

Figure 2. — C-banded metaphase in *Q. robur* showing intensely heterochromatic B-chromosome (arrow) (x 1500).



Figure 3. — Anaphase in *Q. robur* showing late dividing B-chromosome (x 1500).

KUMAR, 1986; OHRI and KOSHOO, 1987). Significant interspecific variation as encountered in many herbaceous groups (c. f. OHRI and KHOSHOO, 1986) has not been found in tree species except for *Cassia* (OHRI et al., 1986). Detailed studies are therefore needed in more species of *Quercus* to assess the extent of intra- and interspecific variation in DNA amounts.

#### B-Chromosomes

One B-chromosome is present in all the three species of *Quercus* investigated. This seems to be the first report of B-chromosomes in any temperate hardwood species. The B-chromosome is much smaller than the smallest chromosome of the complement and is very intensely heterochromatic as revealed by C-banding (Fig. 1a, b, c; Fig. 2). This would mean that DNA amount per unit volume for B's is considerably higher than for A chromosomes on average (JONES and REES, 1982). At anaphase the B-chromosome can be seen to be late dividing (Fig. 3).

For the first time MEHRA and BAWA (1968) reported the occurrence of B-chromosomes in six eastern Himalayan

woody species. According to the recent information, B's are represented in about 3.9% of the chromosomally known 862 woody species from the Himalayas and central India (BEDI et al., 1985). Quite contrary to earlier concepts, the percentage (3.9%) of woody species with B-chromosomes is almost double that of the overall percentage (1.9%) for flowering plants in general (JONES, 1981).

In this regard, it is an interesting observation that all three species of oak investigated show B-chromosomes. This would indicate that these chromosomes may actually be very widespread among temperate hardwoods. Therefore, detailed investigations are needed on the population basis to understand relationship, if any, between the presence of B-chromosomes and growth characteristics, phenological factors, and ecological tolerance.

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## Comparison of Selection Methods for Improving Volume Growth in Young Coastal Douglas-fir<sup>1)</sup>

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#### Summary

Data from a Douglas-fir [*Pseudotsuga menziesii* (MIRB) FRANCO var. *menziesii*] open-pollinated progeny test in Oregon were used for evaluating methods of selection for bole volume. Tree height and bole diameter at breast

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height (DBH) were measured on 12- to 13-year-old individuals from 90 families at each of three plantations, and bole-volume estimates were derived with a quadratic volume equation. Four methods were compared for both parental and progeny selection: (1) indirect selection based on height, (2) indirect selection based on DBH, (3) direct selection based on volume, and (4) selection based on an index that included all three traits. Two-stage selection was also explored, where test trees are culled on the basis of DBH in the first stage; and, height is measured only on the remaining trees, so that final selections (the second stage) are based on volume. Estimated genetic gains in volume from progeny selection were 8% to 11% greater than those from parental selection. The relative efficiencies of the various selection methods, however, were similar for parental and progeny selection. The greatest estimated gains in single-stage selection, which were achieved with the multitrait index, were only 1% better than those from selections based on volume alone. Indirect selection based on DBH produced about 90% of the gain achieved by direct selection for volume, and indirect selection based on height was about 92% to 94% as efficient as direct selection. With two-stage selection, up to two-thirds of the trees could be culled in stage 1 without significantly lower gains in bole volume than those expected if the height of all trees had been measured.

**Key words:** Douglas-fir, bole volume, progeny testing, tree improvement, selection indices, two-stage selection.

### Introduction

For most timber species, bole volume is the most important trait in determining tree value, and genetic improvement in volume growth is therefore the highest priority in many tree improvement programs. Over 1350 test plantations of Douglas-fir [*Pseudotsuga menziesii* (MIRB.) FRANCO var. *menziesii*], involving progenies from nearly 42,000 parent trees, have been established in coastal Oregon, Washington, and British Columbia in the past 15 years (ADAMS *et al.*, 1990). Most, if not all, of these tests will evaluate bole-volume breeding values of families and individual trees. Given the considerable magnitude of this testing program, efforts to develop selection methods which optimize bole volume improvement, while minimizing measurement costs, are well warranted.

Selection for bole volume is commonly based on the phenotypic value of "derived volume", which is calculated from measurements of individual-tree height and diameter (JOURDAIN and OLSON, 1984; TAUER and McNEW, 1985). However, the phenotypic value of an individual is not the only source of information about its breeding value. When the trait being selected has low heritability, any available information on relatives (especially siblings) can also assist greatly (FALCONER, 1981). Theoretically, the optimum selection procedure uses individual phenotypic values and family means to generate a combined breeding-value index for rating each individual.

If the trait of interest is derived from two or more component traits (i. e., height and diameter), incorporation of individual and family information for each component into the breeding-value index should result in more efficient selection for the derived trait (FALCONER, 1981). However, if the component traits are strongly intercorrelated, gains from such selection may be only marginally greater than those attainable with a simpler index (BAKER, 1986), and therefore would not justify the effort of developing complex selection indices.

In many progeny-test plantations of coastal Douglas-fir, final selection decisions will likely be based on 15-

year measurements (SILEN and WHEAT, 1979). At that age, however, height measurement can be difficult and costly because trees are tall (7 m to 11 m) and canopies closed (HOWE and ADAMS, 1988). This encouraged investigation of diameter measurements as a potential basis for indirect selection of bole volume.

In this paper, we explore the relative efficiencies of bole-volume selection criteria in test plantations of young coastal Douglas-fir. We report on the expected response in individual-tree volume when selections are based directly on derived volume, indirectly on height or diameter, or on a multitrait index which includes derived volume, height, and diameter. We also explore the efficiency of two-stage selection (NAMKOONG, 1970), where selection in the first stage is based on DBH alone, and a large proportion of individuals with lower DBH values are removed from further consideration. In the second stage, height of the remaining trees is measured so that final selections are based on derived volume. The strategy is to achieve near maximal gains in bole volume while minimizing the number of height measurements required. Each selection method is examined (1) where family information is used to select among maternal parents (parental selection) and (2) where family and individual-tree data are combined to select the best individuals in the test (progeny selection).

### Materials and Methods

Trees from 90 open-pollinated families were measured at three test plantations in the Noti Breeding Unit of the Douglas-fir Progressive Tree Improvement Program in the central Oregon Coast Range (QUAM, 1988). At each location, three 30-family sets were planted as separate, randomized complete-block experiments with four replications; each family was represented by a four-tree noncontiguous plot in each replication. Seedlings (1-0 plug) were planted at 3.05- × 3.05-m spacing in plantations that were fenced to exclude large animals. Survival at individual sites ranged from 73% to 83%, and dead seedlings were replaced for 3 years after initial establishment; however, only original trees (totalling 3,333) were measured for this study. At the time of measurement (fall 1984), trees in two of the plantations were 12 years old from seed; those in the third plantation were 13 years old. Total height and DBH (diameter at breast height, 1.37 m) were measured on all trees.

#### Calculation of Derived Volume

To estimate the bole volume of the progeny test trees, we developed a quadratic equation with data on bole volumes of Douglas-fir; these data were derived from stem analysis of 277 felled trees of similar size (3 m to 12 m in height) to the trees measured in this study (data provided by DAVID BRUCE, USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA). These bole volumes were regressed on linear and quadratic functions of height (H) and DBH using stepwise multiple regression. The single variable best related to bole volume was  $H \times DBH$  ( $R^2 = 0.945$ ), and the equation selected ( $R^2 = 0.984$ ) was

$$\text{Vol}(\text{dm}^3) = 14.71959 - (0.43964 \times H(\text{dm})) - (2.26591 \times \text{DBH}(\text{cm})) + (0.09012 \times H \times \text{DBH}) \quad (1)$$

where Vol is the derived volume of an individual tree (hereafter referred to as "volume"). The root mean square error of this equation (13.1%) is comparable to that

Table 1. — Form of analysis of variance for bole height, diameter, and volume <sup>a)</sup>.

Source of variation	Degrees of freedom	Expected mean squares <sup>b)</sup>
Plantations	p-1	$\frac{\sigma_w^2}{k} + \sigma_e^2 + r\sigma_{pf(s)}^2 + f\sigma_{r(ps)}^2 + rf\sigma_{ps}^2 + rfs\sigma_p^2$
Sets	s-1	$\frac{\sigma_w^2}{k} + \sigma_e^2 + r\sigma_{pf(s)}^2 + rp\sigma_{f(s)}^2 + f\sigma_{r(ps)}^2 + rf\sigma_{ps}^2 + rpf\sigma_s^2$
Plantations x sets	(p-1)(s-1)	$\frac{\sigma_w^2}{k} + \sigma_e^2 + r\sigma_{pf(s)}^2 + f\sigma_{r(ps)}^2 + rf\sigma_{ps}^2$
Replications/sets/ plantations	(r-1)sp	$\frac{\sigma_w^2}{k} + \sigma_e^2 + f\sigma_{r(ps)}^2$
Families/sets	(f-1)s	$\frac{\sigma_w^2}{k} + \sigma_e^2 + r\sigma_{p(s)}^2 + rp\sigma_{f(s)}^2$
Plantations x families/sets	(p-1)(f-1)s	$\frac{\sigma_w^2}{k} + \sigma_e^2 + r\sigma_{pf(s)}^2$
Plot error	(f-1)(r-1)sp	$\frac{\sigma_w^2}{k} + \sigma_e^2$
Within plot	$\sum_{i=1}^t (n_i - 1)$	$\sigma_w^2$

a) modified from STONECYPHER *et al.*, 1973.

b) p = number of plantations; s = number of sets; r = number of replications per set per plantation; f = number of families per set; n<sub>i</sub> = number of trees in the i<sup>th</sup> plot; t = total number of plots in the experiment; k = harmonic mean number of trees per plot for all sets.

$\sigma_w^2$  = within-plot variance

$\sigma_e^2$  = plot variance

$\sigma_{pf(s)}^2$  = variance due to plantation by families-in-sets interaction

$\sigma_{f(s)}^2$  = variance due to differences among families-in-sets

$\sigma_{r(ps)}^2$  = variance due to differences among replications-in-sets and plantations

$\sigma_{ps}^2$  = variance due to plantation by set interaction

$\sigma_s^2$  = variance due to differences among sets

$\sigma_p^2$  = variance due to differences among plantations

reported by BRUCE and DEMARS (1974) for their volume equation for small (<5.5 m in height) Douglas-fir (12.7%). The R<sup>2</sup> increased by less than 0.005 when terms for height squared, diameter squared, or both were added to the model.

#### Analyses of Variance

Analyses of variance were computed for height, DBH, and volume according to a random model (Table 1). Analyses of covariance between all pairs of traits were computed as in Table 1, but with expected cross-products, instead of expected mean squares. Components of variance and covariance were estimated from the appropriate mean squares and cross-products, and standard errors of these estimates calculated according to NAMKOONG (1979). Individual heritability calculations followed NAMKOONG (1979), and their standard errors followed OSBORNE and PATERSON (1951). The coefficient of relationship among wind-pollinated progenies was assumed to be 1/3 (CAMPBELL, 1986).

#### Selection Indices

The goal of selection in this study is always to improve the single trait, volume. When both height and DBH are measured, volume can be calculated for each tree and selections based on volume directly. When only height or DBH is available, however, it is assumed that selection is

based on these traits alone, with subsequent gains in volume obtained indirectly.

Smith-Hazel selection indices (LIN, 1978; COTTERILL and JACKSON, 1985) were employed to combine family and individual-tree data for progeny selection. They were also used to improve the estimation of breeding values for volume by incorporating height and DBH along with volume in a multitrait index. These indices employ multiple regression to combine sources of information into a single index value which becomes the unit of selection. The weight given to each source of information is such that the correlation between the index and breeding value is maximized, so that individuals with the highest index values are expected to have the highest breeding values for the trait of interest (FALCONER, 1981).

Selection indices were derived which could be applied to effects, i. e., deviations from class or subclass means (STONECYPHER and ARBEZ, 1976; BURDON, 1982). Environmental effects for plantations and replications-within-plantations were thus removed before indices were derived, which resulted in equal weighting of information from each plantation. Because plots were noncontiguous, individual tree values were not corrected for plot effects.

For height, DBH, or volume taken individually, the form of the Smith-Hazel index for progeny selection is

$$I = b_1 X_i + b_2 \bar{X}_i \quad (2)$$

where measurements  $x_i$  and  $\bar{x}_i$  are the respective individual value and family mean for trait  $i$ , and  $b_1$  and  $b_2$  are the corresponding index coefficients. The multitrait index for progeny selection is

$$I = b_1 X_1 + b_2 X_2 + b_3 X_3 + b_4 \bar{X}_1 + b_5 \bar{X}_2 + b_6 \bar{X}_3 \quad (3)$$

where  $X_1$ ,  $X_2$ , and  $X_3$  are individual-tree values for height, DBH, and volume, respectively;  $\bar{X}_1$ ,  $\bar{X}_2$ , and  $\bar{X}_3$  are family means for the respective traits; and  $b_1 \dots b_6$  are the index coefficients. The form of the multitrait index for parental selection is similar to that for progeny selection, but only family means for height, DBH, and volume are included.

Expressed in matrix notation, the equation for determining index coefficients is

$$\underline{b} = P^{-1} \underline{A} \quad (4)$$

in which  $\underline{b}$  is the column vector of index coefficients,  $P$  is the matrix of phenotypic variances and covariances among the measurements in the index, and  $\underline{A}$  is the column vector of additive genetic variances and covariances (LIN, 1978; COTTERILL and JACKSON, 1985).  $\underline{A}$  is a column vector rather than a matrix because index selection, in each case, is applied only to a single trait (FALCONER, 1981). The  $b$  coefficients for each index were calculated with RESI, a computer program described by COTTERILL and JACKSON (1981). Family components of variance and covariance used in RESI to estimate index coefficients for progeny selection are derived from individual-tree variance and covariance components, assuming equal family sizes (FALCONER 1981, Ch. 13). The harmonic mean family size ( $n = 32$ ) was used for all calculations of genetic and phenotypic parameters involving families.

#### Genetic Gains

##### Parental selection

It was assumed that six trees would be selected from each set of 30 parents [selection intensity ( $i$ ) = 1.354] and clonally replicated in a seed orchard with all other selected parents to produce progeny through random mating. Expected genetic gain ( $G$ ) in volume at age 12 to 13 when selection is applied directly to volume or indirectly to height or DBH can be estimated as

$$G = 2i \frac{COV_A(\bar{V}, \bar{X}_i)}{\sigma_{P\bar{X}}} \quad (5)$$

where  $COV_A(\bar{V}, \bar{X}_i)$  is the additive genetic covariance between the family mean for volume and the family mean for the trait to which selection is applied, and  $\sigma_{P\bar{X}}$  is the phenotypic standard deviation of family means for the selected trait. Equation (5) can be derived from the familiar formula for predicting the correlated response (gain) in one trait when selection is applied to another trait (FALCONER, 1981, Chap. 19). The multiplier of 2 is used in this case because, when parents are selected on the basis of progeny performance, the effect of the selection differential on open-pollinated families is doubled (NAMKOONG, 1979). If volume is the selected trait, then  $COV_A(\bar{V}, \bar{X}_i) = \sigma_{A\bar{V}}^2$ , which is the additive variance of volume among family means. When parents are selected on the basis of

the multitrait index, gain is estimated as  $G = 2i \sigma_I$ , where  $\sigma_I$  is the standard deviation of index values (FALCONER, 1981).

##### Progeny selection

It was assumed that six unrelated trees would be selected from each set of 30 families in the field tests and clonally replicated in a seed orchard. Selection intensity was computed empirically from the ranks of the selected individuals in each set. A computer program for that purpose, based on algorithms described by HARTER (1961) and BURROWS (1972), was provided by Dr. ROY STONECYPHER (Weyerhaeuser Company, Centralia, WA). The average  $i$  over all sets and traits (2.500) was used for all subsequent gain calculations. All selections in this case are based on index values, so that expected response is calculated as

$$G = i \frac{COV_A(V, I)}{\sigma_I} \quad (6)$$

where  $COV_A(V, I)$  is the additive covariance between volume and the index value (FALCONER, 1981). When the index estimates the breeding value for volume directly (i.e., when selection is based on volume or the multitrait index),  $COV_A(V, I) = \sigma_I^2$  and  $R = i \sigma_I$ . When the index estimates the breeding value for a correlated trait (i.e., height or DBH), and using equation (2),

$$\begin{aligned} COV_A(V, I) &= COV_A[V, (b_1 X_i + b_2 \bar{X}_i)] \\ &= b_1 COV_A(V, X_i) + b_2 COV_A(V, \bar{X}_i) \end{aligned} \quad (7)$$

where  $COV_A(V, X_i)$  is the additive genetic covariance between individual-tree volume and the correlated trait, and  $COV_A(V, \bar{X}_i)$  is the additive covariance between individual-tree volume and the family mean for the correlated trait [ $COV_A(V, \bar{X}_i) = COV_A(\bar{V}, \bar{X}_i)$ ].

##### Two-stage selection

Two-stage selection is assumed to be equivalent to sequentially truncating a bivariate normal distribution in which the variates are genetically correlated (NAMKOONG, 1970). If  $y_1$  and  $y_2$  are two standardized variates upon which selection in the first and second stages are based, the expected genetic gain from selection on  $y_1$  and  $y_2$  is calculated as

$$G = W_1 E(y_1) \sigma_{y_1} + W_2 E(y_2) \sigma_{y_2} \quad (8)$$

where  $w_1$  and  $w_2$  are weights chosen to minimize errors in estimating the breeding value of  $y_2$ ,  $E(y_1)$  and  $E(y_2)$  are the expected values of  $y_1$  and  $y_2$  and  $\sigma_{y_1}$  and  $\sigma_{y_2}$  are the phenotypic standard deviations of the respective traits. The  $w_i$ 's are calculated by solving index equation (4), where  $w_i$ 's are substituted for the  $b_i$ ,  $P$  is the phenotypic variance-covariance matrix between  $y_1$  and  $y_2$ , and  $\underline{A}$  is the column vector of covariances between the  $y_i$ 's and the breeding value of  $y_2$ . Given the selection differentials for  $y_1$  and  $y_2$ ,  $E(y_1)$  and  $E(y_2)$  can be derived from tables of the univariate and bivariate normal distributions (NAMKOONG, 1970; YOUNG and WEILER, 1961).

For the case of parental selection,  $y_1$  and  $y_2$  are the standardized family means for DBH and volume, respectively. For progeny selection,  $y_1$  is the standardized combined index value for DBH based on individual and family performance. The selected trait in stage 2 ( $y_2$ ) was

Table 2. — Plantation and set means, and ranges among family means (in parentheses) within each plantation and set, for bole height, diameter, and volume.

Unit	Age <sup>a)</sup> (yrs)	Height (dm)	DBH <sup>b)</sup> (cm)	Volume (dm <sup>3</sup> )
<b>Plantation</b>				
1	12	76.3(56.1-87.3)	10.2(6.9-12.3)	29.4(17.3-45.3)
2	12	77.6(65.0-92.3)	11.3(8.8-14.3)	35.2(20.4-61.2)
3	13	78.3(62.0-89.3)	10.8(7.8-12.8)	33.6(14.7-49.5)
<b>Set</b>				
1	-	75.3(62.0-84.9)	10.5(7.8-13.1)	30.4(14.7-48.0)
2	-	79.9(67.9-92.3)	11.2(8.6-14.3)	35.7(20.0-61.2)
3	-	77.0(56.1-89.1)	10.7(6.9-12.7)	32.1(17.3-46.8)
<b>Grand mean</b>		<b>77.4(56.1-92.3)</b>	<b>10.8(6.9-14.3)</b>	<b>32.7(14.7-61.2)</b>

a) Age from seed.

b) Diameter at breast height (1.37 m).

Table 3. — Analyses of variance of bole traits presented as intraclass correlation coefficients (the ratio of individual variance components to the sum of all components).

Source	df	Height	DBH <sup>a)</sup>	Volume
Plantations	2	0	.041	.021
Sets	2	.021	.011	.016
Plantations x sets	4	.006	.001	.004
Replications/sets/plantations	27	.073	.069	.069
Families/sets	87	.036**	.022*	.025**
Plantations X families/sets	174	.023*	.038**	.034**
Plot error	778	0	.005	.015
Within plots	2258	.841	.813	.816

a) Diameter at breast height (1.37 m).

\*) Significant at the 0.05 level of probability.

\*\*\*) Significant at the 0.01 level of probability.

assumed to be either the standardized individual tree value for volume or the combined index value for this trait. In order to select for volume in stage 2 on the basis of the combined index, appropriate weights for individual-tree values and family means must be known. In addition, most if not all sibs of trees selected in stage 1 would need to be measured for height so that family means for volume can be estimated.

The more trees culled in stage 1, the lower the number of trees that will have to be measured for height, but the greater the probability of inadvertently culling trees with superior volume. Thus, we examined the influence of a range of culling levels in the first stage on the eventual gains in volume. We assumed the overall levels of culling after the second stage to be fixed at the same levels chosen previously for parental and progeny selection in a single stage.

## Results

Although the trees in one plantation were one year older than those in the other two, means for height, DBH, and volume were similar across all three sites (Table 2). Set means and the ranges of family means within sets were also similar. Analyses of variance indicated that the effects of plantations, sets, and the plantations x sets interaction were nonsignificant for all traits (Table 3). However, the effects of families/sets and plantations X families/sets were significant for all traits. The size of the plantations X family/sets variance is on the same order of magnitude as the families/sets variance, and thus should not be dismissed lightly. Nevertheless, data from only three of the 10 test sites in the Noti breeding unit are represented in our analysis, and an in-depth study of the magnitude and potential causes of genotype x environment interaction over all sets and plantations has not been done. For the purpose of

Table 4. — Estimates of means ( $\bar{x}$ ), phenotypic variances ( $\sigma_p^2$ ), additive genetic variances ( $\sigma_A^2$ ), and individual heritabilities ( $h^2$ ) for bole height, diameter (DBH), and volume. Standard errors are in parentheses.

Trait	$\bar{x}$	$\sigma_p^2$	$\sigma_A^2$	$h^2$
Height	77.4 dm	159.00 (4.1)	19.24 (5.8)	0.12 (0.04)
DBH	10.8 cm	5.82 (0.15)	0.44 (0.20)	0.08 (0.03)
Volume	32.7 dm <sup>3</sup>	262.46 (6.8)	22.01 (9.0)	0.08 (0.03)

Table 5. — Estimated genetic gains in bole volume resulting from various selection criteria.

Selection criterion	Parental selection <sup>a</sup>		Progeny selection <sup>b</sup>	
	G(%) <sup>c</sup>	RE(%) <sup>d</sup>	G(%) <sup>c</sup>	RE(%) <sup>d</sup>
Multitrait index	13.66	1.01	14.98	1.02
Volume	13.54	1.00	14.70	1.00
Height	12.43	.92	13.84	.94
DBH <sup>e</sup>	12.31	.91	13.28	.90

a) Best 6 parents out of 30 in each set selected on basis of mean progeny performance (selection intensity = 1.354).

b) Best 6 unrelated progeny in each set. Selection intensity (2.500) was calculated empirically (see text).

c) Gain as a percentage of the population mean for volume.

d) Relative efficiency: the percentage of volume gain relative to the gain expected when the selection criterion is volume.

e) Bole diameter at breast height (1.37 m).

this paper, therefore, all genetic parameter estimates are based on the pooled analyses (Table 1). The resulting parameter estimates are those appropriate when the goal of breeding is to produce genotypes which perform well, on average, across all three sites.

#### Single-Stage Selection

Differences among families-within-sets, though significant, accounted for only a small percentage of the total variance (Table 3), which indicates that the ability of this test to elucidate genetic variation among families (as reflected in the low estimates of individual-tree heritability in Table 4) is limited. Nevertheless, because of the large phenotypic variation observed in all three traits (Table 4), genetic gains in volume can still be substantial (Table 5).

Progeny selection produced estimated genetic gains 8% to 11% higher (depending on selection criteria) than those from parental selection (Table 5). The greatest estimated gains for both parental and progeny selection were obtained with the multitrait index but were only 1% to 2% better than gains from selection based on volume. Because the genetic correlations of height and DBH with volume were strong (0.83 and 0.94, respectively), indirect selection for volume was relatively efficient. For parents and progeny, indirect selection based on DBH measurements is expected to produce approximately 90%

of the gain obtained by direct selection; indirect selection based on height appears to be marginally more efficient than that based on DBH.

#### Two-Stage Selection

For various levels of culling in stage 1, estimated gains in volume after two-stage selection were compared to gains from single-stage selection based on volume (Figure 1). Although overall culling levels were assumed to be the same in single- and two-stage selection, the methods used to calculate gains from two-stage selection assume large populations. Thus, absolute gains calculated for parental selection in two stages were slightly greater than those in Table 5. This does not affect the relative efficiencies shown in Figure 1, however, because we assumed large population sizes in gain calculations for both single- and two-stage selection. The results indicate that 60% to 65% of the parents (families) (i.e., 18 to 20 of the 30 in each set) could be culled in stage 1 with little or no negative impact on ultimate volume gains.

Because the heritability of individual-tree volume is low (Table 4), two-stage progeny selection relying on breeding values from individual-tree performance in the second stage resulted in no more volume gain than could be obtained from a single indirect selection based on a combined index for DBH. However, two-stage progeny selection appears to be quite promising when selection in

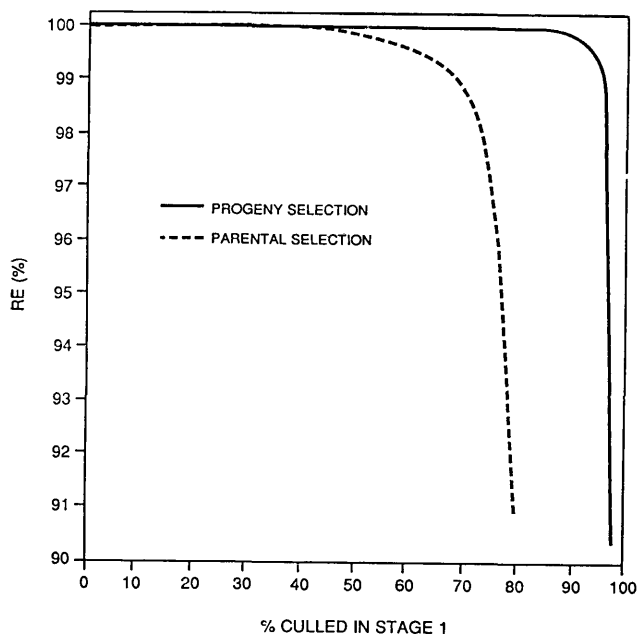


Figure 1. — Genetic gain in bole volume after two-stage selection in progeny tests relative to gain after selection in a single stage (RE). First-stage selection is based on DBH and second-stage (or single-stage) selection on volume. For parental selection, family means are used to rank parents. For progeny selection, individual tree rankings are based on a combined index which utilizes information on both individual-tree and family performance.

the second stage is based on a combined index (Figure 1). When more than 90% of the individuals were culled in the first stage, volume gain was not significantly less than would be achievable if all trees were measured for height. The remaining 10% of progeny represented an average of only 11 families per set. Thus, in this case, only about one-third of the families in each set would require height measurement.

#### Discussion and Conclusions

Despite the low heritabilities of height, DBH, and volume (Table 4), estimated gains for all selection criteria were higher for progeny than for parental selection (Table 5). Thus, for these data, progeny selection based on individual-tree performance combined with family means appears to be an efficient way of achieving genetic improvement in volume of young Douglas-fir. These results may not apply generally to other Douglas-fir breeding populations; relative gains from alternative orchard strategies should be compared for each situation before final decisions are made. Nevertheless, the importance of family information in progeny selection is emphasized in this study by the fact that, in the index equations, family means received 5 to 6 times the weighting of individual-tree values.

According to the calculations in this study, indirect selection based on DBH alone would result in 1% to 1.5% less volume per tree in 12- to 13-year-old coastal Douglas-fir than would be obtained from direct selection based on volume or the multitrait index (Table 5). Economic benefits from these small additional gains could be substantial when spread over the large acreages regenerated during the life of any one seed orchard. Thus, our results seem to justify the additional effort required for height measurement for both parental and progeny selection.

Nevertheless, when resources are limited, the decision to base single-stage selections on DBH or on volume may depend on the amount of additional effort needed for height measurements and on what other tree-improvement activities would be foregone, rather than on a simple cost/benefit evaluation.

Two-stage selection is an appealing alternative. For both parental and progeny selection, about two-thirds of the test trees in our study materials could be culled on the basis of DBH alone (stage 1), without significantly lower volume gains than those expected if the height of all trees had been measured. If weighting coefficients for the combined volume index were not known, both height and DBH measurements would be needed for all trees in 3 to 4 sets in order to develop the index for progeny selection. Nevertheless, because Douglas-fir progeny tests frequently contain 10 or more sets, two-stage selection would still result in considerable reduction of measurement costs. The ability to take advantage of two-stage selection, however, relies on the timely analysis of DBH data so that individuals and families can be identified for subsequent height measurement. The additional costs for these analyses need to be considered when evaluating the efficiency of two-stage versus single-stage selection alternatives. A method of determining the optimum allocation of selection intensity in two-stage selection which takes into account both potential gains and costs associated with the additional stage of selection is presented by NAMKOONG (1970).

The relevance of our results to other tree improvement programs needs to be considered in light of the age and quality of the test plantations in this study. Because stand density tends to affect bole diameter more than it affects height (HUSCH *et al.*, 1972), the heritability of DBH may be decreased proportionally more than that of height in tests with greater mortality. If the heritability of DBH were lower, the relative efficiency of indirect selection based on DBH, or of two-stage selection, would not be as high as reported here. Thus, the heritability of DBH must be part of the decision whether to include height measurements in a selection program for volume.

Even if the true breeding values are known, selecting for 15-year volume represents indirect selection for the true trait of interest, which is bole volume at harvest age. Thus, decisions about whether to measure 15-year-old trees for height, diameter, or both should account for the correlated response of bole volume at harvest age. At present, it seems reasonable to assume that bole volume breeding values for 15-year-old trees are the best available predictors of the same values at harvest age; however, it will be decades before actual juvenile/mature correlations will be available from Douglas-fir genetic tests. Assuming that the relationship between bole volume at early ages and that at harvest age is at least moderately strong, gains per year of effort will be greater if selections are made at early ages, and generations turned over more frequently, than when selections are made at harvest age (LAMBETH, 1980).

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# Impact of Crop Management Practices on Seed Yield in a Douglas-Fir Seed Orchard

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## Abstract

The impact of two crop-management practices, supplemental-mass-pollination (SMP) and overhead cooling, on seed yield in a 13-year-old seedling Douglas-fir [*Pseudotsuga menziesii* (MIRB.) FRANCO] seed orchard was studied. A 2 × 2 factorial trial of SMP/no SMP and cooling/no cooling was applied to four genetically similar blocks of trees. Potential seed yield per cone, average number of successful fertilizations, and average number of filled seeds per cone all showed no significant differences between cooling or SMP treatments and among cooling × SMP treatment combinations. These results indicated that the within-orchard pollen cloud was not a factor limiting seed yield. The average number of seeds infested by the Douglas-fir seed wasp (*Megastigmus spermotrophus* WACHTL) larva was significantly ( $P < 0.05$ ) less when cooling was applied, indicating that the treatment was effective in disrupting the synchrony between presence of ovipositing females and developing cones. It is concluded that the cooling was effective in reducing seed loss due to insect damage and that the added benefits of the SMP and/or cooling in mature Douglas-fir seed orchards are quality oriented rather than quantity oriented.

**Key words:** Douglas-fir, seed orchards, supplemental mass pollination, overhead cooling, seed potential.

## Introduction

Supplemental mass pollination (SMP), the broadcast application of viable pollen to un-isolated strobili, is a common crop-management practice in most Douglas-fir [*Pseudotsuga menziesii* (MIRB.) FRANCO] seed orchards in coastal British Columbia. Since its introduction by WAKELEY *et al.* (1966), the technique has been used to 1) broaden the genetic base by introducing desirable genotypes into seed orchards (WOESSNER and FRANKLIN, 1973; DENISON and FRANKLIN, 1975; HADDERS, 1984), 2) produce inter-specific hybrid seeds (WAKELEY *et al.*, 1966; HYUN, 1969; JOLY and ADAMS, 1983), 3) reduce self-fertilization (WOESSNER and FRANKLIN, 1973; EL-KASSABY and RITLAND, 1986a; EL-KASSABY and DAVIDSON, 1990), pollen contamination (EL-KASSABY and RITLAND, 1986a; EL-KASSABY and DAVIDSON, 1990), and ovule abortion (BRIDGWATER and BRAMLETT, 1982), 4) improve parental balance (EL-KASSABY *et al.*, 1986, 1989; EL-KASSABY and REYNOLDS, 1990; REYNOLDS and EL-KASSABY, 1990), and panmixis (EL-KASSABY *et al.*, 1984, 1986, 1988; FASHLER and EL-KASSABY, 1987), and 5) increase seed yield (DANIELS 1978; BRIDGWATER and TREW, 1981; BRIDGWATER and BRAMLETT, 1982; HADDERS, 1984; WEBBER, 1987; EL-KASSABY and REYNOLDS, 1990) and genetic gain (DENISON and FRANKLIN, 1975).

Overhead cooling of seed-orchard trees, another crop-management practice, was proposed as means of reducing orchard contamination by delaying reproductive bud development relative to background pollen sources (SILEN and KEANE, 1969). This procedure provides temporal isolation of pollen contamination (FASHLER and DEVITT, 1980; EL-KASSABY and RITLAND, 1986b; FASHLER and EL-KASSABY, 1987; EL-KASSABY and DAVIDSON, 1990) and is effective in

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