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John R Barnett, Joseph Gril, Pekka Saranpää

► **To cite this version:**

John R Barnett, Joseph Gril, Pekka Saranpää. The Biology of Reaction Wood Introduction. The Biology of Reaction Wood, pp.1 - 11, 2014, 978-3-642-10813-6. hal-01452015

HAL Id: hal-01452015

<https://hal.science/hal-01452015>

Submitted on 1 Feb 2017

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Barnett J., Gril J., Saranpää P. (2014) Introduction, in: *The Biology of Reaction Wood*, Springer Series in Wood Science, Springer (pub), Gardiner B., Barnett J., Saranpää P., Gril J (eds), p. 1-11.

The Biology of Reaction Wood

Chapter 1. Introduction

J. R. Barnett, Joseph Gril, Pekka Saranpää

“The rings on the cross-section of the branch of a tree show the number of its years, and the greater or smaller width of these rings show which years were wetter and which drier. They also show the direction in which the branch was turned, for the part that was turned towards the north grows thicker than that turned towards the south so that the centre of the stem is nearer to the bark that faces south than to that on the north side.” Leonardo da Vinci.

Leonardo published his observations of stem asymmetry in his notes for a treatise on painting without any attempt at explanation. It must represent one of the earliest references to reaction wood in the literature, although there can be no doubt that carpenters and joiners had long been intuitively aware of its effects on the working and mechanical properties of timber. With the passage of time our understanding of why and how it is formed in the tree has increased, providing a scientific basis for folk knowledge, but despite extensive research, much remains to be explained.

The last major work on this topic was the *Magnum Opus* of Timell (1986), which summarised current ideas on compression wood in gymnosperms. No equivalent work has, however, been produced dealing with tension wood, its counterpart in angiosperm dicotyledonous trees. This reflects to some extent the fact that hitherto, tension wood has been of less commercial importance, although this is now changing with the breeding and development of fast-growing temperate-hardwood species. This book is intended to bring the reader up-to-date with progress in research into reaction wood, particularly with reference to tension wood, but also the developments in compression wood research since the publication of Timell's definitive work.

What is reaction wood?

Reaction wood has been defined by the Committee on Nomenclature of the International Association of Wood Anatomists (IAWA, 1964) as *“Wood with more or less distinctive anatomical characters, formed typically in parts of leaning or crooked stems and in branches and tending to restore the original position, if this has been disturbed. It is divided into two types: tension wood in dicotyledons and compression wood in conifers”*. The Committee further defines compression wood as *“Reaction wood formed typically on the lower sides of branches and leaning or crooked stems of coniferous trees and characterized anatomically by heavily lignified tracheids that are rounded in transverse section and bear spiral wall checks; zones of compression wood are typically denser and darker than the surrounding tissue”*. Tension wood is: *“Reaction wood formed typically on the upper sides of branches and leaning or*

crooked stems of dicotyledonous trees and characterized anatomically by lack of cell wall lignification and often by the presence of an internal gelatinous layer in the fibres”.

As might be expected, and as will become clear in this book, there are many examples of variations in detail from these necessarily succinct definitions. For example in the case of so-called mild compression wood, cell walls may lack spiral wall checks and not necessarily be rounded, while the gelatinous layer is not present in tension wood of many species. The Oxford English Dictionary provides several definitions of the word “reaction” several of which encompass the nature and function of the term when used in conjunction with wood. Perhaps the two most appropriate are: “*The response made by a system or an organ to an external stimulus*” and “*A movement towards a reversal of an existing tendency or state of things.....or desire to return, to a previous condition of affairs*”. The first definition is appropriate to the formation of reaction wood, while the second is appropriate to its function in the tree.

Briefly, reaction wood is formed in response to mechanical stress experienced by a tree. Its formation can work to restore vertical growth (gravitropy) in main stems, providing the stem is not already too thick to make this possible. It can be used also to incline stems in order to move the canopy in towards light (heliotropy). In the case of a branch, reaction wood formation is carefully controlled to balance its continuously increasing weight, either as a buttress in the case of compression wood in gymnosperms, or as a cantilever, in the case of tension wood in angiosperm dicotyledons, thereby maintaining the branches pre-ordained orientation and the architecture of the tree. It is noteworthy that reaction wood in a branch does not tend to force the branch into a vertical alignment unless the dominance of the apical shoot is lost. However, reaction wood is required to change the orientation of a lateral branch to the vertical in the event of damage to or loss of the leading shoot. Compression wood and tension wood sectors in the stem are always associated with local growth stresses which are very different from the normal tensile stress state common to gymnosperms and angiosperms: compressive stress in the case of compression wood, very high tensile stress in the case of tension wood.

There are, however, as will become apparent, variations on the theme. For example, compression wood may form around the entire growth ring in straight vertical fast-growing conifer stems. This may be a result of almost continual movement in the wind of the long, recently formed apical internodes, which are highly flexible owing to the high microfibril angle in the S2 layer in the juvenile tracheids. Also, gelatinous fibres of the type normally associated with tension wood are sometimes found distributed randomly in vertical stems of fast-growing hybrid aspen. These phenomena might be explained by the existence of extraordinary growth stresses in fast growing trees or by some variation in the level of growth regulators.

Some workers have observed cases in which the “normal” pattern of reaction wood formation was not found. For instance, Höster and Liese (1966) described compression wood in angiosperm species whose main axial elements were tracheids, observations confirmed by Yoshizawa *et al.* (1993) and Baillères *et al.* (1977). In contrast, Jacquot and Trenard (1974) described gelatinous fibres in coniferous wood.

Historical Background

The reason why branches and many tree stems are elliptical in cross section, with growth rings having different widths on opposite sides, and pith located to the side of the narrower growth rings, was already a subject of investigation in the nineteenth century. It was noted that in conifers growing on mountain slopes more growth occurred on the side of the stem facing the slope. Attempts were made to explain this in terms of nutrient distribution to the cambium, in that nutrients moved preferentially to areas to stimulate growth. Büsgen and Münch (1929), pointed out that in fact the opposite was the case, as suggested by Cotta (1806), in that growth stimulates the movement of nutrients to where they are required. They suggested that this process was set in motion by stimuli which at that time were unknown. They also noted that in Germany, where south-west and west winds predominate, conifer stems take on an elliptical form with the long axis of the ellipse parallel to the wind direction and greatest growth on the leeward side of the stem. Similarly they noted that in leaning conifer stems, greatest growth occurred on the lower side. Thus the tree presents its least flexible profile to the prevailing stress. It was also noted that those roots aligned with the direction of the stress, whether wind or gravitational pull, also developed an elliptical profile. They proposed that this helped to prevent the stem from falling over.

Hartig (1901) with spruce and Raadorsky (1925) with *Helianthus* induced elliptical stem form by rocking the experimental plant from side to side. Büsgen and Münch (1929) interpreted this to mean that eccentric growth in branches and leaning stems was caused by mechanical stimulation. The fact that this response was also found by Hartig (1901) in a fallen spruce stem supported by the ground and therefore not under any bending stress, led to the view that the force of gravity played the most important part in the eccentricity of branches.

The facts that in conifers, reaction wood is produced on the underside of leaning stems and branches under compressive stress, and that it has a reddish hue, led to its being referred to in the German literature as Druckholz (pressure wood) or Rotholz (red wood). These terms were supplanted by the name compression wood as it was believed to be formed as a result of the tissue being under a compressive load. In contrast, reaction wood produced in angiosperm dicots, which is formed in tissues under tensile stress, and which is light in colour was referred to as tension wood or Weissholz (white wood). As Dadswell and Wardrop (1949) pointed out, the latter name is confusing as it was also used to describe wood formed in conifers on the opposite side of the stem to Rotholz. The terms compression wood and tension wood eventually acquired universal acceptance as reflecting the stress conditions under which they are usually formed.

However, there are circumstances in which tension wood can form in tissues under compressive stress and *vice versa*. Experiments by Ewart and Mason-Jones (1906) in which they bent conifer twigs into vertical loops (Figure 1), demonstrated that compression wood formed on the lower side of the twigs at both the top of the loop (where the developing wood was under pressure) and the bottom (where it was under tension). Jaccard (1938) repeated the experiment and found that in

angiosperm saplings tension wood always formed on the upper side of the top and bottom of the loop. This, coupled with the discovery of auxin and its effects as a growth regulator which moves basipetally in tissues under the influence of gravity, led to the proposition that auxin accumulation on the lower side of conifer branches and leaning stems stimulated compression wood formation, while depletion of auxin from the upper side in angiosperms led to tension wood formation. The work of Wershing and Bailey (1942), who found that external applications of auxin induced compression wood formation, lent support to this view. Conversely, Nečesaný (1958) found that the application of auxin to the upper side of an angiosperm branch inhibited tension wood formation, while Lachaud (1987) applied tritiated auxin to loops made in the manner of Jaccard (1938) and found that it moved to the lower side of the loop while tension wood formed on the upper side. This effect was most pronounced when the loop was still attached to the plant, no movement of auxin taking place in a detached loop.

In essence this theory was accepted until questioned by Boyd (1977), who felt that reaction wood formation was stimulated by stress, rather than auxin concentration changes. His view was supported by Wilson *et al.* (1989) following measurement of auxin levels in bent branches of Douglas fir made using gas chromatography-mass spectroscopy. It was found that auxin levels were higher on the upper side of these branches even though compression wood was formed on the lower side. Sundberg *et al.* (1994) measured auxin concentrations with a relatively high degree of resolution in the cambium of tilted pine stems and also found no difference in auxin distribution between tilted and control stems.

The work performed by the French consortium ASMA (Fournier *et al.* 1991a & b, Thibaut *et al.* 2001) demonstrated that reaction wood is not a consequence of stresses acting on a zone in the tree but rather, its role is to generate specific levels of stress when and where they are needed. The fact that while the main stem of the tree produces reaction wood in an apparent attempt to maintain as vertical an alignment as possible, while branches produce it to maintain a particular orientation has led to the suggestion that the stress imposed by gravitational force does not of itself stimulate reaction wood formation. Rather it is the tree's perception of the effect of the gravitational force in displacing the stem or branch from its pre-ordained alignment that provokes the response.

Recent developments in this area are described in Chapters 4 and 5.

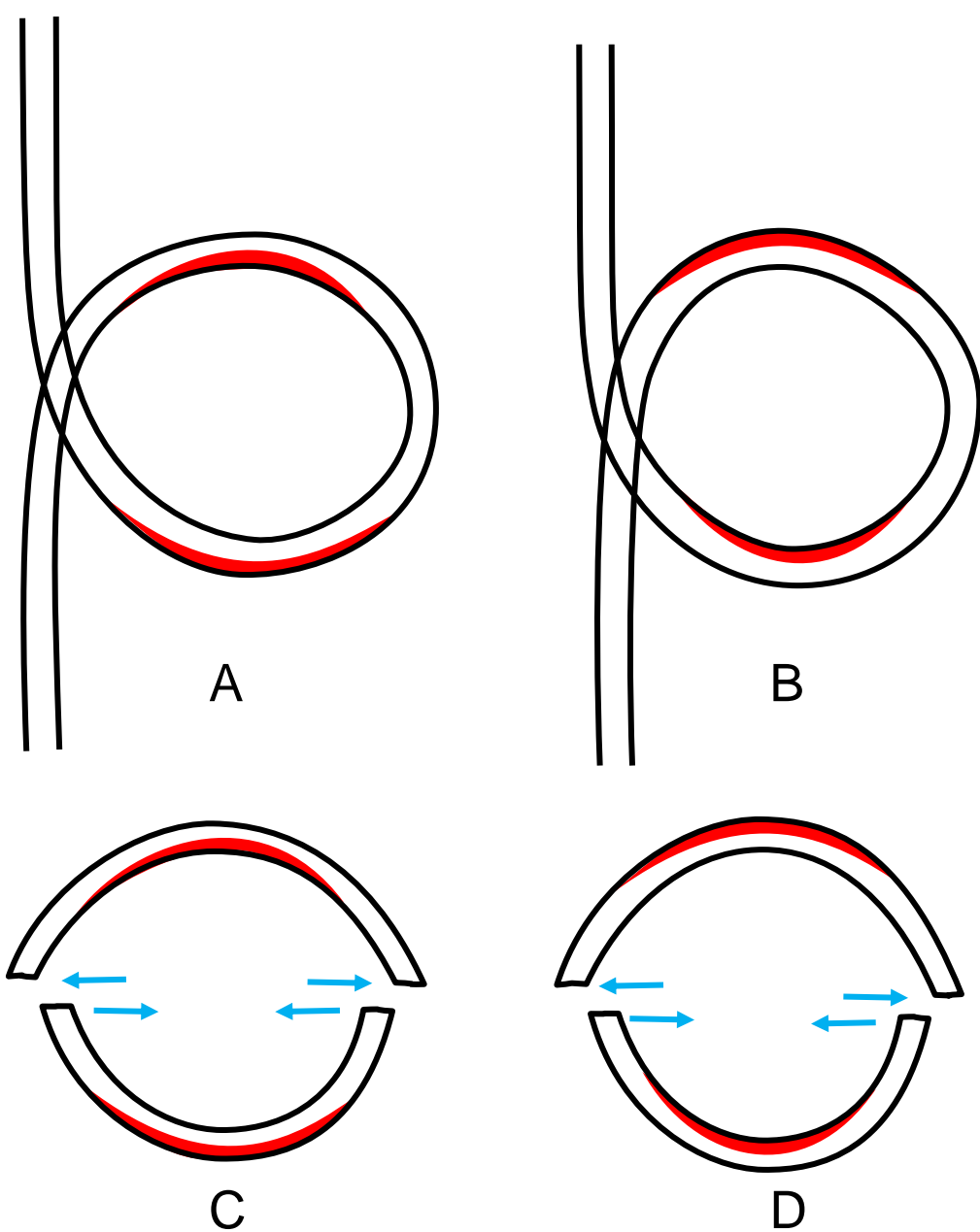


Figure 1: Diagram after Jaccard 1938. Diagrammatic representations of
 A: Loop made in a conifer stem. Compression wood is shown as a thicker line on the lower sides of the upper and lower parts of the loop.
 B: Loop made in a woody dicotyledon stem. Tension wood is shown as a thicker line on the upper sides of the upper and lower parts of the loop.
 C and D: The effect of cutting the loops is similar in each case suggesting compression wood acts by pushing, while tension wood by pulling against the normal wood.

Structure of reaction wood.

The anatomical and structural features of reaction wood are usually described by comparison with so-called normal wood. The latter term actually refers to wood which has those properties most desired by the timber industry, for example, straight grain, high density, high bending strength and uniform shrinkage without distortion on drying. Interestingly there appears to be no definition of normal wood and it is

noteworthy that the IAWA glossary in its definitions of reaction wood, tension wood and compression wood avoids the use of comparatives.

Those features usually associated with what authors refer to as normal wood and which are responsible for the desirable characteristics of good timber are determined by the anatomical structure of the wood and the structure of fibre (hardwoods) and tracheid (softwood) walls. In particular, tracheids and fibres have the classical three-layered secondary wall (Figure 2) with the microfibril angle in the S2 layer being small, resulting in a high modulus of elasticity. In reacting to gravity-induced displacement of the stem or branch, the tree produces fibres or tracheids whose structure differs to a greater or lesser extent from this "ideal". These variations and other differences in reaction wood will be discussed in more detail in Chapter 2.

In brief, compression wood is a darker colour than normal wood, the tracheids are more rounded in cross-section with the result that intercellular spaces are formed. They are also shorter than normal wood tracheids in the same tree. Cell walls of compression wood tracheids are normally thicker than those of normal wood tracheids in the same part of the tree. This coupled with the greater proportion of lignin in the cell wall makes the wood denser, more impermeable and stronger in compression. The microfibril angle in the S2 layer is larger, which reduces the tensile strength, modulus of elasticity and increases the brittleness of the wood, making it unsuitable for uses in which it is likely to experience high stresses. The larger microfibril angle also means that the wood has a higher longitudinal shrinkage on drying, but a lower transverse shrinkage. This explains the distortion on drying of pieces of wood containing both normal and compression wood. In severe cases the S3 wall layer is absent and the S2 layer contains splits which lie parallel to the microfibril angle.

The structure of tension wood fibres is less clear-cut than that of compression wood tracheids. Tension wood fibres are longer than those in normal wood and have been found to contain a lower proportion of lignin than normal wood, giving it a whiter appearance. They are most commonly described as lacking an S3 layer and having variable amounts of the S2 remaining, inside which is a gelatinous layer composed mainly of hydrated cellulose microfibrils (Norberg and Meier 1966) oriented almost parallel to the long axis of the fibre. This gives the wood a glistening gelatinous appearance when wet. Variations on this theme have been reported, however. For example Faruya *et al.* (1970) reported the presence of a gelatinous layer in fibres of *Populus euroamericana* which had retained their S3 layer, while Côté *et al.* (1969) reported an S3 layer inside a gelatinous layer. More and more variations on the structure of tension wood fibres are being reported, with numerous species apparently lacking a gelatinous layer in their fibre walls.

These structural variations, which are adapted to the mechanical role the fibres and tracheids must fulfil, are of course, a normal response by the tree to enhance its chances of survival, either by helping to maintain the upward movement of the crown by the shortest possible route, by restoring verticality of trees partially uprooted by wind, or by maintaining the optimum branch architecture for efficient light capture. As such, for the tree, making reaction wood is as normal as making the normal wood beloved of the timber merchant, engineer, carpenter or joiner. The use of the term normal for the latter carries the implication that reaction wood is abnormal, and by

extension that it is of no value. However, trees as we know them could not have evolved without reaction wood, a fact which needs to be borne in mind by those working to improve wood quality.

The formation of reaction wood demonstrates that the tree is capable of fine tuning the structure of its fibre or tracheid walls to generate growth stress. It does this by adjusting the proportions and arrangement of its major wall components, cellulose, hemicellulose and lignin. The structure and composition of the cell wall in reaction wood forms the subject of Chapter 3.

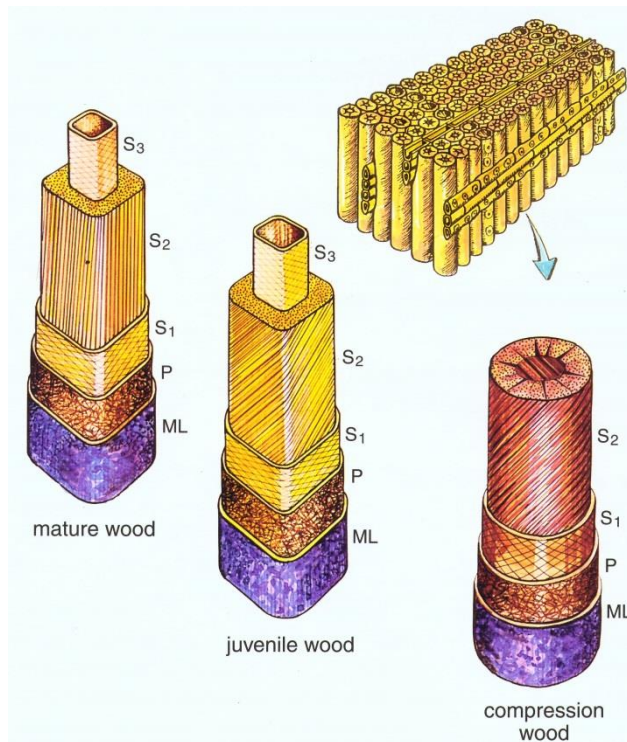


Figure 2: Cell structure of normal (mature) wood, juvenile wood and compression wood (from Jozsa and Middleton 1994)

How Reaction Wood Works

It is now well known that reaction wood effects stem reorientation by generating a long lasting flexure momentum (Alméras et al 2005). This is linked to asymmetry between wood production (new ring) on the two sides of the wooden axis: asymmetry of generated growth stress and often asymmetry of ring width. But it is not yet well understood how growth stress level is tuned during cell differentiation. Various theories have been put forward, but none has so far proved satisfactory. Brodski (1972) proposed that the water in the developing S₂ layer of the compression wood tracheid wall was replaced during maturation by a compound, laricinan, and that this insertion provided the force needed to push the stem upright. Boyd (1978) published a convincing argument against such a role for laricinan. The tensional effect of gelatinous layer of tension wood fibres is also difficult to explain. When gelatinous fibres are severed, the gelatinous layer may be observed to detach itself from the other wall layers and contract. This is despite the fact that its major

component is cellulose microfibrils with their major axis parallel to the direction of shrinkage. As the microfibrils are highly crystalline they would not be expected to shrink in this way. Current thinking on these topics is covered in Chapter 5.

Why is Reaction Wood so important?

It is precisely those properties which enable reaction wood to carry out its function in the tree that render it a problem for the timber industry. When Jaccard (1938) cut loops in which reaction wood had formed, the curvature immediately changed as internal stresses were released (Figure 1). In the case of the gymnosperm loop, in which compression wood had formed on the convex side of the lower curve, and the concave side of the upper curve, the effect of cutting the loop was to increase the radius of curvature of the lower section, and decrease the radius of curvature of the upper section. Thus the compression wood appeared to have been exerting a positive pressure prior to release. In the case of the angiosperm loop, where tension wood formed on the upper sides of the loop, the effect was the opposite, with release prompting a shortening of the tension wood side. These movements illustrate the phenomena associated with growth stress release during wood processing, further amplified by drying-induced deformations. The commercial significance of such effects is enormous, since timber containing reaction wood cannot be used where dimensional stability is required.

Other problems associated with compression wood include the difficulty of working the hard timber. Büsgen and Münch (1929) commented that it is very difficult to drive a nail into it. It is also brittle and prone to brash compression failure. The higher levels of lignin also increase costs for the pulp and paper industry since lignin is expensive to remove and was hitherto difficult to dispose of. However, increasing pressure on non-renewable natural resources mean that research is now looking into utilisation of this abundant waste product.

Tension wood suffers from similar problems of dimensional stability and is also difficult to work. The gelatinous fibres tear rather than cut, giving a wood surface containing tension wood a woolly appearance. On the other hand, the lower levels of lignin might be considered advantageous for the pulp industry. The problems created by reaction wood for industry are discussed in Chapters 6, 8 and 9.

If reaction wood were present in wood in only small amounts, these problems might be ameliorated. However, the fact that tree growth takes place subject to environmental pressures means that trees constantly have to make some reaction wood to brace themselves against the wind, to correct for windthrow and to support branches at the optimum angle. Even those trees which are perfect in form (from the forester's and timber merchant's point of view), with straight and vertical stems, may contain significant amounts of reaction wood. Vertical growth may only be achieved by constant corrections of tendencies to lean under the influence of wind, whose direction may change from day to day. For this reason it is essential that we have the tools for identification of reaction wood. It is not always easy to do this, and methods for doing so are reviewed in Chapter 7.

The evolution of reaction wood was an essential step in the evolution of trees. Without it, tall trees could not exist and there would be no timber of any size for industry to use. It is certain therefore, that the wood-based industries will have to live with reaction wood and allow for its behaviour. However, it is possible to reduce the levels of reaction wood by careful forest management and it may be possible to reduce the levels to the minimum required for successful tree growth through focussed tree breeding. These and other commercial issues are discussed in Chapter 9.

In a world where pressure on forests is increasing as demand for wood for traditional purposes is added to by demand from new uses such as biofuel, it is essential that we grow trees with high quality wood while optimising biomass production. This means that we need to find ways of keeping the amount of reaction wood in timber to a minimum compatible with the safety of the tree. In addition we should be actively seeking ways of using reaction wood and ensuring that wastage is kept to a minimum. This book provides the best scientific understanding of the formation, function and behaviour of reaction wood, which will help achieve these goals.

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