Tension wood and opposite wood in 21 tropical rain forest species. 1. Occurence and efficiency of G-layer

Bruno Clair, Julien Ruelle, Jacques Beauchêne, Marie-Françoise Prévost, Meriem Fournier

To cite this version:

Bruno Clair, Julien Ruelle, Jacques Beauchêne, Marie-Françoise Prévost, Meriem Fournier. Tension wood and opposite wood in 21 tropical rain forest species. 1. Occurence and efficiency of G-layer. IAWA Journal, 2006, 27 (3), pp.329-338. 10.1163/22941932-90000158 . hal-00112579

TENSION WOOD AND OPPOSITE WOOD IN 21 TROPICAL RAIN FOREST SPECIES.

1. OCCURRENCE AND EFFICIENCY OF G-LAYER

by
Bruno Clair [1, 2], Julien Ruelle[1, 3], Jacques Beauchêne [1], Marie Françoise Prévost [4] & Meriem Fournier [1]

Published in IAWA Journal, Vol. 27 (3), 2006: 329–338

SUMMARY

Wood samples were taken from the upper and lower sides of 21 naturally tilted trees from 18 families of angiosperms in the tropical rainforest in French Guyana. The measurement of growth stresses 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 lower tensile stressed wood on the lower side, called opposite wood. Eight species had tension wood fibres with a distinct gelatinous layer (G-layer). The distribution of gelatinous fibres varied from species to species. One of the species, *Casearia javitensis* (Flacourtiaceae), showed a peculiar multilayered secondary wall in its reaction wood. Comparison between the stress level and the occurrence of the G-layer indicates that the G-layer is not a key factor in the production of high tensile stressed wood.

Key words: gelatinous layer, G-layer, French Guyana, tension wood, tropical rain forest, wood anatomy.

INTRODUCTION

Tree stems maintain their orientation (vertical for trunks, oblique for branches) by generating asymmetrical (from one side of the stem to the other) stresses in wood, during cell wall maturation, i.e. lignification and formation of the secondary cell wall (Archer 1986; Fournier et al. 1994a). Angiosperms generate stronger tension stresses on the upper side of the stem (Wardrop 1964; Fisher and Stevenson 1981), contrary to gymnosperms that produce wood with compression stresses on the lower part of the stem. This particular mechanical state is performed through marked changes in anatomical structure (Onaka 1949), that are called tension wood compared to normal wood. The generated asymmetrical stresses produce an internal bending moment at the level of the growing cross section, opposite to the external one induced by gravity and growth in mass (Wilson and Archer 1979; Archer 1986; Fournier et al. 1994b). In dense forests as tropical rainforest understoreys, tree trunk slenderness is extremely high, associated to a low stiffness and a high buckling and bending risk (Kohyama and Hotta 1990). Thus, in such dense tree communities, the above-mentionned gravitropic reactions (i.e. the formation of tension

---

[1] UMR « Ecologie des Forêts de Guyane » CIRAD ENGREF INRA, BP 316, 97379 Kourou, Guyane Française, France

[2] Laboratoire de Mécanique et Génie Civil (LMGC), UMR 5508, CNRS - Université Montpellier 2, Place E. Bataillon, cc 048, 34095 Montpellier Cedex 5, France

[3] Laboratory of Bio-Material Physics, Graduate School of Bioagricultural Sciences, Nagoya University, Nagoya 464-8601, Japan

[4] UMR « Botanique et bioinformatique de l'architecture des plantes (AMAP)» IRD-Cayenne, BP 165, 97323 Cayenne, Guyane Française, France

(e-mail: ruelle_j@kourou.cirad.fr)

wood) should be of great importance to maintain vertical growth. Moreover, tropical rain forests are characterized by a high biodiversity of trees (Richards 1996), and therefore, it is interesting to study the tropical biodiversity of tension wood, i.e. the different tension wood structures generated by the different angiosperm tree species.

For many commonly studied species such as beech, poplar, oak or chestnut, tension wood is characterised by the occurrence of fibres with a particular morphology and chemical composition due to the development of the so-called gelatinous layer (G-layer). This layer is essentially made up of strongly crystalline cellulose (Norberg & Meier 1966; Côté et al. 1969), with a very low microfibril angle (Fujita et al. 1974). However, recent studies demonstrated the presence of lignins (Joseleau et al. 2004) in G-layer. In species where tension wood exhibits a typical G-layer, its occurrence is always correlated with high tensile growth stresses (Trénard & Guéneau 1975; Mariaux & Vitalis-Brun 1983; Combes et al. 1996; Grzeskowiak et al. 1996; Sassus 1998; Clair et al. 2003; Washusen et al. 2003).

However the G-layer is not always present in tension wood. Several studies have shown that the formation of the supplementary G-layer is not constant in tension wood fibres. Out of the 346 species cited by Onaka (1949), fibres with a G-layer were observed in only 136 (39 %) of them. Fisher and Stevenson (1981), working on tension wood in branches on 122 species, demonstrated the G-layer only in 46 % of them. However these studies were based on the assumption that the upper parts of leaning stems would be made of tension wood, *i.e.* should be in very high tensile stress state compared to normal and opposite wood, but growth stresses were not in fact measured. Only a few studies (Détienne 1976; Baillères et al. 1995, Yoshida et al. 2000) have shown the absence of a G-layer in a given species after measurement of the mechanical tensile stress of tension wood.

The aim of this study was 1) to screen a wide range of species and to analyze tension wood in which the growth stresses had been measured to check the presence/absence of G-layer, and 2) analyse whether the occurrence of a G-layer resulted in a more highly tensile-stressed wood.

MATERIAL AND METHODS

Plant material and sampling

In this study only trunks were investigated and occurrence of tension wood was demonstrated by mechanical measurement of released strains on both sides of the leaning tree.

Twenty one species in the tropical rain forest distributed in 18 families (see table 1) were selected (one tree per species).

Sampling was carried out in primary forest along a trail dedicated to the study of the diversity of tree species (spatial distribution and pharmacological evaluation). The site is located on the border of the "Piste de St Elie" (pK 17) about 90 km from Kourou in French Guyana (53°0'W-5°20'N). Tree diameters ranged between 10 and 40 cm.

To be sure of the presence of tension wood, only tilting trees were chosen (tilting angles are given in table 1) with evidence of recovering verticality (bended trees). This visual criterion was confirmed by the measurement of the longitudinal residual strains on the upper and lower side of the tree (see § growth stresses) (Fig. 1).

Wood samples were taken as close as possible to the measuring zone, on both sides of the grooves made for the measurement of growth stress. To be sure that each sample was homogeneous, anatomical sections were made on two fragments (one on each side of the growth stress measurement zone) (Fig. 1).

Growth stress measurements

Growth stresses were measured with the "wap's" method (described in Fournier et al. 1994). This method consists in measuring longitudinal deformation resulting from the manual sawing of two grooves on each side of an extensometer sensor. Growth stress measurement is performed after removing of the bark in the newly formed wood. The longitudinal maturation strain is proportional to the variation in distance measured by the extensometer. Strains were measured with commercial strain gauge sensors (Hottinger Baldwin Messtechnik, DD1 type) connected to a full bridge mode via a battery-powered strain bridge (Alco system, Captels). The sensors were fitted with steel pins spaced 14 mm apart. Pins are placed in the wood after removal of the bark.

Local deformation was calculated by the ratio between the variation in the distance between pins and the distance between these pins: Strain = $(L-L_0) / L_0$ with L_0 = 14 mm.

The distance between the pins is recorded before and after the sawing of the two grooves in order to measure their displacement. Local deformation was calculated by the ratio between this displacement and the initial distance between pins: Strain = $(L-L_0) / L_0$ with L_0 = 14 mm.

At the surface of the tree, this deformation should be equal to the initial tendency of wood to deform during maturation (the grooves allow the peripheral fibres to dissociate themselves from the rest of the trunk), this is referred to as longitudinal residual maturation strain. The higher the strain rate, the higher the mechanical stress of the wood which is then assumed to possess the anatomical characteristics of tension wood.

The accuracy of this system of measurement (taking into account the precision of the device and experimental conditions) is estimated at 30 micro-strains (dimensionless strain unit, i.e. 30 µm/m).

Anatomical observations

Sections (15 µm in thickness) were cut with a microtome (Leitz) equipped with disposable razor blades (Feather N35, A35 or N35H depending on the hardness of the wood).

Double staining with Safranin / Fast Green was used to demonstrate the presence of a G-layer. Safranin stains lignified tissues red, and fast green stains both lignified and un-lignified green. Lignified tissues were red mixed with varying degrees of green while cell wall layer essentially cellulosic, like the gelatinous layer, were green.

RESULTS AND DISCUSSION

Growth stresses

Results of growth strain measurements are presented in table 1. Growth strain values on the upper side were from 2 to 20 times higher than on the lower side. This confirmed both that trees were recovering verticality often with a high growth stress ratio and the presence of wood under very high mechanical tensile stress on the upper side.

However, dispersion was observed in tension wood strain values (from 2000 to 3500 µstrain) which is probably related to intra-tree and intra-species variability rather than to differences between species.

Presence / absence of fibres with a G- layer and their distribution in tensile stressed wood

On the 21 species studied only seven (*Protium opacum* (Burceraceae), *Ormosia bolivarensis* (Papilionaceae), *Ormosia coutinhoi* (Papilionaceae), *Hebepetalum humiriifolium* (Hugoniaceae), *Ocotea indirectinervia* (Lauraceae), *Symphonia globulifera* (Clusiaceae), *Talisia simaboides* (Sapindaceae)) had fibres with a well differentiated G-layer that were very obviously green after double staining with Safranin – Fast Green (Fig. 2). This proportion is close to that found in previous studies (Fisher & Stevenson 1981; Onaka

1949). It should be noted that out of the 122 species observed by Fisher and Stevenson (1981), only one genus was common to both samples (*Casearia* in the Flacourtiaceae) in which these authors found no G-layer fibres whereas we observed a distinct multilayered secondary wall in *Casearia javitensis*. None of the species studied by Onaka 1949) were included in our sample.

In the eight species containing fibres with a G-layer, three types of distribution could be distinguished: in *Hebepetalum humiriifolium*, *Talisia simaboides* and *Symphonia globulifera* all the fibres were gelatinous and normal fibres were scarce; in *Ormosia bolivarensis* and *O. coutinhoi* fibres with a G-layer were diffuse, or occurred in clusters; finally, in *Protium opacum* and *Ocotea indirectinervia*, G-layer fibres were isolated and sparse.

Concerning the appearance of the G-layer itself, some authors have proposed different classifications to describe the different types (Onaka 1949, Wardrop & Dadswell 1955; Höster & Liese 1966; Höster 1971 in Détienne 1976). None of these classifications appeared to us to be perfectly satisfactory because different types of G-layers can be found in the same tree (Araki et al. 1983), and especially because recent results (Clair et al. 2005a; Clair et al. 2005b) showed that classical sectioning with a sliding microtome (i.e. the procedure we used), produced an artefact with respect to the appearance of the G-layer. We consequently decided not classify the diversity in G-layers observed . We would like to draw attention to the special case of *Casearia javitensis* (Flacourtiaceae) where the secondary wall is multilayered and gelatinous fibres exhibit some features of compression wood tracheids with round cells and intercellular spaces (Fig. 3 and Fig. 7g in Ruelle et al. in press 2006). Similar observations were made in another Flacourtiaceae (*Laetia procera*) species which displayed very high tension stress in tension wood and a secondary wall with a multi-layered structure. Studies are now in progress to identify the origin of the layered structure in these two Flacourtiaceae.

Efficiency of G-fibres to produce a high tensile stressed wood…

Analysis of the occurrence of G-fibres as a function of the growth strains measured in tension wood (Fig. 4) showed that some species without a G-layer are able to produce higher stress than other species with fibres having a G-layer. Furthermore, the level of stress can be higher in some woods with isolated G-fibres than in some where all fibres are G-fibres. It can thus be concluded that a G-layer is not the only effective mechanism to produce high tensile stress. Tension wood fibres are able to produce high stress with or without the presence of a G-layer.

… in order to produce bending of trees.

The ability of trees to bend themselves depends not only on the high stress in tension wood but to an even greater extent on the difference in stress between the two sides of the stem. From our study, the stresses produced in tension wood reached a maximum towards 3500 µstrain. If trees cannot exceed this value, the only way to increase the bending moment would be to decrease the stress level in the opposite wood. In this respect, *Casearia javitensis* (Flacourtiaceae) is the most efficient tree we studied. This species combines a strong tension stress on the upper side with the presence of fibre with a layered G-layer, and a very low stress in the opposite wood. These results emphasize the need to study both tension wood and opposite wood to increase our understanding of the biomechanical reaction of trees as argued also in Almeras et al. (2005)

CONCLUSIONS

The observation of tension wood in the 21 species we studied indicated that high growth stress levels can be obtained with a wide range of fibre patterns in the tension wood characterized by a very high level of tensile stress.

In some species, the difference in fibre structure is obvious with the presence of a G-layer in the tension wood. In others, the difference between normal wood and high stressed wood is not really clear from observations based on classical anatomy. However, all angiosperms seem to be able to produce highly tensile stressed wood. So the question is if, independently of the occurrence of G-layer, there are anatomical or ultrastructural features that are characteristic of tension wood. This is the aim of the following paper (Ruelle et al. in press 2006).

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 ADEM and French Ministry of Agriculture.

REFERENCES

Almeras, T., A. Thibaut & J. Gril. 2005. Effect of circumferential heterogeneity of wood maturation strain, modulus of elasticity and radial growth on the regulation of stem orientation in trees. Trees 19: 457-467.

Araki, N., M. Fujita, H. Saiki & H. Harada. 1983. Transition of fibre wall structure from normal wood to tension wood in certain species having gelatinous fibres of S_1+G and S_1+S_2+S_3+G types. Mokuzai Gakkaishi 29: 267-273.

Archer, R.R. 1986. Growth stresses and strains in trees. Springer Series in Wood Science. Springer-Verlag, Berlin Heidelberg New-York, 240 pp.

Baillères, H., B. Chanson, M. Fournier, M.T. Tollier & B. Monties. 1995. Structure, composition chimique et retraits de maturation du bois chez les clones d'eucalyptus. Annales des Sciences Forestières 52: 157-172.

Clair, B., J. Gril, K. Baba, B. Thibaut & J. Sugiyama. 2005a. Precautions for the structural analysis of the gelatinous layer in tension wood. IAWA J. 26: 189-196.

Clair, B., J. Ruelle & B. Thibaut. 2003. Relationship between growth stresses, mechano-physical properties and proportion of fibre with gelatinous layer in chestnut (Castanea Sativa Mill.). Holzforschung 57: 189-195.

Clair, B., B. Thibaut & J. Sugiyama. 2005b. On the detachment of gelatinous layer in tension wood fibre. Journal of Wood Science. 51: 218-221.

Combes, J.G., F. Sassus, H. Baillères, B. Chanson & M. Fournier. 1996. Les bois de réaction: relation entre la déformation longitudinale de maturation et les principales caractéristiques physico-mécaniques, anatomiques et chimiques. In: Haluk (Editor), 4ème Colloque Sciences et Industries du Bois. ARBOLOR, Nancy, pp. 75-82.

Côté, W.A.J., A.C. Day & T.E. Timell. 1969. A contribution to the ultrastructure of tension wood fibers. Wood Science and Technology 3: 257-271.

Détienne, P. 1976. Recherche et nature du bois de tension dans quelques arbres tropicaux, Rapport interne Centre Technique Forestier Tropical, Nogent sur marne.

Fisher, J.B. & J.W. Stevenson. 1981. Occurrence of reaction wood in branches of Dicotyledons and its role in tree architecture. Botanical Gazette 142: 82-95.

Fournier, M., H. Baillères & B. Chanson. 1994a. "Tree biomechanics : growth, cumulative pre-stresses and reorientations." Biomimetics **2**: 229-252.

Fournier, M., B. Chanson, B. Thibaut & D. Guitard. 1994b. Mesure des déformations résiduelles de croissance à la surface des arbres, en relation avec leur morphologie. Observation sur différentes espèces. Annales des Sciences Forestières 51: 249-266.

Fujita, M., H. Saiki & H. Harada. 1974. Electron Microscopy of Microtubules and Cellulose Microfibrils in Secondary Wall Formation of Poplar Tension Wood Fibers. Mokuzai Gakkaishi 20: 147-156.

Grzeskowiak, V., F. Sassus & M. Fournier. 1996. Coloration macroscopique, Retraits longitudinaux de maturation et de séchage du bois de tension du Peuplier (*Populus x euramericana cv. I.214*.). Ann. Sci. For. 53: 1083-1097.

Höster, H.R. 1971. Das Vorkommen von reaktionsholz bei tropenhölzern. *Mitt. Bunderforsh*. Aust. Forst. u. Holzw. 82: 225-231.

Höster, H.R. & W. Liese. 1966. Uber das vorkommen vin reaktiongewehe in wurzen und aster des dikotyledonen. Holzforschung 20: 80-90.

Joseleau, J.P., T. Imai, K. Kuroda & K. Ruel. 2004. Detection in situ and characterization of lignin in the G-layer of tension wood fibres of *Populus deltoides*. Planta 219: 338-348.

Kohyama, T. and M. Hotta. 1990. "Significance of allometry in tropical saplings." Functional Ecology 4: 515-521.

Mariaux, A. & A. Vitalis-Brun. 1983. Structure fine du bois de wapa en relation avec les contraintes de croissance. Bois et Forêts des Tropiques 199: 43-57.

Norberg, P.H. & H. Meier. 1966. Physical and chemical properties of the gelatinous layer in tension wood fibre of aspen (*Populus tremula* L). Holzforschung 20: 174-178.

Onaka, F. 1949. Studies on compression and tension wood. Wood research, Bulletin of the Wood research Institute, Kyoto University, Japan 24: 1-88.

Richards, P. W.. 1996. The Tropical Rainforest. Cambridge, Second edition. Cambridge University Press.

Ruelle, J., B. Clair, J. Beauchêne, M.F. Prevost & M. Fournier. in press 2006. Tension wood and opposite wood in 21 tropical rain Forest species. 2. Comparison of some anatomical criteria. IAWA J.

Sassus, F. 1998. Déformations de maturation et propriétés du bois de tension chez le hêtre et le peuplier : mesures et modèles. Ph.D. Thesis, ENGREF, Montpellier.

Trénard, Y. & P. Guéneau. 1975. Relations entre contraintes de croissance longitudinales et bois de tension dans le hêtre (*Fagus sylvatica* L.). Holzforschung 29: 217-223.

Wardrop, A.B. 1964. Reaction anatomy of arborescent angiosperms. In: H. Zimmermann (Editor), The formation of wood in forest tree. Academic Press, New York. London.

Wardrop, A.B. & H.E. Dadswell. 1955. The nature of tension wood. IV - Variation in cell wall organization of tension wood fibres. Aust. J. Bot. 1: 1-16.

Washusen, R., J. Ilic & G. Waugh. 2003. The relationship between longitudinal growth strain and the occurrence of gelatinous fibers in 10 and 11-year-old *Eucalyptus globulus* Labill. Holz als Roh- und Werkstoff 61: 299-303.

Wilson, B. F. and R. R. Archer. 1979. "Tree design : some biological solutions to mechanical problems." Bioscience 29: 293-298.

Yoshida, M., T. Okuda & T. Okuyama. 2000. Tension wood and growth stress induced by artificial inclination in *Liriodendron tulipifera* Linn. and *Prunus spachiana* Kitamura f. *ascendens* Kitamura. Ann. For. Sci. 57: 739-746.

TABLES

Table 1: list of species studied. Tilting angle (degrees). GS: Growth strains (µstrain); T: Tension side (upper side); O: Opposite side.

n°	Family	Species	Tilting angle (°)	GS (µstrain) T	O	Ratio T/O
1	Annonaceae	*Guatteria schomburgkiana* Martius	10	2130	1110	1.9
2	Annonaceae	*Oxandra asbeckii* (Pulle) R.E. Fries	32	1950	310	6.3
3	Apocynaceae	*Lacmellea aculeata* (Ducke) Monachino	10	2580	120	21.5
4	Burceraceae	*Protium opacum* Swart	10	2090	410	5.1
5	Chrysobalanaceae	*Licania membranacea* Sagot	8	3310	1180	2.8
6	Clusiaceae	*Symphonia globulifera* Linnaeus f.	23	2158	584	3.7
7	Flacourtiaceae	*Casearia javitensis* Kunth	18	3350	140	23.9
8	Goupiaceae	*Goupia glabra* J.B. Aublet	8	2350	770	3.0
9	Hugoniaceae	*Hebepetalum humiriifolium* (Planchon) Bentham	10	2890	650	4.4
10	Icacinaceae	*Dendrobangia boliviana* Rusby	7	2210	120	18.4
11	Lauraceae	*Ocotea indirectinervia* C.K. Allen	13	2650	680	3.9
12	Lecythidaceae	*Eschweilera sagotiana* Miers	13	2970	680	4.4
13	Lecythidaceae	*Lecythis poiteaui* O.C. Berg	16	3000	760	3.9
14	Meliaceae	*Trichilia schomburgkii* A.C. De Candolle	4	2780	680	4.1
15	Mimosaceae	*Inga marginata* C.L. Willdenow	16	3010	680	4.4
16	Myrtaceae	*Myrcia decorticans* De Candolle	2	2020	680	2.9
17	Papilonaceae	*Ormosia bolivarensis* (Rudd) Stirton	5	3260	1210	2.7
18	Papilonaceae	*Ormosia coutinhoi* Ducke	7	2780	1400	1.9
19	Rhizophoraceae	*Cassipourea guianensis* J.B. Aublet	10	2740	1220	2.2
20	Sapindaceae	*Cupania scrobiculata* L.C. Richard	19	2710	770	3.5
21	Sapindaceae	*Talisia simaboides* Kramer		3470	1030	3.4

FIGURES

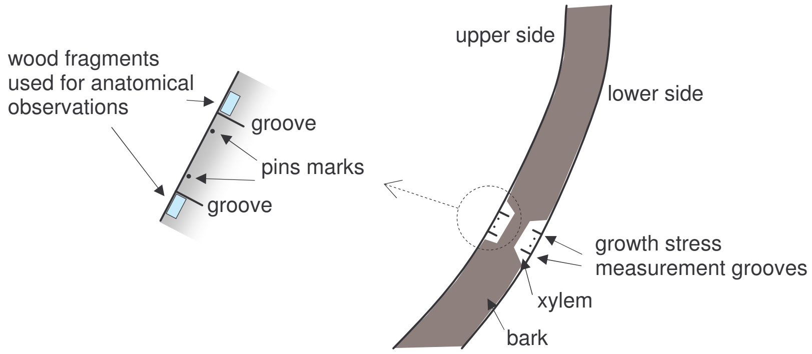

Fig. 1: Schematic drawing of the experimental set up. Right: over-view of the sampling zone on tree. Left: detail on the sampling zone where the wood fragments were extracted for the anatomical observations.

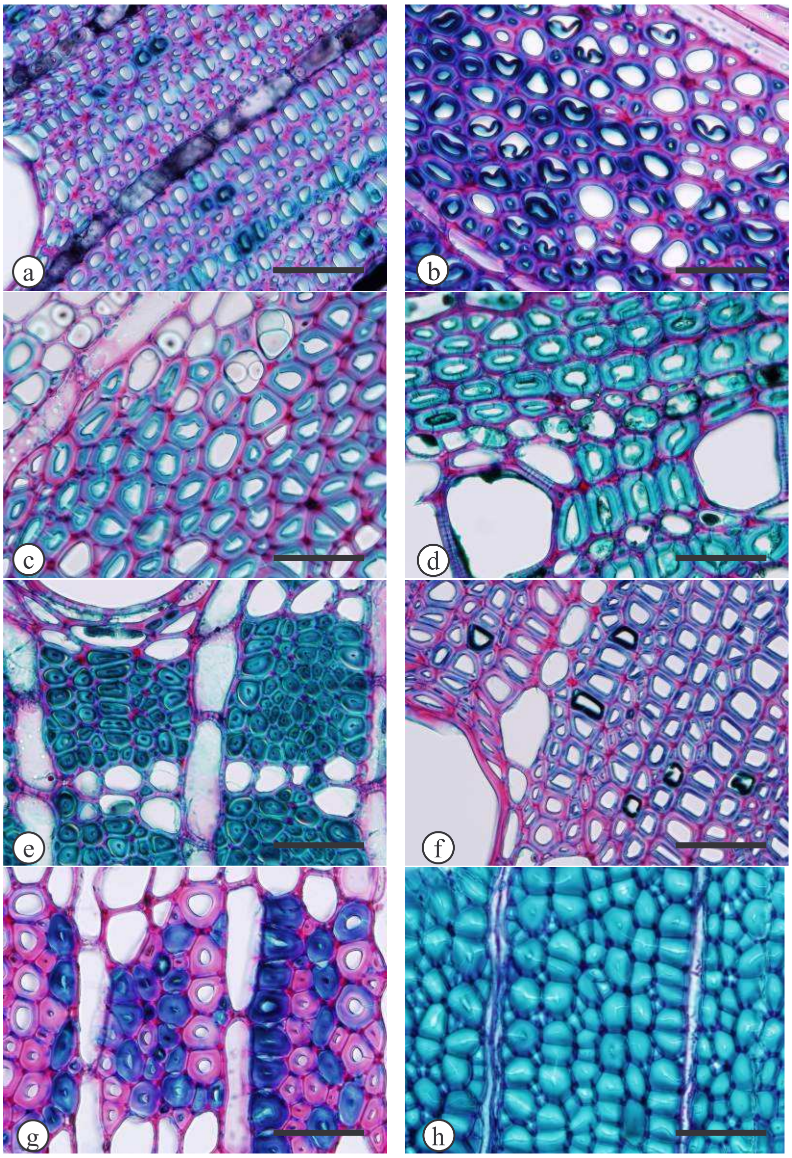

Fig. 2: Detail of fibres with a G-layer in the species containing it. - a: Burseraceae *Protium opacum*; - b: Papilionaceae *Ormosia coutinhoi*; - c: Papilionaceae *Ormosia bolivarensis*; - d: Flacourtiaceae *Casearia javitensis* ; - e: Hugoniaceae *Hebepetalum humiriifolium*; - f: Lauraceae *Ocotea indirectinervia*; - g: Clusiaceae *Symphonia globulifera*; - h: Sapindaceae *Talisia simaboides*. - Staining: Safranin-Fast Green. – Scale bars = 50 µm.

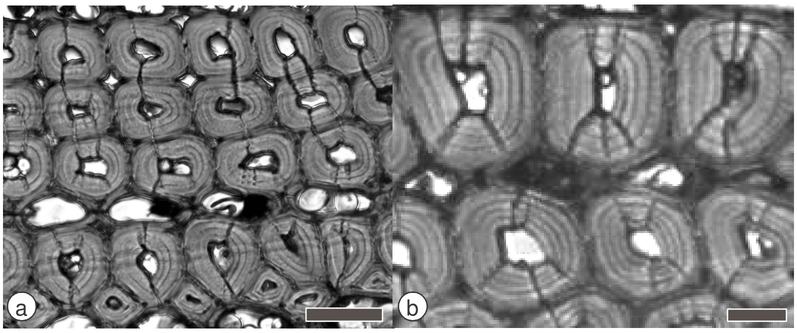

Fig. 3: Tension wood in Casearia javitensis (Flacourtiaceae). (a) Round cells and intercellular spaces. (b) Detail of the multilayered structure of the secondary wall. Scale bars: a = 25 µm; b = 10 µm.

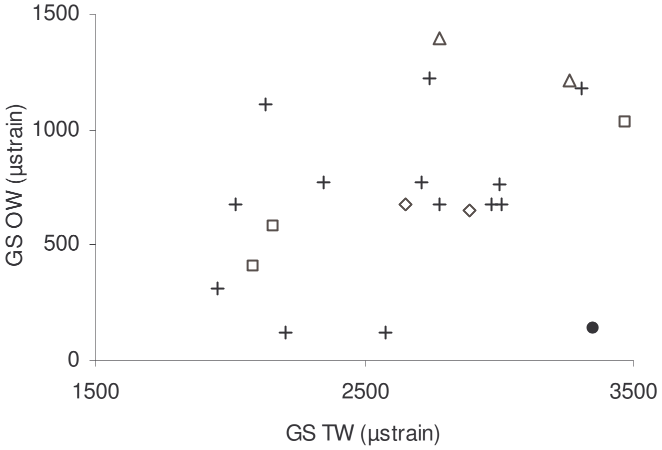

Fig. 4: occurrence and distribution of G-fibres in tension wood with respect to the growth strain in tension wood (GS TW) and opposite wood (GS OW). Cross: without G-fibres; square: all the fibre are G-fibres; triangle: diffuse distribution of groups of G-fibres; diamond shape: isolated and sparse G-fibres; full circle: multilayered secondary wall (*Casearia javitensis*).