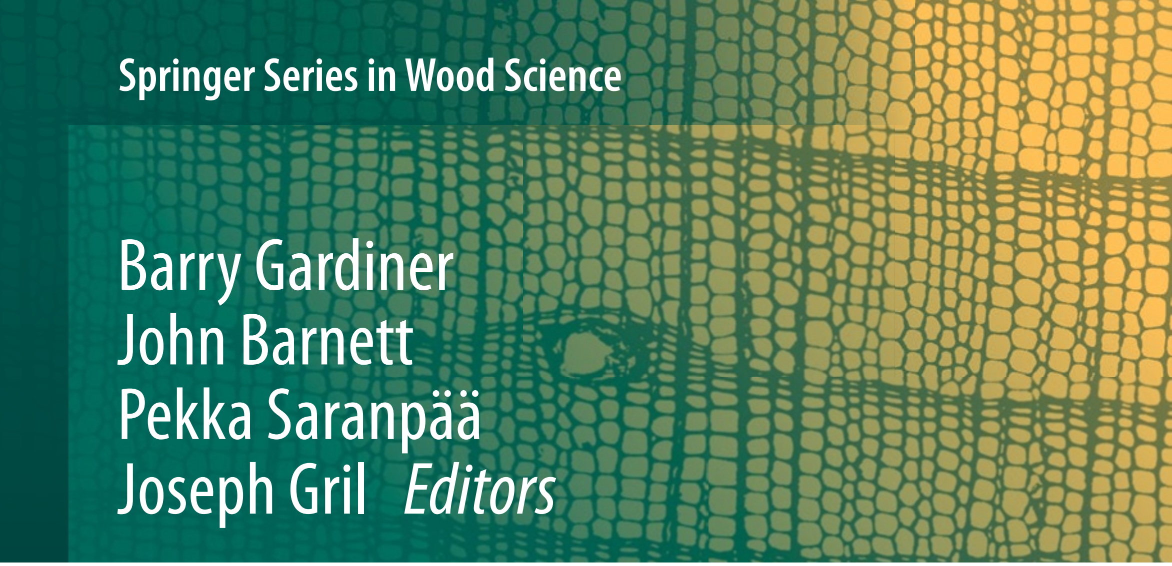

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Barry Gardiner
John Barnett
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Joseph Gril *Editors*

The Biology of Reaction Wood

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Preface

Reaction wood is wood produced by trees in order to orientate stems and branches in response to displacement and the requirements for light. The accompanying changes in the physical and chemical properties of the wood result in its having different mechanical and physical properties compared to normal wood including differences in colour, fibre properties, workability, distortion and strength. These have important consequences for wood-based industries in the processing and serviceability of products containing reaction wood. This has resulted in increased interest among wood scientists in the factors controlling reaction wood formation, the physical and chemical properties of reaction wood cells, and the way such changes are able to generate the stresses required to reposition stems and branches.

The European COST Action program COST E50 "Cell wall macromolecules and reaction wood (CEMARE)", which ran from July 2005 to June 2009, brought together wood scientists from 19 countries. The Action covered the whole range of issues related to reaction wood from cell wall biosynthesis to forest management and wood processing. In this way it attempted to link the environmental influences on reaction wood formation to cell wall formation and cell wall structure and subsequently to the consequences for wood and fibre properties and processing. It very deliberately brought together studies on compression wood and tension wood, the normal types of reaction wood in gymnosperms and angiosperms, respectively.

The genesis of the idea for this book was the realisation amongst the scientists involved in CEMARE that there was no synthesis in one place of all the different aspects of reaction wood. In addition, the definitive work on compression wood by Tore Timell is now almost 30 years old, and no such comprehensive work on tension wood has ever been written. Therefore, it was decided to pull together in one volume the latest understanding of reaction wood and to ensure that we discussed compression wood and tension wood together in order to highlight the similarities and differences in their formation and properties. The book covers everything from reaction wood morphology, anatomy, ultrastructure and cell wall polymers to the molecular mechanisms of reaction wood induction, and the biomechanical action and biological functions of reaction wood. In addition the physical and mechanical properties of reaction wood at all levels are discussed, focussing in particular on the impact of these properties on the utilisation of wood for different end products. Finally, there are chapters on detection techniques, the commercial implications of reaction wood and the influence of forest management.

The book will provide a valuable and important reference source on reaction wood for wood scientists and technologists, plant biologists and chemists, plant breeders, silviculturists, forest ecologists and anyone involved and interested in the growing of trees and the processing of wood. It is hoped that it will also provide a useful introduction to the subject for people new to this scientific area.

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Contents

Chapter 1
Introduction

J.R. Barnett, Joseph Gril, and 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 not only the

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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.

1.1 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" some 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 S_2 layer in the juvenile tracheids. Of all existing types of compression wood the so-called spiral compression wood is most peculiar. A band of compression wood that spirals from the pith towards the cambium may last for decades (Fig. 1.1). The reason for formation of spiral compression wood is unknown. 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. (1997). In contrast, Jacquiot and Trenard (1974) described gelatinous fibres in coniferous wood.

1.2 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

Fig. 1.1 Spiral compression wood in a Scots pine (*Pinus sylvestris* L.) stem from a first thinning site in southern Finland. The *disk* shows a band of compression wood that spirals four times clockwise from the pith towards the cambium. The formation of compression wood began when the tree was 5–6 years old and continued for several decades

gravitational pull, also developed an elliptical profile. They proposed that this helped to prevent the stem from falling over.

Hartig (1901) with spruce and Rasdorsky (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 (Fig. 1.2) 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

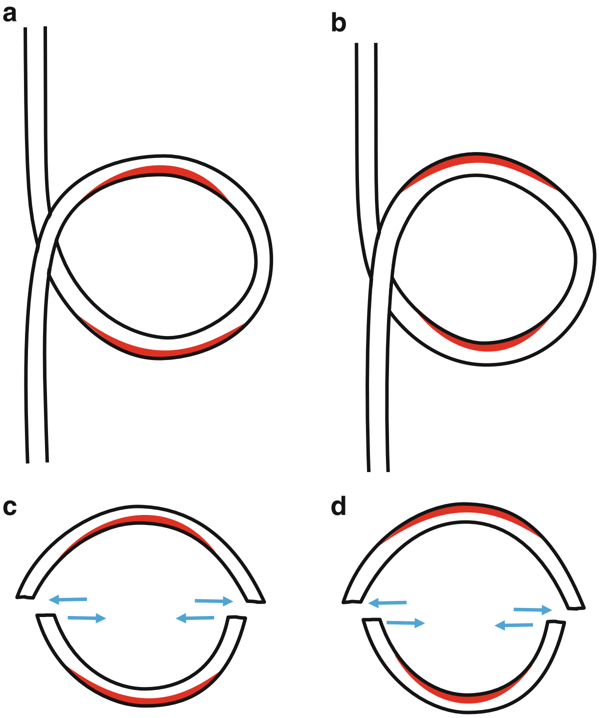

Fig. 1.2 Diagram after Jaccard (1938). Diagrammatic representations of (**a**) Loop made in a conifer stem. Compression wood is shown as a *thicker line* on the lower sides of the upper and lower parts of the loop. (**b**) Loop made in a woody dicotyledon stem. Tension wood is shown as a *thicker line* 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

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