INTRA-RING VARIATIONS IN MATURE DOUGLAS-FIR TREES FROM PROVENANCE PLANTATIONS[1]

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ABSTRACT

Variations in seven intra-ring characteristics were studied in juvenile and mature wood from two Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] genetic plantations. Samples were collected from 30 families representing 10 provenances with two replicates in each plantation. The following characteristics were determined by X-ray densitometry: earlywood density (EWD), latewood density (LWD), average ring density (RD), earlywood width (EWW), latewood width (LWW), total ring width (RW), and latewood proportion (LWP). Variation patterns were analyzed by two models: (1) families pooled across provenances and (2) provenances and families-within-provenances.

Differences between plantations were significant for all traits except juvenile RD and mature RW and EWD. Variance components associated with families (pooled across provenances) remained the same with stand development and were biased upwards as a result of provenance variation. Genetic variation resulting from provenances was evident for RD and EWD, but (except for LWP) was relatively unimportant for RW parameters. Selection for families within populations can contribute to juvenile RW, as well as to mature RD and LWP.

Keywords: Douglas-fir, intra-ring characteristics, variation among families, variation among provenances.

INTRODUCTION

Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] is a primary North American tree species utilized by the Western forest industry, which is becoming increasingly dependent on young-growth trees for its raw material supply. This transition to young growth is accompanied by a reduction in log size and an increase in the volume of juvenile wood. Thus, new technologies are required in the manufacture of desirable, or at least acceptable, wood products (Zobel 1984). Improvements in processing technology and manufactured products are usually made by increasing production inputs and costs, and/or reducing yield and quality of products. Tree improvement programs that foster growing the best of the forest gene pool under optimal silvicultural regimes can alleviate these problems. Although most tree-breeding programs emphasize fast-growing, better-formed, well-adapted, and pest-resis-

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tant trees, these programs could also select for improved wood properties (Zobel and Talbert 1984). In this connection, a basic understanding of the genetic structure of natural variation in the traits of interest is essential. This requires determination of the relative proportion of variation that is controlled genetically and of changes in the performance of genotypes when trees are grown in different environments.

Effective tree improvement programs generally confine efforts to a few characteristics that contribute to the intended use of the wood produced. Many researchers (e.g., Kellogg 1982), however, have suggested that tree improvement programs might simply select for wood density. Recent development of X-radiographic methods has enabled researchers to refine and provide more detailed measurements of various density and ring width parameters, as well as of complete density profiles. The objective of the work presented here was to determine patterns and magnitudes of variation for seven densitometric intra-ring characteristics expressed in two genetic plantations of known parentage.

MATERIALS AND METHODS

Because most genetic plantations are relatively young, tree breeders usually are unable to estimate genetic variability in mature trees. One of the few sources of mature trees of known parentage is the 1912 Douglas-fir Heredity Study established by the USDA Forest Service (described by Munger and Morris 1936). The genetic stock is based on seed from wind-pollinated families (parent trees). Material for the present study was obtained from these Douglas-fir trees, which are located in western Oregon and Washington, in 1979 (McKimmy and Campbell 1982). The sample consisted of 360 trees representing 30 families grown in two replication blocks in each of two plantations. Material analyzed comprised an extra pair of 12-mm cores from each tree collected by McKimmy and Campbell (1982) at north and south cardinal directions 1.4 m from the ground. Six of the 720 cores were missing and could not be replaced. The two plantations were the Columbia National Forest at Wind River (335 m elevation, 45.25°N latitude) and the Mount Hood National Forest (850 m elevation, approximately 45°N latitude). The 30 families were from 10 provenances (three families per provenance): Darrington, Granite Falls, Hazel, Fortson (northwestern Washington), Lakeview (central western Washington), Carson, Racetrack, Wind River (southwestern Washington), and Gates and Palmar (northwestern Oregon). McKimmy and Campbell (1982) measured only the average density (maximum moisture content method) and ring width of core segments for the 10 rings closest to the pith (juvenile wood) and the 10 rings closest to the bark (mature wood), while our study examined intra-ring characteristics measured by X-ray densitometry.

X-ray densitometry

Ring density and width were determined by direct X-ray densitometry as described in detail by Hoag and McKimmy (1988). The earlywood-latewood boundary in a growth ring was established by a density of 0.5 g/cm^3 in the transition zone. All intra-ring variables were based on this boundary.

To represent the juvenile wood zone, 10 rings that had the same biological age (rings number 6–15 from the pith) were chosen from each core. The mature wood sample was selected to avoid systematic variations attributable to seasonal growth conditions. Because growth rings toward the ends of cores were narrow, intra-ring density profiles could not be resolved accurately with the X-ray densitometer; therefore, growth rings 16–25 from the bark were selected to represent mature wood. The mature and juvenile wood samples were separated by from 7 to 17 rings in the various cores. Nonweighted averages for the following variables were identified for the juvenile and mature wood samples: earlywood density (EWD), latewood density (LWD), average ring density (RD), earlywood width (EWW), latewood width (LWW), total ring width (RW), and latewood proportion (LWP).

TABLE 1. *Analysis of variance format and* F*-tests for families pooled across provenances.*

Source	Degrees of freedom	Mean square designation	Expected mean square[a]	*F*-test
Plantation	1	A	$\sigma^2_e + 2\sigma^2_w + 6\sigma^2_{r(l)\cdot f} + 12\sigma^2_{l\cdot f} + 180\sigma^2_{r(l)} + 360\sigma^2_l$	$F_{plantation} = (A + E)/(B + D)^b$
Replication in plantation	2	B	$\sigma^2_e + 2\sigma^2_w + 6\sigma^2_{r(l)\cdot f} + 180\sigma^2_{r(l)}$	$F_{replication(plantation)} = (B/E)^c$
Family	29	C	$\sigma^2_c + 2\sigma^2_w + 6\sigma^2_{r(l)\cdot f} + 12\sigma^2_{l\cdot f} + 24\sigma^2_f$	$F_{family} = (C/D)^d$
Plantation•family	29	D	$\sigma^2_c + 2\sigma^2_w + 6\sigma^2_{r(l)\cdot f} + 12\sigma^2_{l\cdot f}$	$F_{plantation\cdot family} = (D/E)^e$
Replication (plantation)•family	58	E	$\sigma^2_c + 2\sigma^2_w + 6\sigma^2_{r(l)\cdot f}$	$F_{replication(plantation)\cdot family} = (E/F)^f$
Within plot	240	F	$\sigma^2_c + 2\sigma^2_w$	
Error	360	G	σ^2_c	

[a] Numerals are coefficients of the variance components of the mean squares. The following notations are the variance components of the respective effect: σ^2_c = cores within trees; σ^2_w = within plot; $\sigma^2_{r(l)\cdot f}$ = plot error; $\sigma^2_{l\cdot f}$ = plantation•family; σ^2_f = family; $\sigma^2_{r(l)}$ = replication-within-plantation; σ^2_l = plantation.
[b] With $(A + E)^2/[(A^2) + (E^2/58)]$ and $(B + D)^2/[(B^2/2) + (D^2/29)]$ degrees of freedom.
[c] With 2 and 58 degrees of freedom.
[d] With 29 and 29 degrees of freedom.
[e] With 29 and 58 degrees of freedom.
[f] With 58 and 240 degrees of freedom.

Data analysis

Preliminary analysis indicated that adjustments for age differences in the mature wood data by including ring age as a covariate in the analysis were not necessary (Abdel-Gadir 1991). The analyses of variance for each intraring characteristic employed two models. The first model utilized core averages (714 observations) to test for differences among the 30 half-sib families. The variation was partitioned into: plantation locations, replications within plantations, families (30 plots), family interactions with location and replication, and within plot. The ANOVA format and *F*-tests in terms of expected mean squares are given in Table 1. The second model, used also by McKimmy and Campbell (1982), included additional terms to separate the variance resulting from families into variance attributable to provenances and that attributable to families-within-provenances. These analyses were based on the assumptions of additivity, homogeneous variance, zero correlations, and normally distributed variables. All effects, except provenances, were considered to be random. Because some *F*-tests did not have appropriate denominators, approximate *F*-tests were conducted by synthesizing some of the denominators and degrees of freedom (Snedecor and Cochran 1980).

Components of variance were determined for each trait by equating the mean squares to their expectations. Coefficients of variation (C.V.%) were calculated as the square root of each variance component divided by the trait mean to facilitate comparisons among intraring characteristics and between the two zones. All statistical analyses were carried out using Statistical Analysis System procedures (SAS Institute 1988).

RESULTS AND DISCUSSION

General description of the data

Ranges and averages of X-ray densitometry data were calculated based on tree averages (Table 2). For this purpose, X-ray densities (measured at 9% moisture content) were adjusted to an oven-dry weight/green volume basis (ASTM 1985). Unadjusted data, as well as data reported in Table 2, were used for results of ANOVA. Ring density (RD) in juvenile wood varied from 0.324 to 0.498 g/cm³ and averaged 0.409 g/cm³; in mature wood these values were 0.372, 0.612, and 0.467 g/cm³, respectively. Average number of rings per inch was about 6 in juvenile and 14 in mature wood. These values compare well with those reported by McKimmy and Campbell (1982), even though a different technique was used to measure wood density and ring width. Average wood density values published for coastal Douglas-fir are 0.43 g/cm³ (Drow 1957) and 0.45 g/cm³ (USDA Forest Service 1965). Based on the coefficients of variation (Table 2), ring width parameters (EWW, LWW, RW, and LWP) exhibited considerably more variation than did ring density parameters (EWD, LWD, and RD).

Within a juvenile growth ring, wood density increased from earlywood to latewood by an average of 0.27 g/cm³ (81% of EWD). Within a mature growth ring, the average difference between earlywood and latewood density was 67% of the EWD value. In the juvenile zone, average earlywood width was 2.5 times latewood width. When the trees reached maturity, widths of earlywood and latewood were, on average, almost equal.

Based on the juvenile wood values, average increases from juvenile to mature wood were about 16% (0.067 g/cm³) in RD, 11% (0.053 g/cm³) in EWD, and 58% in LWP. By comparison, LWD averaged a 1.5% change. These results suggest that the variation in wood density between juvenile and mature wood was caused primarily by differences in the width of latewood relative to that of earlywood and by differences in earlywood density. The difference in wood density between the two zones is comparable to that known for conifers (Bendtsen 1978), but appears minor in comparison with the findings of Senft et al. (1985). In a study of 60-year-old Douglas-fir, they reported a difference of 32% between the average wood density of the first 15 rings and that of the rings formed thereafter. Results of the present study clearly demonstrate that, in terms of wood density, variation within growth rings is much larger than that between an average ring in juvenile wood and an average ring in mature wood.

TABLE 2. *Simple descriptive statistics for the intra-ring characteristics in juvenile and mature wood.*

Variable[a]	Minimum	Mean	Maximum	C.V.%
Juvenile wood sample				
Earlywood density	0.255	0.327	0.412	6.8
Latewood density	0.490	0.594	0.691	7.1
Average ring density	0.324	0.409	0.498	7.5
Earlywood width	1.46	2.90	5.66	26.0
Latewood width	0.43	1.20	2.53	34.0
Total ring width	2.30	4.09	7.65	26.0
Latewood proportion	0.146	0.293	0.474	18.7
Mature wood sample				
Earlywood density	0.282	0.362	0.442	7.1
Latewood density	0.501	0.603	0.750	8.0
Average ring density	0.372	0.476	0.612	9.7
Earlywood width	0.37	0.95	1.75	28.6
Latewood width	0.38	0.80	1.67	29.3
Total ring width	0.94	1.76	2.96	22.1
Latewood proportion	0.264	0.464	0.690	19.4

[a] Densities are in g/cm³ and widths are in mm.

Analysis of variance

Mean squares and the results of the F-tests obtained from both models are listed in Tables 3 (juvenile wood) and 4 (mature wood). Differences were checked for significance at both $\alpha = 0.05$ and $\alpha = 0.01$. Figure 1 presents graphically the coefficients of variation based on the square roots of the variance components. All error deviations from the second model (i.e., replications within plantations, main plot error, subplot error, and sampling error) were grouped into one error term.

Provenance and family stability.—Although the magnitudes of the variance components of the interactions were in some instances as great as, or greater than, the main effects (Fig. 1), all F-tests of the family-by-location effect were nonsignificant (Tables 3 and 4). Also, in no instance was the provenance-by-location effect statistically significant. Thus, there was no tendency for provenance or family ranking to dif-

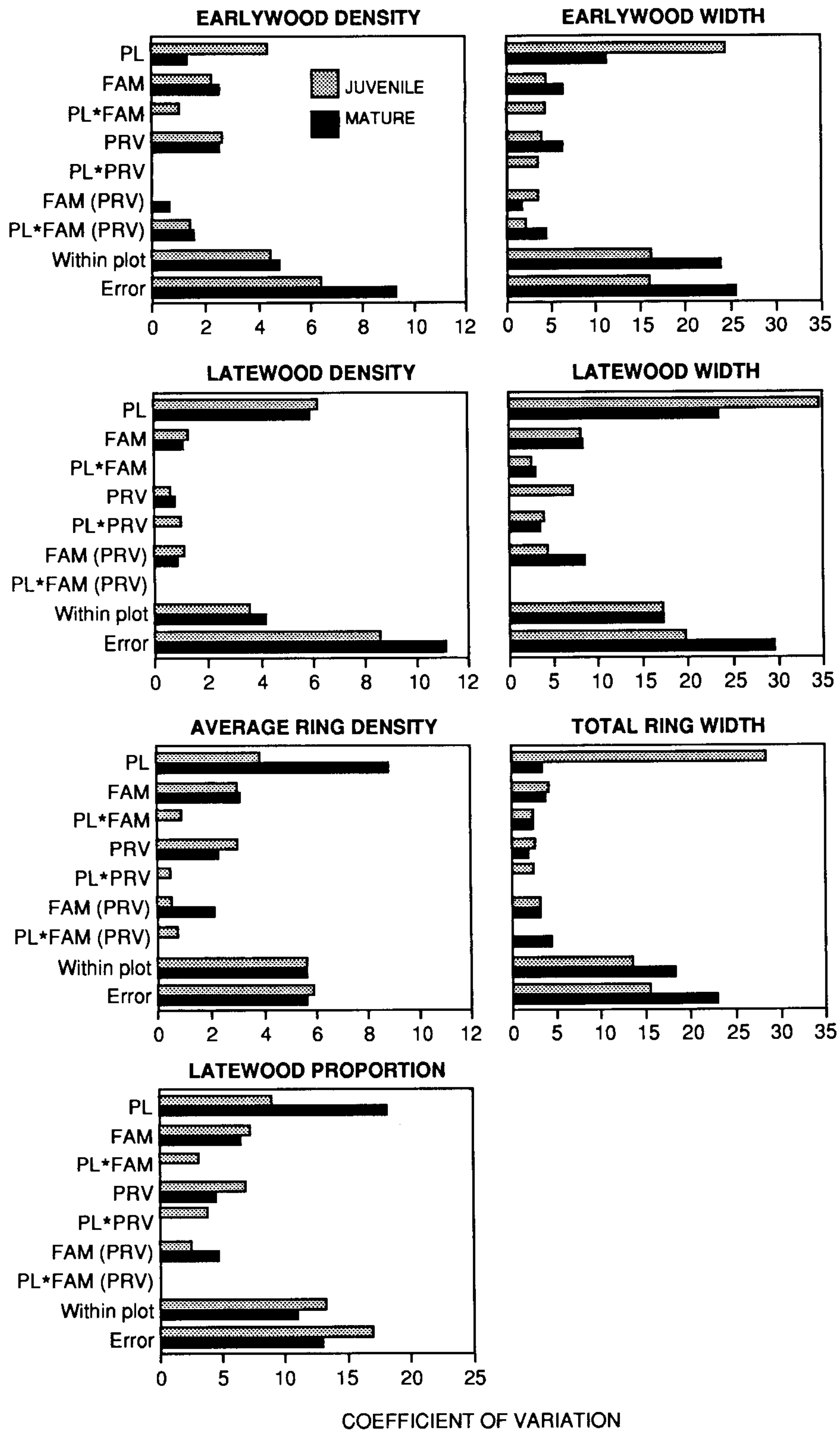

FIG. 1. Coefficients of variation based on variance components for intra-ring variables in juvenile and mature wood. (PL = plantation, FAM = family, PRV = provenance.)

TABLE 3. *Analysis of variance in juvenile wood samples: mean squares and significance tests.*[a]

Source	EWD[b]	LWD	RD	EWW	LWW	RW	LWP
Plantation	13.52*	36.19**	4.94^{ns}	132.75**	252.86**	298.77**	19.32**
Replication in plantation	7.70**	3.61*	6.08**	0.54^{ns}	0.62^{ns}	0.08^{ns}	2.79^{ns}
Family	2.57**	1.53^{ns}	3.61**	1.84^{ns}	2.35**	1.16^{ns}	2.97**
Plantation•family	1.29^{ns}	0.88^{ns}	1.19^{ns}	1.34^{ns}	1.25^{ns}	1.20^{ns}	1.30^{ns}
Replication (plantation)•family	1.03^{ns}	1.33^{ns}	0.84^{ns}	0.94^{ns}	0.91^{ns}	0.98^{ns}	0.97^{ns}
Provenance	5.75**	1.18^{ns}	4.98**	1.50^{ns}	2.49*	1.34^{ns}	3.34**
Plantation•provenance	0.73^{ns}	1.35^{ns}	1.07^{ns}	1.33^{ns}	1.34^{ns}	1.22^{ns}	1.63^{ns}
Replication (plantation)•provenance	1.18^{ns}	1.25^{ns}	0.59^{ns}	1.19^{ns}	1.22^{ns}	1.53^{ns}	0 51^{ns}
Family (provenance)	0.65^{ns}	1.89^{ns}	1.14^{ns}	1.42^{ns}	1.60^{ns}	1.61^{ns}	1.31^{ns}
Plantation•family (provenance)	1.45^{ns}	0.57^{ns}	1.10^{ns}	1.08^{ns}	0.89^{ns}	0.96^{ns}	0.94^{ns}
Replication (plantation)•family (provenance)	0.98^{ns}	1.24^{ns}	0.97^{ns}	0.89^{ns}	0.85^{ns}	0.84^{ns}	1.15^{ns}
Within plot	1.62**	2.02**	3.77**	3.99**	3.50**	3.54**	3.50**

[a] ** = significant at the 0.01 level; * = significant at the 0.05 level; and ns = not significant at the 0.05 level.
[b] EWD = earlywood density, LWD = latewood density, RD = average ring density, EWW = earlywood width, LWW = latewood width, RW = total ring width, and LWP = latewood proportion.

fer between plantations. Both strong and weak genotype-by-environment interactions have been reported for Douglas-fir (McKimmy 1966; Cown and Parker 1979). McKimmy and Campbell (1982) found significant plantation-by-provenance interaction for juvenile RW and plantation-by-family interaction for juvenile RD. In the present study, these interactions, although not statistically significant, were as large as the corresponding genetic main effect (Fig. 1). Calculation of the provenance and family means in each of the two plantations revealed that these interactions had a slight effect on ranking of the means and a larger effect on the scale of mean differences.

In the early growth years, the variance component due to the plantation-by-provenance interaction for growth-rate parameters was greater than that for wood-density parameters. When the trees reached maturity, this interaction term diminished to zero (or small negative values) in all traits except LWW (Fig. 1). However, McKimmy and Campbell's (1982) results suggest that the relative importance of this interaction for RW continues to increase with stand development.

Planting locations.—The analysis of variance indicated significant differences between the two plantations for most of the characteristics studied (Tables 3 and 4). In juvenile wood, plantation variance accounted for more than 55% of the total variation in ring width and its components (EWW and LWW), and for from 6% (RD) to 45% (LWD) of the total variation in ring density parameters. In the mature wood sample, the relative contribution of plantations showed an average of 28% and ranged from about 2% (RW) to above 52% (RD and LWP).

The warmer environment at Wind River produced the wider juvenile RW and the higher mature RD ($P \leq 0.01$). This result is in accordance with the findings of McKimmy and Campbell (1982). Wind River also produced the wider LWW and higher LWP and LWD during both juvenility and maturity (Tables 3 and 4), but there were no significant plantation differences in mature RW and juvenile RD. The results of mature RD and LWP support the findings of Lassen and Okkonen (1969) that wood density and latewood proportion are greater in trees from low elevations than in trees from high elevations. Also, dates of bud burst in the two plantations show that growth starts in Wind River several weeks earlier than at Mt. Hood. Kennedy (1970) found that the greater specific gravity of early-flushing Douglas-fir trees was associated with earlier initiation of latewood formation.

The effect of replication blocks probably re-

TABLE 4. *Analysis of variance in mature wood samples; mean squares and significance tests.*[a]

Source	EWD[b]	LWD	RD	EWW	LWW	RW	LWP
Plantation	2.18^{ns}	24.02*	178.67**	11.47*	23.03*	1.81^{ns}	157.54**
Replication in plantation	2.23^{ns}	3.13^{ns}	1.63^{ns}	1.47^{ns}	7.26**	3.36^{ns}	1.29^{ns}
Family	2.75**	1.26^{ns}	4.49^{ns}	1.61^{ns}	2.36^{ns}	1.33^{ns}	4.82^{ns}
Plantation•family	0.79^{ns}	0.80^{ns}	0.83^{ns}	0.92^{ns}	1.21^{ns}	1.09^{ns}	0.71^{ns}
Replication (plantation)•family	1.46*	1.32^{ns}	0.88^{ns}	1.09^{ns}	1.11^{ns}	1.09^{ns}	1.02^{ns}
Provenance	3.67**	1.26^{ns}	2.76*	1.97^{ns}	0.93^{ns}	1.12^{ns}	2.44*
Plantation•provenance	0.43^{ns}	0.70^{ns}	0.82^{ns}	0.69^{ns}	1.19^{ns}	0.79^{ns}	0.93^{ns}
Replication (plantation)•provenance	3.03**	1.69^{ns}	0.86^{ns}	1.62^{ns}	1.03^{ns}	1.57^{ns}	1.15^{ns}
Family (provenance)	1.09^{ns}	1.24^{ns}	2.54*	1.03^{ns}	2.70**	1.26^{ns}	3.23**
Plot•family (provenance)	1.44^{ns}	0.93^{ns}	0.88^{ns}	1.16^{ns}	0.97^{ns}	1.28^{ns}	0.69^{ns}
Replication (plantation)•family (provenance)	0.90^{ns}	1.08^{ns}	0.92^{ns}	0.91^{ns}	1.10^{ns}	0.92^{ns}	0.98^{ns}
Within plot	2.65**	1.76**	3.50**	5.22**	2.77**	4.47**	3.23**

[a] ** = significant at the 0.01 level; * = significant at the 0.05 level; and ns = not significant at the 0.05 level.
[b] EWD = earlywood density, LWD = latewood density, RD = average ring density, EWW = earlywood width, LWW = latewood width, RW = total ring width, and LWP = latewood proportion.

flects micro-environmental variations (e.g., soil nutrients, competition) within plantation locations. During early years of growth, ring density parameters (EWD, LWD, and RD) are the only traits to be influenced by replications within plantations. During maturity, ring width parameters (LWW and RW) are the characteristics most likely to reveal nonuniformity within plantation sites (Tables 3 and 4).

Expressing the square root of plantation variance for RD and LWP as a ratio of their means (Fig. 1) provides evidence that the increase in the absolute size of the plantation variance with advanced stand development was not simply the result of increasing means. This increasing importance of the plantation effect from the juvenile to mature period was accompanied by a decrease in the cumulative error in LWP, but not in RD. The coefficients of variation (Fig. 1) show that, even after accounting for the decline in the mean values of RW, EWW, and LWW from juvenile to mature wood, plantation variance decreased. This decline was, in all instances, accompanied by a comparable rise in the sum of error deviations. For LWD, the magnitudes of the plantation variance and the coefficients of variation in juvenile and mature wood were the same (Fig. 1), because LWD means in the two zones differed only slightly (Table 2).

Genetic parameters.—The distinctiveness of the family and provenance groupings reflects the strength of the genetic effect. The analysis of variance showed significant variability among the 30 half-sib families for all traits ($P \leq 0.05$) in the juvenile wood zone (Table 3), except for EWW and RW ($P \approx 0.07$) and LWD ($P \approx 0.10$). When families were grouped by their geographic origins (provenances), none of the traits in the juvenile wood exhibited significant differences ($P \leq 0.05$) among families-within-provenances; only LWD and RW showed a slight tendency ($P \approx 0.08$ and 0.10, respectively) to differ among families-within-provenances. At the same time, differences among provenances were statistically significant ($P \leq 0.05$) for EWD, RD, LWW, and LWP. These results, taken together, might suggest that, when the effect of provenances was removed, the remaining variation in juvenile wood traits due to families (within provenances) failed to reach an acceptable level of significance. In other words, the significant difference established among the 30 families for these traits was caused by differences among families belonging to different provenances, rather than by families within the same provenances.

In the mature wood zone (Table 4), variation among the 30 families was significant for EWD, RD, LWW, and LWP. When families were grouped into provenances, the following results were obtained: provenances significantly influenced EWD, RD, and LWP, but not LWW; and families-within-provenances significantly influenced RD, LWW, and LWP, but not EWD. These results suggest that, in mature wood, the significant variability among the 30 families (1) for EWD was caused by variation among families belonging to different provenances; (2) for LWW was caused by variation among families belonging to the same provenances; and (3) for RD and LWP was caused by differences among families representing different provenances, as well as families-within-provenances.

These conclusions about the family effect can be substantiated by a closer look at the relative variance components (coefficients of variation) of the 30 families, provenances, and families-within-provenances (Fig. 1). For example, the relative family components of variance for juvenile EWD (significant at $P = 0.006$) and for mature EWD (significant at $P = 0.004$) were about 2.3 and 2.5%, respectively. When the provenance effect was accounted for in the analysis, almost all the variation in EWD among the 30 families appeared to be based on provenances; the families-within-provenances contributed nothing to the total variation in juvenile EWD and only about 0.5% to that in mature EWD. Similar results were established for juvenile RD. This means that, for the above traits, estimates of the variance components associated with the 30 families were biased upwards when provenances were confounded into families. In contrast, partitioning of the family component of variance for mature LWW (Fig. 1) revealed that provenances contributed nothing to the variation in this trait; the genetic variation was entirely the result of families-within-provenances. Other characteristics varied between these extremes; for example, the relative variance component due to families-within-provenances for juvenile RW was about 1.4 times that due to provenances. Variation in mature RD and LWP among the 30 families was divided almost equally between the provenances and families-within-provenances (Fig. 1).

The results of RD in juvenile wood conflict with the findings of Bastien et al. (1985) who, working in 14-year-old provenance trials in France, reported that genetic variability was much higher at the family than at the provenance level. Such discrepancies can be attributed to differences in both the populations and the environments under study. The possibility exists also that the nonsignificance of the family-within-provenance effect, which was evident for some traits in the present study, resulted from the small number of families-within-provenances involved, which limited variation and degrees of freedom. A significant family-within-provenance effect was detected only where the signals were extremely strong with reference to the plantation by family-within-provenance interaction, which was used as the error term for the *F*-test. Although a larger sample of families-within-provenances is needed before final conclusions can be made, these results indicate different architectures of genetic variation for the various intra-ring components. Apparently, forest trees within provenances had differentiated genotypes in response to the micro-environments surrounding individual trees, as well as to the means and extremes of the macro-environments in which they were found (Campbell 1979). These findings differ from those of Cown and Parker (1979), who worked in five widely separated 17-year-old provenances and reported nonsignificant provenance effects for wood density. Their work supported the hypothesis that the plasticity of Douglas-fir is so great that genetic adaptations often do not occur.

Ignoring the geographic sources, the coefficient of variation due to the 30 families remained almost the same between juvenile and mature wood for all seven traits (Fig. 1). This was not the case when families were grouped by their provenances. No general trend existed among the RW components. Whereas in EWW the coefficient of variation for provenance increased and that for family-within-provenance decreased from juvenile to mature wood, the opposite was true in LWW and LWP. Consequently, the genetic structure in RW remained more or less unchanged with advancing stand development (Fig. 1). Although the effect of families-within-provenances on RW didn't change with age, the importance of this source of variation in mature wood seems to be overshadowed by the relatively large variance associated with the families-within-provenances interaction.

The RD components, EWD and LWD, behaved similarly. Coefficients of variation of both provenances and families-within-provenances remained remarkably similar during the juvenile and mature periods. The genetic structure in average RD followed the trend of LWP rather than that of its components (EWD and LWD); differences among families-within-provenances increased from the juvenile to the mature period, and those among provenances decreased slightly (Fig. 1). McKimmy and Campbell (1982), whose mature wood sample consisted of the 10 rings just to the outside of those used in this study, concluded that the genetic structure for wood density and ring width did not vary appreciably between juvenile and mature wood.

Within plots.—The analysis of variance showed significant heterogeneity among trees-within-families for all traits (Tables 3 and 4). The estimated variance components associated with trees-within-plots accounted for an average of 29% and ranged from 14.6% (juvenile LWW) to 54.4% (mature RW) of the total variation. Because all trees within a plot had a mother tree in common, these differences were the result of the genotypes of the male parents and variations in micro-habitat within plots. Variability among trees-within-plots was generally more pronounced in RW than in RD components (Fig. 1). The within-plot variance for wood density parameters and for LWW and LWP did not differ between the juvenile and mature periods (Fig. 1), thus indicating that differences among trees remained unchanged with advanced age. In contrast, the importance of this source of variation for RW and its major component, EWW, increased from the juvenile to the mature period.

The variation among cores-within-trees accounted for an average of 25.6% and ranged from 12.6% (juvenile RW) to 43.4% (mature LWD) of the total variation. The magnitudes of these subsampling variances reflect circumferential variation plus errors of measurements; they were by far the largest component of the cumulative error deviation shown in Fig. 1. The variation among trees-within-plots was, except for LWD, greater than that within trees.

Provenance means.—The provenances included in the study were from the Pacific Coast region, a population known to consist of one variety of Douglas-fir. The analysis of variance revealed that differences among provenance means were significant for EWD, RD, and LWP in both juvenile and mature wood samples, and for LWW only in the juvenile sample (Tables 3 and 4); for these traits the provenances accounted for from 2.5 to 13.3% of the total variance. Table 5 lists the provenance means for these traits and the results of the Fisher Protected Least Significant Difference test.

The results clearly demonstrate the excellent performance of the Lakeview provenance during the juvenile period. This provenance not only ranked the highest for LWW, RD, and LWP, but also had values that were separated by a wide margin from those of the other provenances. During early years of growth, provenance means for RD ranged from 0.396 to 0.436 g/cm^3. The overall difference in RD was 10% (0.040 g/cm^3), and that between the overall mean and the highest value was about 7% (0.027 g/cm^3). Such differences are not as small as they might seem if the large area over which selection efforts are applied and the volume of wood produced during the entire rotation are considered. Mean differences for LWW and LWP were even greater. For these two traits the difference between the last- and first-ranked provenances was about 27%. These results indicate that some improvement in the quality of juvenile wood can be achieved by provenance selection. Kellogg (1982) pointed to the

TABLE 5. *Provenance (P) means and results of the Fisher Protected Least Significant Difference test for earlywood density, average ring density, latewood width, and latewood proportion in juvenile and mature wood.*

Earlywood density				Average ring density				Latewood width		Latewood proportion			
P[a]	Juvenile	P	Mature	P	Juvenile	P	Mature	P	Juvenile	P	Juvenile	P	Mature
2	0.340A	2	0.375A	5	0.436A	5	0.500A	5	1.40A	5	0.343A	5	0.518A
1	0.336B	5	0.372A	2	0.424B	2	0.493A	2	1.28B	2	0.313B	2	0.494B
5	0.334CB	1	0.370BA	1	0.418C	1	0.479B	10	1.27CB	1	0.308B	1	0.477C
7	0.331CD	7	0.365BC	7	0.409D	7	0.475CB	1	1.23CB	7	0.291C	7	0.458D
3	0.328ED	3	0.360DC	3	0.406D	9	0.475CB	9	1.21CD	3	0.289C	9	0.458D
8	0.326E	6	0.360DC	9	0.405D	10	0.474CB	3	1.15ED	9	0.286DC	10	0.458D
9	0.321F	8	0.358D	8	0.404ED	6	0.469C	4	1.14E	8	0.280DCE	6	0.455ED
6	0.320GF	9	0.356D	10	0.399EF	3	0.469C	8	1.11E	10	0.277DE	3	0.453ED
10	0.318GF	10	0.354D	4	0.398F	8	0.468C	7	1.10E	6	0.273E	8	0.441EF
4	0.316G	4	0.346E	6	0.396F	4	0.459D	6	1.10E	4	0.272E	4	0.428F

[a] Provenances are: 1 = Carson, 2 = Race Track, 3 = Wind River, 4 = Darrington, 5 = Lakeview, 6 = Granite Falls, 7 = Hazel, 8 = Fortson, 9 = Gates, and 10 = Palmer.

huge change in product value associated with a 2% change in raw-material density.

During the mature period, significant variation occurred in RD among provenance means. The means for Lakeview and Race Track were significantly higher and that for Darrington was significantly lower than were means for the other provenances. Differences between the lowest and highest and between the mean and highest mature wood values were of the same magnitudes as were found in the juvenile wood. Similar results were obtained for LWP. Moreover, for average RD and LWP, the top four provenances in mature wood showed exactly the same ranking as existed in juvenile wood. Similarly, ranking of the top five provenances according to EWD differed only slightly between juvenile and mature wood. Within these sampling zones, rankings of provenance means for RD and LWP were exactly the same.

The above results and results from previous studies (McKimmy 1966; McKimmy and Campbell 1982) provide strong evidence of provenance genetic variation in coastal Douglas-fir wood density. If radial growth is highly correlated with volume growth, then any improvement in wood density that can be obtained by provenance selection would be a bonus over normal production, because no significant difference exists in radial rate of growth among provenances.

No definite relationship of any of the above traits (EWD, RD, LWW, and LWP) to altitudinal distribution of the provenances was found. For example, Race Track, Wind River, and Palmer, which are high-elevation provenances, ranked respectively second, fifth, and eighth for juvenile wood density and latewood proportion. In juvenile and mature wood, Race Track had the highest EWD and Palmer had the second lowest EWD. In addition, no definite relationship was found between intra-ring characteristics and latitudinal distribution of the provenances. For juvenile RD and LWP, the southernmost provenance, Carson, ranked sixth and the most northerly provenance ranked fourth. The same two provenances ranked fifth and fourth for mature RD and LWP. The provenance with the highest RD, Lakeview, is midway between the high- and low-latitude provenances. Similar results were found for EWD. However, provenances from similar geographic origins behaved relatively similarly during the juvenile period. For example, the three progenies originating from the Wind River Valley ranked second, third, and fifth for RD and LWP; the four provenances from the Stillaquamish Valley were tailing the lists of RD, LWW, and LWP. The environments within which the sampled seed sources evolved apparently did not have a strong environmental gradient. This resulted in an ecotypic pattern of genetic variation rather than a cline. All provenances were from the western slopes of the Cascade Mountains except Lakeview, which outperformed the rest of the provenances in most of the studied traits.

CONCLUSIONS

The plantation-genotype interaction was found to be of little importance, if any; both provenances and families were stable over locations and showed approximately the same ranking in Wind River and Mount Hood. Progenies included in this study displayed great variation in the properties analyzed within and among trees. Although this variation appears to be controlled to a great extent by environmental conditions, genotype also has a strong influence on tree development.

Differences in wood density between the juvenile and mature wood zones are governed mainly by variations in the structure of wood produced during the early months of the growing season (EWD) and by the rate of growth towards the end of the season (LWW and LWP). Planting site influences all intra-ring characteristics except juvenile RD, mature RW, and EWD. The lack of significance of the plantation effect on juvenile RD and mature RW is the result of an outweighing effect of their components. Considerable genetic variation exists among families (when confounded into their geographic origins) for almost all the traits in juvenile wood, as well as for RD, EWD, LWW, and LWP in mature wood.

The results further show two genetic components, related to provenances and families-within-provenances, to the variation in some of the intra-ring variables studied. Provenance influences ring density but not ring width in both juvenile and mature wood, and family-within-provenance influences RW only during juvenility and RD only during maturity. No definite trend is present for either the wood-density or the growth-rate parameters. The dominant feature of genetic variation for EWD, LWW, and LWP during the juvenile period and for EWD during the mature period is the provenance variation. For juvenile LWD and mature LWW, the dominant feature of genetic variation is the family-within-provenance variation. In other traits the two components of genetic variability are almost equal; they are either both significant as in mature RD and LWP, or both insignificant as in juvenile EWW and mature LWD.

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