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Biomechanical Action and Biological Functions

Meriem Fournier, Tancrede Alméras, Bruno Clair, and Joseph Gril

Abstract The main biological function of reaction wood is to act as “muscle” for trees, enabling them to control their posture. The key property to achieve this function is the development of high mechanical stress during the formation of reaction wood cells, called “maturation strains”. Actually, reaction wood formation is basically the asymmetric formation of wood around the tree circumference, with higher maturation strains on the side where reaction wood is formed than on the opposite side. This asymmetry enables stems to bend upward or to compensate for the downward bending induced by gravity. At the cross section level, the performance in this biological function is linked not only to the magnitude of this asymmetry but also to an effect of the cross-sectional size (diameter) of the stem. Eccentric growth and variations in wood mechanical stiffness are second order effects that can modify this performance. Differences in maturation strains between reaction and non-reaction woods are related to their specific cell wall structure and composition. The swelling of the cell wall matrix during maturation and the effect of microfibril angle explain the differences in maturation strains between normal and compression wood. However, this mechanism fails in explaining the high maturation shrinkage of tension wood, and several hypotheses at the molecular levels are still under debate. How trees perceive their gravitational disequilibrium is also an open question for physiologists. Integrative biomechanical modelling (from the polymer level to the cell wall, cross section and whole tree levels) enables defining key variables that explain the performance of reaction wood as a system that insures the stem motricity. Maturation strains can be precisely measured only

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in recently formed wood at the tree surface, but their changes during the whole tree life can also be estimated by retrospective dendrochronological analysis through structural markers of reaction wood. Lastly, wood in living trees ensures general storage, defence, vascular and skeletal functions, that ask general questions about synergies and trade-offs as the structural characteristics of reaction wood can affect all these functions.

5.1 Introduction

5.1.1 General Questions About the Biological Functions of Reaction Wood

Wood is made of different cell elements and the spatial and temporal organization of this heterogeneous structure allows it to perform several functions. For example, in temperate climates wood structure and functions differ within the growing season, so that earlywood and latewood are structurally and functionally different. Other examples are that due to the ageing process of heartwood formation, only the peripheral wood, i.e. the sapwood, is involved in sap transport and wound tissues are formed by cambial growth in reaction to injuries. Reaction wood is another kind of specialized wood tissue.

Wood anatomists were the first scientists who defined reaction wood, so that reaction wood structural properties are usually better known than its biological functions. Nevertheless, the IAWA definition (IAWA 1964) pointed out not only how reaction wood can be recognized from distinctive anatomical characteristics, but also how reaction wood is linked to tree morphology (reaction wood is “wood with distinctive anatomical and physical characteristics, formed typically in parts of leaning or crooked stems and in branches”). In addition, the IAWA definition also mentions the function of reaction wood as wood “that tends to restore the original position of the branch or stem when it has been disturbed”.

This assumed biological function of reaction wood poses several questions to different scientific disciplines:

- From a mechanical and physical point of view, how can reaction wood restore the position of a rigid woody stem? In particular how can wood formation produce the necessary mechanical energy and stress to bend growing stems?
- Wood technologists know that reaction wood is not just a wood pathological reaction or a peculiar characteristic of crooked stems and branches. Indeed reaction wood can also be observed in straight and vertical trunks. Does it confirm or contradict the assumed function of position restoration?
- Can physiology explain how trees perceive signals that trigger reaction wood formation? How is reaction wood formation genetically and biochemically controlled?

Lastly, wood trait analysis across wide environmental gradients is currently of great interest for plant ecology (Chave et al. 2009), in order to understand how plant distributions and growth are driven by environmental factors. How are wood biological functions that are linked to plant ecological strategies affected by reaction wood structure? To explore such a question, we need to define how all the relevant functional properties of wood differ between non-reaction¹ and reaction wood.

5.1.2 *Plant Movements in Woody Systems*

By analogy with the function of bones in animals, it can be said that wood stiffness and strength provides trees with an efficient “skeletal” system (Mouliia et al. 2006). However, this skeletal function is not the only mechanical function of wood fibres. The other biophysical function of wood is to provide stems with the ability of performing movement, i.e. a “motor” system (Darwin and Darwin 1880; Wilson 1984; Mouliia et al. 2006; Mouliia and Fournier 2009; Martone et al. 2010). Although usually much less often considered than the vascular and skeletal functions, this motricity function is of major importance to the biology of woody plants. Plant stems, and in particular woody stems, seem static at the usual observation timescale of humans, but they are not, and plant movements have been studied at least since Darwin’s works on this issue (Darwin and Darwin 1880). Stem reorientation movements are common, and they are necessary for plants to adapt to their environment, for example to avoid shade and maximize light interception, avoid obstacles or recover from mechanical perturbations. Figure 5.1 (from Alméras et al. 2009) illustrates movements observed in experiments where gravitropism is stimulated by tilting (the aim of such studies is to induce reaction wood in order to compare plant behaviour or analyse reaction wood physiology). Sinnott (1952) made a series of experiments with *Pinus strobus* and observed that tying of vertical shoot axes and lateral branches provoked significant bending movements, which tend to restore the initial position and was associated with compression wood formation. This seminal work on reaction wood induction demonstrated that reaction wood is not a simple response to gravity or mechanical stimuli, but is associated with the more complex regulatory function of posture restoration. Under natural conditions, Collet et al. (2011) observed on advanced regeneration of beech (*Fagus sylvatica* L., age: 10–31 years old, initial basal diameter 0.9–2.4 cm) that a gap opening stimulates radial growth associated with great righting movements (Fig. 5.2): between 2004 and 2008 the global tilt angle of the already lignified trunks changed from 58° to 76° (mean values on 31 trees, 90° is the vertical). All these studies illustrate significant changes of tree shape that

¹Note that in Chap. 2 the term “non-reaction” wood was used in preference to “normal” wood because “opposite” wood can also have different properties from “normal” wood.

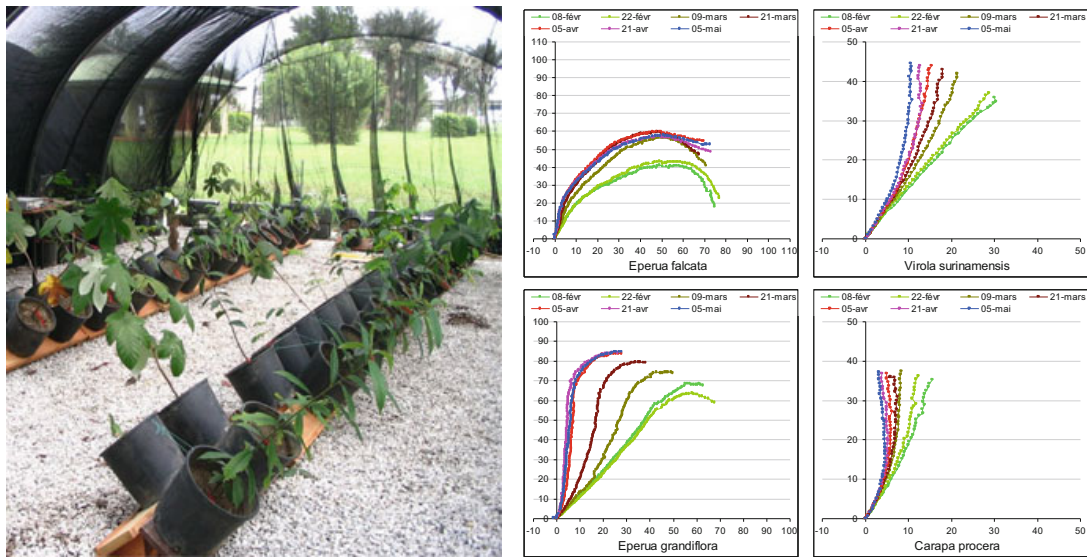


Fig. 5.1 Righting movements of young trees of different tropical species during a period of 3 months. Described in Alméras et al. (2009)

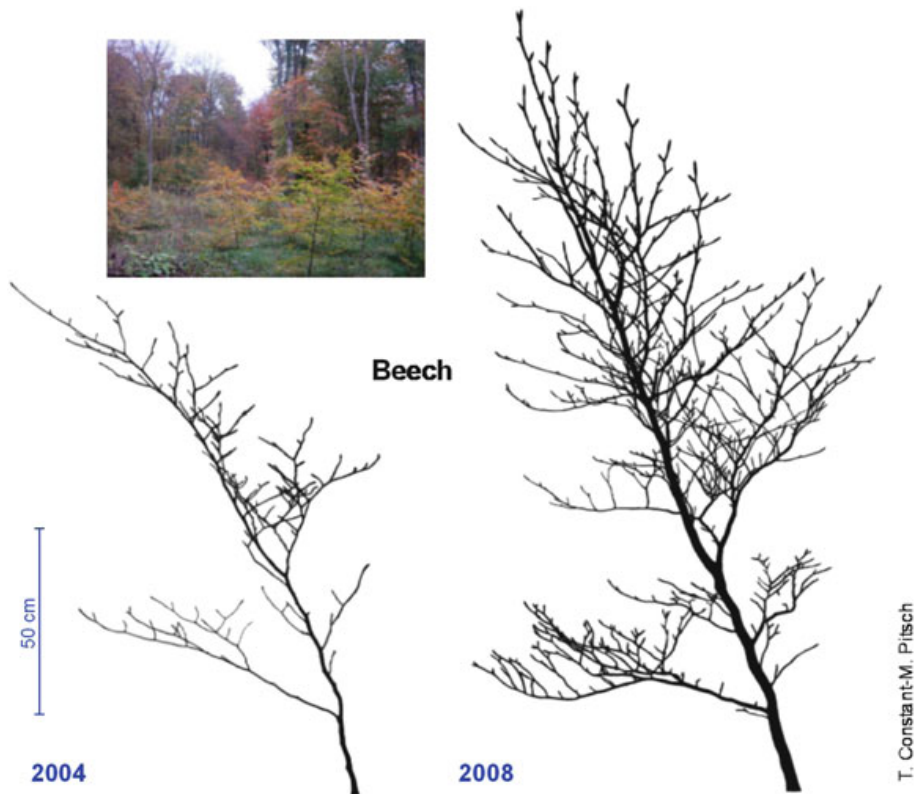


Fig. 5.2 Righting movements of a beech sapling during 4 years of growth. Described in Collet et al. (2011) (pictures T. Constant and M. Pitsch)

involve curvatures of the still lignified stem. This means that stem orientation is not only initially controlled by the direction of primary growth or branching pattern, but also mainly by later movements provoked by cambial activity and wood formation.

Moreover, because plants are slender structures growing in the field of gravity, motricity is necessary even in the absence of visible movement. Indeed, to maintain the orientation of a woody stem while it grows, it is necessary to compensate for the effect of the increasing weight by actively generating counteracting forces within the stem (Alm eras and Fournier 2009). This function has been termed the “posture control” and is more general than the function of stem reorientation. Its necessity can be understood through an analogy with terrestrial vertebrates, in which an active muscular system is necessary not only to perform movements but also to stay immobile because continuous corrections are necessary to compensate for small mechanical perturbations and keep a stable equilibrium position (Mouli a et al. 2006). Both stem reorientation and posture control are achieved by the active generation of mechanical stress during the development and maturation of wood fibres or tracheids. Reaction wood, as a tissue, is functionally specialized to provide this posture control.

5.1.3 Reaction Wood Is the Motor System of Posture Control in Woody Plants

Generally speaking, stem reorientation and posture control requires the generation of motion from bending forces. The basic mechanism for achieving this is similar in most plant stems including fungi, herbaceous and woody plants. It involves differential tissue expansion or shrinkage between the two sides of the stem, which generates a bending moment and thereby induces a change in stem curvature (Wilson 1984; Hejnowicz 1997). This mechanism will be set out in more detail in the following section.

As recently pointed out by Mouli a and Fournier (2009), the efficiency of this mechanism results from the balance between the motor process itself (which provides the mechanical energy for straining the active tissue) and the mechanical resistance of surrounding tissues. In herbaceous stems, the motor process is based on changes in cell turgor pressure, adjusting the swelling and shrinkage of the active tissue. The magnitude of stress generated by turgor pressure changes is sufficient to bend herbaceous stems because their tissues have low stiffness and therefore offer weak resistance to bending. Woody stems are, however, much stiffer, and the magnitude of stress required to efficiently bend them is much larger than for herbaceous stems. To achieve stresses of large magnitude, they use a specific motor process, not based on turgor (which is anyway lost when the cells die) but rather on the development of stresses directly in the cell walls at the end of wood formation. Therefore, the characteristic property associated with the reaction wood motor function is the ability to generate large mechanical stresses during the last

stage of cell development (cellular maturation), and this is achieved by specific transformations of the fibre walls. At the cell wall level, the process generating this stress is not yet completely understood, but current hypotheses and evidence will be discussed below.

The concepts and mechanisms involved in this issue have a general value beyond the question of “reaction wood” itself, because (1) the motor function of wood is also to some extent achieved by non-specialized (normal) wood cells, (2) all maturing cells develop strains in trees (e.g. Archer 1987b; Boyd 1972), or in monocots (Huang et al. 2002) and (3) conversely, specialized fibres found in tension wood are also found in other tissues than wood [e.g. in phloem (Gorshkova et al. 2010; Salnikov et al. 2008)] and in organs other than stems, such as roots (Fisher 2008; Schreiber et al. 2010) or tendrils (Bowling and Vaughn 2009).

5.1.4 Linking Reaction Wood Structure and Function

The structural characteristics of reaction woods have been introduced in Chaps. 2 and 3. At the cellular level, compression wood is not very different from normal wood and tension wood is usually defined by the presence of a gelatinous layer. Ultrastructure and chemical composition are the major features that define reaction wood. However, the distinction is not completely dichotomous because variations between non-reaction and reaction wood suggest a continuum in structure between compression wood, non-reaction wood and tension wood, with only the gelatinous layer in some tension woods as a truly unique characteristic (Mellerowicz and Gorshkova 2011). The general trend along this gradient is a decreasing microfibril angle, decreasing lignin content, and increasing cellulose content and crystallinity. Then, although gelatinous fibres are found in less than 40 % of botanical genera or families of angiosperms, tension wood—as wood defined along this gradient and associated with the reaction wood function—can be found in all angiosperm species. Such a continuum in structure can be a source of confusion. This is because although reaction wood can probably be found in any growing tree, it has been described mainly under extreme conditions (crooked stems or branches), so that many biologists consider reaction wood as an abnormal and scarce phenomenon.

Actually, the characteristic property associated with the posture control function is the ability to generate large mechanical bending stresses during cell development and maturation. The biomechanical analysis developed in the next section aims at understanding how stress is generated in any kind of wood, normal or reaction wood, and then, how transformation of the fibre or tracheid walls explains the stress variations that induce bending at the cross section level, and then the posture control at the whole organism level.

5.2 How the “Tree Muscle” Works: The Biomechanical Point of View

5.2.1 Evidence of Strain Generation in Maturing Cells

Growth stresses have been studied since the beginning of the twentieth century, with several syntheses (Dinwoodie 1966; Archer 1987a; Kubler 1987) of the pioneer works. Studies on this phenomena resulted from tree fellers and sawmillers observing surprising cracks and warp when cutting, sawing or machining green wood. Forest and wood researchers were asked to prevent such problems through silviculture or technological solutions and they tried to understand how mechanical energy could be stored during tree growth before being released by cutting. Synthesizing all the observations, Boyd (1950) concludes that this mechanical energy, namely growth stresses, originates close to the periphery of the tree during secondary wall formation. Actually, only a phenomenon that occurs immediately after cellular expansion can explain mechanical stresses in the youngest wood located just beside the cambium. Moreover, as stresses are always present and high (order of magnitude 10 MPa along the grain), the phenomenon must be closely regulated by wood formation with no requirement for an external source of energy. Actually, as concluded by Munch (1937–1938, cited by Archer 1987b; Dinwoodie 1966), such stresses could only be generated by “chemical forces” involved in the formation of the secondary cell wall and not by gravity or other external forces.

Later Archer and Byrnes (1974) described mechanically and mathematically how wood in growing trees becomes stressed just after its differentiation: during the maturation process, wood tends to strain, with a longitudinal shrinkage of about 0.1 % and a transverse swelling of about 0.2 % in the normal wood of both gymnosperms and angiosperms. As this new wood is “glued” onto the older stiff core of wood, longitudinal and tangential strains are prevented so that wood is in a state of longitudinal tensile stress and tangential compressive stress.

5.2.2 How to Bend a Growing Stem by Generating Maturation Strains in Differentiating Peripheral Wood?

Historically, growth stresses have been described as homogeneous tensions generated continuously around the growing cross section, so that the older internal core is compressed by the younger peripheral wood (Kubler 1959; Archer 1987a). For foresters interested in sorting or breeding trees with low peripheral stresses with the aim of increasing industrial wood quality, the question was how to determine which trees develop high levels of stress, in order to describe the ecological or silvicultural

situations leading to a high risk of felling cracks or timber splitting and distortion during sawing.

Observations of stresses at the stem periphery in different angiosperm tree populations emphasize the fact that high tensile stress values associated with high longitudinal maturation shrinkage and high risk of felling cracks are scarcely homogeneous, but concentrated in small angular sectors of tension wood. In gymnosperms, although high tensile stress values are not observed (so that the occurrence of felling cracks is generally low), an asymmetry of stresses is also observed as longitudinal maturation swelling in compression wood is opposed to maturation shrinkage in opposite wood (Archer 1987a; Fournier et al. 1994b). Then reaction wood is mechanically described as an active guy rope (for non-reaction or tension wood producing tensile stress) or a forestay (for compression wood producing compressive stress) that can bend the stem. This mechanical system can be modelled using the theoretical background developed by Archer and Byrnes (1974), Fournier et al. (1991), or Fournier et al. (1994a). Such mechanical models give the scaling laws of the motricity function from the cell wall to the whole tree (Fourcaud et al. 2003; Fourcaud and Lac 2003; Alméras and Fournier 2009; Coutand et al. 2011).

A first step is to describe how maturation strains generated in the differentiating cells act at the cross section level to provoke local curvatures through asymmetry of growth and/or cell wall properties. The basic but general equation of reaction wood action (Alméras and Fournier 2009) from the tissue to the cross section level expresses the elementary change in stem curvature dC_R (see Moulia and Fournier 2009), in terms of the cross-sectional diameter (D), growth (dD), and a dimensionless efficiency e that is a function of the asymmetry of maturation strains between the reaction wood and wood on the opposite side of the tree and different form factors (asymmetry of growth, and heterogeneity of wood stiffness between the core and the periphery):

$$dC_R = 4e \frac{dD}{D^2}.$$

As the rate of bending with radial growth dC_R/dD scales as $1/D^2$, righting movement kinetics change a lot with the tree size, as noticed by Boyd (1973) who mentioned that compression wood can bend only small trees. Moreover, the model can be applied to the analysis of experimental observations of tree righting movements (Coutand et al. 2007), in order to compare efficiencies between species (Alméras et al. 2009) and genotypes (Sierra-De-Grado et al. 2008) in tilting experiments, or individual responses in the natural environment (Collet et al. 2011), because it allows the separation of size and growth effects from wood properties and shape factors.

In addition, different components of the efficiency parameter e can be analysed including asymmetry of wood maturation strains, growth eccentricity and wood stiffness heterogeneity. The assumption of a sinusoidal variation around the cross

section circumference of ring width, longitudinal maturation strain α and wood modulus of elasticity (MOE) E (Alm eras and Fournier 2009) leads to:

$$e_r = \Delta\alpha \cdot f \cdot \frac{\bar{E}}{E_{\text{section}}},$$

where:

- $\Delta\alpha$ is the difference in maturation strain between the two opposed sides of the stem (along the bending axis).
- $\frac{\bar{E}}{E_{\text{section}}}$ is the ratio between the mean MOE of the new ring, and that of the stem section inside the new ring.
- The effect of circumferential variations in ring width and stiffness is accounted for by a form factor f :

$$f = 1 + \frac{3}{4}k_E \cdot k_O + (k_E + k_O) \cdot \frac{2\bar{\alpha}}{\Delta\alpha},$$

where $\bar{\alpha}$ is the mean maturation strain (around the circumference), k_E and k_O (between -1 and 1) are the relative circumferential variations of, respectively, the MOE and the tree ring width (see Alm eras and Fournier 2009 for details).

If the section is homogeneous and concentric, the form factor is 1 and e is the difference in maturation strain between the lower and the upper side $\Delta\alpha$, as assumed by previous models (Coutand et al. 2007; Fournier et al. 2006). The models show that the effects of eccentricity or stiffness variations can be positive (synergic effects) or negative. For example, in conifers, because the MOE of compression wood is lower, this variation has a negative effect on the righting movement (compared to the theoretical case of no variation of E between normal or reaction wood Alm eras et al. 2005b).

In order to calibrate the model from springback strains (i.e. strains measured at the stem periphery after removing the self-weight), Huang et al. (2010) modified slightly the expression of the efficiency e assuming that the force rather than each component (MOE and radial growth) varies sinusoidally. This assumption of sinusoidal variations provides an easy way to derive analytical formulas, but could be far from the real circumferential variation in wood properties. More general models (Alm eras et al. 2005b; Coutand et al. 2011) allow simulation of the real pattern of reaction wood formation including variable width.

5.2.3 *Is Reaction Wood the Main Way to Produce a “Tree Muscle”?*

Growth eccentricity is a complementary but second order effect often associated with reaction wood formation (Alméras et al. 2005b). Reaction wood is usually but not necessarily associated with faster growth (see synthesis on this subject in Schweingruber 2007, pp. 131–132). For example, Wang et al. (2009) and Tsai et al. (2012) described faster growth in opposite wood of branches. Nevertheless, in extreme conditions of eccentric growth such as buttresses that are known to act as tension members but usually not made of reaction wood (Schweingruber 2007, p. 132; Ter Steege et al. 1997; Fisher 1982), the posture control system can be induced by growth asymmetry alone without a change in wood properties (see Fig. 5.3). Eccentric growth without a clear modification of wood structure has also been mentioned by Fisher and Marler (2006) in *Cycas micronesica*. Similarly, in some species, stilt roots (which is an extreme case of eccentric growth consisting of new, external organs) plays a role in posture control (Leopold and Jaffe 2000) with no absolute requirement for reaction wood, although reaction wood is often present (Fisher 1982) to provide an additional driving force. In summary, in the most common tree species, the main driving force of bending arising from the maturation of new cells during radial growth is the asymmetry of wood properties between opposite wood and reaction wood (Fig. 5.3, case A or B).

As pointed out by Alméras et al. (2005b) and Huang et al. (2010), the asymmetry of the MOE increases the efficiency of tension wood (which is stiffer due to a high crystalline cellulose content with a low microfibril angle) but decreases the efficiency of compression wood (that is less stiff than normal wood because of its high microfibril angle). Moreover, the radial gradient of wood stiffness (Lachenbruch et al. 2011) increases the reaction curvature if the central wood is less stiff (as is the case for the juvenile wood of softwoods) but lowers the efficiency of reaction wood if the central core is stiffer. However, all these effects are of second order so long as the stiffness is within the usual range of variation for wood but things need to be reconsidered in peculiar cases such as hollow stems or plants with very soft cores (Alméras et al. 2009).

Lastly, taking into account the viscoelastic properties of wood, Coutand et al. (2011) demonstrated that creep could significantly catalyse the upward bending of stems even though the value of maturation strain (i.e. the quantitative difference between opposite and tension wood) remained the most influent parameter.

As a conclusion, reaction wood formation means from a functional point of view that wood of different maturation strains is created on each side of a tree and this is how they generate active bending movements to control the stems erect habit. Although some light compressive stress has been reported in opposite wood (Clair et al. 2006), the formation of both tension and compression wood (Fig. 5.3, A + B) that would be the most efficient system for stem redirection has not been observed in trees. For a given gradient of wood properties from reaction to opposite

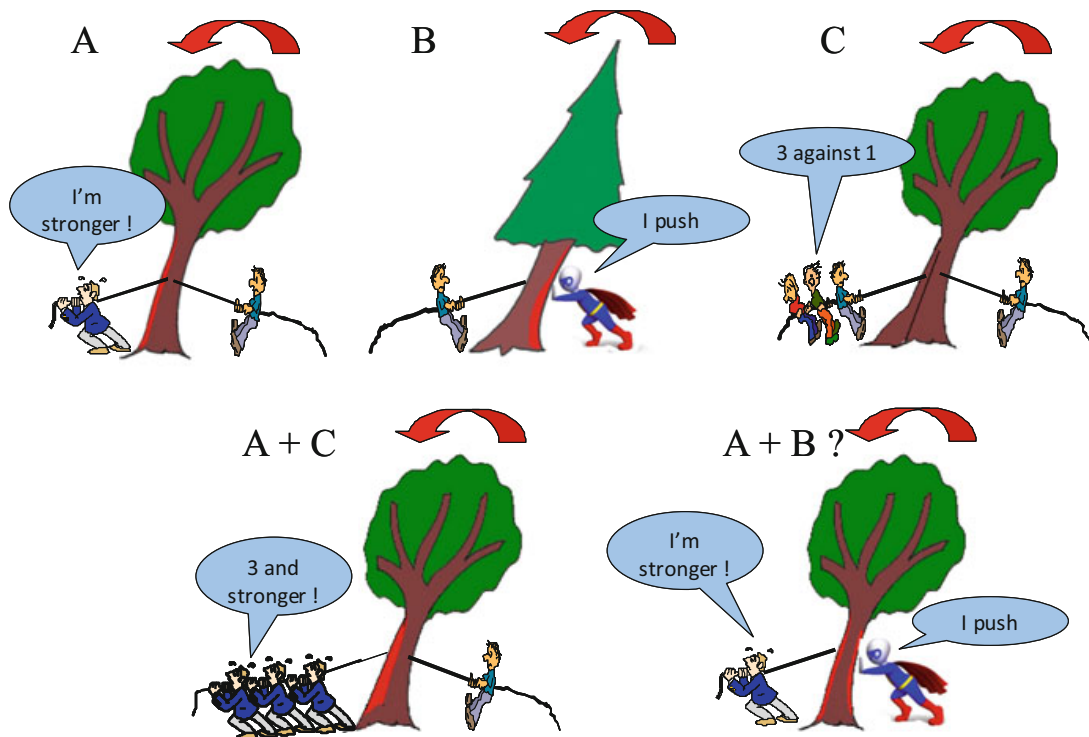


Fig. 5.3 The different ways to create a bending moment in a growing tree cross section: (A) tension wood in angiosperms (higher tension than opposite “normal” wood); (B) compression wood in gymnosperms (compression opposed to the “normal” tension in opposite wood); (C) tensile buttresses in angiosperms, or increasing growth with the same wood quality (i.e. the same tensile stress) so that the tensile force is greater; (A + C) is the commonly (but not systematically) observed situation of faster growth in reaction wood; (A + B) would be the never observed combination of tension and compression wood in the same tree

wood, the smaller the cross section and the faster the radial growth, the more efficient the reactive bending. Synergic effects linked with eccentric growth are also sometimes found.

5.2.4 How to Induce High Mechanical Strains in Differentiating and Maturing Cell Walls?

The question of maturation stress generation at the microscopic level—why and how this “spontaneous tendency to shrink” appears—has long been a matter of discussion. The swelling of the wood matrix substance during lignification has been proposed as the primary cause of maturation stress generation, together with lateral connexion established between microfibrils before lignin polymerization (Boyd 1950, 1972). According to the mechanism proposed by Boyd, the MFA controls the anisotropy of the resulting stress: swelling dominates for compression wood (large MFA), while in normal or tension wood (low MFA) the shortening along the microfibrils directly results in axial shrinkage. However, this mechanism fails to

explain the large tensile stress found in tension wood, and especially in G-layer tension wood, with little or no lignin present in the secondary wall. As an alternative, the hypothesis of shrinkage of cellulose microfibrils was proposed (Bamber 1987, 2001). Results obtained using micro-mechanical models showed that to account for the observed relation between microfibril angle and released maturation strains in conifer woods, a combination of both assumptions was necessary (Okuyama et al. 1994; Yamamoto 1998; Alméras et al. 2005a). However, the proposed mechanisms remain purely hypothetical, and no evidence of such behaviour has yet been provided at the molecular level.

The recent revival of interest in the question of the generation of maturation strains, linked to the acquisition of new knowledge about chemical composition, physical structure and mechanical state of the G-layer (see Chap. 3 for more detail), has generated new hypotheses (Goswami et al. 2008; Mellerowicz et al. 2008b). However, to date no convincing model has been provided and successfully tested (Mellerowicz and Gorshkova 2011). Because of the apparent paradox between the axial stiffness of the G-layer and longitudinal maturation strains of tension wood, some authors suggested that maturation stress must be supported not by the G-layer, but by adjacent layers of the tension wood fibre (Münch 1938; Goswami et al. 2008). This idea arose because the G-layer was often observed partly detached from adjacent layers, and therefore must be loosely connected and not able to transmit the stress to the surrounding tissue. Further observations showed that this detachment was a preparation artefact (Clair et al. 2005a). Based on a number of observations (Clair and Thibaut 2001; Clair et al. 2003, 2005b), it is clear that the G-layer is indeed submitted to axial tensile stress and transverse compressive stress as a result of maturation. Moreover, experimental evidence was recently provided that the cellulose microfibrils of the G-layer are put in tension during their maturation (Clair et al. 2011). This does not solve, however, the question of the primary cause of maturation stress. What mechanism generated tension in the microfibrils? A hypothetical effect of the daily variations in water tension in the cell lumen was suggested (Okuyama et al. 1995), but it was later proved that this external factor is not involved (Alméras et al. 2006). Therefore, the cause must be internal, directly related to a process occurring within the cell wall during or after its formation. It could be either a modification of the cellulose structure after its deposition or a transfer of stress between the matrix and the microfibrils, as is observed during wood drying (Abe and Yamamoto 2005, 2006; Clair et al. 2008). Recently, it was shown that the G-layer, like gels, is characterized by a large amount of water-filled meso-pores, having a mean size of 7 nm (Clair et al. 2008). Moreover, dimensional changes of microfibril aggregates due to variations in water content in the matrix have been observed (Lee et al. 2010). Therefore, changes in water content during maturation could be involved in the appearance of swelling or shrinkage strains in the matrix, depending on the osmotic concentration, the ion concentration and the valence (monovalent or divalent) of the cations (van Ieperen 2007). Figure 5.4 shows mechanisms that could produce longitudinal tension within a G-layer. The preferred mechanism (d) is the only one able to produce lateral compression also and is very similar to the one suggested by Boyd with lignin swelling within a

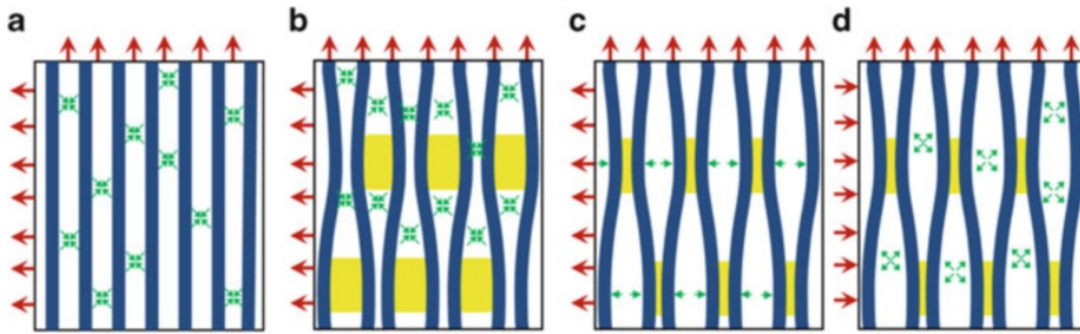


Fig. 5.4 Possible mechanisms of stress generation within a G layer: (a) matrix shrinkage only; (b) matrix shrinkage associated with the presence of stiff zones between microfibrils; (c) active creation of bridges between microfibrils; (d) matrix swelling between bridged microfibrils. Arrays of *red arrows* at boundary indicate the stress direction (outward: tension; inward: compression); *green arrows* within the domain indicate movements (horizontal: lateral movement of the microfibrils; inclined: matrix swelling or shrinkage)

trellis-like microfibrillar network (except that the swelling cannot be attributed to lignin in the G-layer). More studies are needed to explore these hypotheses and to predict their mechanical effect. Moreover, generic models need to be able to describe not only G-layer tension wood but also all types of tension wood characterized by high crystalline cellulose content.

5.2.5 Adjusting the Response to the Stem Requirements: How Do Trees Perceive Posture and React to Control It?

Gravi-perception, mecano-sensing and gravitropism are very general physiological processes in plants and a comprehensive synthesis of these topics goes far beyond the scope of this chapter. The reader could refer to recent review papers such as Moulia and Fournier (2009) or Moulia et al. (2006), or general books such as Wojtaszek (2011) or Gilroy and Masson (2008). However, the function of reaction wood cannot be described without some insight into how the reaction is biologically induced and controlled. As suggested by the terminology “tension” or “compression” wood, reaction wood is usually associated with mechanical stress. Compression or tension stress can be measured in recently differentiated compression or tension wood (see next section) but such stress is a biomechanical response and not a stimulus. The stimuli perceived by the wood remains an open question for molecular and cellular physiology, involving complex interactions between gravisensors such as statoliths, mechanosensitive channels, and photo-receptors. At a macroscopic level, dose response laws can be tested, such as Sachs’ “sine law”. This law states that the local response rate is proportional to the sine of the difference between the current position and a theoretical equilibrium position, called the gravitropic set-point angle, taking into account a time lag (reaction time). The first issue is how to choose the relevant response variable. In any plant

system (coleptils, hypocotils) usually studied by physiologists, observed lean is a confusing variable as the response basically involves bending and curvature rather than just angles of lean (Mouliia and Fournier 2009). Secondary growth induces further artefacts. Firstly, the response in terms of change in curvature is physically linked to the stem's initial radius and internal wood stiffness (see previous analysis in Sect. 5.2.2). Therefore, the slower reaction of bigger stems (or of basal parts of stems compared to distal parts closed to the apex) is not the result of a slower perception or physiological response, but is because bigger stems are stiffer and therefore less easy to bend. Secondly, compared to movement based on hydraulic pressure, the formation of secondary wall involves the mobilization of carbon assimilates with several constraints on the availability of resources, and slow characteristic times. In addition the similar responses of trees grown in very different environments demonstrate that stressed trees (e.g. drought or low-light conditions) have developed a much more efficient response because they need to compensate for their slower growth. Generally speaking, the assessment of stimulus–response curves cannot be based directly on the observation of righting movements, as variations of movements involve not only the gravitropic response but also variations of diameter and tree ring width. Lastly, the apparent lack of response in a leaning stem that maintains its position does not mean that there is no response and no mechanical work, because some sort of response is always necessary to counteract the gravitational bending due to growth in mass of the tree. Understanding how the posture control system reacts and acclimates to gravitational stimuli from the observation of reaction wood occurrence based on structural (chemical, ultrastructure of cell walls, anatomical) analysis should be more accurate than the direct observations of curvature changes provided that the link with the functional efficiency of reaction wood in the posture control is demonstrated through (1) strong relationships between maturation strains and the structural characteristics observed (see Sect. 5.2.4) and (2) a careful spatio-temporal analysis (because the structure is generally only observed retrospectively at the end of the process whereas the stimuli change with time during the movement). Actually, interpretations of experiments where different stimuli are applied (e.g. different initial inclinations) are easier to discuss when they are based on a fixed angle as done by Yamashita et al. (2007) who demonstrated on *Cryptomeria japonica* that the response increases with the tilt angle, up to a saturation level (30° of lean). However, up to now and even after a careful preliminary analysis eliminating the previously described artefacts, no unified theory based on physiological and mechanistic knowledge is able to explain the reaction wood distributions observed in Sinnott's loop experiments (Sinnott 1952) or in other seminal works (Archer and Wilson 1973). Actually, Archer and Wilson observed shifts in the location of compression wood from one side of the stem to the other. This distribution means that an opposite curvature is generated after the first reaction. This is obviously a necessity to ensure posture control as reaction wood formed all on the same side of the stem will lead to an upward curved stem not a vertical and straight one. But, as observed by Wilson and Archer and pointed out by Coutand et al. (2007), the puzzling question remains to explain physiologically the

“autotropic” perception as the shift develops before the stem has passed the vertical, increasing the performance of the shape regulation and avoiding oscillating systems. Recently, Bastien et al. (2013) demonstrated that the proprioceptive sensing of curvature changes is as important as gravisensing to understand gravitropic movements. Furthermore, light is well known to influence gravitropic responses with many poorly understood underlying physiological processes (Iino 2006).

5.3 Practical Assessment of the Functional Performance of the Posture Control

As developed in the previous section, reaction wood is the main motor of posture control, and posture control results from multi-scale processes. We have discussed reaction wood at the stem cross section level in detail in Sect. 5.2.2 and to investigate reaction wood influence at the stem level requires summing curvature changes and cross sections along the whole stem as done by Coutand et al. (2011) or Fourcaud et al. (2003). Maturation strains in reaction wood, because they are different from opposite wood, are the main relevant property at the tissue level to assess the reaction functional performance but, as previously shown, other characteristics at a more macroscopic level (tree size, reaction wood distribution, growth rate) have interactive effects. Moreover, maturation strains are explainable by cell wall structure and chemical composition (Sect. 5.2.4). Table 5.1 summarizes the different scales with relevant variables linked to reaction wood formation, at each level. At the whole tree level, the problem is how to assess the global performance of control as a growth strategy, involving kinetics and spatial patterns of reaction wood formation during the whole life and in the whole tree, and analysing how the shape control by reaction wood formation impacts tree ecological fitness by modifying stem buckling or breakage risk or canopy light capture efficiency.

5.3.1 *How to Measure or Estimate Maturation Strains*

Although the importance of multi-scale analysis must be emphasized, maturation strains (and more accurately the difference of maturation strains from reaction to opposite wood) is probably in many cases the most significant component of the reaction efficiency. Alm eras et al. (2005b) analysed statistically the contribution of different factors on the reaction efficiency of a diversity of tree species (11 angiosperms and 3 conifers) and found that the isolated effect of maturation strains explains 40–110 % of the righting curvature (values greater than 100 % are possible as the eccentricity of growth or stiffness variations can have a negative effect, see Sect. 5.2.3). However, other studies that estimated “ e ” from curvature observations (Coutand et al. 2007; Alm eras et al. 2009; Collet et al. 2011) on seedlings found

Table 5.1 Assessment of the performance of the posture control function due to reaction wood formation: summary of the relevant variables at the successive organization levels from the cell wall to the whole tree

| Level | Performance | Performance components (explicative variables) | Material |
|--|---|--|---|
| Cell wall | Cell wall maturation strain α_{wall} | MFA, cellulose and lignin content, cellulose crystallinity Mesoporosity of the G-layer? Organization of the cell wall (links between matrix and microfibrils)? Type of amorphous polysaccharides? | Cell wall from embedded or frozen sections Wood powder for chemical analyses |
| Wood (tissue) | Tissue maturation strain “ α ” | α_{wall} Area of tension wood fibres or compression wood tracheids | Microscopic sections |
| Maturing wood in a cross section | Efficiency “ e ” (see Sect. 5.2.3) linked to reaction wood formation | Circumferential variations of α Eccentricity of growth Radial variations of modulus of elasticity | Tree ring or peripheral new layer of cells |
| Growing cross section | Reaction curvature induced by reaction wood formation dC_{matur} during growth | Efficiency “ e ” Section size (diameter) Radial growth rate (dR/dt) Wood viscoelasticity | Stem cross section |
| Growing and loaded cross section and tree stem | Balance between reaction curvature dC_{matur} and gravitational curvature dC_{weight} | dC_{matur} and dC_{weight} function of lean, stiffness and viscoelasticity, weight increase (dW/dt) Spatial integration of curvatures along the stem | Successive cross sections along the stem, other organs inducing self-loading (branches, leaves...) |
| Whole life of a whole tree | Spatial and temporal distribution of reaction wood as a global strategy that impact long-term stem buckling and breakage risk and canopy light capture efficiency | Trajectories and cartography of reaction wood formation versus gravitational loads and other disturbances (see Sect. 5.3.3) | Wood retrospective analysis (discs and chronological series of tree rings) at different heights, adding biomass and morphological data (tree architecture analysis) |

very high values of “ e ” of 10^{-2} when the highest values of maturation strains generally measured (see below) are several times lower, suggesting that in small stems, other factors play a greater role.

Fournier et al. (1994a, b) and Yoshida and Okuyama (2002) compared different methods used to measure maturation strains at the stem periphery. The most direct method (Fig. 5.5a) consists of gluing a strain gauge or a small extensometer to the wood surface (after debarking) and then measuring the released strain after drilling two grooves designed to isolate the tissue located under the gauges from the mechanical influence of surrounding wood, so that the initially impeded maturation strains are entirely released. The technique requires a lot of care to measure strains properly (order of magnitude of strains are 1–10 μm for a length of 10 mm) when conducted in the field on wet wood (see Jullien and Gril 2008 for a numerical analysis of the method). A widely used and cheaper technique initially developed by Archer (1987a, b) consists in measuring the variation of distance between two pin targets (distant between 45 and 50 mm) induced by the drilling of a central hole (Fig. 5.5b). The higher the initial stress, the higher the variation of length. Therefore, the measurement estimates the maturation strain, although an accurate quantitative interpretation requires a more intensive analysis because the measurement depends not only on the initial strain but also on the sensor geometry (relative hole size versus distance between pin targets) and wood elastic anisotropy. As this method measures length variations of 10–500 μm , extensometers cheaper than electrical strain gauges can be used.

Whatever the measurement method, some bias can occur because the measured released strain is not always equal to the actual maturation strains (i.e. strains generated during the maturation of the last peripheral wood cells and impeded during growth). Actually, released strains measure all the mechanical strains supported by peripheral wood since its formation. They provide a reliable estimate of maturation strains only if maturation strains are very high compared to other loads that may have acted on peripheral wood since its formation. Such assumptions are generally adequate for big stems, but may be wrong in many specific cases. For example, in very thin (not stiff) and tilted organs such as branches, even in very new and peripheral wood, a quite low variation of weight induces a strain of the same order of magnitude as the maturation strains (and especially in some fruit trees, where fruit loads are an important mechanical component, see, e.g., Alm eras et al. 2004 for an example from apricot trees). Notice that in leaning stems, it is of great importance to measure maturation strains in the natural tilted position without displacing the stem, as suppressing the whole weight induces high non-reversible strains that are not the opposite of the strains provoked by gravity in the growing tree. Actually, these gravitational strains in the youngest wood located at the stem surface are due to the weight increment added during the last millimetres of radial growth, which is generally much lower than the whole weight. Maturation strains will also differ significantly from released strains in very slowly growing organs where the peripheral wood could have undergone a quite complex and long mechanical history. For example, in buttressed trunks (Fig. 5.6), we measured compressive values of released strains far from the ridges and such released strains just expressed the fact that only the ridges are growing, so that the other parts of the trunk have been progressively compressed by the growing ridges.

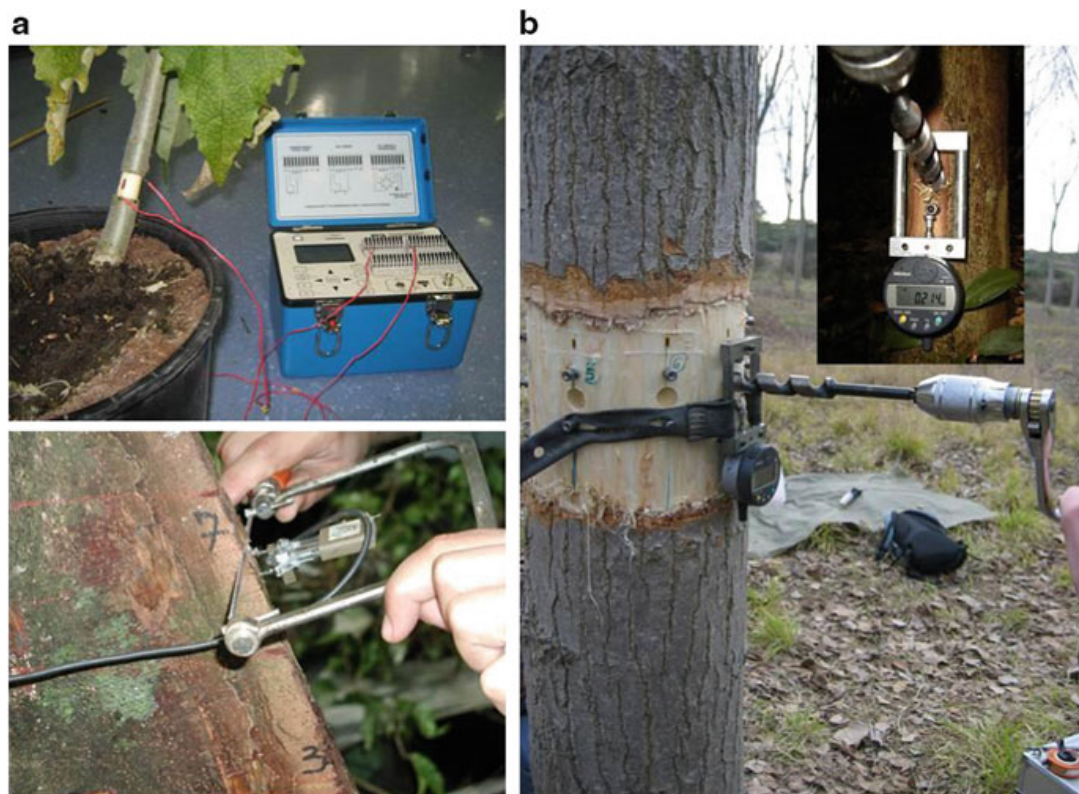


Fig. 5.5 Two different methods to estimate maturation strains: **(a)** the two grooves method using strain gauges or strain sensors. In this method, the measured strain is very localized and gives quite directly an estimation of the initially impeded maturation strain (if grooves are deep enough and not too far from the gauges, see Jullien and Gril 2008). **(b)** The single hole method. This method disturbs the bi-dimensional field of stress so that the measurement is an indirect indicator of the initial maturation strains (but depends also on the hole geometry, wood anisotropy, etc.). See Fournier et al. (1994b), for more details

5.3.2 Retrospective Analysis of Posture Control History Through Structure Analysis

Peripheral released strains are a good proxy of maturation strains because of the hypothesis that maturation strains are completely impeded during the growth process and are the only significant and long-term (rather than short-term such as induced by the wind) stress process in recently formed wood. Therefore, they can be only measured in the youngest peripheral wood. To estimate maturation strains in older wood, dendrochronological approaches must be developed, using quantitative and robust relationships between maturation strains and structural or physical wood characteristics, and using retrospective mapping of the variables chosen as proxies for maturation strains assessment (e.g. Dassot et al. 2012). Although many studies have established good relationships between maturation strains and (1) MFA, chemical composition or other cell wall characteristics or (2) drying shrinkage or other physical characteristics (e.g. Bailleres et al. 1995; Clair et al. 2003; Fang et al. 2008, see also Sect. 5.2.4), they haven't been developed, probably because the mapping of such characteristics for a large number of tree rings, cross sections and

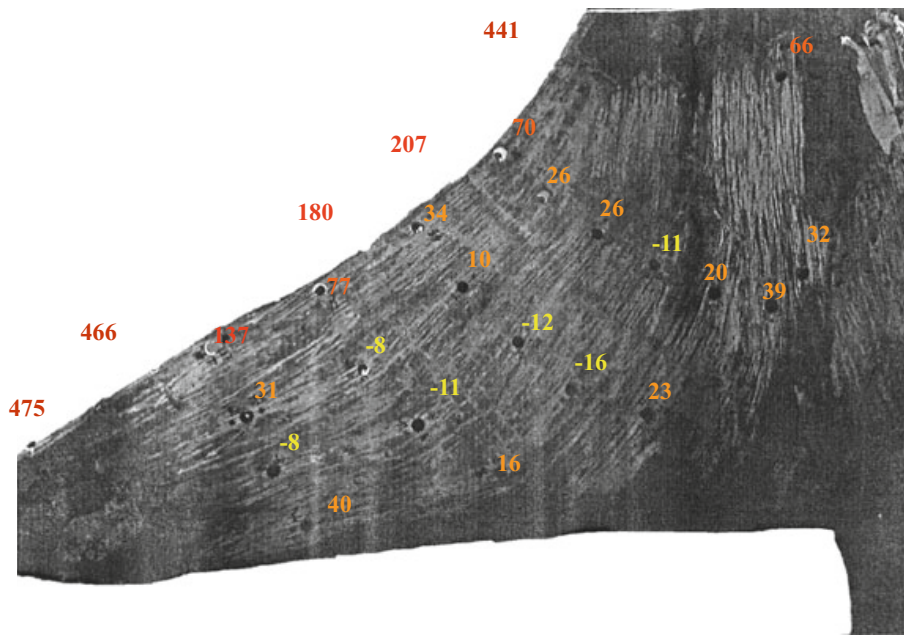


Fig. 5.6 Map of released strains (figures indicate the crude measurements in micrometres made by the single hole method and CIRAD’s sensor) in a buttress trunk (*Ragala sanguinolenta*, Sapotaceae). Compressive values do not mean that compression wood is formed, but that only the ridges are growing significantly (M. Fournier, unpublished data)

trees requires expertise in high throughput metrologies (e.g. Silviscan for MFA, Evans and Ilic 2001). Up to now retrospective analyses have relied on staining methods (e.g. Grzeskowiak et al. 1996; Badia et al. 2005; Barbacci et al. 2008; Dassot et al. 2012). Such methods give binary information (presence/absence of reaction wood) and fail to estimate the “severity” of reaction wood (see Dogu and Grabner 2010), i.e. the continuous variations of structural maturation strains in both types of wood. Although such retrospective works are infrequent and rarely discussed by dendrochronologists (see Duncker and Spiecker 2008, or Stoffel and Perret 2006 for a more in-depth discussion about the potential of reaction wood for dendrochronological methods), they are usually successful in linking reaction wood formation to environmental events such as (1) wind events (e.g. Zielonka et al. 2010), (2) snow fall (Casteller et al. 2011), (3) rainfall on conifers growing on slopes (Furukawa et al. 1988), (4) ice storm damage (Hook et al. 2011), (5) high thinning (e.g. Washusen et al. 2005), (6) establishment and competition periods in fast growing species (Badia et al. 2006) and (7) apical bud death of mature trees (Loup et al. 1991) or young shoots (Delavault 1994)

5.4 Consequences of Reaction Wood on Wood General Biological Functions

In the previous section, we emphasized the specific function of reaction wood as a motor of posture control. As stated in introduction, wood is a multifunctional tissue made of specialized cells or sub-tissue, and the tissue or cell design adapted to one specialized function should therefore impact other functional properties. The aim of this paragraph is to study how other functional properties are modified in reaction wood, in order to discuss trade-offs between different wood functions. The term “functional properties” here refers to properties of the wood in the living tree that characterize its ability to perform a biological function. This excludes a number of properties that are of interest for the use of reaction wood as a product but not directly involved during the tree life, such as drying shrinkage or dry mechanical properties (these are presented in more detail in Chaps. 6 and 8).

5.4.1 Wood as a Multifunctional Plant Tissue: Vascular, Skeletal, Defence, Storage and Motor System

The transport of sap from the roots to the leaves and the mechanical strength and stiffness that allows the erect-against-gravity tree habit are the main wood functions usually considered by plant ecologists (e.g. Chave et al. 2009). Water transport and support are functions performed by dead elements such as vessels and tracheids in the living organism, and their performance and safety against embolism are related to biophysical laws and properties. Vessels or earlywood tracheids in the sapwood form a vascular system that has the primary hydraulic function of sap transport. Fibres or latewood tracheids are specialized in mechanical functions. They greatly improve the stiffness and strength of the stem, providing safe mechanical support for the foliage, which is necessary for the tree to grow in height and extend its crown. Additionally, living elements of wood (ray cells and axial parenchyma) perform physiological functions such as defence against pathogens, and the transport and storage of nutrients. All usual wood cell types can be found in reaction wood tissues: fibres or tracheids, rays, and, in the case of angiosperms, vessels and axial parenchyma. Table 5.2 summarizes the wood functions for each specialized cell or tissue.

5.4.2 “Skeletal” Properties: Mechanical Stiffness and Strength

The two main wood mechanical properties related to the skeletal function of wood are stiffness and strength in the fibre direction. These properties are a function of the

Table 5.2 The multifunctionality of wood, which is composed of specialized cells and tissues

| Function | Specialized tissues | Specialized cells |
|---|--|----------------------|
| “Skeleton” = mechanical strength and stiffness | Latewood (in temperate climates) | Fibres of tracheids |
| “Muscle” = movement | Reaction wood | Reaction wood fibres |
| Sap transport | Sapwood Earlywood (in temperate climates) | Vessels or tracheids |
| Storage of nutrients | No specialized tissue | Parenchyma cells |
| Defence against biotic attacks (insects, fungi, etc.) | No specialized tissue | Resin ducts |

amount of water bound to its walls. In the living tree, where some free water is always present in the vascular system, the walls remain water-saturated regardless of the amount of free water. This implies that the mechanical properties of green wood do not depend on the amount of water in the conduits. However, they differ from the mechanical properties of wood in the hygroscopic domain, i.e. for water contents lower than the fibre saturation point (at approximately 30 % moisture content). Properties in the hygroscopic domain will be specifically discussed in Chap. 6. In the present chapter we will always implicitly refer to reaction wood properties measured in the green or water-saturated state, which are those directly relevant to its biological functions. Although shear and even transverse properties are obviously very important for the skeletal function (e.g. Mattheck and Kubler 1995), it is usually assumed that the most relevant mechanical properties are those measured in tension/compression/bending in the fibre direction. Therefore, structural parameters controlling the growth stress and the motor function, such as MFA, lignin content and composition, mesoporosity in the case of G-layers, all have an effect on other properties with stiffness being the most obvious one, and so indirectly impact the other functions of the tissue.

The stiffness of wood, usually quantified by the MOE, is a measure of the amount it bends or distorts as a function of the load imposed on it. Actually, the whole stem stiffness against gravitational forces combines the wood stiffness (MOE), the cross section diameter and the position of the centre of mass (linked to the stem length). A high wood stiffness (MOE) is thus a necessary condition for stems to maintain their self-standing habit despite their high slenderness (length/diameter ratio). The micro-mechanical design of wood makes it very efficient for this function, mainly because of its cellular structure and the ultrastructure of its secondary walls, that can be described as a polymeric matrix reinforced with oriented microfibrils made of stiff crystalline cellulose. The MOE in the fibre direction of reaction woods often differs from that of normal woods, the general trend being that tension wood is stiffer than normal wood and compression wood less stiff. The stiffness of compression wood has been extensively documented (Timell 1986) and due to the high MFA and low cellulose content of compression wood, it is always significantly lower than that of normal wood of the same species.

Data about tension wood are less abundant in the literature but clearly show the opposite trend. For example, in a study of eleven tropical angiosperm species where tension wood and normal wood were identified based on the values of residual maturation strains (Alméras et al. 2005b), the MOE of tension wood was found to be 10–30 % higher than in normal wood for six species but two species had a slightly lower MOE for tension wood (–10 % and –17 %). Three other tropical species, as well as the poplar tree (*Populus* spp.) examined in the study, exhibited a larger difference with tension wood being approximately 50 % stiffer than normal wood. Coutand et al. (2004) who examined small specimens of poplar tension wood found them to be three times stiffer than opposite wood. In chestnut (*Castanea* spp.) (Clair et al. 2003), the MOE of wood was found to be correlated with the residual maturation strain (indicative of the presence of tension wood), tension wood being approximately 50 % stiffer than opposite wood. This work also demonstrated that variations in stiffness were correlated with the proportion of fibres having a gelatinous layer, characteristic of the tension wood fibres for this species.

Strength is a distinct property, expressing the ability of the material to support mechanical loads without breaking. A large strength is necessary to withstand external loads (such as wind, snow, falling trees or animals) without structural damages. Wood strength can be described by a critical stress (MOR) or a critical strain, at a given stage of failure or at the elastic limit (i.e. the point where the relationship between stress and strain is no longer linear). There is usually a significant correlation between the MOE and the MOR at the elastic or failure limit because both are influenced by wood density. Therefore, because tension wood is usually stronger than other woods, its formation as a “muscle” for the motricity function has a beneficial effect on the performance of the skeleton function of the rest of the wood in a tree, whereas in conifers, because compression wood is generally weaker, trees must manage a trade-off between the “muscle” function and the skeletal function of the wood.

However, such a quick theoretical analysis of trade-offs and synergies can lead to the wrong conclusions. Basically, the skeleton performance at the relevant tree level involves not only wood stiffness and strength but also geometry and load, and therefore, for a given amount of biomass, making a thicker stem with less dense weaker wood is much more efficient for the skeletal function (see Larjavaara and Muller-Landau 2010 for more discussion on this topic). Moreover, even at the tissue level, MOE and MOR are not the only criteria that define the skeletal function. Critical strains at the failure or elasticity limit, in different loading modes (compression, shear, etc.), that are independent of MOE and wood density could be candidate additional criteria. To date they have been scarcely used, probably due to the lack of extensive databases on these properties. As the critical strain at failure for compression wood submitted to compressive loads is very high (due to its high MFA and low cellulose content), this should be a positive trait for the skeletal function.

5.4.3 *Vascular Properties: Hydraulic Conductivity and Vulnerability to Embolism*

Two physical properties are mainly used to quantify the functional hydraulic properties of wood: conductivity and vulnerability to embolism. In wood, water transport is monitored by gradients in negative pressure, i.e. water tension (Tyree and Zimmermann 2002). The conductivity expresses the relation between the water flow in wood and the pressure gradient. A large conductivity allows provision of water to the foliage while minimizing water tension in the conduits. Excessive water tension increases the probability that an embolism will occur. Because an embolized conduit can no longer contribute to water conduction, wood conductivity decreases when water tension becomes larger. Plant vascular systems have varying vulnerability to embolisms and safety against embolisms is directly related to the plant's ability to resist drought and maintain photosynthesis in conditions of large evaporative demand. Unfortunately, there are few studies on the vascular functional properties of reaction woods.

Concerning tension wood, Gartner et al. (2003) examined hydraulic conductivity and vulnerability to embolisms of stem segments of *Quercus ilex* seedlings that had previously been left inclined to induce the production of tension wood. They could not find any difference between the controls and the inclined stems. We did a similar experiment on seedlings of six tropical species (T. Alméras and S. Patiño, unpublished data) and also did not find any significant difference in hydraulic conductivity between controls and previously inclined stems, for any of these species. Note, however, that these two sets of experiments were performed on stem segments containing both tension wood and normal wood, so that normal wood possibly masked the specific properties of tension wood or compensated for them. It is generally considered that tension wood has fewer and smaller vessels than normal wood (Dadswell and Wardrop 1955). In an anatomical study of 21 tropical species, Ruelle et al. (2006) found that vessel frequency was systematically lower in tension wood than in opposite wood, but did not find a systematic pattern for vessel size, except for species with normally large vessels which generally had smaller vessels in tension wood than in opposite wood.

Studies on compression wood hydraulics clearly show that it has reduced conductivity. In Douglas-fir branches, Spicer and Gartner (1998) found that the lower halves, containing compression wood, had a 30 % reduction in conductivity compared to the upper halves. This lower conductivity is probably related to the lower lumen diameter of compression wood (Spicer and Gartner 1998). In a later study, they found that conductivity was 50 % lower in compression wood than in normal wood, but could not find any consequences on the water potential at the whole-plant level (Spicer and Gartner 2002). Working on Norway spruce, Rosner et al. (2007) found that the amount of compression wood in stem segments was negatively correlated with its conductivity, but not with its vulnerability to embolisms. On the same species, Mayr and Cochard (2003) found that compression wood conductivity is 79 % lower than that of opposite wood, and that its

vulnerability to embolisms was slightly higher. Further examination of Norway spruce compression wood (Mayr et al. 2006) revealed that in the compression wood tissue, the first-formed tracheids of an annual ring, called “light bands”, have a primary hydraulic function and partly compensate for the very low conductivity of pure compression wood.

From the above studies, it is clear that reaction woods generally have lower hydraulic performance (especially for gymnosperms) than non-reaction wood, but because other wood parts partly compensate for this, the presence of reaction wood has only a minor influence on the hydraulics at the whole-plant level.

5.5 Conclusions on the Ecological Significance of Reaction Wood

Reaction wood impacts tree ecology in different ways: first, it has indirect effects because it modifies other wood traits that are linked to tree physiological functioning (see Sect. 5.4), it changes the pre-stress system in wood which is designed to prevent the tree from breaking (Mattheck and Kubler 1995), and finally it is the main motor of posture control (see Sect. 5.2).

Section 5.4 reviewed the variations of mechanical and hydraulic properties in reaction wood and concluded that it slightly decreases hydraulic performance and can increase or decrease the skeletal performance. To our knowledge, no one has yet studied the possible impacts of reaction wood on wood storage function (and anyway the storage function is not yet to date quantified as a tissue traits in the same way as hydraulic and mechanical functions). Moreover, as illustrated in Table 5.1 for the “muscle” function, each function is performed at the tree level, and therefore a relevant analysis of performance or safety must be done not only at the scale of tissues and cells but also at larger scales. Although a comprehensive multi-scale analysis of all wood functions is beyond the scope of this chapter, one must keep in mind that trade-off at the tissue level can be compensated for at the organism level, and that ecologically the relevant level is the population. So, for example, a large area of sapwood can compensate for low conductivity or a low MOE, and a high water flow is not required if the leaf area is small. Similarly a low MOE is easily offset by a thicker stem and high stiffness is not necessary to support low weights. Generally speaking, discussing the organism performance should include discussion of mechanical loading or disturbance (not only the intrinsic performance of the involved tissue). Actually, at the level of the whole organism, the performances of wood functions (hydraulics, skeletal, motricity, etc.) are very dependent on the stem size and shape. This is especially relevant to the posture control function where the wood properties (maturation strains) cannot be analysed independently of weight disturbance or cross section diameter and radial growth.

There are also important interactions between the skeletal and the “muscle” functions. Controlling the posture by bending stems from peripheral wood requires

counteracting the stem stiffness, which is a basic skeletal property. Therefore, as shown in Table 5.1, although the main tissue trait involved in the motor function is maturation strain, the MOE and the stem diameter are part of the “muscle” performance. Moreover, maturation strain and stiffness or strength share common anatomical determinants at the cell wall level, such as the microfibril angle.

Reaction wood could also be expected to have an impact on strength at the stem level and not only at the tissue level because it modifies the pre-stressing system. Actually, as wood is less strong in compression, this pre-stressing system that puts the periphery under tension is also believed to prevent the tree from breakage (Mattheck and Kubler 1995; Bonser and Ennos 1998). Therefore, the high peripheral tensions of tension wood should be an advantage in resisting bending forces (wind and gravity) in the living tree. However, no one has observed a significant relationship between the level of peripheral stresses and mortality rate, and moreover, Huang et al. (2002) report a reverse distribution of stresses (periphery under compression) in coconut that is known for its slenderness and its strength along windy coasts. Thus, even if high peripheral tensions are an advantage in the living tree, such a trait is not under strong selective pressure.

The use of wood properties from large databases has had great success in plant trait analysis, which aims at explaining plant strategies in different environments from plant strategy axes defined by reduced sets of independent traits (e.g. Chave et al. 2009). Wood density, which is the construction cost of the tissue per unit of volume, is often found to be a good proxy to the first order in predicting variations of the mechanical properties expressed as stiffness (MOE) or as critical stress at failure (MOR). Wood density (a measure of wood porosity: the ratio of cell wall volume to cell volume) is primarily responsible for the large variations of mechanical properties observed between tree species. However, as mechanical properties depend also on cell wall properties, large variations of mechanical properties can also be observed independently of wood density. For example, compression wood, although denser, has a significantly lower MOE than normal wood. Therefore, although not studied yet by ecologists, genetic and environmental variations of reaction wood occurrence could upset the validity of wood density as a general proxy for wood traits. Moreover, as already mentioned, the relevant level for discussing fitness and functional performances is the whole tree, so that discussing ecological performances through wood or cell wall traits requires an integrative biological view. For biophysical functions such as conductivity, skeletal support, motricity or posture control, biomechanical models are useful for integrating tissue and cell properties within the larger structure, taking into account mechanical loads and tree geometry. Therefore, in-depth and complete ecological studies are required, taking into account simultaneously this integrative biological view, more realistic biophysical views than simple compression-tension bending or maximal conductivity, and the construction costs versus benefits of the different wood tissues.

A last but not least question is to know whether posture control by reaction wood formation is a key ecological process. As shown in Sect. 5.3.2, dendroecological approaches use very severe reaction wood as an efficient marker (associated with

other traumatic reactions) of extreme events and disturbances such as storms. Another point of view is that reaction wood formation is not traumatic but very common and usual in “normal life” as gravitropic movements are a strong requirement to build a long living and gigantic but very slender erect structure such as a tree stem. Therefore, the traits involved in this process, including reaction wood presence and properties, should be studied as part of general plant strategies more or less expressed according to genotypes and conditions of stress, competition or disturbance (and not only in extreme conditions of disturbance). Gravitropism is widely studied by plant scientists (e.g. the book of Gilroy and Masson 2008), but although it is quite easy to demonstrate that without reaction wood, no tree could grow and stand up in the long term (Alméras and Fournier 2009; Fournier et al. 2006), plant ecologists who are unfamiliar with plant biomechanics are reluctant to recognize that posture control is as important a function in trees as hydraulic or skeletal functioning. There are two main reasons for this. First, current ecological studies are based on large databases and there are no equivalent large technological databases for maturation strains as there are for MOE, MOR or wood density. Then, looking only at maturation strains or reaction wood occurrence is not very informative because, as already discussed, the posture control function involves several interacting variables, and only a systemic view (rather than a single plant trait approach) can help to determine the exact effect on plant performance versus constraints. Secondly, posture control is a dynamic process that is not easy to observe or follow. For example, when under perfect control the plant reacts to gravitational constraints but always remains perfectly vertical and straight! Because a small tree with a thin cross section bends more easily the gravitropic process is probably more important in the first ontogenetic stages, with major long-term consequences (Dassot et al.; 2012). Long-term observations in permanent plot studies, for example of survival probabilities of young trees as a function of the performance of their posture control function are necessary for a better integration of reaction wood studies in tree ecology.

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