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Evaluating Efficacy of Early Testing for Stem Growth in Coastal Douglas-fir¹⁾

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Abstract

In a test to evaluate the ability to predict stem growth of families in the field from nursery performance (i.e., early testing), 67 open-pollinated families and 66 full-sib families of coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* MIRB. (FRANCO)) were sown in two nursery conditions, each replicated as separate experiments: two bareroot nursery trials established in successive years in the same nursery, and two container-sown greenhouse trials sown in different greenhouses in the same year. First-year heights in the seedling trials were compared to mean stem volumes of the same open-pollinated families in eight 15-year-old field progeny tests and the same full-sib families in eleven 12-year-old tests.

Family mean nursery-field correlations (r_{xy}) were similar for all four seedling trials for both open-pollinated (OP) and full-sib (FS) families, and generally ranged between 0.30 and 0.40. Although low, it is shown that nursery-field correlations of this magnitude can be quite useful in tree improvement programs. For example, based on the data in this study, it is estimated that a single-stage of family selection for first year seedling height would be about 50% as effective in improving 15-year volume as direct selection for this trait in field tests. Early testing, however, is probably of more practical significance as a tool for culling families prior to out-planting field tests in two-stage selection schemes. It is estimated that 25% of the OP families in this study could have been culled in an early test (first-stage selection), with gain in 15-year volume after subsequent field testing and selection of the remaining families (second-stage selection) being nearly the same as if all families had been field tested. Thus, early testing is an effective tool for reducing the size and cost of field progeny tests without sacrificing genetic gain.

Key words: *Pseudotsuga menziesii*, early selection, two-stage selection, genetic parameters, nursery-field correlations, genotype X environment interaction.

Introduction

Because of the long rotation lengths typically used in forestry, early evaluation of genotypes is often an important component of tree improvement programs (e.g., LAMBETH *et al.*, 1982; LAMBETH, 1983; TALBERT and LAMBETH, 1984; LOWE and VAN BULJTENEN, 1989; CARTER *et al.*, 1990; BRIDGWATER and MCKEAND 1997). Early evaluation can be used in a number of ways, but in this paper, we refer exclusively to *early testing*

defined by LAMBETH, (1983) as the “process whereby trees are selected after being grown at close spacing in a greenhouse, growth chamber or nursery for one or two years.” Early testing can be used to select superior progeny, families, or parents, based on progeny performance.

Early testing may have one of two primary applications in tree improvement programs:

1) *Early single-stage selection* – Superior genotypes are identified based on seedling performance in order to shorten generation intervals and increase genetic gain per unit of time.

2) *Multiple-stage selection* – Screening at the seedling stage is used to identify and cull poor-performing genotypes prior to the establishment of field tests. Final selections are based on one or more additional stages of evaluation in the field. Early testing makes it possible to reduce the size of field tests, thereby increasing their statistical precision and reducing their cost.

Tree breeders may be reluctant to rely on early testing alone because some traits cannot be scored at the seedling stage. Thus, multiple-stage selection may be the most valuable application of early testing. Multiple-stage selection for disease resistance for example, is used routinely (e.g. PHELPS, 1977; WACKINSHAW *et al.*, 1980). There are fewer examples of multiple-stage selection being used for growth (LOWE and VAN BULJTENEN, 1989) although this would be highly desirable if it can be done effectively.

In this paper, we first review the factors influencing the efficacy of early testing in tree improvement programs, then evaluate the potential of early testing for stem growth in coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* MIRB. (FRANCO)). In our analyses, we assume that the purpose of

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early testing is to select the best families of older, field-grown trees based on seedling performance.

Early Testing Theory

Early Single-stage Selection

Early single-stage selection can be thought of as a special case of indirect selection. In the case of family selection, the correlated response in the trait of interest in older, field-grown trees from selection of families at the seedling stage (SSR_y) is:

$$SSR_y = i h_x h_y r_{Gxy} s_y \quad (1)$$

where i is the intensity of selection practiced on families at the seedling stage; h_x and h_y are the square-roots of the family heritabilities for the seedling trait (x) and the field trait (y); respectively; r_{Gxy} is the genetic correlation between the seedling and field traits; and s_y is the phenotypic standard deviation among family means for the field trait.

Environmental covariance between traits measured on seedlings and field-grown trees in the same families should be zero. This is because trees from the two ages are grown in different environments. In addition, any common maternal effects (i.e. due to common seed size or nutritional status) are expected to become minimal within only a few years after planting (ST. CLAIR and ADAMS, 1991; SURLLES *et al.*, 1993). Given that the environmental covariance is zero, the phenotypic correlation between family means for seedling and field traits (r_{xy}) is:

$$r_{xy} = r_{Gxy} h_x h_y \quad (2)$$

$$\text{and } SSR_y = i r_{xy} s_y \quad (3)$$

This relationship demonstrates that the effectiveness of early testing is a function of r_{xy} , something that can be readily measured and interpreted.

To assess the efficacy of early testing in a single stage of selection, the relative efficiency of early single-stage testing (RE_{SS}) can be calculated as the expected correlated response in a field trait from early testing divided by the expected response when the field trait is selected directly (i.e., at the older age, R_y):

$$RE_{SS} = SSR_y / R_y \quad (4)$$

$$\text{and } R_y = i h_y^2 s_y \quad (5)$$

Assuming the same intensity of selection at both ages:

$$RE_{SS} = r_{xy} / h_y^2 \quad (6)$$

RE_{SS} , however, does not account for the reduction in generation time when final selections are based on early single-stage testing. A better measure for evaluating the efficacy of early single-stage selection is the ratio of the responses per unit of time of the selection regimes (E_t), defined by LAMBETH (1983) as:

$$E_t = \frac{(SSR_y / T_x)}{(R_y / T_y)} = RE_{SS} \cdot T_y / T_x \quad (7)$$

where T_x and T_y are the generation intervals under the early testing and field testing regimes, respectively. Thus, early single-stage selection will be more efficient than field selection when $RE_{SS} > T_x / T_y$.

Assuming 13 years to 15 years of field testing (SILEN and WHEAT, 1979; JOHNSON *et al.*, 1997), T_y in coastal Douglas-fir is expected to range between 16 and 20 years, depending on the complexity of the mating design, whereas T_x is expected to range between 6 and 12 years, depending on the mating design and whether early selection occurs after 1 or 2 years of testing (D. L. COPES, USDA Forest Service, Pacific Northwest Research Station, and N. WHEELER, Weyerhaeuser Co., pers comm.). Therefore, T_x / T_y is expected to range between 0.30 and 0.75, and a $RE_{SS} > 0.50$ would often be sufficient, for single-stage

early testing to be more efficient than field selection. Given that family heritabilities for growth traits often range from 0.60 to 0.80 in field tests, an r_{xy} of only 0.30 to 0.40 is required for RE_{SS} to exceed 0.50.

Multiple-stage Selection

In multiple-stage selection culling occurs sequentially, with each stage of selection further truncating the population. In this paper, we examine two-stage selection, where the first stage is based on early test results, and the second stage is based on field measurements.

The theory for estimating the overall response from two-stage selection is based on the properties of the bivariate normal distribution. The expected response in the additive breeding value of a variable, z , from two-stage selection in a large population (Z , expressed in standard deviation units of z) is given by COTTERILL and JAMES (1981, Equation 6) as:

(8)

$$\Delta Z = i_1 r_{vz} + i_2 [(r_{wz} - r_{vw} r_{vz} H) / (1 - r_{vw}^2 H)^{1/2}]$$

where trait v is selected in the first stage and trait w in the second stage, respectively; r_{vz} , r_{wz} , and r_{vw} are phenotypic correlations between the traits; and, $H = i_1 (i_1 - v_1)$, where v_1 is the value of trait v at the point of truncation of selection in the first stage, expressed in standard deviations from the mean. This equation assumes that w and z remain jointly normally distributed after stage-1 selection truncates the population. This is not strictly the case, but when COTTERILL and JAMES (1981) compared response calculations based on equation 8 to more complicated, but exact, gain formulations (NAMKOONG, 1970), the differences were always small (less than 1%). In the case of early testing, the first stage of family selection is based on seedling trait x in the nursery, the second stage on field trait y , and the response variable of interest is the additive breeding value of y . The correlations in equation 8 then become: $r_{vz} = r_{Gxy} h_x$, $r_{wz} = h_y$, and $r_{vw} = r_{xy}$. The expected response in y from two-stage selection expressed in absolute units (TSR_y) is:

(9)

$$TSR_y = i_1 r_{Gxy} h_x h_y \sigma_y + i_2 \sigma_y [(h_y^2 - r_{xy} r_{Gxy} h_x h_y H) / (1 - r_{xy}^2 H)^{1/2}]$$

where $H = i_1 (i_1 - x_1)$. Assuming, as done in the previous section, that the environmental correlation between traits measured in the two stages is zero (i.e., $r_{xy} = r_{Gxy} h_x h_y$), equation 9 can be written as:

(10)

$$TSR_y = i_1 r_{xy} \sigma_y + i_2 \sigma_y [(h_y^2 - r_{xy}^2 H) / (1 - r_{xy}^2 H)^{1/2}]$$

where $i_1 r_{xy} s_y$ is the gain expected from selection in the early test, using a selection intensity of i_1 (see Equation 3), and the remainder is the gain expected when selection intensity i_2 is practiced in the truncated population of the field test.

The relative efficiency of two-stage selection (RE_{TS}) compared to single-stage field selection is:

$$RE_{TS} = TSR_y / R_y \quad (11)$$

RE_{TS} depends primarily on two factors: the magnitude of r_{xy} relative to h_y^2 , and the proportion of individuals culled at the seedling stage. This is illustrated in *figure 1*; where we assume $h_y^2 = 0.60$, and the overall proportion of the original population selected after two stages is 20%. With r_{xy} as low as 0.3 to 0.4, 30% to 40% of the test families could be culled at the seedling stage with nearly the same response in the field trait as if all selections were based on field testing. Note, when r_{xy} is 0.50,

RE_{TS} in this scenario exceeds one. This result is addressed in the discussion.

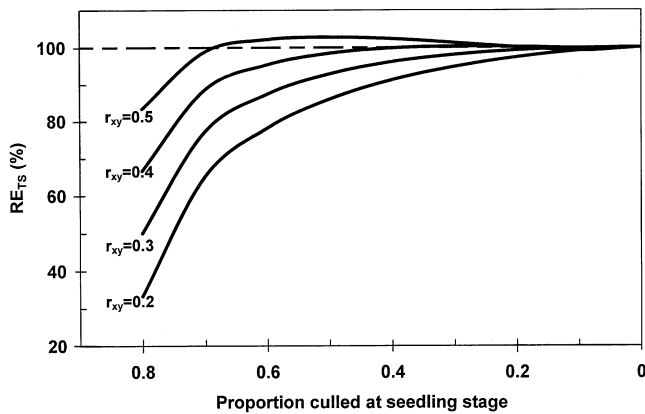


Fig. 1. – Expected genetic gains from two-stage truncation selection [early (seedling) testing plus field selection] of families relative to gains expected from field selection alone (RE_{TS}), for different seedling-field correlations (r_{xy}) and levels of culling at the seedling stage. Based on the methods of COTTERILL and JAMES (1981), assuming the family heritability for the trait selected at the field stage is 0.60 and the final proportion of the original families remaining after all selection is 0.20.

Results from retrospective studies of early testing, where the performance of families in early tests is compared to the same families in older, previously-established field tests, have been reported for a number of coniferous species (e.g., CANNELL *et al.*, 1978; LAMBETH *et al.*, 1982; RIITERS and PERRY, 1987; LOWE and VAN BUIJTENEN, 1989; FRANKLIN, 1989; CARTER *et al.*, 1990; SMITH *et al.*, 1993; WU *et al.*, 1997; JANSSON *et al.*, 1998; HANNERZ *et al.*, 1999). These studies generally show only weak to moderate correlations between family means for seedling and field traits. In Douglas-fir, for example, the average r_{xy} found between seedling height and field height ranged from 0.05 to 0.54 (LAMBETH *et al.*, 1982; RIITERS and PERRY, 1987). For total seedling dry weight and field height, r_{xy} ranged from 0.22 to 0.54 (RIITERS and PERRY, 1987; LAMBETH *et al.*, 1982). Thus, one question of interest is what magnitude of r_{xy} can be expected when early testing is used.

The magnitude of r_{xy} is influenced both by the seedling trait and the early test environment. If genotype-by-environment interactions are strong among seedling test environments, and if test environments differ in their ability to predict field performance as a result, the choice of test environment becomes critical to the success of early testing. In Douglas-fir, however, little genotype-by-environment interaction has been observed among early test environments, especially when more extreme

environments are removed from consideration (LAMBETH *et al.*, 1982; RIITERS and PERRY, 1987). This result, however, may be partly due to the small numbers of families used in earlier investigations (typically 20 or fewer), resulting in poor statistical precision (LASCoux and KREMER, 1994).

In this study, we evaluate the magnitude and repeatability of r_{xy} between (1) seedling performance under more-or-less operational early testing environments and (2) stem volume in 12- to 15-year-old Douglas-fir trees. We used much larger numbers of families than in previous retrospective studies, and included both open-pollinated and full-sib families. In addition, we evaluated the relative efficiency of early selection for volume growth under both single and two-stage selection scenarios using field data available from the open-pollinated families.

Materials and Methods

Materials

Sixty-seven open-pollinated (OP) and 66 control-pollinated, full sib (FS) progenies were included in this study (Table 1). The OP families belonged to sets # 2 (20 families), # 4 (23 families) and # 5 (24 families) of parent trees selected from natural stands throughout the Noti breeding unit (52,000 ha, below 650 m elevation) in the central Oregon coast range (SILEN and WHEAT, 1979). The FS families were sampled from sets # 75 (35 families) and # 77 (31 families) of two-parent crosses made by the British Columbia Ministry of Forests Coastal Douglas-fir Tree Improvement Program. Parent trees used in the crosses came from southwestern British Columbia. Crosses were originally made in a six-tree disconnected half-diallel mating design, with a total of 150 crosses in set # 75 and 135 in set # 77. Because of limited availability of stored seed, however, the families included in the study were sampled from several half-diallels in each set, with the only criterion for selection being to minimize the relatedness among parents in the different crosses.

Field Tests

For the OP families, 1-0 containerized seedlings were planted on eight test sites within the Noti Breeding unit from 1972 to 1975. Each set of families was established as a different randomized complete block design experiment with 4 replications on each site (Table 1). Families were represented by a four-tree non-contiguous plot within each block. Seedlings were planted at a 3.05 m x 3.05 m spacing and the plantations were fenced to exclude large herbivores. Tree height and breast-height (1.37 m) diameter (DBH) were measured at age 15 years from seed. Stem volume was estimated using the equation described by ADAMS and JOYCE (1990) for young Douglas-fir. At this age, average survival across all test sites was 72%.

Table 1. – Origin, number of families, experimental design and number of field test sites for the open-pollinated (OP) and full-sib (FS) materials included in the study.

Family type	Origin	Families	Field test sites	
			Experimental design	Number
OP	Sets 2, 4, and 5, Noti breeding unit, central Oregon coast	67	Same sites for all sets. On each site, each set with 4 randomized blocks; each family represented by one 4-tree non-contiguous plot in each block.	8
FS	Sets 75 and 77, SW British Columbia, B.C. Ministry of Forests coastal Douglas-fir improvement program	66	Separate sites for each set. On each site, 4 randomized blocks with each family represented by one four-tree row plot in each block. Exception was 5 of 11 sites for set 75 which had 2 blocks and 9-tree row plots.	11

Sets # 75 and # 77 of FS families were planted in separate field tests in 1976 and 1978, respectively, using 1-0 containerized seedlings. Each set was planted at 11 test sites, using a randomized complete block design at each site (Table 1). Six of the set # 75 tests had four replications per site with each family represented by a four-tree row plot. The remaining five tests had two replications per site with nine-tree row plots.

All of the set # 77 tests had four replications per site with four-tree family row plots in each block. Stem volume was estimated from height and DBH measurements made when the trees were 12-years old from seed. At this time, survival averaged 90% for the set # 75 plantations and 91% for Set # 77.

Nursery Tests

Both the OP and FS families were sown as germinants into two early testing regimes, "bareroot" and "container". Each testing regime was replicated twice. In the bareroot regime, germinants were sown directly into a nursery in the state of Washington (WA), at a spacing of 8.9 cm within rows, and 15.0 cm between rows. Replication was achieved by sowing the entire experiment in two separate years, 1986 and 1987, in adjacent beds. Within each year, the experimental design was a split-split plot with nine blocks (Figure 2). Family types (OP and FS) were main plots, family sets (within family type) were subplots, and families-within-sets were represented by 4-tree-row sub-subplots. Seedlings were grown using standard operational practices, except that no pre-emergent herbicides were used and the seedlings were not top- or root-pruned. The beds were hand-weeded until seedlings were old enough to survive herbicide applications. Due to poor emergence and survival in some of the blocks, 2 blocks in the 1986 test and 3 blocks in the 1987 test were excluded from the final analyses. Survival in the remaining blocks was 78% in the 1986 test and 90% in the 1987 test.

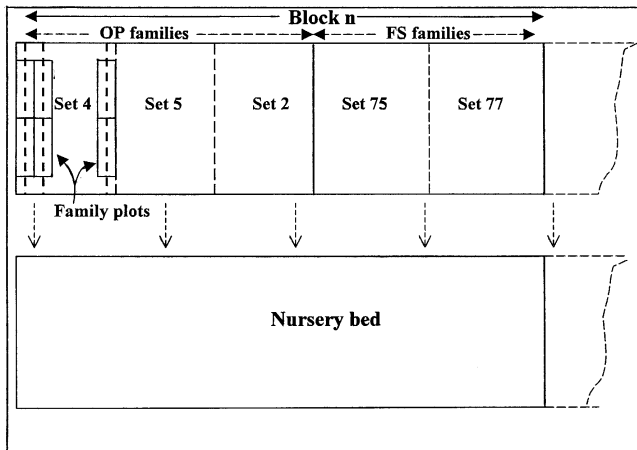


Fig. 2. – Experimental layout used for each nursery trial. The bareroot regime was replicated in two years (1986 and 1987); the container regime was replicated in two greenhouses (WA and OR, see text).

In the container regime, germinants were sown in 1987 into Ray Leach Super Cells (164 cm³) filled with a standard greenhouse medium. The entire experiment was replicated in two commercial greenhouses, one in WA, the other in Oregon (OR). The greenhouse tests had the same experimental design as the nursery tests (Figure 2), but with eight blocks. The containerized seedlings were grown using similar standard operational practices in both greenhouses, except that the onset of water stress in the WA greenhouse occurred earlier (early July), and more abruptly than in the OR greenhouse (late July). This reduced first-year growth in the WA greenhouse. Due to poor

emergence and survival in the WA greenhouse, the eight original blocks were consolidated into six blocks. Survival in the final blocks was 98% in OR and 97% in WA. Seedlings were grown for one season in the greenhouse, then transplanted into two bareroot nurseries for a second year of growth. In each nursery trial, seedling height was measured to the nearest mm at the end of the first and the second growing seasons. Because analyses of the first- and second-year heights yielded similar results, only first-year height will be considered in this paper.

Genetic Parameters

Genetic parameters for 15-year stem volume in the OP families were estimated using the data pooled over the eight test sites, because the tests were located within a single breeding zone. Variance components were estimated using the REML option of PROC VARCOMP (SAS, 1990) and the following linear model for individual-tree data:

$$(12)$$

$$Y_{ijklm} = \mu + T_i + S_j + TS_{ij} + B_{k(ij)} + F_{l(ij)} + TF_{il(ij)} + e_{ijkl} + w_{ijklm}$$

where y_{ijklm} is the performance of individual m from family l in block k of set j and test site i ; μ is the overall mean; T_i is the random effect of the i^{th} test site [$E(T_i) = 0$, $\text{Var}(T_i) = s^2_{T_i}$]; S_j is the random effect of the j^{th} set [$E(S_j) = 0$, $\text{Var}(S_j) = s^2_{S_j}$]; TS_{ij} is the random interaction effect of the i^{th} test site and j^{th} set [$E(TS_{ij}) = 0$, $\text{Var}(TS_{ij}) = s^2_{TS_{ij}}$]; $B_{k(ij)}$ is the random effect of the k^{th} block in the j^{th} set and i^{th} test site [$E(B_{k(ij)}) = 0$, $\text{Var}(B_{k(ij)}) = s^2_{B_{k(ij)}}$]; $F_{l(ij)}$ is the random effect of the l^{th} family in the j^{th} set [$E(F_{l(ij)}) = 0$, $\text{Var}(F_{l(ij)}) = s^2_{F_{l(ij)}}$]; $TF_{il(ij)}$ is the random interaction effect of the i^{th} test site and l^{th} family within the j^{th} set [$E(TF_{il(ij)}) = 0$, $\text{Var}(TF_{il(ij)}) = s^2_{TF_{il(ij)}}$]; e_{ijkl} is the random plot error of the l^{th} family in the k^{th} block of the j^{th} set in the i^{th} test site [$E(e_{ijkl}) = 0$, $\text{Var}(e_{ijkl}) = s^2_{e_{ijkl}}$]; and w_{ijklm} is the within-plot error [$E(w_{ijklm}) = 0$, $\text{Var}(w_{ijklm}) = s^2_{w_{ijklm}}$]. Family heritability (h^2_f) was estimated as:

$$h^2_f = (\sigma^2_F) / (\sigma^2_{\bar{p}}) \quad (13)$$

where $s^2_{\bar{p}} = s^2_F + (s^2_{TF}/t) + (s^2_e/tb) + (s^2_w/tbh)$ is the phenotypic variance of family means (NAMKOONG, 1979); t is the number of test sites; b is the number of replications; and h is the harmonic mean number of trees per plot. Since most of the unbalance was at the within-plot level (i.e., in the number of trees per plot), this approach provides an acceptable level of approximation for $s^2_{\bar{p}}$. Family heritability estimated this way is appropriate for estimating gains from deployment of selected families in a planting program (i.e., without further mating). If the individuals within OP families are related as half-sibs (i.e., coefficient of relationship = 0.25), h^2_f estimated in this manner is equivalent to the proportion of variation among family means due to additive genetic effects (i.e., narrow-sense family heritability). Because individuals within OP families of Douglas-fir are thought to be more closely related than half-sibs (CAMPBELL, 1986), narrow-sense family heritability is probably slightly lower than this h^2_f estimate.

For the FS families we only had field data on family means of stem volume across all test sites at age 12, so we did not estimate heritability for this trait. However, analysis of variance done by the B.C. Ministry of Forests over all families and test sites for each set showed significant ($p < 0.05$) family differences in volume growth at this age (A. YANCHUK, B.C. Ministry of Forests, pers. comm.).

Variance analyses for seedling data were done separately for each nursery test replicate (i.e., two bareroot and two container tests), because each replicate was designed to stand alone as an independent early test. Analyses of variance using PROC

GLM showed significant ($p < 0.05$) family-within-Set differences in first-year height for both types of families, and variance components were estimated using the REML option of PROC VARCOMP (SAS, 1990) with the same model as for field data (Equation 12), but without the terms for test site and with “blocks” as a crossed factor instead of nested within Sets. To compare the precision of early tests, h^2_f was estimated for each type of family using equation 13.

Although family means for first-year height growth were positively correlated with seed weight, unadjusted values were used in our analyses, because they provided slightly higher estimates of h^2_f and similar estimates of r_{xy} with volume growth in the field tests, when compared to the adjusted values. There is evidence from other studies that the relationship between seed weight and early seedling growth has genetic as well as environmental components, and adjustments may reduce useful genetic variance (SORENSEN and CAMPBELL, 1993; SURLLES *et al.*, 1993).

The ability of each early testing regime to predict field performance of families was evaluated by comparing estimates of r_{xy} . The correlation between seedling height and volume growth in the field was estimated as the PEARSON’S correlation between those traits using family-mean values. This was done separately for each Set of families (i. e., Sets # 2, # 4 and # 5 in OP families and Sets # 75 and # 77 in FS families), then weighted mean estimates of r_{xy} across sets were calculated for each type of family and test replicate using the methods described in STEEL *et al.* (1997; Section 11.5). A c^2 test of heterogeneity was used to compare the magnitude of mean r_{xy} estimates between test replicates and nursery regimes.

Similar values of r_{xy} in different seedling tests do not necessarily mean that families are ranked the same in the different tests. To help evaluate the similarity of r_{xy} estimates and the repeatability of family rankings, a VARCOMP analysis was done for all pair-wise combinations of nursery trials with data standardized for each trial ($\mu=0$, $s^2=1$). Type-B genetic correlations (r_g , BURDON, 1977) were subsequently estimated using the equation:

$$r_g = (\sigma^2_F) / (\sigma^2_F + \sigma^2_{TF}) \quad (14)$$

where s^2_F and s^2_{TF} are the REML variance components for family and for test x family interaction, respectively. LU *et al.*, (1999) showed that this method provides satisfactory estimates even when the data are slightly or moderately unbalanced as long as the data are standardized to remove scale effects between trials.

Potential for Early Testing

The efficacy of early testing was examined by calculating RE’s for both single and two-stage selection, with parameters

estimated for OP families in the field (i.e., pooled across all sites) and in each nursery trial (i.e., separately for each replicate). For single-stage selection, RE was estimated using equation 6; for two-stage selection, using equation 11. Two scenarios were considered for two-stage selection, the use of early testing (1) to reduce field test size; and, (2) to increase overall selection intensity. In both scenarios, we assumed a maximum of 300 families can be tested in the field and that 60 (20%) of the families will be retained after both stages of selection. In scenario 1, 300 families are tested at the seedling stage, and 25% of them are culled in the nursery ($i_1=0.424$) on the basis of first-year height. The remaining 225 families are tested in the field and final selections (60 families) are made on the basis of stem volume at age 15 ($i_2=1.233$). In scenario 2, 400 families are tested at the seedling stage, 25% are culled in the nursery ($i_1=0.424$), and 300 are field tested, with final selections (60 families) made on the basis of volume growth ($i_2=1.400$).

Results

Genetic Parameters

For OP families, 15-year stem volume averaged 57.3 dm³ across the eight field tests. Families within sets varied widely in this trait, with mean values ranging from 45.5 dm³ to 68.3 dm³. The estimated h^2_f was 0.68. Twelve-year stem volume averaged 22 dm³ and 18.4 dm³ for sets # 75 and # 77. Stem volume also ranged widely among families (14.4 dm³ to 28.0 dm³ in Set # 75 and 12.2 dm³ to 24.1 dm³ in Set # 77). Narrow-sense family heritability for stem volume estimated using all diallel crosses made in each set was 0.88 for set # 75 and 0.89 for set # 77 (A. YANCHUCK, B.C. Ministry of Forests, pers comm.). This suggests that if we had calculated h^2_f for the subset of FS families used in the early testing analysis, that estimate would be similar in magnitude or greater than what was found in the field for the OP families.

Average first-year height for both family types was fairly similar in three of the nursery trials (Table 2). However, average seedling height for both OP and FS families in the OR greenhouse was over 50% greater than in the other nursery trials, probably because of the extended growing period in that greenhouse. Despite this difference, comparable ranges of variation among family means within sets were observed for seedling height across all nursery trials. An exception was the FS families in the OR greenhouse, which showed a much wider range of variation (Table 2), primarily because three families (one from Set # 75 and two from Set # 77) grew poorly in this trial (below 130 mm). Family heritabilities for first-year height were similar in the different nursery trials for each family type, and were similar in magnitude to h^2_f for stem volume across the field test sites, averaging 0.71 and 0.83, respectively, for OP and FS families (Table 2).

Table 2. – Estimates of overall means, ranges of family means within sets, and family heritabilities (h^2_f) for first-year height (mm) in nursery trials, and family-mean correlations (r_{xy}) between this trait and stem volume in field tests for open-pollinated (OP) and full-sib (FS) families.

Nursery trial	OP Families				FS Families			
	Mean	range	h^2_f [†]	r_{xy}	Mean	range	h^2_f [†]	r_{xy}
Bareroot:								
1986	142	107-174	0.74	0.31	142	110-174	0.79	0.31
1987	167	135-194	0.79	0.34	157	128-183	0.83	0.39
Container:								
OR	265	232-292	0.73	0.30	241	112-284	0.88	0.32
WA	167	150-186	0.56	0.36	160	126-183	0.80	0.57
Mean			0.71	0.33			0.83	0.40

[†] Upper bound estimates of the standard error of h^2_f (DICKERSON, 1969) ranged 0.17 to 0.18 (mean = 0.18) in OP families and 0.24 to 0.26 (mean = 0.25) in FS families.

Table 3. – Estimated type B genetic correlations in first-year seedling height between pairs of nursery trials for open-pollinated families (above the diagonal) and full-sib families (below the diagonal).

Nursery trial	Bareroot 1986	Bareroot 1987	Container OR	Container WA
Bareroot 1986	----	0.99	0.63	0.60
Bareroot 1987	1.00	----	0.63	0.63
Container OR	0.49	0.50	----	0.80
Container WA	0.72	0.80	0.53	----

Table 4. – Relative efficiency (RE, expressed as %) of early selection for stem volume in 15-year-old trees of OP families based on single stage (first-year height in early test) or two-stage selection (early testing plus field selection for 15-year volume), for different seedling trials^a.

Nursery trial	Single-stage	Two-stage ^b	
		Scenario 1	Scenario 2
Bareroot:			
1986	45.6	98.0	109.4
1987	50.0	98.5	109.8
Container:			
OR	44.1	97.8	109.2
WA	52.9	98.8	110.0

^a Relative efficiency is expected response in 15-year stem volume from early testing alone or by two-stage selection, divided by the expected response in stem volume if all selection takes place at age 15.

^b Two-stage selection scenarios assume a maximum of 300 families can be tested in the field, with a goal of 60 families remaining in the final selected population (after both stages of selection). In scenario 1, 300 families are tested at the seedling stage and 25% (75) families culled; the remaining 225 families are tested in the field. In scenario 2, 400 families are tested at the seedling stage; 25% (100) are culled, and 300 are subsequently field tested.

Seedling-field correlations (r_{xy}) were relatively homogeneous among nursery trials; ranging between 0.31 and 0.36 (mean = 0.33) for OP families and between 0.31 and 0.57 (mean = 0.40) for FS families (Table 2). In fact, in both cases the c^2 test was non-significant, suggesting that nursery test conditions did not influence seedling-field correlations.

Type-B genetic correlations (r_g) for first-year height were essentially unity between bareroot replicate trials for both family types, and moderately strong (0.49 r_g 0.80; mean = 0.64) for all other pair-wise comparisons of nursery trials (Table 3). The lowest correlations were found for the FS families in comparisons where the OR greenhouse was involved, indicating that FS families were more interactive in the greenhouse trial, but not greatly so.

Potential for Early Testing

Given the homogeneity of r_{xy} estimates, relative efficiency of single-stage early selection for 15-year volume in OP families was similar across nursery trials, with values ranging between 44% and 53% (Table 4). Thus, in terms of response per unit of time, early selection for stem volume in these materials is expected to be more efficient than field selection under scenarios where flower induction and breeding can be completed rapidly.

For two-stage selection, RE across nursery trials under scenario 1 was nearly 100% (Table 4), so similar gains in volume growth could be obtained as for direct selection, but with reduced size of field tests. Under scenario 2, RE across nursery trials was around 110%. Thus, this scenario would produce higher gains than those expected from direct selection, primarily because of the higher cumulative selection intensity. Yet, this option would not increase the size of field tests over that required if only a single stage of field selection was employed.

The efficacy of two-stage selection for volume growth is illustrated using data for OP and FS families in the 1987

bareroot trial (Figure 3). These data are representative of what was observed in all nursery trials. In both scatter-plots, only one (out of 16) of the shortest 25% of the families at age 1 was among the largest for stem volume at age 15 (OP families) or age 12 (FS families) (coincidentally, the 10th ranked family in the field in both cases). Thus, early testing can be quite effective for identifying and culling families with the poorest potential for stem volume growth at later ages.

Discussion

Nursery-field Correlations: Single vs. Two-stage Selection

Although family mean correlations between seedling and field traits appear to be low in coastal Douglas-fir, they are large enough to be useful in tree improvement programs. If flowering can be stimulated at an early age, gain per unit of time in stem growth could be substantially increased with early single-stage selection. Alternatively, multi-stage selection can be valuable if long-term evaluation is desired. Compared to traditional single-stage selection, multi-stage selection could be used to achieve either greater genetic gain with no increase in field-testing, or about the same genetic gain with smaller field tests.

Early test environment did not influence the relative efficiency of early selection. Estimates of r_{xy} were relatively consistent across two different nursery testing regimes and replicates of these trials for both OP and FS families. In addition, precision of early tests (measured by h^2_p) was similar and repeatability of family rankings (measured by r_g) was relatively consistent across nursery trials in both family types.

The lack of significant differences in r_{xy} across nursery testing regimes is consistent with previous findings in Douglas-fir (LAMBETH *et al.*, 1982; RIITTERS and PERRY, 1987), and in other coniferous species (CARTER *et al.*, 1990; ERICKSSON *et al.*, 1993; JANSSON *et al.*, 1998). The primary interest of most pre-

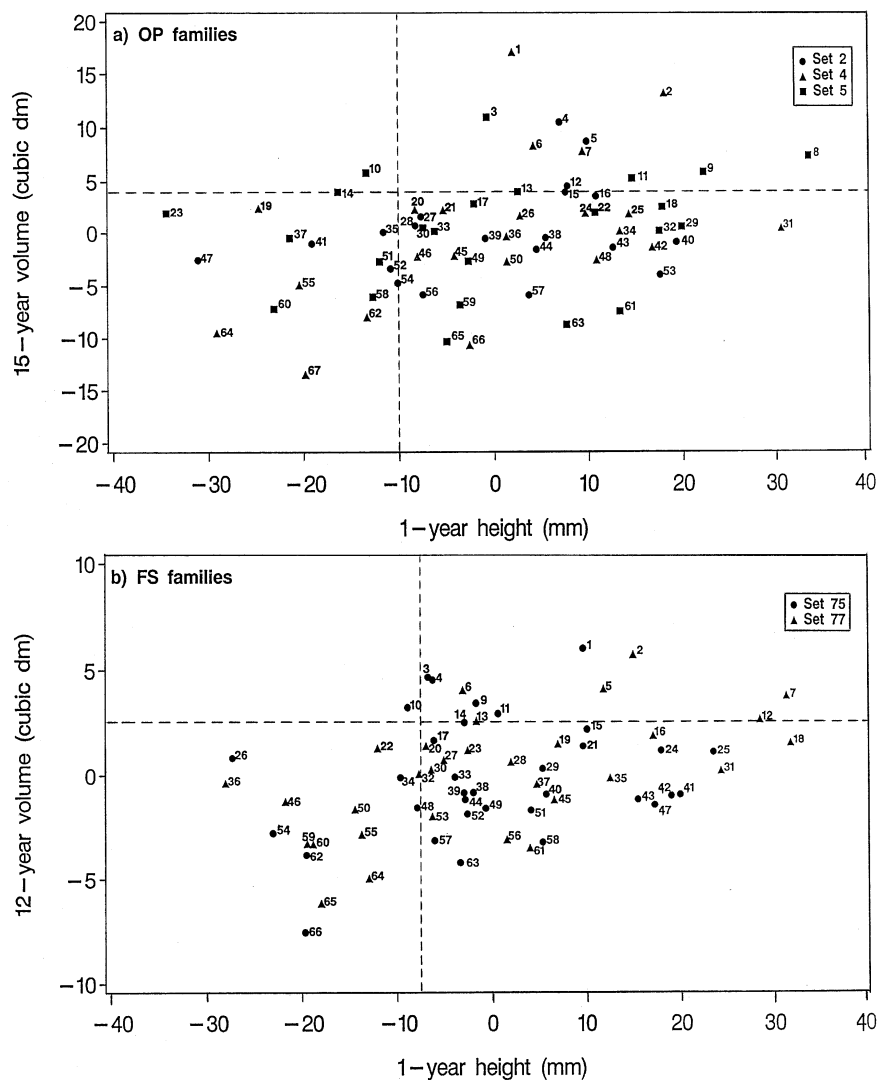


Fig. 3. – Scatter plots of mean first-year height in the 1987 bareroot nursery trial versus mean 15-year stem volume (over all test sites) for open-pollinated (OP) families (a; 67 total) and mean 12-year stem volume for full sib (FS) families (b; 66 total). Family means are expressed as deviations from respective set means. The shortest 25% of the families in the nursery trial occur to the left of the vertical dashed line, while the top 20% of the families for stem volume occur above the horizontal line. The numbers rank the families from best (1) to worst (66 or 67) for stem volume in the field. Only 65 out of 66 FS families are shown in the scatter plot because one family (ranked 8th in the field test) was missing in this nursery trial.

vious retrospective studies of early testing was to determine whether r_{xy} can be substantially improved by choosing the “most appropriate” test conditions (i.e., CANNELL *et al.*, 1978; LAMBETH *et al.*, 1982; RITTERS and PERRY, 1987). Even though those experiments are somewhat difficult to interpret because of the small numbers of families generally used, there is little evidence that r_{xy} is substantially improved by altering growing conditions, as long as they are generally favorable. However, extreme early test environments that are particularly sub-optimal (very high or very low nutrient concentrations, etc.) can reduce r_{xy} (LI *et al.*, 1991; ERIKSSON *et al.*, 1993). An exception might be when selection for growth in particular stress conditions is of interest (e.g., drought, cold, disease) and the nursery environment mimics these conditions (CANNELL *et al.*, 1978).

The magnitude of r_{xy} and RE also depends on the seedling trait used for early selection (LAMBETH *et al.*, 1982; RITTERS and PERRY, 1987). In this study, first-year height had similar genetic control and similar r_{xy} with stem volume growth in the

field as two-year height, and both height traits were consistently the best predictors of field growth performance when compared to several other seedling traits measured in the nursery trials (ADAMS, unpublished). First-year height is a desirable trait to use for selection because it is easy to measure and is evaluated in the first growing season. Because Douglas-fir progeny tests are generally established with one-year-old stock, early test results obtained in the first growing season would avoid any unnecessary delay in field planting, reducing the generation interval. This is of particular value in two-stage selection. If all families are sown in the early test at the same time they are sown for producing field-test planting stock, information will be available at the time of lifting to cull the poorer families. Correlations between seedling and field performance might also be improved by including multiple seedling traits in an index (SMITH *et al.*, 1993).

Two-stage selection would even be more efficient if the second stage of selection was based on an index combining

family information for both the field and seedling traits (COTTERILL and JAMES, 1981; WU, 1998). Given that the index is needed in the second stage, the information required might be obtained along the way, although the population would have a slightly modified distribution after the first-stage of culling. COTTERILL and JAMES (1981), however, found that gains from independent culling without a stage-two index were nearly as good as those with the index, and indicated that two-stage selection without the second-stage index would usually be preferred because it is simpler to use.

Cost of Early Selection vs. Field Tests

Cost factors were not considered in our estimates of relative efficiency. Given that seedling tests are considerably less expensive than field-testing, the RE's of early testing for either single-stage indirect selection or two-stage selection are even more favorable, if gain per unit of cost is of greatest importance. The magnitude of the savings by utilizing early testing in two-stage selection (scenario 1) can be evaluated from typical costs of establishing, maintaining and measuring second-generation Douglas-fir progeny tests in the Pacific Northwest. Assume that a testing program calls for evaluating a total of 400 families on 6 test sites with final selections made at age 12. Using the projected costs of this testing program, the relative total costs of two hypothetical alternatives can be compared (Table 5). In the first alternative, all 400 families are tested in the field, similar to the approach employed in first-generation testing in the region. In the second alternative, early testing is used to cull 25% of the families based on first-year height, and only the remaining 300 families are field-tested. Despite the additional expense of a nursery test, the total cost of testing drops from \$371,000 without nursery culling, to \$306,000 with nursery culling prior to field-testing. Thus, it is possible to achieve cost savings of approximately 18%, with almost no projected loss in overall genetic gain. In addition to potential cost savings associated with two-stage selection, reduction in field test size has two other advantages. Locating uniform sites of sufficient size for test purposes is difficult in the mountainous terrain of the Pacific Northwest, and reducing test size makes this task easier. Furthermore, the reduced

heterogeneity associated with smaller, more uniform test sites makes it possible to increase the statistical precision of tests.

Genetic Gain and Early Selection

The curve for RE in figure 1, when $r_{xy} = 0.50$, suggests that gains after two stages of selection may exceed that achievable when all selection occurs at a single stage in the field or in an early test. The equation we used to estimate gain after two stages of selection (Equation 10) is an approximation that assumes the target trait of interest (i. e., the field trait) is still normally distributed after truncation of the population in the first stage of selection. This is not strictly true, so that a small amount of bias ($< 1\%$) is expected in genetic gain using this procedure (COTTERILL and JAMES, 1981), relative to that predicted with an exact method (NAMKOONG, 1970). This small bias, however, is not enough to account for RE values exceeding 100% in figure 1 (the highest RE value is 103%). Thus, it appears that two-stage selection may be slightly more efficient than selecting all families in a field test, in situations where r_{xy} is nearly as large as h_y^2 , and the proportion of the population culled at the seedling stage is intermediate. WU (1998) came to a similar conclusion based on theoretical considerations. Apparently, indirect selection has less impact than direct selection on the phenotypic variance of the field trait, such that the lower efficiency of indirect selection in the first stage is compensated by more phenotypic variation available for selection in the second stage.

This study examined the effectiveness of early testing for 15-year stem volume because final selections in coastal Douglas-fir are recommended to be made at this or even younger ages (SILEN and WHEAT, 1979; JOHNSON *et al.*, 1997). Of course, the trait breeders are interested in is stem volume at rotation, which in coastal Douglas-fir is 40 + years. The extent to which seedling height is related to volume at rotation is unknown, but presumably ranking of families for stem volume at ages 12 to 15 gives reasonably accurate rankings of families for stem volume at rotation. For instance, the estimated additive genetic correlation for DBH between ages 12 and 24 was 0.84, based on 90 families from same breeding zone as OP families in this study (TEMEL and ADAMS, 2000), and genetic correlations be-

Table 5. – Estimated costs of progeny testing for a Douglas-fir breeding program with and without early testing (culling 25% of the families in the nursery) to reduce the size of the field tests^a).

Activity	Estimated cost (U.S. \$) ^b	
	Without early testing	With early testing
Seedling production	\$ 36,000	\$ 34,000
Nursery test	0	12,000 ^c
Site preparation and fencing	152,000	122,500
Planting and mapping	46,000	34,500
Site maintenance (1-12)	53,000	40,000
Measurement (age 12)	84,000	63,000
Total	\$ 371,000	\$ 306,000

^a) Assumes a total of 400 families at the onset. All 400 are tested at 6 field sites when there is no early test. With early testing, 100 of the families are culled before outplanting and only 300 are planted at the 6 field sites. The typical design includes 20 test-trees/family on each site (20 randomized complete blocks, 1 tree/family/block) plus filler trees in un-plantable spots and a 2-tree border row around the entire test (the number of border and filler trees was assumed to be 30% of the test tree number). Trees are planted at 8 x 8 foot (2.4 m x 2.4 m) spacing.

^b) Costs for each activity were estimated from data provided by WILLIAM K. RANDALL, Daniels and Associates, Centralia, Washington; and DAN CRESS, Regenetics, Seattle, Washington.

^c) Costs for establishing and measuring a nursery test (400 families, 8 blocks and 4 seedlings/family/block) to rank families based on height at age 1 were estimated with data provided by RICHARD MILES, U.S.D.A. Forest Service, Pacific Northwest Research Station, Corvallis, Oregon.

tween ages 15 and 25, averaged over six Douglas-fir breeding zones in western Oregon, were 0.93 and 0.87 for height and DBH, respectively (JOHNSON *et al.*, 1997). Thus, it looks like family rankings for stem growth traits may be quite stable after age 15 in coastal Douglas-fir. As long as this is true, selection of the best performing families at ages 12 to 15 is a reasonable objective and early testing can be used to increase the efficiency and/or cost effectiveness of this process.

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