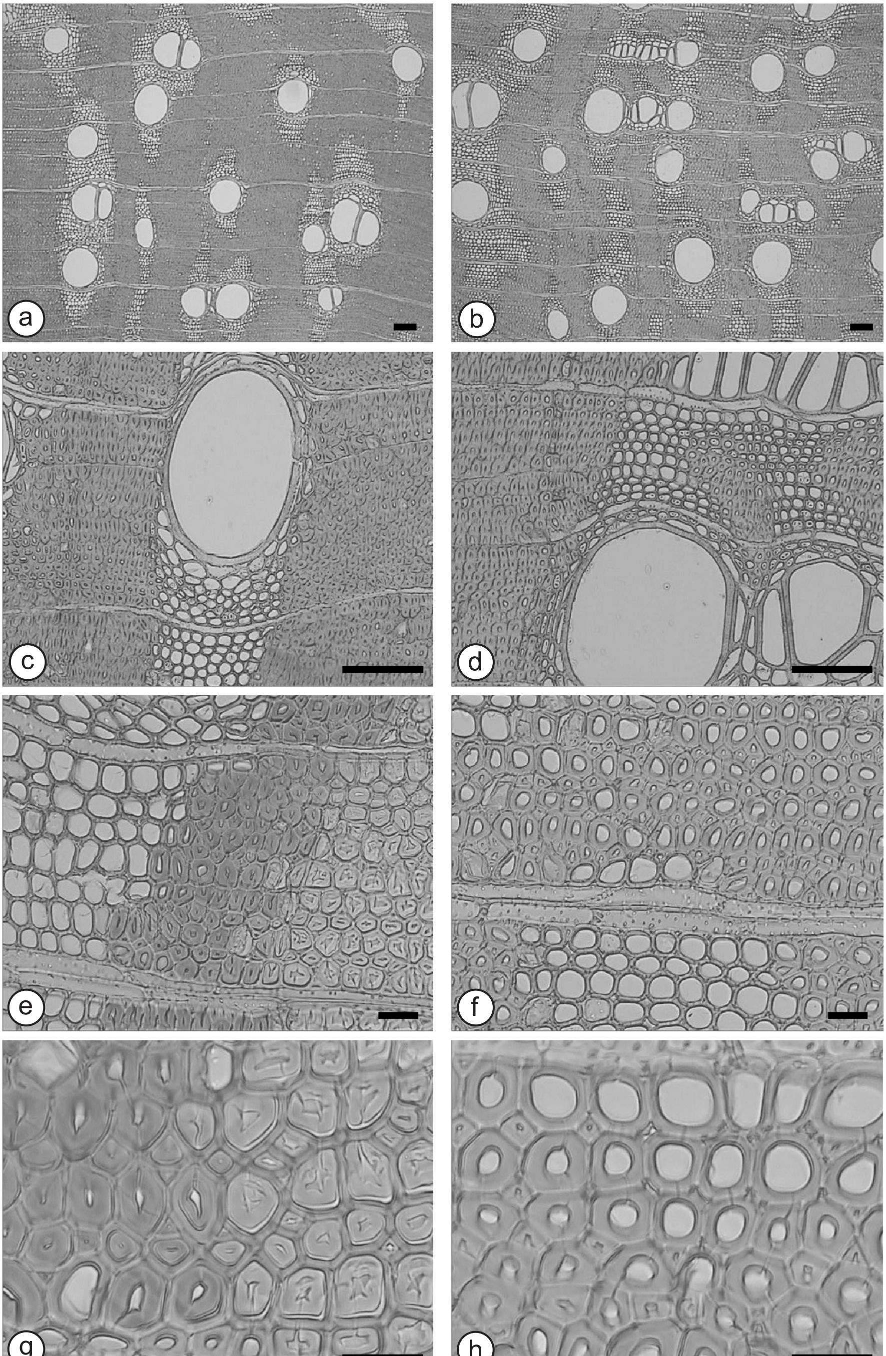


Fig. 15. Comparison of transverse sections of tension wood (a, c, e, g) and opposite wood (b, d, f, h) of *Inga marginata* (Mimosaceae). — Scale bars of a–d = 100 µm, of e–h = 25 µm.

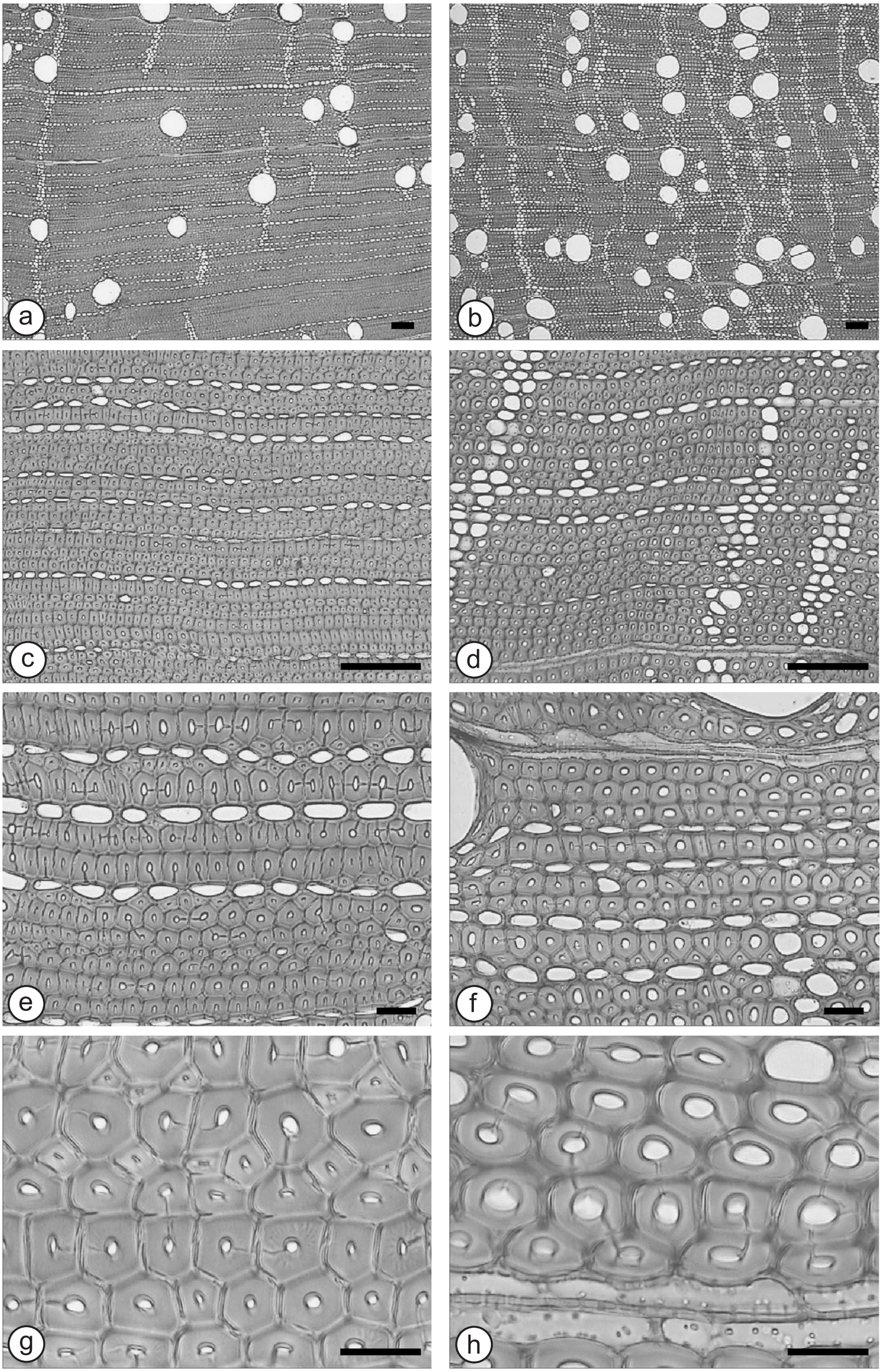


Fig. 16. Comparison of transverse sections of tension wood (a, c, e, g) and opposite wood (b, d, f, h) of *Myrcia decorticans* (Myrtaceae). — Scale bars of a–d = 100 μm, of e–h = 25 μm.

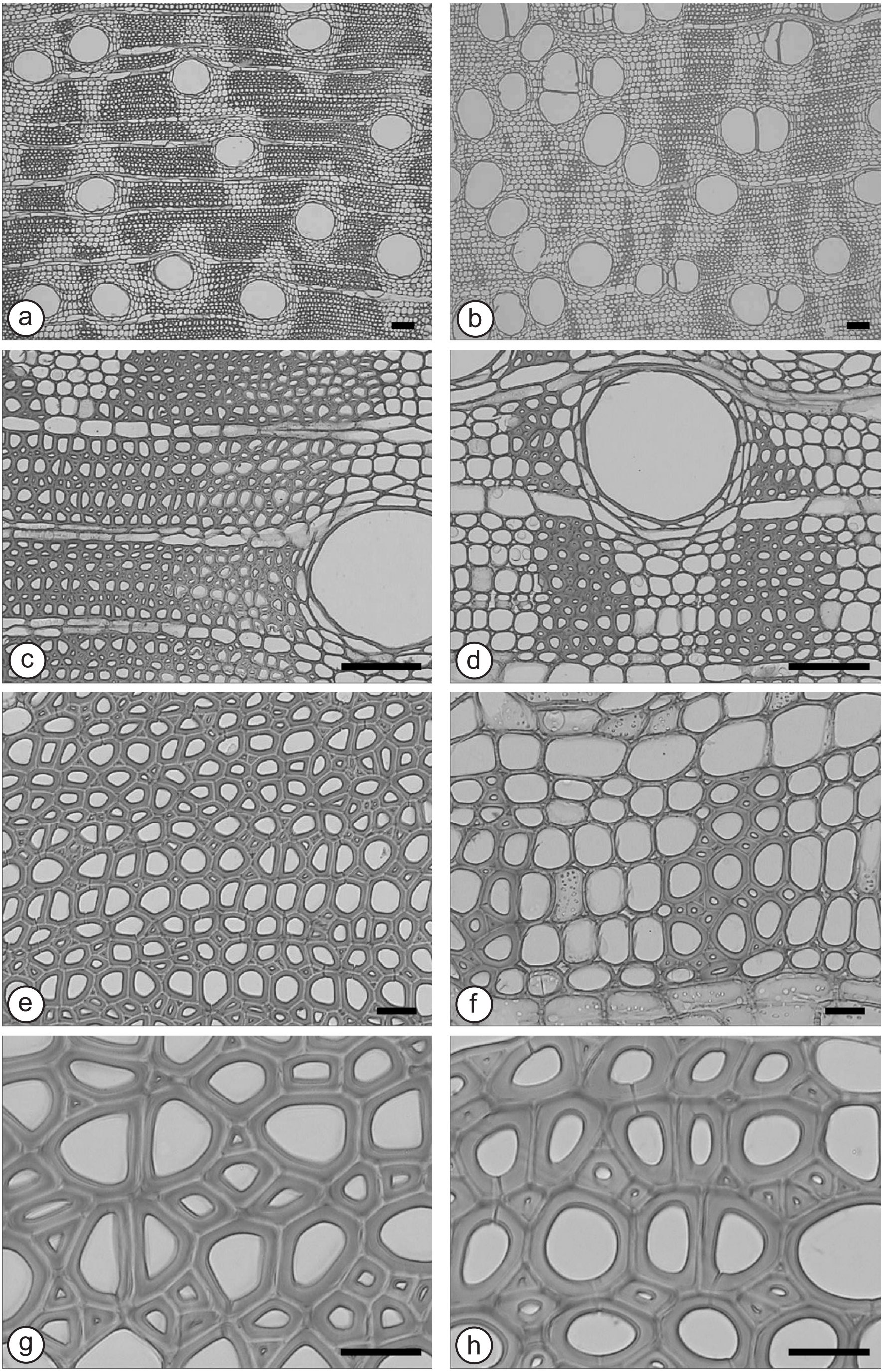


Fig. 17. Comparison of transverse sections of tension wood (a, c, e, g) and opposite wood (b, d, f, h) of *Ormosia bolivarensis* (Papilionaceae). — Scale bars of a–d = 100 µm, of e–h = 25 µm.

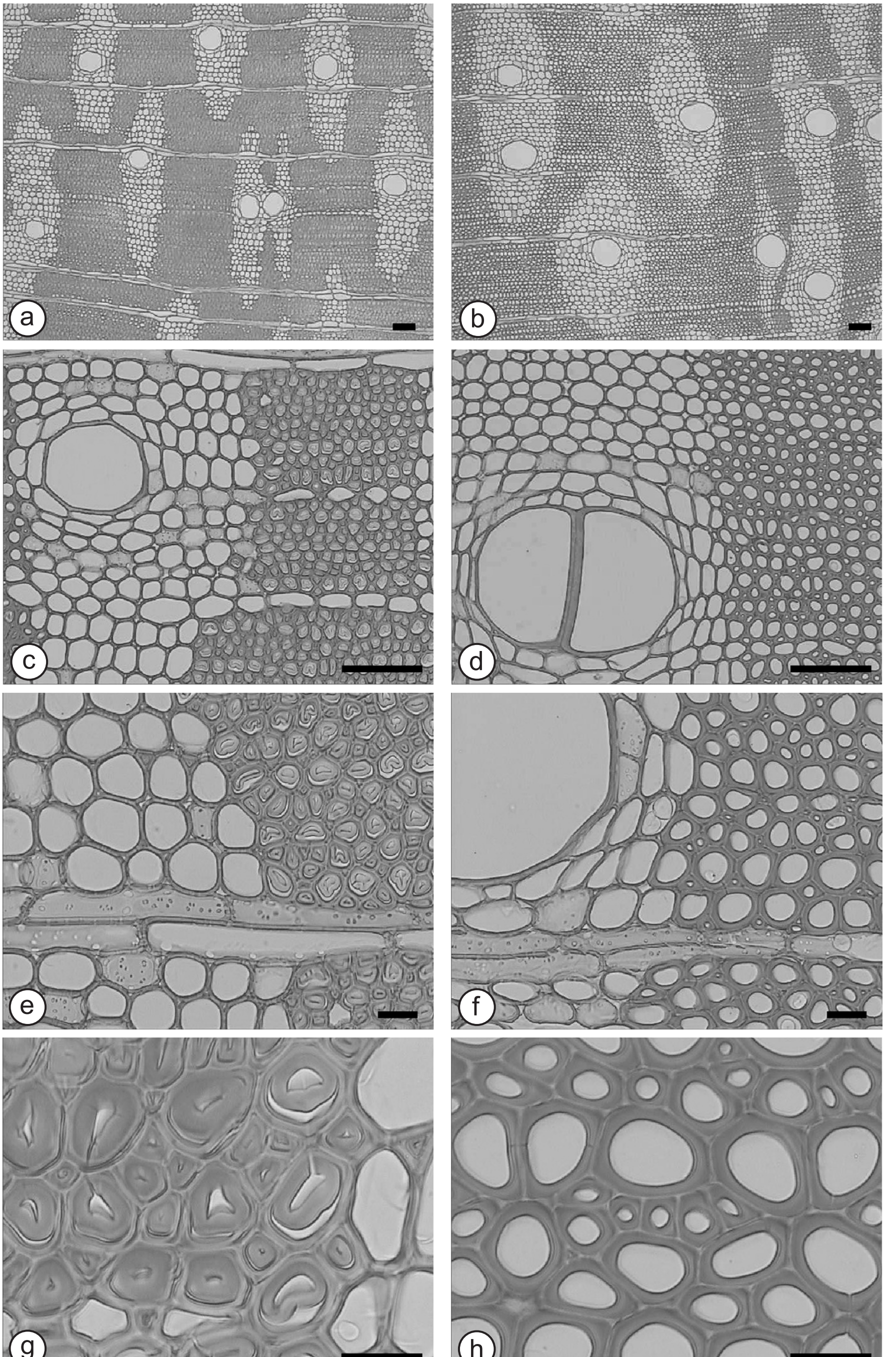


Fig. 18. Comparison of transverse sections of tension wood (a, c, e, g) and opposite wood (b, d, f, h) of *Ormosia coutinhoi* (Papilionaceae). — Scale bars of a–d = 100 µm, of e–h = 25 µm.

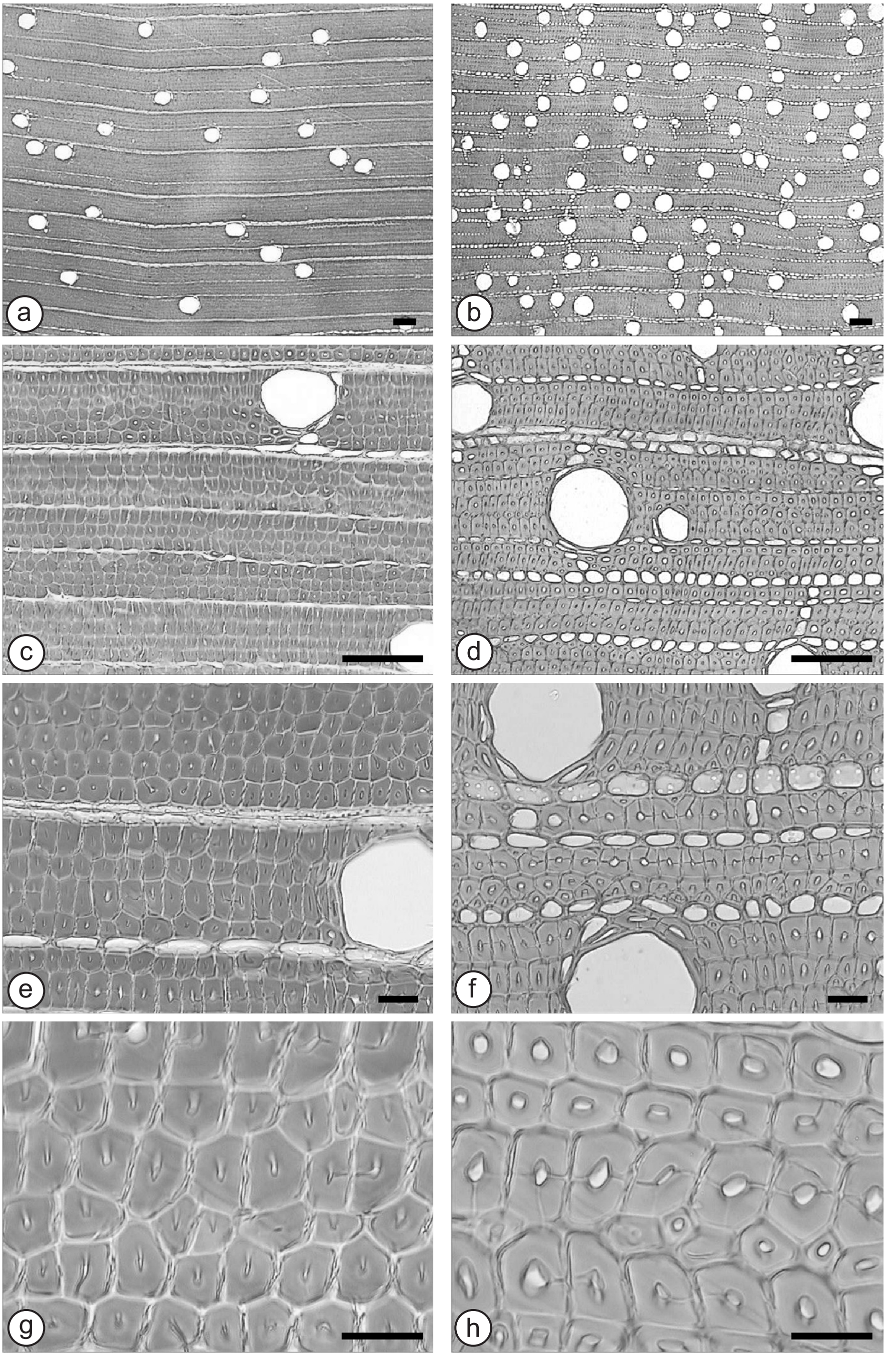


Fig. 19. Comparison of transverse sections of tension wood (a, c, e, g) and opposite wood (b, d, f, h) of *Cassipourea guianensis* (Rhizophoraceae). — Scale bars of a–d = 100 μm, of e–h = 25 μm.

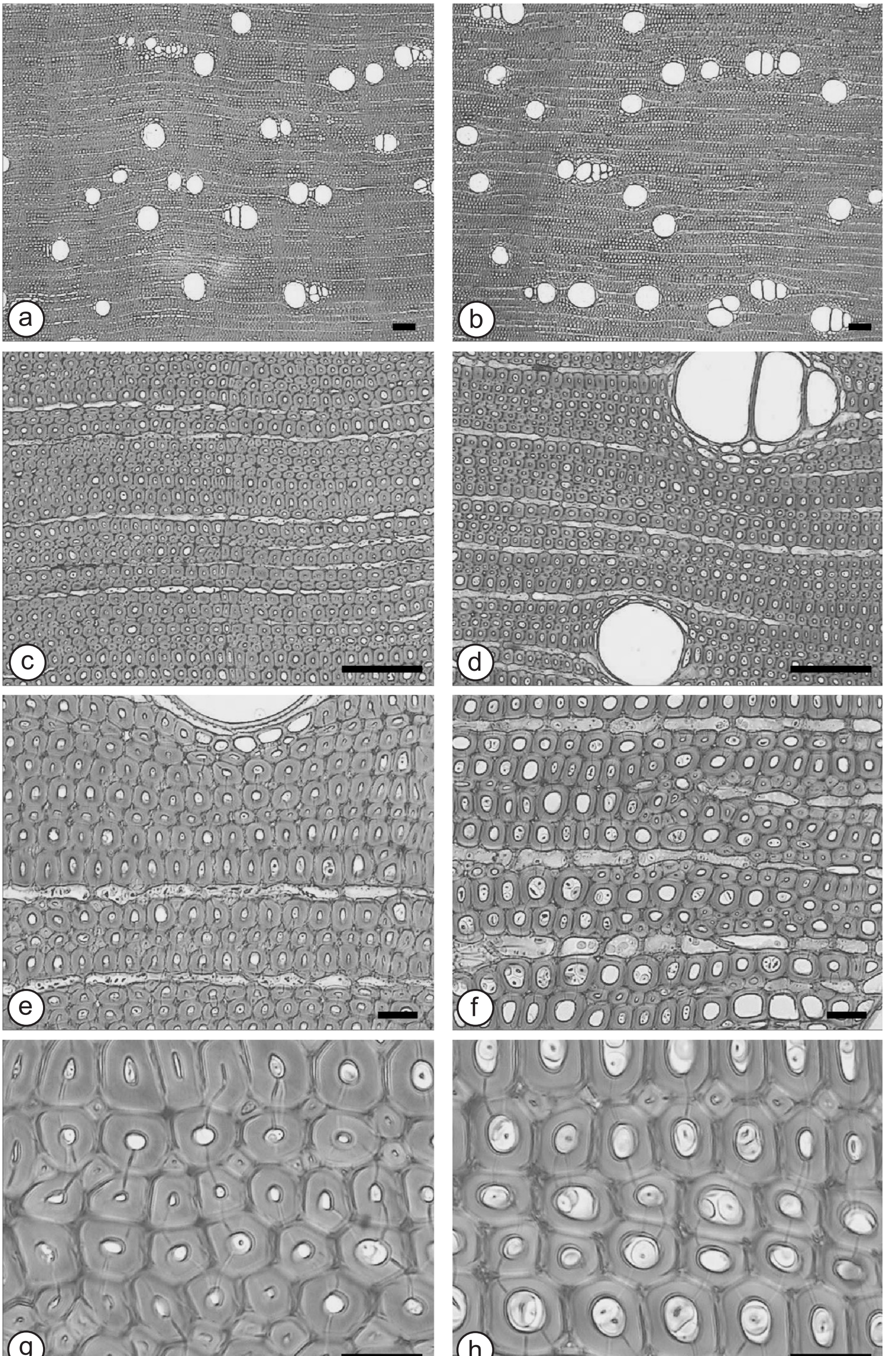


Fig. 20. Comparison of transverse sections of tension wood (a, c, e, g) and opposite wood (b, d, f, h) of *Cupania scrobiculata* (Sapindaceae). — Scale bars of a–d = 100 µm, of e–h = 25 µm.

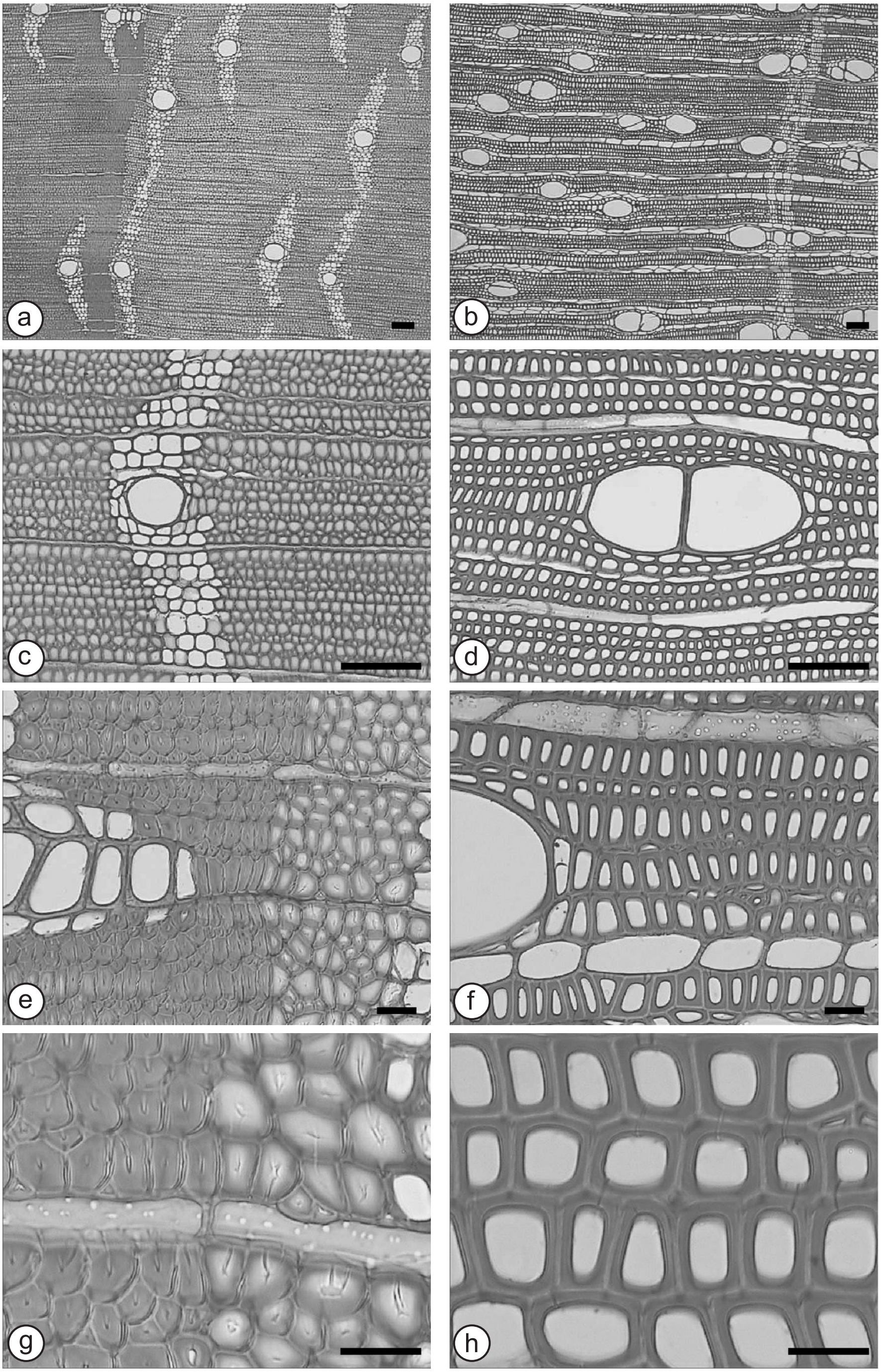


Fig. 21. Comparison of transverse sections of tension wood (a, c, e, g) and opposite wood (b, d, f, h) of *Talisia simaboidea* (Sapindaceae). — Scale bars of a–d = 100 µm, of e–h = 25 µm.

Comparison of radial–tangential directions

Table 2 gives relative differences in measurements of anatomical criteria as a function of tangential and radial directions ((radial dimension–tangential dimension) / radial dimension) × 100 for the 21 trees.

These results show that, irrespective of whether opposite or tension wood is concerned, there is a significant difference between radial and tangential dimensions in fibre diameter, lumen diameter, cell wall thickness, relative cell wall thickness and vessel diameter. In most of the species, ovalization of fibres and their lumen can be observed in the tangential direction. Cell wall thickness does not seem to have a preferential direction that is shared by the majority of trees. Considering tension wood and opposite wood separately, general trends are apparent for all 21 trees. Vessels do not display any systematic orientation in opposite wood ($p = 0.09$), but in tension wood they are mainly radially oriented ($p < 0.001$).

Variability within individuals

For each tree, averages of each parameter measured in tension wood and opposite wood are presented in Table 3. The values are then compared in order to highlight significant differences. Probabilities resulting from the Student test on the average differences are presented in Table 4. In order to visualize the direction and the amplitude of the difference between TW and OW, Table 4 also gives the relative difference (TW–OW) / TW for each tree and each parameter.

The missing values for the opposite side of tree 6 are due to repeated damage to vessel elements during sectioning, which made measurements impossible.

Analysis of the variation within individuals showed that certain anatomical parameters differ more between opposite wood and tension wood than others. Parameters for which one generally finds significant differences between tension wood and opposite wood are the absolute and relative wall thickness of fibres. Concerning the vessels, diameter and surface also seem to show a rather strong contrast within individuals. The limited number of measurements on shape index, vessel group index and vessel frequency did not enable us to perform analysis of variability between individuals.

Certain trees have tension wood that is anatomically very different from opposite wood both with respect to vessels and fibres. The most highly contrasted case was *Talisia simaboides* (Fig. 21), but the contrast was also very strong in *Protium opacum* (Fig. 4), *Hebepetalum humiriifolium* (Fig. 9), *Trichilia schomburgkii* (Fig. 14), and *Cassipourea guianensis* (Fig. 19). In *Ormosia coutinhoi* (Fig. 18), the difference was highly significant for element size (diameter, surface area and wall thickness), whereas no difference was apparent in the shape, the index of vessel grouping and the frequency of the vessels. It should also be noted that in 5 trees (Fig. 8, 10, 13, 14, 20), there was a significant difference ($p < 0.0001$) in lumen diameter whereas no significant difference was observed in fibre diameter, thus indicating a significant difference in the absolute and relative thickness of fibre walls.

Conversely, some trees did not show significant differences in the majority of the parameters measured, particularly *Licania membranacea* (Fig. 5) where fibres were very similar, and *Eschweilera sagotiana* (Fig. 12) where there was no significant difference in vessel parameters.

Table 2. — Top: relative difference in the measurement of anatomical parameters in tangential and radial directions (radial dimension–tangential dimension)/radial dimension) × 100 for the 21 trees and significance thresholds of differences within individuals. FD = fibre diameter; FLD = fibre lumen diameter; ReFWT = relative fibre wall thickness; FWT = fibre wall thickness; VD = vessel diameter. The bold characters in the table highlight the positive differences (value of the criterion higher in the radial than in the tangential direction) in contrast to negative differences. — Bottom: comparison between individuals of tangential and radial measurement for each criterion (Test of paired Student). NS = non significant (p > 0.05); *: p < 0.05; **: p < 0.01; ***: p < 0.001 blank = values did not allow a Student test to be performed. — T = tension wood, O = opposite wood. — Units = %.

	FD		FLD		ReFWT		FWT		VD	
	T	O	T	O	T	O	T	O	T	O
1	**19** ***	**11**	**18 ns**	**3 ns**	**1 ns**	**8 ns**	**19** **	**19** **	**6**	-10 ns
2	-21 ***	-19	-43 ***	-60 ***	**4** *	**8** **	-16 ***	0	**0 ns**	-2 ns
3	0 ns	-35 ***	**7 ns**	-44	-13 ns	**12**	-14 ns	-16 **	**27** ***	**17**
4	-13 *	-21 ***	-29 **	-23 ***	**13**	**7 ns**	**1 ns**	-11 ns	**12** ***	-1 ns
5	-67 ***	-57 ***	-208 ***	-73	**9** ***	**2**	-53 ***	-48 ***	**14** *	***
6	**1 ns**	**4 ns**	**22**	**2 ns**	-2	**1**	**0 ns**	**4 ns**	**6 ns**	-3 ns
7	-2 ns	-9 ns	-2 ns	-29 ***	**7 ns**	**10** ***	**4 ns**	**2 ns**	**13** ***	**6 ns**
8	-45 ***	-32 ***	-171 ***	-64	**11** ***	**6** ***	-27 ***	-24 ***	**15** ***	**7** *
9	-20 **	-23 ***	-51 ***	-59 ***	**5** ***	**4** **	-12 **	-19 ***	**12** ***	**19** ***
10	-21 **	-22	-51 ***	-53 ***	**5** **	**7** *	-16 **	-16 *	**5**	-5 ns
11	-25 ***	-28	-49 ***	-52 ***	**18** ***	**18** **	**0 ns**	-5 ns	**2 ns**	-6 ns
12	-21 ***	-8	-125 ***	-16	**6** ***	**5 ns**	-11 **	**2 ns**	**4 ns**	**12** *
13	-18 **	-27 ***	-82 ***	-51	**10** ***	**3**	-5 ns	-20 ***	**12 ns**	**5 ns**
14	-31 ***	-33 ***	-64 ***	-76 ***	**6** **	**12** ***	-23 ***	-16 ***	**4 ns**	**5 ns**
15	-25 ***	-8 ns	-58 ***	-26 ns	**10** **	**9 ns**	-8	**1 ns**	-7 ns	-11 *
16	-4	**10** **	-12 ns	-4 ns	**3 ns**	**6** *	**1 ns**	**15** ***	-10 *	-12 **
17	-1 ns	**5**	**6 ns**	**7 ns**	-6 ns	-3 ns	-1	**1 ns**	**15**	**1 ns**
18	**2 ns**	**19** ***	**28**	**20** **	-8	-4 ns	-10 *	**15** *	**9** **	**13** ***
19	-36 ***	-49	-109	-97 ***	**7** ***	**8** ***	-24 ***	-39 ***	**17** ***	-11 ***
20	**4 ns**	-9 *	-2 ns	-21 **	**4 ns**	**7** *	**9** **	-1 ns	-3 ns	-1 ns
21	-15 **	-37 ***	-52	-53 ***	**3**	**20** **	-11 **	-8 ns	**13** **	**34** ***
	0.0028 **	0.0017 **	0.0054 **	0.0007 ***	0.0010 **	<0.0001 ***	0.0162 *	0.0569 ns	0.0005 ***	0.1860 ns
	<0.0001 ***		<0.0001 ***		<0.0001 ***		0.0020 **		0.0016 **	

Table 3. Summary of the averages obtained for each parameter in tension wood and opposite wood for the 21 trees. — FD = fibre diameter (µm); FLD = fibre lumen diameter (µm); ReFWT = relative fibre wall thickness (%); FWT = fibre wall thickness (µm); VF = vessel frequency (mm^{-2}); VGI = vessel group index; VSI = vessel shape index; VD = vessel diameter (µm); VS = vessel surface (10^3 $µm^2$); VA, APA, RA and FA = relative amount of vessels, axial parenchyma, rays and fibres on a transversal plan (%). — T = tension wood; O = opposite wood.

N°	FD		FLD		ReFWT		FWT		VF		VGI		VSI		VD		VS		VA		APA		RA		FA	
	T	O	T	O	T	O	T	O	T	O	T	O	T	O	T	O	T	O	T	O	T	O	T	O	T	O
1	22.3	24.3	6.9	10.0	69	59	15.2	13.9	2.2	2.4	0.52	0.63	0.4	-15.4	195	167	23.8	23.8	11.0	6.8	16.9	16.6	21.6	22.2	50.5	54.3
2	12.8	11.8	2.6	3.1	80	75	10.1	8.4	18.4	20.1	0.58	0.57	-0.8	-2.7	83	86	5.4	5.9	6.1	5.5	10.8	8.1	10.1	15.2	72.9	71.2
3	19.0	20.8	12.2	12.0	36	42	6.8	8.5	15.8	21.6	0.36	0.29	26.6	14.6	105	85	8.6	5.7	9.0	7.8	8.7	7.6	22.4	22.8	59.9	61. 8
4	13.7	17.2	6.8	12.5	51	27	6.8	4.5	18.1	19.9	0.73	0.63	11.3	-3.7	111	134	9.7	14.4	12.0	19.3	1.8	0.0	8.7	10.7	77.5	70.0
5	17.6	18.4	2.6	2.1	86	88	15.0	15.8	3.1	5.1	0.98	0.69	12.4		145		17.6		6.6	4.1	3.6	13.5	14.0	13.2	75.7	69.1
6	21.2	22.8	1.6	9.2	92	60	19.4	13.3	3.3	3.9	0.83	0.73	4.1	-3.7	179	211	25.8	35.2	9.5	12.4	21.5	34.2	22.7	19.2	46.3	34.1
7	22.5	23.9	9.5	9.1	55	62	12.5	14.7	30.0	47.9	0.45	0.36	11.6	3.1	63	67	3.2	3.5	6.3	9.6	0.0	0.0	28.0	24.3	65.6	66.1
8	24.7	22.9	4.2	5.1	84	78	20.3	17.8	6.6	10.8	0.91	0.84	15.0	5.5	126	104	12.6	8.6	6.0	7.4	6.1	3.4	31.0	33.0	56.9	56.2
9	16.5	18.8	3.1	2.7	82	86	13.3	16.1	5.6	7.8	0.99	0.98	10.5	18.2	135	151	14.6	18.2	8.2	12.6	4.2	2.9	15.9	16.8	71.7	67.7
10	43.8	42.1	8.0	10.7	82	74	35.4	30.6	5.4	5.8	0.80	0.76	4.7	-7.8	188	209	28.4	34.8	14.9	18.9	7.7	7.0	25.8	30.0	51.6	44.1
11	17.0	19.4	9.5	9.9	45	50	7.5	9.4	8.6	11.7	0.67	0.38	1.2	-6.7	140	149	15.5	17.8	8.9	9.0	4.3	5.9	11.9	14.3	74.9	70.8
12	13.4	14.6	1.4	6.0	90	59	11.9	8.4	4.1	6.3	0.60	0.62	1.5	9.2	127	113	13.3	10.5	5.6	4.9	20.5	23.7	18.0	14.8	55.8	56.5
13	15.1	15.6	3.2	2.2	80	86	11.7	13.2	6.3	14.8	0.43	0.46	11.0	2.5	122	114	11.9	10.3	4.6	5.0	18.9	27.4	14.4	14.7	62.1	52.8
14	14.3	14.3	3.0	4.0	79	72	11.3	10.1	11.4	27.8	0.58	0.43	3.5	2.9	98	90	7.7	6.5	5.1	4.8	7.9	8.0	13.4	18.4	73.6	68.7
15	15.9	18.2	4.5	6.6	72	65	11.1	11.2	4.9	6.2	0.51	0.50	-8.2	-13.4	182	195	26.4	30.6	8.6	12.4	23.3	22.9	9.3	9.4	58.8	55.3
16	17.3	18.7	4.1	5.2	76	72	13.1	13.4	7.6	12.3	0.89	0.86	-13.0	-14.3	124	112	12.7	10.2	9.5	8.7	5.5	8.1	17.1	20.0	67.9	63.1
17	22.2	25.3	13.7	14.9	39	41	8.3	10.0	3.0	6.6	0.88	0.70	14.7	-0.6	207	226	34.1	40.0	13.5	17.2	28.8	38.3	11.7	13.8	46.0	30.7
18	19.5	23.9	4.2	14.2	79	41	15.3	9.4	1.9	3.0	0.86	0.67	8.8	12.5	140	164	15.4	21.4	5.0	7.6	40.6	44.1	6.7	9.4	47.7	38.9
19	17.6	20.3	2.5	4.5	86	79	14.9	15.9	6.4	18.8	1.00	1.00	16.2	-13.2	90	82	6.4	5.4	5.3	8.9	0.8	2.5	13.5	18.2	80.4	70.4
20	18.9	19.1	6.1	8.0	68	58	12.7	11.1	9.3	10.2	0.51	0.55	-3.6	-2.3	103	123	8.7	12.0	5.7	6.9	1.5	1.6	8.2	15.0	84.4	76.5
21	16.9	22.7	1.5	14.2	91	38	15.2	8.2	3.0	9.8	0.88	0.41	13.0	32.3	99	127	7.9	12.5	2.8	6.3	12.6	2.8	8.5	23.3	76.1	67.5

Table 4. Summary of the relative differences (100 × (TW–OW) / TW in %) and of the probabilities resulting from the paired Student test comparing opposite wood and tension wood for 10 anatomical parameters. — ns = non significant ($p>0.05$); *: $p<0.05$; **: $p<0.01$; ***: $p<0.001$. The bold characters highlight the positive differences (value higher in tension wood than in normal wood) in contrast to negative differences. — RD = relative difference (%).

Trees	FD		FLD		FWT		ReFWT		VD		VS		VA		APA		RA		FA	
	Student (p=)	RD	Student (p=)	RD	Student (p=)	RD	Student (p=)	RD	Student (p=)	RD	Student (p=)	RD	Student (p=)	RD	Student (p=)	RD	Student (p=)	RD	Student (p=)	RD
1	0.028 *	-9	<0.001 ***	-45	**0.066 ns**	**9**	**<0.001** ***	**15**		**14**	**0.214 ns**	**23**		**38**		**2**		-3		-8
2		**7**		-19	***	**17**	**<0.001** ***	**6**	<0.001 ***	-4	0.121 ns	-9		**9**	**<0.001** ***	**25**	<0.001 ***	-49		**2**
3	0.031 *	-9		**1**	<0.001 ***	-24		-16	**0.003** **	**19**	**<0.001** ***	**34**		**13**		**13**		-2		-3
4	<0.001 ***	-25	<0.001 ***	-83	**<0.001** ***	**33**	**<0.001** ***	**47**	<0.001 ***	-21	<0.001 ***	-48	<0.001 ***	-61	**TW only**	**100**		-22	**<0.001** ***	**10**
5	0.381 ns	-4	0.239 ns	18	0.076 ns	-5		-2					**<0.001** ***	**38**	<0.001 ***	-271	**<0.001** ***	**6**	**<0.001** ***	**9**
6	0.043 *	-8		-477	**<0.001** ***	**31**		**36**	<0.001 ***	-18	<0.001 ***	-36		-30	<0.001 ***	-59	**0.002** **	**15**	**<0.001** ***	**26**
7	0.062 ns	-6	**0.100 ns**	**4**	<0.001 ***	-18	<0.001 ***	-13	<0.001 ***	-6	0.091 ns	-10	<0.001 ***	-51				**13**		-1
8	**0.179 ns**	**8**	<0.001 ***	-21	**0.004** **	**12**	**<0.001** ***	**7**	**<0.001** ***	**18**	**<0.001** ***	**32**		-24		**44**		-6		**1**
9	0.003 **	-14	**0.033** *	**13**	<0.001 ***	-21	<0.001 ***	-6	<0.001 ***	-12	<0.001 ***	-24	<0.001 ***	-55	**0.001** **	**31**		-6	**0.028** *	**6**
10	**0.394 ns**	**4**	<0.001 ***	-35	***	**13**	**<0.001** ***	**10**		-11	0.003 **	-23	0.003 **	-27		**9**		-16	**0.022** *	**15**
11		-14	0.400 ns	-4	<0.001 ***	-25	0.048 *	-10	0.826 ns	-7	0.041 *	-15		-1	0.003 **	-38	0.006 **	-20	**0.004** **	**6**
12	0.036 *	-9	<0.001 ***	-319	**<0.001** ***	**29**	**<0.001** ***	**34**	**0.074 ns**	**11**	**0.046** *	**21**		**13**	<0.001 ***	-16	**<0.001** ***	**18**		-1
13	0.609 ns	-3	**<0.001** ***	**31**	<0.001 ***	-13	<0.001 ***	-8	**<0.001** ***	**6**	**0.249 ns**	**14**		-11	<0.001 ***	-45		-2	**<0.001** ***	**15**
14	**0.988 ns**	**0**	<0.001 ***	-34	**<0.001** ***	**10**	**<0.001** ***	**9**	**<0.001** ***	**8**	**<0.001** ***	**16**		**5**		-3	<0.001 ***	-37	**<0.001** ***	**7**
15	0.009 **	-15	<0.001 ***	-47	***	-1	**<0.001** ***	**10**	0.008 **	-7	0.076 ns	-16	<0.001 ***	-44		**2**		-1		**6**
16	0.013 *	-8	<0.001 ***	-28	0.090 ns	-2	**<0.001** ***	**6**	**0.020** *	**10**	**0.005** **	**19**		**9**	0.001 **	-49	<0.001 ***	-17	**0.004** **	**7**
17		-14	0.076 ns	-9	<0.001 ***	-20	0.196 ns	-6	<0.001 ***	-9	0.004 **	-17	0.015 *	-27	<0.001 ***	-33	0.040 *	-18	**<0.001** ***	**33**
18	<0.001 ***	-23	<0.001 ***	-239	**<0.001** ***	**39**	**<0.001** ***	**49**	<0.001 ***	-18	<0.001 ***	-39	<0.001 ***	-51		-9	0.045 *	-40	**<0.001** ***	**18**
19	0.004 **	-16	<0.001 ***	-79	0.053 ns	-7	**<0.001** ***	**9**	**<0.001** ***	**9**	**<0.001** ***	**15**	<0.001 ***	-68	<0.001 ***	-233	<0.001 ***	-34	**<0.001** ***	**12**
20	0.552 ns	-2	<0.001 ***	-33	**<0.001** ***	**13**	**<0.001** ***	**14**	0.470 ns	-19	<0.001 ***	-38		-21		-2	<0.001 ***	-80	**<0.001** ***	**9**
21	<0.001 ***	-34	<0.001 ***	-864	**<0.001** ***	**46**	**<0.001** ***	**58**	<0.001 ***	-28	<0.001 ***	-59	<0.001 ***	-127	**<0.001** ***	**78**	<0.001 ***	-175	**<0.001** ***	**11**

Results on relative amounts of tissues help us to quantify variations concerning modification of wood structure between tension and opposite wood. We can see clearly that for some trees like *Lacmellea aculeata* or *Goupia glabra* these amounts do not show strong variations. On the contrary, trees like *Protium opacum*, *Ormosia bolivarensis, Cassipourea guianensis* and *Talisia simaboides* show strong variations concerning the whole tissue areas. The strongest variations concern vessel area and axial parenchyma area for *Protium opacum* (in this case hardly any axial parenchyma was discernable in opposite wood), axial parenchyma area for *Licania membranacea* and *Cassipourea guianensis*, vessel area, axial parenchyma area and ray area for *Talisia simaboides*.

Variability between individuals

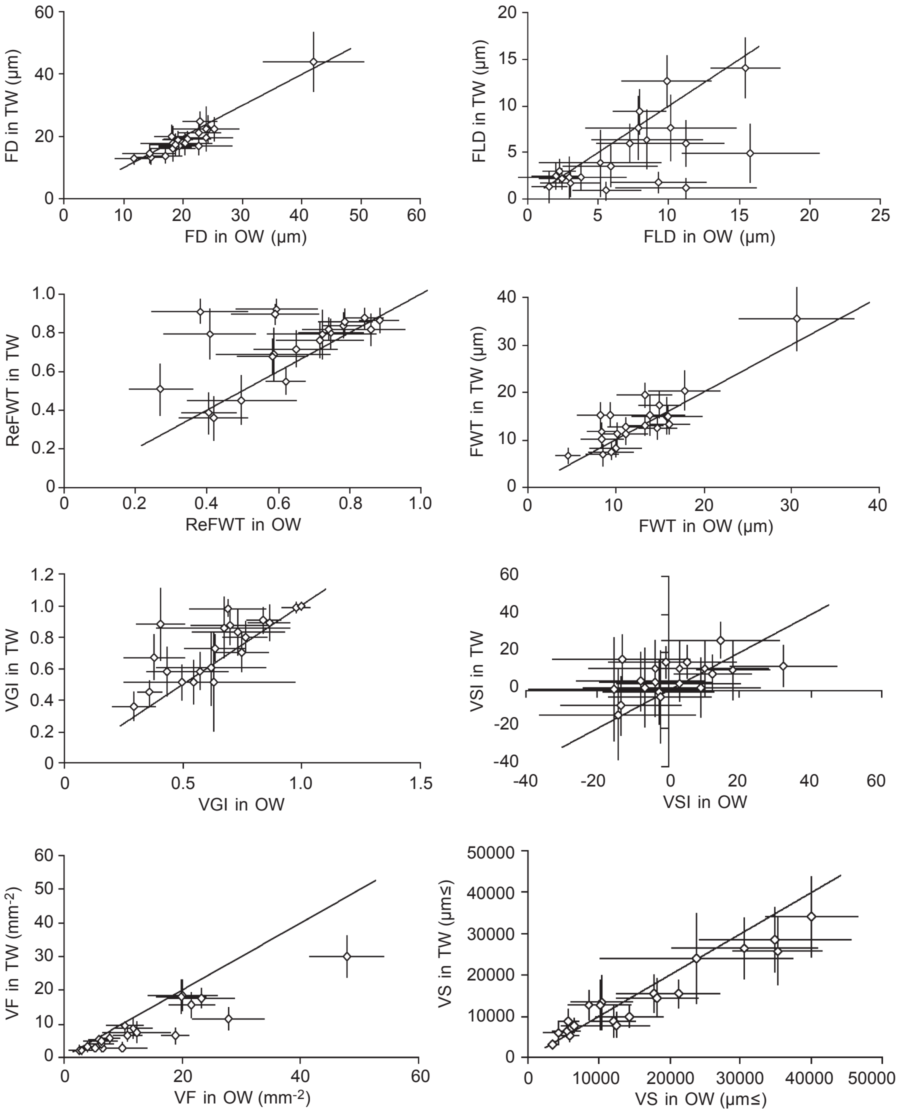
Figure 22 compares tension wood to opposite wood for twelve parameters. This figure does not enable each tree to be distinguished individually, but highlights general trends in the difference between tension wood and opposite wood. As a complement to the preceding tables, this figure also shows the standard deviation around the average value.

Table 5 shows the results of the Student test for each parameter and for all trees.

Table 5. Averages of the average variation (T-O) / T [%] and results of the Student test for 13 anatomical parameters for all trees. — FD = fibre diameter (µm); FLD = fibre lumen diameter (µm); ReFWT = relative fibre wall thickness (µm); FWT = fibre wall thickness (µm); VF = vessel frequency (mm^{-2}); VGI = vessel group index; VSI = vessel shape index; VD = vessel diameter (µm); VS = vessel surface ($µm^2$); VA, APA, RA and FA = relative amount of vessels, axial parenchyma, rays and fibres on a transversal plan (%). — ns = non significant (p>0.05); *: p<0.05; **: p<0.01; ***: p<0.001. — T = tension wood; O = opposite wood.

	FD	FLD	ReFWT	FWT	VF	VGI	VSI	VD	VS	VA	APA	RA	FA
(T-O)/T	-9	-108	12	6	-66	11	229	-3	-8	-1.53	-1.57	-2.16	5.26
p =	0.1*		1.1*	9.4ns	0.05***		3.0*	26.1ns	15.9ns	1.90*	17.56ns		0.01***

Vessel dimensions were not significantly different in the analysis of variability between trees. Measurements on fibres were significant but less so than in the analysis of variability within trees. However, in tension wood fibres had smaller diameters and thicker walls (relative and absolute). In most cases, the index of vessel grouping differs (vessels were more often grouped in tension wood) and the most relevant parameter is vessel frequency where there is a significant difference ($p<0.0001$) between frequency in tension wood (lower) and in opposite wood (higher). This phenomenon has already been observed in many other trees from various species (29 species sampled by Onaka (1949), and in poplar by Jourez *et al.* (2001), *etc.*). It seems that during the production of tension wood, the tree mobilizes its resources for the production and the effectiveness of its elements of support (fibres) to the detriment of conduction. However, if one considers that the production of tension wood is often accompanied by increased cambial activity (of which the macroscopic consequence is pith eccentricity), it would be interesting to see if the total production of conducting elements is really lower per growth unit.



continued on the next page

Fibre area increases in tension wood specimens for 17 trees. For 15 of these and two of the other 4, ray area decreases. For 14 trees the vessel area is higher in opposite wood. Axial parenchyma area is higher in the tension wood of 10 trees and lower in 11 (Table 4, 5 and Fig. 22).

We were unable to find any relation between all of the criteria considered in this study of variability between individuals and the tilting angle of trees or their growth stress ratio between tension and opposite wood.

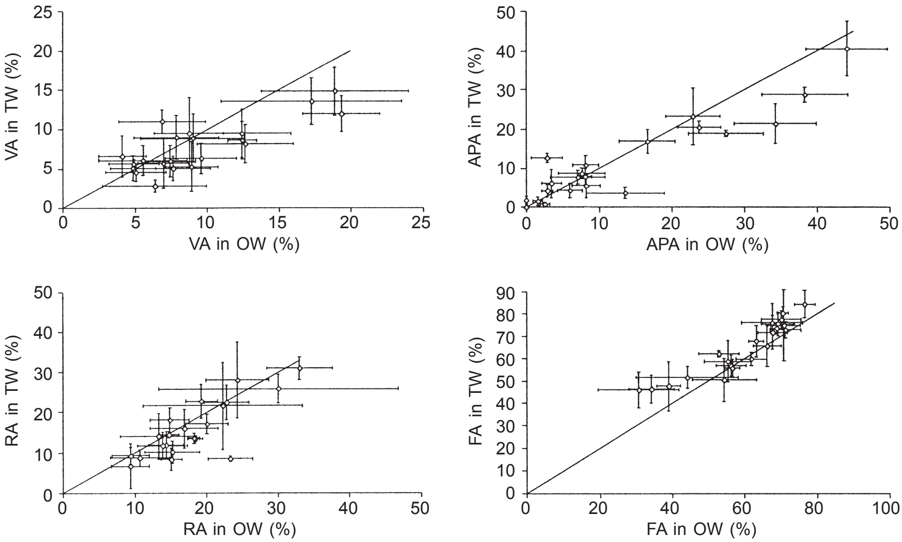


Fig. 22. Distribution of the 21 trees in the comparison of tension wood (TW) and opposite wood (OW) for 8 anatomical parameters. — FD = fibre diameter; FLD = fibre lumen diameter; ReFWT = relative fibre wall thickness; FWT = fibre wall thickness; VGI = vessel group index; VSI = vessel shape index; VS = vessel surface; VF = vessel frequency. — VA, APA, RA and FA = relative amount of vessels, axial parenchyma, rays and fibres on a transversal plan (%).

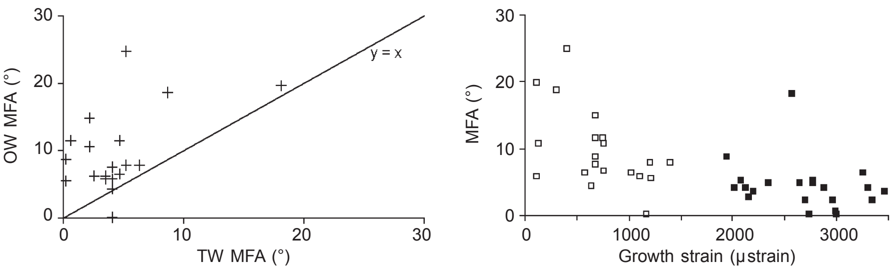


Fig. 23. Left: distribution of the 21 trees in the comparison of the MFA (in degrees) between tension wood (TW) and opposite wood (OW). — Right: MFA (in degrees) versus growth strain for tension wood (full squares) and opposite wood (empty squares).

Microfibril angle (MFA) estimation

Table 6 shows MFA in tension and opposite wood for each tree. Figure 23 compares average MFA in tension wood and opposite wood and shows their relation with growth stresses. It can be seen that for all the trees, except *Licania membranacea*, the MFA was lower in tension wood specimens even in species without a G-layer. Similar observations were made by Hori *et al.* (2003) and Yoshida *et al.* (2000) for the upper side of branches of *Liriodendron tulipifera*. This shows that even if the fibre wall of

Table 6. MFA (in degrees) from tension and opposite wood specimens for all the trees studied. Trees with gelatinous layer in their tension wood are indicated with *.

Trees	MFA estimation in tension wood specimen	MFA estimation in opposite wood specimen
1	4.1	5.8
2	8.7	18.7
3	18.1	19.7
4*	5.2	24.8
5	4.1	0.2
6*	2.6	6.3
7*	2.2	10.7
8	4.7	6.6
9*	4.1	4.4
10	3.5	5.8
11*	4.7	11.5
12	2.2	14.8
13	0.6	11.5
14	4.7	11.5
15	0.2	8.7
16	4.1	7.6
17*	6.3	7.8
18*	5.2	7.8
19	0.2	5.5
20	2.2	10.7
21*	3.5	6.3

species with high tensile-stressed wood without a G-layer does not undergo a qualitative change in its anatomical structure, it reacts to produce an external stress through a quantitative modification in its ultrastructure. Despite the considerable anatomical diversity observed, all of these trees were able to produce high tension stress. Thus, the origin of the stress is likely to be found in the modification of the ultrastructure.

In the tree (*Licania membranacea)* that does not show a lower MFA in tension wood, we were unable to find a correlation between this peculiar result and an anatomical parameter of the sample studied; we thus suspect a change in the chemical composition, but this was not analysed.

CONCLUSIONS

Anatomical differences between a highly stressed wood, qualified as tension wood, and a normally or weakly stressed wood are variable and sometimes weak. Tension wood in angiosperms is usually linked with its biomechanical function in living trees as "reaction wood": its formation on the upper side allows bending of the stem that counteracts gravitational forces. In this study, tension wood is defined from a mechanical point of view with respect to pre-stresses associated with its genesis in the living tree. Mechanically speaking, tension wood is thus under far stronger tension stress than that observed in the remainder of the tree periphery. As the mechanical imbalance induced by the more tensile side of the stem leads to a restoration of verticality in the tree, mechanically defined tension wood is thus directly related to functional tension wood. However, general relations between these mechanical or functional definitions of tension wood and anatomical variations that would allow a reliable anatomical definition of tension wood have not yet been found. Among quantitative anatomical criteria only the decreasing of vessel frequency seems to be a general feature. Whereas one could have assumed that certain parameters such as fibre wall thickness could partly explain certain properties, it appears that even this criterion is not generally applicable. As the results of average MFA suggest, the proper structural definition of tension wood is probably to be found at finer scales, in particular in the ultrastructural organization of the cell wall.

ACKNOWLEDGEMENTS

Many thanks to Pieter Baas, Bernard Thibaut and Joseph Gril for their critical review of this paper. This work was performed in the framework of the programme "Reaction wood" funded by ADEME and the French Ministry of Agriculture.

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