GENETIC DIFFERENCES IN WOOD TRAITS AMONG HALF-CENTURY-OLD FAMILIES OF DOUGLAS-FIR[1]

M. D. McKimmy and D. D. Nicholas

School of Forestry, Oregon State University, Corvallis 97331

ABSTRACT

Variations in tracheid length and wood specific gravity were analyzed in half-century-old Douglas-fir trees that represent progeny from five half-sib families each from a single parent tree. All of these five families were sampled at three provenance plantations in widely different climatic conditions.

Both plantation (environment) and family (parent in race) had highly significant effects on tracheid length and specific gravity in the three plantations studied.

Progeny from one parent had the longest tracheid length at all three plantations. Progeny from another parent had the shortest tracheid length in all three plantations. Although progeny from one parent had the highest specific gravity in each of the three plantations, progeny from another had the lowest specific gravity in only two of the plantations and next to the lowest in the third.

INTRODUCTION

Considerable interest has developed recently in the relation of wood-growth quality to genetic differences. In this paper, we report the influence of genetic and environmental factors on wood properties, family by family, in a half-century-old study of heredity in Douglas-fir. The study was established by the U.S. Forest Service in 1912, from known female parents. This portion of the investigation on some wood properties of five families on three widely different sites, conducted by the School of Forestry, Oregon State University, is part of a cooperative effort in which the Pacific Northwest Forest and Range Experiment Station is coordinating many aspects of a long-term study.

No general agreement has been reached on which wood property is most important for the evaluation of wood quality, because the desirability of wood properties differs according to specific end use. In general, the literature reveals that specific gravity, tracheid length, fibril angle, cellulose content, lignin content, cell-wall thickness, and extractive content are regarded as important indices of wood quality. We measured tracheid length and specific gravity for our study.

No effort has been made to review the extensive literature on the relation of wood-growth quality to genetic differences. The Forest Biology Committee (1962), Goggans (1962), Stonecypher (1966), and Zobel (1964) have reviewed aspects of the literature in this field.

AREAS SAMPLED

The Douglas-fir trees we studied came from six provenance plantations that were established from known parents. The trees sampled for wood traits were from three of these plantations and were 47 years old at the time of sampling. The plantations were established in 1915-1916 by the U.S. Forest Service, as described by Munger and Morris (1936). We studied only the plantations started in 1915. The seed was collected from 120 different open-pollinated trees that grew in 13 localities in western Washington and Oregon. It was sown in a nursery in 1913, and, when the seedlings were 2 years old, they were outplanted in selected, burned-over areas. Each plantation was laid out by the same planting diagram (Fig. 2), and contained equal numbers of progeny from the same mother tree.

PROCEDURES AND RESULTS

To sample as many trees as possible, we took one 10-mm increment core at breast height from each tree. On the basis of data

[1] Paper 702, School of Forestry, Oregon State University, Corvallis, Oregon 97331.

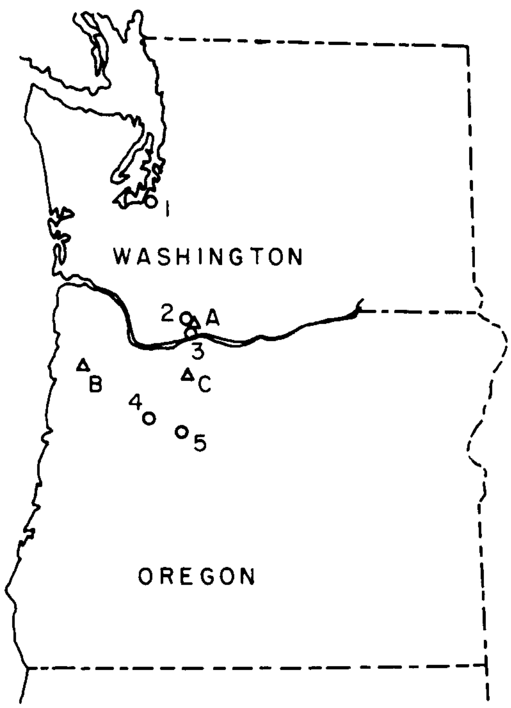

FIG. 1. Seed collection sites (circles) and plantations (triangles): 1, Lakeview; 2, Race Track; 3, Carson; 4, Gates; 5, Santiam; A, Wind River; B, Siuslaw; and, C, Mt. Hood.

previously reported by Dadswell (1957), Dadswell et al. (1961), Echols (1955), Kramer (1957), Wellwood (1952, 1960), and Zobel and McElwee (1958), we assumed that a wood sample outside of about 15 annual rings from the pith in a cross section should give an adequate measure of the specific gravity and tracheid length in the mature portion of the tree. Thus, growth from years 25 (assuming the tree took 10 years to reach breast height) to 47 was sampled, but only the outermost eight annual rings (years 40 through 47) next to the cambium were measured for tracheid length and specific gravity.

Selection of trees

In all three plantations, progeny from a single parent from Carson, Race Track, Lakeview, Gates, and Santiam races were chosen for study. They had been planted in long rows, following the planting pattern shown in Fig. 2. Five of the rows, one from each of the five locations of parent trees, were selected for sampling. Half-sib trees in a given row from a specific mother tree will hereafter be called a family.

We selected progeny for sampling by first dividing each row into units of 10 trees and then selecting the tallest tree from each unit. This provided 10 dominant trees for each family and represented five parent tree locations, which gave a total of 50 dominant trees from each plantation and 150 trees for the entire study. Thus, the mean value obtained for a family in each plantation is the average for 10 progeny grown from seed collected from a single open-pollinated mother tree. The height and diameter of these same trees were measured by personnel at the Pacific Northwest Forest and Range Experiment Station for a growth study. The growth study data were compared with the values for tracheid length and specific gravity obtained in our study.

Maceration and measuring techniques

For the measurement of tracheid length, the three outermost annual rings of each increment core were macerated by the sodium chlorite method of Spearin and Isenberg (1947).

Five slides of macerated fibers were prepared for each tree, and 10 intact tracheids were measured from each slide. This provided a total of 50 tracheids from each tree, which was the number required to provide an accuracy of 0.1 mm at the 5% level of probability. We measured the tracheids with an ampliscope with 27× magnification, similar to the one described by Echols (1959). Both summerwood and springwood tracheids were measured, and the average tracheid length for each tree includes summerwood and springwood tracheids in about equal numbers from each tree.

We determined specific gravity in the five growth rings toward the pith and next to the tracheid length samples (age 40–45), by the method of maximum moisture content as described by Smith (1954). To reduce

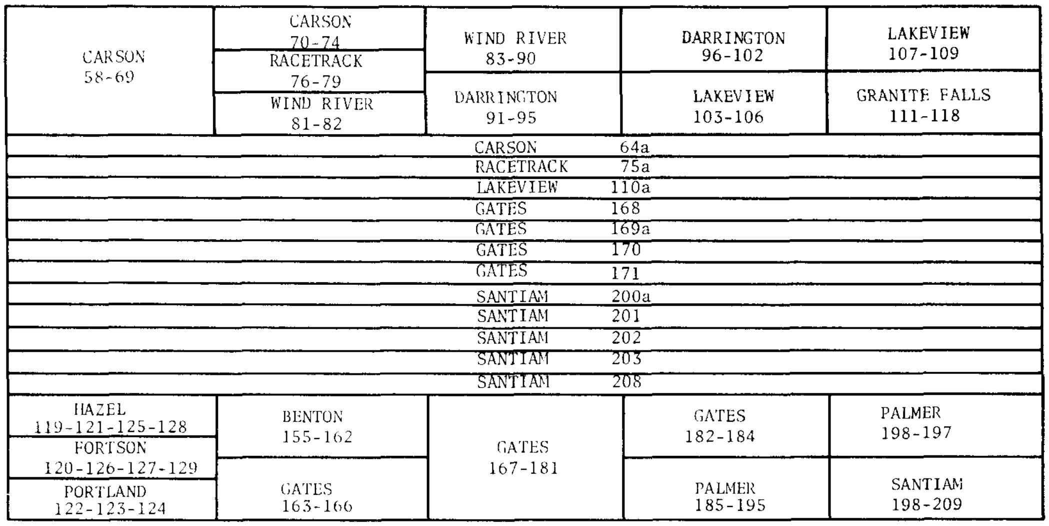

FIG. 2. Planting scheme at each plantation. [a]Trees in this study. Numbers indicate parent trees.

weighing errors, all samples were weighed in glass weighing bottles on a microbalance to an accuracy of 0.1 milligram.

Genetic and environmental effects

The significance of variation in specific gravity and tracheid length among plantations and among families and the interaction between them were tested by a factorial analysis of variance, described by Li (1957). For tracheid length, an individual tracheid was the sampling unit and, as indicated, fifty measurements per core were obtained. The average of these fifty tracheids then comprised an observation for statistical analysis.

Genetic effects in this study were estimated by analyzing the data for consistent differences in specific gravity and tracheid length among families at the three planta-

TABLE 1. *Comparison of average specific gravity of the various parents at three plantations*

Elev. (ft)	Seed source	Plantation			
		Siuslaw	Wind River	Mt. Hood	All
400	Carson	0.483	0.482	0.391	0.452
2,600	Race Track	0.421	0.453	0.401	0.425
100	Lakeview	0.467	0.503	0.431	0.467
950	Gates	0.422	0.484	0.405	0.437
2,800	Santiam	0.489	0.506	0.459	0.485
—	All sources	0.456	0.486	0.417	

Analysis of variance

Source of variation	Degrees freedom	Sum of squares	Mean square	F.
Plantations	2	0.116691	0.058345	19.13**
Source (parent in a race)	4	0.067071	0.016768	5.50*
Plantation × source (Error)	8	0.024399	0.003050	

* Significant at the 5% level of probability.
** Significant at the 1% level of probability.

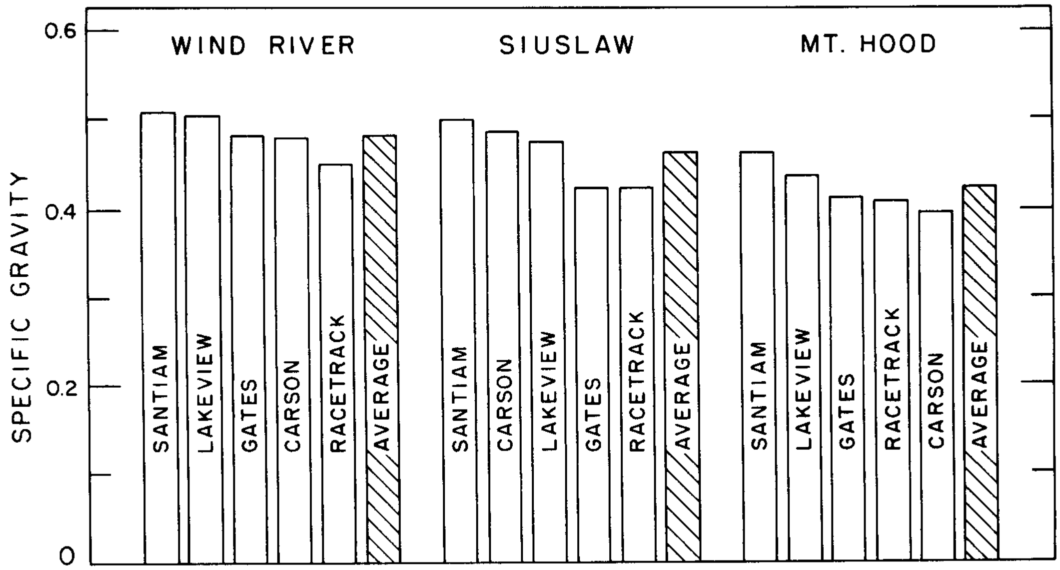

FIG. 3. Comparison of specific gravities of families at three plantations.

tions. A consistent difference of these properties at all plantations among the various families would be an indication of genetic influence. Furthermore, a consistent pattern in the quantitative ranking of the families according to tracheid length and specific gravity would be expected at each plantation if a strong genetic influence is present, because, in this instance, specific genotypes would react similarly at the different locations. It should be pointed out that a consistent pattern in family ranking might be significantly altered by genotype-environment interaction.

Specific gravity

A summary of the above analysis of variance is shown in Table 1 and reveals that

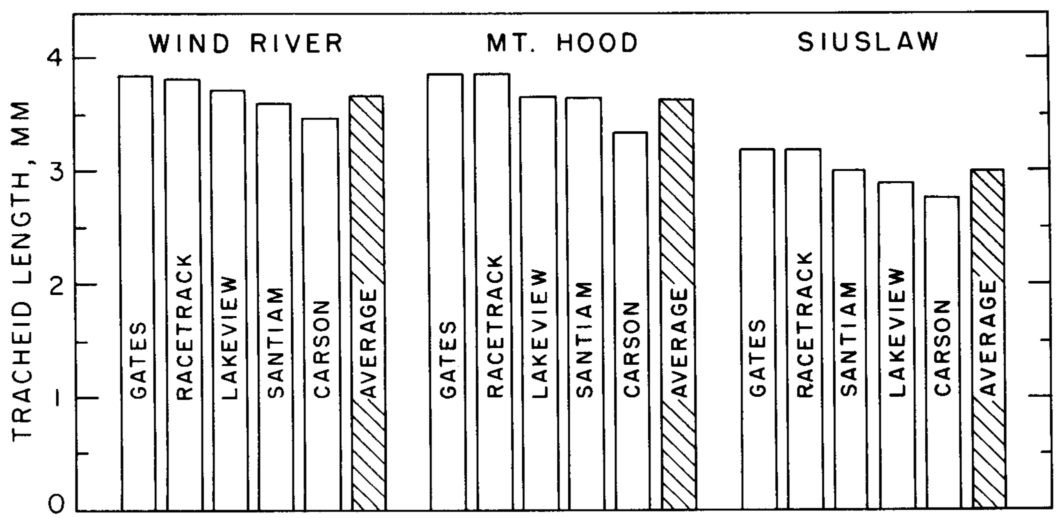

FIG. 4. Comparison of tracheid lengths of families at three plantations.

TABLE 2. *Comparison of average tracheid lengths, in millimeters, of the various parents at three plantations*

Elev. (ft)	Seed source	Plantation			
		Siuslaw	Wind River	Mt. Hood	All
400	Carson	2.8[a]	3.5	3.3	3.2
2,600	Race Track	3.2	3.8	3.8	3.6
100	Lakeview	2.9	3.7	3.6	3.4
950	Gates	3.2	3.8	3.8	3.6
2,800	Santiam	3.0	3.6	3.6	3.4
—	All sources	3.0	3.7	3.6	

[a] Each value is an average of 10 trees and 50 tracheids per tree.

Analysis of variance

Source of variation	Degrees freedom	Sum of squares	Mean square	F.
Plantations	2	13.6776	6.83880	153.54**
Source (parent in a race)	4	3.4423	0.86058	19.32**
Plantation × source (Error)	8	0.3563	0.04454	

** Significant at the 1% level of probability.

the variation in specific gravity of the wood among plantations and families is significant at the 1% level. Table 3 shows the proportion of total variance from specific gravity for the variables in Table 1. This analysis indicates that the environmental component, represented by the among-plantation and error variation, and genetic component, represented by the among-family variation, are both significant factors affecting specific gravity. The interaction between plantation and family specific gravity is significant at the 5% level and indicates that the ranking of families according to specific gravity is not consistent from one plantation to another.

Figure 3 shows the general patterns of variation in specific gravity. As can be seen, the Santiam family consistently averages higher in specific gravity at each plantation, and the Race Track family averages among the lowest in specific gravity at each plantation. Note that, for specific gravity, the ranking of the families was different than it was for tracheid length (Fig. 4). Furthermore, the combined average specific gravity of all families is highest at the Wind River plantation and lowest at the Mt. Hood plantation, again a different pattern from that seen for variation in tracheid length.

Tracheid length

Figure 4 shows the patterns of variation in tracheid length (age 45–47). The average tracheid length for all trees is much shorter at the Siuslaw plantation than at the Wind River and Mt. Hood plantations, illustrating the effect of environment within families. At all plantations, the average tracheid length is longer for the Gates and Race Track families than for the Carson family, illustrating the overriding genetic effect of a parent within a plantation.

The average tracheid length for each family at each plantation and a summary of the factorial analysis of variance are shown in Table 2. This statistical analysis

TABLE 3. *Proportion of total variance because of specific gravity and tracheid length*

Components	Specific gravity (%)	Tracheid length (%)
Plantation	37.4	54.5
Source (parent in a race)	17.0	10.4
Plantation × source	6.0	0
Error	39.6	35.1

TABLE 4. *Evaluation of the effect of growth rate on tracheid length in adjacent rings. Averages are from 70 tracheids measured per ring*

Tree[a]	Ring width narrow[b]	Ring width wide	Tracheid length narrow ring (mm)	Tracheid length wide ring (mm)	Narrow minus wide (mm)
		WIND RIVER PLANTATION			
200-22	53	87	2.9	3.0	–0.1
200-94	26	72	3.4	3.4	0.0
200-94	16	24	3.8	3.7	0.1
169-19	29	118	2.9	3.2	–0.3
169-53	33	49	4.3	4.0	0.3
110-44	35	52	3.7	3.7	0.0
75-23	61	95	3.1	3.1	0.0
75-47	35	52	3.9	3.6	0.3
64-99	19	32	3.6	3.3	0.3
64-77	41	60	3.2	3.0	0.2
Total	348	641	34.8	34.0	0.8
Average	34.8	64.1	3.5	3.4	0.1
		SIUSLAW PLANTATION			
200-46	11	19	3.2	3.1	0.1
200-40	11	20	2.9	2.9	0.0
200-94	20	35	3.1	2.7	0.3
169-40	11	26	3.3	3.2	0.1
169-79	19	30	3.1	3.0	0.1
75-82	21	40	3.1	3.1	0.0
75-21	13	26	3.4	3.2	0.2
64-46	20	30	2.7	2.8	–0.1
64-40	22	46	2.8	2.4	0.4
110-87	16	33	3.1	2.9	0.2
Total	164	305	30.7	29.3	1.4
Average	16.4	30.5	3.1	2.9	0.14

Paired t-test: $t = 3.11$ (significant at the 1% level of probability).
[a] Tree 200—Santiam, 169—Gates, 110—Lakeview, 75—Race Track, 64—Carson.
[b] Values are in units. One hundred units = 0.24 inch.

tested the significance of variation in tracheid length among plantations and among families, and the interaction between them. Because the variation among plantations and among families is significant at the 1% level, the environmental component, represented by the among-plantation variation, and the genetic component, represented by the among-family or source variation, are both important factors affecting tracheid length. The interaction between plantation and tracheid length of the parent is not significant and implies that the quantitative ranking of parents by tracheid length is consistent from one plantation to another. Table 3 shows the proportion of variance from tracheid length for the variables from Table 2.

Tracheid length versus growth rate

Preliminary evaluation of the increment borings indicated that a difference in growth rate existed in the sampling area in various families. Because Goggans (1962) reported that growth rate affects tracheid length, we attempted to evaluate this effect by the method outlined by Kramer (1957). It consists of selecting from each family at two plantations several borings from progeny that exhibited annual rings with a growth rate differential of about 1 : 2 between two adjacent rings. To eliminate possible bias, the sequence was reversed for about half of the samples, with a growth ring differential of about 2 : 1. These two adjacent growth rings exhibiting the growth rate differential were then macerated separately and 70 tracheids, both springwood and summerwood, were measured from each ring.

We evaluated the significance of the effect of growth rate on tracheid length by a paired *t*-test described by Li (1957). All trees for this test from the Wind River and Siuslaw plantations were combined in a single analysis and the results are shown in Table 4. These data show a definite pattern, with an increase in growth rate resulting in a decrease in tracheid length. This supposition is verified by the paired *t*-test, which is significant at the 1% level. This relation is apparently more consistent at the Siuslaw plantation than at the Wind River plantation.

Correlations

We tested possible correlations between specific gravity, tracheid length, tree height, and tree diameter at all three plantations by a linear regression analysis described by Li (1957). For this analysis, all families were combined at each plantation and correlation coefficients were calculated from the error sum of squares, rather than the total sum of squares, which statistically removed the family effect from the correlation coefficients.

A summary of this linear regression analysis is given in Table 5. The strongest relation appears to be between specific gravity and tree diameter. For this relation, the negative correlation coefficients are significant at Siuslaw and Wind River plantations, but not at the Mt. Hood plantation. The relation between tracheid length and tree height shows a significant negative correlation coefficient at the Mt. Hood plantation, indicating that taller trees have shorter tracheids. Other relations are not significant at any other plantation.

DISCUSSION

The rare circumstances of having half-century-old trees, some taller than 100 feet, existing as identifiable families at three locations make the data of unusual significance. Racial differences in specific gravity already have been shown to occur in these plantations (McKimmy 1966).

Genetic and environmental effects

Significant differences shown by analysis of these data leave little doubt that tracheid length and specific gravity are at least partially genetically controlled at the family or source level. The consistent variation of these properties among the various families verifies this assertion.

Table 3 is a simple summary of the analyses of variance in Tables 1 and 2 to show the proportion of total variance in specific gravity and tracheid length for source or family and plantations and the interaction between them. Clearly, Table 3 shows that both plantations and source have a large influence on specific gravity and tracheid length.

Perhaps the most significant finding of this analysis is the consistency with which a long-fibered family (Gates-169) or a short-fibered one (Carson-64) maintains its position in such diverse environments as the 2,000-ft elevation in the Coast Range, the 1,100-ft elevation near the Columbia Gorge, and the 2,600-ft elevation near Mt. Hood. Essentially the same situation prevails for the family with high specific gravity (Santiam-200) and that with low specific gravity (Race Track-75, in two of the three plantations). This is an important finding for future improvement in these traits of trees, because plantations over wide geographic and environmental ranges of any family in future breeding are probably not contemplated.

Another point of interest is the comparison of geographic location of the parent trees and the average tracheid lengths and specific gravities of their families within the plantations studied. The Carson and Race Track sources are from opposite ends of the Wind River Valley, about 13 miles apart. The Gates and Santiam sources are from opposite ends of the Santiam Valley, about 22 miles apart. In all plantations, a con-

TABLE 5. *Correlation coefficients for all variables at three plantations*

	Siuslaw		Wind River		Mt. Hood	
	Specific gravity	Tracheid length	Specific gravity	Tracheid length	Specific gravity	Tracheid length
Specific gravity	1.00	–0.054	1.00	–0.011	1.00	–0.002
Tree height	–0.071	–0.311*	–0.212	+0.097	+0.004	+0.229
Tree diameter	–0.370*	–0.037	–0.445**	–0.056	–0.033	+0.239

*Significant at the 5% level of probability.
** Significant at the 1% level of probability.

sistent difference occurs in tracheid length in the families from parent trees located in the same valley. The same relation is true for specific gravity, although these two traits were not related.

Tracheid length and growth rate

The effect of growth rate on tracheid length has been a subject of considerable controversy over the years. Although the sample size in this experiment is fairly small, an increased growth rate apparently results in slight decrease in tracheid length. Because a growth rate differential of 1 : 2 results in a decrease of only about 0.1 mm in tracheid length, this effect appears negligible.

In a previous study, Kramer (1957) applied the same technique for comparing tracheid length in adjacent rings in loblolly pine and concluded that growth rate had no influence on tracheid length.

Correlations

None of the correlations investigated in this study and shown in Table 5 is consistent. A correlation between two characteristics may be significant at one or two plantations, but not at all three. This discrepancy could possibly be attributable to two factors. First, little biological basis may exist for expecting a correlation; hence, the relation may be a chance one. Second, any relations that are real may be influenced by change in environment from one plantation to another. Furthermore, the data may have been insufficient to provide an adequate basis for the particular factors that were analyzed.

SUMMARY AND CONCLUSIONS

From this study, we drew the following conclusions:

1) Douglas-fir families from individual parents from different seed sources show heritable differences in both tracheid length and specific gravity at age 47 years. A surprising consistency in families with long tracheids or high specific gravity to remain so over all sites occurred, which indicates an overriding genetic effect of parents within a plantation.

2) The influence of both genetics and environment on specific gravity and tracheid length is highly significant.

3) Both specific gravity and tracheid length varied considerably from one plantation to another. Environment caused tracheid length to range from 3.0 to 3.7 mm and specific gravity from 0.42 to 0.49.

4) Increased growth rate resulted in a decreased tracheid length. Though highly significant, this growth rate differential of about 1 : 2 resulted in only about 0.1 mm decrease in tracheid length.

5) Correlations between specific gravity, tracheid length, tree diameter, and tree height did not show a consistent pattern. A correlation between any two characteristics was not significant at all three plantations, and sometimes the correlation coefficient changed sign from one plantation to another.

An expansion of this study is needed so that we can evaluate differences caused by individual parent trees as distinct from racial differences.

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