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Diversity in the organisation and lignification of tension wood fibre walls – A review

Barbara Ghislain* and Bruno Clair

CNRS, UMR EcoFoG, AgroParisTech, Cirad, INRA, Université des Antilles,
Université de Guyane, 97310 Kourou, France

*Corresponding author; e-mail: barbara.ghislain@gmail.com

ABSTRACT

Tension wood, a tissue developed by angiosperm trees to actively recover their verticality, has long been defined by the presence of an unlignified cellulosic inner layer in the cell wall of fibres, called the G-layer. Although it was known that some species have no G-layer, the definition was appropriate since it enabled easy detection of tension wood zones using various staining techniques for either cellulose or lignin. For several years now, irrespective of its anatomical structure, tension wood has been defined by its high mechanical internal tensile stress. This definition enables screening of the diversity of cell walls in tension wood fibres. Recent results obtained in tropical species with tension wood with a delay in the lignification of the G-layer opened our eyes to the effective presence of large amounts of lignin in the G-layer of some species. This led us to review older literature mentioning the presence of lignin deposits in the G-layer and give them credit. Advances in the knowledge of tension wood fibres allow us to reconsider some previous classifications of the diversity in the organisation of the fibre walls of the tension wood.

Keywords: Tension wood, fibres, G-layer, $S_1 + S_2 + S_3 + G$, lignification, multi-layered tension wood fibre walls, diversity.

[In the online version of this paper Figure 2 is reproduced in colour.]

INTRODUCTION

Definition of tension wood

Historical definition of tension wood

Trees are fascinating slender structures as they can combine reasonable trunk diameter with impressive height. This performance is possible thanks to the ability of the tree to form pre-stressed material (Archer 1987). This internal stress is the result of a process which occurs during cell maturation and enables control of tree posture (Moullia & Fournier 2009). When the trunk or branches need reorientation, asymmetric stress distribution is induced thanks to a special kind of wood called reaction wood. More precisely, compression wood, which generates compressive stress on the lower part of the tilted stem in gymnosperms, can be distinguished from tension wood, which generates tensile stress on the upper part of the tilted stem in angiosperm trees. This tissue allows the tree to continuously adjust its position to the multiple disturbances that occur throughout its life.

Studies on compression wood were exhaustively summarized by Timell (1986) and recently updated by Gardiner *et al.* (2014a). This most recent book, “The Biology of Reaction Wood” (Gardiner *et al.* 2014a), also dedicated a large section to tension wood in which the structure, function, and properties of tension wood are described in detail from the scale of the tree down to that of macromolecules. Ruelle (2014) reported the structure of tension wood from macroscopic scale to nanometric scales. In this paper we thus focus on the organisation and composition of the tension wood cell wall, with particular attention to its diversity in angiosperms (excepting the few angiosperms which form compression wood), and reinterpret old data in the light of recent results.

Today, tension wood is defined by measuring the mechanical strain resulting from the release of stress around the tree circumference, independently of the anatomy of the wood which is formed (Fournier *et al.* 2014). This mechanical definition finally allows the description of the anatomical diversity of tension wood.

However, in the literature only a few studies included strain measurements on the living tree. Most studies identified tension wood thanks to the tree shape: tilted trees with the trunk recovering verticality or branches where the mechanical effort to maintain branch angle is obvious. Additionally several studies were performed on young trees artificially tilted to ensure the production of tension wood. Unfortunately, we found no literature comparing the tension wood anatomy caused by different mechanical stimuli (artificial or natural) or occurring in trunks or branches. One can however suspect that tension wood cell wall type does not depend on the stimulus, based on the numerous studies on *Populus* sp. where the tension wood cell wall is always reported with a similar structure regardless of the type of stimulus or axis studied.

From an anatomical point of view, tension wood has often been defined by the presence of an internal gelatinous layer in the fibres (IAWA 1964). The so-called gelatinous layer, or G-layer, was discovered in the 19th century by Hartig (after Sanio 1860a cited in Potter 1904). Because of its high cellulose content and its anatomically swollen, detached and jelly-like aspect, the layer was originally called cellulosic layer, mucilaginous layer, cartilaginous layer, or gelatinous layer (Sanio 1860a, 1860b, 1863; Potter 1904; Metzger 1908). Ultimately, gelatinous layer or G-layer became the official name. Its detached and jelly-like aspect was later reported to be a border artefact occurring during sectioning due to the high tensile stress in the G-layer compared to the S₂ layer and the weak transverse stiffness of the G-layer (Clair *et al.* 2005a & b). Unless the wood specimen is embedded in resin and the first 100 µm are trimmed, the detachment and swelling of the G-layer should be observable. Therefore, on 20–50 µm unembedded sections, the G-layer is usually swollen and detached from the other layers. Evidence for the presence of a gel in the G-layer was provided much later thanks to the characterisation of its mesoporous texture, with pores ranging from 2 to 50 nm (Clair *et al.* 2008).

Poplar as a model for studies of tension wood with a G-layer

Although early on it was known that some species lack G-layers (Onaka 1949), most studies were carried out on tension wood with G-layers, but instead of studying the G-layer in different species, the literature converged on poplar as a model tree (the

Appendix illustrates the increasing focus on poplar in tension wood studies). Poplar was chosen for its many advantages: it is a fast-growing species which makes it possible to obtain results rapidly; it is a wood of commercial interest in which tension wood is responsible for wood defects including a woolly surface; tension wood is anatomically easy to locate thanks to its thick G-layer; and more recently it has become possible to choose different well-characterised genotypes thanks to the description of the poplar genome (Pilate *et al.* 2004b; Tuskan *et al.* 2004).

The G-layer is an internal layer in the cell wall of fibres, which replaces the S₃ and part of the S₂ layer in poplar (Wardrop & Dadswell 1955). It was historically described to be mostly, or even only, composed of cellulose. More recently, several authors demonstrated the presence of other polysaccharides and proteins (Lafarguette *et al.* 2004; Andersson-Gunnerås *et al.* 2006; Nishikubo *et al.* 2007; Bowling & Vaughn 2008, whose study was on *Celtis* and *Liquidambar*; Kim & Daniel 2012). The cellulose microfibrils of the G-layer are highly crystalline and are almost aligned with the axis of the fibre (Fujita *et al.* 1974; Chaffey 2000; Daniel *et al.* 2006). In the process of G-layer deposition during cell wall maturation, a strong tensile stress occurs in its cellulose microfibrils (Clair *et al.* 2011) associated with the swelling of the mesopores (Chang *et al.* 2015). And indeed, the thicker the G-layer, the greater the maturation stress (Fang *et al.* 2007).

The absence of lignin in the G-layer of poplar tension wood has been demonstrated in several studies (Norberg & Meier 1966; Pilate *et al.* 2004a; Yoshinaga *et al.* 2012), whereas other studies reported the presence of lignin (see below). However, the most frequently cited paper providing evidence for lignin (Joseleau *et al.* 2004) only qualifies its presence as ‘traces’. As a result, the lack of lignification has become a strong criterion to define the G-layer of poplar. As this species has been extensively studied, the criterion is used by extension to define tension wood in many other hardwood species. Tension wood thereby became easy to locate thanks to different types of staining which made it possible to distinguish the cellulose G-layer from the other lignified layers. As lignification does not occur in the G-layer, when tension wood did show slight lignin staining, the sample was often discarded (Gartner *et al.* 2003). At that time, stains such as safranin/alcian blue were considered to be insufficiently specific and the traces of safranin in the G-layer were often considered as a staining problem. Indeed, observations with UV light (which highlighted the lignin in unstained samples thanks to their auto-fluorescence) or the use of Wiesner or Mäule tests are known to be more specific. However, comparison of safranin/alcian blue with observations using UV light demonstrated the reliability of such double staining (Roussel & Clair 2015; personal observations) as long as the sample is sapwood and does not contain heartwood extractives. Therefore, in a number of observations reported in the literature, safranin staining of the G-layer may not have been a staining problem but, in contrast, may have revealed traces of lignin in the G-layer.

It should be noted that G-layer fibres can also be found in straight trees, scarcely dispersed, or as tangential bands around the circumference of the trunk (Badia *et al.* 2006). These observations reveal that short reactions were needed to maintain the tree upright. The few G-fibres on one side enabled vertical recovery at the time of their

development. Then, later in tree growth, an imbalance in another direction made it necessary to produce G-fibres on the other side of the stem, etc.

Different organisation of the cell wall layers in gelatinous fibres

Three types of organisation of the cell wall of G-fibres were proposed by Wardrop and Dadswell (1955): 1) S_1+S_2+G ; 2) S_1+G ; and 3) $S_1+S_2+S_3+G$. They found that tension wood of *Eucalyptus gigantea* had S_1+S_2+G in latewood and S_1+G in earlywood. S_1+S_2+G is the most common type and occurs in 10 out of the 12 species studied by Saiki and Ono (1971). Only *Cercidiphyllum japonicum* presented two types, S_1+G and S_1+S_2+G , in the same portion of tension wood. The third type is quite rare. The only reports we found in the literature were by Wardrop and Dadswell (1955), Saiki and Ono (1971) and Araki *et al.* (1983). Unfortunately, in the first paper, Wardrop and Dadswell (1955) did not mention the position of the sampling, *i.e.* they did not specify if sampling was done during the process of maturation or in a transition zone between normal wood and tension wood. Furthermore, it cannot be checked, since the observation was made on an unidentified Flacourtiaceae (currently split into two families Achariaceae and Salicaceae *sensu lato*) and, as we now know, many Flacourtiaceae newly classified as Salicaceae *sensu lato* are able to form multi-layered fibre walls in their tension wood (Ghislain *et al.* 2016). The illustration of Wardrop and Dadswell (1955) does not allow us to confirm the presence of an S_3 layer or a multi-layered G-layer, since Ruelle *et al.* (2007c) described the thin lignified layers in multi-layered tension wood as similar to the S_3 layer. Saiki and Ono (1971) also mentioned the third type of organisation ($S_1+S_2+S_3+G$) in thin sections of resin-embedded samples of *Celtis sinensis* for which methacrylate was removed before Pt-Pd shadowing, but were unable to confirm it in thin sections of Epon-embedded samples stained with potassium permanganate. Finally, Araki *et al.* (1983) also found the third type, but only in the transition zone between normal wood and tension wood. This is in agreement with the results of Abedini *et al.* (2015) on poplar, in which the authors reported the establishment of a G-layer on an S_2 layer formed before the tilting of the tree. It could therefore be hypothesised that in the study by Araki *et al.* (1983) the S_3 layer was formed just before tilting and the formation of a G-layer, thus explaining the presence of the organisation $S_1+S_2+S_3+G$ in the transition zone only.

It would thus seem that the type $S_1+S_2+S_3+G$, can only be observed in the transition zone from normal wood to tension wood, and that only two types of cell wall organisation can occur in tension wood: S_1+S_2+G and S_1+G . Further investigations are required to clarify this issue.

Tension wood classified as with or without a G-layer

Onaka (1949) was the first to carry out a large study on both compression and tension wood and investigated the latter in 219 species belonging to 84 genera of dicotyledons. His classification, although very interesting, is sometimes a little confusing due to the use of the growth eccentricity as a criterion for classification (Fig. 1).

At first, when an eccentricity was present on the upper side, it was classified as being present either both in the wood and in the bark or only in the wood, even if the

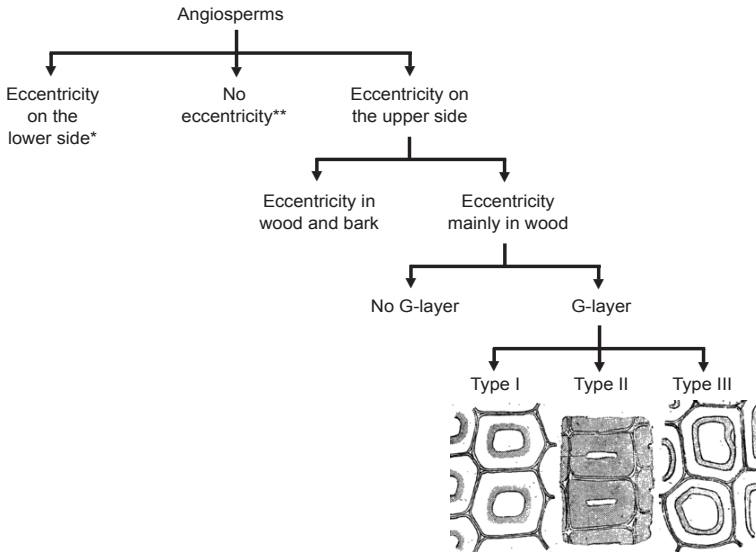


Figure 1. Schematic diagram of the classification proposed by Onaka (1949). *: Class containing only *Gardenia* and *Buxus*. **: Class represented by shrubs or vines and two trees, *Paulownia tomentosa* and *Catalpa ovata*. Pictures of the cells are the original drawings by Onaka (1949), the unignified G-layers are in gray.

bark developed more on the upper side. The author then divided the latter according to the presence or absence of the G-layer. Finally, when the G-layer was present, the author defined three types (I, II and III). These three types are not easily distinguishable but Wardrop and Dadswell (1955) presumed the types corresponded to the S_1+G , S_1+S_2+G and $S_1+S_2+S_3+G$ types.

Type II looks like the S_1+G type and both Onaka (1949) and Saiki and Ono (1971) confirmed that *Cercidiphyllaceae* belonged to this type. Type III is similar to the S_1+S_2+G type which is the most common type. Onaka (1949) cites among other families the *Salicaceae* (at that time only including the genera *Salix* and *Populus*). However, type I cannot correspond to the $S_1+S_2+S_3+G$ type. Onaka (1949) described “a lessening of the degree of lignification towards the center, and a gradual change to the gelatinous layer.”

Several species have been classified in the three classes of eccentricity, or in two types of G-layers. In most cases, eccentricity is an efficient way to detect the formation of tension wood. However, a tree forming tension wood specifically on one side of the stem does not systematically show clear eccentricity, as is the case in *Castanea sativa* (fig. 9.1 in Gardiner *et al.* 2014b) or *Bagassa guianensis* (Bossu 2015). Furthermore, tension wood serves the biological function of controlling tree posture and may consequently be found in several parts of the trunk depending on the past history of the tree and the need to reorient the tree axis. Using eccentricity to predict tension wood is thus less easy, which is why eccentricity should be used with caution when classifying tension wood.

After Onaka (1949) the diversity of tension wood was classified more simply, as either forming G-layers or lacking them, which facilitated the comparison of different studies. Höster and Liese (1966) surveyed the branches of 110 tropical and temperate tree species, and found 75% had G-layers in their tension wood, compared to 35% for shrubs. In tilted branches or young axes, only 46% of the 122 species studied by Fisher and Stevenson (1981) presented tension wood with G-layers. Among buttresses and aerial roots of 48 tropical species, however, only 10% had distinct G-layers (Fisher 1982). No G-layer was found in nine Japanese shrub species (Sultana *et al.* 2010). However, do shrubs, branches, buttresses and aerial roots produce high tensile stresses? Preliminary studies suggest that tensile stress in buttresses correspond to those in normal wood (fig. 5.6 in Fournier *et al.* 2014). Finally, in a study on 21 tropical species from 18 families, 38% were shown to have a G-layer in their tension wood despite the higher growth stresses recorded on the tension wood side of all the trees considered (Clair *et al.* 2006). Thus, although tension wood with a G-layer has been more widely studied, it is much less common than tension wood without a G-layer.

Unusual observations of tension wood reported in the literature

Figure 2 gives a schematic representation of the anatomy of tension wood fibres described or deduced from the literature. All the observations presented in the text are summarized in Table 1.

Simarouba amara: from lacking a G-layer to having a G-layer with late lignification

The tension wood of several species without a G-layer has been characterised thanks to measurements of growth stress combined with anatomical observations. Amongst

(text continued on page 254)

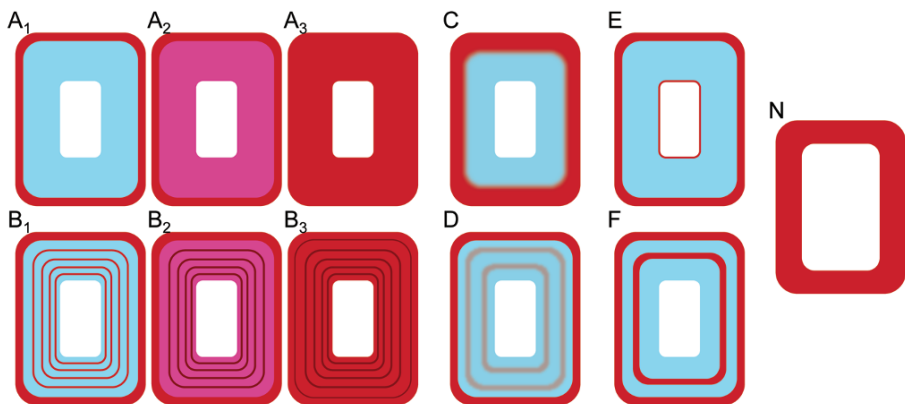


Figure 2. Schematic representation of the anatomy of tension wood fibres presenting S and G-layer (S₁ layer and S₂ layer - if any - are presented as a single layer) (A–F), compared to a normal wood fibre (N). – A₁–A₃: Unlignified to highly lignified G-layer. – B₁–B₃: Unlignified to highly lignified multi-layered G-layer. – C: Progressive decrease in lignin content from the S₁ or the S₂ layer to the G-layer. – D: Concentric lignin deposition in the G-layer. – E: Inner thin lignified ring in the G-layer. – F: Thick lignified ring inside the G-layer. – N: Normal wood fibre, including S₁, S₂, S₃.

Table 1. Summary of the tension wood type, sampling location, tilting condition and occurrence of stress measurement in the cited literature.

Axes: T = trunk, B = branch, Bu = buttress, Bo = board, HW = heartwood. – **Tilting condition:** A = artificially tilted, N = naturally tilted, S = straight tree, NM = tension wood not mentioned. – **Stress meas.:** Y indicates a study where measurements of maturation stress were performed. – **Classif. Fig. 2:** Tension wood type (A–F) is given according to the classification pictured in Figure 2; H = tension wood without G-layer. Letters in parentheses refer to less common types. Question marks indicate uncertain classification. – **References** *: additional observations to the cited study.

Family	Species	Axes	Tilting condition	Stress meas.	Classif. Fig. 2	References
Altingiaceae	<i>Liquidambar styraciflua</i>	T	N		A ₁	Bowling & Vaughn 2008
Annonaceae	<i>Annona</i>	B, T	N, S		H?	Fisher & Stevenson 1981
Annonaceae	<i>Annona</i>				H	Onaka 1949
Betulaceae	<i>Alnus pendula</i>	T	A		C	Araki <i>et al.</i> 1983
Bignoniaceae	<i>Catalpa</i>	B, T	N, S		H?	Fisher & Stevenson 1981
Cannabaceae	<i>Celtis sinensis</i>	T	N		A ₁	Bowling & Vaughn 2008
Cannabaceae	<i>Celtis sinensis</i>	B, T	N		A ₁	Saiki & Ono 1971
Casuarinaceae	<i>Casuarina equisetifolia</i>				F?	Sanio 1863
Cercidiphyllaceae	<i>Cercidiphyllum japonicum</i>	T	A		A (C)	Araki <i>et al.</i> 1983
Cercidiphyllaceae	<i>Cercidiphyllum japonicum</i>	B, T	N		A (C)	Saiki & Ono 1971
Cornaceae	<i>Cornus controversa</i>	T	A		A (C)	Araki <i>et al.</i> 1983
Daphnaceae	<i>Daphne odora</i>				H	Onaka 1949
Euphorbiaceae	<i>Hevea brasiliensis</i>	T			A & B	Encinas & Daniel 1997
Euphorbiaceae	<i>Hevea brasiliensis</i>	T	N		B	Sujan <i>et al.</i> 2015
Euphorbiaceae	<i>Mallotus japonicus</i>	T	A		B	Nakagawa <i>et al.</i> 2012
Fabaceae	<i>Caragana korshinskii</i>	T	S		A ₁ , A ₂ , A ₃	Furukawa & Ohashi 1999
Fabaceae	<i>Carmichaelia arborea</i>				B	Butterfield & Meylan 1980
Fabaceae	<i>Hedysarum scoparium</i>	T	S		A ₁ , A ₂ , A ₃	Furukawa & Ohashi 1999
Fabaceae	<i>Inga marginata</i>	T	N	Y	A ₁ & A ₃	Clair <i>et al.</i> 2006
Fabaceae	<i>Inga marginata</i>	T	N	Y	A ₁ & A ₃	Ruelle <i>et al.</i> 2006
Fabaceae	<i>Koompassia malaccensis</i>	T, HW			B	Schmitt <i>et al.</i> 1995
Fabaceae	<i>Koompassia malaccensis</i>	Bo, HW	NM		B	Singh <i>et al.</i> 2004
Fabaceae	<i>Robinia pseudoacacia</i>	T	A		A ₁ (B ₁ or D)	Araki <i>et al.</i> 1982
Fabaceae	<i>Robinia pseudoacacia</i>	T	A		E	Araki <i>et al.</i> 1982
Fabaceae	<i>Robinia pseudoacacia</i>	B, T	N		A ₁ (F)	Saiki & Ono 1971
Fagaceae	<i>Fagus crenata</i>	B, T	N		E	Saiki & Ono 1971

→

Table 1 continued)

Family	Species	Axes	Tilting condition	Stress meas.	Classif. Fig. 2	References
Fagaceae	<i>Fagus sylvatica</i>				B ?	Wardrop & Dadswell 1955
Fagaceae	<i>Fagus sylvatica</i>				A (B ?)	Wardrop 1964
Fagaceae	<i>Fagus sylvatica</i>	T	N		A1 & E	Lehringer <i>et al.</i> 2009
Fagaceae	<i>Fagus sylvatica</i>	T	N		A1 (A2 & A3)	Schwarze & Fink 1998
Fagaceae	<i>Quercus ilex</i>	T	A		A1 & A2	Gartner <i>et al.</i> 2003
Fagaceae	<i>Quercus lyrata</i>	Bo			A & E	Wahlgren 1957
Fagaceae	<i>Quercus robur</i>	B, T			D	Casperson 1967
Fagaceae	<i>Quercus robur</i>	B			E	Lehringer <i>et al.</i> 2008
Fagaceae	<i>Quercus robur</i>	B			D	Lehringer <i>et al.</i> 2009
Irvingiaceae	<i>Irvingia</i>	Bu			A3 ?	Fisher 1982
Lauraceae	<i>Ocotea indirectinervia</i>	T	N	Y	A1 & A3	Ruelle <i>et al.</i> 2006
Lauraceae	<i>Sextonia rubra</i>	T	N	Y	A1 (B1)	Chang <i>et al.</i> 2009*
Lauraceae	<i>Sextonia rubra</i>	Bo			A1 (F)	Jutte 1956
Lecythidaceae	<i>Eschweilera sagotiana</i>	T	N	Y	A3	Clair <i>et al.</i> 2006
Lecythidaceae	<i>Eschweilera sagotiana</i>	T	N	Y	A3	Ruelle <i>et al.</i> 2006
Lecythidaceae	<i>Eschweilera</i> sp.	Bu			A1 & A3	Fisher 1982
Magnoliaceae	<i>Liriodendron tulipifera</i>	T	A		A3 ?	Hiraiwa <i>et al.</i> 2014
Magnoliaceae	<i>Liriodendron tulipifera</i>	T		Y	A3 ?	Okuyama <i>et al.</i> 1994
Magnoliaceae	<i>Liriodendron tulipifera</i>	T	N	Y	A3 ?	Yoshida <i>et al.</i> 2002
Magnoliaceae	<i>Magnolia kobus</i>	B			A3 ?	Yoshizawa <i>et al.</i> 2000
Magnoliaceae	<i>Magnolia obovata</i>	T	A		A3 ?	Yoshizawa <i>et al.</i> 2000
Magnoliaceae	<i>Magnolia verecunda</i> , <i>Michelia compressa</i>				H ?	Onaka 1949
Malvaceae	<i>Apeiba</i> , <i>Heliocarpus</i> , <i>Tilia</i>	B, T	N, S		H	Fisher & Stevenson 1981
Malvaceae	<i>Entelea arborescens</i>				H	Patel 1988
Malvaceae	<i>Lagunaria patersonii</i>	T	A		H	Bland & Scurfield 1964
Malvaceae	<i>Lagunaria patersonii</i>				H	Scurfield 1973
Malvaceae	<i>Ochroma</i> , <i>Durio zibethinus</i>	B, T	N, S		H ?	Fisher & Stevenson 1981
Malvaceae	<i>Tilia cordata</i>	B	N		H	Böhlmann 1971
Malvaceae	<i>Tilia</i> , <i>Hibiscus syriacus</i> , <i>Firmania platanifolia</i>				H	Onaka 1949
Myrtaceae	<i>Eucalyptus andreaana</i>	T	S	Y	A1, A2, A3	Hirohashi <i>et al.</i> 2012
Myrtaceae	<i>Eucalyptus bicostata</i>	T	A		A (B or D)	Scurfield 1972
Myrtaceae	<i>Eucalyptus camaldulensis</i>	T	A		A (B or D)	Bland & Scurfield 1964
Myrtaceae	<i>Eucalyptus elaeophora</i>				E	Wardrop 1964
Myrtaceae	<i>Eucalyptus maidenii</i>	T	S	Y	A1, A2, A3	Hirohashi <i>et al.</i> 2012
Myrtaceae	<i>Eucalyptus nitens</i>	T	N, S	Y	A1, A2, A3	Clair <i>et al.</i> 2013*
Myrtaceae	<i>Eucalyptus regnans</i>	T	S	Y	A3 ?	Chafe 1977



(Table 1 continued)

Family	Species	Axes	Tilting condition	Stress meas.	Classif. Fig. 2	References
Myrtaceae	<i>Eucalyptus smithii</i>	T	S	Y	A1, A2, A3	Hirohashi <i>et al.</i> 2012
Myrtaceae	<i>Eucalyptus</i> sp.	T	A		A1 & A2?	Scurfield & Wardrop 1963
Myrtaceae	<i>Lophostemon confertus</i>	T	A		B ?	Scurfield & Wardrop 1963
Myrtaceae	<i>Lophostemon confertus</i>	T			B ?	Scurfield 1973
Myrtaceae	<i>Lophostemon confertus</i>				B ?	Wardrop 1964
Oleaceae	<i>Fraxinus sieboldiana</i>	B, T	N		A (C)	Saiki & Ono 1971
Oleaceae	<i>Osmanthus fragrans</i>	T	A		A3 ?	Hiraiwa <i>et al.</i> 2007
Oxalidaceae	<i>Averrhoa</i>	B, T	N, S		H	Fisher & Stevenson 1981
Proteaceae	<i>Grevillea robusta</i>	T	A		B ?	Scurfield & Wardrop 1963
Proteaceae	<i>Grevillea robusta</i>	T			B ?	Scurfield 1973
Proteaceae	<i>Grevillea robusta</i>				B ?	Wardrop 1964
Proteaceae	<i>Hakea laurina</i>	T	A		A1 & A2?	Scurfield & Wardrop 1963
Salicaceae	<i>Casearia javitensis</i>	T	N	Y	B	Clair <i>et al.</i> 2006
Salicaceae	<i>Homalium foetidum</i>		NM		B	Bailey & Kerr 1935
Salicaceae	<i>Homalium luzoniense</i>	Bo	NM		B	Daniel & Nilsson 1996
Salicaceae	<i>Laetia procera</i>	T	N	Y	B1 & B2	Ruelle <i>et al.</i> 2007c
Salicaceae	<i>Olmediella betschleriana</i>	Bo	NM		B	Daniel & Nilsson 1996
Salicaceae	<i>Populus × euramericana</i>	T	N, S		A1	Badia <i>et al.</i> 2006
Salicaceae	<i>Populus deltoides</i>	T			A1 ?	Joseleau <i>et al.</i> 2004
Salicaceae	<i>Populus deltoides × nigra</i>	T	N		A1	Chang <i>et al.</i> 2015
Salicaceae	<i>Populus deltoides × nigra</i>	T	A		A1	Yoshinaga <i>et al.</i> 2012
Salicaceae	<i>Populus euramericana</i>	T	A		A1	Fujita <i>et al.</i> 1974
Salicaceae	<i>Populus I4551</i>	T	N	Y	A1	Fang <i>et al.</i> 2007
Salicaceae	<i>Populus nigra × deltoides</i>	T	A		E	Gierlinger & Schwanniger 2006
Salicaceae	<i>Populus</i> sp.				A1	Pilate <i>et al.</i> 2004
Salicaceae	<i>Populus tremula</i>	T	N		A1	Kim & Daniel 2012
Salicaceae	<i>Populus tremula</i>	T	N		A1	Norberg & Meier 1966
Salicaceae	<i>Populus tremula, P. alba</i>	B, T	N		A1	Nishikubo <i>et al.</i> 2007
Salicaceae	<i>Populus tremula × alba</i>	T	A		A	Lafarguette <i>et al.</i> 2004
Salicaceae	<i>Populus tremula × tremuloides</i>	T	N		A1	Chaffey 2000
Salicaceae	<i>Populus tremula × tremuloides</i>	T	N		A1	Daniel <i>et al.</i> 2006
Salicaceae	<i>Populus tremula × tremuloides</i>	T	A		A1	Nishikubo <i>et al.</i> 2007



(Table 1 continued)

Family	Species	Axes	Tilting condition	Stress meas.	Classif. Fig. 2	References
Salicaceae	<i>Populus tremula</i> × <i>tremuloides</i> , <i>Populus tremula</i>	T	A		A1	Andersson-Gunnerås <i>et al.</i> 2006
Salicaceae	<i>Salix lucida</i>	B, T	N		A1, A2 & A3	Ghislain <i>et al.</i> 2016
Sapindaceae	<i>Acer</i>	Bo			A1, B1 & E	Lehringer <i>et al.</i> 2009
Sapindaceae	<i>Acer</i>	T	S		A (B?)	Morey & Cronshaw 1968
Sapindaceae	<i>Aesculus hippocastanum</i>				D	Casperson 1961
Simaroubaceae	<i>Simarouba amara</i>	T	A, N		A3	Roussel & Clair 2015
Siparunaceae	<i>Siparuna bifida</i>		NM		D	Bailey & Kerr 1935
Tetrameristaceae	<i>Tetramerista glabra</i>		NM		D	Bailey & Kerr 1935
Thymelaceae	<i>Wikstroemia trichotoma</i> , <i>Edgeworthia papyrifera</i>				H	Onaka 1949
Trochodendraceae	<i>Trochodendron aralioides</i>	T	A		A1 & B1	Hiraiwa <i>et al.</i> 2013

these species, *Simarouba amara* has been extensively studied (Ruelle 2006; Ruelle *et al.* 2007a, 2007b, 2011). Strong tensile stress was recorded on the upper side of leaning trunks, but neither the development of G-layers, nor a difference in cell wall thickness was observed. The angle of the microfibrils of cellulose and the size of cellulose aggregates were the only parameters which differed between opposite wood and tension wood (Ruelle *et al.* 2007b).

However, Roussel and Clair (2015) recently demonstrated that in *Simarouba amara* tension wood, a G-layer is visible during cell wall maturation, and that it becomes lignified at a later stage than in normal wood. The G-layer starts its lignification after more than 60 days of tilting in saplings. These authors also documented other species with similar patterns. This means that the usual unlignified nature of the G-layer may be masked by late deposition of lignin, and that the usual staining no longer identifies tension wood fibres. Therefore, to assess the occurrence of a G-layer in tension wood, one needs to look at the maturation process. The tension wood of *Simarouba amara*, thought to be without a G-layer, is now known to develop a G-layer, which later becomes lignified (Fig. 2A).

***Laetia procera*: multi-layered G-layers**

A peculiar multi-layered fibre structure has been described in the xylem fibres of Salicaceae *sensu lato*: *Homalium foetidum*, *H. luzoniense* and *Olmediella betschleriana* (Bailey & Kerr 1935; Daniel & Nilsson 1996). A similar multi-layered structure with an “S₂” composed of two to five thick and thin layers were observed in the fibre walls in a heartwood sample of a member of the Fabaceae, *Koompassia malaccensis* (Schmitt *et al.* 1995; Singh *et al.* 2004). This multi-layered structure was later linked to the occurrence of tension wood in *Casearia javitensis* and *Laetia procera* thanks to measurements of maturation strain (Clair *et al.* 2006; Ruelle *et al.* 2007c). These multi-layered fibres occur in the tension wood of most of the former Flacourtiaceae

now classified as Salicaceae *sensu lato* (Ghislain *et al.* 2016). They not only occur in tension wood but have also been reported in reaction phloem fibres (Nanko *et al.* 1982; Nakagawa *et al.* 2012, 2014). The fibre cell wall is composed of thick layers with a low cellulose microfibril angle separated by thin lignified layers. This peculiar tension wood has been reported in *Carmichaelia arborea* (Fabaceae) (Butterfield & Meylan 1980), *Hevea brasiliensis* (Euphorbiaceae) (Encinas & Daniel 1997) and *Mallotus japonicus* (Euphorbiaceae) (Nakagawa *et al.* 2012).

Early reports of lignin deposition in the G-layer: what do we know?

Even though the presence of lignin in the G-layer has long been rejected in the literature, its occurrence has nevertheless been suggested several times. Bailey and Kerr (1935) already described lignin deposition in the G-layer, even if this layer was not yet related to tension wood. Jutte (1956) discussed the definition of G-layers as being unlignified. Casperson (1967) described lignin deposition in G-layers of tension wood.

We reviewed all the reports of lignin in G-layers. It is always important to consider the sampling location in the sapwood or heartwood, which is, alas, not always specified in the papers we reviewed. It is important since the cellulose/lignin staining used to locate G-layers is not specific to lignin but may also stain other polyphenolic compounds, especially from heartwood extractives which have to be distinguished from lignin deposited in the G-layer during maturation, in the vicinity of the cambium. It is known that the G-layer of *Fagus sylvatica* can be encrusted by lignin or other polyphenolic compounds during the formation of the false heartwood (Baum *et al.* 2000) and the G-layer of *Schinopsis balansae* (Anacardiaceae) has been reported to display encrustations of tannins during heartwood formation (Streit & Fengel 1995). So particular care should be taken when tension wood is taken from a piece of wood in the absence of any other specification concerning its location.

More lignin in the latewood of temperate species

In temperate species, only traces of lignin have been found in the G-layer of *Populus deltoides* tension wood (Joseleau *et al.* 2004). However, a larger proportion of lignin is present in the G-layer of latewood fibres: its deposition in the G-layer of *Quercus robur* (Fagaceae) is either scattered or concentric (Casperson 1967) while it is confined to the outer part of the G-layer in the latewood of *Cercidiphyllum japonicum* and *Fraxinus sieboldiana* (Saiki & Ono 1971). This is why the two last rows of latewood cells in a tension wood sample of *Fagus sylvatica* (Fagaceae) presenting a higher content in lignin were said to be normal wood (Schwarze & Fink 1998). This may also explain why Ruelle (2014) noted that “*tension wood is preferentially observed in earlywood of temperate species.*”

Inner thin lignified layer and outer gradual change from S₁ to G

A thin inner lignified layer in the G-layer (Fig. 2E) has been observed in the following temperate species: *Fagus crenata* (Saiki & Ono 1971), *Robinia pseudoacacia* (Araki *et al.* 1982), *Quercus lyrata* (Wahlgren 1957), *Eucalyptus elaeophora* (Wardrop

1964), *Populus nigra* × *Populus deltoides* (Gierlinger & Schwanninger 2006), *Quercus robur* (Lehringer *et al.* 2008), *Acer* sp. and *Fagus sylvatica* (Lehringer *et al.* 2009).

Within the G-fibre itself, Prodhan *et al.* (1995a) proposed two types of microfibril deposition in *Fraxinus mandshurica* var. *japonica*. Cellulose microfibrils are progressively deposited from the S₂ layer to the G-layer with an angle either ceasing at 0° or passing by 0° and ending at maximum 25°. Interestingly, in the second type of microfibril deposition, the inner part of the G-layer has a varying angle. In addition, the transition between the S₁ layer and the G-layer is progressive and the G-layer stained weakly for lignin in this outer zone (Prodhan *et al.* 1995b; Fig. 2C); this resembles in fact the type I of Onaka (1949), with a gradual change from S₁ to G. Saiki and Ono (1971) made a similar observation concerning the G-layer of *Fraxinus sieboldiana*. Araki *et al.* (1983) also reported lignin staining in the outer G-layer, in what the authors called the G', which shows a gradual change of the orientation of the microfibrils from an angle similar to the one in an S₂ to an angle close to 0° as in G in *Cercidiphyllum japonicum*, *Cornus controversa* and *Alnus pendula*.

Broad distribution of lignin in G-layers

In *Lophostemon confertus* (Myrtaceae, formerly *Tristania conferta*), lignin precursors penetrate the G-layer when the fibre is far enough away from the cambium (Scurfield 1973). This author suggested that these lignin precursors may be released during the terminal stage of cell senescence (Scurfield 1972).

Irregular lignin deposition has been observed in the tension wood of *Eucalyptus* sp. (Myrtaceae) and *Hakea laurina* (Proteaceae) (Scurfield & Wardrop 1963). Some tension wood cells differ in the intensity of deposition. Only some G-layers of *Salix lucida* (Salicaceae) stained strongly for lignin while, in some other species, all the G-layers stained for lignin (Ghislain *et al.* 2016).

G-layers are also present in various shrubby Fabaceae. In *Caragana korshinskii* and *Hedysarum scoparium* three types of G-layers in tension wood have been distinguished: unligified, partly lignified and lignified (Furukawa & Ohashi 1999). Lignified G-layers have also been described in *Ephedra aspera* and *E. viridis* (Ephedraceae), although the authors doubt their role in stem reorientation (Montes *et al.* 2015). The lignin content in the G-layer of these shrubs increases with stem age.

Multi-layered fibre walls and lignification

Jutte (1956) observed tension wood with abnormal fibres in a board of *Ocotea rubra* (currently *Sextonia rubra*, Lauraceae). This author defined three types of tension wood fibres. Type I: fibres with an inner unligified layer (G-layer). Type II: fibres like type I but with an additional inner lignified layer which can be thick or thin. Type III: fibres like fibre II but with an additional inner unligified layer. In this species, Chang *et al.* (2009) described the tension wood as having a thick unligified G-layer. In the same sample, we also observed a few fibres exhibiting unligified multi-layered G-layers (additional observation to the study published by Chang *et al.* 2009).

Ruelle *et al.* (2007c) showed that some multi-layered G-layers of *Laetia procera* are slightly lignified in some fibres and not in others in the same portion of tension wood.

Ghislain *et al.* (2016) added that in some species all multi-layered G-layers become lignified (Fig. 2B). But types II and III of Jutte (1956) are the first reports of lignification in only one thick layer while others remained unlignified. As Jutte (1956) did not mention where in the tree the samples came from, we do not know if this observation can be attributed to heartwood formation.

In tension wood of *Robinia pseudoacacia* thin concentric rings within G-layers were stained with KMnO_4 and divided into two or more sublayers (Araki *et al.* 1982). In this species, an extraordinary sublayer, thicker than the thin layer in a multi-layered G-layer, was stained with KMnO_4 (Saiki & Ono 1971; Fig. 2F). The authors do not specify if the fibre was located in latewood and/or heartwood. A lignified ring has been observed in the G-layer of *Casuarina equisetifolia* (Casuarinaceae) (Sanio 1863). The G-layer of *Eucalyptus camaldulensis* (Myrtaceae) is divided into two sublayers by a thin lignified ring (Bland & Scurfield 1964).

Does tension wood lacking G-layers really exist?

Do some species develop a kind of tension wood, with no unlignified or lignified G-layers? Onaka (1949) described tension wood with thin cell walls and no difference in lignification from normal wood in *Annona* (Annonaceae), *Firmania platanifolia*, *Hibiscus syriacus*, *Tilia* (Malvaceae), *Daphne odora* (Daphnaceae), *Edgeworthia papyrifera* and *Wikstroemia trichotoma* (Thymelaeaceae), *Liriodendron tulipifera*, *Magnolia verecunda*, and *Michelia compressa* (Magnoliaceae). However, in recent observations on *Liriodendron tulipifera* (Hiraiwa *et al.* 2014) the cell wall in tension wood was reported to be rather thick, so this sample probably had G-layers masked by late lignification.

Lagunaria patersonii (Malvaceae) has thinner fibre walls in tension wood than in normal wood fibres (Bland & Scurfield 1964; Scurfield 1973). Böhlmann (1971) observed *Tilia cordata* (Malvaceae) and found no G-layers in its tension wood. Instead, this author observed the phloem and proposed a stress generation mechanism based on phloem instead of wood. Indeed, Onaka (1949) observed greater development of bark on the upper side of *Tilia* and even proposed a class called “eccentricity in wood and bark” (Fig. 1).

Fisher and Stevenson (1981) assumed that the same mechanism of reaction phloem could occur in *Apeiba*, *Heliocarpus*, *Tilia* (Malvaceae), *Averrhoa* (Oxalidaceae) and possibly in *Annona* (Annonaceae), *Catalpa* (Bignoniaceae), *Durio zibethinus* and *Ochroma* (Malvaceae).

Furthermore, these authors noted that *Cananga* (Annonaceae), *Alstonia angustiloba* (Apocynaceae), *Cordia alliodora*, *C. lutea*, *C. panamensis* (Boraginaceae), *Garcinia nigrolineata* (Clusiaceae), *Apeiba*, *Durio zibethinus*, *Ochroma*, *Sterculia ceramica*, *S. foetida* (Malvaceae), and *Hamelia* (Rubiaceae) have enlarged unlignified parenchyma in their tension wood. However, *Sterculia foetida* was said to have either no G-layer or G-layers on the upper side of the leaning branch.

Patel (1988) described a non-homogeneous distribution of what the author called pith-like parenchyma in a tree of *Entelea arborescens* (Malvaceae) with high eccentricity, and concluded it was reaction wood.

It therefore appears that tension wood really lacking G-layers does exist, with fibres with thinner cell walls, different distribution/size of parenchyma cells and a thicker phloem. However, growth stress measurements coupled with anatomical studies are necessary to conclude on the mechanism underlying such tension wood lacking a G-layer.

New light on old data

Acknowledging the occurrence of late lignification in the G-layer of *Simarouba amara*, of lignin deposits in the G-layer of many species, of multi-layered G-layers, and of tension wood with thin cell walls and no G-layers, throws new light on reports in the literature on tension wood previously considered to be unusual. Indeed, species previously believed to be lacking G-layers might actually have lignified ones, while others really do lack them.

Observations of late lignification such as in tension wood of *Simarouba amara*

Unusual fibres of *Eschweilera* sp. (Lecythidaceae) with delayed lignification of their inner wall were observed by Fisher (1982) in tension wood. *Eschweilera sagotiana* is not reported to have G-layers although a strong tensile stress has been observed on the upper side of the leaning trunk (Clair *et al.* 2006; Ruelle *et al.* 2006). However, the swollen aspect of a G-layer and its weak adherence to outer layers is clearly visible, even though it is lignified. Similarly *Irvingia* (Irvingiaceae) has been described as having an inner layer that becomes lignified in mature wood but remains separate from the other layers (Fisher 1982). These observations suggest that late lignification masks the expected unligified aspect of the G-layer as described by Roussel and Clair (2015). *Osmanthus fragrans* (Oleaceae) tension wood has no G-layer but the cell wall fibres lack an S₃ and have an S₂ with a reduced microfibril angle (MFA) and less lignin than normal wood (Hiraiwa *et al.* 2007). Similar observations have been reported in *Magnolia kobus* and *M. obovata* (Magnoliaceae) (Yoshizawa *et al.* 2000) and *Liriodendron tulipifera* (Magnoliaceae) (Yoshida *et al.* 2002; Hiraiwa *et al.* 2014). These species might thus all have lignified G-layers. Increasing maturation stresses have indeed been linked to decreasing MFA, increasing α -cellulose content and increasing cellulose crystallinity in *Liriodendron tulipifera* (Okuyama *et al.* 1994).

Irregular deposition of lignin

Trees of *Eucalyptus regnans* with high maturation stresses might have gelatinous layers partly hidden by lignification (Chafe 1977). This would explain the anatomical differences with the fibres of normal wood. Although the authors did not describe it in that way, autofluorescent photographs of *Eucalyptus andreana*, *E. maidenii* and *E. smithii* showed the occurrence of unligified G-layers next to lignified G-layers and partly lignified G-layers, with either the outer or the inner part of the G-layer containing lignin (Hirohashi *et al.* 2012). Similar observations were made in *E. nitens* (additional observation to the study published by Clair *et al.* 2013).

A confocal fluorescence micrograph of *Populus nigra* was overexposed in order to visualize the G-layer, yet it is interesting to note the heterogeneity of staining of the

G-layer, with the inner part looking brighter (Donaldson 2001). In *Ocotea indirectinervis* (Lauraceae), lignified G-layers can be seen in the vicinity of unligified ones (Ruelle *et al.* 2006). In *Inga marginata* (Fabaceae), no G-layer was mentioned (Clair *et al.* 2006; Ruelle *et al.* 2006), although lignified and unligified G-layers appear in the figure.

Concentric deposition of lignin and/or multi-layered tension wood fibre walls

The concentric deposition of aromatic compounds or lignin described in the G-layer of *Quercus* sp. and *Aesculus* sp. (Casperson 1961, 1967; Lehringer *et al.* 2009) appear to be an intermediate stage between the usual G-layer and a multi-layered G-layer in which the alternating deposition of thick and thin layers is regular (Fig. 2D). It is not clear whether *Eucalyptus bicostata* has multi-layered G-layers in its tension wood or whether it has concentric deposition like in *Quercus* sp. (Scurfield 1972). In tension wood of *Trochodendron aralioides* (Trochodendraceae) (fig. 5 in Hiraiwa *et al.* 2013) a few multi-layered G-layers can be seen among the usual G-layers.

The occurrence of two sublayers in some G-layers of *Acer* species (Lehringer *et al.* 2009) can also be observed in some fibres in the figures of Morey and Cronshaw (1968). Two sublayers are also present in the G-layer of *Hevea brasiliensis* var. *Gondang Tapen* in which maturation stresses and MFA were measured (Sujan *et al.* 2015). The lamellae of the G-layer of *Lophostemon confertus* (Myrtaceae, formerly in *Tristania*), and *Grevillea robusta* (Proteaceae) (Scurfield & Wardrop 1963; Wardrop 1964; Scurfield 1973) appears to correspond to multi-layered tension wood fibres, as does *Fagus sylvatica* (Wardrop & Dadswell 1955; Wardrop 1964).

CONCLUSIONS

After reviewing the diversity of tension wood reported in the literature, we are now able to look at tension wood with fresh eyes, and advances in our understanding of tension wood allow us to re-interpret past observations.

This study confirms that tension wood shows a wide range of anatomical structures which make it impossible to use anatomical criteria to define it, but require instead the use of stress measurement in the living tree. Indeed, tension wood can have lignified or unligified G-layers or even no G-layer at all. To determine if tension wood has formed, it is thus indispensable to know the history of the tree sampled. In the ideal case, we should work with artificially inclined material. If this is not possible, we should either be able to retrace the history of the material under study or measure its stresses, or at least be aware of the limitations of our methods.

In future studies on tension wood diversity, we will still maintain at least two classes, considering the mechanisms that produce stress. The first group will include species which produce tension wood with G-layers. These G-layers may be unligified or contain varying amounts of lignin and/or have many layers, even in temperate species. In unligified G-layers, the generation of stress during maturation was shown to occur during the thickening of the G-layer. When the G-layer is lignified, lignification occurs late, after wall thickening is complete, and one would expect that the maturation stress

has already been generated and that lignification will not produce additional stresses but only fix the tensile stress while causing reinforcement of the cell wall. In this group, knowledge of the mechanism behind the generation of maturation stress is progressing and poplar will probably continue to be the model used to advance our understanding of its functioning. The second group includes the species with tension wood with fibres which do not produce G-layers, with thin cell walls, and with apparently different size and distribution of parenchyma cells. In these species, the mechanism (or mechanisms) behind the generation of tensile stress remain(s) unknown and studies combining stress measurements and microscopic and ultrastructural development are needed to propose a classification able to incorporate more species.

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Appendix

Number of publications mentioning (1) “tension wood” and (2) “tension wood” and poplar or *Populus* or aspen in the text. The ratio (2):(1) illustrates the increasing focus on poplar in research on tension wood (sources: Web of Science, 04/04/2016).

	(1) “tension wood”	(2) “tension wood” and poplar or <i>Populus</i> or aspen	Proportion (2):(1)
1950–1995	36	8	22%
1996–2005	106	39	37%
2006–2013	247	129	52%
2014–2016	62	41	66%