TENSION WOOD AND OPPOSITE WOOD IN
21 TROPICAL RAIN FOREST SPECIES
1. Occurrence and efficiency of the G-layer

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

SUMMARY

Wood samples were taken from the upper and lower sides of 21 naturally tilted trees from 18 families of angiosperms in the tropical rain forest 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, tropical rain forest, tension wood, 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 & 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), referred to as tension 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 & Archer 1979; Archer 1986; Fournier *et al.* 1994b). In dense forests such as tropical rain forest understoreys, tree trunk slenderness is extremely high, and associated with a low stiffness and a high buckling and bending risk (Kohyama & Hotta 1990). Thus, in such dense tree communities, the above-mentioned gravitropic reactions (*i.e.* the formation of tension wood) should be of great importance to maintain vertical growth. Moreover, tropical rain forests are characterised 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 the 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%). Fisher and Stevenson (1981), working on tension wood in branches of 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 analyse tension wood in which the growth stresses had been measured to check the presence/absence of the G-layer, and 2) analyse whether the occurrence of a G-layer was associated with 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).

Table 1. List of species studied. Tilting angle (degrees); GS: growth strains (μstrain); T: tension side (upper side); O: opposite side.

| nº	Family	Species	Tilting angle (°)	GS (μstrain)		Ratio T/O
				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	Burseraceae	*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	Papilionaceae	*Ormosia bolivarensis* (Rudd) Stirton	5	3260	1210	2.7
18	Papilionaceae	*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
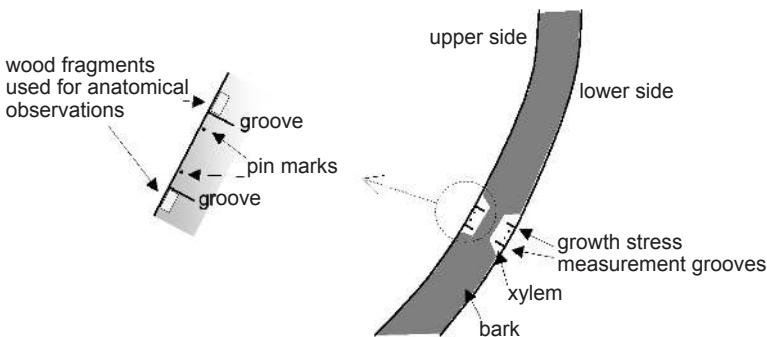
Fig. 1. Diagram of the experimental setup. Right: overview of the sampling from the tree trunk. Left: detail of the sampling zone where the wood fragments were extracted for anatomical observation.

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 § Results: 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*. 1994b). 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 from 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.

The distance between the pins was 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 these 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 unlignified cell walls green. Lignified tissues were red mixed with varying degrees of green while essentially cellulosic cell wall layers, like the gelatinous layer, were green.
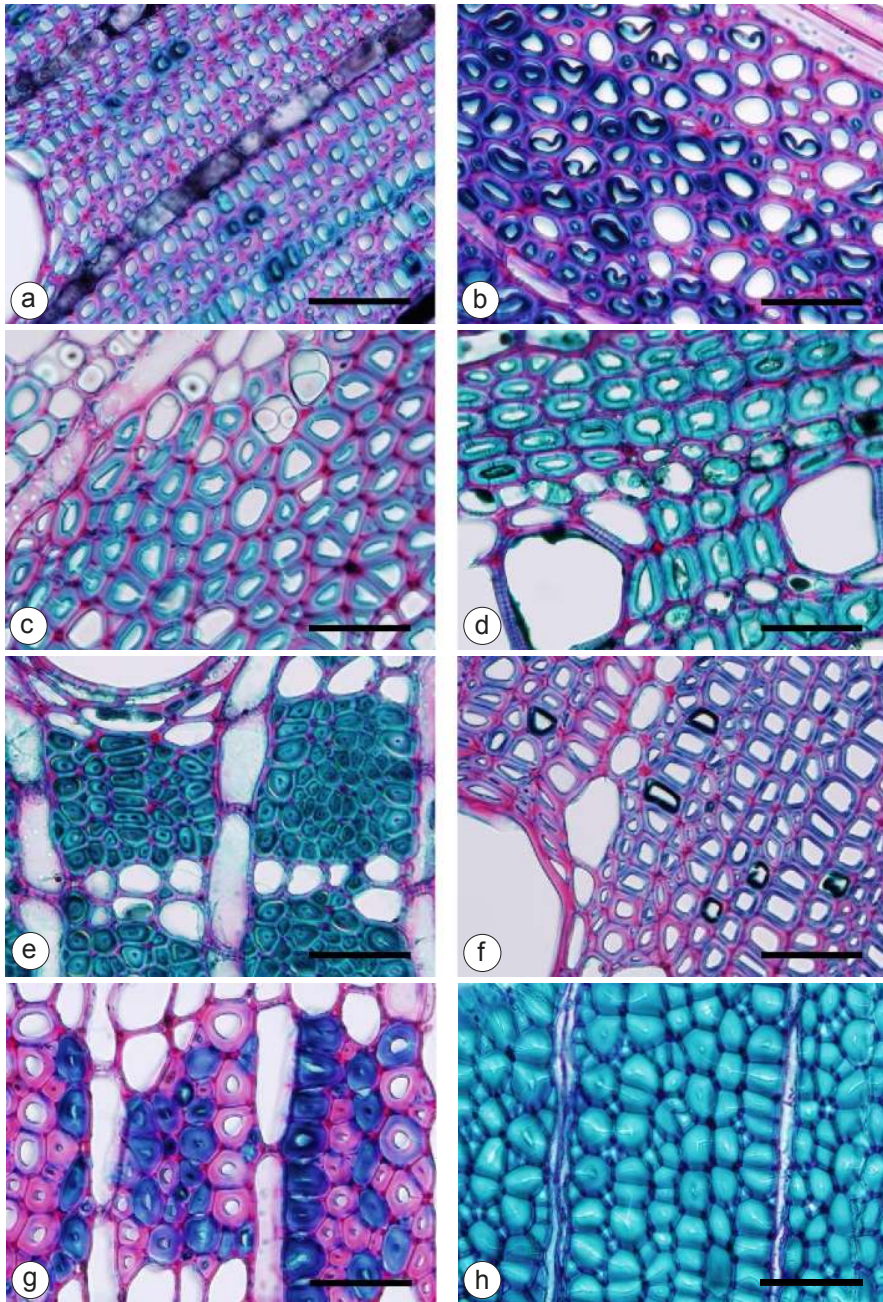
Fig. 2. Detail of fibres with a G-layer in the species containing it. – a: Burseraceae *Protium opacum* – b: Papilionaceae *Ormosia coutinhoi* – c: Papilionaceae *Ormosia bolivarensis* – d: Flacourtiaceae *Casearia javitensis* – e: Hugoniaceae *Hebepetalum humiriifolium* – f: Lauraceae *Ocotea indirectinervia* – g: Clusiaceae *Symphonia globulifera* – h: Sapindaceae *Talisia simaboides*. – Staining: safranin / fast green. — Scale bars = 50 μm.

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 those 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, a large range of variation was observed in tension wood strain values (from 2000 to 3500 µstrain) which probably is due 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

Of the 21 species studied only seven (*Protium opacum* (Burseraceae), *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 and were very obviously green after double staining with safranin / fast green (Fig. 2). This proportion is close to that found in previous studies (Onaka 1949; Fisher & Stevenson 1981). 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 multilayered secondary wall distinctly stained in green in tension wood of *Casearia javitensis*. None of the species studied by Onaka (1949) were included in our sample.

In the seven 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 to 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 tension wood fibres exhibit some features of compression wood tracheids with round cells and intercellular spaces (Fig. 3, and fig. 7g in Ruelle *et al*. 2006). Similar observations were made in another Flacourtiaceae species (*Laetia procera*) which displayed very high tension stress in tension wood and a secondary wall with a multilayered structure. Studies are now in progress to identify the origin of the layered structure in these two Flacourtiaceae.
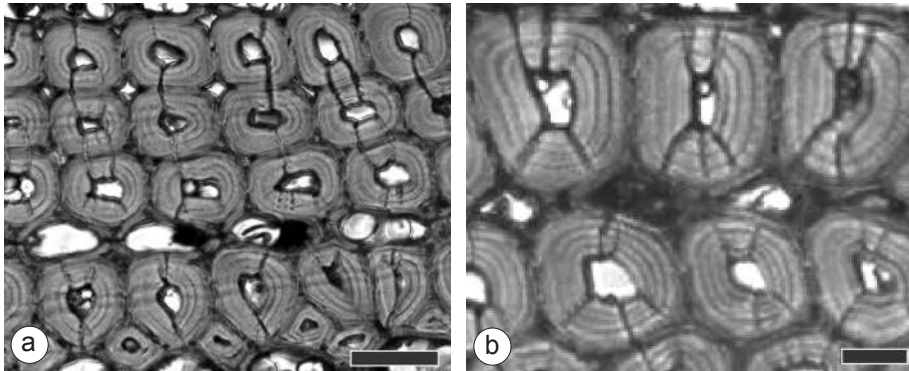
Fig. 3. Tension wood in *Casearia javitensis* (Flacourtiaceae). – a: Round cells and intercellular spaces. – b: Detail of the multilayered structure of the secondary wall. — Scale bars: a = 25 μm; b = 10 μm.

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.
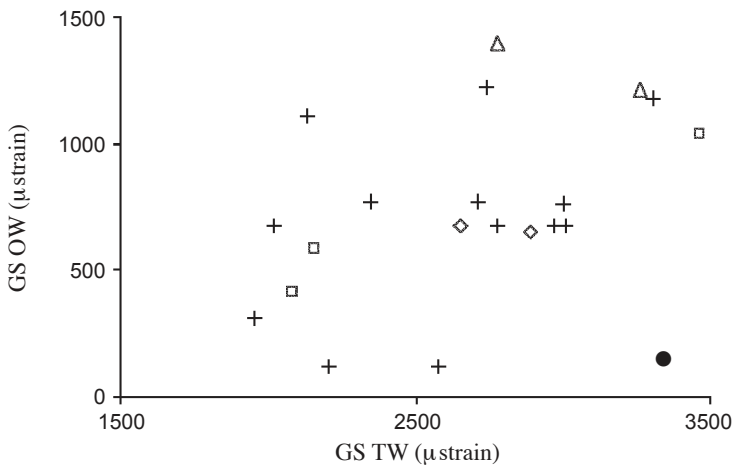

Fig. 4. Occurrence and distribution of G-fibres in tension wood in relation to the growth strain in tension wood (GS TW) and opposite wood (GS OW). +: without G-fibres; □: all the fibres are G-fibres; Δ: diffuse distribution of groups of G-fibres; ◇: isolated and sparse G-fibres; ●: multilayered secondary wall (*Casearia javitensis*).

… 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 fibres with a layered secondary wall, and a very low stress in the opposite wood. These results emphasise 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 characterised 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 the 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*. 2006).

ACKNOWLEDGEMENTS

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.

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. Ann. Sci. For. 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. J. Wood Sci. 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 (ed.), 4ème Colloque Sciences et Industries du Bois: 75–82. ARBOLOR, Nancy.

Côté, W.A.J., A.C. Day & T.E. Timell. 1969. A contribution to the ultrastructure of tension wood fibers. Wood Sci. & Technol. 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. Bot. Gaz. 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. Ann. Sci. For. 51: 249–266.

Fujita, M., H. Saiki & H. Harada. 1974. Electron microscopy of microtubules and cellulose micro-fibrils in secondary wall formation of poplar tension wood fibers. Mokuzai Gakkaishi 20: 147–156.

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

Höster, H.R. 1971. Das Vorkommen von Reaktionsholz bei Tropenhölzern. Mitt. Bundesforsch. Aust. Forst. u. Holzw. 82: 225–231.

Höster, H.R. & W. Liese. 1966. Über das vorkommen von Reaktionsgewebe in Wurzeln und Ästen 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. & 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 con-traintes 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. Ed. 2. Cambridge University Press, Cambridge, UK.

Ruelle, J., B. Clair, J. Beauchêne, M.F. Prevost & M. Fournier. 2006. Tension wood and oppo-site wood in 21 tropical rain forest species. 2. Comparison of some anatomical criteria. IAWA J. 27 (4) [in press].

Sassus, F. 1998. Déformations de maturation et propriétés du bois de tension chez le hêtre et le peuplier: mesures et modèles. PhD 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 (ed.),
     The formation of wood in forest trees. 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 Roh- u. Werkstoff 61: 299–303.
Wilson, B.F. & R.R. Archer. 1979. Tree design: some biological solutions to mechanical prob-
     lems. 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.