

## A GENERAL THEORY FOR THE ORIGIN OF GROWTH STRESSES IN REACTION WOOD: HOW TREES STAY UPRIGHT

by

**Richard Kenneth Bamber**

4/19 Nicholas Drive, Kingston Beach, Tasmania 7050, Australia

### SUMMARY

A general theory for the origin of growth stresses in the reaction wood of trees is presented. In both gymnosperms and arboreal dicotyledons, stress is considered to arise from the cellulosic component of the wood. It is suggested that in gymnosperms, cellulose microfibrils behave as helical springs. The helical springs are thought to be laid down in a compressed state and thus exert a compressive force which acts to right or stabilise the tree.

In arboreal dicotyledons the cellulose microfibrils are laid down as extended, longitudinally oriented springs and thus exert a tensile force tending to right or stabilise the tree.

Contrary to the prevailing view, lignin is not considered to be involved in the generation of growth stress in reaction wood. It is suggested that the sole function of lignin is to cement the cellulosic constituents into a whole, thus ensuring the transmission of stresses through the wood. The low values of lignin often reported from tension wood and especially from gelatinous fibres is seen as a mechanism to facilitate the contraction of microfibrils thus maximising longitudinal tensile stress. The high values of lignin in of compression wood is seen as a mechanism to increase the compressive strength of compression wood.

**Key words:** Reaction wood, compression wood, tension wood, microfibrils, lignin.

### INTRODUCTION

The natural habit of trees is upright growth. If the natural habit is disturbed, for example by soil subsidence or exposure to strong prevailing winds, the resultant leaning stem develops abnormal wood which serves either to reorient the stem, if the stem is not too large, or to stabilise the tree and prevent further lean. This abnormal wood is known as reaction wood. The cambium responds to resulting asymmetrical distribution of stresses in the leaning stem by accelerated wood cell formation. In gymnosperms (softwoods) this occurs on the lower side of the lean whereas in arboreal dicotyledons (hardwoods) this occurs on the upper side so as to produce eccentric stems. In softwoods such wood is known as compression wood and in hardwoods as tension wood.

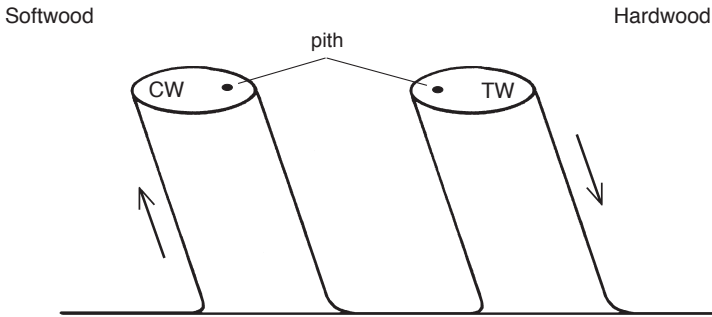


Fig. 1. Leaning stems showing direction of growth-stress-induced forces acting to maintain upright habit or stabilise the stems. CW = compression wood; TW = tension wood.

To effect righting of the tree, compression wood develops a compressive strength that serves to push the stem upright or stabilise it whereas tension wood develops a contractile stress which serves to pull the stem upright or stabilise it (Fig. 1). While stresses are no doubt present in all tree trunks they are more or less evenly distributed. In reaction wood, however, growth stresses are unevenly distributed and as a consequence can cause considerable problems during conversion and drying. Boards containing reaction wood may distort during sawing or drying with resultant degrade of timber.

Because of its biological and economic significance reaction wood has been extensively researched for over a hundred years. Recent reviews such as Timell (1987) and Kubler (1987) cover this research in considerable detail. However, despite the intensive interest in the phenomenon, there is no consensus as to the origin of growth stress in reaction wood.

## DISCUSSION

### Tension wood

The two principal theories advanced to explain the development of growth stress in tension wood are the "lignin swelling theory" (Boyd 1985) and the "cellulose tension theory" (Bamber 1979, 1987). The lignin swelling theory rests on the premise that the deposition of lignin between the microfibrillar cellulosic framework of the cell wall causes the wall to expand laterally. Because of the elastic nature of the cell wall such swelling induces a longitudinal contractile stress in the wall and consequently in the wood.

I disputed lignin swelling as a cause of growth stress in tension wood (TW) and supported my case with detailed argument in several papers (Bamber 1979, 1987). In contradiction I suggested that growth stress in tension wood originated in the contractile nature of cellulosic crystallites and that lignin played no part in stress production. The only role of lignin was to bond the microfibrils and the cells into a cohesive mass so that stress is transmitted through the wood.

In recent years the cellulosic tension concept has received elegant support from Japanese workers (Okuyama et al. 1990; Yamamoto et al. 1992; Sugiyama et al. 1993; Okuyama et al. 1994). Yamamoto et al. (1992), in particular, related microfibrillar angle (in relation to cell axis) to longitudinal growth stress in an eccentric stem of *Liriodendron tulipifera* L., finding a negative correlation between microfibrillar angle and released strain. A similar correlation ( $r = -0.63$ ) was found in the tension wood of *L. tulipifera* for microfibrillar angle and longitudinal growth stress by Okuyama et al. (1994).

### Compression wood

Numerous theories have been advanced to account for the generation of longitudinal compressive stress in compression wood. These have been critically reviewed by Timell (1987). The theory which has received most support is the lignin swelling theory. In the absence of a credible alternative this theory is in danger of being accepted as fact. For example in Desch and Dinwoodie (1996) this theory is stated as being confirmed by Boyd (1985). Likewise Abasolo et al. (1999) say “lignin content above 30% produces longitudinal compression stress” and again in reference to lignin swelling they comment “This hypothesis was proved quantitatively by Okuyama et al. (1985), Yamamoto et al. (1991) and Yamamoto (1998).”

The evidence on which these conclusions are based does not stand up to scrutiny. The lignin swelling theory is based on two principal points: 1) the high correlation between lignin concentration and stress level and 2) the deposition of lignin between the cellulosic microfibrils causes expansion of the cell wall, this expansion leading to longitudinal expansion of the tracheids and thus generating longitudinal compressive stress.

While it is well established that lignin concentration is positively correlated with the severity of stress in compression wood, how the stress is generated is subject to some contention. The swelling hypothesis is dependent on the microfibrillar angle. Where the angle is large it can be argued that if lignin did cause swelling, then logically longitudinal compressive stress could result. For geometrical reasons, however, this situation can only arise where the microfibrillar angle exceeds 40 degrees or so in respect to the cell axis. This aspect has been carefully examined by Timell (1987). He points out that the literature is replete with references to longitudinal compressive stress occurring at microfibril angles much less than 40 degrees. In reference to Boyd's (1985) continuing adherence to the lignin swelling theory, when faced with this fundamental objection, Timell (1987) comments “Boyd dismisses all these measurements as being unreliable or erroneous.” Furthermore the concept of ‘lignin swelling’ and resultant lateral expansion of the tracheid wall does not agree with the observed morphological changes of the wall during maturation. Transversely the tracheid wall is initially rectangular. However, as the cell matures it becomes rounded. Rather than expansion such change suggests contraction, i.e., shrinkage.

Because of this major flaw of the lignin swelling theory one must look elsewhere to provide an explanation for compression wood stress. As microfibrillar angle is also

strongly correlated with degree of stress (Yamamoto et al. 1991) it seems logical to consider the cellulosic components of the wall as the source of stress. This is emphasised by the fact that the deposition of cellulose occurs before lignin, confirmed in respect to the formation of compression wood cell wall fissures by Côté et al. (1968) and Timell (1979).

Support for a causal relationship between microfibril angle and stress in the compression wood of gymnosperms is given by the findings of Archer (1987) that the transition from tensile stress in normal wood cells to compressive stress in compression wood cells is found with increasing microfibril angle.

I argued (Bamber 1979, 1987) that the longitudinal tensile stress in tension wood was produced by the cellulosic crystallites behaving like extended springs. I further suggest that the cellulosic components of the compression wood cell likewise behave as springs, in this case compressed helical springs. Microfibrillar angle in the  $S_2$  layer of normal wood of conifers is around 15 degrees and forms a steep helix of right hand configuration. In compression wood this angle increases with degree of stress often to well over 45 degrees (see review by Timell, 1987).

In extreme compression wood where helical ribs are developed the similarity between this structure and the mechanical coil springs used in automotive suspension systems is obvious (see Fig. 2). Such mechanical coil springs are often encased in a

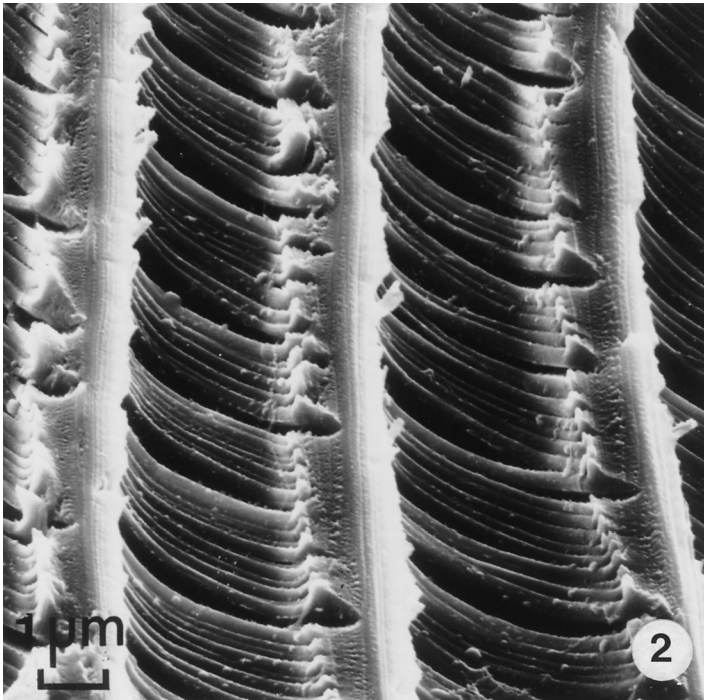


Fig. 2. SEM of compression wood tracheid in *Pinus sylvestris* showing helical configuration of wall cavities and considered to be analogous to coiled springs used in automotive suspension systems (Timell 1987, by permission).

cylinder which prevents lateral distortion when the spring is compressed. In the secondary wall of wood cells the  $S_2$  layer is encased in the  $S_1$  layer, the crossed lamellae structure of which would provide lateral support for the compressed spring structure of the  $S_2$  layer.

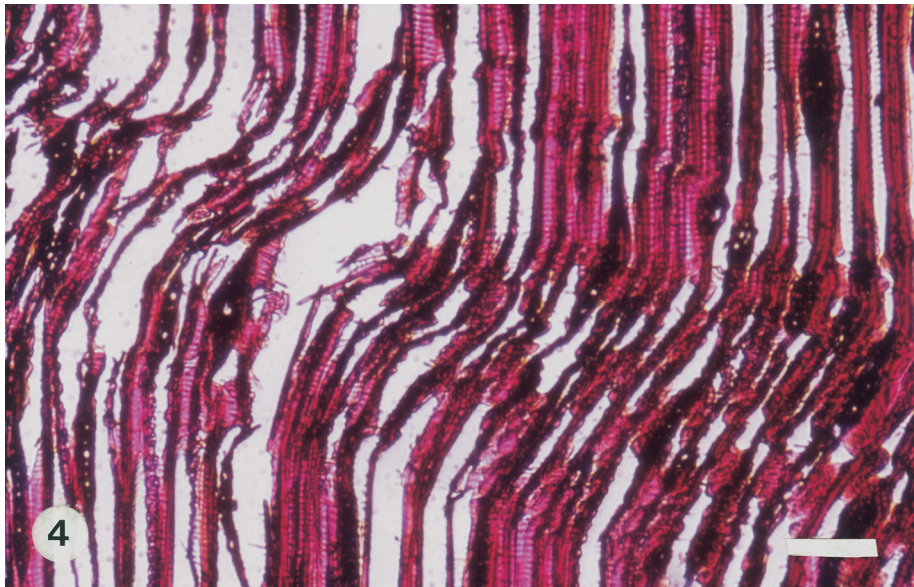
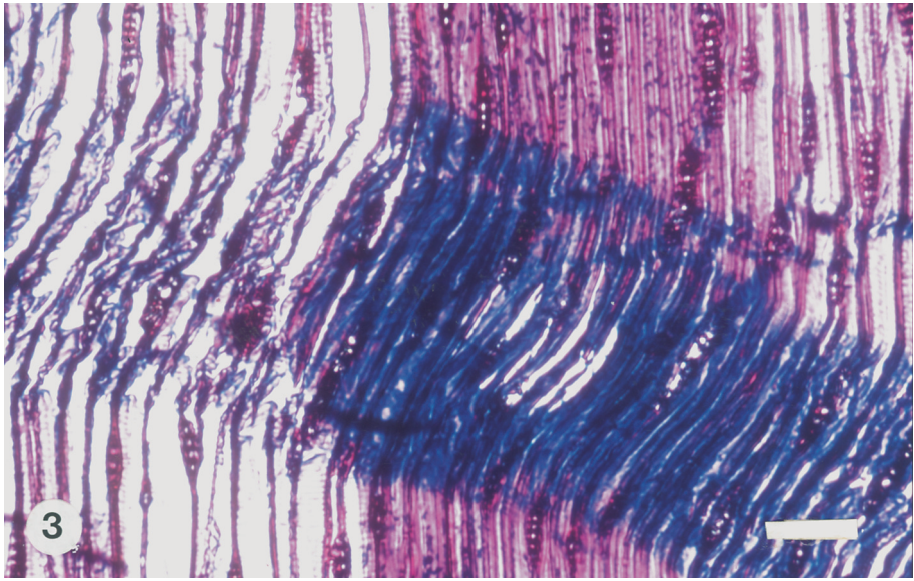


Fig. 3 & 4. Tangential longitudinal sections of *Pseudotsuga menziesii* showing compression creases. — 3: Stained with safranin/aniline blue. — 4: Stained with phloroglucinol/HCl. — Scale bar = 100  $\mu$ m.

Clearly tracheids develop in reaction wood under conditions of compressive stress as it has been shown that intrusive growth of the cell tips is limited and compression wood tracheids develop truncated ends (see review by Timell, 1987). Therefore it could be assumed that the stress which prevents intrusive growth is transmitted throughout the developing tracheid. In the model proposed here it is suggested that this compressive stress prevents the transition of the microfibril angle from about 70 degrees in the  $S_1$  layer to the 10–15 degrees in the  $S_2$  of normal wood and instead causes the microfibrils to be laid down in a much greater angle.

Another feature of compression wood (CW) tracheids is the rounded transverse shape. In respect to the proposed model of the microfibrils as helical springs, the rounded transverse form of the tracheids would appear to be stronger in compression than the rectangular form of normal tracheids.

Because of the high correlation between lignin content and growth stress in CW, lignin has been proposed as the cause of growth stress. For reasons advanced above and elsewhere (Bamber 1979, 1987) this is argued not to be the case. However, the question does arise as to what function lignin plays in CW. It is here suggested that the high lignin content of CW provides for its increased compressive strength (Timell 1987). The role of lignin in wood is to bond the microfibrillar skeleton into a coherent whole. An increase in lignin content could be expected to bond the microfibrillar structure together more strongly and thus to better resist the increased compressive force to which CW is subject.

The importance of the bond between lignin and cellulose in respect to compressive strength is demonstrated in Figures 3 & 4. These figures show tangential longitudinal sections of a wood block of *Pseudotsuga menziesii* (Mirbel) Franco. The wood block was compressed longitudinally to the point of failure. The sections have been cut through a compression crease, that is, a region of compression failure. The section in Figure 3 was stained with the double staining procedure of safranin/aniline blue. It will be observed that the tracheid walls in the creased areas are stained blue whereas the walls in the areas which have not failed, are stained red. The section shown in Figure 4 was stained with phloroglucinol/HCl. In this preparation both the creased walls and the non-creased areas are stained similarly.

The double stain safranin/aniline blue differentiates lignified from non-lignified cells in plant tissue, lignified cell walls staining red and non-lignified walls staining blue. Although all plant cell walls contain cellulose, the presence of lignin masks the cellulose presumably because lignin occupies all the reactive positions on the cellulose. Phloroglucinol/HCl is a specific stain for lignin and the staining pattern in Figure 4 indicates that lignin is present in both creased and uncreased cell walls. The staining pattern shown in Figure 3 indicates that the reactive sites on cellulose have been exposed by the creasing of the walls and suggests that the ligno-cellulose bond has been broken leading to compression failure.

### **General theory for growth stress development in reaction wood**

A case has been argued for microfibrils being the origin of growth stress in reaction wood. In tension wood, microfibrils behave like stretched longitudinal springs which

generate longitudinal tension thus tending to *pull* a leaning stem upright. In compression wood the microfibrils, as a consequence of their large angle, behave like compressed helical springs thus tending to *push* the leaning stem upright.

Lignin is not considered to play a role in the generation of stress in reaction wood. Its absence from the gelatinous fibres of tension wood in fact allows the microfibrils to generate maximum tensile stress. In compression wood, lignin appears to be important to maximise the compressive strength of the wood hence the positive correlation of lignin content and the severity of compression of wood.

### How trees stay upright

In the above discussion only leaning stems were considered. Upright or so-called normal stems, however, are continually subject to bending forces such as winds. While thicker and stronger stems can resist such forces, thinner stems are easily bent but readily return to their natural orientation.

While peripheral tensile stresses are present in upright trees (Timell 1987; Wilkins & Kitahara 1991) such stresses can be considered to be in equilibrium and as pre-stressing in the tree stem. If however the stems are bent, it is suggested that the reaction wood mechanisms as outlined above will come into play and right the stem. Thus in softwoods the microfibrillar helical springs of the  $S_2$  layer of the secondary wall become compressed and exert a compressive force to push the stem upright. Telewski (1989) in fact found that stems of *Abies fraseri* (Pursh) Poiret, when subjected to sustained flexure, produced tracheids which had similar characteristics to CW. In case of hardwoods the microfibrillar springs of the  $S_2$  layer become stretched thus developing a tensile stress which acts to pull the stem upright.

It is argued that the spring-like property of the microfibrils is the basis for the elastic nature of stems and enables young stems to constantly return to their normal orientation no matter from which direction the force arises.

### CONCLUSIONS

Argument is presented for a general theory for the origin of growth stress in reaction wood. It is based on a proposed spring-like property of cellulosic microfibrils in the secondary wall. In softwoods the microfibrils of the  $S_2$  layer are considered to behave as helical springs. In compression wood these helical springs become compressed and thus exert a compressive stress acting to either push the stem upright or to stabilise it. In hardwoods the microfibrils of the secondary wall and/or the gelatinous layer are considered to behave as linear springs. In tension wood these springs are stretched thus developing a tensile stress which acts either to pull the stem upright or to stabilise it.

Qualitative evidence is presented indicating the strong relationship between lignin and cellulosic components in respect to compressive strength. This, together with the positive relationship between lignin concentration and the severity of compression wood, suggests that the role of lignin is to increase the compressive strength of compression wood rather than contribute to the development of growth stress.

## ACKNOWLEDGEMENTS

I wish to acknowledge critical comments of Prof. R. Kitahara of Miyazaki University. Extensive use of the encyclopedic publication of Prof. T.E. Timell, *Compression Wood in Gymnosperms*, has been made in the preparation of this paper. The cooperation of the library staff of Forestry Tasmania is gratefully acknowledged.

I thank Dr. Scott Bamber for editorial assistance.

## REFERENCES

- Abasolo, W., M. Yoshida, H. Yamamoto & T. Okuyama. 1999. Internal stress generation in rattan canes. *IAWA J.* 20: 45–58.
- Archer, R.R. 1987. On the origin of growth stresses in trees. Part 1. Micro mechanics of the developing cambial cell wall. *Wood Sci. Technol.* 21: 139–154.
- Bamber, R.K. 1979. The origin of growth stresses. *Forpride Digest* 8: 75–79.
- Bamber, R.K. 1987. The origin of growth stresses: a rebuttal. *IAWA Bull.* n. s. 8: 80–84.
- Boyd, J.D. 1985. The key factor in growth stress generation in trees. Lignification or crystallisation. *IAWA Bull.* n. s. 6: 139–150.
- Côté, W.A., Jr., N.P. Kutscha & T.E. Timell. 1968. Studies on compression wood. VII. Formation of cavities in compression wood tracheids of *Abies balsamea* (L.) Mill. *Holzforschung* 22: 138–144.
- Desch, H.E. & J.M. Dinwoodie. 1996. *Timber structure, properties, conversion and use.* 7<sup>th</sup> Ed. Macmillan Press Ltd, London.
- Kubler, H. 1987. Growth stresses in trees and related wood properties. *For. Prod. Abstr.* 10: 61–119.
- Okuyama, T., H. Yamamoto, M. Iguchi & M. Yoshida. 1990. Generation process of growth stresses in cell walls. II. Growth stresses in tension wood. *Mokuzai Gakkaishi* 36: 797–803.
- Okuyama, T., H. Yamamoto, M. Yoshida, Y. Hattori & R.R. Archer. 1994. Growth stresses in tension wood: role of microfibrils and lignification. *Ann. Sci. For.* 51: 291–300.
- Sugiyama, K., T. Okuyama, H. Yamamoto & M. Yoshida. 1993. Generation process of growth stresses in cell walls: relation between longitudinal released strain and chemical composition. *Wood Sci. Technol.* 27: 257–262.
- Telewski, F.W. 1989. Structure & function of flexure wood in *Abies fraseri*. *Tree Physiol.* 5: 113–121.
- Timell, T.E. 1979. Formation of compression wood in balsam fir (*Abies balsamea*). II. Ultrastructure of the differentiating xylem. *Holzforschung* 33: 181–191.
- Timell, T.E. 1987. *Compression wood in Gymnosperms.* 3 Vols. Springer-Verlag, Berlin.
- Wilkins, A.P. & R. Kitahara. 1991. Relationship between growth strain and rate of growth in 22-year-old *Eucalyptus grandis*. *Aust. For.* 54: 95–98.
- Yamamoto, H. 1998. Generation mechanism of growth stresses in wood cell walls: role of lignin deposition and cellulose microfibrils during cell wall maturation. *Wood Sci. Technol.* 32: 171–182.
- Yamamoto, H., T. Okuyama, K. Sugiyama & M. Yoshida. 1992. Generation process of growth stresses in cell walls. IV. Action of the cellulose microfibrils upon the generation of tensile stresses. *Mokuzai Gakkaishi* 38: 107–113.
- Yamamoto, H., T. Okuyama, M. Yoshida & K. Sugiyama. 1991. Generation process of growth stresses in cell walls. III. Growth stresses in compression wood. *Mokuzai Gakkaishi* 37: 94–100.