TREE GROWTH STRESSES

III. THE ORIGIN OF GROWTH STRESSES

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Summary

Evidence available indicates that tree growth stresses originate in newly differentiated cells towards the periphery of a tree.

It is considered that an origin connected with the structural development of peripheral cells would explain both the longitudinal and lateral distribution of growth stress effects more satisfactorily than other hypotheses suggested.

The cause of growth stress development may be explained by the theory that cells tend to shorten in length, and simultaneously to increase in cross section during or immediately after differentiation. The resistance of the mature cells throughout the tree to such a shortening could induce the stress effects which occur.

I. Introduction

A number of observers, including Martley (1928) and Koehler (1933), have noted reactions of sawn planks, logs, and trees which suggested that significant stresses existed in directions respectively parallel and transverse to the height of growing trees. Jacobs (1938, 1939, 1945) not only confirmed the existence of these stresses in trees, but his many measurements indicated their magnitude and distribution. Clarke (1939) reviewed the information then available. His discussion referred to results to be expected in trees under the conditions of normal growth, and also to features associated with the development of tension wood and compression wood. Additional information and development of data on stresses in trees is now available (Boyd 1950a).

It is concluded that these manifestations of stress are related in some way to the growth conditions of the tree, but from this point proposed hypotheses on the origin of growth stresses are frequently inadequate to explain observed effects. Stress distributions indicated by the induced strains measured by Jacobs (1938, 1945) suggested to him that both longitudinal and transverse stresses have an origin close to the periphery of the tree. This conclusion arose from the fact that strains measured were of uniform magnitude at the periphery, throughout the wide range of diameter classes investigated. Though most measurements were made on alpine ash (Eucalyptus gigantea Hook. f.) similar results were obtained for a wide range of species. At the same time, it was shown that the tendency to develop and increase longitudinal compressive strains in the area towards the pith was a function of tree diameter—a result which might be anticipated if the causative stress generation occurred at the periphery and always tended towards an approximately uniform value.

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Though Jacobs's data (1938, 1945) on stresses existing in a plane transverse to the length or height of a tree are scanty and conflicting, these and subsequent data and consideration (Boyd 1950a) point to a relatively constant peripheral value and origin of these stresses. The peripheral origin could explain the distribution of both ring and radial stresses (Boyd 1950a).

Hypotheses on stress generation have been proposed by Martley (1928), Koehler (1933), Münch (1938), Clarke (1939), and Jacobs (1945). However, lack of compatibility of the proposed hypotheses appears to warrant their critical examination.

II. LIMITATIONS OF EXISTING HYPOTHESES

Some hypotheses of stress generation within trees have been based on inadequate data. Frequently, theories were proposed to explain particular features such as longitudinal stress reactions, transverse stress reactions, or the effect of special tissue, and little attempt has been made to correlate all such manifestations in one general explanation. Hence, besides examining the adequacy of the theories within the particular limitations proposed, it is felt that this wider basis of appraisal may justify consideration.

(a) The Effect of Tree Weight

After observing that a nominally flat end of a beam became curved in profile after cross-cutting, Martley (1928) reasoned that this was caused by stresses naturally present in the timber. He proceeded to calculate the stress which might develop from tree weight on the basal section of trees of various sizes and species, and concluded that values up to 200 or 300 lb./sq. in. were the maximum which could be expected. On the other hand, he estimated that the observed elongations towards the centre of a cross-cut face must have been the result of stresses of a considerably higher magnitude. Subsequent investigations (Boyd 1950a) have shown that the observed elongations are directly related to longitudinal strain energy movements in the log, rather than to the longitudinal stress alone, but measurements of this stress in hardwoods have indicated values of approximately 3,000 lb./sq. in. (Jacobs 1945; Boyd 1950a).

In addition, the longitudinal strain pattern established (Jacobs 1945; Boyd 1950a) indicates that an annulus or zone of tension exists round the full periphery of the tree—a condition incompatible with the weight effect arising from either symmetrical or asymmetrical growth of the crown. Further, the peripheral tension is approximately constant both round any particular section, and over the height of the tree (Jacobs 1945). On the other hand, tree weight would be expected to cause either compressive stresses only on a tree cross section, or an unsymmetrical distribution of tensile and compressive stresses. Variation of stress with height could also be anticipated if weight were the cause. In pendant branches of eucalypts, it might be anticipated that tensile stresses would predominate if weight were the most significant factor, but actually these branches exhibit a stress distribution similar to that of the bole of the tree (Jacobs 1945).
In a transverse plane, it might be anticipated that tree weight would have some effect. Considering a hardwood, and assuming the normal elastic relationship between primary stresses in a longitudinal direction and induced reactions in a transverse direction, then if the values of the modulus of elasticity in the longitudinal and transverse directions are 3,000,000 and 100,000 lb./sq. in. respectively, and the corresponding Poisson's ratio is 0.45, it can be shown that a longitudinal compressive stress of 300 lb./sq. in. may induce a tensile stress of 4.5 lb./sq. in. in the transverse plane. Although the elastic moduli of a tree may vary appreciably from those assumed above, the order of value of the calculated figure, and the stress character (tensile) appear to be incompatible with measured peripheral, transverse, compressive stresses of the order of magnitude of 300 lb./sq. in. (Jacobs 1945; Boyd 1950a).

Undoubtedly its own weight has some effect in producing stresses within a tree, but the estimated value of these stresses, their character, and distribution appear inadequate to explain the stress equivalents of measured strains. Obviously then, the main cause of stress development must be sought elsewhere.

(b) Koehler's Theories on Stress Generation

Koehler (1933) was concerned with stresses which developed in a transverse plane and caused “rift cracks” or shakes across a cross-cut face. He suggested three possible explanations of the observed stress effect — greater circumferential than radial growth, reduction in the turgidity of the older tissues, and chemical changes of the older wood.

Normally, the wood cells developed within a tree are oriented in a direction parallel to the stem or branch (except the ray cells) and are arranged in any cross section so as to form radial lines from the pith. Consequently, as the tree grows, the increasing girth requires a change in the expanse of the new sheaths of cells, and therefore some variation in the number or shape of cells. From time to time it is necessary that new radial lines of cells be developed. Koehler envisaged that this mechanism of growth involved squeezing or possibly stretching of cells to fill the available space, and that this adjustment might be responsible for the stresses developed.

However, it appears that all substantial adjustments in shape that are necessary would occur in the newly differentiated tissue prior to development of the secondary walls. On this assumption, the secondary walls of the cells would be built up with the primary walls already suitably disposed in position and shape to meet the requirements of the growing tree. Because of its great thickness and strength compared with the primary wall (Preston 1947), the secondary wall must be considered as the most significant in growth stress considerations. Consequently, as this secondary wall is probably not subject to external stresses due to the non-compatibility of uniform cell size and radial and circumferential growth, the corresponding stress effect on the complete cell is likely to be small. Consideration of the elasticity of the wood structure will indicate that in the longitudinal direction, any induced stresses would be much smaller still. Doubts in the validity of this theory of stress development
are increased when it is proposed that some sheaths of cells are squeezed while others are stretched, or at least squeezed to a varying degree. Such an arrangement may render it difficult to explain the relatively uniform strain pattern observed as the tree grows (Jacobs 1945).

That the reduction in turgidity of the older tissue within a tree cross section may cause the development of radial tension and circumferential compression has been proposed (Koehler 1933). Although, in some species, certain cells may retain their turgidity for a considerable number of years, in most species the small proportion of living cells in the sapwood suggests that the effect of their turgidity in inducing transverse stresses throughout the whole cross section of the tree is probably small. Furthermore, after the formation of heartwood has commenced, there is a tendency for the volume of sapwood in proportion to the total tissue in a tree cross section to decrease as the tree grows in diameter (Trendelenburg 1939). To a corresponding degree it might be anticipated that the effect of the turgid tissue in stressing the tree would decrease, and that in a relatively old tree the effect would be small compared with that in a younger tree. Though in some cases immature trees develop severe heart shakes and therefore show evidence of appreciable stresses, this effect is by no means confined to small trees of the particular species (Boyd 1950b). In addition, the peripheral transverse stress development has been shown to be approximately uniform in a variety of tree diameters and species (Boyd 1950a) even though some of the logs investigated were entirely of sapwood. The evidence therefore appears to be at variance with the hypothesis proposed.

Koehler suggested an alternative hypothesis that chemical shrinkage of cells subsequent to their death might be responsible for the observed indication of stress. If this were so, arguments similar to those above would apply, except that the stress effect of chemical shrinkage, though at first negligible, would gradually become of ever-increasing importance. Again this is not in accordance with observed effects and experimental results.

A combination of the effects of turgidity and chemical changes might be argued as a possibility. However, this, too, would leave unexplained the observed stress development in very young trees (Jacobs 1945).

(c) The Effect of Sap Stream Tension

In view of the considerable amount of investigation of growth stresses by Jacobs, and the facts that, after considering a wide variety of possible causes he stated (1945) that “present evidence points to sap stream tension being the cause of the longitudinal stresses of erect hardwood stems and larger coniferous stems,” and that it may be responsible for the lateral stresses also, detailed analyses may be justified.

Many physiologists have examined the phenomenon of sap ascent within a tree, and various hypotheses have been suggested. The different theories proposed imply different sap pressure or suction distributions with correspondingly different stress effects within the tree. However, the hypothesis most
generally held (Thomas 1937) is that the active transpiration of the leaves causes suctions of sufficient strength to draw water to the top of the highest trees. Dixon (1924) has shown that the sap stream could sustain the necessary tension to achieve this end, but in the matter of how the suction is generated, and also the intensity of forces involved, considerable difference of opinion exists. Beyond assuming that the motive force is created in the region of the leaves, it is not proposed to consider the mechanism of sap ascent further. However, the intensity of forces generated will be discussed.

Suction intensities ranging from 10 to hundreds of atmospheres have been estimated by different workers. Thomas (1937) states that suctions equivalent to 10-20 atmospheres are not uncommon in the leaves of trees, and that the forces of adhesion between water and cell wall materials may be over 1,000 atmospheres. Dixon's work (1924) indicates that for some plants, the frictional resistance to flow through the conducting passages may require that the suction exerted be equivalent to twice their height. Obviously this will vary with the particular tree or species, but if one were 340 ft. high, a suction magnitude of 20 atmospheres may be anticipated.

The manner in which sap tension might transfer stresses to the cell wall probably depends upon the mechanism of sap movement, diameter and continuity of the sap columns or conducting passages, rate of transpiration, etc. However, if peripheral longitudinal tensions of the magnitude of 2,000 lb./sq. in. (Boyd 1950a) in the mature wood formed over a period of a few years are to be explained in this way, the average suction exerted in the sap stream over this period must have been very large. Even if the suction developed at the leaves could be transferred as equivalent stress to the cell walls—an unlikely possibility—then a suction intensity of at least 140 atmospheres would be indicated. Taking account of variation of transpiration rate with temperature, relative humidity, wind strength, and seasonal conditions, a considerably higher peak suction intensity may be required to account for the measured stresses in the wood. If such sap stream suction intensities were produced, evidence may be available from other considerations of tree growth. Some possible implications will be examined.

(i) The Effect of Suction on Cell Walls.—Little information is available, but on the basis of published cell sizes and wall thicknesses, and on the assumption that on the cambium side the immature cells add little to the strength of adjacent cells, and that in such a species as alpine ash the nominal ultimate strength of wood is only approximately one-third of the stress within the cell wall at failure (when allowance is made for the cellular nature of wood), then a calculation of strength may be made. The internal suction intensities which might be required to produce flexure failures in the walls of vessels, early wood, and late wood fibres are estimated at 30, 150, and 1,500 atmospheres respectively. If these cells are subject to suction forces of the magnitude of 140 atmospheres and perhaps considerably more (which appears necessary if sap tension is to account for measured longitudinal stress development in the wood), then the possibility of fracture or collapse of vessels and early wood fibres must be very real.
The absence in published literature of evidence of inward collapse of green tissue of growing trees therefore raises doubts as to whether the supposed high-intensity suction forces are developed, and whether sap stream suction intensities could be responsible for the tree growth stresses measured.

If the calculations indicated above are not even approximately correct (the problem is a complex one), at least it would appear that the supposedly large suction forces may give rise to considerable stresses, and have an appreciable effect on the reactions and characteristics of the wood tissue. A little thought on the hydraulic factors associated with sap flow suggests that if a suction of 140 atmospheres or more were created within the leaves, this large flow potential must be dissipated in overcoming the resistance to sap movement through the small channels and past the many obstructions en route. For this reason, and because of the static pressure difference due to the height of the tree, only a fraction of the suction effect would exist towards the base of the tree. In fact, Tiemann (1937) reported that suctions of appreciably less than one atmosphere have been measured by pressure gauges attached to the base of a tree and connected to the sapwood. Therefore, if the hypothesis of very large suction intensities in the leaves is valid, from the considerations above it would appear likely that a vastly different internal stress existed within conducting wood tissue and any connected tissue near the top of the tree, as compared with similar tissue at its base.

In reference to the cross-sectional shape of cells at different heights within a tree, no very obvious differences have been reported which would suggest that the cells near the top have been subjected to extremely high suction stresses, while those near the base were free of that effect. The absence of reported differences casts doubt on the sap stream theory as the major origin of growth stress development.

(ii) Lack of Variation in Peripheral Longitudinal Strain with Variation in Size of Tree.—In discussing the mechanics of sap flow, Thomas (1937) suggested that the suction necessary depends directly upon the length and size of the conducting channels and the height of the tree. If this is approximately correct, then when a sapling 20 ft. high is compared with a tree 200 ft. high, it might be expected that the sapling would require to develop at its leaves only a fraction of the suction required at the leaves of the large tree. The possibility that the leaves of both trees may be capable of inducing the same suction intensity is not questioned, but the continuous generation of greater sap tension than would satisfy the sap flow needs of the tree appears unlikely. On the other hand, it is possible that any tendency to do so may be immediately counterbalanced by the resulting surfeit of sap flow. Although it is not known if differences in sap stream suction have been investigated in two such examples, on the hypothesis that growth stresses result from the sap stream tension it may be logical to expect significantly different growth stress intensities in the two tree sizes quoted.
However, measurements of the longitudinal tensile stress at the periphery indicate that the same growth stress is developed in small saplings and large trees (Jacobs 1938). This casts additional doubt on the sap tension growth stress theory.

(iii) Lack of Variation of Longitudinal Stress with Variation in Height in the Tree.—As a corollary of the comparison of likely sap stream suction differences in small and large trees, it is possible that appreciable variation occurs with change in height within a single tree. Again, if the intensity of sap tension is an important factor in the development of growth stresses, then considerable stress variation with change of height in the tree might be anticipated. No such wide variation of peripheral longitudinal stress has been measured. On the contrary, Jacobs (1938) reported an approximately constant longitudinal stress in the sapwood at different heights.

(iv) Lack of Variation of Peripheral Circumferential Stress with Diameter and Height Variation.—It has been shown that peripheral longitudinal stresses are approximately constant with variation of tree size (Jacobs 1945). Peripheral circumferential stresses have been similarly demonstrated as uniform (Jacobs 1945; Boyd 1950a). It appears that these are either dependent upon one another—a condition shown to be unlikely (Boyd 1950a)—or they are both produced by some other agency. If the sap stream tension is visualized as that agency, then its possible wide variation with tree height does not appear compatible with the relative constancy of peripheral circumferential stress with both diameter changes in different stems and height variations within a particular stem.

(v) The Relationship of Sap Stream Forces and Measured Longitudinal Stresses.—It is desirable to check whether the stresses which might be anticipated from the effect of sap stream forces are of the same character (tensile or compressive) as those measured in the tree. Jacobs (1945) suggested that “the contraction measured when an outer strip is cut from a plank would represent an adjustment of the dimensions of the woody elements of the strip as a reaction to the tension remaining in the sap columns. In the stem itself, the sap tension of each new outer sheath of cells would compress the cross section as a whole.” Thus, with this theory, he envisages that the measured contraction in length of wood at the periphery actually represents a compression imposed as the sap columns are cut across, and not, as he suggests elsewhere (1938, 1945), a tension which is relieved when the piece is freed of the restraint of the tree. He says the sap columns “will contract until the capillary force exerted at the apertures in the pit membranes, or other obstructions in the lumina of the cells, balances the tension remaining in the columns. The remaining tension will then be held, and a longitudinal compressive reaction will be imposed on the woody substance.” The increase of length of wood from the core is explained as a reaction to the compressions developed over a period by the natural breaking of sap columns within the tree.
This hypothesis implies that when the sap columns are continuous in the growing tree, they do not impose significant stresses on the tissue through which they pass, but develop stresses in adjacent tissue as a result of a tendency to suck out the fluid contained in its broken sap columns. However, when a tree has been felled the continuity of all columns between roots and crown has been broken, and therefore there must be a tendency to develop the full tension within these as discussed above. Presumably the sap tension developed under such circumstances would depend largely on the tendency to dry out or remove moisture from the columns. With vessels within the wood, the removal of fluid may be comparatively easy, but because of the relatively large diameters of cells concerned, the sap tensions developed would be equivalent to a capillary rise of not more than a few feet (Thomas 1937) and the corresponding stresses must be insignificant in relation to the measured stresses in trees. With wood fibres, the removal of fluid corresponding to the development of stresses would probably be considerably slower. Yet, as a tree is cross-cut under experimental conditions (Boyd 1950a), all observable stress reactions, both in the sapwood and towards the pith, occur immediately after cutting, and no significant addition to the stress development occurs over a period of hours in ordinary atmospheric conditions. In Jacobs's experiments (1945) also, no effect due to the probable wide range of atmospheric conditions during measurement was noted.

If the initial cross-cutting of a log severs the sap columns, on this theory the corresponding tension must soon be established in them, and a compression imposed on the wood. Then additional cross-cutting should not affect either the general intensity of sap tension or the imposed longitudinal compression in the wood. In fact, in Jacobs's experiment (1938, 1939, 1945), strips 8 ft. long reacted to the full stress development of uniform intensity along their entire length. However, if strain gauges are placed on the sapwood at a position between the ends of a log, it can be shown (Boyd 1950a) that reduction of length equivalent to the full measured peripheral stresses (Jacobs 1945) occurs as a result of additional cross-cutting. It appears, therefore, that the longitudinal stress in the sapwood of a tree is not caused by the breaking of sap columns, such as results from felling or cross-cutting, but rather that cross-cutting or stripping the tree into beams may release stresses previously present in the tree. In the sapwood the stresses released are tensile, but the sap tension theory indicates compressive stresses.

Jacobs (1945) has shown that a progressive compression is imposed on the wood towards the pith. This may be difficult to explain in terms of sap tension. When the sap columns break, the compressive forces supposedly imposed by them upon the wood towards the pith are relieved. The development of new sap columns may reimpose the same force, but a cumulative stressing effect is doubtful. Actually, Trendelenburg (1939) shows that the proportion of sapwood tends to decrease as the tree matures, and therefore the effect of forces applied through the sap stream to the heartwood may conceivably decrease. Thus, instead of a cumulative compression of the core, a reduction of compression may occur.
Consequently, from the many aspects considered it is doubtful if growth stresses could be explained in terms of sap stream forces.

(d) The Effect of Vacuolation Forces

A vacuolated living plant cell may be regarded as an osmotic system (Thomas 1937). The pressures generated as a result of osmosis may account for growth stress development within a tree. Jacobs (1945) states that "the pressure of vacuolation must be great enough to rupture the bark and enable a tree to accomplish diameter growth," and he suggests that transverse growth stresses may be explained in this way.

In regard to the pressure required for splitting the bark, it is conceivable that a few pounds per square inch would suffice. For example, if a radial pressure of 5 lb./sq. in. were exerted on the inside face of the bark of a 10 in. diam. tree, the splitting force per inch of length (vertical) of bark considered would amount to 25 lb. This force would tend to increase with diameter increase and undoubtedly a force of this order of magnitude could account for splitting the bark of many species. However, it has been shown (Boyd 1950a) that a radially directed pressure intensity $R$ at the periphery induces a peripheral circumferential stress equal to $R \times E_T/E_R$, where $E_T$ and $E_R$ represent the elastic moduli for forces applied in the tangential and radial directions respectively. Measurements made in this laboratory on several green specimens indicate that the ratio $E_T/E_R$ approximates 0.5 for Eucalyptus regnans and 0.6 for Pinus radiata. Similar results for a variety of species may be derived from published data of the U.S. Forest Products Laboratory, Madison, Wis. (Report Series No. 1528, 1945-6). Thus the peripheral circumferential stress equivalent to a radial pressure of 5 lb./sq. in. would be of the order of 3 lb./sq. in. This is considerably less than measured peripheral transverse stresses in a wide range of species which range from a "probable minimum of 30 lb./sq. in. to a probable maximum of 360 lb./sq. in." (Jacobs 1945). Consequently it is considered that forces much greater than necessary to split the bark are probably operating.

In an attempt to determine vacuolation pressures, Jacobs (1945) applied pressure pads to growing trees of Pinus radiata. He found that circumferential growth continued in the local area under a pad of 1 sq. in. area and loaded with a force of 150 lb. From this he concluded that growth could, and normally probably did occur with pressures of vacuolation approximating 150 lb./sq. in. (10 atmospheres).

However, reservation should be placed on conclusions drawn from this test. In a general way, it is felt that the knowledge that a tree can generate sufficient force under stimulus to continue circumferential growth against restraint may be an insecure basis for concluding that a like force is constantly or normally generated without that particular stimulus. This doubt is reinforced by Jacobs's own observations and photomicrograph (1945), which indicate that, when the tree was subjected to a pressure on the load pad of 100-150 lb., the shape of cells formed was significantly different from normal.
Jacobs assumed that the pressure equivalent of a pad load of 150 lb. was 150 lb./sq. in. However, this intensity may be much greater than the actual pressure intensity under the pads. As the square loading pads were applied to the outside of the bark, its stiffness would tend to support the load on all four sides of each pad. Very little side support beyond the edges of the pad would cause the effective area of application of the load to be considerably increased, and a spread of less than ½ in. on all sides would reduce the intensity of the 150 lb. load application to 75 lb./sq. in. To allow of checking this point, Dr. Jacobs kindly made available the load pad area of one of his specimen trees. A radial saw cut was made through the centre of a load area and a photograph of the exposed face is shown in Plate 1. It may be seen that the grain of the wood towards the bottom of the photograph is straight. This wood was formed before the pad was applied. The curvature of the resins ducts in the wood formed after application of the pad indicates the general disposition of tissue, and confirms the fact that the applied pressure is distributed for an appreciable distance beyond the edge of the 1 in. square pad. A cut made in the transverse direction showed a similar spread of the pressure effect.

In addition, Jacobs states that an applied force of 25 lb. had a positive effect in restricting diameter growth. Again allowing for pressure distribution, it appears that relatively very low pressure intensities may restrict the effect of vacuolation forces. For this to be so, probably the vacuolation forces themselves are correspondingly small under normal growth conditions and consequently they appear inadequate to explain transverse growth stresses.

Vacuolation forces will have a direct effect in the longitudinal direction of the cells and the trees. However, by comparison with stresses in a closed cylinder, and on the assumption of approximate cell dimensions, it may be estimated that a vacuolation pressure of 10 atmospheres would develop a longitudinal stress in the cells of 100-200 lb./sq. in. As these calculations are based on vacuolation stresses which may be high, and the values obtained are very much below measured peripheral longitudinal stresses of 1,000-2,000 lb./sq. in. (Boyd 1950a), the vacuolation pressure origin does not provide a satisfactory explanation of longitudinal stresses. Also, adopting approximate values of the relation of induced longitudinal strain resulting from transverse strain (Kollmann 1936) it may be estimated that, even if vacuolation pressures of 10 atmospheres or more were developed, these would induce stresses probably very much less than 100 lb./sq. in. in the longitudinal direction, and either alone, or in combination with the direct longitudinal effect of these forces, could not explain the origin of longitudinal growth stresses. Furthermore, as vacuolation pressure or the effect of turgidity of cells diminishes and possibly disappears with the completion of the cell wall of structural wood tissue, its effect in stressing the wood is apparently not cumulative. On the contrary, as the trees grow the stress effect would tend to become smaller and could not explain the actual stress distributions observed.
(e) Development of Stress in Compression Wood

It is generally acknowledged that the characteristics of compression wood are very variable, and even in the one tree the most extreme type of abnormal tissue is associated with other tissue whose properties gradually merge into those of normal wood (Pillow and Luxford 1937). Münch (1938) considered some of the possible mechanisms by which a leaning tree might tend to grow straight under the influence of compression wood. He postulated that the corrective force arose from a positive longitudinal growth of compression wood cells as they matured, and a resistance offered by adjacent tissue to that growth. In this way he envisaged the generation of a dynamic stress in the wood structure.

Brown (1944) stated that the "secondary wall is not formed until the enlargement entailing sliding growth is practically complete." Also, Frey-Wyssling (1948) stated that the secondary walls are "deposited by apposition against the fully grown primary wall during the corresponding growth of the membrane in thickness." During growth, it is probable that the primary wall, because of its extremely fragile character (Preston 1947), could not impose large forces on the mature wood tissue. Hence there is a definite doubt that the necessary stresses required for straightening a tree of a coniferous species have their origin in a positive lengthening of the relevant wood tissue.

III. Cell Wall Shortening as an Origin of Tree Growth Stresses

Münch (1938) suggested that the extremely large longitudinal stresses presumed to be associated with tension wood arise from a tendency of these cells to increase in cross section and simultaneously to reduce their length. The abnormal stress development of this reaction wood is confirmed by Jacobs (1938). Clarke (1939) remarked that the same tendency to shorten and broaden the cells may well be present in normal wood and account for the transverse compressive stress mentioned by Koehler (1933). Though ultimately Jacobs (1945) preferred the sap stream hypothesis he initially suggested that "the most reasonable theory for the cause of fibre tension on present knowledge would be that as the wood elements solidify from the gelatinous cambium they tend to shrink slightly, the tendency being resisted by their adhesion to the inner core." As no known attempt has been made to develop these hypotheses in conjunction with experimental data, it is proposed to test them in the light of information available.

Apart from the actual mechanism involved, Münch's suggestion of a simultaneous shortening and dilation of the maturing cells, if applicable to normal wood, may explain the simultaneous peripheral development of longitudinal tension and ring compression. A notable feature of this stress arrangement is the approximately constant intensity of stress generation in both directions at all stages during growth.
(a) Strain Capacity of Wood Cells

As a convenient method of investigation of tree growth stresses, Jacobs measured the normally associated longitudinal strain or proportional change in length of measured sections under the influence of growth forces. These strain determinations were made on strips of sapwood of varying radial thickness ranging up to ½ in. (which was generally adopted for trees 6 in. diam. and greater).

A study of Jacobs's measurements, and particularly the graph prepared by him (1945) to show the radius of the tree plotted against the unit contraction (strain) rate of the core under the influence of the longitudinal strain developed in the sapwood, reveals that the wood in the sapwood zone develops remarkably different strains in trees of different radii. At the same time, it must be pointed out that the strain recovery of the sapwood when released from the restraint of the tree is approximately constant over the wide range of diameter classes measured (from 0.1 to 30 in.). In alpine ash, the mean recoverable sapwood strain (tensile) was 0.0008, and a similar figure was obtained in many other species of pored timber. The tensile stress equivalent of this strain in alpine ash is 1,200 lb./sq. in. (Jacobs 1945).

A conclusion which may be drawn from the graph is that, for the diameter classes ½ in., ¾ in., 1 in., 2 in., 5 in., and 20 in., the respective strains imposed by the peripheral tissue on the whole enclosed core are 16, 8, 5, 2½, 1, and ¾ times the residual or measurable strain at the periphery. Since the residual peripheral strain is constant with variation of height within the tree, it may be expected that individual cells would have mean strains equivalent to that measured in the wood of which they form part. In this range of diameter classes then, not only do peripheral cells exhibit residual strains of 0.0008, but also they impose strains on the cells enclosed by the peripheral sheaths ranging in ratio from 64 to 1, and equivalent to as much as 16 times the measured residual peripheral strains. This implies that a change in length of peripheral cells occurs during the process of stress development, resulting in a maximum shortening during maturity in peripheral cells differentiated while the diameter is small, and progressive proportional change in peripheral tissue with increasing diameter.

Since the changes in peripheral cell length are always greater than, and range up to many times the maximum recoverable strain, it may be deduced that at the stage of stress development, or over the limited period after cell formation represented by the width of sapwood strip examined, a tensile strain of 0.0008 (approximately) is the maximum which can be elastically sustained within the cells. Therefore, other changes of length must be accomplished under conditions of plastic strain or irrecoverable change of length of the cell walls. If then the structural characteristics of the cell walls can generally be regarded as similar over most of the tree diameter, the forces successively developed in the peripheral tissue as the tree grows must be such as would tend to shorten these cells in conformity with the greater measured shortening associated with cells developed towards the pith. With increasing diameter,
the restraint exerted by the mature core of wood on free reduction of cell length would have the effect of increasing the plastic flow and causing a corresponding permanent strain in the cell walls.

It may be of interest to note here that such a system of strain generation and restraint, if imposed on cells which were originally of uniform length over the range of tree diameters, would result in somewhat longer cells as the tree diameter increased. From the early stages of tree growth to the later stages, the rate of cell length increase would at first be relatively rapid, later a constant length would be approached. However, it should be realized that the extreme change in length of cells in the tree diameter range of \( \frac{3}{4} \) in. to 30 in. would approximate only 1/100 of the cell length. Even in the ideal case this would be difficult to measure, but the changes in cell lengths which occur under the various growth stimuli and independently of the stress effect would completely mask it in any practical example.

(b) The Relationship of Growth Stresses and Cell Wall Deformations

Cell wall deformations have been the subject of considerable investigation by a number of workers. It is proposed to discuss them in some detail in a separate paper, but because of their possible bearing on the study of tree growth stresses brief mention will be made below.

Wardrop and Dadswell (1947) have stated that "slip planes occur commonly in nearly all fibres and tracheids with perhaps some exception in the case of the wood in close proximity to the pith of the main stem or branch. They have definitely been observed in the cell walls of the last-formed fibres of many trees, i.e. in the fibres just differentiated from the cambium." The same workers have shown that these distortions have the appearance of a crinkle or fold very much akin to that of a compression failure.

As growth stresses appear to be developed in cells close to the cambium zone, it is perhaps reasonable to consider that cell wall distortions may be connected with that development. However, if growth stresses resulted from sap stream tension, longitudinal tension would be general throughout the cell walls of conducting tissue in the sapwood. This would appear incompatible with the compression-type cell wall distortion. On the other hand, if growth stresses resulted from some mechanism causing shortening of the differentiating cell wall, then newly formed cells would be subject to considerable compressions by younger cells just maturing from the cambium. This compression may be sufficient to cause the distortions.

The distribution in tension wood zones of the more severe cell wall distortions known as "minute compression failures" (Wardrop and Dadswell 1947) may provide additional confirmation. In comparing the reaction of normal wood and tension wood, if it is assumed that the orientation of the cellulose molecular chains is similar in the wall layers common to both types of cells, then the application of a particular force with an origin external to the cell wall might be expected to have a less severe effect in stressing the relatively thick-walled tension wood fibres than would be expected in normal wood.
Yet minute compression failures are more common in tension wood tissues than adjacent normal wood tissue. As it does not appear likely that sap tensions would be relatively greater in tension wood, again the sap tension theory appears incompatible; but if the tensions generated were in some way related to the volume and other characteristics of the material in the maturing cell walls, then exceptionally high stress intensities in tension wood cells might be expected. The reaction of the attached cells on the pith side (whether tension wood or normal wood) may induce compression intensities sufficient to cause severe distortion in them.

(c) The Mechanism of Growth Stress Development

The foregoing deductions, which are based on experimental results and observations discussed, are consistent with the idea that the wood cells shorten in length. Generally, this shortening could result either from forces generated external to the cell wall structure or from forces developed within the actual wall; but detailed consideration of possible external agencies such as tree weight, sap tension, etc., have raised considerable doubt that these could explain the observed results. Consequently, the hypothesis which may best fit the facts is that there is a tendency for the cell walls to shorten under the effect of some compelling mechanism within their structure, and that the restraint applied by the relatively rigid mature core of the tree to their free adjustment of length and cross section is responsible for the generation of growth stresses.

In tension wood, Münch (1938) has suggested that, at the time of its formation, the secondary wall undergoes an irreversible swelling, as a result of which it exerts a radial pressure on the outer layers of the wall, tending to compress the spiral windings and shorten the cell. If, as Clarke (1939) suggests, this mechanism in a less extreme form occurs in normal wood, it may well explain the longitudinal and transverse stress distribution which has been observed.

At this point it is desirable to recall that transverse stresses induced as a result of longitudinal stresses alone could not account for the measured values (Boyd 1950a). Consequently, a theory which presupposed shrinkage of the peripheral cells would be unsatisfactory, in that the cross section of cells would be required to increase to account for the measured transverse growth stresses. On the other hand, if increase of cell cross sections occurs either from the effect of fibre swelling or some other cause, this could produce the peripheral circumferential compression required to explain the distribution of radial and ring stresses.

Jacobs (1938) has shown that tension wood is characterized by the development of much greater tensions than normal wood. Also, Wardrop and Dadswell (1948) have shown that tension wood is very similar to normal wood of the same species, except for the addition of a relatively thick un lignified tertiary inner wall in the tension wood fibres. This tertiary wall replaces the more normal thin inner layer of the secondary wall. It appears likely then, that the increased volume of cellulose within the cell walls may be directly related to the greater stress development of tension wood tissue.
Münch (1938) has suggested that compression wood achieves the purpose of correcting the lean of a tree by the process of positive cell lengthening. Though this is open to doubt, the same purpose could be achieved if the compression wood fibres shortened to a smaller degree than new tissue on the opposite side of the stem. Compression wood cell shortening may appear to be incompatible with observations of Jacobs (1938), Pillow and Luxford (1937), and others that the compression wood is in a state of compression in the tree, but such observations can be explained by consideration of mechanics quite independent of wood structure. If it is conceded that cell shortening is proportionately less than normal, then it is of interest to note that this occurs in cells which contain proportionately more lignin than normal (Pillow and Luxford 1937).

The particular process responsible for the reduction in length of the cells is at present obscure. However, it could conceivably be due to changes in the chemical composition of the cell walls or to changes in the physical state of some or all of the cell wall constituents. It is also possible that lignin, which is normally associated with rigidity in plant tissue (Thomas 1937) may modify the degree to which cells shorten.

IV. Conclusions

After consideration of various hypotheses, it appears that the cause of tree growth stresses may be found in reactions developing in the differentiating cell walls and causing the cells to shorten and dilate. The reason for the cell shortening (and dilation) is not yet apparent, but consideration of the relative reactions of normal wood, tension wood, and compression wood, and the comparative amounts of cellulose and lignin materials present in each, suggests that the cellulose material may be primarily responsible, though possibly modified in effect by the amount and disposition of the lignin and carbohydrate constituents.

V. References

Disturbance of wood growth and compression of bark under 1 in. square load pad in a specimen of *Pinus radiata*. Applied load was approximately 100 lb. Graduations on scale shown each represent 1/32 in.

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