The form of a tree stem and the properties of the wood comprising a stem may be determined by the strength requirements of that stem. If this is true, a tree will react physiologically to stresses which are imposed on a stem. This study was designed to investigate the influence of static bending stress on the growth and wood characteristics of Douglas-fir. Twenty-four nine-year-old Douglas-fir trees from two geographic sources were divided into three treatments. The treatments used were control, low bending stress, and high bending stress. Trees in the low and high treatments were bent with a horizontal force at a point 4.5 ft. from the base, so that a low and high bending stress, respectively, would be produced in the trees. Bending caused another variable to be introduced into the experiment. That variable was a transverse component of gravity which influenced the low and high treatment trees.
The influence of stress and gravity was studied on the diameter, radial, and leader growth of the trees and also on the specific gravity and tracheid length of the wood which was produced.

Treatments did not cause a significant change in diameter growth. Radial growth was increased in treatment trees on the side of stems which was under compressive stress. The greatest increase in radial growth occurred in the lower parts of stems from 2.5 ft. to the base. Leader growth was significantly decreased by the treatments with the greatest decrease in high stress trees. The treatment thus caused a redistribution of wood formation from the higher parts of stems to the lower parts of stems. Stress is thought to be the factor influencing this downward redistribution of wood and causing the increase in radial growth in the lower parts of stems.

Specific gravity of wood formed was increased by treatments, but only on the side of stems containing compressive stress. The greatest increase was at 4.5 ft. and 2.5 ft., with only a small increase at the base. The increase in specific gravity was associated with compression wood formation. The increase in specific gravity and associated compression wood formation is believed caused by the transverse component of gravity rather than by any stress influence.

Treatments also caused a decrease in tracheid length of wood formed on the sides of stems containing compressive stress. This
decrease in tracheid length appeared to be associated with the increase in radial growth which occurred on treatment trees and also with compression wood formation.

This study indicates that the function of compression wood is not to resist stresses in trees, but rather possibly to cause a bent or leaning tree to reorient itself in the vertical position. In order to resist stresses in stems, trees produce increased amounts of normal wood. In this way a greater cross sectional area of a stem is available to resist the imposed stresses.
INFLUENCE OF STATIC BENDING STRESS ON GROWTH AND WOOD CHARACTERISTICS OF NINE-YEAR-OLD DOUGLAS-FIR FROM TWO GEOGRAPHIC SOURCES

by

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# TABLE OF CONTENTS

## INTRODUCTION .............................................................. 1

## REVIEW OF LITERATURE ............................................. 3

- Mechanical Strength Requirements of Trees .................. 3
- Effect of Wind and Sway on Tree Form ......................... 4
- Cambial Activity and Compression Wood Formation ......... 6
- General Properties of Compression Wood ..................... 6
- Effect of Stress on Compression Wood Formation .......... 8
- Effect of Gravity on Compression Wood Formation ......... 9

## METHODS AND MATERIALS ............................................. 13

- Experimental Design ................................................ 13
- Growth Characteristics ............................................. 17
  - Diameter Growth .................................................. 17
  - Ring Width .......................................................... 17
  - Leader Growth and Needle Length and Number on Leader .... 18
- Wood Characteristics ................................................ 18
  - Specific Gravity .................................................. 18
  - Tracheid Length ................................................... 20
  - Lumen Diameter and Cell Wall Thickness ..................... 20

## RESULTS AND DISCUSSION ........................................... 21

- Growth Characteristics ............................................. 25
  - Diameter Growth .................................................. 25
  - Ring Width .......................................................... 29
  - Leader Growth ...................................................... 30
  - Length and Number of Needles from Leader .................. 33
- Wood Characteristics ................................................ 34
  - Specific Gravity .................................................. 34
  - Tracheid Length ................................................... 41
  - Lumen Diameter and Cell Wall Thickness ..................... 46
  - Postulated Mechanism Causing Treatment Effects .......... 47

## SUMMARY AND CONCLUSIONS ......................................... 51

## BIBLIOGRAPHY ............................................................. 55
# LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>Overall view of provenance plantation and seed sources 3 and 10 (center).</td>
<td>14</td>
</tr>
<tr>
<td>2.</td>
<td>Diagram showing bending treatment, location of heights of measurement, and location of growth ring samples.</td>
<td>15</td>
</tr>
<tr>
<td>3.</td>
<td>Bending force applied at 4.5 ft. to low stress tree (left) and high stress tree (right).</td>
<td>15</td>
</tr>
<tr>
<td>4.</td>
<td>Disks cut from three heights in trees, at the base, 2.5 ft. and 4.5 ft., from one tree each of control, low and high treatments and from seed sources 3 and 10.</td>
<td>19</td>
</tr>
<tr>
<td>5.</td>
<td>Theoretical stress distribution for treatment trees.</td>
<td>24</td>
</tr>
<tr>
<td>6.</td>
<td>Average ring width of four trees per treatment.</td>
<td>29</td>
</tr>
<tr>
<td>7.</td>
<td>Average leader growth of all trees for 1964 and 1965.</td>
<td>32</td>
</tr>
<tr>
<td>8.</td>
<td>Treatment difference in leader growth.</td>
<td>32</td>
</tr>
<tr>
<td>9.</td>
<td>Average specific gravity of 1965 growth ring for 12 trees.</td>
<td>35</td>
</tr>
<tr>
<td>12.</td>
<td>Mild form of compression wood.</td>
<td>38</td>
</tr>
<tr>
<td>13.</td>
<td>Severe form of compression wood.</td>
<td>39</td>
</tr>
<tr>
<td>14.</td>
<td>Average tracheid length of 12 trees.</td>
<td>43</td>
</tr>
</tbody>
</table>
# LIST OF TABLES

<table>
<thead>
<tr>
<th>Table</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>Mean net diameter increase in inches for all trees from April 1, to October 8, 1965.</td>
<td>26</td>
</tr>
<tr>
<td>2.</td>
<td>Area and volume increase of all trees for the 1965 growing season.</td>
<td>27</td>
</tr>
<tr>
<td>3.</td>
<td>Fiber length change from 1964 to 1965.</td>
<td>44</td>
</tr>
<tr>
<td>4.</td>
<td>Table of mean squares.</td>
<td>50</td>
</tr>
</tbody>
</table>
INFLUENCE OF STATIC BENDING STRESS ON GROWTH AND WOOD CHARACTERISTICS OF NINE-YEAR-OLD DOUGLAS-FIR FROM TWO GEOGRAPHIC SOURCES

INTRODUCTION

From the time of Schwendener in 1874 (Larson, 1963), the question as to what factor determines the shape of the stem of a plant has been of interest. Many theories as to what this factor is have been proposed. One of these is the mechanistic theory developed by Metzger in 1893 (Larson, 1963).

The essence of Metzger's theory is that the shape of a tree stem is determined by the mechanical requirements of the stem. The stem of a tree is required to support the weight of that tree, and in addition, resist horizontal forces caused by wind. Most tree stems perform this function adequately, and probably more important, tree stems perform their support functions efficiently. However, the strength of the tree is not completely determined by the shape of the stem, but also by the strength properties of the material that comprise the stem, namely wood. The mechanistic theory may not explain all variations in stem form or wood quality; however if the theory is partially valid, then imposition of a mechanical stress should result in a change in stem form to accommodate the new stress situation.

The objectives of this study were to measure differences in
stem form and wood characteristics as a result of variation in stress conditions. Also, it was desired to determine if a relationship exists between reaction wood formation and support function of a tree stem.
REVIEW OF LITERATURE

Mechanical Strength Requirements of Trees

According to Trendelenburg and Mayer-Wegelin (1955) only a small percentage of the actual cross section of the tree stem is required to support the weight of the tree itself. Kübler (1959) elaborated this idea further and stated that the function of a tree trunk is to support the crown, and in this capacity it is stressed much less by the weight of a tree than by forces of wind which tend to bend a tree. Further, because compressive strength of wood is about half of the tensile strength of wood, wind stresses will affect the concave or leeward side of the tree much more than the windward side.

Schwendener in 1874 (Larson, 1963; Optowski, 1946) first introduced the concept that the shape of a plant stem is dictated by its mechanical requirements. Metzger in 1893 (Larson, 1963) developed this tenet into true mechanistic laws. His theory was based on the assumption that wood formation in a stem is governed by the requirements of a tree for mechanical strength. He envisioned that the stems of spruce were beams of uniform resistance, that is, a beam whose taper is so adjusted that it presents the same resistance throughout its entire length to a bending force applied to one end. The condition of maximum strength clearly implies that stress must be
the same in cross sections at all heights in the trunk (Opatowski, 1944).

This condition of equal vertical strength in a tree can be attained by either varying the amount of wood formed at any given height or by varying the quality of the wood formed. Schniewind (1962) and Doerner (1964) explain vertical variation in radial growth and horizontal variation in specific gravity of stem wood with age as the most efficient use of available material to produce the required strength in the stem.

**Effect of Wind and Sway on Tree Form**

Larson (1963) notes that open-grown trees reflect higher external wind stresses by their greater taper than stand-grown trees which are sheltered to some extent from the wind by their neighbors. Dominant trees which rise above the shelter of their neighbors and are exposed to greater wind forces also have greater tapers while suppressed trees have virtually no taper. Taper of forest trees growing in a thick stand can be readily increased by thinning the stand and permitting wind stresses to increase.

Haberlandt (1914) reported an experiment where one group of apple trees was supported so that a portion of their stems was restricted in movement by wind, while in another group a portion of their stems was permitted to sway in only one primary direction.
The unsupported portions of the first group of trees accumulated much new wood during the growing season while the supported portions increased very little in size. The group that was allowed to sway in only one direction produced eccentric growth, the axis of eccentricity being in the direction of sway. Jacobs (1939, 1954) performed a similar experiment on Pinus radiata. Trees in a young forest were stayed with guy wires to a height of about 25 feet. He measured the diameter and height growth of stayed and unstayed trees over a 15-year period and found that free swaying trees grew more in diameter in the lower portions of the trunk than stayed trees. Sway caused increased diameter growth near the roots and produced eccentric growth along the line of the predominant winds. Above the guy lines, diameter increase of stayed trees was comparable to unstayed trees, but the effect of staying on reducing diameter growth was noticeable immediately below the guy lines. Jacobs further noted that individual reaction of trees to the stimulus of sway appeared to be one of the factors that contributes to the assertion of dominance by certain trees. Also, because trees of Pinus radiata were no longer stable under normal conditions when first allowed to grow vigorously without sway, he concluded that the stimulus of sway was very important in allowing a tree to adjust its strength properties and roots.

In other experiments in which trees either were artificially
stimulated by sway or were prevented from swaying by supports
(Büsken and Münch, 1931; Fielding, 1940; Mergen, 1958; and Larson,
1965) the general conclusion was that swaying stimulated diameter
growth and affected height growth. Swaying in one primary direction
caused eccentric growth. Prevention of sway caused less diameter
increases than in swaying trees. Westing (1965) concluded that
stresses and strains resulting from stem swaying stimulated cambial
activity in some manner in proportion to the degree of stimulation and
perhaps at the expense of height growth. He noted that while sway
stimulated cambial activity, it did not cause compression wood to
form and this phenomenon was unrelated to the geotropic righting
mechanism.

Cambial Activity and Compression Wood Formation

The cambium of trees not only can be stimulated to produce
increased amounts of normal wood, as for example by sway stimulus,
but it can be also stimulated by other means to produce abnormal
wood. In the case of gymnosperms this abnormal or reaction wood
is commonly referred to as compression wood.

General Properties of Compression Wood

Compression wood is characterized by a higher specific grav-
ity than normal wood (Brown, Panshin and Forsaith, 1959; Cieslar,
1896; and Dadswell and Wardrop, 1949) in part due to increased amounts of latewood produced in the ring (Côte, 1965; Dadswell and Wardrop, 1949) and in part due to thicker cell walls (Trendelenburg, 1932). In cross section compression wood tracheids are rounder than normal tracheids and thus create abnormally large intercellular spaces (Côte, 1965; Dadswell and Wardrop, 1949; Kennedy and Farrar, 1965; Westing, 1965; Brown, Panshin and Forsaith, 1949). Because of increased amounts of latewood in compression wood and also because of the slightly thicker cell walls of earlywood tracheids, the transition from earlywood to latewood in a compression wood ring becomes more gradual (Brown, Panshin and Forsaith, 1949; Dadswell and Wardrop, 1949; Côte, 1965; and Larson, 1965). The tracheid length of compression wood is typically shorter than that of normal wood in the same growth ring (Cieslar, 1896; Brown, Panshin and Forsaith, 1949; Dadswell, 1958; Sinnott, 1952; Wardrop and Davies, 1964; Low, 1964; Côte, 1965; and Westing, 1965). In addition, strength properties of compression wood are different from normal wood. In bending, compression wood generally is weaker than normal wood at comparable densities (U. S. Forest Service Wood Handbook, 1955; Dadswell and Wardrop, 1949; and Côte, 1965). However, Ollinmaa (1961) stated that the compressive strength of compression wood is greater than normal and correlates with the amount of compression wood in the ring. Wardrop (1965) and
Wardrop and Davies (1964) noted that the structure and properties of compression wood tracheids are particularly adapted to resist compressive stresses along the grain and that the mechanical properties of compression wood confirm this.

Effect of Stress on Compression Wood Formation

There has been much interest in the possibilities of stress, either in the form of longitudinal compressive stress or bending stress, stimulating cambial activity to cause compression wood formation. In trees, it appears that static stresses do not cause compression wood to form (Ewart and Mason-Jones, 1906; Büsgen and Münch, 1931; Pennington, 1910; Sinnott, 1951, 1952, 1960; Wareing, 1958; Wardrop and Davies, 1964; and Westing, 1965). Ewart and Mason-Jones (1906) showed by forcibly bending stems into loops that compression wood only formed on the lower horizontal sides of the bent stems, regardless of whether the stem was in tension or compression. In those portions of the stem that were vertical, even though they were under stress, no compression wood formed. However Ewart and Mason-Jones did not report whether or not the vertical portions of the stem under stress showed any increased normal cambial activity. Similar experiments of this nature support the conclusion that static stresses in trees do not stimulate compression wood to form (Westing, 1965).
Effect of Gravity on Compression Wood Formation

While the experiment of Ewart and Mason-Jones (1906) described above indicates that stress is not the compression wood stimulus, it does indicate that perhaps the compression wood stimulus is gravity since in stems bent into loops the compression wood formed only the lower sides of the stem. Scott and Preston (1955) showed that centrifugal force would produce compression wood in much the same manner as gravity would on leaning stems. In general it is accepted that gravity is the stimulus for compression wood formation (Ewart and Mason-Jones, 1906; Westing, 1965). Sinnott (1951, 1952) believed that compression wood forms irrespective of either stress or gravity and the compression wood forms primarily to restore or maintain a specific pattern or relationship among plant parts, and is thus regulatory in nature. Low (1964) citing Hartmann's work, and Spurr and Hyvarinen (1954) support Sinnott's contention.

The amount of gravity that is necessary for compression wood formation is slight; a small deviation from the vertical would be sufficient to induce compression wood (Ewart and Mason-Jones, 1906). However, the amount of gravitational stimulus, that is, in leaning trees the amount of lean, is positively correlated with the amount of compression wood formed (Wardrop, 1965) and the amount of compression wood is believed to be proportional to the sine of the
stems angular displacement from the vertical (Westing, 1965).

The length of time that the gravitational stimulus needs to remain on the stem to induce compression wood is quite short. In Douglas-fir this presentation time is less than 12 hours (Westing, 1965) and in tilted 3-month-old Jack pine, compression wood was formed within two days (Kennedy and Farrar, 1965).

Mechanism of Gravitational Perception—Auxin. Westing (1965) in his review of compression wood stated that the perception of compression wood stimulus (gravity) occurs locally since compression wood forms essentially only in an inclined portion of a stem, irrespective of the verticality of the super and subjacent regions. It is generally believed that auxin stimulates the initiation of cambial activity in the spring (Larson, 1960, 1965). Fraser (1949, 1952) has shown that applications of heteroauxin such as IAA will stimulate cambial activity and the continuous production of spring wood. Wareing (1958) showed that there was an interaction between indoleacetic acid (IAA) and gibberellic acid (GA) in cambial stimulation. Mirov (1941) noted that hormone concentration in ponderosa pine was always higher in fast growing than in slow growing trees. Wardrop (1965) observed that the site of the initial cambial stimulus was in the apex and that once the cambium was stimulated, it could continue without the apex. Westing (1965) suggested that after the initial stimulus, the cambium could develop an ability to produce a certain amount of
auxin autonomously or get it by some other means.

High concentrations of auxin have been shown to produce typical compression wood (Fraser, 1949, 1952; Nečesaný, 1958; Low, 1964; Kennedy and Farrar, 1965; Wershing and Bailey, 1942). In natural leaning trees the formation of compression wood is believed to be the result of supra-optimal concentrations of auxin (Spurr and Hyvarinen, 1954; Mergen, 1958; Larson, 1965; Wareing, 1958, 1964; Nečesaný, 1958). Wardrop and Davies (1964) showed that there was no evidence of any structural difference between the tracheids of natural and chemically induced compression wood.

If gravity is the stimulus for compression wood formation and possibly auxin a link in the mechanism, does gravity affect the movement of auxin in order to cause compression wood to form? Wareing and Nasr (1961) and Lyon (1962) agree that gravity is an effective mechanism in the transport of auxin vertically in a plant. Wareing and Nasr (1961) also support the view that gravity is the means by which auxin tends to accumulate on the lower side of horizontal organs, so that there is a lateral redistribution of auxin in leaning stems. Lyon (1962) states that the effect of gravity on the erect stem is to equalize differences in auxin content of growing tissues, presumably by the same mechanism by which a nonvertical axis is caused to assume the erect position. On the other hand, Wareing, Hanney, and Digby (1965) suggest that the differential cambial
activity between the upper and lower halves is not due primarily to redistribution of auxin, but possibly to differential sensitivity of the cambium on the two sides.
METHODS AND MATERIALS

Experimental Design

The purpose of this experiment was to observe the effects of static bending stress on Douglas-fir trees. Twenty-four trees were initially selected from a provenance plantation located at Dorena, Oregon. The 24 trees were divided evenly between two geographically different seed sources. The two seed sources were planted adjacent to each other and were nine-years-old from seed (Figure 1). One seed source was from low elevation in British Columbia (570-750 ft., Mesachic Lake), which will be referred to as seed source 3, and the other was from high elevation in Oregon (3200-3800 ft., Molalla area), which will be referred to as seed source 10.

Trees were selected for total height. Six trees from each seed source were selected to represent the tallest trees of that seed source. The remaining 12 trees, six from each seed source, were nearly equal in height and were selected to represent the "average" height of both seed sources.

The 12 trees in each seed source were randomly divided into three treatment groups of four trees each. Each treatment group contained two "tall" trees and two "average" trees. The three treatments were control, low bending stress, and high bending stress. Of the 24 trees, eight were control, eight were "lows", and eight were
Figure 1. Overall view of provenance plantation and seed sources 3 and 10 (center).

Treatments for low and high stress trees consisted of bending these trees with a horizontal force applied at 4.5 feet from the base (Figures 2 and 3). The magnitude of force to be applied was calculated for each individual tree using the formula

\[ P = \frac{(t_{\text{max}})(d_o^2(d_l - d_o))}{1.5(L)} \]

where:

- \( P \) = the force necessary to produce the desired maximum bending stress
Stem bent at 4.5 ft.

Figure 2. Diagram showing bending treatment, location of heights of measurement, and location of growth ring samples.

Figure 3. Bending force applied at 4.5 ft. to low stress tree (left) and high stress tree (right). Note spring scale used to measure forces, attached between chain and stake (left).
the maximum bending stress desired (see below for clarification)

d_o = the average diameter of the tree in inches at 4.5 ft.

d_1 = the average diameter in inches at the base of the tree

L = the distance in inches from the base of the tree to the applied load.

With this equation the force necessary to produce a given stress can be calculated for a homogeneous, linearly tapered, cantilevered beam. In order to apply this equation, treatment trees were assumed to have a linear taper between the base and 4.5 ft. and to be homogeneous. The average diameter of each tree was measured at the base and at 4.5 ft.

For high stress trees, the maximum bending stress desired \( t_{\text{max}} \) was arbitrarily selected to be 90% of the fiber stress at proportional limit in static bending for Douglas-fir with low specific gravity and high moisture content (Specific gravity = 0.41, 48% moisture content. See Wood Handbook (1955), page 75). This value of \( t_{\text{max}} \) was 3,420 pounds per square inch (psi) or 90% of 3,800 psi for the high stress trees. For low stress trees 45% of 3,800 psi or 1,710 psi was used.

Appropriate forces were applied to each tree on April 1, 1965.
Remeasurement of the applied forces during the interval from April 1, to June 10, indicated that relaxation had occurred in either the stem of the trees or at the root collars, and the forces had to be increased to the original values. After June 10, the trees began to grow in resistance to the forces, and the forces increased above the original values. In this case the forces were readjusted downward to the original values.

Growth Characteristics

Diameter Growth

Diameter measurements were made on each tree beginning March 1, 1965, and were remeasured at subsequent intervals ranging from one to four weeks throughout the growing season until October 8, 1965. Diameters were measured at three heights on each tree; at the base, at 2.5 ft., and at 4.5 ft. from the base (Figure 2). At each height the diameter was measured in two directions, one measurement being made in line with the direction of the applied forces, and the other measurement being 90° to the first.

Ring Width

Sections of the last two growth rings at three heights and in four directions from six harvested trees were prepared on a sliding
microtome. Ring widths were measured on each of these sections using an optical micrometer at 52.5 magnifications. For another six harvested trees where no slides were prepared, ring widths were measured to the nearest 0.001" directly on the specific gravity samples (described below) using a machinist's micrometer. In spite of the diversity of the two measuring techniques, values obtained for ring widths were uniform in magnitude.

**Leader Growth and Needle Length and Number on Leader**

At the end of the growing season leader growth was recorded for each tree and samples of needles from leaders were taken in order to measure average needle length and average needle number for the leader. Needle length was measured to the nearest 0.1 mm.

**Wood Characteristics**

At the end of the growing season, two "tall" trees were harvested from each treatment in a seed source, for a total of four trees per treatment. These 12 trees were analyzed for differences in wood characteristics.

**Specific Gravity**

Cylindrical disks about 1/2" thick were cut from each of the 12 harvested trees, one disk from the base, one from 2.5 ft., and one
from 4.5 ft. (Figures 2 and 4). Each disk was then divided into four quadrants. Quadrant 1 contained the area of the disk which received compressive stress while quadrant 3 contained the portion which received tensile stress. Quadrants 2 and 4 contained the area of the "neutral axis" of the disks (Figure 2). A narrow section of the last two complete growth rings was taken from the central portion of each quadrant. Specific gravity was determined for each growth ring using the maximum moisture content method described by Smith (1954). Therefore, for each of the 12 harvested trees specific gravity was determined for the last two growth rings (1965 and 1964) at three heights in a tree and in four directions at each height.

Figure 4. Disks cut from three heights in trees, at the base, 2.5 ft. and 4.5 ft., from one tree each of control, low and high treatments and from seed sources 3 and 10.
Tracheid Length

After the specific gravity was measured on the growth ring sections, small radial strips of each of the last two growth rings in quadrants 1 and 3 only were macerated separately in a sodium chlorite, acetic acid solution. Slides of these macerations were prepared and the lengths of 50 tracheids on a slide were measured by projecting the slides onto a screen. Magnification was 100x. Tracheid lengths on the projected image were measured to the nearest mm, or to the nearest 0.01 mm actual length.

Lumen Diameter and Cell Wall Thickness

Sections were made on the sliding microtome of wood samples from the same areas where the specific gravities were determined (but for only six trees). Samples represented one tree of each treatment in each seed source. On these sections cell wall thickness and lumen diameter was measured in the radial direction. This was done using an optical micrometer at 645 magnifications. Three samples of ten cells each were measured in the primary early wood, in the zone of transition between earlywood and latewood, and in a portion of latewood nearest the bark, in each growth ring section.
RESULTS AND DISCUSSION

Compression wood was extensively discussed in the literature, particularly possible causes of compression wood formation. Yet, in the results and discussion compression wood per se will not be stressed as much as in the literature review. The reason is that in literature certain growth characteristics and wood properties are associated with compression wood formation and are described as properties of compression wood. Some of these characteristics associated with compression wood are increased cambial divisions, increased specific gravity and decreased tracheid length of wood. But in fact, these characteristics may not be properties of or associated directly with compression wood, but simply may be caused by similar factors which also cause compression wood to form. Thus, I am more interested in these characteristics and the influence of bending stress on them than their association with compression wood and its formation specifically. That these characteristics occur along with compression wood is clear in the literature, but their correlation quantitatively with compression wood is not. It is my purpose to observe whether bending stress influences these characteristics and also whether stress influences compression wood formation. The assumption is not made that changes in tracheid length for example, are correlated with compression wood formation.
Initially it was intended that there be only one independent variable, namely static bending stress. This was to be a simple treatment variable caused by bending the trees over. However, in bending trees over another variable is introduced, namely a gravitational component acting transversely on the trees. Since the high stress trees would normally be bent over further than the low stress trees, their transverse gravitational component would be greater than the low stress trees, and the relative magnitudes of stress and gravity would be the same between treatments. Thus, high gravity is associated with high stress, low gravity with low stress, and in the controls, there is no gravity or stress. The situation between treatments thus appears simple, at least in terms of defining the independent variables involved. But in analyzing the dependent variables, it proved difficult to separate the individual effects of stress and gravity between treatments.

The independent variables not only vary between treatments, but they also vary within individual trees, and not only do these variables vary within trees, but they vary independently and differently from each other. For example, a tree bent with a force at 4.5 ft. will start out essentially vertical at the base and because of the taper will lean over more until at 4.5 ft. the lean of the tree will be the greatest. Thus, the transverse component of gravity in a bent tree will start at zero at the base and increase to a maximum at the
bending force, in this case at 4.5 ft. Stress, on the other hand, does not vary in such a direct manner. If the trees were "beams of uniform resistance" to a horizontal force applied at 4.5 ft., then stress would be uniform throughout the stem of a tree. But taper of these trees does not conform to a beam of uniform resistance to a force applied at 4.5 ft., although they may approximate beams of uniform resistance to some other force distribution such as a wind load. Figure 5 shows the theoretical calculations for the average stress distribution in the high and low stress treatment trees of seed source 10 to a force applied at 4.5 ft. These figures were calculated using the initial average diameters of the trees for the initial stress distribution, and the final average diameters of the trees for the final stress distribution and the same force is used for both the initial and final stress distributions. At the point of application of force, 4.5 ft., stress is always zero. From the figures it can be seen that the stress in both the high and low stress treatments rapidly increases to a maximum at about 2.5 ft., and decreases from there to the base, the stress at the base being about 50-60% of the maximum value. Thus, while at 4.5 ft. gravity has its greatest value, the stress there is zero. At 2.5 ft. stress is maximal while the transverse component of gravity is intermediate in value.

Transverse gravity at the base is zero while stress becomes intermediate in value.
Treatment effects on wood quality were apparent only in the zone of compression, quadrant 1 of the analyses. Quadrants 2 and 4 contained the "neutral axis" in regard to stress and these zones were relatively unaffected by the treatment. Quadrant 3 was the zone of tensile stress, the upper side of the bent trees, and except for nonconsistent changes in radial growth, this zone was also relatively unaffected by the treatments. Because quadrant 1 is the only quadrant in which differences were apparent in the analyses,
subsequent discussion referring to treatment differences in cambial activity will refer primarily to quadrant 1 unless otherwise stated. Statistical data are summarized in Table 4 at the end of this section.

**Growth Characteristics**

**Diameter Growth**

As stated previously, a record of the diameter growth of all trees was kept throughout the growing season. These data were analyzed statistically to determine if the treatment levels caused an actual difference in either the magnitude of diameter increase between treatments or in the distribution of diameter growth within treatments. Diameter data were analyzed first as "increment" diameter increase, which was the difference in diameter measurements between any two successive dates of measurement. Secondly, diameter data were analyzed as "net" diameter increase, which was the difference in diameter readings between the initial date of measurement and any subsequent date of measurement.

Analysis of variance on these data indicated there was no significant difference in either the net or increment diameter increase between any dates of measurement. Four factors were analyzed: seed source, treatment, height, and direction, and none of these factors nor any of the interactions were significantly different
at the 5% level of significance.

While no significant difference in diameter growth between seed sources appeared in the 1965 data, there was a seed source difference in the initial diameters of the experimental trees. Trees of seed source 10 had a greater initial average diameter than did the trees of seed source 3, although all the trees were of comparable heights between seed sources. Thus it might be expected that the trees of seed source 10 would have a potential for greater or faster radial growth. Table 1 indicates that trees of seed source 10 did have a greater mean net diameter increase, but statistically this increase was not significant.

<table>
<thead>
<tr>
<th>TABLE 1. Mean net diameter increase in inches for all trees from April 1, to October 8, 1965.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seed Source</td>
</tr>
<tr>
<td>Control 0.612</td>
</tr>
<tr>
<td>Low 0.636</td>
</tr>
<tr>
<td>High 0.700</td>
</tr>
<tr>
<td>Base</td>
</tr>
<tr>
<td></td>
</tr>
</tbody>
</table>
There are two primary reasons why differences between any of the factors were not significant. It can be seen from Tables 1 and 2 that the treatments did cause an increase in diameter growth. The first reason that these treatment differences are not statistically significant is that the increase in diameter growth in any one tree is small compared to the variation in diameter increase between trees. The second reason is that the diameter growth in the treatments increased in quadrant 1, but tended to decrease in quadrant 3, and remained about the same as the controls in quadrants 2 and 4. Thus the diameter measurement in line with quadrants 2 and 4 would not be different from the controls. The measurement across quadrants 1 and 3 would reflect the average of the increase in growth in quadrant 1 and the decrease in growth in quadrant 3 from that of the controls and this averaged out the possible differences that actually occurred. (This fact is derived from the ring width measurements.)

TABLE 2. Area and volume increase of all trees for the 1965 growing season.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Height of measurement</th>
<th>Average area increase (in.)</th>
<th>Average volume increase from base to 4.5 ft. (in.³)</th>
<th>Volume increase over controls (percent)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>4.5 ft.</td>
<td>1.0</td>
<td>86.9</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2.5 ft.</td>
<td>1.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Base</td>
<td>2.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Low</td>
<td>4.5 ft.</td>
<td>1.0</td>
<td>89.8</td>
<td>3.4</td>
</tr>
<tr>
<td></td>
<td>2.5 ft.</td>
<td>1.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Base</td>
<td>2.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>High</td>
<td>4.5 ft.</td>
<td>0.8</td>
<td>104.2</td>
<td>19.8</td>
</tr>
<tr>
<td></td>
<td>2.5 ft.</td>
<td>1.6</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Base</td>
<td>4.0</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Even though the differences in net diameter increase shown in Table 1 are not significant, the data are valuable for the trends they show. It was previously stated that the initial average diameters of seed source 10 trees were greater than those of seed source 3, even though the trees were all of uniform height. Table 1 shows seed source 10 also having a slightly greater mean diameter increase in 1965 than seed source 3 which reinforces the initial diameter difference. This table also points out the increase in mean diameter growth with increase in bending stress. There was less of a net diameter increase at 4.5 ft. than at 2.5 ft. or at the base. In relation to the leader growth reduction in the treatments, and the area and volume increase data of Table 2, this indicates that treatments caused a redistribution of wood formation from the upper portion of the stem to the basal portion of the stem. Since the gravitational variable decreased from a maximum at 4.5 ft. to zero at the base, the increase in wood formation in the lower parts of the stem suggests that the dominant stimulus was stress, which was highest in the lower parts of the stem. Lastly, the greatest net diameter increase was in the direction of bending. This increase could possibly indicate that the response of the tree was to the tensile and compressive stresses, but it does not rule out gravity as the stimulus.
Ring Width

Average ring widths for 1964 and 1965 are depicted in Figure 6. Seed source differences were not significant and are averaged in this figure. For 1964 there was no significant variation between trees and so values for all trees are averaged together. In 1964 it can be seen that there was very little difference in ring width between the three heights of measurement. This variation with height changes markedly in 1965 as seen in the control trees. The difference here is mainly that the ring width at the base in 1965 is greater than in 1964.
The treatment affected ring width primarily in the zone of compression in the bent trees. The general trend was that at 4.5 ft. a decrease in ring width occurred in both low and high treatments. This decrease in the treatments, while not significantly different than the controls, is apparent in all four quadrants at 4.5 ft. This is especially significant in that it possibly indicates a diversion of food supplies from the upper portions of the stem, and is not necessarily related to a direct local treatment effect at 4.5 ft. At 2.5 ft. there is an increase in ring width in the treatment trees in quadrant 1 only. This increase is possibly in direct response to either the stress or gravitational stimuli acting directly at 2.5 ft. The same observation is possible at the base, although at the base it is likely that the gravitational stimulus is close to zero. It appears that the predominant stimulus affecting ring width is stress since the greatest change is in the lower parts of the tree where stress is highest and gravity is zero. Also the decrease in ring width at 4.5 ft. does not seem due to gravity since this would be a reverse of the effect gravity might have at 2.5 ft. and at the base.

**Leader Growth**

Trees in this experiment were initially selected for uniformity of height between seed sources, but it was observed that the average height of all the trees in seed source 3 including those not selected
for this study, was greater than all trees in seed source 10. The 1964 leader growth was first measured, and after the 1965 growing season the current leader growth was also measured. An analysis of variance was performed separately on each of the sets of data for leader growth.

Analysis of the 1964 leader growth data showed no difference between any of the trees or between seed sources. Analysis on the 1965 or treatment year leader growth showed a significant treatment difference in leader growth. Both 1964 and 1965 averages for leader growth are shown in Figure 7. The 1965 treatment difference is apparent from this figure and also from Figure 8. As bending stress increased, leader growth decreased. The proportional decrease in leader growth with increase in stress is almost perfectly linear when leader growth is averaged between seed sources. The analysis of variance on the 1965 leader growth also indicated a seed source difference. This seed source difference barely failed to make the 5% significance level, but the data indicated that the leader growth of seed source 10 was less than seed source 3 in 1965. Accompanying the general increase in cambial activity in the lower portions of the stems of the treatment trees in 1965 is a decrease in the cambial activity in the higher portions of the stem (e.g. at 4.5 ft.), and a decrease in leader growth. It is possible that the bending treatment, whether or not the actual stimulus is stress or
Figure 7. Average leader growth of all trees for 1964 and 1965. Treatments are control (C) and Low (L) and high (H) bending stress.

Figure 8. Treatment difference in leader growth. High stress tree on left, control in center, and low stress tree on right.
gravity, is stimulating or necessitating an increase in cambial activity in the lower portions of the trees. Because of the limited stored food reserves in the tree and because of the limited photosynthetic capacity of the tree, the increase in cambial activity at 2.5 ft. and at the base, with the associated increase in food material required, necessitates a translocation of food material from the higher portions of the tree, 4.5 ft. and the leader, where the functional requirements for food supplies are possibly not as great as at 2.5 ft. and at the base.

Length and Number of Needles from Leader

An analysis of variance was performed on the average length and number of needles from leaders of all 24 trees. This analysis indicated that differences in these factors either between seed sources or between treatments were not significant. Sterling (1946) stated that leaf primordia of Douglas-fir are formed in the bud prior to bud set of the previous year. Thus one would not expect the bending stress during a selected growing season to influence needle number for that same season, although the stress may influence the number of needle primordia formed during the treatment for the subsequent year. That the length of needles on leaders was not different between treatments indicates that possibly the mechanism regulating needle growth is not influenced by the bending treatment.
Wood Characteristics

Specific Gravity

Specific gravity of the ring sections was measured at three heights in each of 12 trees, and in four directions at each height. A five factor analysis of variance was performed on the resulting data. These factors were seed source, treatment, height, direction and growth ring.

Figure 9 represents a summary of specific gravity data. In the statistical analysis, seed source differences were not significant, so that in Figure 9 specific gravity data for both seed sources were averaged together. The only real specific gravity differences that were significant appeared in quadrant 1, the zone of compression, in the 1965 or treatment year growth ring. In Figure 9, the data for quadrant 1 in 1965, for the treatments is kept separate, while the rest of the data for the two growth rings and three quadrants at each height has been averaged together.

Except for quadrant 1 in 1965, no differences in specific gravity were apparent between either the 1964 or 1965 growth rings, between heights of measurement, or between treatments. In 1965 treatments caused a significant increase in specific gravity in quadrant 1 at all three heights of measurement. The difference in increase
between heights in quadrant 1 was not significant between 2.5 ft. and 4.5 ft., but it was significant between both 2.5 ft and 4.5 ft., and the base. The increase in specific gravity in quadrant 1 at the base was much less than at 2.5 ft. and 4.5 ft.

![Graph showing specific gravity at measured heights for control, low, and high treatments.](image)

**Figure 9.** Average specific gravity of 1965 growth ring for 12 trees. Specific gravity at each measured height averaged for quadrants 1, 2, 3 and 4 in controls, and quadrants 2, 3, and 4 in low and high trees (Broad line). Narrow line for low and high is quadrant 1 only.

Ewart and Mason-Jones (1906) showed that a transverse gravitational stimulus induced compression wood to form, regardless of stress conditions. If it is true that the amount and severity of compression wood is correlated with the severity of the stimulus, or
the degree of lean of the stem (Westing, 1965; Wardrop, 1965), then a gradient of compression wood quantity and quality should be observed from zero at the base to a maximum at 4.5 ft., and between the high stress trees and the low stress trees. This gradient follows because in the treatment trees there is a gradient of transverse gravitational force from zero at the base to a maximum at 4.5 ft., and an average maximum of gravitational stimulus in the high stress trees compared to the low stress trees. In this experiment increases in specific gravity are associated with compression wood formation. Specific gravity data was supplemented with optical observations of compression wood on the prepared slides. In the treatments, at the base where there is no transverse gravitational force, it might be expected that there should be no compression wood formation. From Figure 9 there is shown however, a slight increase in specific gravity at the base and optical observation bears out the fact that compression wood did form at the base. The compression wood that formed at the base in both treatments occupies only about 50% of the actual ring width and is of a "mild" type. Mild compression wood has on the average, larger cells and thinner cell walls than severe compression wood, with less lignification and less round or more rectangular cell cross-sections (Figures 10-13). There are several possible explanations for the existence of compression wood at the base. There could have been a small inclination of the basal portion
Figure 10. Normal earlywood of Douglas-fir (675x).

Figure 11. Normal latewood of Douglas-fir (675x).
Figure 12. Mild form of compression wood. Note the nearly rectangular cross section of cells, the thin cell walls, and the lack of pronounced intercellular spaces. Compare with Figure 13. (Top, 675x, Bottom 1395x, oil immersion.)
Figure 13. Severe form of compression wood. Note the round cross section of the fibers, the thickened cell walls, and the pronounced intercellular spaces. (Top 675x, Bottom 1395x, oil immersion.)
of the stem due to movement of the roots in the soil and thus a small, but sufficient transverse gravitational stimulus was present to induce compression wood formation or there could have been no gravitational stimulus at the base, but either stress stimulated the compression wood formation or there was a longitudinal downward translocation of some factor, possibly auxin, to the base which stimulated compression wood formation. Since under the bending treatment a slight leaning of the tree could be expected not far above the sampling point at the base, it would be feasible to assume that compression wood would have formed at this point above the base and that some of the stimulus factor could have been longitudinally translocated downward. This factor could induce the formation of a mild form of compression wood in the latter half of the ring at the base.

That bending may be part of the explanation is observed in Figure 9 where the specific gravity at the base is slightly higher in the high treatments than in the low.

Also, from Figure 9 it is apparent that there is little or no difference in the amount or degree of compression wood between 2.5 ft. and 4.5 ft. in quadrant 1. Optical observation shows that at both of these heights, about 100% of the ring was compression wood, and of a much more severe kind than at the base. Within trees at least, the severity of the gravitational stimulus between 2.5 ft. and 4.5 ft. is not reflected in any concomitant difference in
compression wood. This apparently conflicts with the statements of Wardrop (1965) and Westing (1965) previously referred to that the severity of compression wood is correlated with the severity of the stimulus. However, these observations are in agreement with Ewart and Mason-Jones (1906) who stated that a slight deviation from the vertical is sufficient to produce a perceptible response, while the maximum possible morphogenetic stimulus appears to be exercised by a comparatively small angle of deviation, beyond which little further increase in compression wood formation occurs. Not only does this statement support the observations at 4.5 ft. and 2.5 ft. but it also might explain the "perceptible response" at the base on the basis that there was a slight deviation from the vertical at the base.

It seems likely that gravity causes compression wood formation, based on both the literature and the observations that increase in specific gravity and associated compression wood formation are related to the within tree variation of gravity. Also, these variations do not follow the within tree variation of stress.

**Tracheid Length**

Tracheid length was determined for the same growth ring samples where specific gravity was measured. However, tracheid length was measured in quadrants 1 and 3 only. Analysis of variance was used to test differences in seed source, treatment, height of
measurement, quadrant, and growth ring.

In young conifers, tracheid length normally increases in each succeeding growth ring, from the pith to the bark (Dadswell, 1958; Duffield, 1964; Richardson, 1964). Within a particular growth ring, tracheid length increases from the base of the tree to a point which is about 1/3 stem height, and then decreases (Richardson, 1964). Thus the point of maximum tracheid length is located at progressively higher levels in each succeeding ring. Figure 14 shows average tracheid length of 12 trees in 1964 and 1965, at three heights of measurement. The first column shows the average tracheid length of all 12 trees in 1964. The greatest tracheid length occurs at 2.5 ft. which is a little less than 1/3 stem height. The next column shows the average tracheid length of normal wood of 12 trees in 1965. Normal wood is defined as the wood in both quadrants 1 and 3 of control trees and in only quadrant 3 (quadrant of tensile stress) of low and high treatment trees. The data for normal wood in 1965 shows a general increase in tracheid length from 1964 at all heights of measurement except the base. The tracheid length at 4.5 ft. in 1965 increased more than at 2.5 ft. reflecting that the 4.5 ft. height is becoming 1/3 stem height and thus the location of maximum tracheid length is that growth ring.
Tracheid lengths of quadrant 1 in 1965 for the low and high treatments are also shown in Figure 14. Instead of the increase in tracheid length which occurred in normal wood in 1965, in quadrant 1, the side of tree containing compressive stress, the tracheid length decreased. Notice also the difference between low and high treatments. Tracheid length for low trees follows the same height pattern as normal 1965 wood, but high trees have a different pattern and a greater decrease in tracheid length at 2.5 ft. Table 3 amplifies the tracheid length differences and shows the average tracheid length change in a given quadrant and height from 1964 to 1965.
Tracheid length for 1964 was subtracted from 1965, a positive difference indicated an increase in tracheid length whereas a negative difference indicated a decrease in length. Tracheid length of normal wood increased from 1964 to 1965. Very little change has occurred at the base while a very large increase has occurred at 4.5 ft. This pattern is changed in quadrant 1 of the treatments where again, a decrease occurred. At 4.5 ft. in both low and high trees, instead of the very great increase which occurred in normal wood, very little change in tracheid length was noted. Significant decrease is seen at 2.5 ft. and at the base. Note also the treatment difference between the low and high trees.

**TABLE 3.** Fiber length change from 1964 to 1965. This change represents the average increase or decrease in tracheid length at every measured point.

<table>
<thead>
<tr>
<th>Height</th>
<th>Average tracheid length change (mm.)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>for normal wood</td>
</tr>
<tr>
<td></td>
<td>all trees</td>
</tr>
<tr>
<td>4.5 ft.</td>
<td>+0.21</td>
</tr>
<tr>
<td>2.5 ft.</td>
<td>+0.09</td>
</tr>
<tr>
<td>Base</td>
<td>-0.04</td>
</tr>
<tr>
<td></td>
<td>Direction 1 only</td>
</tr>
<tr>
<td></td>
<td>Low stress</td>
</tr>
<tr>
<td>4.5 ft.</td>
<td>+0.03</td>
</tr>
<tr>
<td>2.5 ft.</td>
<td>-0.10</td>
</tr>
<tr>
<td>Base</td>
<td>-0.13</td>
</tr>
<tr>
<td></td>
<td>High stress</td>
</tr>
<tr>
<td>4.5 ft.</td>
<td>-0.06</td>
</tr>
<tr>
<td>2.5 ft.</td>
<td>-0.29</td>
</tr>
<tr>
<td>Base</td>
<td>-0.25</td>
</tr>
</tbody>
</table>

Note: + values indicate an increase in tracheid length, - values a decrease in tracheid length from 1964 to 1965.

In the literature review it was stated that compression wood tracheids are shorter than normal tracheids. In particular, tracheid
length of compression wood is generally shorter than from the opposite side of the ring (quadrant 1 vs. quadrant 3 in this study) (Neesan, 1958). It could be inferred that short tracheids are associated with or are a result of compression wood formation. However, if this were true, the greatest decrease in tracheid length should occur where the greatest amount of compression wood formed. The greatest amount of compression wood was formed at 4.5 ft. and at 2.5 ft. in both low and high trees. At the base only about 50-70% compression wood was formed, which was of a more mild form than at 2.5 ft. or 4.5 ft. There is thus no relationship between amount and degree of compression wood and short tracheids. The decrease in tracheid length at the three measured heights does not follow the variation of either gravity, which proportionally decreases with height until no transverse component occurs at the base, or of stress which is zero at 4.5 ft. and maximal at 2.5 ft.

Decrease in tracheid length may be a consequence of increased cambial division associated with compression wood (Dadswell and Wardrop, 1949; Low, 1964; Wardrop and Davies, 1964; Westing, 1965). If so, a relationship may exist between ring width of quadrant 1 and decrease of tracheid length. It was shown that in fact, the greatest increase in ring width was at 2.5 ft. and the base in both low and high trees. It was a more or less linear increase which began actually with a slight decrease in ring width at 4.5 ft. and then increased to a
maximum value at the base. Tracheid length decrease is not however, quite as linear, although the same general relationship holds with ring width. Perhaps the decrease in tracheid length is a consequence of an increase in cambial activity, but it seems more likely that tracheid length decrease is a result of both increased cambial divisions and compression wood formation per se. In effect, both compression wood formation without any associated increases in cambial divisions, and increase in cambial divisions caused by other factors than compression wood formation, may both result in additive decreases in tracheid length.

Lumen Diameter and Cell Wall Thickness

Preliminary analysis of the lumen diameter and cell wall thickness data indicated no consistent differences between treatments or between heights of measurement. There may have been some differences between average values of cell wall thickness and lumen diameter between treatments, but it would possibly require extensive sampling of complete growth rings to accurately reveal this. Because measurements of specific gravity indicated qualitative differences in lumen diameter and cell wall thickness of growth rings, the actual measurement of these factors was discontinued.
Postulated Mechanism Causing Treatment Effects

In the literature review, it was shown that auxin stimulates normal cambial activity and that possibly this stimulation of normal cambial activity is not the result of only IAA, but rather, possibly a result of an interaction between different growth hormones such as IAA and GA. It was further shown that supra-optimal concentrations of auxin will induce compression wood to form which is anatomically similar to naturally occurring compression wood. It is believed that gravity is the sole stimulus of compression wood formation, the mechanism of which is to cause a lateral redistribution of auxin towards the lower side of the stem.

Stress by itself does not induce compression wood to form, although stress may be the factor in the sway stimulus which stimulates increased normal cambial activity. With sway however, the stimulus may be the dynamic application of stress, or some component of gravity may interact to stimulate cambial activity. In static experiments it has been shown that gravity, regardless of stress conditions caused compression wood formation. The reverse has not been shown, namely, that static stress, regardless of gravity, will stimulate either normal or abnormal cambial activity, except in herbaceous plants. A reason this reverse mechanism has not been shown is that it is difficult to obtain high magnitudes of
stress without introducing a gravitational factor.

In this study the greatest increase in radial growth occurred at the base where the transverse gravitational component was near zero, and this radial increment at the base was composed of about 50% normal earlywood with the other 50% being mild compression wood. It might be assumed that part of this radial increment was due to the stress factor. If the high radial increment at the base was due to a vertical translocation of some of the supra-optimal concentrations of auxin from a higher point in the tree where gravity induced a transverse translocation of auxin, why wasn’t the radial increment greater at that point where the concentration of auxin was greater?

Perhaps stress causes an increase in normal cambial activity while gravity causes the stimulation of abnormal wood or compression wood formation associated with increased cambial activity. The nature of the stimulatory mechanism may be similar for both stress and gravity, this mechanism being auxin. In the case of stress, increased normal cambial activity is brought about by either a slight increase in auxin concentration, or by an alteration in the concentrations of interacting growth hormones such as IAA and GA. Gravity causes a transverse translocation of auxin which results in a supra-optimal concentration of auxin thus causing compression wood formation. High magnitudes of stress might also
cause supra-optimal concentrations of auxin to accumulate with consequent compression wood formation. Low magnitudes of stress cause only increased normal wood production. It is known that high concentrations of auxin induce compression wood, and compression wood is typically of higher specific gravity wood than normal wood.

If there is only a given amount of material available for wood formation at a given location, and the supra-optimal concentrations of auxin dictate compression wood formation which is of high specific gravity, then the radial increment will be less than the same amount of material used for normal wood of lower specific gravity as at the base. This could explain the less increase in ring width at 2.5 ft. from that at the base.

One weakness in this postulation is that no mechanism for the translocation of auxin under stress stimulus is available. However, it is not necessary for auxin to be translocated from another place in the tree in order to stimulate increased amount of normal cambial activity, but only that the stress stimulus cause either a differential sensitivity of the cambium to auxin, or cause in some manner the ability of the cambium to draw upon locally bound auxin or develop an ability to produce a certain amount of auxin autonomously.
Table 4. Table of mean squares.

<table>
<thead>
<tr>
<th></th>
<th>Initial Diameter</th>
<th>Net Diameter Increase (4-1-66 to 10-8-66)</th>
<th>Ring width</th>
<th>Leader growth 1964</th>
<th>Leader growth 1965</th>
<th>Specific gravity</th>
<th>Tracheid Length 1964 to 1965</th>
<th>Tracheid Length difference 1964 to 1965</th>
</tr>
</thead>
<tbody>
<tr>
<td>Seed Source (SS)</td>
<td>0.492++</td>
<td>0.0103 n.s.</td>
<td>4.405 n.s.</td>
<td>15,000 n.s.</td>
<td>57,820 n.s.</td>
<td>5.476 n.s.</td>
<td>0.04 n.s.</td>
<td>5.265 n.s.</td>
</tr>
<tr>
<td>Treatment (T)</td>
<td>0.098 n.s.</td>
<td>1.760 n.s.</td>
<td>5.313 n.s.</td>
<td>530.293+++</td>
<td></td>
<td>30.049+++</td>
<td>0.769 n.s.</td>
<td>16.255+++</td>
</tr>
<tr>
<td>Height (H)</td>
<td>16.724+++</td>
<td>0.0187 n.s.</td>
<td>124.790+++</td>
<td></td>
<td></td>
<td>5.110 n.s.</td>
<td>37.571+++</td>
<td>27.625+++</td>
</tr>
<tr>
<td>Direction (D)</td>
<td>0.000 n.s.</td>
<td>0.0515 n.s.</td>
<td>17.483+++</td>
<td></td>
<td></td>
<td>62.012+++</td>
<td>19.301+++</td>
<td>52.207+++</td>
</tr>
<tr>
<td>Year (Y)</td>
<td>66.574+++</td>
<td></td>
<td>9.293 n.s.</td>
<td>16,833 n.s.</td>
<td></td>
<td>1.588 n.s.</td>
<td>1.449 n.s.</td>
<td>5.203 n.s.</td>
</tr>
<tr>
<td>SS x T</td>
<td>0.0094 n.s.</td>
<td>7.863 n.s.</td>
<td>9.293 n.s.</td>
<td>16,833 n.s.</td>
<td></td>
<td>1.588 n.s.</td>
<td>1.449 n.s.</td>
<td>5.203 n.s.</td>
</tr>
<tr>
<td>SS x H</td>
<td>0.039 n.s.</td>
<td>0.0023 n.s.</td>
<td>0.000 n.s.</td>
<td></td>
<td></td>
<td>0.027 n.s.</td>
<td>0.161 n.s.</td>
<td>3.528 n.s.</td>
</tr>
<tr>
<td>SS x D</td>
<td>4.461+++</td>
<td>0.0012 n.s.</td>
<td>1.131 n.s.</td>
<td></td>
<td></td>
<td>0.216 n.s.</td>
<td>0.528 n.s.</td>
<td>0.006 n.s.</td>
</tr>
<tr>
<td>SS x Y</td>
<td>0.669 n.s.</td>
<td></td>
<td>1.713 n.s.</td>
<td></td>
<td></td>
<td>1.713 n.s.</td>
<td>2.635 n.s.</td>
<td></td>
</tr>
<tr>
<td>T x H</td>
<td>0.0315 n.s.</td>
<td>6.412 n.s.</td>
<td></td>
<td></td>
<td></td>
<td>3.997 n.s.</td>
<td>1.767 n.s.</td>
<td>2.759 n.s.</td>
</tr>
<tr>
<td>T x D</td>
<td>0.1778 n.s.</td>
<td>4.033 n.s.</td>
<td></td>
<td></td>
<td></td>
<td>15.140+++</td>
<td>13,056+++</td>
<td>5.167 n.s.</td>
</tr>
<tr>
<td>T x Y</td>
<td>3.987 n.s.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>8.819+</td>
<td></td>
<td></td>
</tr>
<tr>
<td>H x D</td>
<td>0.007 n.s.</td>
<td>0.0213 n.s.</td>
<td>1.692 n.s.</td>
<td></td>
<td></td>
<td>4.265 n.s.</td>
<td>1.749 n.s.</td>
<td>2.639 n.s.</td>
</tr>
<tr>
<td>H x Y</td>
<td>66.725+++</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>14.982+++</td>
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</tr>
<tr>
<td>D x Y</td>
<td>19.067+++</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>53.477+++</td>
<td>11.503+</td>
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</tr>
<tr>
<td>Error</td>
<td>0.019</td>
<td>0.0392</td>
<td>3.066</td>
<td>7.126</td>
<td>13,316</td>
<td>3.575</td>
<td>2.321</td>
<td>1.811</td>
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Note: + indicates significance at 5%
++ Indicates significance at 1%
+++ indicates significance at 0.05%
SUMMARY AND CONCLUSIONS

Form of the stem of a tree may be in part determined by the strength requirements of a tree. If it is, a tree would react physiologically to variations in stresses to which it is subjected. This study was initiated to observe the effects of imposed static bending stresses on the growth and wood characteristics of trees. Twenty-four, nine-year-old Douglas-fir trees from two geographic sources were selected for the study. One-third of the trees were grown as controls, 1/3 were bent with a force applied at 4.5 ft. from the base, which produced a low bending stress, while the other 1/3 were bent in the same manner to cause a high bending stress. While bending stress was intended to be the only variable, during the bending treatment another variable was introduced. This variable caused by bending was a transverse component of gravity which also influenced the trees.

During the growing season (1965) the diameter of all trees was measured at three heights and in two directions at each height. At the end of the growing season leaders of all trees were measured. Twelve of the trees were then harvested and the ring width, specific gravity, and tracheid length of these trees was measured at the same three heights of diameter measurement, and in four directions at each height in both the 1964 and 1965 growth rings.
The treatments did not cause any significant differences in diameter growth although some trends were noted. When the diameter measurements were used to calculate area growth, it was observed that there was a greater increase in area growth at the base than at 2.5 ft., and a greater area growth at 2.5 ft. than at 4.5 ft.

Measurements of ring widths indicated a significant increase in radial growth in the treatments, but this increase was apparent only on the side of the tree which contained the compressive stress. The greatest increase in radial growth occurred at the base of the tree. At the 2.5 ft. height there was still an increase in radial growth from the control trees, but at 4.5 ft. there was a slight decrease in radial growth from the controls, although this decrease was not significant. The difference between the low and the high treatments was not significant.

Leader measurements of trees showed a significant treatment effect. Low stress trees had less leader growth than the control trees, while the high stress trees had less leader growth than the low stress trees. The decrease in leader growth with increase in stress was approximately linear.

Measurements of diameter growth, radial growth, and leader growth all indicated that the treatments caused a redistribution of wood formation from higher parts of the trees to lower parts of the trees. It is thought that the stimulus causing the increase in radial
growth in the lower parts of the trees is stress. Stress increases
the functional requirements of the tree for wood formation in the
lower parts and thus brings about a redistribution of wood formation
downward in the tree.

Treatments caused a significant increase in specific gravity
from the control trees, but this increase was again only apparent
in the direction of compressive stress in the trees. The specific
gravity in this direction increased to about the same values at both
4.5 ft. and 2.5 ft. in the two treatments. The specific gravity at the
base of both treatments increased less than at either 2.5 ft. or 4.5 ft.
The increase in specific gravity was associated with and indicated
compression wood formation. Growth rings at 4.5 ft. and 2.5 ft.
(in direction of compressive stress only) contained almost 100%
compression wood of a severe type. Growth rings at the base con-
tained between 50% and 70% compression wood, and this compression
wood was less severe than the type which formed at 2.5 ft. and 4.5 ft.

Formation of compression wood is generally thought to be
stimulated by gravity rather than by stress, but the formation of
compression wood at the base of the treatment trees where there
was no transverse gravitational component indicates that perhaps
stress is a factor in compression wood formation.

Measurements of tracheid length also indicated a significant
treatment difference. The normal pattern of tracheid length
variation from year to year at a given location in young Douglas-fir is for the tracheid length to increase. This normal increase was observed in the trees, except in the direction of the compressive stress in the treatment trees. Here the tracheid length significantly decreased. The greatest decrease occurred at 2.5 ft. and at the base. At 4.5 ft. there was very little change in tracheid length from the year prior to the treatment year. The decrease in tracheid length was greatest in high stress trees than in low stress trees.

The variation of decrease in tracheid length within treatment trees did not correlate meaningfully with the variation of stress or gravity within these trees. It did however, correlate in a general manner with the variation of increase of radial growth within trees, and partially with the formation of compression wood. The decrease in tracheid length is thus believed to be associated with both increased cambial divisions and compression wood formation independently, but not necessarily directly.

The function of compression wood formation is believed to be to cause a reorientation of leaning stems to the vertical position. A transverse component of gravity is the stimulus for compression wood formation. The function of increased normal cambial activity in bent trees is perhaps to bring about a greater cross sectional area of tree stems thus decreasing the magnitude of stress in the trees.
BIBLIOGRAPHY


