

of Geneva entails, has technical consequences. It forces the designers to make use of the latest technical developments, for example superconducting magnets, in order to obtain such high energies within so little space. The new project will, therefore, necessarily be much more modern than the one planned earlier.

I think I have presented most of the arguments which played a part in the final decision. Let me repeat them in a few words. First of all, there is the satisfaction of working on a meaningful cooperative project, but also uncertainty with respect to the forthcoming results with the new instrument, the question whether the experience gained with the earlier accelerators may not suffice to comprehend the world of elementary particles. There is the further question of progress in technology; might it not be the case that in a few years accelerators with the required energies can be built much more cheaply than now by using new technical processes? An additional difficulty was the necessity for the participating nations to come to a fair decision with respect to the site, and for each of the individual governments to renounce plans or projects of their own in favor of the international accelerator. It seems to me that in view of all these difficul-

ties the final decision is a very good solution, an appropriate compromise between the various interests, and a valuable contribution to the strengthening of the European community.

Motives behind the Building of Giant Accelerators

In conclusion, however, let me leave this level of practical considerations, scientific reasoning, and political negotiations and, descending to a somewhat deeper level, ask: Why, after all, do we humans make such strenuous efforts to build a large accelerator, why do we spend billions on a scientific instrument which, at least for the moment, does not promise any economic return? When I once put this question to the American ambassador in Bonn, I received the following reply: In ancient Egypt pyramids were built, in the Christian Middle Ages magnificent cathedrals, and in our time we are building giant scientific instruments. In ancient Egypt the royal ancestors represented a bond to the deity, and the trust in help and support deriving from this bond manifested itself in the erection of these giant tombs. In the Christian Middle Ages the believers went into the cathedrals firmly con-

vinced of obtaining deliverance from their suffering. In our time we trust almost blindly in science and rational thought, and we are bringing enormous material sacrifices to further science, to increase our knowledge of the world. The American ambassador's comparison contains without doubt part of the truth, and if we mean by religion in a very general way the center of trust forming the kernel of a society, it must be admitted that religious motives are the driving force behind the building of these giant accelerators. Still, one must ask oneself here whether the power of the goddess "Reason" is, indeed, as large as it was hoped at the time of the French Revolution. The experiences of our century seem to indicate that it is rather limited. However one may judge this power, our minimal demand must be that we do not blindly commit ourselves to it, but that we act sensibly and critically if it is a question of investing enormous funds in large scientific projects. This has certainly been the case with regard to the Geneva giant accelerator, and it must be hoped that in the future, too, similar scrupulous care will be taken in deciding on such large projects.

Note

1. This article was translated by Sonja Bargmann.

Reaction Wood: Its Structure and Function

Lignification may generate the force active in restoring the trunks of leaning trees to the vertical.

G. Scurfield

The Problem Stated

Wherever trees are found, but perhaps most often on exposed seacoasts, high mountains receiving heavy snow, unstable slopes with shifting rocks or scree, and the banks of uncertain rivers, it is not uncommon to find

some with main stems which have not grown upright during part or all of their lifetime. The form of the stems of these trees is usually such as to suggest that, after being bent or tilted, they have striven to regain a vertical position. We are to be concerned with the mechanism of this recovery process.

Morphology

There are two morphological consequences of displacing the main stem of a tree from the vertical.

1) If the displacement is severe, as when large trees are partially uprooted without being killed, but especially when stems are caused to overarch (naturally, as under snow load, or artificially, as in trellising, for example), stem growth is continued from a lateral bud so placed that the stem it produces is as nearly vertical as possible. That part of the tilted main stem which lies beyond the sprouting lateral may subsequently die, the lateral taking over the role of main stem. If more than one lateral grows out, a tree may develop a stem similar to that shown in Fig. 1a.

Should the displacement from the

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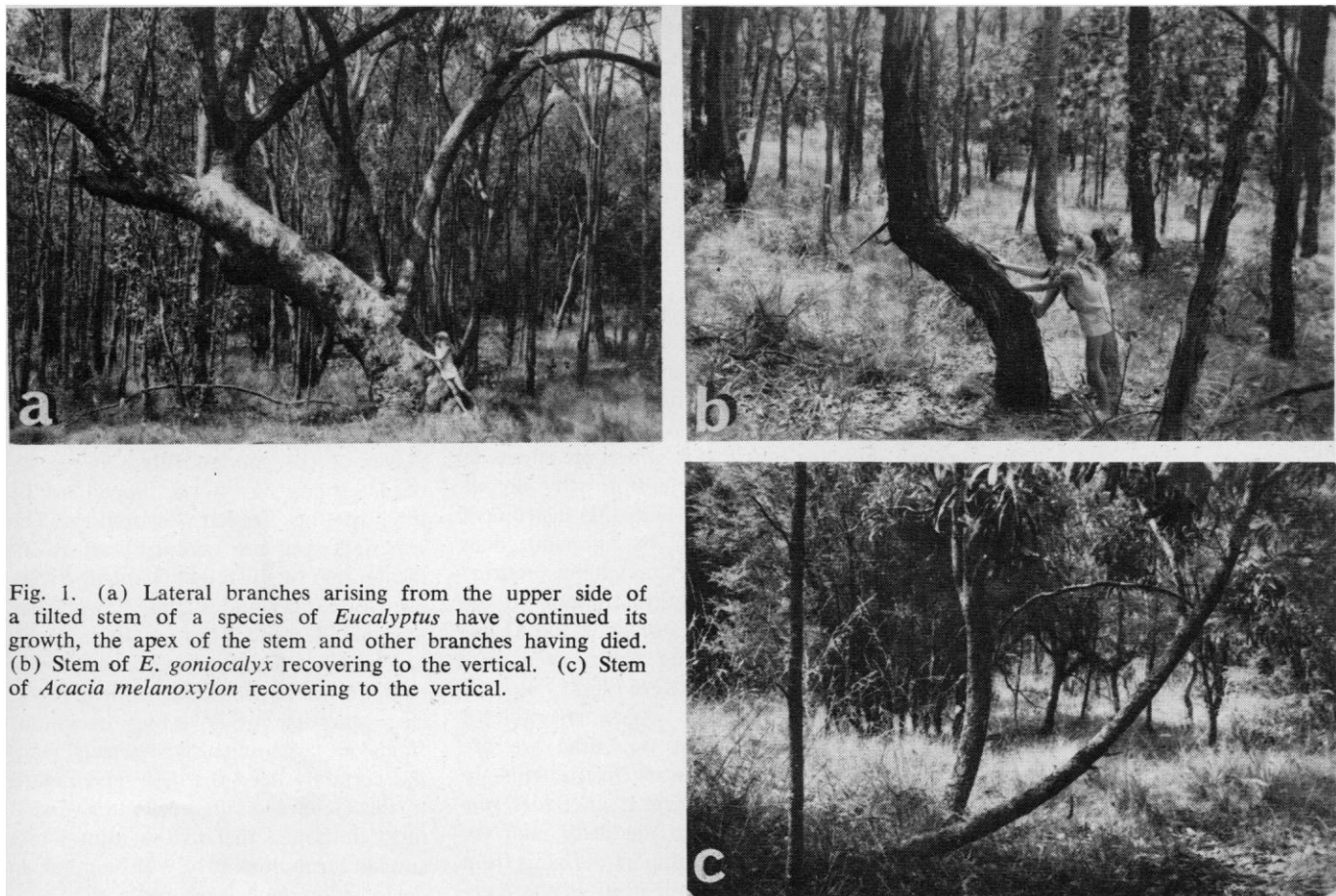


Fig. 1. (a) Lateral branches arising from the upper side of a tilted stem of a species of *Eucalyptus* have continued its growth, the apex of the stem and other branches having died. (b) Stem of *E. gonicalyx* recovering to the vertical. (c) Stem of *Acacia melanoxylon* recovering to the vertical.

vertical be less severe, and especially if the tree is young and actively growing, the almost immediate consequence is that its stem tip undergoes realignment so that it is again upright. It then continues to grow upward. After a lag period during which the displacement of the tree from the vertical may actually increase (1, 2), the tilted

or bent portion also tends to recover toward its original position over a period of time and with a degree of success related to factors such as stem size and weight. This tendency, greater in the upper (younger) than in the lower (older) portions of the stem, leads eventually to the development of main stems having in them bends or sweeps

or curves of wide variety. Examples are shown in Fig. 1, b and c.

The sequence of events outlined above can be demonstrated experimentally (Fig. 2). The value of a mechanical-mathematical model of the process of recovery in softwoods is currently being assessed (3).

2) A second morphological consequence of displacing the whole or part of the stem of an actively growing tree from the vertical, irrespective of its age, is that the whole or part so displaced undergoes asymmetric radial growth. The remarkable fact is that in gymnosperms (softwoods) growth is greater on the under side (Fig. 3) and in angiosperms (hardwoods) usually on the upper side of the whole or part (Fig. 4).

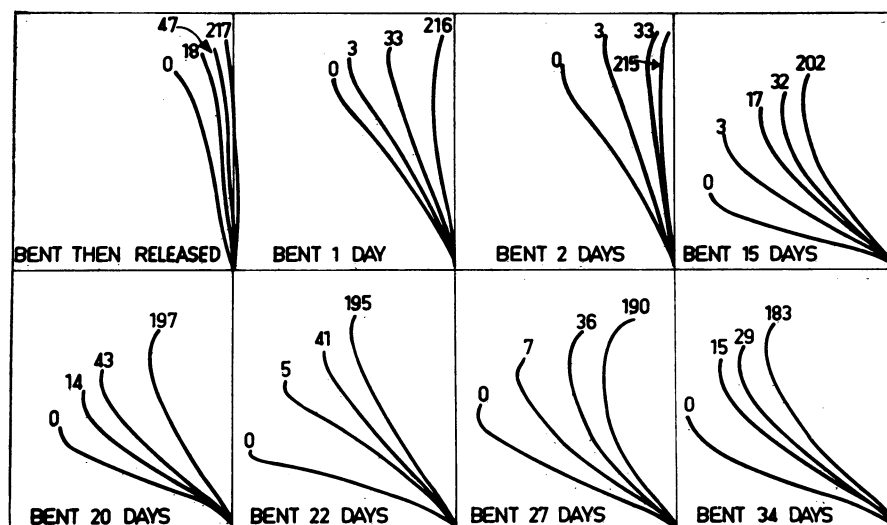


Fig. 2. Seedlings of *Tristania conferta* bent at right angles to the vertical in the second oldest internode for various periods (0 to 34 days) and then released. Their positions during the remainder of the growth season are shown, the numbers being days after release.

Role of Reaction Wood Formation

Since in most trees asymmetry of cross section appears to be accounted for largely on the basis of accentuated development of wood rather than bark, it is relevant to ask if the wood (reaction wood) plays an active role in the recovery of a bent or tilted stem to the vertical. If we bear in mind that reaction wood is structurally different

from normal wood (see below) in both hardwood and softwood trees, the following evidence supports the view that its role is an active one: (i) Boards cut tangentially and parallel with the under side of a softwood stem that has formed reaction wood tend to expand longitudinally. Boards cut from the upper side of a hardwood stem that has formed reaction wood tend to contract (4, 5). (ii) Asymmetric radial growth of a vertical stem of a softwood can be brought about by lateral application of β -indolylacetic acid (IAA). The stem bends in the direction opposite to the side to which the IAA is applied, the wood formed on this side having a structure similar to that of reaction wood formed on the under side of a tilted stem of the same species (6, 7). (iii) Jaccard (8) showed that if vertical loops (Fig. 5c) are cut horizontally across, the upper chord expands while the lower chord contracts in hardwood stems. Reaction wood, since it is located along the upper side of such chords, is evidently associated with stem contraction. In a similar way, reaction wood formed by softwood stems can be associated with stem expansion. (iv) The structure of wood formed around the circumference of aerial roots of *Ficus* species when they undergo secondary growth (after penetrating and becoming anchored in the soil) is similar to that of reaction wood formed in tilted stems of the same species. The reaction wood formed by the roots is associated with their contraction since free-hanging roots allowed to penetrate soil in containers will eventually lift the containers (9).

Questions concerning the location and origin of the force generated in reaction wood next arise. Answers require consideration of its structure, differentiation, and chemical composition.

Gymnosperm Wood

This consists of a vertical system of tracheids with pitted walls, tracheid contact being interrupted here and there by resin canals, and a horizontal system of ray parenchyma cells. The number of resin canals is markedly reduced in reaction wood formed by seedlings of *Pinus radiata* (Fig. 3). Reaction wood tracheids frequently have distorted tips (10) and tend to be shorter in length than normal tracheids.

The wall of a normal tracheid consists of an outer primary wall and an inner secondary wall. The latter is het-

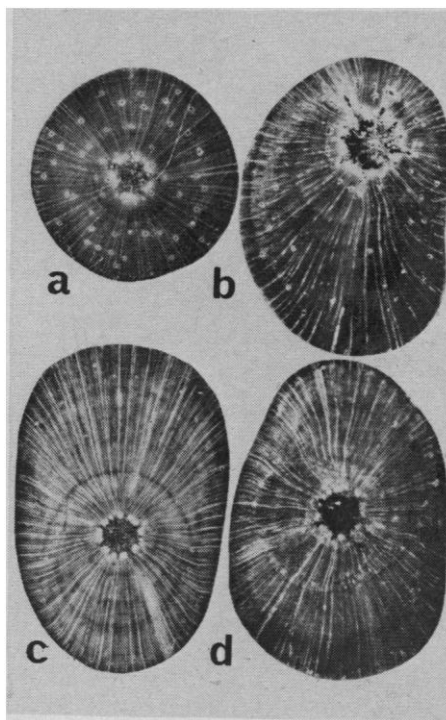


Fig. 3. Seedlings of *Pinus radiata* grown (a) vertically, (b) horizontally, (c) horizontally for 1 month and then turned through 180°, and (d) horizontally and then rotated twice through 180° with an interval of 1 month between each rotation. Asymmetric growth is confined to the under side of horizontally grown stems.

erogeneous in optical, staining, and other properties—a transverse section, for example, viewed between crossed Nicol prisms, shows a middle layer with little or no birefringence sandwiched between birefringent outer and inner layers. For convenience, the outer, middle, and inner layers are designated S1, S2, and S3, respectively,

S2 making up something like 75 percent of the wall thickness. Surface warts cover the innermost (lumen) surface of S3. The wall is made up of cellulose microfibrils organized into lamellae (4 to 6 in S1, about 30 in S2, and up to 6 in S3) in an amorphous matrix of lignin and hemicelluloses (11). The orientation of the microfibrillar helices is important: they are relatively flat (70° to 50° to the cell length) in S1 and S3, while in S2 they are relatively steep (40° to 10° to the cell length).

Reaction wood tracheids have round cross sections and abnormally thick walls. The secondary wall consists of only two layers, S1 and S2, both thicker than normal and lamellate. Cellulose microfibrils run more or less transversely in S1, while in S2 they run for the most part at an angle of 30° to 45° to the longitudinal axis of the cell. The lumen side of S2 is ribbed, the ribs forming helices which run in the same direction as the cellulose microfibrils (7, 12). The fissures separating the ribs are

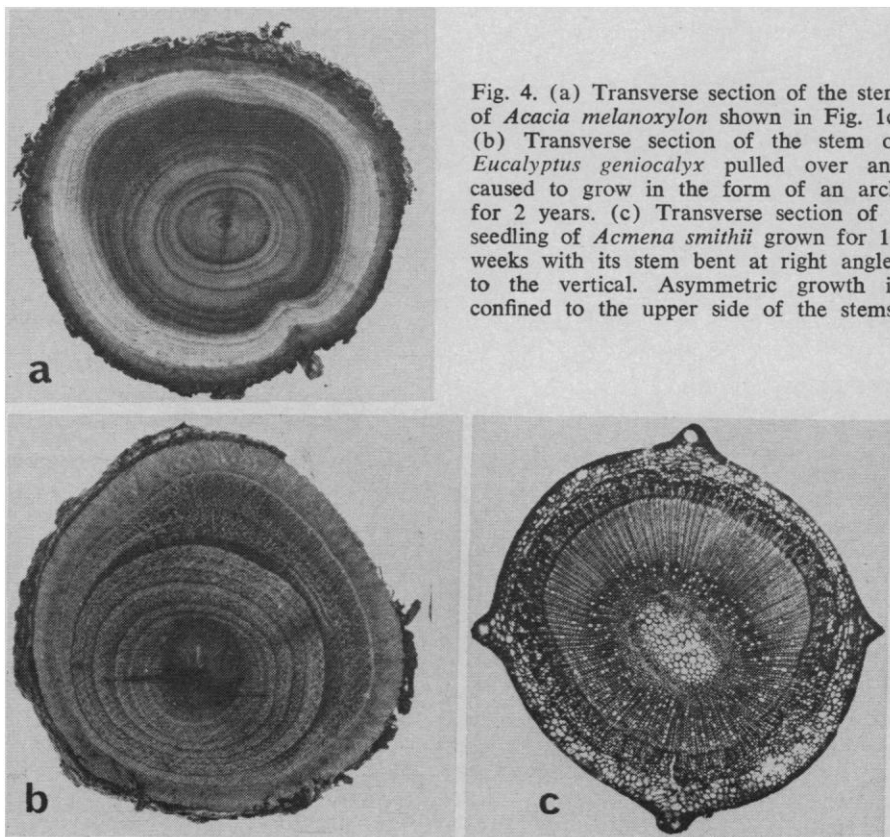
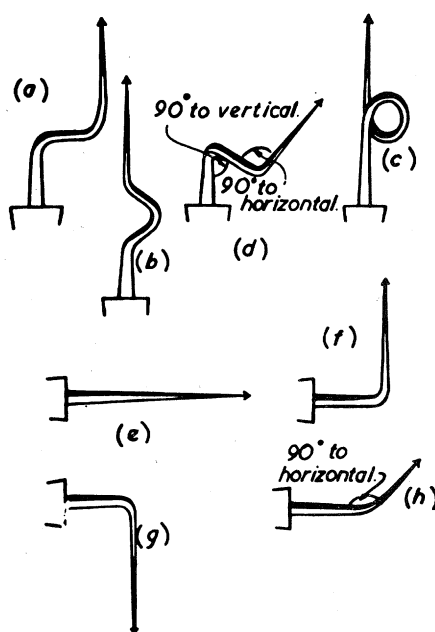


Fig. 4. (a) Transverse section of the stem of *Acacia melanoxylon* shown in Fig. 1c. (b) Transverse section of the stem of *Eucalyptus genicocalyx* pulled over and caused to grow in the form of an arch for 2 years. (c) Transverse section of a seedling of *Acmena smithii* grown for 10 weeks with its stem bent at right angles to the vertical. Asymmetric growth is confined to the upper side of the stems.

Fig. 5. Experiment to show that reaction wood forms along the upper side of the stems of seedlings of *Tristania conferta* irrespective of the method of mechanically deforming the stem. Reaction wood formation appears, therefore, to be related to a change in the orientation of cambial initials.



deep-seated: they originate close to S1 and often coalesce in passing through S2 to the cell lumen. Fewer warts occur on the lumen surfaces than in normal tracheids. They tend to be confined to fissures (13). Cracks occur in the walls, the result presumably of ribs having been pulled apart. Large intercellular spaces occur, intercellular material tending to be restricted to regions between cell walls in contact (Fig. 6).

The differentiation of gymnosperm reaction wood involves an increase in the number of anticlinal divisions of cambial initials (14).

Reaction wood tracheids are reported to differentiate completely in less time than the 20 or so days taken by normal tracheids (15). The acquisition by them of a rounded cross section and the associated development of intercellular spaces take place before secondary wall formation (7, 16). It may be assumed that in reaction wood tracheids, as in normal tracheids (11), formation of this wall begins about the middle of the cells and progresses toward their tips as the cells elongate by apical intrusive growth.

Lignification follows close on the heels of cell wall differentiation (17).

The fissures in S2 are detectable at "a time when lignification passes from the primary to the secondary wall" (16). Compared with normal tracheids, the lignin content of S2, but not S1, is high. The outer region of S2 is highly lignified, more so than the inner region. Frequent reports that there is a gradient of lignin concentration ranging from high at the S1-S2 interface to somewhat less about the cell lumen have been denied (18). The possibility that lignification has not spread uniformly throughout S2 by the time the cell dies, but that chemical changes, associated perhaps with lignin condensation and

polymerization, subsequently occur has been mooted (19). Lignin deposition reduces the birefringence of the walls, makes them less porous, and produces changes in their histochemical properties. One such change is loss of a positive response to tests for peroxidase (19).

Gymnosperm reaction wood contains more lignin and β -D-(1-4)-linked galactan and less cellulose than normal wood (20). The cellulose is said to be less crystalline in reaction wood (21), while the lignin is released in larger amount on ball-milling (22, 23).

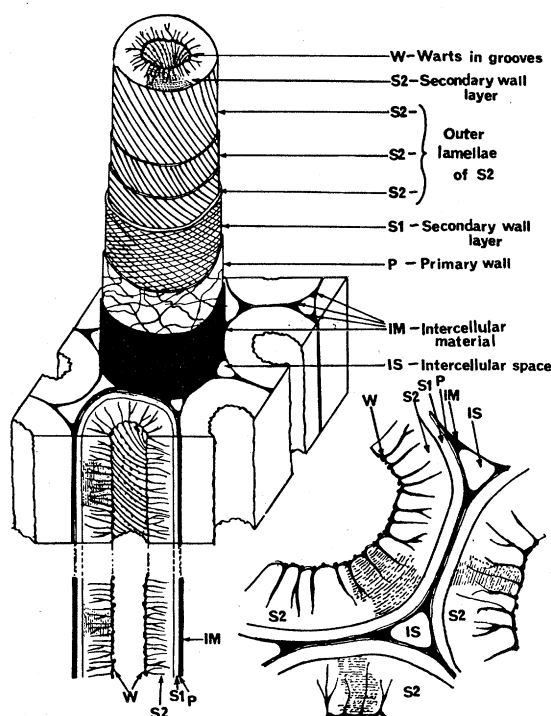
Angiosperm Wood

Typical hardwood consists of a vertical system of vessels, fibers or fiber tracheids or both, and xylem parenchyma, and a horizontal system of ray parenchyma cells. Reaction wood contains fewer vessels, more fibers, and fewer rays than normal wood. Vessels and ray and xylem parenchyma cells are often laterally compressed by surrounding fibers and sometimes obliterated (24). Reaction wood fibers show reduced wall pitting, but the walls contain a greater number of slip planes (25). There are no intercellular spaces.

Fibers or fiber tracheids can be regarded as having a primary wall, P, and a secondary wall consisting of lamellated layers S1, S2, and S3. The cellulose microfibrils making up the lamellae are orientated in ways comparable with those in the similar layers of softwood tracheid walls. However, the sort of wall structure developed by reaction wood fibers depends on the stage of differentiation they have reached when the stem is bent or tilted. Normal cells, if they are still alive at this time, form an extra wall layer (designated G). Cells which have not yet formed S3, but only S1 and S2, or which have not formed S2 or S3, but only S1, form G in addition. We thus obtain reaction wood cells with walls consisting of P + S1 + S2 + S3 + G, P + S1 + S2 + G, or P + S1 + G (Figs. 7a and 8b), the thickness of G increasing in passing from first to last. The important structural features of layer G are that it is multilamellate, certain of the interlamellar boundaries (indicated by arrows in Fig. 7a) being better defined than others, and that the cellulose microfibrils making up these lamellae are axially orientated (Fig. 7, b and c) (24, 26, 27).

A reversion to the formation of normal fibers, which occurs as a bent

Fig. 6. Diagram to show the structure of the walls of a reaction wood tracheid in a softwood stem.



or tilted stem recovers to the vertical, and in cell rows on the flanks of reaction wood arcs as the growth season advances, involves the formation of a fourth kind of reaction wood fiber. Its walls consist of layers P + S1 + G + another layer or layers, the extra layers differing from G in optical and histochemical properties. As the thickness of the additional layers increases that of G declines until the changeover to the formation of normal fibers is complete (28, 29).

The differentiation of angiosperm reaction wood involves an increase in the number of anticlinal divisions of cambial initials and periclinal divisions of their derivatives. Layer G has been detected in the walls of the latter within 10 days of bending a stem (24). Reaction wood fibers still possessing protoplasts lie much deeper within the stem than do comparable normal fibers, but whether this indicates that the former survive longer is uncertain.

When first formed, the lamellae of G, at least in some species, are convoluted and birefringent in cross sec-

tion. The convolutions tend to disappear as the lamellae retract to the cell wall and, in so doing, they lose their birefringence and ability to stain with Congo red. These facts are interpreted as indicating a progressive tendency for the cellulose microfibrils in each lamella to align themselves in an axial direction, closer lateral alignment resulting in the removal of lamellar convolutions, a decrease in the porosity of G, and the appearance of radial striations in the retracted lamellae (Fig. 9) (24).

Layers P and S1 lignify strongly, but G lignifies scarcely at all, in cells with walls consisting of layers P + S1 + G. Wall layers external to G in the other kinds of reaction wood cells also lignify strongly, G lignifying to a lesser extent (Figs. 8 to 10). The distribution of lignin in these latter cells is such as to suggest that its origin is extracellular (29).

Layer G gives strong positive tests for peroxidase in living reaction wood cells. Intense staining also occurs if an appropriate phenol is provided as substrate and hydrogen peroxide is

added (29). The innermost lamellae of G in such cells absorb ultraviolet light (28) and give positive tests for phenolics (Figs. 8 and 10). So do the additional layers in cells with walls consisting of P + S1 + G + additional layers (29).

Angiosperm reaction wood contains more cellulose, rather less glucomannan, and often more galactan than normal wood, but the same amount of lignin per unit of cellulose (30). Layer G consists entirely (31) or almost entirely (32) of cellulose that is more highly crystalline than normal (33). Less lignin is released from reaction wood than normal wood on ball-milling (23).

Location and Origin of the Active Force

The bending moment of the force tending to pull a bent or tilted tree farther out of the vertical as the tree continues to increase in size and weight is much less if the apex of the main stem reerects itself and grows vertically, or

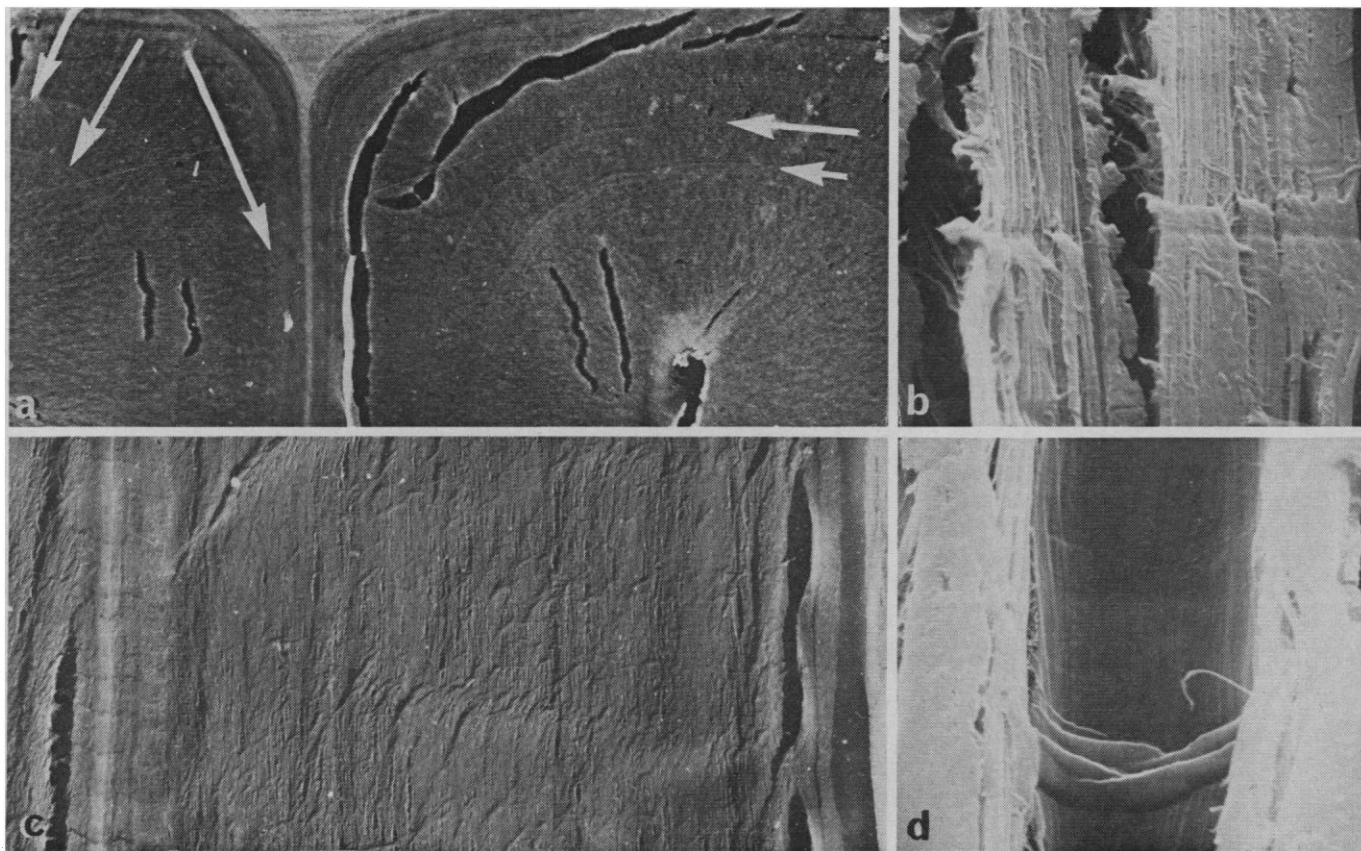


Fig. 7. Transverse section of reaction wood fibers of *Tristania conferta* (a), and tangential longitudinal sections of reaction wood fibers of *Eucalyptus gonicalyx* (b) and (d) and *Liquidambar styraciflua* (c). The walls of the cells in (a) consist of layers P + S1 + G. Layer is multilamellate (a) and (b), certain interlamellar boundaries (arrows) being more obvious than others (a). Note the axial orientation of the microfibrils in the G layer of the walls shown in (c) and (d), and the occurrence of slip-planes in the wall of the cell shown in (d). Panels (a) and (c) are transmission electron micrographs, the cells fixed in potassium permanganate, embedded in araldite, and stained with lead; (b) and (d) are scanning electron micrographs. (a) $\times 11,000$, (b) $\times 4900$, (c) $\times 15,000$, (d) $\times 4300$.

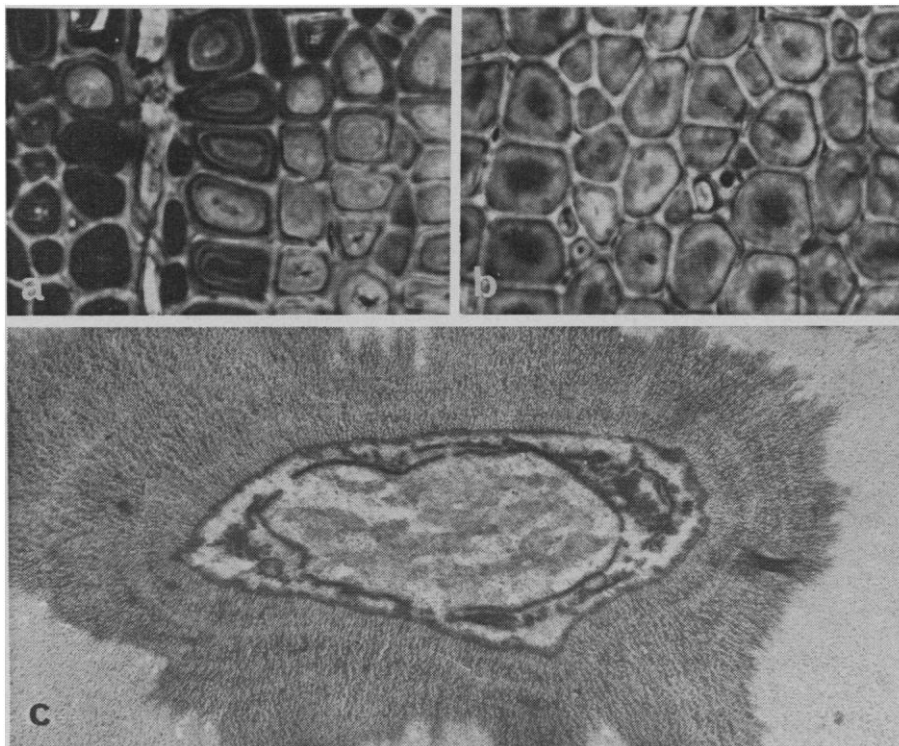
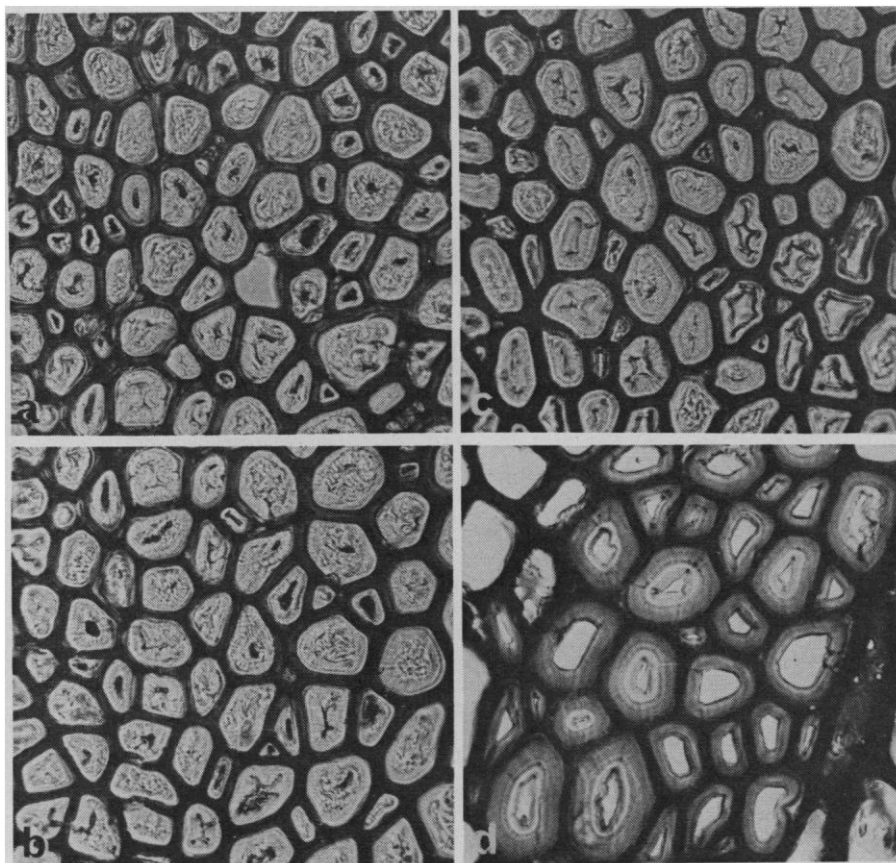


Fig. 8. (a) Transitional reaction wood cells on the flank of an arc of reaction wood in the stem of *Eucalyptus goniocalyx*. Note the histochemical heterogeneity of layer G, the intensity of staining of G being related to the extent of its penetration by lignin precursors. In (b) reaction wood cells have walls consisting of layers P + S1 + G, the innermost lamellae of G staining most intensely. Cells in (a) and (b) are stained with silver methenamine reagent, a test for reducing groups. Panel (c) is a transmission electron micrograph of a cell comparable with the cells in (b); the cell was fixed in potassium permanganate and stained with lead to show the staining of G layer lamellae about the cell lumen, the staining being indicative of the presence of phenolic hydroxyl groups. (a) $\times 690$, (b) $\times 810$, (c) $\times 16,200$.



is replaced by a vertically growing lateral branch, than if the tree continues to grow in the direction in which it is tilted or bent. Asymmetric stem growth, the consequence of stimulated cambial cell division, involves a lessening of any longitudinal stresses imposed on each cell by dispersing them over more cells. This is especially so since the additional cells are formed in a direction normal to the plane in which the stem is bent or tilted. That mechanical stresses are not the cause of asymmetric growth and reaction wood formation, however, can be shown experimentally as illustrated in Fig. 5. It is shown too by experiments in which reaction wood (georeaction wood) can be made to form in vertical stems of both hardwood and softwood trees appropriately rotated on a clinostat (34), and it can be inferred from the fact that reaction wood (pathoreaction wood) can form around stems of apple trees infected by virus (35) and stems of balsam fir following aphid attack (36).

It seems reasonable to assume that in both softwood and hardwood stems the force responsible for their reerection is located in the differentiating reaction wood. A mechanical advantage of such a location is that the farther this moves out from the center of the stem, the greater the moment arm (leverage) it can exert to reerection the stem. A more precise location depends on the view one takes as to its origin. If lignin deposition is merely a method for mechanically consolidating or strengthening an attained cell form, then presumably the recovery force is located in the region of unlignified cells—the cambial zone (37). On the other hand, if lignin deposition alters the form of reaction wood cells, causing them to expand in the longitudinal direction in a softwood and contract in a hardwood, the recovery force would be located in the region of differentiating cells undergoing lignifi-

Fig. 9. Ultraviolet photomicrographs of transverse sections of differentiating reaction wood cells of *Grevillea robusta*. (a to c) Cells at increasing distances from the cambium. Lamellae of layer G are initially convoluted, but retract to the cell wall as differentiation proceeds. Retraction appears to be associated with the development of radial striations in G (a) and (b) in this and some other species. The multilamellate structure and partial lignification of layer G in reaction wood cells in a changeover region (from normal to reaction wood) is shown in (d). [$\times 560$]

cation. The third possibility is that it is located within the whole region of differentiation.

Let us explore the consequences of associating the support of the increasing weight of a still-growing stem displaced from the vertical with the idiosyncracies of secondary wall formation shown by reaction wood cells, and its reerection with lignification of these walls. These functions are comparable with what Münch (4) described as the static and dynamic properties of reaction wood.

Gymnosperm reaction wood cells sacrifice the intimacy of normal cell contact and acquire a rounded cross section; that is, other things being equal, they adopt the form least likely to buckle under load applied parallel to their long axes. Lignification intensifies and, because the cell walls are poor in cellulose of less than normal crystallinity and highly porous, the lignin penetrates them more easily and is deposited in larger quantity, notably at the S1-S2 interface, than is normal. Now, it has been shown that lignin deposition can cause plant cell walls to swell (38) and that removal of lignin from wall layers causes an increase in their birefringence (39). If lignin deposition in reaction wood cell walls causes them similarly to swell (to an extent related to the reduction in their birefringence during differentiation), and if the shape, neighbor-to-neighbor contact, and wall structure of the cells are such as to direct the force generated largely in the longitudinal direction, then it could be responsible for reerecting the stem. The higher lignin content of gymnosperm reaction wood tracheids would acquire, in this way, functional significance. Restriction of their capability to slide past one another as they elongate by apical intrusive growth, a consequence of the early onset of lignification, could lead to tip distortion and an associated dislocation of normal wall development to the development of fissures in S2 (19). The development of cracks in the walls may be the aftermath of stem reerection, but its timing requires investigation.

The reaction wood cells in a bent or tilted hardwood stem develop a thicker than normal secondary wall characterized by a layer G which consists entirely (31) or almost entirely of cellulose (32), the cellulose microfibrils lined up in a direction parallel to the long axes of the cells. Insofar as orientation and crystallinity can

be distinguished as separate properties of such microfibrils (40), crystallinity is generally regarded as the effect and not the cause of orientation (41). What causes the microfibrils to align themselves in an axial direction is uncertain, but a change in the physiological polarity of cambial initials is probably involved. It seems reasonable too that the high degree of orientation brings into play interchain forces which give the microfibrils a strong lateral cohesion, especially in the tangential plane (24, 42). This implies an increase in resistance to deformation, an ability, in other words, to support better the increasing weight of the growing stem; it implies, somewhat paradoxically, that a greater force will be needed to effect the subsequent recovery of the stem to the vertical than if the cellulose microfibrils were less well oriented; and it implies restricted access of lignin precursors to G.

Touching the last point, bear in mind

that layer G is rich in peroxidase and that provision of a suitable phenolic substrate and hydrogen peroxide causes it to stain intensely (29). This, of course, gives no indication of the ease of penetration of G by lignin precursors in vivo. It does suggest, however, that the inability or reduced ability of G to lignify is due either to a dearth of lignin precursors or to restriction of their access to G. Since the lignin content of reaction wood is not unlike that of normal wood, lignin precursors apparently undergoing polymerization in layers external to G, it seems reasonable to conclude that in vivo access of precursors to G is restricted. This is consistent with the observation that, when a high degree of microfibril orientation is no longer maintained, as in cells with walls consisting of layers P + S1 + S2 + additional layers, deposition in the additional layers of phenolics originating from within the cells becomes possible (29, 43). It is consistent

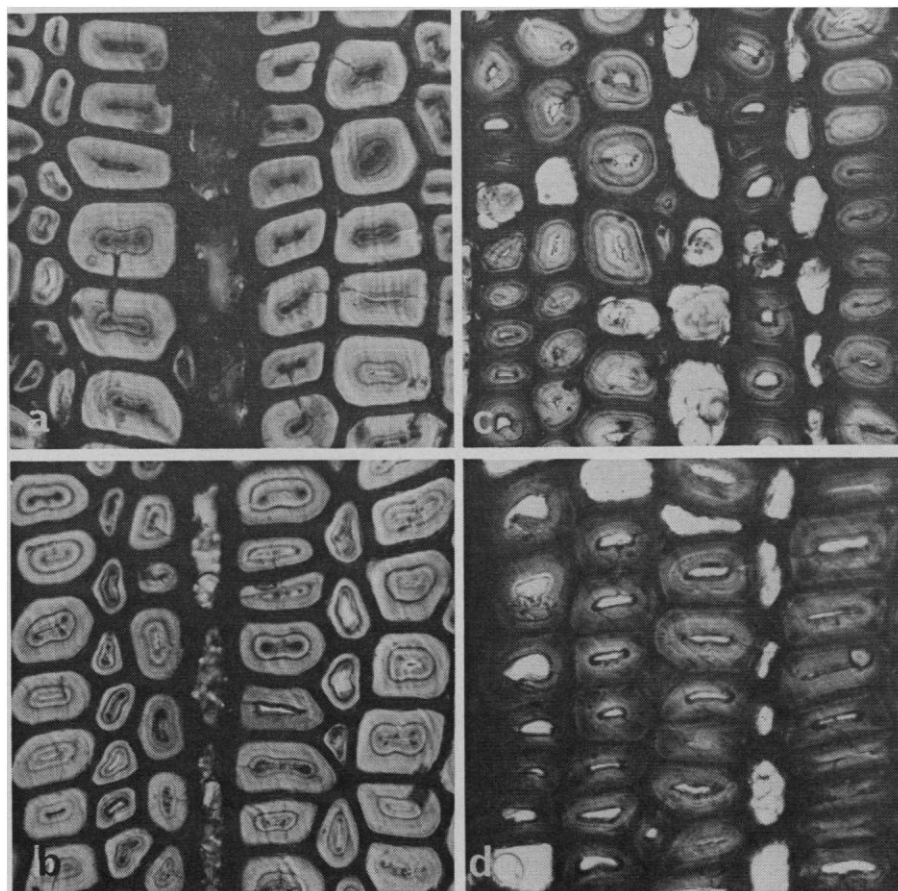


Fig. 10. Ultraviolet photomicrographs of transverse sections of differentiating reaction wood cells of *Tristania conferta* at increasing distances (a to d) from the cambium. Absorption of ultraviolet light about the centers of the cells in (a) and (b) is presumed to be due to the release of phenolics as a result of protoplast damage during sectioning (compare Fig. 8, b and c). Absorption of ultraviolet light by layer G of the walls of the reaction wood cells in (c) and (d) is due to penetration of G by lignin, lignin precursors arriving from outside the cells. Note the penetration of lignin at the corners of the cells shown in (d). (a) $\times 550$, (b and c) $\times 530$, (d) $\times 600$.

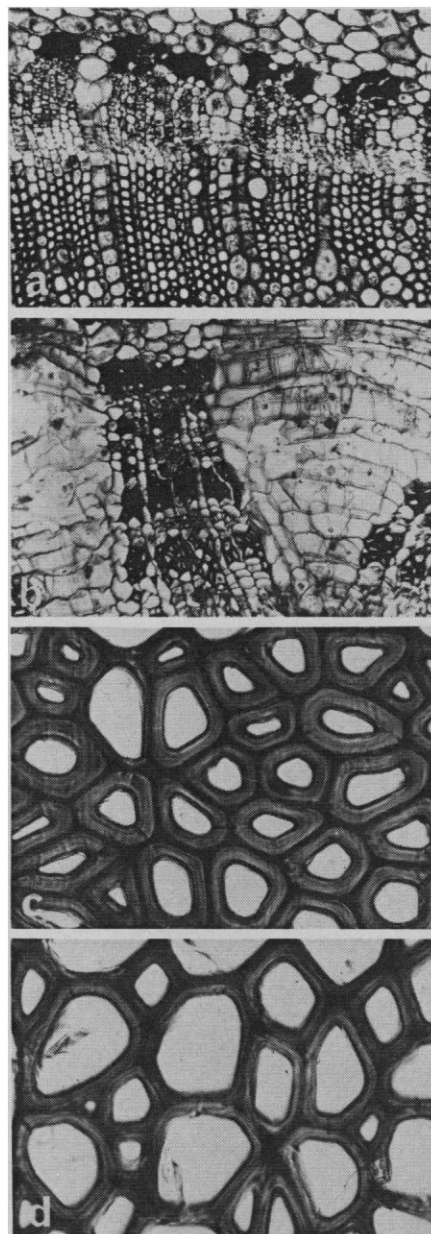
Fig. 11. *Lagunaria pattersonii*: (a) phloem on the under side of a stem grown bent at right angles to the vertical, (b) phloem on the upper side, (c) ultraviolet photomicrograph of normal wood fibers, and (d) ultraviolet photomicrograph of reaction wood fibers. (a) and (b) $\times 110$; (c) and (d) $\times 540$.

also with the observation that when reaction wood fibers produce large amounts of phenolics, as in diseased stems of *Exocarpus* (44), these tend to be confined largely within cell lumina. On the other hand, it is inconsistent with the penetration of the innermost lamellae of G by phenolics in cells such as those shown in Figs. 8 and 10, even though here such release may be the result of damage to cell protoplasts during sectioning (29). This difficulty is unresolved and seems likely to remain so until more is known about the nature of the phenolics released either as a result of sectioning or during cell senescence.

This brings us to the question whether lignification generates the force responsible for reerecting a bent or tilted hardwood stem. The location of lignin being largely in layers external to G, presumably it is these layers which swell when lignin is deposited in them. Belief that the force so created is directed in large part transversely by virtue of the resistance offered by G to longitudinal expansion is consistent with the evidence of lateral compression of vessels and parenchyma cells in reaction wood (24), and the indications of poor lateral cohesion of G with outer wall layers of the fibers (44). By contracting in length, the fibers bring about stem reerection. Overcoming the enhanced buckling stability due to G accounts for the larger number of slip planes reported to occur in reaction wood fiber walls (25). The situation is comparable with that found during the loading, parallel to the grain, of polymer impregnated wood (45).

The Functional Role of Lignin Questioned

1) The stem apex of a woody monocotyledon which is grown horizontally tends to reerect itself, but the stem as a whole does not. Asymmetric radial growth of the stem does not occur, but more vascular bundles may be produced on its upper than on its lower side. Fibers surrounding these bundles have thicker walls than normal, a con-



sequence perhaps of their higher degree of lignification. If so, then such enhanced lignification, since the stem does not reerect itself, may serve instead merely to strengthen the stem as it continues to grow and increase in weight (25).

2) Some hardwoods, for example, *Lagunaria pattersonii* (26), *Tilia cordata*, and *Liriodendron tulipifera* (44), do not produce typical reaction wood. Tilted or bent stems of these species undergo asymmetric radial growth, but this is achieved by increased production of both xylem and phloem on the upper side of the stems (Fig. 11). There are fewer vessels than normal in the reaction wood of *Lagunaria* and they have a smaller cross-sectional area. In this, *Lagunaria* reaction wood is comparable with that produced by other hardwoods.

It is different, however, in that the cross-sectional area of fibers and of ray and xylem parenchyma cells is markedly increased. The texture of the fiber walls is uncertain, but they are thinner than normal due to a reduction in the thickness of S2 and they do not form layer G (Fig. 11). The structure of the phloem appears to be normal (23). The lignin content of the reaction wood is much the same as in normal wood (46).

These features are consistent with the conclusion that for reerection of a displaced stem asymmetric radial growth, coupled with the differentiation of cells having a wall structure different from normal, must occur; that the force bringing about reerection resides in the region of cell differentiation, although here this covers both xylem and phloem; and that the differentiation of layer G plays no active part in stem recovery. The difficulty is to maintain the view that lignification leads to swelling of fiber walls, and that the swelling force is channeled in such a way as to bring about longitudinal contraction of the fibers and reerection of the stem. An alternative is that tangential dilation of the rays causes phloem strands to veer more and more from the longitudinal direction and that the pull they exert first supports, and then perhaps reerects, the stem (47).

3) Asymmetric radial growth either on the upper or lower side of the stems of *Eucalyptus* trees displaced from the vertical has been observed where the structural features of the wood do not appear to correspond with those of the reaction wood described above. These stems are currently being investigated with a view to ascertaining the mechanism of their recovery to the vertical (48). The fact of their occurrence, however, emphasizes the possibility, not only that the mechanism of recovery of a hardwood stem may differ from that of a softwood stem, but that different mechanisms may prevail among individual trees of the same species.

Equally, lignification may not have the same role in all cases. As already mentioned, allocation to it of a passive role shifts the location of the recovery force to the cambial zone. Presumably it is then the resultant of the forces of tension and compression generated by an abnormally rapid rate of division of cambial initials, the increase in volume of the derived cells, and the overall increase in stem circumference accomplished by asymmetric radial growth (1, 37, 49).

Summary

The mechanism by which the stems of trees recover after being bent or tilted out of the vertical is considered. The mechanical consequences of the tendency for the main stem apex to reerect itself and grow vertically or to be replaced by a vertically growing lateral branch, and of the asymmetrical radial growth of displaced stems, are pointed out. The asymmetry usually develops on the upper side of a bent or tilted hardwood stem and on the under side of a softwood stem. Since such asymmetry can usually be accounted for on the basis of accentuated development of wood rather than bark, the question of the possible functional significance of the wood arises. Experiments are cited to demonstrate that the wood (reaction wood) is effective as a means for assisting displaced stems to recover, contracting longitudinally on the upper side of a hardwood stem and expanding on the under side of a softwood stem. Consideration is then given to the structure, differentiation, and chemical composition of the reaction wood formed by hardwoods and softwoods with a view to locating the force active in aiding recovery and determining its origin. The consequences of associating the support of a still-growing stem displaced from the vertical with the idiosyncracies of secondary wall formation of reaction wood cells, and the reerection of such a stem with lignification of

these walls, are explored. On this basis, the hypothesis is advanced that the recovery force is located in the region of differentiating reaction wood cells undergoing lignification, the active force arising from the swelling of cell walls as a result of deposition in them of lignin. Objections to the hypothesis are mentioned.

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50. I am grateful for the comments of R. Pearson, North Carolina State University, and my colleagues J. D. Boyd and R. H. Leicester.

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