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Douglas-Fir Wood Quality Studies
Part I: Effects of Age and Stimulated Growth on Wood Density and Anatomy*

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Abstract

Douglas-fir trees about 21 years old and growing on a poor site were thinned and fertilized causing accelerated growth. The characteristics of the wood across the 30-year age span were studied for 7 trees from the treated plot. Four trees of nearly uniform ring growth were also studied for some characteristics. Radial and tangential tracheid diameters, tracheid length and percent latewood were correlated quite well with log of age, coefficients ranged from 0.76 to 0.88 on pooled data. All tracheid dimensions when correlated with log of age gave high coefficients on a within-tree basis. The strongest relationship in all age-related factors was between 0 and 12 to 14 years. Specific gravity increased with age in all trees to about 16 to 18 years, then leveled off.

Fertilization and thinning caused immediate production of lower density wood with somewhat lower percent latewood, a slight decrease in tracheid diameter tangentially but slightly greater radially, and a small decrease in tracheid length. The effects were mainly in the first 3 to 4 years after treatment, then there was recovery to normal wood density and cell dimensions. Wood from the trees of uniform growth showed no significant change over the same time period in percent latewood, specific gravity, and tracheid length.

Introduction and review

The implications of cultural practices for producing a greater wood supply are now well known and much research has been done on many tree species to measure the growth responses to intensive forest management. Relatively less effort has been expended on the relationship of wood quality to increased rate of wood production, but the amount of work done in this area in the last 15 years has become impressive nevertheless.

Although there are generalizations on what causes changes in wood quality which hold fairly well among a number of species, there is adequate evidence that studies are needed on important species in a variety of locations and forest treatments if we are to be able to make practical decisions on what to do to a forest to obtain the optimum quantity of wood of a quality that we shall find useful for wood products.

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Several years ago we investigated some relationships between morphology and chemical composition of young Douglas-fir as influenced by age from pith and by accelerated growth caused by thinning and fertilization. Part of the work was reported in unpublished Master's Theses. This paper is a condensed presentation of our data presented by Harrison [1963] of this laboratory, combined with new results from much new data from the original experiment and a more extensive statistical analysis. For this reason, the calendar years on the graphs appear older than might be expected. This information should be made available to others interested in wood quality studies.

A second paper is planned which will deal with fibril angle changes and chemical analysis of the major components of these Douglas-fir trees during their total 30-year growth span including their period of accelerated growth.

As long ago as 1916, Gerry reported there was an increase in radial and tangential tracheid diameter during approximately the first 20 years of growth. Similar conclusions have been reported by many workers on other species. Likewise there are reports which state that tracheid length increases with rings from the pith but there is less information and agreement on how much and if the rate of change is variable. In a significant study, Dinwoodie [1963] reported that in Sitka spruce, in the first 15 rings age was most important and in rings beyond 50, ring width became most important. In the intermediate zone, age and distance from pith are both important. Tracheid length fluctuated after reaching a maximum and could be related inversely to ring width. These findings and some others of similar results have special meaning in relation to the results to be reported in this paper. In numerous reports involving a number of species there are conflicting conclusions regarding the effect of growth rate on tracheid length.

In Douglas-fir it generally has been found that specific gravity is closely correlated with percent latewood. Smith [1956] stated that the specific gravity was dependent on it regardless of the location of the ring with respect to the pith. For wide-ring wood the relationship was linear from 16 to 60% latewood. A relationship was found between growth rate and percent latewood. Wellwood and Smith [1962] said percent latewood was very important in controlling specific gravity. Drow [1957] found that the percent latewood of Douglas-fir tends to increase with a decrease in growth rate in wood less than 20 rings per inch but specific gravity is higher in slowly grown wood at a given percentage of latewood. Paul [1963] also has pointed out the application of silviculture to control specific gravity by regulating the growth rate. Kennedy [1961] obtained a correlation between high earlywood increment, low water deficit and high auxin level, and high latewood increment for the opposite conditions. Wellwood and Smith [1962], working on Douglas-fir in British Columbia, and Knigge [1962], using samples from western Washington and Oregon, have good presentations on growth and specific gravity related to site and growth conditions. The latter found that ring width and age were important but several growth effects accounted for only one third of the density variation. McKimmy [1966] studied a 46-year old stand and found dercent latewood, growth rate, age, seed source and plantations had a large effect on specific gravity. He also pointed out that density of juvenile wood was unreliable for predicting density of mature wood. Duffield [1964] measured tracheid lengths on the last portion of latewood in increment cores of Douglas-fir in western

Washington and Oregon and found very diverse patterns with rings from the pith. A second degree polynomial curve described the tracheid length change with age from 10 years to 50 years of age. Similar patterns of tracheid length were often found in trees in close proximity.

Only a few studies have been made on the effects of accelerated growth due to fertilization and thinning on wood quality. Erickson and Lambert [1958] reported the diameter growth in a fertilized and thinned stand, 30 years old, was faster than the growth in a fertilized stand which was greater than in untreated stands. The percent latewood decreased after fertilizing and thinning. Specific gravity also decreased the most with that plot treatment, but the growth rate and volume increment increased and more than compensated the density loss. Harrison [1963] reported good correlations with tracheid dimensional changes and log of age, and also, only a slight change in these dimensions due to accelerated growth. Sastry [1967] reported a general decrease in specific gravity, percent latewood and mean tracheid length in wood of three Douglas-fir trees after they were fertilized. Fertilization of four Douglas-fir trees from 38 to 45 years of age caused a 74% increase in volume, a 10% decrease in specific gravity, a slight increase in pulp yield per unit weight of wood, and a small decrease in extractive content [Siddiqui, Gladstone, Martin 1972]. Megraw and Nearn [1972] reported that fertilizing and/or thinning of six Douglas-fir trees starting at 8 to 10 years old caused more intermediate density fiber because of lowered latewood density and increased earlywood density. Overall specific gravity was not affected. The trees were fertilized, however, during the juvenile period and may have prolonged the juvenile period.

Material

The trees were cut from a $^1/_{10}$ acre plot, which had been heavily thinned, then fertilized for 9 years, in an experimental forest of the University of Washington near LaGrande, Washington. The soil is gravelly sandy loam to 18 inches and gravelly loamy sand to 10 to 15 feet. The area had been burned before establishment of the stand and has a site index of 92 equal to a high Site V for Douglas-fir.

Fertilizer was applied in April, 1950, as ammonium nitrate and ammonium phosphate at the rate of 100 lbs. of N per acre and also 80 lbs. of P_2O_5, 30 lbs. of K_2O and 50 lbs. of CaO. Additional nitrogen (100 lbs. in 1951 and 50 lbs. through 1958) was added each year, some as ammonium nitrate but mainly as urea.

The thinning, done in the spring of 1949 and 1950, favored crop trees of the upper crown classes and removed 80% of the trees and 64.7% of the basal area. The residual stand had 610 trees per acre with a mean diameter of 3.9 inches and a basal area of 51.7 sq. ft. The trees used were from 10 to 17 cm (4 to 6.5 inches) in diameter, breast high and ranged from 27 to 31 years of age at the time they were cut.

The main study is on seven trees from the treated plot which clearly showed increased diameter growth after treatment but for comparitive purposes on some wood characteristics four trees were used which had uniform growth rate in the last 16 to 18 years spanning the period before and after plot treatment. Two trees were from the same plot and two were from the adjacent plot which had been thinned only. This provided comparison, then, with uniform growth rate, not just the slow-down of growth normally expected and shown in the trees of the main study.

The material for this study was one-inch thick discs from 5-foot sections cut at breast height for use in a previous growth study. Generally, the values reported are from the diameter of two equal and opposite radii.

Procedures

For measuring tangential and radial diameters, microtome sections were cut from opposite radii, stained with safranin, mounted, and measured. For tangential measurements, 5 strips on each radius were measured, counting from 400 to 500 tracheids per ring. The standard error at the 95% confidence level was 1.1 μm based on one tree. Late earlywood tracheids were measured instead of latewood tracheids because of better uniformity.

To obtain the radial tracheid diameters, the first 10 tracheids in 20 radial rows were measured in each ring of each of the two radii, not counting cell tips. The standard error was 1.2 micrometers.

Tracheid lengths were measured using macerated latewood from each ring. The wood was macerated with 50% glacial acetic acid and 12% hydrogen peroxide. Drops of the fiber suspension placed on a slide and dried at 40° C were stained with 0.25% chlorozol black, dried, washed free of excess stain, and dried. A photochanger and projection attachment were used which made it easy to detect broken ends by viewing through the microscope when necessary. Forty tracheids (20 from both radii) were measured. The average standard error of the mean was 0.11 mm calculated on one tree.

The latewood percentage was measured at 30× with a measuring microscope, on a microtomed surface of the green block. The boundary was selected where there was a definite increase in cell wall thickness. This was usually accompanied by a color change. In Douglas-fir, cell wall thickness increases rapidly, but not necessarily uniformly laterally, after this point. This was a practical method to indicate major density change instead of some other arbitrary standard such as a ratio of cell wall thickness to lumen diameter.

Several statistical techniques were applied. Regressions were calculated on the main variables using linear regression on both variables, logarithm of the dependent variable only, and a log-log regression. Multiple regression was used to assess the second and even the third most important dependent variable. Analyses were made on the individual tree data and on the pooled data for the group of trees. In some cases, the data were split into periods before and after the first 12 years of growth to assess the effect of juvenile wood on the regressions.

Results

Growth increments and growth rate

In the initial phase of the study, the percent of latewood was measured in each quadrant of trees 1 and 2. The use of opposite radii gave an average nearly as good as that using all quadrants, usually within 2%. Therefore, the same two quadrants were used for this purpose as were used for measurement of cell dimensions. Fig. 1 shows a typical control tree and a variable-growth tree from the treated plot. The difference in rings before and after thinning and the start of fertilization, indicated by the arrow, are evident. The rings are wider and the latewood appears less dense generally. The low percentage of latewood in the early years of both samples is also shown.

The average increase in radius of the seven trees, the earlywood increment, and the latewood increment for each year after age 6 (for most trees) are shown in Fig. 2.

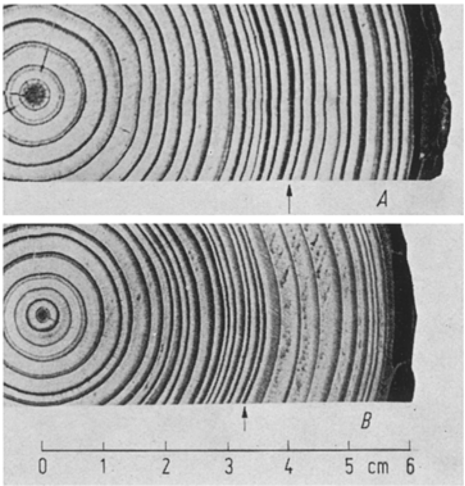

Fig. 1. Typical wood samples; (A) uniform growth and (B) variable growth from the time of thinning and fertilizing indicated by the arrow

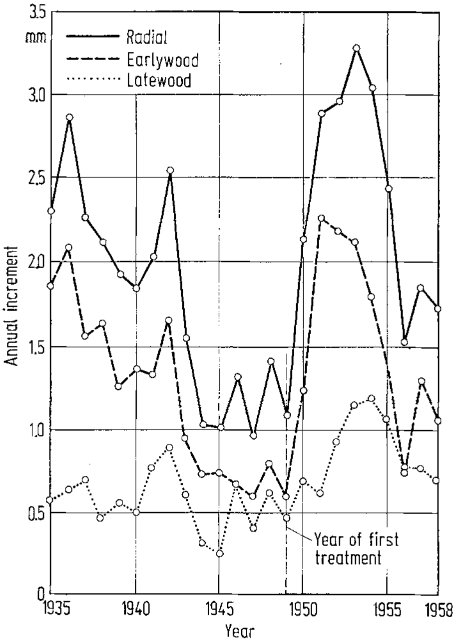

Fig. 2. Incremental growth on the radius of the 7 trees of the main study before and after plot treatment

The few years before the first data points represent the rings very near the pith and the unequal age factor of a 4-year spread in total age. During the earlier years, the radial increment was generally good but dropped rapidly and was low for a period of approximately 5 years until plot treatment accelerated the growth which responded immediately. There was a second decline in growth rate in the last 4 years of the treatment period but it still was 0.5 mm greater than the earlier slow growth rate. Considering the results of other variables, reported elsewhere in this, relative to growth rate, there are indications that a radial growth rate of 1.0 mm may be a critical value above which increased growth rate up to the maximum growth rate encountered in this study, 3 mm approximately, has only little influence on wood characteristics. This concept should be studied more thoroughly as it has relevance to stability of wood properties. It is obvious from Fig. 2 that annual ring width is not well controlled by age in these trees of variable growth rate. The total correlation of the pooled data of ring width with the log of age yielded a coefficient of only -0.194, $r^2 = 3.8\%$. Without the semi-log transformation, the coefficients were even smaller.

The latewood incremental variation was small in the earlier years and remained steady during the middle or slow-growth period. During the same time, the earlywood increments were reduced greatly until, through the slow-growth period, latewood and earlywood increments were nearly equal. During the faster growth after plot treatment, the earlywood increments again exceeded the latewood increments but not by the high ratio found near the pith.

The percent latewood was correlated with age from the pith; the logarithm of age gave a better relationship than the non-log basis. The individual regressions are shown in Fig. 3 with the percent of variance explained by the log of age. The average of the explained within-tree variances from the regressions of the trees was 49% (correlation coefficient of 0.70). A table of latewood percentages, not included here, showed large yearly fluctuations. When only the years before plot

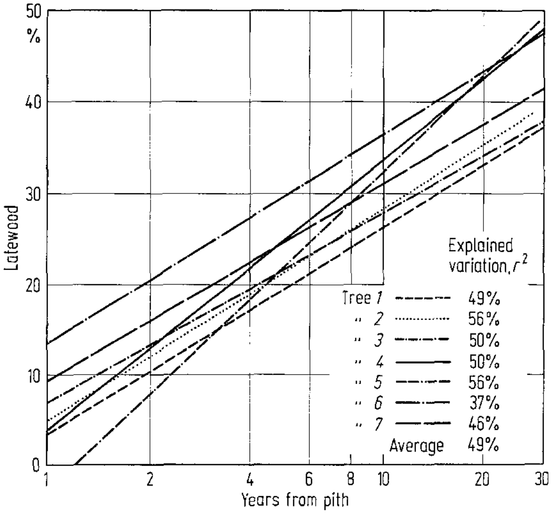

Fig. 3. Regression lines and coefficients of determination (r^2) of percent latewood and log of age for the 7 variable growth trees

treatment were used (mostly juvenile years) the average of the tree correlation coefficients was 0.76 and the explained variation was 57%. The slopes were generally similar except for two trees, Nos. 4 and 5. It will also be shown in regressions involving other factors that Tree 4 was often different in regression slope from the other trees.

Multiple regression analysis on total age data showed the most significant factor associated with percent latewood was either age (4 trees) or the width of earlywood (3 trees). However, the explained variation of 52.6% was only a little better than for age only. Latewood increment was the second most important factor in most trees (it added 23% to explained variance) and inclusion of ring width with the other 3 factors brought the explained variance for all factors to 92% (average for the seven trees). Radial growth rate contributed the least, probably because the two parts of the ring were used as separate factors.

When the first 12 years were omitted, not age but earlywood increment was the factor of first importance for percent latewood in most trees. Some of the other three factors were not significant as separate factors but in total they gave an explained variation of 90%. Smith [1956] and Drow [1957] found that the percentage of latewood tends to increase with a decrease in growth rate. In the present study, however, the analysis showed that for all 30 years of age, growth rate was a significant factor in only 2 trees out of 7. For the first 12 years, growth rate was a significant factor in 2 trees, with earlywood increment being a more important factor.

The total linear correlation of the pooled data of latewood percentages with age for the 7 trees was 0.65; with log age $r = 0.67$ ($r^2 = 45\%$). The latter values are almost as high as the average of the coefficients for the separate trees, $r^2 = 49\%$. The variability of latewood percentage induced by stimulated growth would tend to hold down the correlation. A pooled data analysis using only the first twenty years (before plot treatment) was not made but probably would have been higher, judging by the average of the within-tree correlations, 0.76, given earlier in this paper. If the data by three-year age classes are used the correlation is higher, $r = 0.71$ vs. 0.65 for the data from each year. The correlation for yearly data of the 4 control trees was not computed but must be higher because of its smoother curve.

The general curve for percent latewood against age is shown in Fig. 4A for both the variable-growth trees and the control trees. Each plotted point is the mean of the trees in each 3-year age class starting at 4.3 years average for the variable growth and 3.5 years for the controls. The curves are similar except for most of the period of accelerated growth. The means of the 9 age classes show a close relationship between percent latewood and age. The curve for the variable-growth trees is different from the increment curve of latewood shown in Fig. 2. Again, a semilog relationship is indicated, and the correlation of the points shown was 0.92 for percent latewood with log of age for the 7 variable growth trees and 0.95 for the 4 even-growth trees. Each group confirms the other, and also the inherent association with age when between-tree variation is averaged.

The radial growth and age graph, Fig. 4C, are plotted on the same 3-year age class basis as are A and B to enable comparison of effects on each combination of variables. Part B, dealing with specific gravity, is presented next.

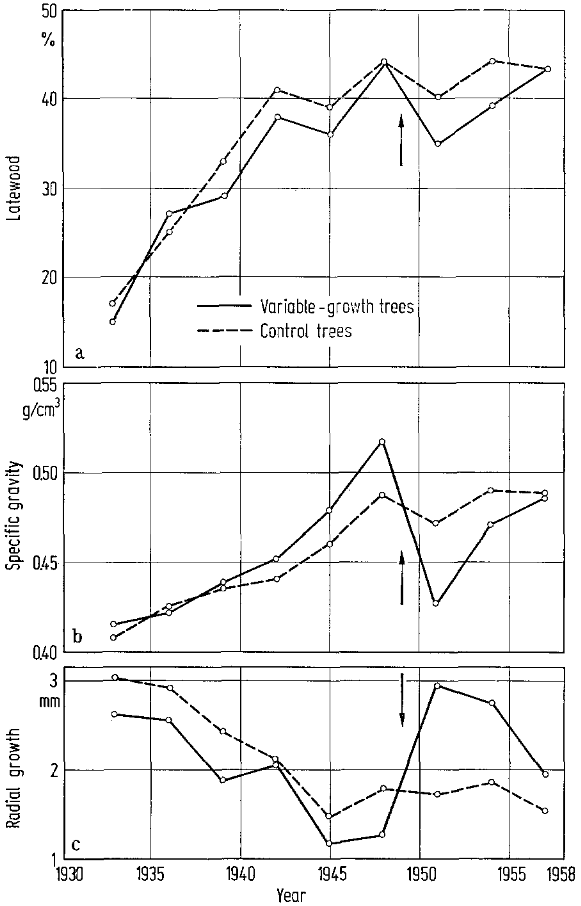

Fig. 4. (A) Percent latewood vs. age, (B) specific gravity vs. age, and (C) Radial growth vs. age for 7 variable growth trees and 4 control trees plotted by tree means of 3-year age classes starting at 4.3 years average age for the 7 trees and 3.5 years for the 4 control trees and ending at 28.3 years and 27.5 years respectively. The arrow indicates plot treatment

Specific gravity

The change in specific gravity with the total age of the trees is shown in Fig. 4B except for the first 2 or 3 years of most trees where adequate sampling is very difficult. All data are plotted by 3-year age classes. Specific gravity values are based on oven-dry weight and green volume. For both groups of trees specific gravity increased with age to an approximate age class of 16 to 18 years. The trend of increase was proved statistically.

In the 3 years before fertilization and thinning the average specific gravity was 0.517 and in the 3 years after this plot treatment it was 0.425. The difference of —0.092 was highly significant. Using 6-year periods before and after treatment the values were 0.498 vs. 0.448, and the difference of —0.500 was also highly significant. There was not significant change in specific gravity in the 4 control trees of slower and nearly uniform growth over this same period of 12 years. Therefore, plot treatment and accelerated growth truly affected the specific gravity.

The wood density tends to recover several years after treatment, and the graph shows that it has risen to an estimated normal value 8 years after plot treatment began, even though the growth rate (Fig. 4C) is equal to or greater than the growth rate in the 10 years prior to the plot treatment. The decrease in latewood percentage shown in Fig. 4A must account for much of the decrease in wood density.

The correlation between age from the pith and specific gravity was computed for the data shown in Fig. 4 B, in which the means of the 3-year age classes are plotted. However, linear regressions and correlations were calculated for both groups of trees using the total data of the age classes unless indicated otherwise. The control trees had a regression coefficient of 0.00353 for specific gravity against age as compared to a lesser regression of 0.00246 for the variable-growth trees. For the control trees ($N = 63$) the r was 0.84 and r^2 was 0.70; for the variable-growth trees ($N = 36$) r was 0.51 and r^2 was 0.26. Clearly, the changes in specific gravity from a few years before to a few years after plot treatment reduced the normally high association with rings from pith. Plot treatment and accelerated growth in maturing trees must be assumed to be the dominant causes.

The total correlation of specific gravity with percent latewood in the 7 variable-growth trees was 0.63, slightly greater than it was with age (0.52). Neither factor was a good predictor of specific gravity ($r^2 = 0.40$ and 0.26 respectively) but percent latewood was the better. Multiple correlation of age and percent latewood with specific gravity gave only a slightly better coefficient, $R = 0.64$, than the better of two independent correlations (percent latewood). This may be due largely to the rather close correlation between age and percent latewood which was 0.71 for these same age classes of samples.

Partial correlation showed that specific gravity was only moderately correlated with percent latewood when the effect of age was removed, $r\,12.3 = 0.44$ as compared to 0.63 for latewood without partial correlation. Specific gravity was slightly more related to age when determined independent of the percent latewood $r\,13.2 = 0.58$, than for age without partial, $r = 0.51$. One concludes that there is some interaction between the two factors of age and percent latewood in predicting specific gravity because removing the effect of age tends to decrease the relation to percent latewood and removing the effect of latewood percentage causes some increase in the relation to age. Much of the variation in percent latewood and specific gravity is related to age of the wood in young trees.

The tree means of percent latewood and specific gravity within each of the 9 3-year age classes of trees of variable growth are plotted in Fig. 5 to show the relationship implied in Fig. 4A and B. The correlation coefficient for the means shown in 0.78, which is higher than 0.63 for the total data. Using the means of the variables in each age class reduces the variance from the regression. The graph shows that the point at 15% latewood, point No. 1, is not in the linear pattern of the other points. That point represents an average age of 4.3 years, definitely juvenile wood. If a correlation is computed omitting this first age class, the coefficient r rises to 0.84 and r^2 to 0.71. This shows a closer relationship of the two variables beyond the age of 4 to 6 years. The regression line shown is based on the means exclusive of the first age class. The second lowest point on the graph at 27% latewood, No. 2, represents wood of age class averaging 7.3 years. The third lowest point at 36% latewood, No. 7, represents the 3-year age class following

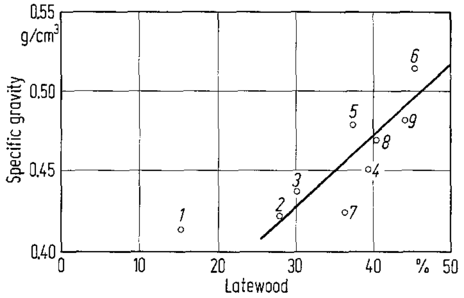

Fig. 5. Specific gravity—percent latewood relationship of variable-growth trees using tree means of age classes as in Fig. 4, $r = 0.84$; class No. 1 is not included in the regression. Numbers are by sequence of age classes. Plot treatment occurred between No. 6 and 7

thinning and fertilization. No. 6 is the pair of values just prior to the plot treatment. The change in both latewood and specific gravity is substantial. It also indicates that the specific gravity of the wood in the first-formed accelerated growth is lower than expected for the percent latewood present which probably is due to a lower overall density of the latewood such as reported by Megraw and Nearn [1972].

Radial tracheid diameter

The relationship between radial diameter of earlywood tracheids and age from the pith for the 7 trees of variable growth is shown in the composite curve in Fig. 6. Since the trees were not exactly the same age, the disparity in age was absorbed at the older age side of the curve because changes in radial diameter in the older wood were not as pronounced as in the very young wood. The radial diameter increased sharply from an average of 25 to almost 40 micrometers during the middle part of the period of slower growth at approximately ring 17. This was a small decrease of 2 to 3 micrometers until the plot treatment was made (about 21 rings from pith) after which radial diameter recovered and went slightly beyond the previous maximum to 42 micrometers. The slight decline from this maximum may be associated with a new decline in growth rate, which the growth data show,

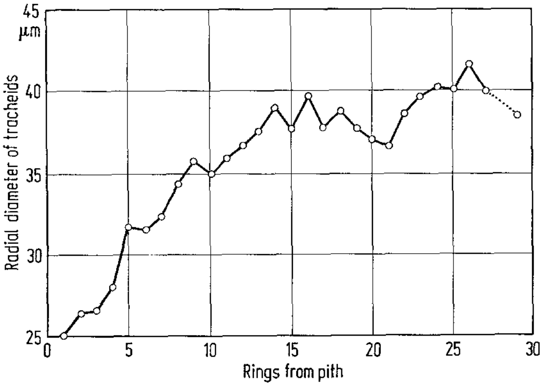

Fig. 6. Radial tracheid diameter as it is influenced by age from pith, not necessarily the same calendar year. The plot treatment is approximately at 18.3 years. Some year-to-year variation is averaged out

but there are insufficient years to establish certainity. The dotted line and final point are not highly meaningful, because this area includes the adjustment of slight differences in tree age; hence, fewer trees are represented in the final plot, and the average shifts a little. Since the same ring from pith does not, in this graph, represent the same calendar year for all trees, environmental differences are not the same for each ring, and such differences will be averaged out to some extent. However, in Fig. 7, radial tracheid diameter is plotted by calendar year to show the effect of annual environmental influences. The dotted line at the left indicates that the tree age discrepancies are now placed in the early-age period. The curve shows numerous and sharper changes in radial diameter than does Fig. 6. The tracheid diameter seems to coincide somewhat with the major ring-width changes in Fig. 2 for the years before and after plot treatment, but a greater sampling is needed to draw firm conclusions.

Radial tracheid diameter was correlated with age from the pith to show the regressions of each tree and determine the variance explained by age. The logarithm of age gave a better fit of curve than either numerical age or a log-log relationship. The average of linear regressions with logarithm of age explained 71% of the variance (r^2) of tracheid radial diameter based on the average of the 7 tree regressions. The individual regressions and their percentages of explained variance are shown in Fig. 8. The correlations were highly significant. Four trees had nearly 80% explained variance (r^2). A multiple regression analysis, using the data for all years of growth and employing radial growth rate, logarithm of age, and earlywood increment as three factors tested, against radial tracheid diameter showed that age was the most important factor, and the inclusion of the other two factors produced a total explained variance of 74%, only 3% greater than that of age alone. Most of this small increase came from significance of growth rate for one tree. The slopes of the regressions vary among the trees, and a tree with a high initial radial tracheid diameter is not necessarily the highest at a later age. Growth rate was only of minor influence.

When the first 12 years were not included (the approximate period before definite slow-down of growth) the effect of age was greatly decreased. It was the most significant factor in only 2 trees and then only at the 95% level. The analysis

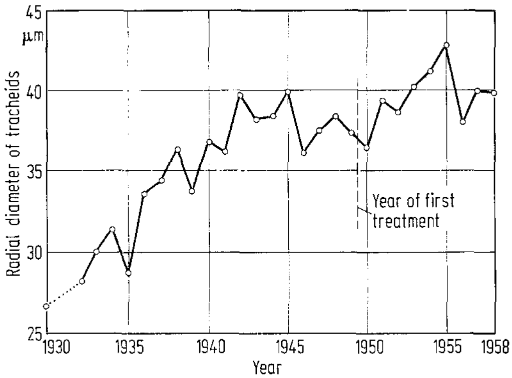

Fig. 7. Radial tracheid diameter by calendar year for the 7 variable-growth trees showing annual fluctuations and before and after plot treatment

showed that none of the factors tested against radial tracheid diameter was very important, either singly or in combination. The average of explained variance for each tree, all factors included, was only 30%, and much of this was not at high confidence levels. Therefore, other undetermined factors not included in the regression analysis have more influence on the moderate increase in radial diameter of tracheids after 12 years of age.

The predicted grand mean of radial diameter after the years of silvicultural treatment when calculated from the trend before treatment was the same (only 0.2 micrometers more) as the grand mean using the regression of all years, and was only 0.3 micrometers more than the grand mean from observed diameter data. This indicates a return to normal radial tracheid width several years after the start of plot treatment when some slowing of growth occurred.

The overall correlation of radial tracheid diameter with total age on a pooled data basis (Fig. 6) was $r = 0.63$ ($r^2 = 40\%$) and when the log of age was used $r = 0.71$ ($r^2 = 50\%$). The regression equation was $\hat{Y} = 23.397 + 11.514 \log X$. Since the change in radial diameter was small during the stimulated growth period, this probably is a fairly true relationship for trees in the plots for this age group. The explained variance of 50% of the pooled data is substantially less than it was for the average of the individual tree correlations which was 71% ($r = 0.84$), because the former includes the differences between means.

The important influence of age during the juvenile period upon radial tracheid diameter of Douglas-fir agrees with investigations on other coniferous species. In general, a rapid increase in radial diameter takes place in the early years of growth. In the present study, growth rate had little influence on radial tracheid

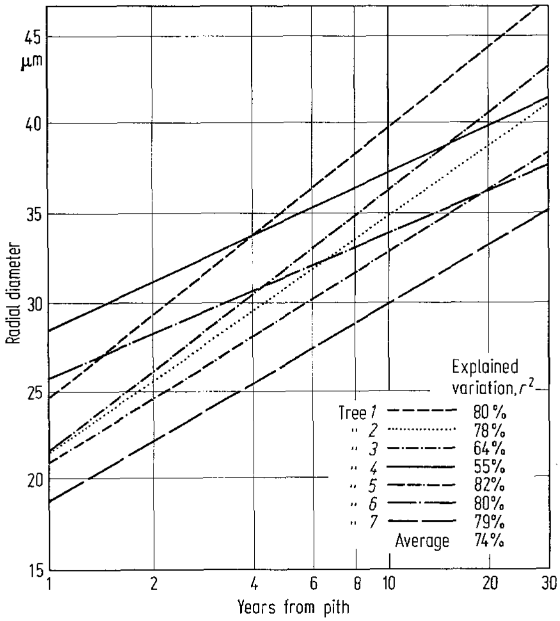

Fig. 8. Within-tree regressions and coefficients of determination, r^2, for radial tracheid diameter and log of age. Some slopes are distinctly different

diameter when tested over the total age span. It should be pointed out, however, that slow growth rates of about 1 mm radius were encountered in this study and none of the material had wide annual rings approaching 1 cm as might be the case with trees from better sites. The relationship with faster average growth remains to be determined.

Tangential tracheid diameter

Although it is customary to measure tangential tracheid diameter at the outer part of the latewood band, a number of measurements in that zone and in the late earlywood led to the conclusion that tangential diameters in the late earlywood were more uniform and more easily measured than in the later latewood. The latter zone, with its greater number of smaller cells toward the end of the growing season made it difficult to accurately decide what cell sizes or cell tips to count.

For comparative purposes, tangential diameter was measured in both late earlywood and late latewood in the same rings across two quadrants of one tree. The tangential diameter of the late earlywood tracheids averaged 2 to 3 μm larger than the latewood tracheids, omitting cell tips.

The relationship between moderate elliptical shape of tree cross sections (15 to 20% diameter variation) and tangential tracheid diameter was determined by measurements in each quadrant of two trees, over the total age span. The differences among quadrants up to age 16 years, approximately, were small, usually 0 to 2 μm. Most of the differences were in the period after plot treatment to stimulate growth. Although different quadrants had different tracheid diameters, the accuracy of the mean tracheid diameter for each year was only slightly increased by measuring the cells in all quadrants rather than across one diameter of two equal radii. Differences could be expected to be less in truly circular cross sections. The variation within a ring in one quadrant was similar to that in other quadrants. For these reasons the extra work of preparing sections for each quadrant was not practical.

The increase in tangential tracheid diameter with age is shown in Fig. 9 for the 7 trees of variable growth. The difference in tree age is represented in the dotted line at the youngest age in this case, and the data are plotted by calendar year to match the time of plot treatment for each tree to show any differences in tangential diameter due to treatment.

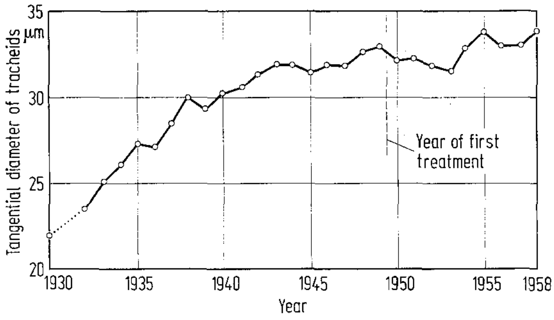

Fig. 9. Tangential tracheid diameter by calendar year for the 7 variable-growth trees. Differences in tree ages are absorbed in the dotted zone at the left

Tracheid diameter increased rapidly from 22 µm in the first ring to about 32 µm in the first 12 to 15 years, then leveled off during the period of retarded growth rate. Some decrease occurred for 4 years after plot treatment but then a recovery of cell diameter took place. The final average cell diameter was only about a micrometer greater than it was in the lower growth period before plot treatment.

The correlation coefficient of tangential tracheid diameter to age using the pooled data of the 7 trees and on a linear basis was 0.79, and the r^2 was 62.6%. The correlation was improved when the log of age used to a coefficient of 0.88 with an explained variance r^2 of 78.1%. The equation is $\hat{Y} = 20.14 + 9.12 \log X$ where $\hat{Y}$ is tracheid tangential diameter and X is age. Probably the correlation would be improved if no great change in growth rate had taken place, but, since the tracheid diameter did not change much, the coefficients of correlation and regression should not be greatly different for uniformly growing trees.

The relation of log of age to tangential diameter within individual trees was excellent. It was highly significant and accounted for an average of 91.5% of the variance within trees. The mean of the correlation coefficients was 0.956. The separate regressions are shown in Fig. 10. Multiple regression showed that growth rate was a second rank factor of significance in 5 of the 7 trees, but even so it added only 1.8 percent to the explained variance of tangential tracheid diameter which already was very high.

When the first 12 years of growth were excluded in the multiple regression analysis, age was still more important than growth rate but now age explained

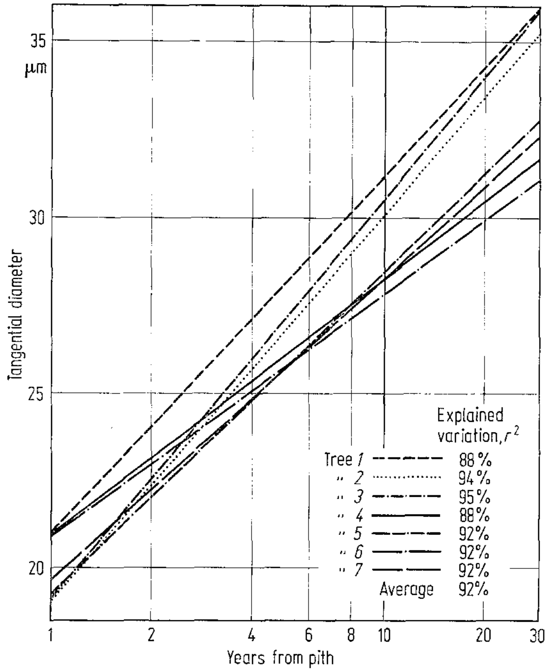

Fig. 10. Tangential tracheid diameter regressions for within-tree variation with logarithm of age

only 33.5% of the variance on the average as compared to 91.5% when the first 12 years were included. Growth rate as a second factor was significant in only 2 trees and added only 9 percent to the total explained variance.

The range of the actual diameter values for the last 2 years (approximately age 30) of each tree was from 30.5 to 35.6 μm with an average of 33.1. For both radial and tangential tracheid diameters, trees No. 4 and 6 had a flatter regression slope than the other trees, and it happened that these trees also had a slower growth rate during the period before plot treatment.

The trend of increasing tangential tracheid diameter outward from the pith in young trees agrees with early work on Douglas-fir [Gerry 1916] and with reports on other species. Likewise, the very small influence of growth rate on tangential diameter agree with most studies on other species.

Tracheid length

The general curve for the relationship between tracheid length and age from pith is shown in Fig. 11. The averages of trees for each year are shown and the last 7 years are plotted by calendar year in order to put all 7 trees on the same time basis with respect to plot treatment. The data of the 4 control trees of almost uniform growth around the time of plot treatment are also plotted to enable some comparison of the two groups.

A linear regression analysis on the pooled data of the 7 trees of variable growth over their total age, including the time of plot treatment, gave a correlation coefficient for tracheid length against age of 0.828 ($r^2 = 68.6\%$). A higher correlation was obtained using the logarithm of age, $r = 0.913$, $r^2 = 83.4\%$. Clearly, the log of age is closely related to tracheid length even when between-tree variation and slight changes in tracheid length due to plot treatment are included.

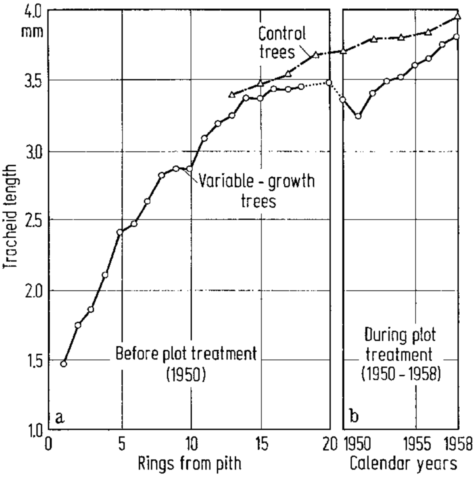

Fig. 11. Tracheid length of both groups of trees as related to age from pith and by changing growth rate due to heavy thinning and fertilization of the one group

The equation for predicting tracheid length from age for these data is $\hat{Y} = 1.32 + 1.63 \log X$.

The graph shows that the decrease in tracheid length during faster growth is temporary and becomes essentially equal to the even-growth trees after a few years.

It was concluded that tracheid length in this sampling of Douglas-fir normally increased rapidly up to approximately 15 years of age after which the rate of increase slowed substantially. Some increase was indicated even near age 30. It would appear that tracheid length after this age, if the trees had not been harvested, would increase at a very slow-rate. Deceleration of growth rate reduced the normal development of longer tracheids as the wood approaches the mature zones. Sudden stimulation of growth caused a quick decrease in length of 0.2 to 0.3 mm; but with continued growth, even before much decrease in rate of growth later on, tracheid length increased toward a maximum which appeared to be normal for that age for this particular tree population.

The data were analyzed on a within-tree basis also which would indicate how well tracheid length is related to age and growth variables when the differences between tree means are removed.

Over the total ages of the trees, the influence of age on latewood tracheid length was highly significant in every tree and the log of age accounted for an average of 92% of the total variance in tracheid lengths ($r^2 = 0.92$, $r = 0.96$). This is the average of the individual tree regression values which are shown in Fig. 12 for the 7 trees of the main experiment. Growth rate was second in importance

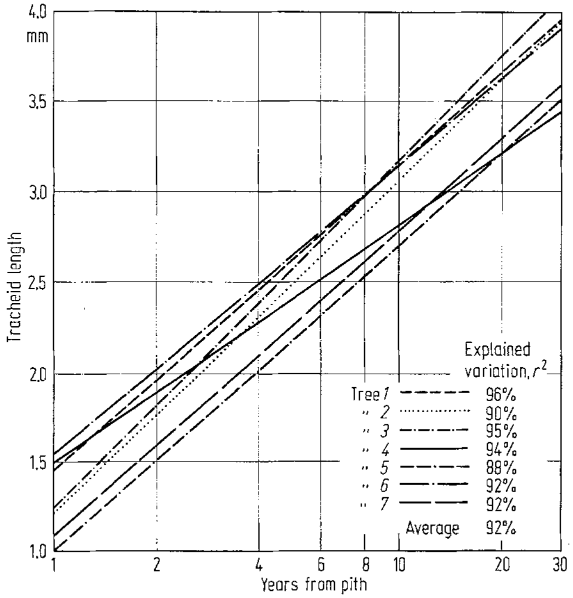

Fig. 12. Within-tree regressions and correlations for tracheid length with log of age. Explained variances are very high, tree 4 has the greatest departure from the other slopes but still a high r^2

and significant in every case, but when it and other variables were included (distance from the pith, latewood width) the additional explained variance averaged only 3 percent; so the added effect of growth rate must be considered very minor mainly because the explained variance due to age was already high. In a later study it was found that tracheid length correlated better with the log of distance from the pith than with actual linear distance but neither was as good as log of age.

When the first 12 years were omitted from the analysis for each tree, the effect of age was greatly reduced and the most significant factors were linear distance from the pith in 4 trees, age in 2 trees, and growth rate in one tree. Growth rate was the most common factor of second importance however. With all factors included (distance, growth rate, age, latewood increase) an average of 71 percent (r^2) of the within-tree tracheid length variance was explained. In Fig. 12 the slopes for each tree were very similar except for tree number 4 and to a lesser extent, number 6 which also had less slope than other trees in radial and tangential tracheid diameters. These had relatively large cell dimensions initially but enlarged at a slower rate to maturity. So the tracheid length in mature wood can be predicted from very young wood in most trees, but not in all.

If 92% of the variation of tracheid length within each of these trees 27 to 31 years old could be explained by the logarithm of age and include the slight dip in the curve associated with induced accelerated growth, then the percent of explained variation should be slightly higher for trees with nearly uniform growth rate for the same age period. The tracheid lengths reported in this study are about 10 percent longer at ages 20 and 30 and about 7 percent longer at age 10 than those reported by Duffield [1964], who used borings from young Douglas-fir in western Washington and Oregon. These results are not necessarily in conflict as his samples included a wide geographical range of samples. He used only the latest portion of the latewood in his study instead of the entire band, as in this study. He reported very diverse patterns in the relation of tracheid length at breast height to rings from the pith, but similar patterns were found among trees within the stand. The slight but continuing increase in tracheid length at age 30 reported herein agrees with the general shape of the curve which he reports. A second degree polynominal curve was applied to his data on rings ten years and older.

Summary

Several wood quality characteristics were studied on Douglas-fir trees from a stand of average age of 30 years on a poor site, high Site V. The test plot had been fertilized and thinned 9 years prior to cutting the trees. Seven of the trees had a slow-growth period for about 5 years prior to plot treatment. For certain parts of the study 4 additional trees were used which had nearly uniform growth during the last 15 years.

1. The dependent variables, radial and tangential tracheid diameters, tracheid length, and percent latewood were more closely correlated to the logarithm of age than to age or to a log-log relationship of the variables.

2. On the variable-growth trees from the treated plot, growth rate was not significantly correlated with total age due to responses to plot treatment.

3. Latewood percentage was quite well correlated with log of age, $r = 0.67$. The within-tree values averaged slightly higher, 0.70, and correlations for the 20 years before stimulated growth were higher yet. When the first 12 years were omitted, earlywood increment was the factor of first importance. Growth rate over the total age was not as important as age. The control trees with uniform growth after the juvenile period tended to have a consistent percentage of latewood.

4. There were indications that a ring width of 1 mm may be a critical value above which increase in growth rate has only a small effect.

5. The use of two radii or quadrants was nearly as good as using four quadrants for measuring percent latewood and cell dimensions.

6. Specific gravity increased with age in all trees to about 16 to 18 years of age.

7. Accelerated growth of 20-year old trees caused a significant decrease in gravity in the first few years but there was recovery after 6 years. There was no significant change in gravity in the trees of uniform growth in the same period.

8. The correlation of specific gravity with percent latewood was 0.63 as compared to 0.52 with age. Multiple correlation caused no substantial improvement of the coefficient. Partial correlation, with the effect of age removed, gave a low correlation between specific gravity and percent latewood.

Analysis of the age-class tree means of these two variables showed the nonconformity of wood less than 4 to 6 years and to some extent the wood formed soon after stimulated growth to a linear regression.

9. The radial diameter of earlywood tracheids increased from the pith outward to about age 17. Growth stimulation shortly after this age caused an increase in diameter of a few micrometers.

10. The pooled data correlation of radial tracheid diameter with log of total age was 0.71 ($r^2 = 50\%$). Within tree correlations averaged 0.84 ($r^2 = 71\%$). Growth rate added very little to the explained variance. The correlation with age in the period after the first 12 years and through the period of stimulated growth was low and sometimes not significant.

11. Tangential tracheid diameter was measured in the late earlywood rather than the late latewood of wood sections because of greater ease of measurement and uniformity of cells. Tangential diameter of late earlywood tracheids averaged two to three μm larger than the tracheids of the latewood.

12. The tangential tracheid diameter in tree discs of moderate elliptical shape was nearly the same in all quadrants to age 16. After plot treatment, differences were greater but the results were almost the same for one diameter of 2 equal radii as for all four radii.

13. Tangential tracheid diameter increased rapidly with age from the pith to about 12 to 14 years then it tended to level off. With stimulated growth, a temporary slight decrease occurred but diameter then slowly increased to normal values.

14. The pooled data correlation of tangential tracheid diameter with log of age was 0.88 ($r^2 = 78\%$). Within-tree correlations averaged 0.96 ($r^2 = 91.5\%$). The first 12 years contributed the most of this close relationship. Growth rate in the years after age 12 had a minor and sometimes non-significant relation to tracheid diameter.

15. Tracheid length was highly correlated with log of age, $r = 0.91$ and $r^2 = 83\%$ (pooled data for 7 trees), even with some decrease in length during part of the stimulated growth period. The greatest change occurs in about the first 15 years. The accelerated diameter growth after about age 20 caused a small but definite decrease in length which subsequently recovered to be equal to projected normal length and to the tracheid length of the trees which had uniform growth after age 15. On within-tree data, log of age accounted for 92% of the variance of tracheid length ($r = 0.96$). Growth rate had a minor added relationship. The age relationship is much less after age 12 when the length begins to level off rapidly. At age 30 there is still some increase in tracheid length.

16. The trees of uniform ring growth showed a steadily increasing tracheid length over the same period of years that the trees of accelerated growth showed their decrease in tracheid length. On this limited sampling, the indication is that thinning or fertilizing by themselves do not cause changes in the wood, but a sudden increase from previous growth rate does cause changes. This important concept needs further work.

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