GROWTH INCREMENT, CHEMICAL COMPOSITION AND CELLULOSE ULTRA-STRUCTURE OF DOUGLAS-FIR STEM WOOD FORMED UNDER ARTIFICIAL LONGITUDINAL COMPRESSIVE LOADING

by

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ABSTRACT

A Douglas-fir stem was artificially subjected to longitudinal compressive load equivalent to an estimated green weight of its crown. The wood subsequently formed under the load was compared with that produced before treatment and above the point of loading after seven growing seasons following treatment. The rate of incremental growth was considerably reduced in both volume and weight, while wood density somewhat increased. Holocellulose and alpha-cellulose yields increased and lignin content decreased. A higher holocellulose crystallinity and a smaller cellulose microfibril angle were observed. These changes were immediate and more apparent in the first 2 years after treatment, then there was a recovery to seemingly normal growth increments. The recovery was confounded with possible effects of the changed wood distribution during the 2 consecutive years immediately following treatment.

There were marked differences in the responses of incremental growth zones and also at different heights in the loaded stem with respect to the point of loading. The differences could be explained by the expected magnitude of applied stress and resultant strain.

It was concluded that the longitudinal compressive stress due to tree weight, to a large extent, influences wood forma-

tion and plays a role limiting stem growth, especially its volume. Stem form and the distributional patterns for wood characteristics within a stem are basically shaped by the stress.

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1.0 INTRODUCTION

Tree's own weight has been recognized by earlier workers as a mechanical force which may influence wood formation and its distribution in the stem and as a possible cause of growth stresses in the tree. Meanwhile, there have been numerous discussions for and against its significance as a factor controlling tree growth. In support of the mechanistic theory, after reviewing the literature on the theories of stem form development, Larson (27) stated that,

> "From the standpoint of strength requirements and support function, the mechanistic theory provides a realistic interpretation that has survived experimental study reasonably well.", and that "It is evident that the stem must be constructed sufficiently strong to withstand not only its own weight but also the weight of ice and snow, and the forces of the wind impringing on the stem."

Although a few studies, done mostly in the earlier years by using the technique of artificial compressing over the stem, have reported the influence of their treatments on tree growth (27,46), their experimental results are contradictory. Furthermore, there is to the writer's knowledge no report available on the information about the wood chemical or ultrastructural characteristics related to the compression. Experimental observations of reaction wood formation in stems and branches subjected to changes in their normal orientation to the direction of gravitational force (52) suggest that wood formation may be regulated by gravity due to tree weight.

Recently the mechanics of living trees have been studied as a field of tree science. Tree mechanics is concerned with a broad spectrum of tree statics, strength and dynamics. Ultimately, these relate to the earth's gravitational effects on tree stability and may have a decisive influence on the physiological and biochemical response of living trees. The gross structural architecture of trees is believed to be the direct result of tree mechanics.

For a project initiated by Adamovich and Walters (1) in 1965, with the purpose of studying the mechanics of standing coniferous trees, Douglas-fir trees were loaded with a weight equivalent to the estimated green weight of their crowns to evaluate the role of tree weight in the wood strength and chemical properties. Since physiological and biochemical responses to the loading are highly confounded and complex, it was logical to seek the tree's response in the observable changes in wood anatomical, physical and chemical characteristics. Preliminarily, a microscopical examination of the wood formed under the load was reported (24). The present paper will describe the changes in chemical composition and ultrastructure of a Douglas-fir stem wood formed under the load. These include holocellulose, alpha-cellulose and lignin contents, crystallinity and microfibril angle. Data of growth increment width and density are also presented for additional information on the tree.

2.0 LITERATURE REVIEW

2.1 Effects of Mechanical Forces on Wood Formation

There are several mechanical forces which may influence wood formation in the stem, such as bending by wind action, compression by tree's own weight and the additional weight of snow and ice, and growth stresses. Among these forces, tree weight and wind are mainly concerned with particular reference to coniferous tree stems. Although a very considerable amount of work on the subject has been reported, the subject is so complex theoretically and technically that the writer is undoubtedly not qualified to review it critically. Moreover, some of the published works are contradictory, inconclusive and sometimes confusing.

Schwendener (44), early in 1874, introduced the mechanistic theory of stem form development that the response of tree to the bending stresses originated by wind determines stem form. This introductory proposal has been criticized, modified and developed by following investigators. Since the work done in the early years was not available to the writer, some historical developments on the mechanistic theory are summarized from the comprehensive review compiled by Larson (27):

i) The weight of tree itself was first recognized by

Metzger (1893) as a vertical mechanical force, still believing the wind to be a governing factor on the assumption that the stem is a beam of uniform resistance to bending.

ii) Hohenadl (1922) claimed, contrary to Metzger, that stem form is primarily established by the tree weight and regarded the stem as a beam of uniform resistance to the compression exerted by its own weight.

iii) Subsequent investigators of Hohenadl's proposal maintained that tree weight may contribute only a minor part to stem form variations.

The definite role of these mechanical forces in influencing wood formation and, subsequently, its distribution in the stem, has not been determined, despite the numerous controversies. Nevertheless, the early contributions seem to indicate that stem form is affected by complex variables and tree weight is not an exclusively dominant factor.

In later years, studies on the stem form - mechanical forces relationship have been directed mostly to wind. Jacobs (19,20), who was the first to study experimentally the effect of wind swaying on stem development, reported that wind sway was an important factor in determining the distribution of radial increment on the lower part of stem. Comparing free-swaying trees with stayed trees with guy-wires attached at the middle part of their stems, he found increased diameter growth at the lower level in the free-swaying trees and above guys in the stayed trees, and reduced radial increment over the stayed stem part. His observations on the effect of wind to stimulate growth of the lower stem have been confirmed by Larson (28) and Burton and Smith (6). In their studies evaluating the effect of wind, it has been maintained that the prevention of wind caused reduction in radial increment of the lower stem.

However, the results of their experiments require careful interpretation, since the experimental trees were exposed to not merely wind loading and no wind treatment (the stayed trees were used for a control), but also completely different kinds of mechanical forces. The free-swaying trees receive geotropic stimuli as well when they are displaced from their normal vertical orientation. In fact, the mechanical forces acting on the stayed stems are complicated, as shown in Figure 1. The tensions on the wires, T_1 and T_2, exert compression and the x-directed forces over the stem. In addition, the stem received geotropic stimuli if $T_1 \neq T_2$ or $\theta_1 \neq \theta_2$, that is, when the stem is out of its normal vertical direction. These forces would be considerable when winds are loaded, even more so in high wind. The problems encountered during their experiments explain the actual magnitude and are manifestations of these forces. Thus, the reduction in the rate of incremental growth observed over the stayed stems is believed to have been a response to these forces, rather than

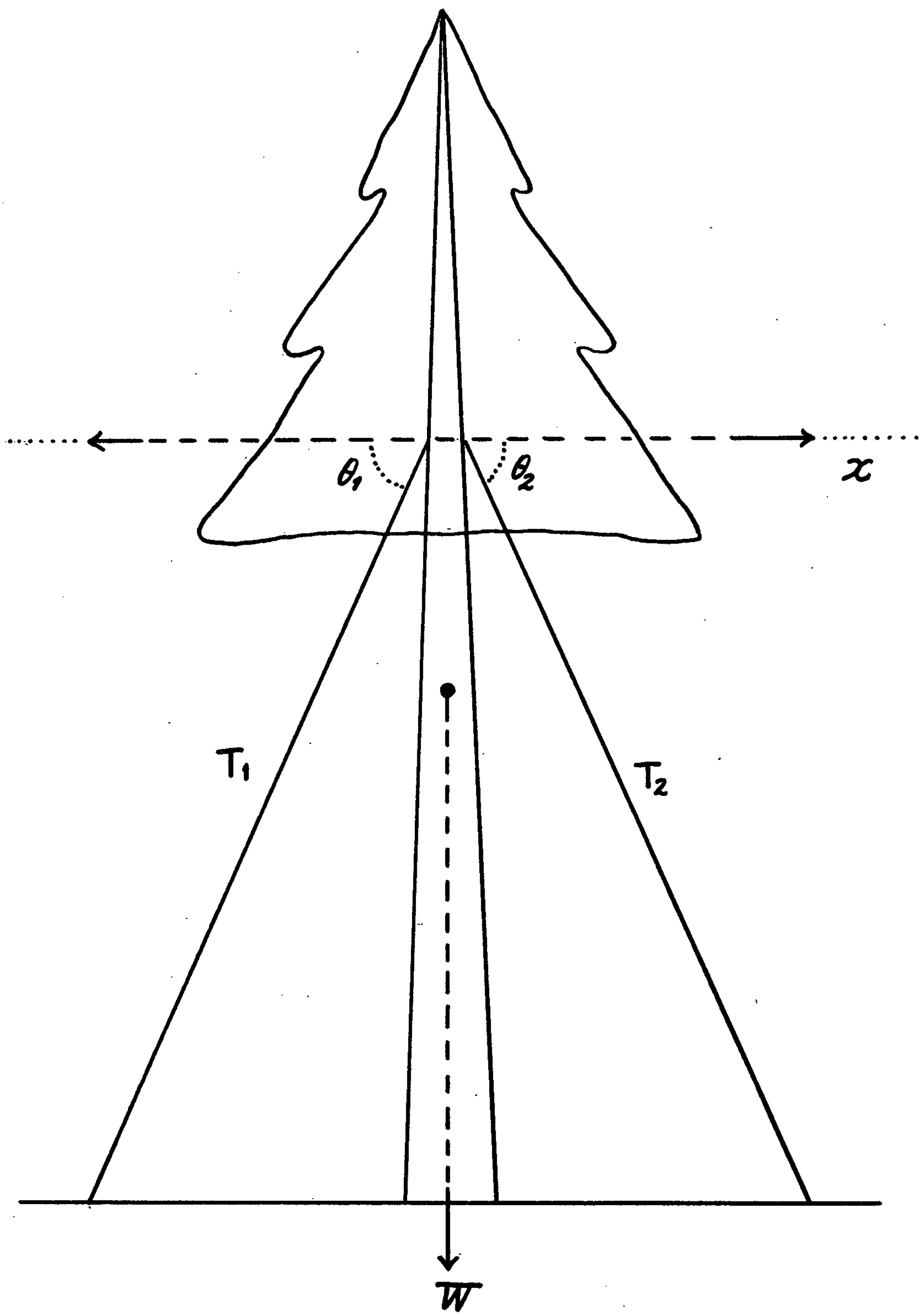


Figure 1. Diagram showing mechanical forces acting on the stayed stem.

their no-wind treatments, perhaps mostly to the compression. The increased rate of growth above the guy may be traced to the wide increment found generally during juvenile wood formation, judging from the high positions in the stems of relatively young trees.

Steucek and Kellogg (47) employed a rather different experimental approach to the study on stem wood development in relation to mechanical forces. Assuming that the introduction of a discontinuity by removing a rectangular (3.8 x 10 cm) core from the stem creates concentrated mechanical stresses at that point when winds are loaded, they examined the distribution of stem growth around the discontinuity. The stems showed a reduced radial increment in the plane of and directly above the discontinuity, and no apparent differences in the percentage of latewood, as compared among the stem cross sections taken from varying distances above and below a discontinuity. Perhaps the results obtained by this experimental approach were a response to the complex mechanical stresses originated by their experimentation, assuming that the observed changes around the discontinuity zone were the response to mechanical forces. Obviously, the reduction in the area of cross section by removing a stem core induces proportionally increased compression stress on the cross section which was supporting the compression of the tree weight above that point.

Many observations of radially eccentric development in the stem exposed to winds (20,28,35) suggest that the eccentricity is due to wind loading and may introduce variations in the stem wood properties. Unfortunately, little information is available on this. Bannan and Bindra (3) found that growth increment was wider on the leeward side and the wider increment was associated with shorter tracheids, as compared with other cardinal points around the stem base. Their data on the windward side showed longer tracheids and narrower increments. These variations were ascribed to the prevailing wind.

Unlike the wind, tree weight received little attention from investigators. Martley (33) examined tree weight as a possible cause of growth stresses and reported that the pressure gradient due to the weight of tree growth was not sufficiently great to contribute the observed stresses. His theoretical calculations of the pressure which might develop from tree weight on the basal cross section of an average 30-year-old Douglas-fir tree showed 16.5 kg/cm^2 (235 green lb/in^2). The tree weight hypothesis on growth stresses was opposed by Boyd (5) on the grounds that the estimated value and character of the stresses due to tree weight is inadequate to explain the measured, high state of growth stresses in the trees. He conceded, however, that tree's own weight has some effect in originating growth stresses.

The effect of artificially-applied longitudinal compression by hanging weights over the stem has been studied mostly with herbaceous plant stems (27,46). The results of these experiments were contradictory. No experimental results are available on stem wood properties of the coniferous trees weighted with load.

From the fact that tree weight is the earth's gravitational force and also the well-known geotropic responses in general tree's growth, the effect of gravity has been investigated as a possible cause of compression wood formation. Observation supporting the theory is that the compression wood is always formed on the lower side of inclined stems or loops made by bending stems. Details on these experiments were described by Wardrop (52) and will not be reiterated here.

Conclusively, the effects of mechanical forces on stem wood formation and subsequently its distribution are much more complicated and greater than is generally appreciated. The results of experimental studies on them may be confounded by the fact that experimentation for a specific mechanical force induces undesirable, different kinds of mechanical forces as well. The pattern of radial incremental growth under wind loading is reasonably well established, although detailed wood physical and chemical properties as influenced by wind are still relatively unknown. Information on the role of tree weight on wood formation is lacking.

2.2 Variability in Wood Chemical and Ultrastructural Properties Within a Douglas-Fir Stem

It is well documented in the literature that wide variations exist in chemical composition and ultrastructure of a single stem of coniferous trees in regard to radial positions or age and growth zones, as well as normal and abnormal wood. However, information on the variations along heights in the stem and with cardinal directions on a stem cross section is relatively lacking for a clear and certain picture of the patterns, even though a few published works indicate a variety of trends (21,22,29,38,43,56,58). The literature pertinent to cellulose, lignin, crystallinity and microfibril angle of Douglas-fir stem wood is reviewed with regard to radial positions and growth zones. Since the variation trends prevailing in other coniferous normal and abnormal wood is generally, but not always, prevalent in Douglas-fir, some findings on the species are also included.

2.2.1 Growth increment and wood zone levels

Quantitative analyses of cellulose in coniferous stem cross sections indicated an increasing pattern in progressive increments from the pith to the cambium. Early in 1951 the data of Cross & Bevan cellulose contents obtained for Douglas-fir and Monterey pine showed a tendency for cellulose contents to increase radially

(51). Examining the variation in cellulose content expected in Douglas-fir, Kennedy and Jaworsky (25) found that most of the variation in cellulose content (from low 57.4 to high 63.3%) occurred during the first 15 years. Their data on the Cross and Bevan cellulose showed a steady increase up to 81 years of growth after the rapid increase for the first years of growth. A similar pattern was reported by Erickson and Arima (13) who studied the effects of age and stimulated growth on chemical composition of Douglas-fir. Holocellulose yields increased relatively fast to age 18-20 years and at a moderate rate thereafter, while alpha-cellulose contents rose from the pith to age 25 or more. During the early 15 years, a rather rapid increase in alpha-cellulose contents was apparent in their data.

Comparative analyses of juvenile and mature wood suggested that the increased cellulose content in the early stage of growth is maintained or still progressively increased during the mature years of growth. The data for a single Douglas-fir (25) showed consistently higher yields of cellulose in the outer wood than in the juvenile wood. Wellwood and Smith (54) also found considerably higher alpha-cellulose content in the 41-50th increments from the pith, when compared to the 6-20th increments in Douglas-fir and hemlock. However, they found little difference (still slightly higher values for the outer increments) in holocellulose contents between the two increment groups. Similar patterns have been observed in pines (43,50,60). The variation between the two wood zones of loblolly pine was 3.5% higher in water-resistant carbohydrates and 7.5% higher in alpha-cellulose for the mature wood.

In a Douglas-fir showing 430 increments, Hale and Clermont (15) found lower alpha-cellulose yields from the 27-32nd and 322-400th increment groups, as compared to those from the increments in between them. The low alpha-cellulose yields of the inner and outermost wood were attributed to the wider increment with lower percentage of latewood, and the thin-walled prosenchyma cells generally found in the overmature wood, respectively. Their data, meanwhile, showed a moderate decrease in holocellulose contents from the inner increments, outward. This declining holocellulose pattern shows incompatibility with the results by Zobel and McElwee (60), who found that the yields of water-resistant carbohydrates and alpha-cellulose from loblolly pines were highly correlated (significant at the 1% level). The relationship has been also noted in Douglas-fir trees, even though one of the trees (ages of 70-85 years) gave slightly lower water-resistant carbohydrates and alpha-cellulose yields in the five outermost increments than in the 16-25th increments from the pith (25). Examinations on relatively older Douglas-fir trees indicated that a decrease in cellulose content was evident in about 300-400 years of growth due to overmaturity (15,42).

In general, lignin pattern for the variation with radial positions on a stem cross section is opposite to those of holocellulose and alpha-cellulose. Erickson and Arima (13) found in 30-year-old Douglas-fir trees that the highest lignin content near the pith gradually declined with age until very little changes after 23-25 years. A gradually decreasing tendency in lignin contents was also prevailing in older Douglas-fir, except the residual increase due to overmaturity.

2.2.2 Incremental growth zone (earlywood and latewood) level

Marked differences in chemical composition and ultrastructure between earlywood and latewood have been shown in the studies on growth zones. In general, latewood has higher cellulose content and degree of crystallinity, less lignin percentage and smaller (steeper) microfibril angle, as compared to corresponding earlywood. Douglas-fir earlywood lignin values were 3-4% higher than those for comparable latewood (15,40,59). The difference was much greater with alpha-cellulose (15) and microfibril angle (10). These differences between earlywood and latewood have been reported similarly for other species (29,32,40,59).

Radial patterns for individual growth zones were examined by Sastry and Wellwood (42) while studying tracheid weight-length relationships in Douglas-fir. Their results obtained for single tracheid weights (holo- and alpha-cellulose fractions obtained after delignification with peracetic acid) showed an increasing trend for both earlywood and latewood to about 150 years and then a moderate decreasing toward the bark. An increasing pattern for Cross & Bevan cellulose was noted in the earlywood of Monterey pine (51). Larson (29) made a study on the variations in lignin and constituent carbohydrates of red pine earlywood and latewood with age. He observed in both growth zones that glucose and mannose contents followed a progressively increasing tendency, whereas the yields of galactose, xylose, arabinose and lignin were decreasing with age.

Crystallinity pattern for individual growth zones of Douglas-fir was examined by Wellwood, et al.(53). They found the same patterns for both earlywood and latewood, in which crystallinity values increased rapidly from the pith to 20 years and then gradually till 400 years. The steady increase even in overmature wood is rather different from what is expected from the observed decrease in alpha-cellulose content of overmature wood (15,42) and the significant correlation (at the 5% level) between crystallinity and the amount of alpha-cellulose in tracheids (53). In a slightly different pattern found in western hemlock (31) and Norway spruce (34), crystallinity of both earlywood and latewood increased rapidly for the first few years, then gradually levelled off and finally became more or less constant. Contrary to the reports indicating increasing pattern, Preston, et al. (39) found that crystallinity in Monterey pine decreased from the 5th to the 15th increments.

Measurements of latewood microfibril angles in Douglas-fir showed a decreasing trend in the progressive increments from the pith outward (13,51). The high initial values over 30 degrees declined rapidly to about 10 degrees in 15 years, and the angle was still declining thereafter but at a slower rate. Similar patterns were observed in loblolly pine (38) and slash pine (18), and so were for both earlywood and latewood of Monterey pine (51) and Norway spruce (34), with an exception in the latter which showed more or less constant values after a rapid decrease in the first 15 years. However, little variations in both growth zones were also reported among the inner (1-10th), middle (11-20th) and outer (21-30th) increment groups sampled from fifty loblolly pines (32).

2.2.3 Abnormal wood

The presence of compression wood is well-known to introduce considerable variations in chemical and ultrastructural properties of coniferous wood. Compression wood has been characterized, as compared to normal or opposite wood, chemically (8,9) by the presence of abnormally higher lignin and lower cellulose contents, and ultrastructurally (31,34) by irregularly lower degree of crystallinity and greater microfibril angle.

Opposite wood has been compared with comparable compression wood and recognized to differ from normal or side wood. The opposite wood of pines was reported to have higher cellulose and lower lignin contents than normal side wood (9,30). In the meantime, other studies (29,49) claimed that opposite wood had the same carbohydrate and lignin contents as had comparable side wood.

2.2.4 Summary and the tree used for the study

There is considerable evidence suggesting that chemical and ultrastructural wood properties of a stem wood exhibit wide range of variations in regard to growth zone level as well as gross wood level. The variability in wood properties should be well appreciated and defined in the studies on tree growth and wood utilization.

Generally, the patterns for the raial variations in wood chemical composition and ultrastructure are the same, whether examined with gross increments or individual growth zones. Increasing patterns are for cellulose content and crystallinity, and lignin content and microfibril angle decrease. Most of the variation occurs in the juvenile wood (the first 15 years), showing some degrees of erratic changes and fluctuations. The variation in mature wood is moderate or little, until eventually opposite trends to those in juvenile wood are observed, due to overmaturity. These variation patterns are more apparent with alpha-cellulose and individual growth zones.

Under a normal growth condition, little differences in holocellulose and lignin contents and microfibril angle would be expected during the experimental period of seven years in the moderately mature Douglas-fir when compared with respective earlywood and latewood from the two incremental groups of before and after loading. A slight increase in alpha-cellulose content and crystallinity, however, might be anticipated. Undoubtedly, the variations including unusual radial growth and compression wood formation which might be expected in response to the treatment for the study, are not considered in the above conclusions.

3.0 MATERIALS AND METHODS

3.1 Experimental Tree and Loading

Douglas-fir trees in a second-growth stand at the southern part of the University of British Columbia Research Forest, Maple Ridge, B.C. were selected for a study by Adamovich and Walters (1). In 1965 they applied compressive (loading-down) and tensile (pulling-up) loads to two trees, respectively, to study the effect of tree weight on some wood properties, and have described their experiments in detail. Compressive loads were applied by hanging lead weights to the point in the stem where the lowest living branch whorl in the crown was located.

One of the two trees grown under compression loading was examined in this study. In March, 1966 the tree was 20.1 m (67 ft) in height, 30 cm (12.0 in) in DBH, and had 26 growth increments at the height of 0.3 m above ground. The tree stem below the loading point (9.3 m above ground) has been placed under weight equivalent to 362 kg (800 lb) for 7 years. The load was based on an estimated green weight of the crown (1). It should be noted that the experiment was not designed to test the mechanistic theory of stem-form development and actual stresses and strains in the stem were not measured.

3.2 Wood Sample Preparations for Chemical Analysis

In 1971 the tree was felled and 8 cm long disks were obtained from its stem, starting at 0.3 m above the ground with an interval of 1 m distance. Only three disks taken from the heights of stem base (0.3 m), 1 m below (8.3 m) and above (10.3 m) the loading point were examined.

From each disk a wood block (6 cm wide) with the growth increments 1960-71 was sectioned from the south and north cardinal directions. The outermost 7 increments for the 1965-71 period were designated as after loading, and the 5 increments formed during 1960-64, before loading, respectively, and split into 2 groups (see Table 1). Earlywood and latewood were separated for every increment within each increment group and then collected. The wood prior to 1959 was excluded from the preparations.

Thus, a total of 24 samples (3 heights x 2 directions x 2 radial positions x 2 growth zones = 24) were prepared and ground in a Wiley mill and screened. The fractions from -40 mesh to +80 mesh were used for chemical analyses.

The wood meal samples were extracted with ethyl ether, absolute ethanol and finally, hot water and conditioned to equilibrium moisture content, sealed in plastic bags and stored in a constant temperature and humidity room. The

TABLE 1: WOOD SAMPLE POSITIONS IN THE STEM

Height of disk (m)	Cardinal Direction (South & North)	Radial Position from Pith	
		Number in Growth Increment Series (1960 - 1971)	Distance (cm) (1960-1965-1971)
0.3	S	20th - 31st	12.1-15.0-17.8
	N	21st - 32nd	13.4-16.8-20.6
8.3	S	12th - 23rd	6.8- 9.9-12.1
	N	12th - 23rd	7.1-10.4-12.2
10.3	S	9th - 20th	5.4- 8.9-12.4
	N	9th - 20th	5.1- 8.1-10.6

equilibrium moisture content was checked from time to time throughout the course of analyses and showed relatively constant values (8.1% for earlywood, 8.3% for latewood).

3.3 Procedures

3.3.1 Holocellulose and alpha-cellulose

In a recent review of the literature on isolation of the total wood carbohydrates (26), the Wood Science Procedure AM/H-1/62-r66 (57) based essentially on the chlorite holocellulose method of Wise, et al. (55) was recommended for the study because of the relatively mild action of chlorite on wood carbohydrates and the alleged quantitative reproducibility. Some advantageous features in the procedure are:

i) uniform mixing and temperature by using a submerged, rotating mixing head,

ii) several determinations can be carried out at the same time,

iii) elimination of the continuous and laborious several sequential additions of chloriting solution with certain intervals by using a single chlorite treatment in a closed system.

A slightly modified method from the procedure was used and is given below:

0.500 g of wood meal (prepared as described above), 7 ml of acetate buffer solution (60 ml acetic acid and 1.2 g sodium hydroxide per liter) and 3.0 ml of 20% sodium chlorite solution are placed in a polyethylene tube (20 ml capacity) and the tube is tightly capped. A mixture of chloriting and buffer solution in the same proportion should give an initial pH 3.2-3.8. Six tubes prepared thus are fixed to a mixing head. The mixing head is submerged in a water bath (50 ± 2°C), being held in an inclined position and rotated slowly. After chloriting for 20 hr, the tubes are transferred to an ice water bath (5°C). Contents in the tubes are washed in Pyrex filtering crucibles (tared sintered glass, coarse porosity, 30 ml capacity) by using 200 ml acetic acid under gentle suction and 20 ml of acetone (gravity-drain) and the washing is concluded by applying suction for 3 min. The chlorite holocellulose in the crucibles is conditioned in a constant temperature and humidity room for at least 24 hr. Two of the four holocelluloses prepared for each sample (see Appendix) are oven-dried at 102 ± 2°C (no more than 4 hr) to determine the equilibrium moisture content upon which the calculations of holocellulose and alpha-cellulose yields are based.

No corrections for residual lignin in the chlorite holocellulose were made, although the inventor of the chlorite procedure insisted on the need for the correction. There are reports of chlorite-resistant lignin (17), modified lignin during chloriting (4,7) and difficulties in removing the lignin in intimate association with carbohydrates (2). These reports indicated doubts on the reliability of an accurate determination of residual lignin content in the chlorite holocellulose. On the other hand, it has been recognized that the loss of carbohydrates due to the degradation and depolymerization by oxidative action of acidified chlorite is quite possible. Perhaps the correction is not worth-while in a study of this magnitude. Rather, a rapid, simple and reproducible procedure was demanded. Moreover, the lignin procedure adopted for the study is not suitable for residual lignin corrections because wood lignin treated with chlorite gives no maxima at 280 nm in the UV-spectra (23,41).

Since the selected holocellulose method was expected to give a reasonable reproducibility, a preliminary examination of the method was made to determine experimental precision obtainable with the method. The result showed that 4 observations for each sample would be required for the desired precision ($t_{0.05}$, $S_{\bar{x}}$ = 0.588, the estimate to be within 0.8% of the population mean) (Appendix).

For alpha-cellulose determination of the remaining two chlorite holocellulose (never oven-dried), the modified procedure by Erickson (12) from TAPPI Standard T 203 m-58 (48) was followed, except using beakers (50 ml capacity) instead of his 'specially designed water bath' for holding crucibles.

3.3.2 .Lignin

Earlier, Johnson, et al. (23) described an acetyl bromide method for the quantitative determination of wood lignin. The technique has been re-examined and slightly modified by Wu and Wilson (59). The modified procedure was followed in dissolving the extracted wood meal with acetyl bromide in acetic acid and measuring the absorbance of the resulting solution at 282 nm on a Beckman DU spectrophotometer. The lignin content was determined from the measured absorbance on a standard (Klason lignin of Pacific silver fir) calibration curve prepared by them. A preliminary examination of the technique showed that two observations for each sample would be required for estimating the mean lignin values at the desired precision ($t_{0.05}$, $S_{\bar{x}}$ = 0.374, D = 0.8%)

(Appendix).

3.3.3 Crystallinity of the chlorite holocellulose

The chlorite holocellulose obtained for holocellulose determinations of the samples was conditioned to a constant moisture content and used for determining the crystallinity. Rectangular (1.3 x 3.2 cm) pellets were prepared by compressing 0.30 g of the holocellulose and 1 drop of glue (a solution of 10 ml Duco cement in 100 ml amyl acetate) in a 'specially designated die' under a pressure of 106 kg/cm^2 (1500 lb/in^2) for 1 min. The pellets were conditioned in a constant temperature and humidity room. The average thickness was 1.38 mm (range, 1.23-1.75) and 1.26 mm (range, 1.06-1.46) for earlywood and latewood, respectively.

After placing a pellet in an aluminum specimen holder, the specimen was scanned over the range 2θ = 6 to 30° in a Phillips X-ray diffractometer equipped with a Cu X-ray (nickel-filtered). The diffractometer was operated at 36 kV and 14 mA and the scanning speed was 1° per min with a rate of cps = 4×10^2 and time constant of 4 sec for the counter. Detailed description of the scanning procedure was given elsewhere (11). For evaluating the produced X-ray diagrams, the crystallinity index proposed by Segal, *et al*. (45) was computed.

3.3.4 Microfibril angle

An X-ray technique for estimating cellulose microfibril angle was described recently by El-Osta, *et al.* (10) and this was adopted for the study. Six wood blocks obtained as described for chemical analyses (3 heights x 2 cardinal directions) were freeze-dried. Specimen having dimensions of 1.5 mm for earlywood and 1.0 mm for latewood, radially, 1.0 cm tangentially and longitudinally, were machined on a micro-saw from each growth increment. The specimens were stored in teflon vials prior to X-ray radiation.

The specimens were mounted on a Phillips 1009 X-ray diffractometer equipped with a Phillips 1078 texture goniometer and scanned according to the procedure. The intensity patterns of X-ray diffraction were analyzed by a computer program (14). Unlike the X-ray technique based on measurement of the diffraction intensity pattern on the paratropic (002), $(10\bar{1})$ and (101) planes, this method directly gives the average orientation of cellulose crystallites in wood by measuring diffractions from the diatropic (040) plane. A computer program is used for resolving the (040) diffraction intensity pattern and calculating the mean orientation angle.

4.0 OBSERVATIONS AND DISCUSSION

4.1 Growth Increment Before Loading

Individual growth increment characteristics from the pith throughout the tree's life were measured by the staff at the Western Forest Products Laboratory, Department of the Environment, Vancouver, on an X-ray densitometry system using a computerized tree growth increment scanning densitometer. The technique has been described elsewhere (16,36,37).

Data on growth increment width and density, out of the measurements, are presented in Figures 2 and 3 to show their variations in the stem. The figures reveal that systematic variation patterns for increment width and density in a stem can be attained when the increment characteristics are plotted by the calendar year of formation. In general, however, the density of earlywood remains constantly low with the years. The distinctiveness of 0.3 m height is made evident in the great fluctuation of its increment width and the smallest difference in density between earlywood and latewood. The height has the highest density for earlywood and lowest for latewood. With regards to height and cardinal direction, there are no consistent variation patterns although some variations are apparent.

Figure 2. Variation in growth increment width at different stem heights before loading, with reference to cardinal directions.

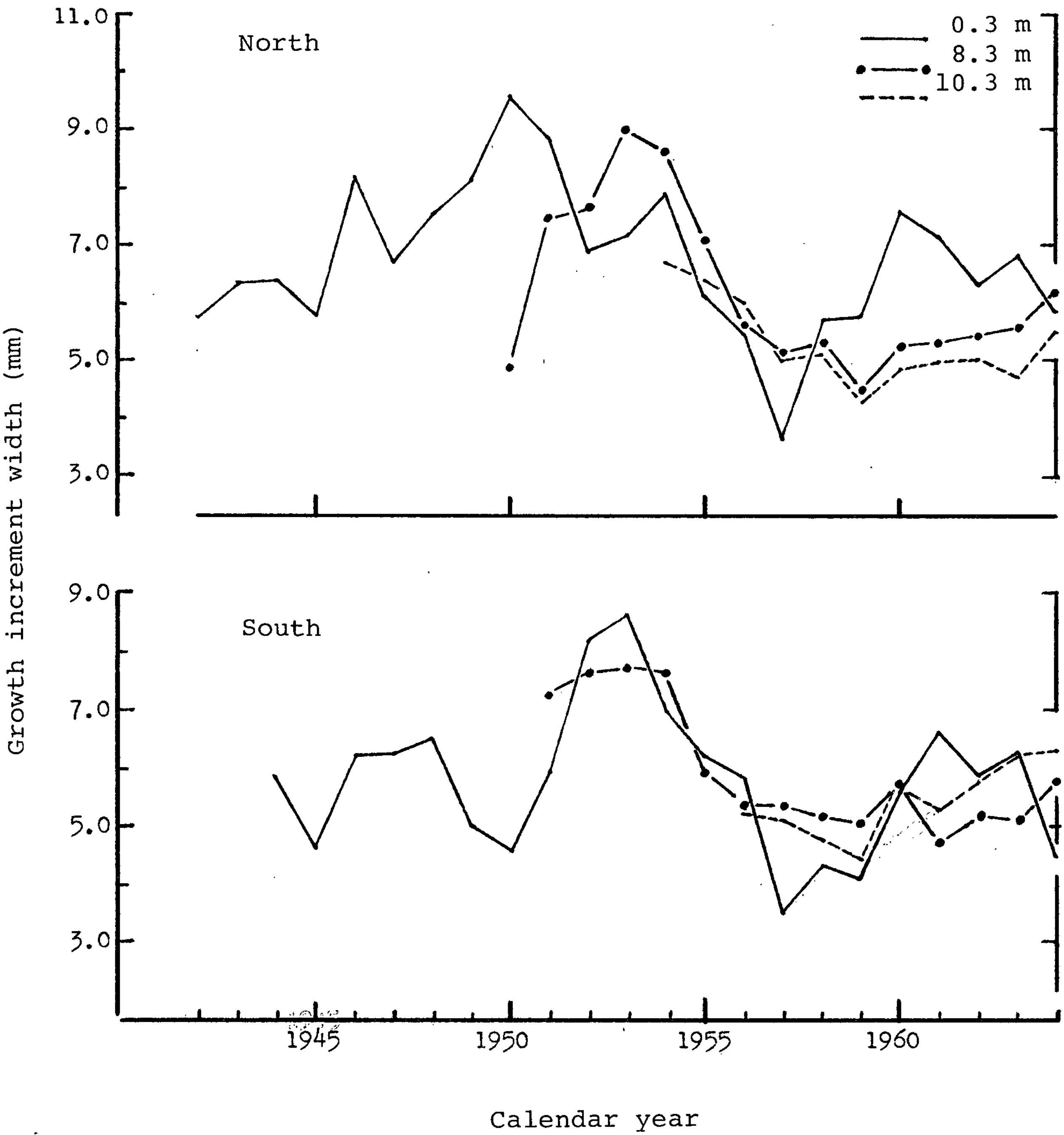
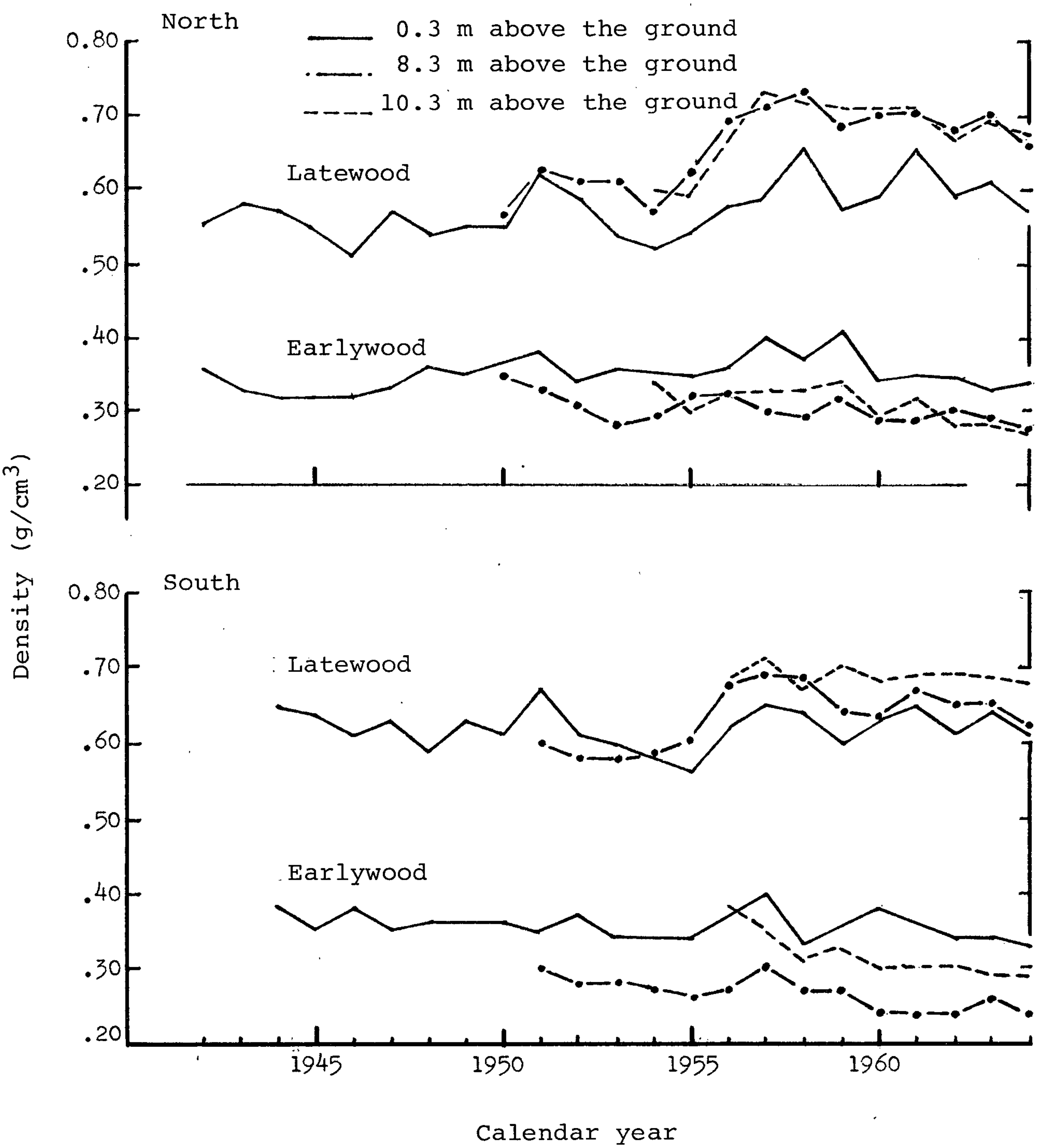


Figure 3. Variation in incremental growth zone density at different stem heights before loading, with reference to cardinal directions.



Thus, during the early stage of growth the tree formed increments having relatively low density, while increasing radial increment up to a maximum in the tree's lifetime. This young growth was terminated in 1954 as the age became relatively mature. The juvenile wood formation during about 15 years was followed by 3 years of transition to mature growth. In the transition period, substantial changes took place. Increment width became much narrower and latewood density increased substantially. Beyond this point, namely in the mature growth, the variations were very little in both increment width and density. Meanwhile, earlywood increment has maintained its initially low density to the year 1964.

These growth patterns observed in the moderately mature Douglas-fir are in agreement with those reported in the literature, in which little or moderate changes in wood properties during mature wood formation were indicated.

4.2 Wood Formation After Loading

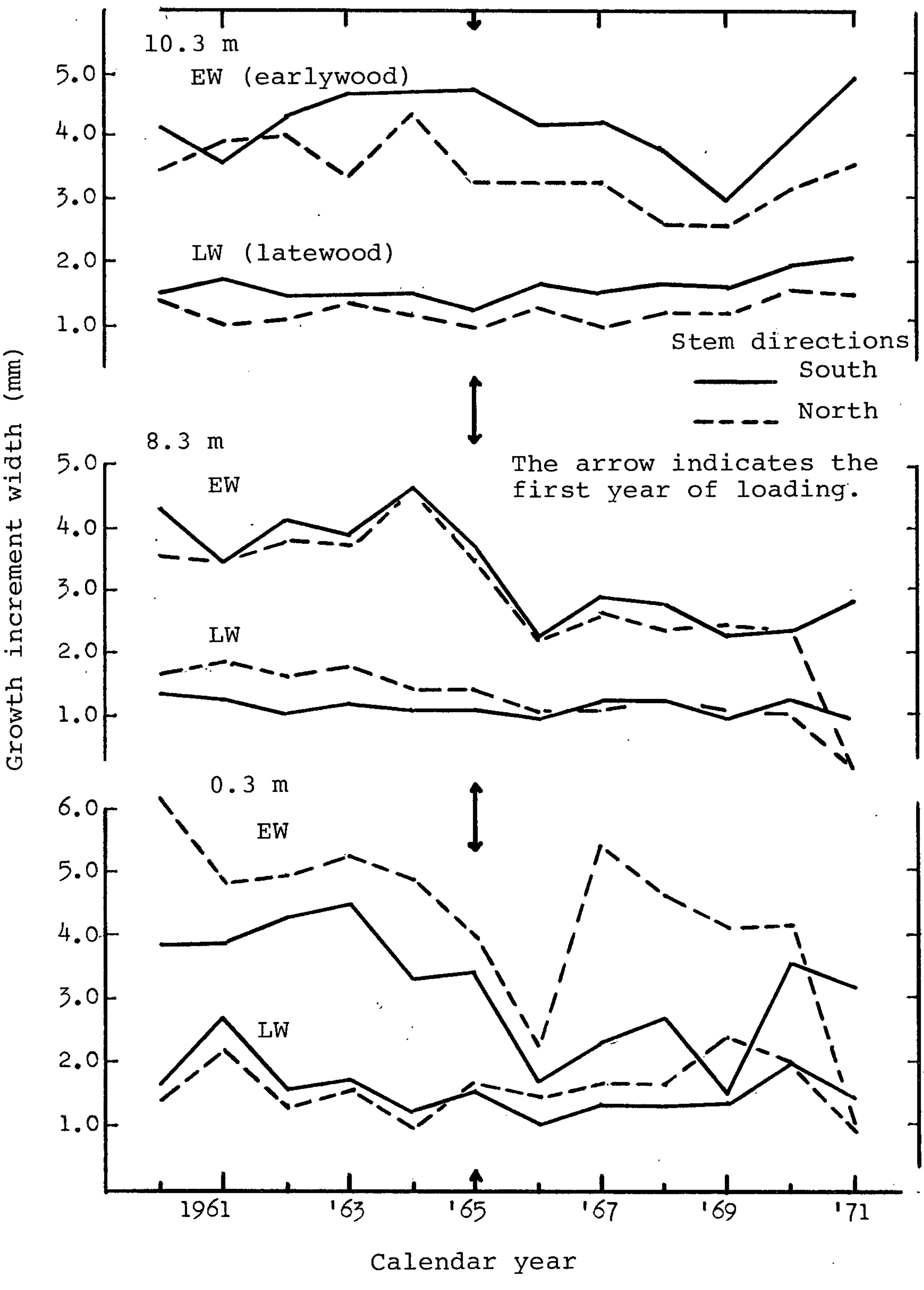
The influence of artificial compression loading on wood formation was evaluated by comparing wood characteristics of the 1960-64 increment group (before loading) with those of the succeeding 1965-71 increments (after loading). Simultaneously, differences in the wood formed below and above the plane of load were also examined.

The load would have forced the stem portion below the point of load into mainly further longitudinal compression, in addition to the tree's own weight. The compression stress due to the load plus tree's own weight was transmitted to every cross section throughout the length of the loaded stem portion. These assumptions may be justified by the fact that the loading was applied in such a way to be parallel to the stem axis and the ratio of length to diameter for the loaded stem was small enough not to introduce a bending moment. Therefore, the increased compression stress by the loading on each cross section would have been greater with ascending heights up to the greatest on the plane of loading.

4.2.1 Growth increment width and density

A reduction of approximately 50% in the earlywood increment at the heights below the load is observed in the two years following loading (Fig. 4). This contrasts sharply with almost no changes in comparable latewood, which give rise to a considerable increase in the percentage of latewood. In the same period, the height of 1 m above the load shows slightly decreased increment. Reduced increment due to artificially increased compression stresses has been indicated in the stayed stems and also the stem part with a discontinuity.

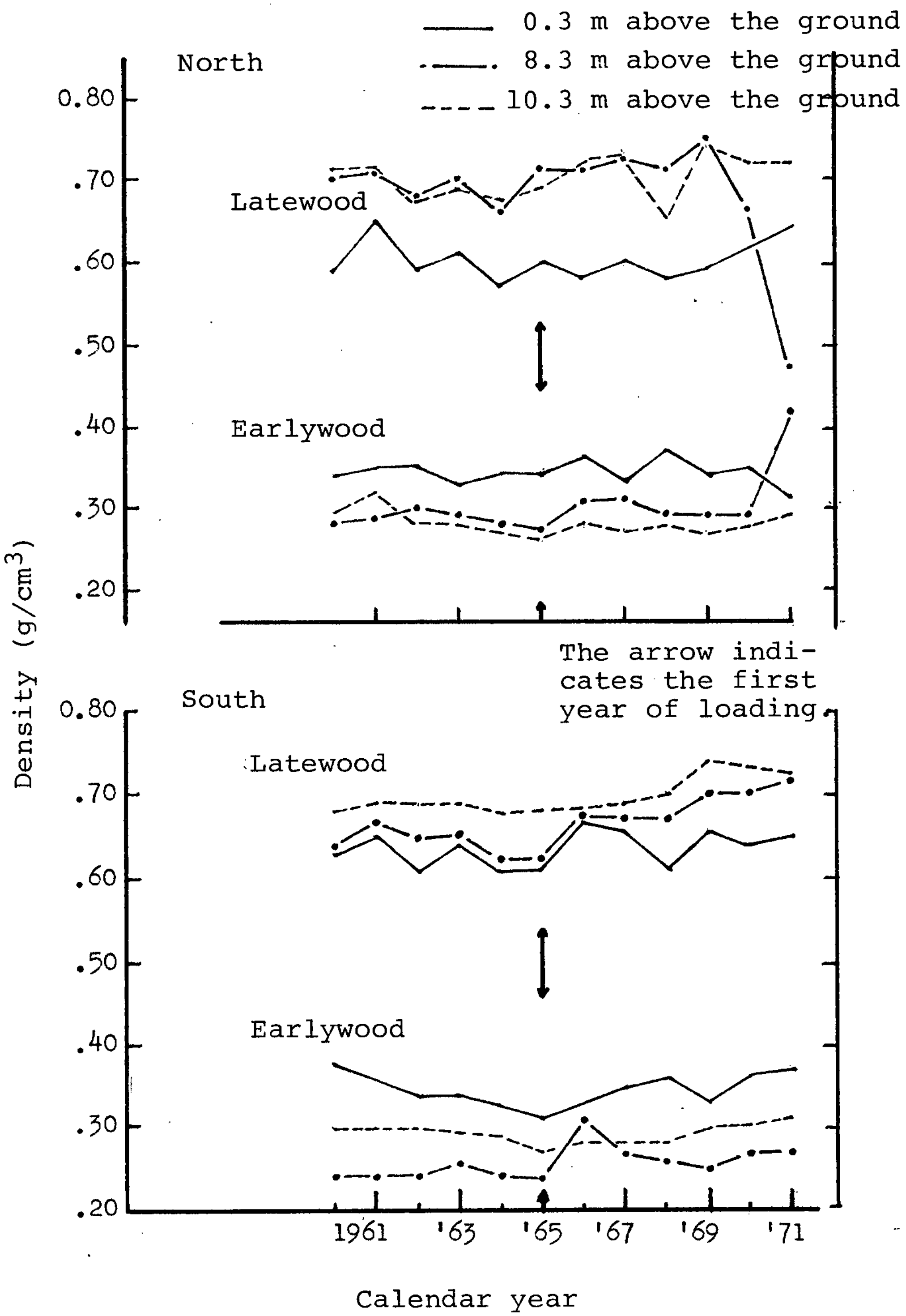
Figure 4. Growth increment width at different stem heights before and after loading.



The variations in wood density since the loading is shown in Figure 5. Although the changes are not consistent with respect to stem direction and year, increased density is noticeable in the loaded stem. In comparison, no apparent changes are observed at the height of 1 m above the load.

The growth increments formed under suddenly increased compression stresses are characterized by a narrower increment and probably an increased density. The magnitude of the changes in increment is much greater in earlywood than in latewood. This difference may be explained by the inherited differences in their respective structures. Earlywood tracheids normally tend to have larger lumina, thinner walls and consequently lower density, as compared to those of latewood. When wood is formed under a stress, the following strain is dependent not only on the size of the stress applied but also on the stiffness of each component. From the structures of growth zones, the earlywood is expected to show greater strain and perhaps equally greater response to the same stress level. It is, in fact, surprising that latewood shows no responsive changes in its width. This suggests that the size of loading was not great enough to affect the width of latewood increment, although some changes are indicated in its density. It

Figure 5. Incremental growth zone density at different stem heights before and after loading, with reference to cardinal directions.



is possible, however, that when the magnitude of stress is great enough, the width of latewood zone will be changed in much the same way as earlywood. Reduced radial width in both earlywood and latewood increments in the same proportion have been reported in the stayed loblolly pine stems (6) and the zone of discontinuity in a Norway spruce stem (47), where presumably much greater compression stresses were artificially introduced.

Even in earlywood, a recovery from the drastic changes is indicated after two years of loading. The recovery is more evident at the height of 0.3 m than that of 1 m below the load. It is quite likely that growth increments during the recovery period reflect changes in stem form and tree weight distribution. In other words, the distributional pattern of compression stress in the stem has changed with time as wood was distributed in response to loading. During the consecutive two years following loading, the reduction in volume growth was accompanied by comparable decline in weight growth as well (Table 2). Obviously, this suggests that more, probably preferentially, wood was distributed in the stem portion above the load, causing a higher wood weight concentration in the top of the stem.

Table 2. Growth increment weight* in the compressed Douglas-fir stem before and after loading.

Height in the stem (m)	Growth Zone	Cardinal Direction	Before				After			
			1961	1962	1963	1964	1965	1966	1967	1968
0.3	EW	South	11.3	12.4	13.6	10.0	10.2	5.5	7.9	9.8
		North	15.9	16.7	17.3	17.3	14.7	8.8	20.3	20.1
	LW	South	14.6	8.2	10.3	7.1	9.1	6.7	9.0	8.3
		North	13.3	7.6	9.7	5.5	10.8	9.5	11.5	11.7
8.3	EW	South	3.9	5.0	5.4	6.4	5.4	4.5	5.1	4.9
		North	4.9	6.0	6.1	7.6	5.9	4.6	5.6	4.8
	LW	South	4.1	3.7	4.4	4.0	4.1	3.9	5.3	5.8
		North	6.5	6.0	7.2	5.9	6.5	5.7	5.8	6.2
9.3	The point of loading									
10.3	EW	South	4.1	5.5	6.3	6.9	6.9	6.7	7.3	6.8
		North	4.6	4.5	4.0	5.4	4.2	4.7	4.7	4.1
	LW	South	4.9	4.4	5.0	5.4	4.6	6.7	6.6	7.7
		North	2.8	2.9	4.2	3.7	3.4	4.7	4.0	4.4

*Oven-dry weight in grams for 1 cm thick disk

*The data presented here were measured by the staff at the Western Forest Products Laboratory.

EW - earlywood, LW - latewood

Observations on the wood distribution in response to loading suggest that the stress pattern is ever-changing and also that stem form is basically shaped by the stress pattern.

4.2.2 Chemical composition

Results of comparative analyses of the wood formed before and after loading are summarized in Table 3. Analysis of variance and multiple range test for the results are given in Table 4, which reveal that growth zone, height, loading, cardinal direction, and some of their interactions are significant (over the 95% probability level) factors in the variability of chemical composition of the stem. The mean holocellulose, alpha-cellulose and lignin yields from the stem are 73.4% (range 70.6-76.0; standard deviation, 0.177), 43.9% (37.7-48.7; 0.344) and 28.2% (24.5-32.6; 0.24), respectively. These values were calculated on the basis of the results for individual growth zones.

Summations of holocellulose and lignin yields, which were determined separately, are an average of 101.6% (range 99-104). This variable result is possibly due to some deficiencies of the methods adopted for the present study. Particularly the chloriting method tends to yield higher values (26). It should be, there-

Table 3. Chemical composition of the compressed Douglas-fir stem wood before and after loading.

Height in the stem (m)	Growth Zone	Cardinal Direction	Holocellulose		Alpha-cellulose		Lignin	
			Before	After	Before	After	Before	After
0.3	EW	South	70.6	72.5	41.4	43.8	29.7	27.4
		North	71.3	71.4	41.8	42.1	30.6	29.1
	LW	South	72.9	73.9	47.4	48.1	26.4	25.3
		North	72.6	73.9	44.8	46.5	29.6	26.6
8.3	EW	South	73.3	73.6	41.7	42.6	31.0	28.2
		North	73.0	73.7	41.2	42.8	31.1	28.8
	LW	South	75.5	75.7	47.8	48.6	25.5	24.5
		North	75.1	75.9	47.3	48.7	26.3	25.9
9.3	The point of loading							
10.3	EW	South	70.7	71.8	37.7	38.4	32.6	29.7
		North	72.4	73.4	38.8	29.3	31.9	30.4
	LW	South	73.9	72.8	45.7	44.2	27.2	27.5
		North	75.4	76.0	46.6	47.6	26.5	24.4

i) all percentage yields are based on oven-dry weight of extracted wood.
ii) each value is the mean percentage yield on n = 4 (holocellulose) or n = 2 (alpha-cellulose, lignin) observations.
iii) EW - earlywood, LW - latewood

Table 4. Analysis of variance and Duncan's multiple range test for the chemical composition data, and chemical composition of growth zones and heights before and after loading.

A. Analysis of variance

Source	DF	F values		
		Holocellulose	Alpha-cellulose	Lignin
Height (H)	2	42.68**	130.14**	16.96**
Direction (D)	1	9.49**	0.05	11.38**
EW vs. LW (E)	1	138.91**	1628.45**	578.11**
Before vs. After loading (B)	1	12.28**	38.51**	121.56**
H x D	2	14.46**	32.28**	26.36**
H x E	2	0.62	37.56**	24.63**
H x B	2	1.40	6.15**	0.73
D x E	1	0.49	0.03	0.03
D x B	1	0.23	1.69	0.26
E x B	1	1.09	1.07	10.99**
H x D x E	2	0.42	5.59*	9.02**
H x D x B	2	1.74	3.74*	1.49
H x E x B	2	1.51	0.81	3.61*
D x E x B	1	3.61	9.12**	11.53**
H x D x E x B	2	0.75	2.17	3.73*
Error	DF	72	24	24
Total	DF	95	47	47

* Significant at P = .05
** Significant at P = .01

Table 4.

B. Duncan's multiple range test

Chemical Component	Height in the stem (m)			Growth Zone		Before	After	Direction	
	0.3	8.3	10.3	EW	LW	Loading		South	North
Holocellulose	72.4	74.5	73.3	72.3	74.5	73.1	73.7	73.1	73.7
Alpha-cellulose	44.4	45.1	42.3	40.9	46.9	43.5	44.4	43.9	43.9
Lignin	28.1	27.7	28.8	30.1	26.3	29.0	27.3	27.9	28.4

i) range for alpha = .05

ii) any two means differ significantly, homogeneous subjects

Table 4.

C. Chemical composition of growth zones and heights in the stem before and after loading.

	Holocellulose		Alpha-cellulose		Lignin	
	Before	After	Before	After	Before	After
Growth zones						
Earlywood	71.9	72.7	40.4	41.5	31.2	28.9
Latewood	74.2	74.7	46.5	47.3	26.9	25.7
Heights in the stem (m)						
0.3	71.9	72.9	43.7	45.1	29.1	27.1
8.3	74.2	74.7	44.5	45.7	28.5	26.9
9.3	The point of loading					
10.3	73.1	74.5	42.2	42.4	29.6	28.0

fore, pointed out that the data reported in the study are not absolute, but rather reasonably reproducible. As a result, small differences can not be detected or showed with any certainty.

Furthermore, some difficulties lie in evaluating the effect of loading on wood chemical composition unless the observed variations are definitely consistent and great. Unfortunately, the manifest response in the two years immediately following treatment, as shown in individual growth increments, was somewhat discounted by sampling the seven consecutive increments formed after loading. Nonetheless, there are strong indications that under increased compression stress, holocellulose and alpha-cellulose percentages increase, while that of lignin declines.

A. Earlywood and Latewood

In both growth zones (growth zone x loading) an increased cellulose and a decreased lignin content are apparent. The magnitude of the changes is greater in earlywood (EW) than in latewood (LW), which is in accordance with the result on growth increment.

The two incremental growth zones differ markedly in their chemical compositions, as in their anatomical characteristics. They present the most significant difference among the variables examined in the study and the data for them agree with those reported previously. On the average, the difference in holocellulose yields is 2.2% higher for LW. The difference in their alpha-cellulose contents is even higher, with 6.0%. The higher cellulose content for LW is associated with a lower lignin content. The EW yields 3.8% higher lignin. A higher lignin content for EW is due partly to a greater proportion of the middle lamella (rich in lignin) of EW substance per unit weight (40), but mostly to the evidence that the lignin concentration in the secondary wall is higher in EW than in LW (56). It is interesting to note that these differences between growth zones are the greatest at the height of 10.3 m and the smallest at 0.3 m. This indicates that the difference in chemical composition between incremental growth zones of Douglas-fir becomes greater with ascending heights in the stem, even though three heights are not enough to generalize the tendency for the entire stem. The smallest difference found at 0.3 m is consistent with the result for density of the height.

B. Heights in the Stem

The tendencies of increasing in cellulose and decreasing in lignin are also indicated at all the three heights (height x loading), yet greater changes are found in the stem portion placed under the load. In comparison, the height of 1 m above the load exhibits a little increase in cellulose content.

Although the variability of chemical composition in regard to height in the stem is not so great as the growth zone, there are some differences among the heights studied. The highest holocellulose value is found at the height of 8.3 m, while 0.3 m has the lowest value. With regard to alpha-cellulose, the heights of 8.3 and 0.3 m show a higher percentage yield than 10.3 m. Maximum lignin is yielded from 10.3 m and minimum from 8.3 m. The differences in holocellulose, alpha-cellulose, and lignin contents between maximum and minimum values are 2.1, 2.8 and 1.1% respectively.

C. Growth Zones at Different Heights

The effects of loading appear to be unique, when examined with the individual growth zones along the heights (growth zone x height x loading). Both growth zones of the stem part under the load show much greater variations than anticipated in the adjacent two increment groups of a normal mature wood.

Of all the variations since loading the most noteworthy is at 1 m above the load. Exceptionally substantial decreases in holo- and alpha-cellulose yields and a slight increase in lignin content are indicated in the LW after loading, specifically on the south side of the height. This is a rather unusual situation in a stem development, in which the otherwise normal patterns of increasing in cellulose and declining in lignin content would be expected. The unusual growth pattern can be found in compression or overmature wood. However, the possibilities are quite unlikely, because of the age of the tree and the observed normal growth increment width and density. The comparable EW and both growth zones on the north stem part of the height show a similar change to that described for the loaded stem part. Probably these differences in responding to the load in regards to growth zones and cardinal directions resulted from the confounded, complex responses of the tree to the environment, but no clear explanation of the results can be given.

D. Directions in the Stem

Generally, in the stem (direction x loading), no significant variations are observed since loading. There are, however, a variety of variations with the south and north directions in the responses of individual growth zones at different heights, as mentioned in the preceding section. The differences in wood formation between directions have been claimed to be due to wind action.

4.2.3 Crystallinity and microfibril angle

Results of crystallinity, expressed by an X-ray crystallinity index, are included in Table 5. Multiple range test for the results (Table 6) show no significant changes by the loading, but close inspection of Table 5 discloses definite changes and also an unusual variation. In both cardinal directions, an increased crystallinity is observed in the stem under the load, except for the LW at 0.3 m height which shows a reduced crystallinity. The reduction in crystallinity after loading is also found for both growth zones at the height above the load (10.3 m). These opposite trends explain the statistically insignificant changes. It is noted that above the load more pronounced reduction in crystallinity has resulted in LW than in EW.

Linear regressions of cellulose microfibril angle on age (calendar year) are presented in Figure 6. The effect of loading on the angle is indicated in the EW of the heights at 0.3 m above ground and 1 m above the load, but the variations are not consistent with respect to directions of the heights. Slightly larger and smaller

Table 5. Crystallinity of the compressed Douglas-fir stem wood before and after loading.

Height in the stem (m)	Growth Zone	Cardinal Direction	Crystallinity index (%) Before	After
0.3	EW	South	61.3	63.1
		North	60.7	61.6
	LW	South	64.0	63.2
		North	63.1	62.0
8.3	EW	South	64.8	65.2
		North	63.2	64.6
	LW	South	66.5	68.3
		North	67.3	68.0
9.3	The point of loading			
10.3	EW	South	61.4	60.7
		North	63.3	63.2
	LW	South	66.7	62.9
		North	67.7	66.7

i) each value is the mean percent holocellulose crystallinity of two observations.

ii) EW - earlywood, LW - latewood

Table 6. Duncan's multiple range test for the crystallinity data, and crystallinity of growth zones and heights before and after loading.

A. Duncan's multiple range test

Height in the stem (m)			Growth zone		Before	After	Direction	
0.3	8.3	10.3	EW	LW	Loading		South	North
62.4	66.0	64.1	62.8	65.5	64.2	64.1	64.0	64.3

i) range for alpha = .05

ii) any two means differ significantly, homogeneous subjects.

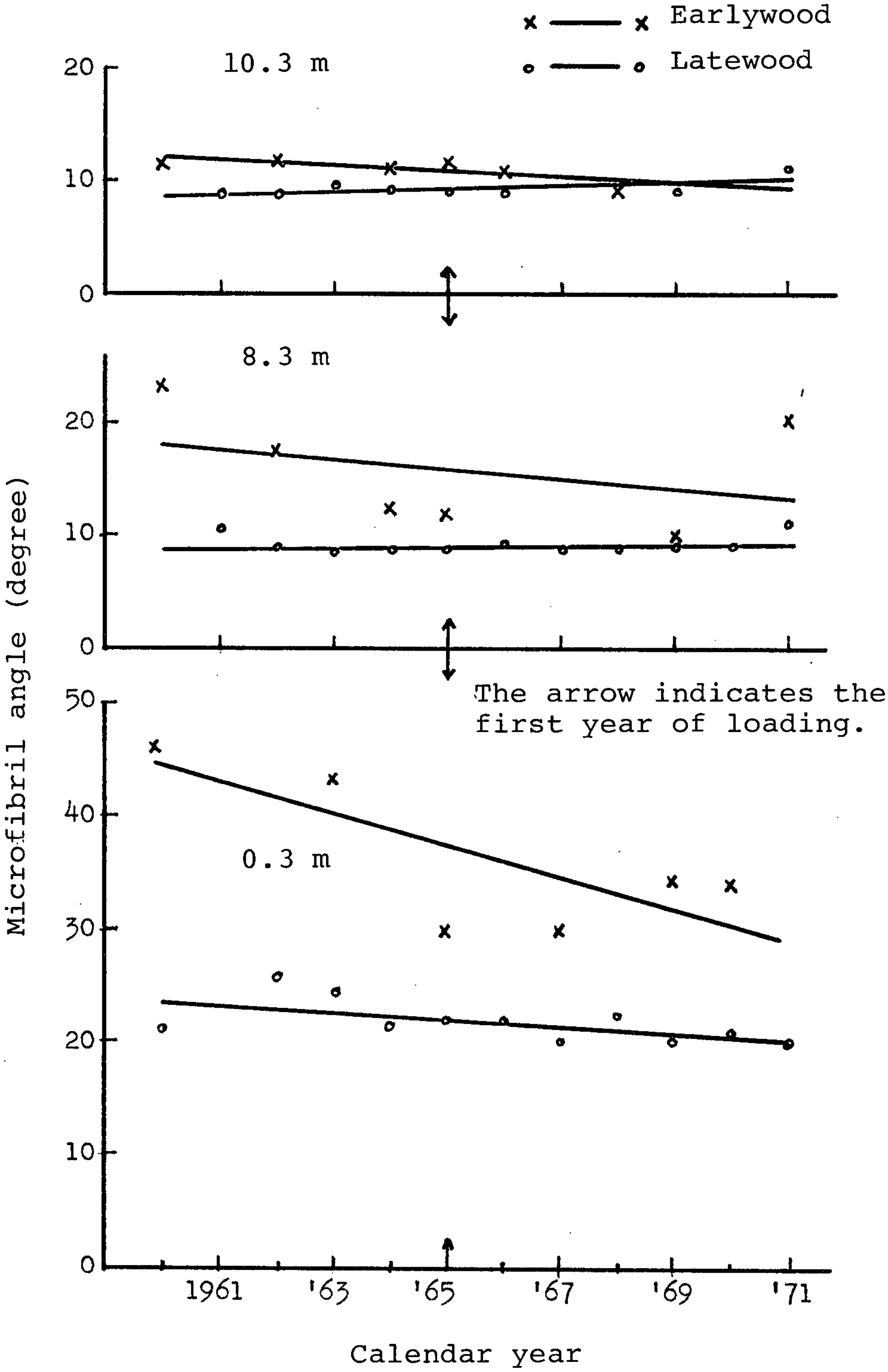
Table 6.

B. Crystallinity of growth zones and heights in the stem before and after loading.

	Crystallinity index (%)	
	Before	After
Growth zones		
Earlywood	62.5	63.1
Latewood	65.9	65.2
Heights in the stem (m)		
0.3	62.3	62.5
8.3	65.5	66.5
9.3	The point of loading	
10.3	64.8	63.4

Figure 6. Microfibril angle of incremental growth zone at different stem heights before and after loading, with reference to cardinal directions.

A. North



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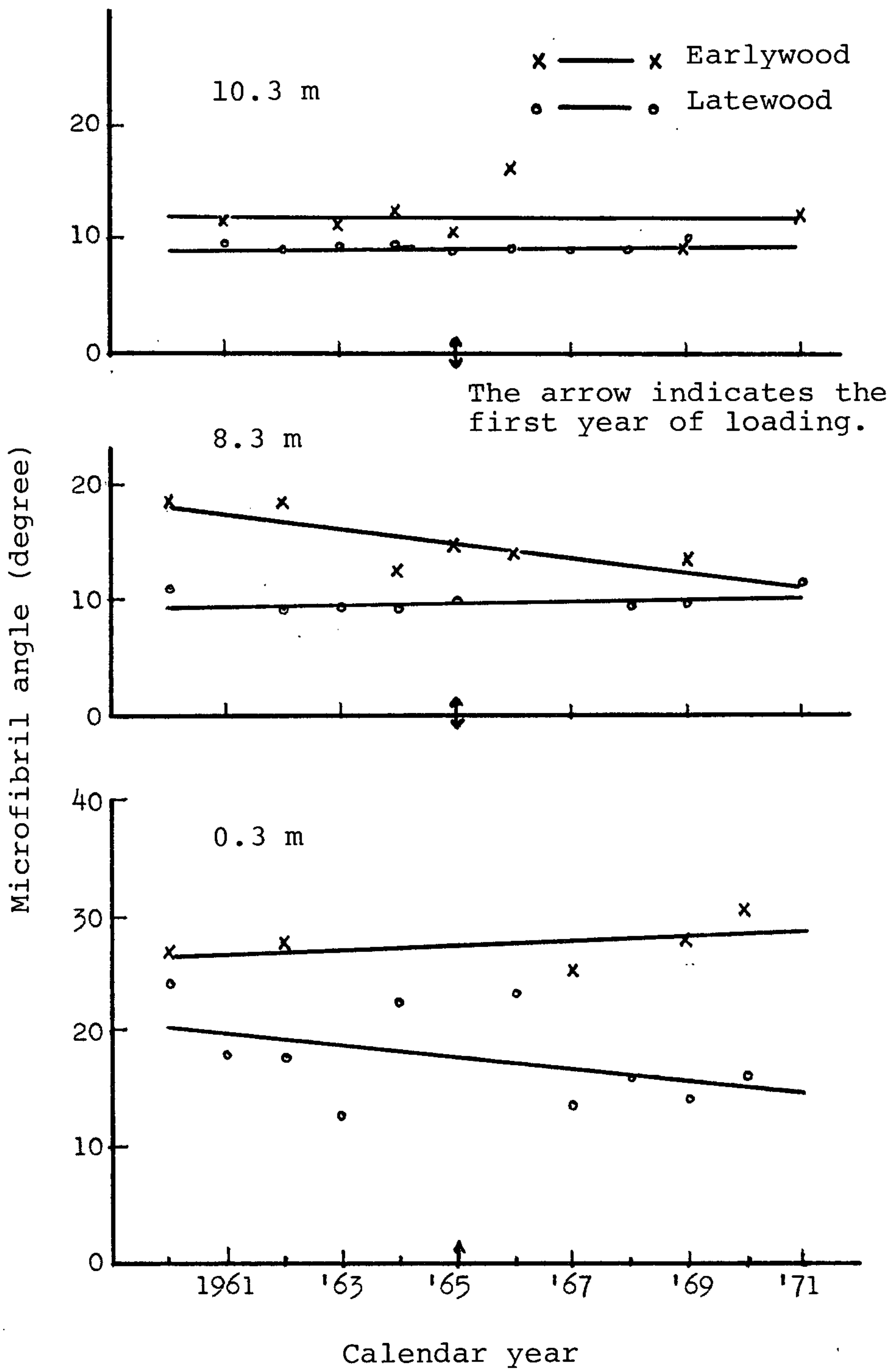
....Continued

B. South



angles are observed on the south side of 10.3 m and the north side of 0.3 m height, respectively.

4.3 About the Experiment

Artificial compression loading was employed in this study to evaluate the influence of tree weight on wood formation in the stem, on the assumption that the compression load would be a predominant factor on the growth of the stem. But all the variations observed in the wood formed since the loading can not be definitely attributed to the loading, since many factors other than the treatment may be involved in the formation of wood.

The effects of wind and physical wounding, among others, are unavoidable mainly because of the technical difficulties in controlling them. The influence of prevailing wind could be somewhat limited by examining the south and north directions of the stem (3,20), yet variations with different directions prove otherwise in the data of the present study. However, neither pronounced stem eccentricity nor compression wood was noticed in the stem sections examined. No attempt was made to explore the development of traumatic resin canals or any changes in normal resin canals, even though minor wounds were evident in the region of loading.

To learn more about the effects of growth factors, including climate, other than treatment on earlywood growth, the yearly differences in the widths of earlywood and latewood in the young Douglas-fir stems sampled near the experimental area of this study are documented in Table 7. A moderate variation in earlywood width prevailed for the period 1960-71 in the area, while unusually increased variability was evident in the loaded stem after loading (see Fig. 4).

Even if the substantial changes in growth increments for the two years immediately following loading are mostly due to the treatment, the changes after the first two years may be confounded with the effect of increased tree weight for the period. While the increased tree weight is relatively small in magnitude, this gives rise to a change in compression stress distribution pattern in the stem as the rate of incremental growth declines in the loaded stem and the stem growth is concentrated above the load with time.

Part of the observed variations in the wood formed after loading has been evidently, at least to a limited degree, caused by other factors. But it is believed to be hard to detect their specific influences, considering the complex interactions between their actions and the experimental loading on the biological system of wood formation. It may be, however, reasonable to state that highly significant differences or unusual growth trends are mostly attributed to treatment.

Table 7. Average radial growth at breast height for the 180 young Douglas-fir trees at Univ. of B.C. Research Forest for the years 1960-71*.

Year	Width .01 mm	
	Earlywood	Latewood
1960	377.90	166.30
1961	366.10	171.30
1962	367.40	188.80
1963	394.80	212.50
1964	424.90	169.10
1965	339.20	155.60
1966	338.70	158.60
1967	308.40	137.10
1968	292.70	164.90
1969	240.30	148.60
1970	346.60	177.00
1971	321.10	138.50

* The data presented here were compiled by Dr. J. Harry G. Smith, Faculty of Forestry, University of British Columbia, Vancouver, B.C.

5.0 CONCLUSIONS AND PRACTICAL APPLICATION

The experiment has shown immediate and definite influence of longitudinal compressive stress on the formation of stem wood. This evidence suggests that the stress due to tree weight is an important factor in governing wood formation and distribution in the stem. The extent of influence by tree weight depends on the magnitude of applied stress and resultant strain locally and appears to be much greater than the stress level might suggest. Defining the specific influence of the weight requires further, refined studies on the physiological and biochemical pathways to the observed variations in wood characteristics.

If the findings from the study based on a single tree can be verified in other trees and other species, they would be of considerable importance to knowledge of the variations of tree growth and wood distribution in the stem. The longitudinal compressive stress pattern obtainable by stem form and green weight distribution pattern in a stem may be used in predicting the distributional pattern for wood properties of the stem. Such information may explain the conflicting results in the earlier studies on the longitudinal variations in stem wood characteristics. It may also be a helpful and sound guide to the silvicultural practices affecting the green weight or weight distribution of trees.

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APPENDIX: Sample Size for the Desired Precision in Selected Holocellulose and Lignin Procedures

A. Holocellulose

A preliminary determination for a sample of ISEA was made to estimate the mean percent holocellulose content, according to the modified Wood Science Procedure. The result gave a standard deviation among 6 determinations of 0.5882.

The result is given below:

1) 71.39
2) 72.33
3) 72.59
4) 72.83
5) 72.84
6) 73.02

$\bar{x} = 72.50$ $S^2 = 0.3460$ $S = 0.5882$

Sample size was estimated by the formula:

$$n = \frac{t^2 S^2}{D^2}$$

Where $t^2_{0.05} = 2.571^2 = 6.61$

$S^2 = 0.3460$

$D^2 = 0.8^2 = 0.64$ (the estimate to be within 0.8% of the population mean)

$n \doteqdot 3.57$

The sample size (n) must be an integral value and, because 3.57 is too small, a sample of n = 4 observations would be required for the desired precision.

B. Lignin

5 determinations for a sample of ISLA were made to estimate the mean percent lignin content, by using the modified acetyl bromide method (59).

The result is:

1) 25.02

2) 25.08

3) 25.30

4) 25.50

5) 25.92

$\bar{x} = 25.30$ $S^2 = 0.14$

The formula:

$$n = \frac{t^2 S^2}{D^2}$$

Where $t^2_{0.05} = 2.776^2 = 7.70$

$S^2 = 0.14$

$D^2 = 0.8^2 = 0.64$

$n \doteq 1.68$

Therefore, 2 observations would be required for the desired precision.