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

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

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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,

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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.

| n° | Family | Species | Tilting angle (°) | GS (μstrain) T | GS (μstrain) 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 | 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 |

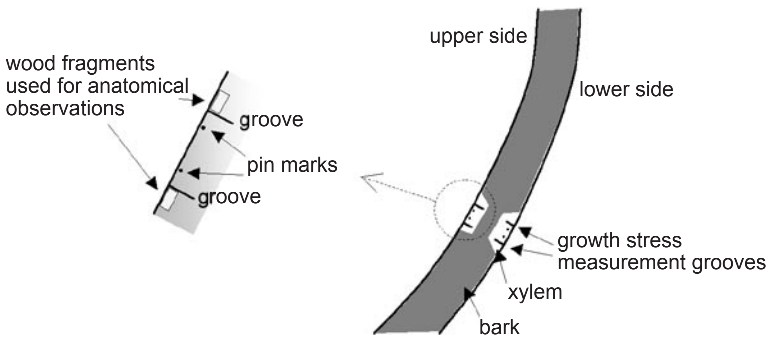


Fig. 1. Diagram of the experimental setup. Right: overview of the sampling from the tree trunk. Left: detail of the sampling zone where the wood fragments were extracted for anatomical observation.

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.* 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 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.

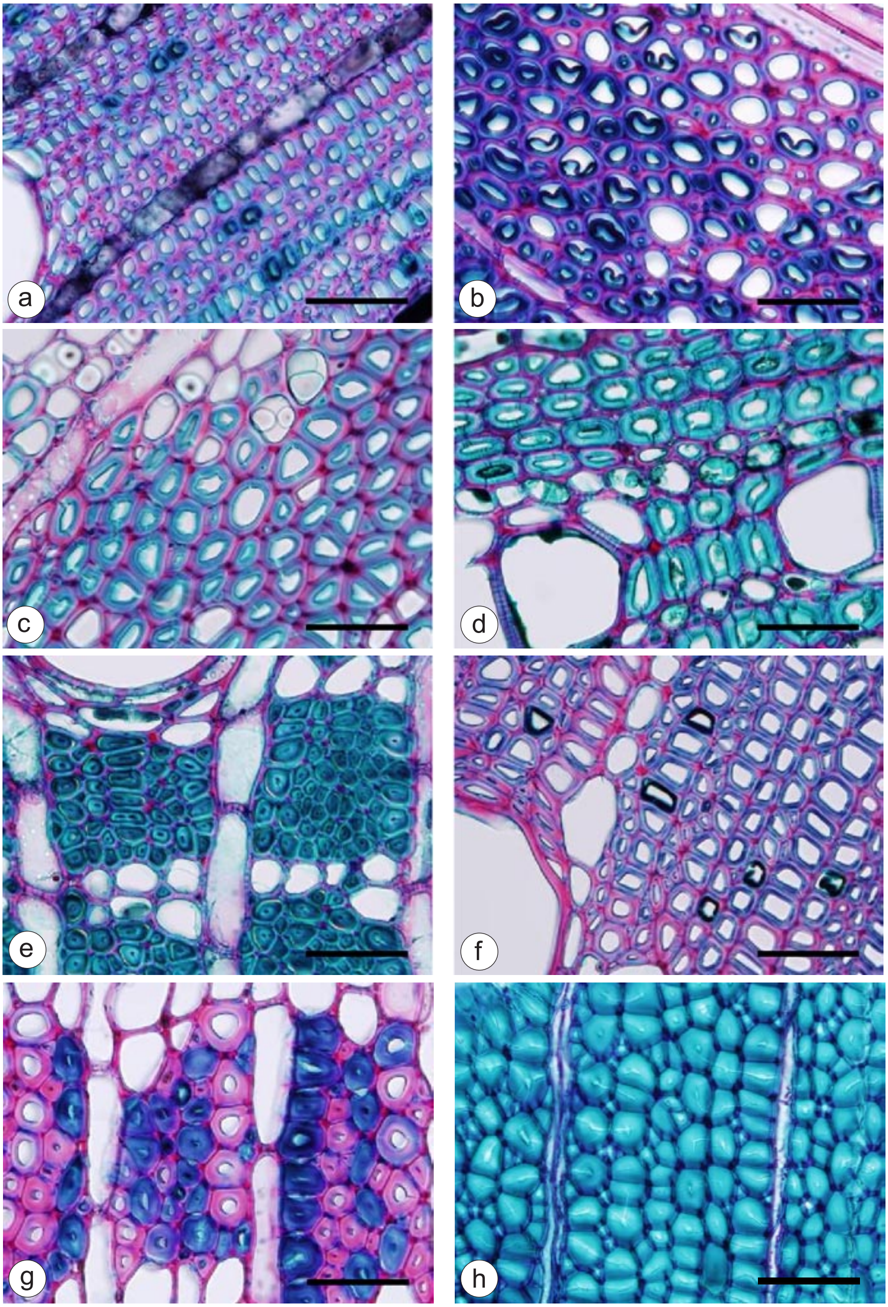


Fig. 2. Detail of fibres with a G-layer in the species containing it. – a: Burseraceae *Protium opacum* – b: Papilionaceae *Ormosia coutinhoi* – c: Papilionaceae *Ormosia bolivarensis* – d: Flacourtiaceae *Casearia javitensis* – e: Hugoniaceae *Hebepetalum humiriifolium* – f: Lauraceae *Ocotea indirectinervia* – g: Clusiaceae *Symphonia globulifera* – h: Sapindaceae *Talisia simaboides*. – Staining: safranin/fast green. — Scale bars = 50 $\mu$m.

## 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 distinct multilayered secondary wall 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.

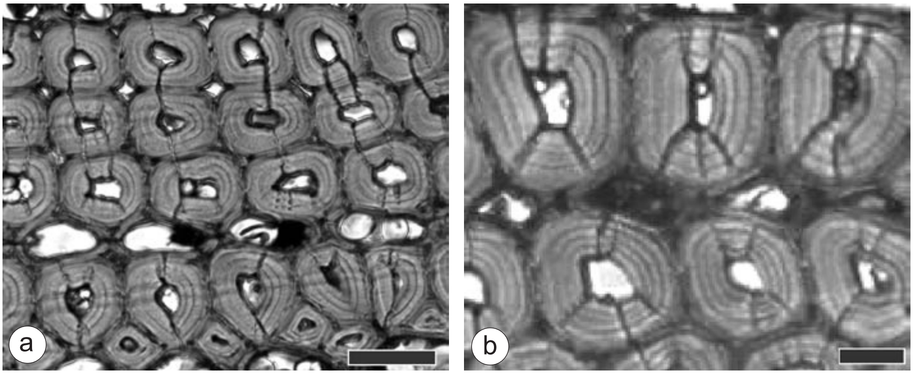


Fig. 3. Tension wood in *Casearia javitensis* (Flacourtiaceae). – a: Round cells and intercellular spaces. – b: Detail of the multilayered structure of the secondary wall. — Scale bars: a = 25 µm; b = 10 µm.

***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.

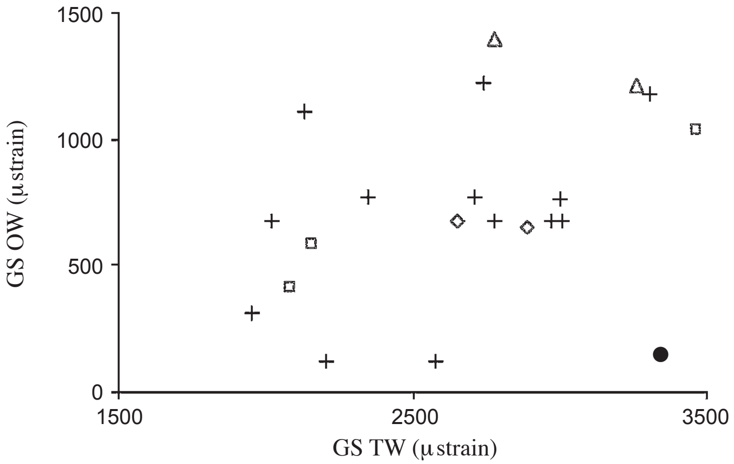


Fig. 4. Occurrence and distribution of G-fibres in tension wood in relation to the growth strain in tension wood (GS TW) and opposite wood (GS OW). +: without G-fibres; □: all the fibres are G-fibres; Δ: diffuse distribution of groups of G-fibres; ◇: isolated and sparse G-fibres; ●: multilayered secondary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

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 the French Ministry of Agriculture.

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