COMPRESSION WOOD FORCE GENERATION AND FUNCTIONAL MECHANICS

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ABSTRACT

Evidence shows that lignification causes significant dimensional changes during differentiation of wood cells. Because lignin occupies sites in the cell wall similar to those occupied by water, the theory of anisotropic shrinkage can be used to deduce that compression wood tends to expand longitudinally during lignification. Consequently, large forces are generated on the underside of a leaning stem; with assistance from forces in tissue elsewhere in the cross-section, these cause reorientation movements. The characteristic mechanical properties of compression wood cells contribute to maximising their functional value in supporting the displaced tree, and in its reorientation movements.

INTRODUCTION

Compression wood is formed in gymnosperms on the lower side of branches, and of the stem or trunk of a leaning tree. Hartmann (1942) and others consider that where the attitude of the stem, or the relationship of the branches to the stem has been changed by external forces such as ground disturbance, strong prevailing winds, or a broken leader, compression wood is formed to restore the structural organ to its optimum position. In stems, compression wood is found at and below the position of the bend, crook or comparable deformation developed by the corrective mechanism.

In trees growing vigorously, generally there is a local stimulation of rate of growth at the position where compression wood is being differentiated (Westing, 1965). Thus on the lower side of a leaning stem, xylem forms at a faster rate than elsewhere, and the cross-section becomes eccentric relative to the pith. Because of its location and association with corrective reactions, Münch (1938) and others have suggested that compression wood generates strong, active pressures, which push the displaced stem or branch back towards the optimum position. It is compatible with this that, in whatever direction branches may be forced away from their normal angle to the stem, compression wood is differentiated below, above or on either side of the branch, depending on which position would be most effective for the location of a counter-pushing force designed to restore its normal attitude (Hartman, 1942; Sinnot, 1952).

Much research has been reported on factors associated with compression wood, including stimuli thought to cause its differentiation, anatomical, chemical and physical characteristics, and the manner in which it is presumed to affect a functional mechanical response in the tree. Extensive reviews of the resulting literature have been published by Onaka (1949), Low (1964), and Westing (1965, 1968). Münch (1938) suggested that the intrusive longitudinal growth of the primary wall of the compression wood cell was a necessary factor associated with the forces involved in reorientation movements.

Also, Münch and other investigators have postulated that the secondary walls of the cells may have the most important influence on the generation of corrective forces. He proposed that this force generation and righting action could result from longitudinal expansion within the secondary wall. He suggested that it could be a consequence of the relatively large angle to the cell axis at which the cellulose microfibrils were disposed, the high intensity of lignification, and the thick cell walls.

It has been assumed that experimental demonstrations, showing substantial longitudinal expansion of compression wood when cut out of the tree (Jacobs, 1945; Münch, 1938), indicated that in the tree it expands and pushes longitudinally within the lower side, and so bends the stem upwards to achieve reorientation movement. However, that expansion does not prove that the measured strains were autogenerated, rather than a "locked-in" result of the external forces bending the tree, and so causing a corresponding shortening on the lower side of the bend. Westing (1965) sought to demonstrate that reorientation was achieved as a result of compression wood causing a substantial increase in the length of the lower side of the stem, and a corresponding decrease in the upper side. In calculations related to measurements of upward-curving trees of *Picea* sp. and *Tsuga canadensis,* he assumed the distribution of consequent strains would be identical with that in a simple cantilever beam which was fixed in the ground and then bent by a lateral force. However, there were serious errors involved in his method of calculation. These will be discussed later.

Hypotheses on the method of generation of strong reactive forces in compression wood have lacked vital supporting data. However, now there is evidence that lignification is a factor responsible for significant dimensional changes in wood cells. Earlier, it was reported for a number of species by Frey (1926), Alexandrov and Djaparidze (1927), Preston and Middlebrook (1949), Onaka (1949) and others, that lignification during differentiation leads to a swelling in the thickness of walls of fibres. Recently, deductions made by Boyd (1972), from the data of Grozdits and Ifju (1969), showed that during differentiation but subsequent to completion of the primary wall and the S_1 layer of the secondary wall, there was a significant increase in overall radial width of normal wood cells of a gymnosperm. For the successive stages of development of the cellulosic framework of the cell wall, the data enable this swelling to be correlated with the progress of lignification.

An analysis of the consequences of these and associated dimensional changes has been facilitated by the studies of expected dimensional changes in wood during shrinkage. The estimated changes were related to the microfibril angle in the cell wall (Preston, 1942), and additionally to the matrix material (Barber and Meylan, 1964). The mathematical model, as developed by Barber and Meylan, enables the anisotropic shrinkage behaviour of wood to be deduced from a knowledge of the microfibril angles in its dominant cell wall layers, and the corresponding relative stiffness of the microfibrils and the matrix and encrusting materials including lignin.

By an inverse analogy, for which justification has been discussed previously (Boyd, 1972, 1973), it was shown that the theory of anisotropic shrinkage could be used as a basis for prediction of the physical effects of lignification. Thus consequent relative changes in length, width and thickness of the several layers of the cell wall may be deduced. Further, it was shown that the dimensional changes in cell walls, that resulted from their lignification, would lead to the development of substantial stresses in normal wood (Boyd, 1972). It was pointed out that these stresses were identical in nature (longitudinal and transverse tensions and compressions) with those that constitute the system of growth stresses known to occur in trees of all species. In addition, for gymnoperms it was demonstrated that they were quite adequate to account for the high intensities of longitudinal growth stresses that have been measured in straight trees, and also for the magnitudes of the radial and circumferential stresses.

The foregoing evidence of a strong causative relationship between growth stresses and lignification, and the demonstrated practicability of estimating the associated dimensional changes within cells, on the basis of shrinkage theory, provide good general justification for continued use of the method. Extensive additional confirmation of the validity of this analytical procedure is adduced, as its use can explain the presence and all characteristics of helical fissures in compression wood (Boyd, 1973). This situation is indicative of a firmly-established basis, for applying the same method of analysis, to test the hypothesis that significant lengthening tends to occur in compression wood cells at the time of their lignification. If a lengthening tendency is so deduced, it then becomes practical to extend the study to investigate whether substantial stresses would be generated as a consequence.

In compression wood, the unusually large compressive stresses that have been measured at the periphery, on the underside of the stem, are in marked contrast with the tensile stresses which are normally present in a straight stems of otherwise similar trees that are more than a few years old (Jacobs, 1945; Boyd, 1950a; Boyd and Schuster, 1972). Of that total compressive stress, some would be accounted for by the centre of gravity of the tree not being vertically above the centre of its base section. However, auto-generated functional stresses must also exist if reorientation movements are caused by the compression wood. Therefore, it is proposed to investigate whether the particular anatomical features of compression wood could account for the development of unusual auto-forces, and for the special functional mechanics attributed to this tissue.

II. SIGNIFICANT MORPHOLOGICAL AND ANATOMICAL FACTORS

A number of characteristics of compression wood could be of significance in an investigation of its supposed tendency to increase in length, and thus to generate large reaction forces during differentiation. Those pertinent to the analysis are listed below; they have been identified by many different investigators, and reviewed by Onaka (1949), Low (1964) and Westing (1965).

1. *Cell Form and Wall Arrangement*

Compression wood cells tend to round in cross-section, may have large corner spaces between them, and often exhibit distorted and bifurcated tips (illustrated by Wardrop, 1965), that are indicative of intrusive growth. The thickness of the cell wall is approximately twice that of normal earlywood, and similar to normal latewood. As with normal wood, the primary wall (P) and S_1 are thin relative to the S_2 layer of the secondary wall. Frequently the S_1 layer is considerably thicker than in normal wood, particularly near the corner spaces (Casperson and Zinsser, 1965). Often the secondary wall contains a special, electron-dense zone at the S_1/S_2 boundary, but the typical S_3 layer of normal wood is absent. Generally numerous splits, through the full thickness of the S_2 layer, occur at approximately equally-spaced positions around the cross-sections; these run parallel to the microfibrils in S_2.

2. *Lignification*

Summarising the literature, Westing (1965) stated that on average compression wood contains 28 per cent more lignin than normal wood, but "the excess lignin appears in large part to be associated with the middle lamella". However, there is also a high concentration of lignin in the S_1/S_2 layer (Wardrop and Davies, 1964).

3. *Microfibril Angles in the Cell Wall*

As with normal wood, the P and S_1 layers have their microfibrils oriented at angles of about 70° to 90° to the cell axis. Wardrop and Davies (1964) were uncertain whether the cellulosic framework of the S_1/S_2 layer had an S_1 or S_2 arrangement of microfibrils, but Côté *et al.* (1968) considered it has S_1 orientation.

For the S_2 layer, most authors, including Münch (1938), Onaka (1949), Westing (1965), and Wardrop (1965), have not made precise statements on microfibril angles or cited extensive measurements; but generally they indicated microfibril angles of about 45° or 50°. Sonntag (1909) reported angles of 48° to 71° for Douglas fir. In two trees of *Pinus radiata,* Wardrop and Dadswell (1950) measured cells "from the last-formed latewood"; angles were from 23° to 42° in tissue having "compression wood present". However, the latter values probably are not typical for compression wood cells; it was not stated that they were for cells with characteristic helical fissures. Similarly, Harris and Meylan (1965) reported X-ray measurements of angles that did not exceed 40° for radiata pine compression wood. Judged on recent observations at this laboratory, which identified very wide variability of microfibril angle between cells in each of a range of tissues including typical compression wood, normal cells were almost inevitably included in the *tissue* measured by Harris and Meylan. The normal (and transition) cells would substantially depress the average (X-ray value) below the value representing true compression wood *cells.*

III. RATIOS OF MODULUS OF ELASTICITY OF CELLULOSE TO MODULUS OF RIGIDITY OF MATRIX MATERIALS

To estimate strains generated in compression wood cells, as a result of their lignification, the procedure is based on Barber and Meylan's (1964) analysis for shrinkage. Thus for each wall layer, it is necessary to have a reasonably approximate estimate of the ratio (MR) of modulus of elasticity* of the cellulose microfibrils, to modulus of rigidity (shear modulus) of the matrix and encrusting materials, including lignin. The determination of the required MR values has been based on the work of Sakurada *et al.* (1962), Mark (1965), Goring (1963), Srinivason (1941), Dulmage and Contois (1958), Mark and Gillis (1970), Barber and Meylan (1964), Barber (1968), and Westing (1965). Details of the derivations are given by Boyd (1973).

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* In this context, the modulus of elasticity of the cellulose represents the force required to extend by unit amount longitudinally all microfibrils within unit area of the cross-section of a wall layer. It involves the distribution density (proportional volume) of the cellulose in the complex of matrix and encrusting material.

While the MR values cannot be precisely determined, it will become obvious that the results of the following analyses are not highly sensitive to likely extreme variations in those values. Accordingly, values listed in Table 1 provide a good working base.

TABLE 1—Wall layer moduli ratios

Wall layer	Moduli ratio (MR)
M & P	5 to 10
S_1	10 to 20
S_1/S_2	5 to 10
S_2	50

IV. DIMENSIONAL CHANGES IN CELLS DURING LIGNIFICATION

For the estimation of proportional dimensional changes induced by lignification, it is required to know the equivalent strain ratios corresponding to particular microfibril angles and MR values. Typical strain values, as derived directly from Barber and Meylan's analysis, are given in Table 2. An approximate value of Poisson's ratio is also

TABLE 2—Strains* associated with lignification of wood cells

Micro-fibril Angle (Degrees)	For Moduli Ratio = 50			For Moduli Ratio = 20		
	Cell Length	Cell Width	Wall Thickness	Cell Length	Cell Width	Wall Thickness
0	0.03	1.48	1.48	0.06	1.46	1.46
10	—0.01	1.48	1.52	0.04	1.45	1.50
15	—0.07	1.46	1.59	—0.01	1.44	1.56
25	—0.24	1.38	1.83	—0.15	1.35	1.79
35	—0.39	1.01	2.34	—0.23	1.01	2.16
40	—0.27	0.56	2.70	—0.10	0.64	2.39
45	0.13	0.11	2.97	0.26	0.24	2.51
50	0.59	—0.26	2.74	0.63	—0.08	2.37
55	0.98	—0.37	2.27	0.96	—0.24	2.14
65	1.41	—0.26	1.78	1.35	—0.19	1.76
	For Moduli Ratio = 10			For Moduli Ratio = 5		
40	0.12	0.69	2.13	0.33	0.77	1.86
45	0.43	0.36	2.23	0.55	0.53	1.91
50	0.72	0.10	2.12	0.79	0.34	1.86
55	1.01	—0.05	1.94	1.00	0.20	1.77
65	1.31	—0.02	1.69	1.26	0.14	1.55

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* The listed strains are expressed in the form of "strain ratios", i.e., as fractions of the strains which would be expected in the matrix material if there were no modifying influence of the cellulose microfibrils.
The "moduli ratio" is the ratio of the modulus of elasticity of the microfibrils to the modulus of rigidity of the matrix material.
Negative values in the table indicate that those strains are contractive in nature; other strains are expansive.
The data in this Table are based on the effects of water causing anisotropic swelling of dry wood cell-wall substance (Barber and Meylan, 1964). There is circumstantial evidence (Boyd, 1972), that at least in the sense of comparative strains at particular microfibril angles, the data are equally applicable to dimensional changes associated with lignification.

required for compression wood, particularly for the S_2 layer. This has been based on data given by Kollmann and Côté (1968) for normal wood tissue, that given by Mark and Gillis (1970) for the several wall layers of normal wood cells, and on its characteristic anatomical structure. Using all these data, in conjunction with those in Table 1, and also those on the anatomy and morphology of compression wood cells, the strains induced by lignification of each wall layer can be calculated, as demonstrated by Boyd (1973).

In this way it is shown that, for each wall layer except S_2, there is a small tendency for an overall circumferential expansion during lignification. Further, it was deduced that the outer wall layers effectively prevent circumferential contraction of S_2, despite its strong inherent tendency. In addition, because of similar and simultaneous strain tendencies induced in adjacent differentiating cells, the slight lateral expansion tendency of each is prevented, except radially towards the cambium. Nevertheless, it was deduced that the restraint in the tangential direction could induce only a negligible effect in the longitudinal direction.

It was demonstrated that all cell wall layers expand in thickness as a consequence of lignification. However, partly because the inter-cellular spaces lead to only limited restraint being placed on minor modifications of the initial circular cross-section of the cell, the secondary longitudinal effects of wall swelling were proved to be negligible, compared with the primary longitudinal dimensional effects of lignification. Primary longitudinal effects in the outer layers are very similar to each other, and therefore compatible. In accordance with a temporary assumption of no interaction, these longitudinal effects have been listed in Table 3, with several alternative microfibril angles in the S_2 layer.

TABLE 3—Longitudinal strains* (ratios) caused by lignification

For the outer layers of the cell wall	+ 1.42 (expansive)
For the S_2 layer	
with a microfibril angle of 43°	— 0.03 (contractive)
with a microfibril angle of 55°	+ 0.98 (expansive)
with a microfibril angle of 75°	+ 1.58

* The magnitude of a particular strain, or change in length per unit length of cell wall, could be found by multiplying its "strain ratio" by the value of the strain which would occur in the three coordinate directions parallel and perpendicular to the cell wall, if that were composed only of isotropic matrix material, i.e., if it were presumed that there were no cellulose microfibrils present.

V. INDEX OF LONGITUDINAL FORCE POTENTIAL

In the context of this paper, the strains caused by lignification are considered in relationship to their force-generation potential, and the functional responses of the tissue. The index of longitudinal force generation is derived by multiplying the area of the inner and outer wall layers, expressed as a ratio relative to the whole cell wall, by the elastic modulus (stiffness index E) for the respective layers, and then multiplying the products by the corresponding strain ratios given in Table 3. The estimates of these areas and stiffness values are discussed in Appendix I. In Table 4, the sums of the corresponding force-potential ratios† for the inner and outer layers are given for three alternative representative microfibril angles in S_2.

TABLE 4—Longitudinal force-potential ratios for compression wood

Microfibril angle in S_2	Force-potential ratio
43°	+ 0.4 (expansive)
55°	+ 3.1
75°	+ 4.7

The force-potential ratios indicate that, with increasing microfibril angles greater than about 40° in S_2, differentiating compression wood cells generate a correspondingly more powerful autoforce, which tends to extend their length. Nevertheless, until a substantial volume of compression wood is formed, the longitudinal expansive tendency would be overwhelmed by the effect of unbalanced external forces such as gravity; i.e., the actual expansion would be much less than the compressive strain imposed by the external forces. However, in a vigorously-growing tree, the net effective expansion would ultimately exceed the imposed compression, and lead directly to reorientation movements. On the other hand, it is not essential to the functional mechanics of stabilisation and reorientation movement, that in the tree there should be a net expansive effect of the newly-differentiated compression wood; this will be discussed later.

Preliminary to consideration of functional mechanics, it would be helpful if the force-potential ratio for compression wood cells could be converted into stress equivalents. Unfortunately necessary data for this are not available; but an indirect estimate can be made. As a consequence, the auto-force potential, due to lignification of the thick secondary wall of the compression wood cell, can be compared with alternative proposed sources of auto-forces, that some investigators have thought capable of affecting reorientation movements in trees.

VI. ESTIMATED AND MEASURED STRESSES IN COMPRESSION WOOD

1. *Assessment of Stresses Induced by Lignification*

As estimate of the stresses (stress potential) induced by lignification of normal wood has been made by Boyd (1972). At the same time, the general validity of the result was shown by comparison with the measurements of growth stresses developed in the xylem in the vicinity of the cambium. Multiplying that calculated stress potential, by the ratio of the calculated strains due to lignification of compression wood and normal wood respectively, gives an approximation to the stress-generation potential of compression wood.

Justification for the method, and the detailed procedure in the calculations are given

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† The "force-potential ratio" is used here as a comparative index of potential for auto-force development in the differentiating cell. It includes the same multiplying factor as the "strain ratio", i.e., one third the volumetric swelling due to lignification. It also includes the constant conversion factor for transforming into force equivalents, the product of the weighted values of layer areas, corresponding values of moduli of elasticity, and relevant longitudinal strain ratios.

in Appendix II. From these it has been concluded that compression wood cells, having a microfibril angle in S_2 of about 50°, are capable of generating an expansive auto-force having a compressive-stress equivalent of about 10.35 MPa.

2. *Alternative Source of Auto-stress Development*

Münch (1938) considered that an unexplained resistance, encountered during intersusception growth, was an essential factor in the development of longitudinal pressure leading to reorientation movements in trees. Apparently he thought that the longitudinal forces could be transferred only through the tightly-intergrown tips of the cells. However, repeated experimental observations (Wardrop and Addo-Ashong, 1963; Mark, 1967; Koran, 1967; Davies, 1968; Grozdits and Ifju, 1969; Keith and Côté, 1968) show that when wood has been subjected to failure loads in either tension, compression, bending or shear, the ultimate failure mode always involves splitting within or between cell wall layers, parallel to their length, and usually also breaking across the length of the wall layers. Theoretical studies, such as those of Mark and Gillis (1970), confirm the manner of stress transfer, and its dependence upon bonds along the whole length between cells, wall layers, and lamellae, rather than on end-to-end contact between the cells. Consequently a physical barrier, to intersusception growth of the primary wall, is not a necessary factor in auto-force generation leading to reorientation; and forces generated within the secondary layer of the cell wall could readily be applied to reorientation.

However, with a hypothesis somewhat similar to that of Münch, Frey-Wyssling (1952), supported by Wardrop (1965), suggested that with the intercession of viscoelastic action the turgidity involved in the intrusive growth of the primary wall, or protoplasmic pressure, might be the origin of significant expansive forces and reorientation movements in trees. That potential has been estimated in Appendix III. There it was deduced that such forces could not be applied to reorientation movements. In any case, the maximum auto-stress potential that could be developed in the primary wall zone would be two orders of magnitude smaller than that generated by lignification of the S_2 layer; therefore it could not be significant.

3. *Evidence on Stresses Generated in Compression Wood*

Numerous authors have reported qualitative evidence of reactive stresses in compression wood that are so high that they cause the bending of moderately-large tree stems during reorientation movements (Westing, 1965). For such stresses to be effective, generally intensities should be much greater than normal growth stresses. Explicit evidence on the relatively high potential for auto-stress generation in compression wood is provided in Appendix IV.

Using data published by Hallock (1966), Watanabe (1965), and Jacobs (1938, 1945), it is shown that compression wood generates expansive auto-stresses of about 10.35 MPa. Also, for each set of results, a ratio of about five exists between stress intensities in compression wood and normal wood. Further, it was demonstrated that the same ratio applied between the reaction wood (tension wood) and normal wood of angiosperms. These data indicate that most tree species could have a comparable potential for increase in auto-stress generation, as cell wall anatomy was changed from a normal to reaction type, when reorientation movements are stimulated. The compression wood anatomy also causes a reversal of the normal type of stress due to lignification, from contractive to expansive.

VII. MECHANICAL PROPERTIES OF COMPRESSION WOOD AND THEIR FUNCTIONAL SIGNIFICANCE

1. *Mechanical Properties of Compression Wood*

At the normal moisture content in the tree, compression wood is stronger in compression than normal wood, by an average of about 30 per cent (Onaka, 1949; Rothe, 1930; Trendelenburg, 1932; and Pillow and Luxford, 1937). It exhibits unusually great extensibility before failure when stressed in tension; Sonntag (1909) reported corresponding maximum strain values of 3.6 to 7.0% for compression wood of Douglas fir, whereas in normal wood the strain causing failure is of the order of 1% (unpublished data). The modulus of elasticity (E) for compression wood subject to compression is low, being on average little more than half and occasionally even a lower proportion of the corresponding value for normal wood (Hartig, 1899; Rothe, 1930; Trendelenburg, 1932). The E in tension also is only about half that of wood from the opposite side of the tree (Hartig, 1899).

2. *Functional Effect of Cell Extension During Differentiation*

Because of the natural tendency for differentiating compression wood cells to extend longitudinally, a gradual lengthening, albeit proportionately small, occurs in the under-side of a leaning tree. It has been suggested by Münch (1938) and others that this is the mechanism responsible for the displaced structural organ being forced back towards the normal position. This appear to be the basis of Westing's (1965) calculations of the lengthening of the underside, and forced compression and consequent shortening of the upper side of the stem, in the process of correcting the lean of a tree. Accordingly, it may be thought that if the bending stress due to gravity or any external agency were greater than the auto-stress potential of the compression wood tissue, the expansive tendency would be negated, and a net shortening effect imposed by the external force. However, because proper consideration of the functional effects and consequences must include the whole tree, and all forces acting at or with effect on any particular cross-section in it, the viewpoints above do not adequately represent the actual situation.

In the part of the tree subject to corrective bending, normal wood tissue, which is located on the sides parallel to the plane of lean, and also the tissue situated on the side opposite to the compression wood, in any cross-section of the stem, each have a natural tendency to contract in length during differentiation, as has been discussed for normal wood by Boyd (1972). The tissues to the sides confer a mutually-balanced stiffening against external forces transverse to the lean, while those at the upper face tend to pull the tree back towards the vertical. Thus the action of compression wood alone does not counteract the bending moment; the effective restoring moment is developed jointly by the tendency for auto-lengthening of tissue on the lower side of the stem, and auto-shortening of that on the upper side. Indeed, even without any auto-expansive cells being differentiated on the lower side, a counter moment could be developed and cause effective reorientation after the less-extreme displacements. There is a requirement only that the tissue on the lower side should tend to contract to an extent significantly smaller than that on the upper side.

Where compression wood is being formed, usually differentiation at that position is stimulated to a rate much faster than elsewhere in the cross-section (Burns, 1920;

Casperson, 1963; and Westing, 1965), and particularly so relative to the opposite side of the stem; there it is usually suppressed relative to normal. An important effect of rapid differentiation of compression wood cells is to reduce the maximum stress on the lower side of the bend, and thus reduce the possibility or extent of damage by excessively-high external forces. Simultaneously, there is a reduction in the compressive shortening of tracheids there, and therefore some reduction in the total deflection of the stem.

A special functional significance could also attach to the tissue which forms on the upper side of the stem at the same time; this often "exhibits a slight tendency towards tension-wood structure", as noted by Westing (1965) and a number of other observers. The implication of the variation from normal in this "opposite" tissue, is that it may generate greater stress of a tensile character than does normal wood. In such case, it would increase its contribution to corrective or righting action in conjunction with the compression wood.

Measurements made here, of peripheral longitudinal stresses in two radiata pine trees growing in very similar conditions in a plantation, indicate something of the significance of the foregoing statements. The trees were 22 yr old and growing vigorously. One was 1.63 m girth under bark at the measuring section at height 0.6 m, and had a bend in the basal 2 m such that the nominally vertical top of the tree was displaced 0.75 m relative to the base. The "major diameter" (in the plane of the initial lean) was 0.53 m, and that at right angles 0.45 m. Maximum compressive stress was 1.38 MPa at the periphery in the plane of lean. On the high side of the periphery, maximum tensile stress was 4.14 MPa. As the upper length of the stem was vertical, evidently it had stabilised its attitude. A microscopic examination of the tissue at the position of highest compression revealed that no typical compression wood had been differentiated in the last year.

It is significant that the compressive stresses on the lower side of the bend were about equal to the margin by which the tensile stresses on the upper side exceeded average for a straight, vertical tree of the species. From an estimate of the weight of the tree and the present horizontal displacement of the top, it was calculated that the eccentric centre of gravity would induce maximum compression stress at the lower station and maximum tensile stress at the upper station, each between 1.7 and 2.1 MPa. Thus, with minimum variation from average growth stresses in normal wood, the tissues on opposite sides of this stem were together producing an auto-stress reaction moment which effectively just counterbalanced the moment imposed by the external force. By so moderating its reaction, the tree had minimised encroachment on the margin of strength, which is given by the normal tensile growth stresses all around the periphery, to offset damaging compressive stresses due to bending by strong winds. Measurements showed that in achieving its stability, the less eccentric radiata tree developed a lower counter-force with smaller variations from stresses in normal trees.

Prior to generation of corrective auto-forces in a substantially-displaced stem, the external force induces intense compressive stresses on the under side of the stem, and similar tensile stresses on the upper side, with a gradual transition between. This simple distribution interacts with the more complex distribution of normal growth-stresses in the tree. The intensity pattern for the latter is dome-shaped; the tensions round the periphery reduce to zero at about one-third of the radius towards the pith, and then change to compressive stresses increasing towards the centre of the cross-section (Boyd, 1950a).

As auto-forces increase on the lower and upper sides, to counteract the displacement, their interaction with the original growth-stresses and the externally-applied stresses causes a continually changing composite stress pattern. The neutral line, which separates the resultant tensile and compressive stresses, is a curve of changing shape and position. All other lines joining points of equal stress similarly change shape and position. The auto-stressing of tissue, which is differentiated on the sides parallel to the plane of bending, adds complications to the determination of the pattern of resultant stresses. Therefore there is no simple, direct relationship between the internal stress distribution and the external bending forces. For these reasons, Westing's (1965) calculation of reorientation forces is misleading.

Comparable stress measurements on angiosperms confirm that the reorientation system is dependent on auto-force generation on both the upper and lower sides of the stem. For example, Nicholson *et al.* (1972) reported high tensile stresses on the upper side of a tree which had corrected its lean, and considerably smaller tensile stresses in its lower side. These auto-forces, in conjunction with the extant system of growth stresses, were counterbalancing the external bending forces.

This evidence, that expansive action of compression wood may not be essential to counteract displacements, supports a hypothesis for which the main principle was stated much earlier (Boyd, 1950b). Thus depending on the seriousness of the initial and subsequent displacements, differentiation of "modified normal wood" alone may bring about a counter-balance and even reorient the stem. This is confirmed by an extensive study of the anatomy* of tissues, and other factors for the bent radiata tree referred to above.

3. *Other Relevant Statements on Mechanics of Reorientation*

(i) *Evidence Implying Unilateral Correction*

In experiments on gymnosperms, Wardrop (1956) showed that when very young trees were placed on a tilted position and the cambium removed from the upper side of the stem, compression wood formed on the lower side, and effective reorientation movement occurred. Correspondingly, he showed that when the cambium was removed from the lower side of similar angiosperm stems, tension wood developed on the upper side and reorientation occurred. He concluded that for "recovery . . . it was only necessary for the cambium to be active on the side of the reaction wood formation."

However, Wardrop overlooked the interaction forces with the extant growth stresses in the tissue differentiated before the cambium was removed, and he did not note that a stronger and quicker-acting restoring force would develop when new tissue was allowed to form on both upper and lower sides. Generally the latter condition would be essential to reorient larger trees.

(ii) *Corrective Forces Associated with Visco-elastic Effects*

Frey-Wyssling (1952) suggested that reorientation movements could be explained by

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* Details of this study will be published as part of another paper.

visco-elastic action induced by turgor and protoplasmic pressure in the differentiating cells. Westing (1965) remarked on errors in Frey-Wyssling's calculations, but supported the idea that righting would be achieved by forces substantially smaller than indicated by the short-duration effects. Wardrop (1965) also argued that "a study of the differentiation of compression wood is consistent with such a (Frey-Wyssling's) hypothesis."

However, forces arising in the cambium cannot interact significantly with or impose permanent stresses on the xylem (Appendix III), and be responsible for reorientation movements. Before there can be *any* reorientation, the internally-generated *primary* forces and moments *must* be sufficient to *fully* counterbalance the external bending forces associated with the displacement. Until then, the externally-induced visco-elastic action (creep) will reduce the effectiveness of the auto-forces. Indeed, creep arising from the dominant external forces tends to increase the displacement, and in extreme cases it could prevent ultimate recovery. After primary auto-forces fully counterbalance the external bending moment, additional increments would induce favourable visco-elastic action, but its effect would be small compared with that of the primary force.

(iii) *Damage to Tissue During Reorientation*

Because of aforementioned factors, it should not be surprising that Westing (1965) could not find the compression failures he anticipated on the upper side of upward-bending gymnosperms. Correspondingly, tension failures which he observed on the lower side, at a position coincident with the periphery at the time of the initial displacement, would be effects of that displacement and the mechanics of reorientation. A direct effect of a large displacement would be to cause compression folds (incipient failures) in the tissue of tthe lower side of the stem. As reorientation developed, that tissue would be stretched by the longitudinally-expanding compression wood differentiated outside it. The incipient failures would cause stress-concentrations, and these would render that tissue particularly vulnerable to failure under increasing tension as reorientation proceeded.

4. *Functional Significance of Mechanical Properties*

(i) *Passive Role*

Initially, the compression wood must offer maximum resistance to damaging effects of the displacement. It must bolster the resistance of the normal tissue, and thus safely sustain the abnormal compressive stresses imposed on the lower side of the stem. The relatively low longitudinal modulus of elasticity of its outer wall layers assists this function.

The low modulus is a consequence of the very large microfibril angles in the outer layers, the abnormally large volume of matrix material in the vicinity, and the presence of large inter-cellular spaces. Thus substantial reductions in length (relative to strains in normal tissue) may be imposed on those layers, without inducing damaging high stresses in them. Yet their intense lignification ensures maintenance of bonding between them, and effective transfer of forces to the thicker and stiffer S_2 layer (Boyd, 1973).

The open helical splits in the S_2 layer, which are well illustrated by Meylan and Butterfield (1972), and by Jutte and Levy (1972), confer the characteristics of a long compression spring. Application of large compressive forces tends to close the helical "ribs" firmly together. At that time, because the fibrils in the outer layers are disposed nearly perpendicular to the tracheid length, they act as reinforcing hoops and offer strong resistance to lateral expansion of the cell. The greater-than-normal thickness of the outer layers assists this function. Together, these mechanisms increase longitudinal compressive strength and maximise passive resistance to undesirable displacement of the tree.

(ii) *Dynamic Role*

Although compression wood cells tend to expand in length, because only a limited number constitute the initial reaction to the dominant displacement force, at first they would not achieve auto-strain extension equal to their theoretical potential, or even develop a net expansion against the imposed compression. Nevertheless, each new group would contribute to a reduction in the externally-imposed compressive strain, and simultaneously induce increments of tension in tissue towards the pith. Therefore the first compression wood cells would gradually be relieved of externally-imposed compressions and correspondingly they would extend.

Acting like a pre-compressed spring, the closed helical gaps in S_2 would tend to open during this elastic recovery response. In the process, the compression wood cells would lose some of their passive supporting capacity. However, until expansion closely approached the auto-strain potential generated during their differentiation, they would retain most of their capacity to counterbalance externally-imposed compressive forces. Also, the need for support so lost would have been more than offset by the younger cells.

As additional compression wood cells differentiated and extended, the initial ones would become distant from the periphery, gradually relieved of all compression, and ultimately subjected to tension. Then, their low modulus of elasticity in tension, and unusually large extensibility, would ensure that they offered minimum resistance to the function of the outer tissue then performing the prime support and reorientation roles. Thus at all stages compression wood cells exhibit optimum characteristics when making their functional contribution to structural support, and to reorientation movements.

VIII CONCLUSIONS

Based on anatomical features of the cells, evidence that lignification causes significant changes in dimensions, and analyses using an adaptation of the theory of anisotropic shrinkage, it has been demonstrated that longitudinal expansion tends to occur during differentiation of compression wood. Because of restraints preventing free extension during lignification, corresponding substantial longitudinal expansive forces are generated. These are applied initially to counteract severe external forces displacing the stem, or branch; subsequently they cause reorientation towards the optimum position.

Longitudinal auto-generated expansive stresses in compression wood are about five times greater than the auto-generated tensile growth stresses at the periphery in normal earlywood of gymnosperms. Although compression wood alone could affect reorientation of a very small tree displaced from the vertical, a more powerful combination of corrective forces is usually operative. Thus the expansive push of the compression wood on the lower side is assisted by the pull of the nominally-normal cells near the periphery on the upper side of the stem. On the other hand, turgor or protoplasmic pressure in differentiating cells could not cause reorientation movements in trees.

As an immediate response to an extended displacement of a gymnosperm tree there is an enhanced rate of differentiation on the lower side, compared with elsewhere; this maximises early effective primary reaction, and thus limits both structural damage due to the displacement, and critical secondary (creep) deflection. Continued accelerated differentiation minimises the time required for reorientation.

Unique mechanical properties of compression wood, including high compressive strength, low longitudinal moduli of elasticity in compression and tension, and large extensibility, all contribute to it having optimum functional qualities for both its passive and dynamic roles in a displaced stem or branch.

Evidence and deductions on the forces generated in compression wood are compatible with the widely-reported observations on the function of this tissue. Therefore they indicate that the manner of generation of forces is as stated herein, and that the method of analysis is valid. Thus they supplement previously-reported indications that lignification is a prime factor influencing the important mechanical properties of wood cells, and the development of their structural functions.

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APPENDIX I

CELL WALL DATA FOR ESTIMATING LIGNIFICATION FORCES

The effective longitudinal strain, arising from lignification in compression wood, depends on the relative stiffness of its wall layers, and the fact that the strong lignin bonds between outer and inner layers of the wall ensure they act together. As test data on the elastic modulus for each are not available, values must be derived; however, only approximate comparative values are needed for determining interactions.

For these estimates, account is taken of the following—modulus of elasticity (E) for the S_2 layer of normal wood is about 5 times that of the outer layers (Mark and Gillis, 1970), cross-sectional area of S_2 plus S_3 in earlywood is approximately 3½ times that of the outer layers (Mark, 1967), and in latewood the thickness of S_2 is generally at least twice that in earlywood; wall thickness in compression wood cells is about that in latewood, and the primary wall, immediately-associated middle lamella (excluding intercellular spaces) and

S_1 are anatomically similar to normal wood, although S_1 tends to be thicker, and E is 0.56 times (av.) that for normal wood (Onaka, 1949).

An approximate ratio of E, for S_2 and the outer layers of a tracheid, may be obtained by treating the stiffness of each layer as the product of its cross-section and respective E, and by substituting in the formula: $E_t = (E_i A_i + E_o A_o)/(A_i + A_o)$. In this, "A" represents the area of wall, and subscripts "t, i and o" represent the complete cell, and inner and outer wall zones respectively. Accordingly, for compression wood it has been deduced that E_i = approx. $4E_o$. Even if this estimate were in error up to 50 per cent (unlikely), there would be no change in the significance of conclusions when it is used to determine lignification forces.

APPENDIX II

CALCULATION OF AUTO-FORCE GENERATION IN COMPRESSION WOOD

An estimate of the potential for stress generation in normal earlywood (Boyd, 1972) was based on dimensional changes occurring during lignification. It was shown that the longitudinal contractive auto-stress was about 3.86 MPa (560 lb/sq in.). This calculation involved the conservative assumptions that: no significant permanent auto-force was generated before commencement of differentiation of the S_2 layer; and that half the residual potential to generate force would be inffective, because the framework of S_2 was far from complete when its expansion and strain development were initiated by lignification of the older lamellae, and its capacity to sustain the strains elastically would be limited accordingly.

For the earlywood of gymnosperms, Onaka (1949) stated microfibril angles in the S_2 layer of 20° to 35°, and Nakato (1958) gave values for seven species that averaged 21°; therefore about 25° is considered compatible with the above estimate of its stress potential. For S_2 in compression wood cells, an angle of 50° is assumed, with MR = 50 as in normal wood. Assume that the thickness of S_2 in normal earlywood and compression wood cells is one-tenth and one-fifth the respective diameters.

Accordingly, Table 2 indicates that lignification tends to induce strain ratio changes in cell length of —0.24 (contractive) and +0.59 (expansive) for S_2 in. normal wood and compression wood respectively. Therefore, with due allowance for the S_2 cross-sections, the relative tendencies for length changes in the two types of tissue, their stiffness indices, and the previously-established auto-stress potential in normal wood, an estimate* of the auto-force potential in compression wood is:

$$-3.86 \times \frac{0.59}{-0.24} \times \frac{0.20}{0.10} \times 0.56 = +10.62 \text{ MPa (compressive).}$$

APPENDIX III

POTENTIAL OF PRIMARY WALL FOR DEVELOPING REORIENTATION FORCES

1. Significance of Turgor and Protoplasmic Pressure

Stresses imposed by turgor or protoplasmic pressure were analysed by Boyd (1950b); calculations indicated that the maximum conceivable pressures were unlikely to induce stresses of the order of magnitude of normal growth stresses, the origin of which is now

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* Calculations for normal wood, which were based on lignification effects and the same methods of analysis (Boyd 1972, 1973), gave values which were probably conservative, but clearly compatible with relevant observed phenomena. Therefore, the corresponding calculated stress potentials for compression wood may be regarded as substantially dependable.

attributed to lignification. Further, as shown in Appendix IV herein, compression wood generates very much higher auto-stresses than normal growth stresses.

Putting aside those conclusions, if sufficiently large forces were presumed to be generated in differentiating cells, before the secondary wall was formed, they could induce reorientation only if transferred to offset the large forces in the mature wood, which are a consequence of the displacement imposed. However, where the primary wall is undergoing growth, lignification has not commenced, and there would be no adjacent structural support. Because of lack of strong bonds to mature material, at this stage the wall could not transfer any forces in it. Also, due to its extreme thinness, large microfibril angle of its cellulosic framework, and absence of effective physical restrains on its bending, it would be very flexible.

At this stage, the primary wall could be bent and deformed at its growing end by very small forces, or any obstruction to its growth on a particular direction, and it could not exert significant counter-force. Prior to its lignification, therefore, the primary wall and associated turgor or protoplasmic pressures would not have a capacity to exert forces adequate for reorientation of a stem or branch.

2. Forces Induced by Lignification of the Primary Wall

In assessing the possibility that lignification of the primary wall could be a significant factor in auto-force generation in compression wood, it a "generous" assumption that its thickness is one-tenth the combined thickness of wall layers excluding S_2, and thus not more than one-twentieth of that of S_2. Extrapolation of Table 2 or Barber and Meylan's (1964) curves shows the relative strain ratio for P and S_2 is about 1.6/0.59, for microfibril angles of 75° and 50° respectively. Assume a corresponding ratio for their moduli of elasticity, of 1/4 (Appendix I).

Then the relative force-generation potential in the primary wall would be not more than 1.6/0.59 × 1/20 × 1/4, or about 3 per cent of that in S_2. However, the microfibril angle may be larger than assumed for P and even for S_2, P may be thinner than assumed, and it would be impracticable to harness most of the force-generation potential. Hence lignification of P could not be a force of significance in reorientation movements.

APPENDIX IV

EVIDENCE ON STRESS GENERATION IN REACTION WOOD

The limited data, which directly indicate the intensity of auto-stress development in compression wood, can be supplemented with other significant relevant data for both gymnosperms and angiosperms.

1. Qualitative Data

Münch (1937) reported stresses in the reaction wood of **Picea** sp., that were much higher than in normal wood. Also, Jacobs (1939) demonstrated that, when four **Pinus radiata** trees of age 3 to 7 yr, and ranging in diameter at breast height from 25 to 100 mm (1 to 4 in.), were bent experimentally, the force initially necessary to hold them in the bent position was exceeded rapidly and substantially after about a month, as a result of formation of compression wood. Additionally, Jacobs (1939, 1965) visually illustrated the large expansive reaction of green compression wood.

2. Stress Measurements in Pinus taeda

Hallock (1966) made measurements on building timber, from 432 **Pinus taeda** logs with diameters from 150 × 300 mm (6 to 12 in.), some of which undoubtedly contained compression wood. Indicated mean longitudinal growth stresses averaged about 1.38 MPa (200 lb/sq in.) and generally ranged up to above 4.82 MPa (700 lb/sq in.) in both tension and compression, with one extreme value of about 10.35 MPa (1500 lb/sq in.). However, those stress levels, which were deduced from the natural curving after straight sawing of green 100 × 50 mm

× 2.4 m (4 × 2 in. × 8 ft) long timbers, did "not necessarily reflect the true growth stresses," but rather "the net stress" in each piece.

The latter comment implied that undoubtedly there were higher stresses in parts of the sections, and the results showed only the average differential stress across the piece. Other data on peripheral growth stresses, meaured before and after felling hardwood trees (Nicholson, 1973), indicate that extreme stresses would generally be higher in trees than in logs and timber cut from them.

3. **Stresses in** *Cryptomeria japonica*

Watanbe (1965) gave values of peripheral compressive strains in 3-yr-old sugi trees, that were about three times the average tensile strain generated at the periphery of straight 5-yr-old trees of that species, and more than four times the average for some of the trees.

Jacobs (1945) explained that very young gymnosperms often exhibit peripheral compressive stresses, associated with compression wood, but later the trees appear quite straight and the normal stresses generated at the periphery are tensions.

4. **Stresses in** *Pinus radiata*

Jacobs (1938) reported strains in compression wood from one tree of **Pinus radiata.** The values were approximately six times the average contractive-strain measured by Jacobs (1945) in normal wood at the periphery of six straight **Pinus radiata** trees. For the latter, his results indicated an average stress was 1.93 MPa, with an extreme tree value of about 4.14 MPa. The estimated stress in the compression wood was about five times that in average normal wood, and about 2½ times the quoted extreme.

5. **Relative Intensities of Stresses in Straight and Leaning Angiosperms**

Qualitative observations, made by Lenz and Strassler (1959), indicate that the stresses in reaction wood in **Fagus silvatica** are much greater than in the normal wood of straight trees of the species. For normal wood of straight trees of **Eucalyptus** sp., measurements by Jacobs (1945), Boyd (1950a), Boyd and Schuster (1972), and Nicholson **et al.** (1972), showed tensile longitudinal growth stresses at the periphery, averaging about 10.35 MPa (1,500 lb/sq in). However, Jacobs' (1938) measurements of strains in **Eucalyptus** sp. showed that stresses in tension wood were about five times those in normal wood.

Stresses measured by Nicholson **et al.** (1972), on a bent tree of **Eucalyptus regnans,** showed that tensions existed at all points around the periphery of a longitudinally-curved section of the stem. At one section, they ranged from about 2.07 MPa (300 lb/sq in) on the lower side in the plane of the bend, to about 44.8 MPa (6500 lb/sq in) on the upper side of the stem. His unpublished data on other bent trees show comparable maxima. Thus maximum-intensity peripheral reactive-stresses can be four to five times the average of about 10.35 MPa in straight angiosperms.