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EARLY TESTING OF DOUGLAS-FIR: WOOD DENSITY AND RING WIDTH

J. Krakowski[1], Y.S. Park[2] & Y.A. El-Kassaby[1]

[1] Forest Sciences Dept., Faculty of Forestry, University of British Columbia, 3616-2424 Main Mall, Vancouver, B.C. Canada V6T 1Z4.
[2] Natural Resources Canada, Canadian Forest Service – Maritimes Region, P.O. Box 4000, Fredericton, N.B. Canada E3B 5P7.
Corresponding author: Y. A. El-Kassaby, Phone: (604) 822-1821; Fax: (604) 822-9102; E-mail: y.el-kassaby@ubc.ca.

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ABSTRACT

Early genetic control over juvenile ring width, ring density, and earlywood-latewood density ratio in coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) was assessed using seven disconnected diallel crosses with six clones in each set. Annual and composite traits were measured for 104 families over three years. Variance due to general combining ability for density traits was significant. Heritability estimates were consistent with earlier reports on the same species (annual: 4–22 %; combined: 9–34 %). Variance due to specific combining ability and heritability increased with age. Year by family interaction was always significant, except for composite wood density ratio. Random error variance accounted for 64–82 % of total phenotypic variance for individual years, and 50–78 % cumulatively. The relatively stable general combining ability variance over years indicates that wood properties will respond incrementally to selection in a breeding program and that genetic trends in early traits will strengthen over time. Although inversely correlated, coarse-filter selection for wood density and diameter growth is feasible on three-year-old progeny based on ranks of the top and bottom few crosses; however, selections should be made on older trees since genetic parameters vary before stabilizing by age twelve to fifteen in this species.

Key words: diallel mating design, general combining ability, *Pseudotsuga menziesii*, ring width, specific combining ability, wood density.

INTRODUCTION

Wood properties are focal traits in tree improvement programs. Different traits affect product quality, depending on the desired end-product: for dimension lumber, a straight grain with a low fibril angle is important, while for high quality pulp, strong, long cellulose fibres and low lignin content are essential. Wood density and the relative proportions of earlywood and latewood affect structural integrity and ability to withstand warping both during processing and utilization (VARGAS-HERNANDEZ & ADAMS 1991).

Heritabilities, breeding values and general and specific combining abilities of parent trees in a tree breeding program can be ascertained using progeny tests (ZOBEL & TALBERT 1984). Age-age correlations can also be determined from progeny trials, facilitating early selection and thus, increasing efficiency by accelerating the breeding cycle (VARGAS-HERNANDEZ & ADAMS 1991, 1992). Diallel mating designs are fairly efficient and accurate for estimating genetic parameters, particularly for trees which have long generation times (NAMKOONG & ROBERDS 1974; JOHNSON 1998b).

Investigations of quantitative traits in Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) have been progressing for decades in the Pacific Northwest (KING *et al.* 1988; ST. CLAIR 1994), and using material planted in Europe (*i.e.*, ROZENBERG 1993; ROZENBERG *et al.* 2001) and New Zealand (LAUSBERG 1997). Douglas-fir is prized for its rapid growth, straight bole, low incidence of diseases and pests, and high quality wood. Current breeding programs in the Pacific Northwest are on their third generation (KING *et al.* 1988; JOHNSON 1998b). Douglas-fir breeding and deployment programs use both traditional breeding techniques and clonal forestry, incorporating somatic and zygotic seedlings (ROZENBERG *et al.* 2001; BENOWICZ *et al.* 2002). Genetic gains have been substantial in many traits. Improvement programs focus primarily on growth and yield, and secondarily on wood quality (LOO-DINKINS & HERNANDEZ 1991; ST. CLAIR 1994; JOHNSON 1998b), although the importance of wood quality is increasing (ROZENBERG *et al.* 2001).

The objective of this study was to quantify early genetic control of wood density, diameter growth and earlywood-latewood density ratios of Douglas-fir parent trees based on progeny trials. Prior studies found fairly high juvenile-mature correlations of growth and wood quality parameters (often $r > 0.5$) by age seven. It may be feasible to select top-ranking crosses or, more pragmatically, rogue poorly performing parents earlier if performance and genetic parameters are comparable to those several years later (VARGAS-HERNANDEZ & ADAMS 1992).

MATERIALS AND METHODS

Seven sets of disconnected diallel crosses with six parents in each diallel set, representing 42 parents, were planted in a uniform farm field in Saanichton, British Columbia (48°35' N, 123°24' W). Parent trees were represented in the breeding program of Pacific Forest Products (now Western Forest Products), originally selected from low-elevation (0 to 450 m) provenances throughout Vancouver Island and southwestern British Columbia. Seeds were collected and grown in a commercial greenhouse in containers, watered and fertilized according to standard industry protocols. Overall, progeny from 104 full-sib families were produced using a completely randomized block design with two replicates.

One-year-old container-grown seedlings were planted in a five-tree-row plot spaced at 15 cm within rows and 30 cm between rows. After the third growing season, three seedlings per cross were harvested and a 3-cm stem sample was taken at the root collar. Density of earlywood, latewood, total ring, and ring width were determined using X-ray densitometry for each annual ring (LOO-DINKINS & GONZALEZ 1991). Composite wood density was derived by measuring the entire stem cross-section by X-ray densitometry resulting in a single cumulative value; the relative density threshold to distinguish between earlywood and latewood was 0.45. Composite ring width was the mean over the entire cross-section. This measure reduces the bias towards wider rings closer to the pith in these very young trees as the annual volume increment is distributed over a larger vertical distance and a correspondingly smaller radial difference.

Variance and covariance components were estimated using a modified version of the DIALL program (SCHAFFER & USANIS 1969) to accommodate diallel set effects of this experimental design. Epistatic effects and linkage disequilibrium were assumed to be non-significant in terms of net phenotypic effects (HALLAUER & MIRANDA 1988). Analyses of variance (ANOVA), cross-products, and model coefficients of variance components and error terms for ring width, ring density, and ratio of earlywood to latewood density were calculated from the following additive linear model:

$$y_{ijklmn} = \mu + R_i + Y_j + RY_{ij} + D_k + G_{kl} + G_{km} + S_{klm} + YF_{jklm} + E_{ijklmn} \qquad [1]$$

where: y_{ijklmn} = the n^{th} observation in the lm^{th} family in the k^{th} diallel set in the i^{th} replicate of the j^{th} year ($n = 1, 2, 3$); μ = the grand mean; R_i = the i^{th} replicate effect ($i = 1, 2$); Y_j = the j^{th} year effect ($j = 1, 2, 3$); RY_{ij} = the interaction effect of the i^{th} replicate and j^{th} year; D_k = the k^{th} diallel set effect ($k = 1, 2, \ldots 7$); $G_{kl}(G_{km})$ = the m^{th} general combining ability (GCA) effect within the k^{th} diallel set ($l, m = 1, 2, \ldots 6$); S_{klm} = the lm^{th} specific combining ability (SCA) effect within the k^{th} diallel set; YF_{jklm} = the interaction effect of the j^{th} year and the klm^{th} family; and E_{ijklmn} = the random error component.

The ANOVA and cross-products for diameter, core density, and earlywood-latewood density ratio based on a composite of the three year data were calculated from the following additive linear model:

$$y_{ijklmn} = \mu + R_i + D_k + G_{kl} + G_{km} + S_{klm} + YF_{jklm} + E_{ijklmn} \qquad [2]$$

where: y_{ijklmn} = the n^{th} observation of the klm^{th} family in the i^{th} replicate; RF_{iklm} = the interaction effect of the i^{th} replicate and klm^{th} family, and E_{iklmn} = the random error component while all other terms are as previously defined.

Standard deviation of the components were analyzed using formulae of ANDERSON & BANCROFT (1952), and significance was tested using the *F*-test and SATTERTHWAITE'S (1946) approximation after comparing expected mean square (EMS) coefficients at the $\alpha = 0.05$ level. Narrow-sense heritability (h^2) was calculated as:

$$h^2 = 4\sigma^2_{GCA}/\sigma^2_P \qquad [3]$$

where: σ^2_P = the total phenotypic variance, calculated as:

$$\sigma^2_P = \sigma^2_{SET} + 2\sigma^2_{GCA} + \sigma^2_{SCA} + \sigma^2_{YF} + \sigma^2_E \text{ for model [1]} \qquad [4.1]$$

$$\sigma^2_P = \sigma^2_{SET} + 2\sigma^2_{GCA} + \sigma^2_{SCA} + \sigma^2_{RF} + \sigma^2_E \text{ for model [2]} \qquad [4.2]$$

σ^2_{SET} = the variance due to diallel set (the six parents in each mating design); σ^2_{GCA} = the variance due to GCA; σ^2_{SCA} = the variance due to SCA; σ^2_{YF} = the variance due to year by family interaction; and σ^2_E = the variance due to random error.

To examine relationships among traits, genetic correlations (r_{xy}) were calculated as follows:

$$r_{xy} = \sigma^2_{GCAxy} / (\sigma^2_{GCAx} \times \sigma^2_{GCAy})^{0.5} \qquad [5]$$

where: σ^2_{SCA} = the additive covariance component between the traits x and y; σ^2_{SCA} = the additive variance due to general combining ability for trait y; and σ^2_{SCA} = the additive variance due to general combining ability for trait x.

Descriptive statistics for traits were calculated using PROC GLM in SAS (SAS Institute, Cary, NC) according to the models described above.

RESULTS

Significance of the respective variance components for individual years and composite variables and the percentage of the total phenotypic variance each accounted for are presented in Tables 1 and 2. Diallel set means, standard errors, and heritability estimates for measured traits are presented in Figure 1 and Table 3. Rings grew wider with age, with an increase in latewood, leading to a decrease in the ratio of earlywood to latewood density; however, individual year ring density remained similar over the three years (Fig. 1). Residual error terms contributed the vast majority of variation for all variables: 64.2–81.8 % for individual years and 49.8–77.8 % for composite data, with ring density showing the lowest proportion of residual variance (Tables 1 and 2).

With respect to ring width, there were no significant differences across replicates, but year-to-year variation was significant (Table 1). After the residual error term, variances due to the interaction between year and family as well as diallel set were significant accounting for the largest proportion of phenotypic variance (11.3 and 4.15 %, respectively, Table 1). Both GCA and SCA variances were not significant and contributed very small amounts to total variation (Table 1). Narrow-sense heritability for ring width was very small (0.04, Table 3). Composite diameter growth had a significant interaction between replicates and families (8.1 %, Table 2). The variance due to GCA for ring width was significant but accounted for only 2.3 % of total phenotypic variance, resulting in a heritability estimate of 0.09 (Table 2).

The significant amounts of variation due to individual year ring density was explained by both GCA (5.8 %) and SCA (17.7 %), the latter accounted for 3 times more variance than the former (Table 1). Year-by-family interaction was highly significant, accounting for 18.2 % for the total variation (Table 1). Narrow-sense heritability was 0.22 (Table 3). Composite wood density residual variance explained the largest proportion of phenotypic variance (49.8 %), followed by significant SCA variance (27.4 %, Table 2). Composite wood density variance attributed to GCA was approximately one-third that of SCA (9.2 vs. 27.4 %, Table 2), yielding a narrow-sense heritability of 0.34 (Table 3).

Annual earlywood-latewood density ratio had significant variance contributed by GCA (1.9 %), but year-by-family interaction was responsible for the majority of the variance (18.2 %, Table 1), after

Table 1. Model [1] annual variables: estimates and percentages of phenotypic variance for each variance component. See text for variable and model details. Asterisks indicate significant terms (α = 0.05).

Variance component	Ring width		Ring density		EW/LW density	
	Estimate (S.D.)	% σ^2_P	Estimate (S.D.)	% σ^2_P	Estimate (S.D.)	% σ^2_P
Replicate (R)	0.18 (0.17)	–	-1.19 (0.28)	–	-0.92 (1.79)	–
Year (Y)	47.82 (33.8)*	–	235.52 (68.0)*	–	2275.64 (1611.0)*	–
R × Y	0.02 (0.06)	–	4.68 (3.62)	–	5.29 (4.48)	–
Set	1.10 (0.75)*	4.15	8.22 (10.6)	3.92	11.32 (9.65)	2.71
GCA	0.29 (0.25)	1.10	12.14 (6.20)*	5.79	7.76 (3.94)	1.86
SCA	0.41 (0.51)	1.56	37.52 (9.01)*	17.70	-11.44 (7.06)	0.00
Y × F	3.02 (0.67)*	11.39	17.17 (3.98)*	8.19	76.04 (12.9)*	18.20
Error	21.69 (0.78)	81.81	134.54 (4.84)	64.19	322.74 (11.6)	77.24

Table 2. Model [2] composite variables: estimates and percentages of phenotypic variance for each variance component. See text for variable and model details. Asterisks indicate significant terms ($\alpha = 0.05$).

Variance component	Ring width		Ring density		EW/LW density	
	Estimate (S.D.)	% σ_P^2	Estimate (S.D.)	% σ_P^2	Estimate (S.D.)	% σ_P^2
Replicate (R)	7.45 (7.33)*	–	0.42 (0.60)	–	1.13 (1.31)	–
Set	38.78 (26.73)*	8.50	6.48 (9.64)	5.12	13.05 (10.94)	8.25
GCA	10.61 (9.09)	2.33	11.63 (6.09)*	9.20	9.18 (4.14)*	5.81
SCA	16.58 (20.10	3.63	34.59 (9.20)*	27.37	6.00 (6.37)	3.80
R × Family	36.85 (23.47)*	8.08	10.71 (4.72)*	8.47	6.91 (7.42)	4.37
Error	353.38 (24.89)	77.46	63.00 (4.44)	49.84	123.00 (8.67)	77.77

Table 3. Means and standard deviations (in parentheses) and narrow-sense heritabilities (h^2) for annual and composite wood properties by diallel set.

	Annual			Composite		
	Ring width	Ring density	EW/LW density	Ring width	Ring density	EW/LW density
Set 1	18.8 (6.8)	0.54 (0.06)	0.71 (0.14)	112.3 (18.4)	0.54 (0.03)	0.70 (0.04)
Set 2	21.0 (7.8)	0.52 (0.06)	0.73 (0.14)	125.8 (20.6)	0.52 (0.03)	0.72 (0.04)
Set 3	19.4 (7.5)	0.52 (0.06)	0.71 (0.13)	116.6 (22.4)	0.52 (0.04)	0.70 (0.04)
Set 4	20.0 (7.8)	0.51 (0.06)	0.70 (0.14)	119.8 (24.2)	0.51 (0.03)	0.69 (0.04)
Set 5	19.4 (7.8)	0.51 (0.06)	0.69 (0.13)	116.2 (20.1)	0.51 (0.04)	0.68 (0.04)
Set 6	18.5 (7.0)	0.51 (0.07)	0.69 (0.14)	110.3 (17.6)	0.51 (0.04)	0.68 (0.04)
Set 7	21.8 (8.3)	0.50 (0.06)	0.70 (0.14)	130.6 (19.7)	0.50 (0.03)	0.69 (0.04)
h^2	0.04	0.22	0.07	0.09	0.34	0.22

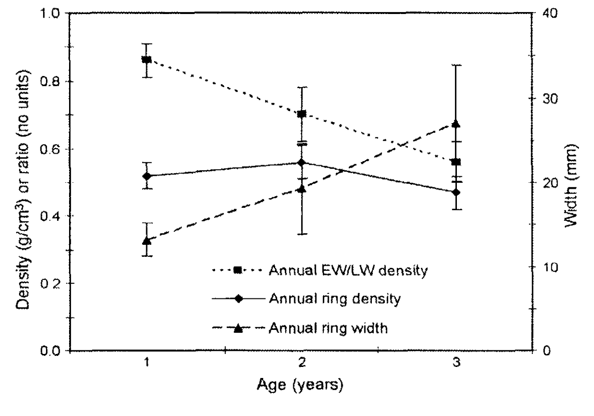

Figure 1. Mean and standard deviations of annual wood properties with progeny age.

the residual error. The heritability estimate for annual earlywood-latewood density ratio was 0.07 (Table 3). For composite wood density ratio, only GCA accounted for a significant proportion of phenotypic variance (5.8 %, Table 2), yielding a heritability estimate of 0.22 (Table 3). Variance due to diallel set was not significant for composite wood density ratio, but contributed the highest non-error proportion of variance (8.3 %).

Composite and individual year correlations of genetic and phenotypic traits were of similar magnitude and sign, except for the weak phenotypic correlations between ring density and earlywood-latewood density ratio (-0.017, 0.109 phenotypic, Table 4). Diameter growth and density were strongly and negatively correlated, as were wood density and earlywood-latewood density ratios (Table 4). Ring width and earlywood-latewood density ratio were positively correlated. Wood density and density ratio were only weakly correlated.

DISCUSSION

Variation in mean individual year and composite ring width among families increased from age 1 to 3, while the range of values for wood density variables was stable (Table 3, Figure 1). Density variables

Table 4. Genotypic (above diagonal) and phenotypic (below diagonal) correlations among composite and annual wood quality traits.

	Ring width	Ring density	EW/LW density
Annual traits			
Ring width	–	–0.541	0.398
Ring density	–0.316	–	0.029
EW/LW density	0.290	–0.017	–
Composite traits			
Ring width	–	–0.545	0.311
Ring density	–0.280	–	0.101
EW/LW density	0.253	0.109	–

alone may thus provide a fairly accurate index for juvenile wood properties. Selections on the basis of ring width alone at such an early stage can likely guide very preliminary roguing (*e.g.*, the lowest 5-10 % of families due to fairly strong age-age correlations (VARGAS-HERNANDEZ & ADAMS 1992)). Data from early progeny tests may be used in 3 ways: (1) estimation of genetic variances to characterize the parental (breeding) population; (2) to rogue seed orchards, usually based on GCA or breeding value; and (3) progeny are evaluated and retained to form the next breeding generation. The latter two options could prematurely eliminate some families from breeding programs, since very early composite juvenile wood density in Douglas-fir tends to fluctuate relative to mature wood values for the first six to seven years (LOO-DINKINS & GONZALEZ 1991). Taking both growth and density into account ensures a more stable selection technique, given their negative correlation (Table 4; VARGAS-HERNANDEZ & ADAMS 1991, 1992).

Estimates of GCA and SCA were considered robust since each parent was represented by five crosses (JOHNSON 1998a). General combining ability variance was significant for density-related traits, although specific combining ability variances accounted for far more variation in both yearly and composite ring density (Tables 1 and 2). This reflects the stable nature of individual year ring density relative to composite ring density, which often decreases with age (YANCHUK 1996). This trend was also found for other early growth traits in this species (*e.g.*, YEH & HEAMAN 1987; EL-KASSABY & PARK 1991). Other studies have shown strong juvenile-mature correlations between traits of interest in Douglas-fir. Values for traits at age three tend to vary slightly before stabilizing several years later, generally by age 12 to 15 in this species (KING *et al.* 1988; LOO-DINKINS & GONZALEZ 1991; YANCHUK 1996; JOHNSON *et al.* 1997).

Diallel sets were extremely consistent with respect to wood properties, although a prior study had shown significant differences in phenological and growth traits (EL-KASSABY & PARK 1991). These contrasting results indicate that wood density traits are independent of phenological and growth traits. This concurs with the fairly narrow variation in wood properties also found in the same species by VARGAS-HERNANDEZ & ADAMS (1991). The maternal parent was found to have a much stronger influence on progeny performance than the pollen parent (LOO-DINKINS & GONZALEZ 1991), but YANCHUK (1996) calculated a correlation of 0.94 between values of maternal and paternal Douglas-fir parents in a replicated diallel for growth traits. He also found highly consistent values among diallel sets, also noted in this study (Table 3). Although ring width variances were significantly different among diallel sets in this experiment, the range of actual means did not show any unusual deviation. Disconnected diallel sets comprise an effective design to produce the next generation breeding population, and to obtain detailed genetic information. With no significant differences among sets, a breeder can select progenies with equal weight. In practice, the parents used in each diallel set may be considered as sub-lines.

As found in other coastal Douglas-fir studies, there was a trade-off between density and diameter (KING *et al.* 1988; VARGAS-HERNANDEZ & ADAMS 1991, 1992; ROZENBERG 1993; ST. CLAIR 1994; LAUSBERG 1997). VARGAS-HERNANDEZ & ADAMS (1991) also suggested that the various density traits they examined were under similar genetic control since they expressed similar trends; the same pattern was also found in this study. This supports YANCHUK'S (1996) assertion that epistasis probably does affect traits more than models currently allow. Ultimately, negative and positive epistatic effects on phenotypic traits may result in little net effect, since the relative magnitude of their effects on total variation is likely small when compared with the main genetic effects (*i.e.*, GCA and SCA, respectively). Other studies have found variable correlations between early diameter growth and mature volume (KING *et al.* 1988; ST. CLAIR 1994; LAUSBERG 1997; ROZENBERG *et al.* 2001). Diameter tended to correlate better with volume than with early height, since the latter is subject to substantial microsite and temporal variation in this species (YEH & HEAMAN 1987; KING *et al.* 1988; ST. CLAIR 1994; JOHNSON 1998b). This also could be a byproduct of the relationship between diameter and early volume (OMULE *et al.* 1987).

The mean values, heritabilities, and levels of genetic variability in traits found in the present study were consistent with previous studies on the same species (YEH & HEAMAN 1987; VARGAS-HERNANDEZ & ADAMS 1991, 1992; LOO-DINKINS & GONZALEZ 1991; ST. CLAIR 1994; YANCHUK 1996; JOHNSON *et al.* 1997). Age-age correlations between juvenile and mature growth and wood quality traits of coastal Douglas-fir tend to increase to a stable maximum between ages 12 and 15. While some traits such as latewood density may be stable relative to mature values and family ranks as early as age seven (LOO-DINKINS & GONZALEZ 1991; VARGAS-HERNANDEZ & ADAMS 1992), age three is too young to select parents for diameter and wood properties based on progeny performance: variance is too high and means too unstable (see early testing caveats noted by KING & EL-KASSABY 1990). Coastal Douglas-fir breeding programs currently focus on GCA rather than SCA to capitalize on additive variance, and the declining magnitude of SCA with age supports this strategy, since GCA is more robust (YANCHUK 1996).

Properties of juvenile wood such as density and latewood proportion differ somewhat from mature wood, making determination of mature wood characteristics based on early traits not completely reliable (VARGAS-HERNANDEZ & ADAMS 1992; LOO-DINKINS & GONZALEZ 1991). This type of very early testing could still be beneficial for truncating the tested population by eliminating crosses with very low breeding values. Wood attribute field evaluation on the remaining individuals in the tested population would be more efficient and economical. Depending on the specific objectives and resources of the breeding program, some early roguing of the parent population may be based on results by age three since ranks at the top and bottom of a breeding program tend to be fairly stable for phenotypic traits (EL-KASSABY & PARK 1991).

Continued activity in Douglas-fir breeding programs incorporating simultaneous selection for negatively correlated traits as diameter and density is feasible (VARGAS-HERNANDEZ & ADAMS 1991; JOHNSON 1998b), but will proceed relatively slowly due to the inherent trade-offs between these traits. Based on the variation found in this and other studies, gains can be made for both diameter and wood quality. The inverse relationship between the traits necessitates carefully planned breeding and selection strategies where additive variance could be exploited. A selection index approach may be used to optimize tradeoffs between traits with apparently contradictory outcomes, but accurately predicting economic weights at rotation age based likely has too much uncertainty to derive a practical selection index at such an early stage. Multiple lines and polycrosses, where families and lines are bred separately for maximum gains in diameter and in wood quality, may be interbred in a two-trait tandem selection design or a multiple-trait independent design to achieve gains simultaneously in both traits (NAMKOONG *et al.* 1988).

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