GENETIC VARIATION IN THE AGE OF DEMARCATION BETWEEN JUVENILE AND MATURE WOOD IN DOUGLAS-FIR[1]

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ABSTRACT

Variation in the age of demarcation between juvenile and mature wood based on wood density was studied in 180 Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) trees. Ring density profiles were generated from X-ray densitometry of increment cores from each of 3 randomly selected trees from each of 30 wind-pollinated families (parent trees) grown in 2 replication blocks. The families represented 10 provenances (3 families per provenance). Two boundary points were determined: the age at which a significant change occurred in the slope of the density-age relationship (using piecewise regression techniques), and the age at which species average density was reached. The period of juvenile wood production ranged from 11 to 37 years among the trees sampled. Most of the variation was among trees-within-plots; however, significant differences among families-within-provenances indicated that the period of juvenile wood production for this population of Douglas-fir was under appreciable genetic control.

Keywords: Douglas-fir, genetic variation, juvenile-mature wood demarcation, wood density.

INTRODUCTION

Many studies on variation in wood properties have shown a definite radial pattern in the wood of coniferous trees that is frequently described as juvenile and mature wood. These wood types are produced from normal physiological growth processes (Larson 1962) and are expected in each tree. The properties of juvenile wood (Thomas 1984; Krahmer 1986) generally have an unfavorable effect on the use of wood and wood-based products (Kellogg 1982; Senft and Bendtsen 1984; Maloney 1986; Megraw 1986).

Understanding the factors that affect how long juvenile wood is produced by a tree species could lead to methods to shorten that period. Megraw and Nearn (1972) conjectured that juvenile wood production in 16- to 18-year-old Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) trees was prolonged by treatments that increased crown vigor. Clark and Saucier (1989) reported that the transition from juvenile to mature wood for slash and loblolly pine in the southeastern United States was influenced by environmental factors related to geographic location rather than to initial planting density.

Genetic manipulation of juvenile wood production should also be considered. Apparently, genetic variation in the specific gravity of juvenile wood in Douglas-fir is sufficient to warrant improvement by breeding (McKimmy and Campbell 1982; King et al. 1988; Abdel-Gadir et al. 1993). However, in addi-

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tion to breeding trees with improved juvenile wood properties, it may be possible to breed for shorter periods of juvenile wood production (Loo et al. 1985). Ladrach (1986) indicated that the age (ring number from pith) of attaining mature wood properties varies considerably among trees, and he proposed using this variation to make mass selections for tree improvement programs. Burdon and Harris (1973) suggested that the pith-to-bark wood density gradient could be controlled by clonal selection in radiata pine. Loo et al. (1985) furnished conclusive evidence that the age of attaining mature wood based on wood density and fiber length is genetically controlled in loblolly pine.

Genetic control of juvenile wood formation in Douglas-fir had not been thoroughly studied. The objectives of this work were to: (1) investigate the extent and nature of genetic influence on a statistically determined index point (age) in the phase transition for wood density from juvenile to mature wood in Douglas-fir, and (2) examine the correlation between this index point (age) and selected wood properties in juvenile and mature wood samples.

MATERIALS AND METHODS

Materials used were part of a sample collected from Douglas-fir trees for previous studies (McKimmy and Campbell 1982; Abdel-Gadir et al. 1993). Two increment cores extracted at breast height were available from each of 180 trees. The trees were growing in two blocks in the Wind River plantation in Washington (lat. 45°15′N, 335 m elev.), which was established as part of a genetic experiment in 1912 (Munger and Morris 1936). Increment cores were taken from three trees grown from the seeds of each seed parent tree. Our sample was drawn from 30 wind-pollinated families (female seed parent trees), 3 from each of 10 provenances (seed sources; the growing sites on which the female parents evolved). Four of the provenances were from the Stillaquamish River drainage in northwestern Washington (Darrington, 152 m elev.; Granite Falls, 122 m elev.; Hazel, 274 m elev.; and Fortson, 152 m elev.; approximately lat. 48°N); three were from the Wind River drainage in southwestern Washington (Carson, 122 m elev.; Racetrack, 793 m elev.; and Wind River, 335 m elev.; approximately lat. 45°30′N); one was from central western Washington in the Puget Sound Trough (Lakeview, 31 m elev.; lat. 47°N); and two were from northwestern Oregon (Gates, 290 m elev.; and Palmar, 610 and 914 m elev.; lat. 45°12′ and 45°48′N, respectively).

Ring density measurements (at 9% moisture content) for each increment core were made with a direct scanning X-ray densitometry system (Hoag and McKimmy 1988; Hoag and Krahmer 1991). The ring density profiles were averaged for the 2 cores from each of the 180 trees. A previous report (Abdel-Gadir and Krahmer 1993) documented the applicability of piecewise regression analysis to characterize the variation of wood density with age (ring number from pith), and to objectively estimate an age of maturity. In this study, piecewise regression (Neter et al. 1989) was fitted to data from the age with the lowest wood density in the juvenile wood zone up to age 50 from the pith. This procedure identifies an index point (age) in the phase transition for density from the juvenile wood zone to the mature wood zone. This index point is called the age of demarcation in this report.

Two piecewise regression models were used; one assumed a slow (gradual) transition at the age of demarcation (Eq. 1), and the other (Eq. 2) assumed a rapid (abrupt) transition (Abdel-Gadir and Krahmer 1993):

$$Y_i = \beta_0 + \beta_1 X_i + \beta_2 D_i (X_i - X_{i*}) + \epsilon_i \qquad (1)$$

$$Y_i = \beta_0 + \beta_1 X_i + \beta_2 D_i (X_i - X_{i*}) + \\ + \beta_3 D'_i + \epsilon_i \qquad (2)$$

where

Y_i = wood density of individual rings,
β_0 = intercept of the regression line of the juvenile zone,
β_1 = slope of the regression line of the juvenile zone,

β_2 = difference between the slopes of the regression lines for mature and juvenile wood,
β_3 = the difference in expected values of wood density (Y_i) for the two regression segments at the age of demarcation (X_{i*}),
X_i = ring ages, from the one with lowest wood density to 50,
X_{i*} = age of demarcation (ring age after which the density-age slope changes),
D_i = 1 if $X_i > X_{i*}$ (ring ages in the mature wood zone); 0 if otherwise (ring ages in the juvenile wood zone),
D'_i = 1 if $X_i > X_{i*}$ (ring ages in the mature wood zone); 0 if otherwise (ring ages in the juvenile wood zone), and
ϵ_i = independent, normally distributed random error term.

Because the demarcation was not known, both models were repeatedly fitted to each of the 180 data sets; in each iteration, one of the X_i values was used as the age of demarcation (X_{i*}). The regression results were retained if the regression coefficients were statistically significant at the 0.05 probability level, if the slope of the mature wood line was zero or positive and less than that of the juvenile wood ($\beta_1 + \beta_2 \geq 0$ and $\beta_2 < 0$), and, in rapid transitions, if the abrupt change in density at the age of demarcation was positive ($\beta_3 \geq 0$). The residual sums of squares produced by all admissible regressions were then evaluated for each tree profile to determine the model and index point (age of demarcation) combination that was best supported by the data (had the smallest error mean square (MSE)).

The age at which ring density started to increase above the species average density for Douglas-fir (0.45 g/cm³) (USDA Forest Service 1965) was also determined.

Analyses of variance for a random model were performed to test the significance of provenance and family-within-provenance related effects on the demarcation age, slope of the density-age regression line for juvenile wood (β_1), difference between the slopes of the regression lines for mature and juvenile wood (β_2), slope of the mature wood line ($\beta_1 + \beta_2$), and the age of species average density:

$$Y_{ijkl} = \mu + b_k + p_j + (bp)_{kj} + \\ + f_i + (bf)_{ki} + e_{3jkl} \qquad (3)$$

where

Y_{ijkl} = the observation of tree I of family i within provenance j in block k,
μ = overall mean,
b_k = effect of block k,
p_j = effect of provenance j,
$(bp)_{kj}$ = interaction of block k and provenance j (block error),
f_i = effect of family i within provenance j,
$(bf)_{ki}$ = interaction of block k and family i within provenance j (plot error), and
e_{ijkl} = the normally and independently distributed random error associated with the ijklth tree.

Because a direct *F*-test could not be made for the provenance effect, the approximate test procedure of Snedecor and Cochran (1980) was used to synthesize mean squares with the same expected values, except for the effect of provenance. Variance components for the sources of variation were also estimated. Correlation coefficients were calculated to assess the relationship between the age of demarcation and age of species average density, and between each of these ages and averages of intra-ring properties in juvenile wood (rings 6 to 15 from the pith) and mature wood (rings 10 to 20 from the bark) samples. Seven intra-ring properties were examined: average ring, earlywood, and latewood densities; total ring, earlywood, and latewood widths; and percent latewood. All analyses used the Statistical Analysis System package (SAS Institute Inc. 1988).

RESULTS AND DISCUSSION

The age of demarcation between juvenile and mature wood ranged from 11 to 37 years among the sampled trees; the average was 25, with a standard deviation of 5 years. This wide range indicates broad phenotypic variability.

TABLE 1. *Analysis of variance: mean squares and significance tests.*[a]

Source of variation	Degrees of freedom	Age of demarcation	β_1[b]	β_2[c]	$\beta_1 + \beta_2$[d]	LOGIT-R[e]	Age of acceptable density
Block	1	170.14**	88.06**	39.98$^+$	9.82$^+$	22.11**	25.69ns
Provenance	9	103.38$^+$	16.79ns	16.57ns	2.51ns	33.72*	128.63ns
Block × Provenance	9	15.81ns	8.05ns	10.02ns	1.31ns	1.66ns	48.05$^+$
Family-within-Provenance	20	48.79*	12.82ns	14.56ns	2.15$^+$	14.52*	47.87*
Block × Family-within-Provenance	20	20.94ns	17.41*	16.92*	1.04ns	6.89	22.87ns
Within plot	120	15.28	9.11	9.69	1.39	—	31.85

[a] ** = significant at the 0.01 level; * = significant at the 0.05 level; $^+$ = significant at the 0.10 level; ns = not significant at the 0.10 level.

[b] Slope of juvenile wood line.

[c] Difference between the slopes of juvenile and mature wood lines.

[d] Slope of mature wood line.

[e] The ratio of abrupt to gradual transitions in trees/plot; log-transformed data.

Analysis of variance results are summarized in Table 1. The age of demarcation was sensitive to differences in growing conditions between replication blocks ($P = 0.01$). Genetic variation among the 30 families was partitioned into effects due to provenances (seed sources) and effects due to families-within-provenances (parent trees). The interactions of replicates by provenances (block error) and families-within-provenances (plot error) were not significant, suggesting that genotypes performed similarly in the replicate blocks. However, while there was not sufficient power in the test to indicate significant differences for the interaction of replicates by families-within-provenances for age of demarcation, β_1 and β_2 were statistically significant, indicating caution in concluding similarity of genotype performance.

The age of demarcation differed significantly in provenances and families-within-provenances ($P = 0.08$ and 0.03, respectively). Mean ages ranged from 21.6 (Racetrack) to 28.9 (Gates) years for provenances and from 17.1 to 29.8 years for families. Results from this study indicate that establishing improved plantations of Douglas-fir based on selection of genotypes with short juvenile-wood production periods may be feasible. Similar results were obtained for loblolly pine (Loo et al. 1985). The width of the juvenile zone is a function of the growth rate of the tree when wood is formed in the vicinity of the pith. The proportion of juvenile wood in the stem is related to the growth rate, rotation age, and age of demarcation. Our results indicate that it is possible to genetically control the number of years that juvenile wood is produced and thereby control the proportion of juvenile wood by means other than suppressing tree growth during juvenile wood production.

Although the slope of the density-age relationship for juvenile wood (β_1) and the difference between the slopes for juvenile and mature wood (β_2) did not differ among genetic sources of variation, the regression slope for mature wood ($\beta_1 + \beta_2$) varied among families-within-provenances ($P = 0.055$) (Table 1). β_1 and β_2 were sensitive to microsite differences between replication blocks ($P = 0.009$ and 0.08, respectively); this sensitivity, however, varied among families-within-provenances (interaction significant at $P = 0.017$ and 0.035, respectively). The rate that wood density increased with age appears to be based on genetic and environmental responses in mature wood, but on an environmental response that varies among families in juvenile wood.

Of the trees sampled, 38.5% exhibited an abrupt transition (Eq. (2)) in the values of wood density from juvenile to mature wood. The ratio of abrupt to gradual transitions in trees per plot was analyzed with a model similar to Eq. (3), except for the within-plot effect, on log-transformed data $\{Y = \log_e[(P + 0.05)/(1.5 - P)]\}$. Because the ratio varied among provenances ($P = 0.06$) and families-within-provenances ($P = 0.05$) (LOGIT-R; Table 1), differences in the other profile criteria were tested between trees with and without an abrupt tran-

TABLE 2. *Means and standard errors (SE) for the types of transition between juvenile and mature wood.*

Type of transition	Age of demarcation		β_1[b]		β_2[c]		$\beta_1 + \beta_2$[d]	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Gradual	25.32	0.43	8.65	0.27	7.22	0.28	1.43	0.11
Abrupt	26.06	0.70	5.82	0.44	4.60	0.45	1.21	0.17
P-value[a]	0.37		0.0001		0.0001		0.30	

[a] The probability of rejecting the hypothesis that the means are equal.
[b] Slope of juvenile wood line.
[c] Difference between the slopes of juvenile and mature wood lines.
[d] Slope of mature wood line.

sition in the density profiles. Analysis results showed that trees with a gradual transition at the boundary point had demarcation ages and mature wood regression slopes similar to the trees with an abrupt transition (Table 2). Trees with a gradual transition had higher rates of density increase in juvenile wood (β_1) and greater differences between the slopes of juvenile and mature wood lines (β_2) than those with an abrupt transition (Table 2).

The age of demarcation estimated by regression defines juvenile wood as the zone of maximum variability in wood density with respect to age; mature wood starts when the slope of the density-age relationship is significantly reduced. For practical purposes, it is meaningful to set a boundary between the two zones based on wood property values that are acceptable for the intended end uses. Unfortunately, such values are scarce in the literature, even for thoroughly investigated properties such as wood density. In this study, the average wood density for coast Douglas-fir (0.45 g/cm^3) (USDA Forest Service 1965) was considered acceptable for both current and predicted end uses, and was hence used to delineate the zone of less satisfactory wood. The age at which this species average density was reached ranged from 1 to 37 years among trees; the average was 19, with a standard deviation of 6 years. The analysis of variance (Table 1) revealed significant differences in the age of acceptable density among families-within-provenances ($P = 0.04$). Variation among provenances was not significant ($P = 0.17$), probably because provenances showed differences approaching significance from one replication block to the other ($P = 0.07$ for block X provenance interaction).

Variance estimates and their standard errors are listed in Table 3. The variance component due to within-plots (σ^2_e) was clearly the major source of variation in all traits. It contributed 56% (for demarcation age) to 81% (for slope

TABLE 3. *Variance component (V.C.) estimates and standard errors (SE).*

Variance[a]	Age of demarcation		β_1[b]		β_2[c]		$\beta_1 + \beta_2$[d]		LOGIT-R[e]		Age of acceptable density	
	V.C.	SE	V.C.	SE	V.C.	SE	V.C.	SE	V.C.	SE	V.C.	SE
σ^2_r	1.715	1.54	0.889	0.80	0.322	0.37	0.095	0.09	0.682	0.60	0.000	0.326
σ^2_p	3.318	2.63	0.740	0.57	0.495	0.59	0.005	0.08	4.072	2.53	3.043	3.372
σ^2_{rp}	0.000	1.03	0.000	0.69	0.000	0.74	0.030	0.07	0.000	0.73	2.887	2.402
σ^2_f	4.643	2.67	0.000	1.09	0.000	1.12	0.187	0.12	3.815	2.42	4.302	2.666
σ^2_{rf}	1.887	2.20	2.764	1.79	2.409	1.75	0.000	0.12	6.890	2.08	0.000	2.670
σ^2_e	15.278	1.96	9.115	1.17	9.690	1.24	1.392	0.18	—	—	31.856	4.078

[a] σ^2_r, σ^2_p, σ^2_{rp}, σ^2_f, σ^2_{rf}, and σ^2_e are variance components for block, provenance, block error, family-within-provenance, plot error, and within-plot, respectively. Negative estimates are shown as zero.
[b] Slope of juvenile wood line.
[c] Difference between the slopes of juvenile and mature wood lines.
[d] Slope of mature wood line.
[e] The ratio of abrupt to gradual transitions in trees/plot; log-transformed data.

of mature wood line) of the total phenotypic variation. This variance reflects genetic variation among trees-within-families and deviations induced by microenvironmental differences among the planting sites. Differences in early height growth among trees may also have contributed to this variance. All trees were sampled at breast height, and if they reached sampling height at different ages (as would be inferred from the report by Namkoong et al. 1972), the wood material near the pith would have been produced in different growing seasons and conditions in separate trees.

Genetic variance components due to families-within-provenances (σ^2_f) were relatively high, positive, and exceeded their standard errors for the age of demarcation, slope of mature wood line, and age of acceptable density (Table 3). For the age of demarcation and age of acceptable density, families-within-provenances accounted for 18% and 10%, and provenances accounted for 13% and 7%, respectively, of the total variance within provenances ($\sigma^2_{w-p} = \sigma^2_p + \sigma^2_{rp} + \sigma^2_f + \sigma^2_{rf} + \sigma^2_e$). The proportion of variation attributable to both families and provenances was greater for the age of demarcation than for the age of acceptable density. Nevertheless, the ratio of family-within-provenance variance to provenance variance was identical (1.4) for both ages, which indicates similar patterns of genetic structure for these boundary points. The magnitude of this ratio and the *F*-test results (Table 1) reveal that the genetic differentiation in response to the average environment at each provenance location was slightly less important than in response to microhabitat of the parent trees. The former determinant would result in reduced within-provenance variation and the latter would favor the maintenance of a variety of genotypes within provenances (Hamrick 1976). However, examining provenance effect in a single test environment, as in this study, might underestimate the provenance variance; any single test environment would allow the expression of only part of this genetic variation (Campbell 1979).

The total phenotypic variance within families-within-provenances was estimated as $\sigma^2_{w-f} = \sigma^2_f + \sigma^2_{rf} + \sigma^2_e$. The intraclass correlation ratio ($r_i = \sigma^2_f/(\sigma^2_f + \sigma^2_{rf} + \sigma^2_e)$) measures resemblance among individuals in a family. The ratios for the age of demarcation, slope of mature wood line, and age of acceptable density were 0.21, 0.12, and 0.11, respectively. These estimates indicate that there was a positive correlation between responses by individual trees within a family and surrounding conditions. It can be assumed that σ^2_f approximates ⅓ of the additive variance (Campbell 1979), and the ratio can be multiplied by 3 to obtain an approximate heritability estimate. Such values are sufficiently large to be useful for tree breeding programs. However, these results were based on data from only a few families grown in a relatively uniform environment and should be extrapolated with care.

Correlation coefficients based on individual trees (n = 180) and on overall family means (n = 30) are given in Tables 4 and 5, respectively. Most tree-based, phenotypic correlations for the age of demarcation had small coefficients; the strongest correlation was between the age of demarcation and the age of acceptable density ($r = 0.38$) (Table 4). Trees with high juvenile wood density (rings 6 to 15 from the pith) tended to have shorter periods of juvenile wood production ($r = -0.28$) and reached acceptable density at younger ages ($r = -0.78$). No relationship was found between juvenile ring width and either of the boundary ages (Table 4). The rate of density increase in rings 6 to 15 was poorly correlated with the age of demarcation ($r = -0.30$) and moderately correlated with the age of acceptable density ($r = -0.41$).

The weak tree-based correlations between the age of demarcation and juvenile wood properties, and the intercorrelations between these properties make it difficult to precisely predict the age of demarcation in individual trees. There was also no relationship between this age and intra-ring properties in mature wood (rings 10 to 20 from the bark). The correlations were significant between the age of acceptable density and all the mature wood

TABLE 4. *Correlation coefficients based on individual trees ($n - 1 = 179$). Significance probabilities of correlations are given beneath the coefficients.*

	Age of demarcation	β_1[a]	β_2[b]	$\beta_1 + \beta_2$[c]	Age of acceptable density
Age of acceptable density	0.38 0.0001	−0.26 0.0004	−0.22 0.0028	−0.10 0.1759	—
Correlations with intra-ring properties in juvenile wood					
Ring density	−0.28 0.0002	0.03 0.7318	0.02 0.8256	0.02 0.7476	−0.78 0.0001
Earlywood density	−0.17 0.0263	−0.11 0.1410	−0.13 0.0879	0.05 0.4865	−0.52 0.0001
Latewood density	−0.21 0.0053	0.18 0.0177	0.18 0.0149	−0.02 0.7948	−0.51 0.0001
Ring width	−0.01 0.9043	0.16 0.0281	0.16 0.0338	0.01 0.9116	0.06 0.4534
Earlywood width	0.09 0.2385	0.14 0.0648	0.14 0.0698	<0.01 0.9871	0.31 0.0001
Latewood width	−0.20 0.0059	0.13 0.0713	0.13 0.0919	0.02 0.8051	−0.50 0.0001
Percent latewood	−0.28 0.0012	0.01 0.8696	0.01 0.8477	−0.01 0.9336	−0.72 0.0001
Density-age slope in rings 6–15	−0.30 0.0001	0.15 0.0428	0.13 0.0860	0.06 0.4500	−0.41 0.0001
Density-age intercept in rings 6–15	0.08 0.3061	−0.17 0.1179	−0.10 0.1695	−0.03 0.6503	−0.16 0.0343
Correlations with intra-ring properties in mature wood					
Ring density	−0.09 0.2198	0.32 0.0001	0.28 0.0002	0.10 0.1818	−0.72 0.0001
Earlywood density	0.10 0.1751	−0.05 0.5456	−0.06 0.4575	0.03 0.6864	−0.29 0.0001
Latewood density	−0.20 0.0063	0.34 0.0001	0.31 0.0001	0.07 0.3354	−0.50 0.0001
Ring width	−0.04 0.5525	−0.05 0.5089	−0.02 0.8027	−0.08 0.2710	0.02 0.8287
Earlywood width	−0.03 0.7001	−0.15 0.0483	−0.11 0.1368	−0.09 0.2139	0.30 0.0001
Latewood width	−0.05 0.5090	0.08 0.3051	0.09 0.2161	−0.05 0.5362	−0.32 0.0001
Percent latewood	0.02 0.8247	0.23 0.0031	0.19 0.0106	0.07 0.3400	−0.60 0.0001

[a] Slope of juvenile wood line.
[b] Difference between the slopes of juvenile and mature wood lines.
[c] Slope of mature wood line.

properties (except ring width), but weaker than the corresponding correlations in juvenile wood (Table 4).

Most family-based coefficients for correlations between either age of demarcation or age of acceptable density and juvenile wood properties were 2 to 3 times higher than the respective tree-based coefficients (Tables 4 and 5). When family structure was considered, the correlation between the age of demarcation and juvenile wood density was negative and moderate ($r = -0.56$) (Table 5). The correlation between family age of demarcation and age of acceptable density was on the same order, apparently as a result of a strong relationship between the age of acceptable density and juvenile wood density ($r = -0.86$). Both boundary ages were negatively correlated with the

TABLE 5. *Correlation coefficients based on overall family means ($n - 1 = 29$). Significance probabilities of correlations are given beneath the coefficients.*

	Age of demarcation	β_1[a]	β_2[b]	$\beta_1 + \beta_2$[c]	Age of acceptable density
Age of acceptable density	0.58	−0.31	−0.17	−0.33	—
	0.0010	0.0964	0.3738	0.0710	
	Correlations with intra-ring properties in juvenile wood				
Ring density	−0.56	0.08	−0.03	0.27	−0.86
	0.0013	0.6906	0.8652	0.1451	0.0001
Earlywood density	−0.51	−0.04	−0.15	0.29	−0.71
	0.0042	0.8528	0.4414	0.1202	0.0001
Latewood density	−0.23	0.10	0.09	0.03	−0.40
	0.2267	0.5821	0.6403	0.8734	0.0270
Ring width	0.11	0.42	0.44	−0.10	>−0.01
	0.5613	0.0207	0.0145	0.6114	0.9840
Earlywood width	0.32	0.33	0.38	−0.18	0.34
	0.0817	0.0792	0.0360	0.3299	0.625
Latewood width	−0.37	0.31	0.24	0.14	−0.66
	0.0439	0.0975	0.1943	0.4714	0.0001
Percent latewood	−0.51	0.09	0.01	0.22	−0.78
	0.0037	0.6194	0.9714	0.2480	0.0001
Density-age slope in rings 6–15	−0.45	0.36	0.20	0.38	−0.64
	0.0125	0.0537	0.2984	0.0396	0.0001
Density-age intercept in rings 6–15	0.01	−0.30	−0.23	−0.17	−0.03
	0.9392	0.1014	0.2263	0.3693	0.8826
	Correlations with intra-ring properties in mature wood				
Ring density	−0.23	0.35	0.17	0.45	−0.77
	0.2199	0.0571	0.3831	0.0133	0.0001
Earlywood density	−0.26	0.25	0.10	0.37	−0.56
	0.1696	0.1836	0.6053	0.0461	0.0012
Latewood density	−0.06	0.19	0.12	0.18	−0.43
	0.7594	0.3249	0.5707	0.3294	0.0179
Ring width	−0.08	>−0.01	<0.01	−0.02	−0.13
	0.6576	0.9821	0.9882	0.9250	0.4813
Earlywood width	0.09	−0.22	−0.10	−0.27	0.32
	0.6425	0.2536	0.5924	0.1455	0.0840
Latewood width	−0.21	0.18	0.09	0.21	−0.49
	0.2660	0.3338	0.6211	0.2614	0.0058
Percent latewood	−0.23	0.31	0.14	0.41	−0.73
	0.2143	0.0922	0.4525	0.0242	0.0001

[a] Slope of juvenile wood line.
[b] Difference between the slopes of juvenile and mature wood lines.
[c] Slope of mature wood line.

slope of the density-age relationship in the juvenile wood sample (Table 5). These associations suggest that breeding for increased juvenile wood density may shorten the juvenile wood production period.

Of the juvenile wood properties studied, ring density had the strongest family correlation with both age of demarcation and age of acceptable density. Each of these boundary ages was negatively correlated with latewood width and positively correlated with earlywood width; consequently, there was no apparent relationship between either of the ages and total ring width in the juvenile wood sample (Table 5). This suggests that the period of juvenile wood production is independent of radial growth rate in the juvenile wood zone. Because none of the correlations between the age of demarcation and intra-ring properties of the mature wood was significant (Table 5), selection against a prolonged juvenile period may reduce variability across the stem without lowering wood density or radial growth rate in mature wood in this population. Families with higher rates of density increase from the age of minimum density to the demarcation age (β_1) appeared to have wider rings of the juvenile wood ($r = 0.42$) and higher wood density in the mature wood ($r = 0.35$) samples. However, there was no correlation between β_1 and ring density of the juvenile wood or ring width of the mature wood samples (Table 5).

A separate analysis was conducted to determine how well the ages of demarcation and acceptable wood density of families can be predicted with data from rings 6 to 10 from the pith. Correlations between these ages and ring data (not shown here) were only slightly weaker than the corresponding correlations with data from rings 6 to 15 (Tables 4 and 5). Independent variables considered in stepwise multiple regression analyses were average values of intra-ring properties, and intercepts and slopes from simple regressions of each of these properties on age. The best single predictor of the age of demarcation in families was the rate of ring density change with age, which explained about 24% of the variation. The addition of ring density significantly improved prediction (adjusted $R^2 = 30\%$) and the response equation was:

$$\mathrm{DA} = 51.9 - 0.056(\mathrm{RD}) - \\ - 0.33(\mathrm{RD\text{-}SLOPE}) \qquad (4)$$

where

DA = age of demarcation,
RD = ring density (kg/m^3),
RD-SLOPE = rate of ring density change with age (kg/m^{3}year).

The maximum predictable proportion of the variance of the demarcation age from significant regression variables ($P \leq 0.05$) was 34% (adjusted R^2); the independent variables were the intercept of the density-age regression line, and the slopes from regression of earlywood density, latewood density, and percent latewood on age. About 50% of the variation in the age of acceptable density could be explained by variation in density of rings 6 to 10 from the pith. Up to 60% of the variance within this age range could be explained by regression of age of acceptable density on ring density and on the rate of change with age of either ring density or percent latewood. The response equations were, respectively:

$$\mathrm{ADA} = 72.7 - 0.11(\mathrm{RD}) - \\ - 0.33(\mathrm{RD\text{-}SLOPE}) \qquad (5)$$

$$\mathrm{ADA} = 78.6 - 0.12(\mathrm{RD}) - \\ - 0.197(\mathrm{LWP\text{-}SLOPE}) \qquad (6)$$

where

ADA = age of acceptable density,
LWP-SLOPE = rate of change in percent latewood with age (%/year).

These multiple regression equations provide acceptable estimates of the age of demarcation and the age of acceptable density based on data from rings 6 to 10 from the pith.

This study examined the period of juvenile wood production in terms of wood density, a characteristic that is closely related to increases in cell-wall thickness and percent latewood with distance from the pith as the tree ages. There are also changes in grain alignment, fiber length, and fibril angles of the cell walls, but changes in density might not accurately index changes in all components of juvenile wood. It is the cumulative effect of these changes that defines juvenile wood; however, for a given end use, the patterns of variation in some wood properties are more critical than others. For example, strength properties and shrinkage of wood are influenced both by the amount (wood density) and the attributes (e.g., microfibril angle) of the material. Data presented by Erickson and Arima (1974) suggest that fibril angle in Douglas-fir exhibits the features of mature wood by about age 15. The age of maturity for strength properties or shrinkage may be younger than that suggested by the pattern of wood density variation. More research is needed in order to better define the extent of the juvenile wood zone; special consideration should be given to those properties that are important to specific end uses.

CONCLUSIONS

The age of demarcation between juvenile and mature wood based on wood density is extremely variable in Douglas-fir; in this study it ranged from 22 to 29 years for provenances and from 17 to 30 years for families. We found that a significant portion of the variation is attributable to families-within-provenances. Therefore the potential exists for reducing the period of juvenile wood production by genetic manipulation.

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