

Early Selection of Coastal Douglas-fir in a Farm-Field Test Environment

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(Received 4th May 1995)

Abstract

Farm-field tests are progeny tests established using intensive site preparation, close spacing and nearly complete weed control. Early growth and wood density of coastal Douglas-fir in a farm-field environment up to 7 years from seed are compared with stem volume and wood density from 11 field sites at age 13 (20% to 25% of commercial rotation). Family heritabilities are high for almost all traits in both the farm-field and field sites. Breeding-value correlations of farm-field heights with field stem volume at age 13 increase from a low of 0.5 for farm-field age 1 and level off at about 0.7 by farm-field age 3. Farm-field diameter with field volume age 13 breeding-value correlations are initially lower than those for height, but increase to 0.82 by age 7. Wood density breeding value correlations between field pilodyn assessments at age 13 and farm-field stem sections at age 6 are 0.83. Maximum family-selection efficiency per year (including a 5-year breeding delay), relative to direct selection on field volume 13, reaches 162% using index selection on farm-field height and diameter at age 3. Within-family selection efficiencies per year are highest at age 1 and decline quickly. All selection in the farm-field test has a higher efficiency per unit time than selection in field tests. It is concluded that correctly established farm-field tests will provide greater per year gains in stem yield and wood density traits than field sites.

Key words: Early selection, breeding, genetic gain, Douglas-fir, progeny testing.

FDC: 165.43; 165.62; 232.11; 232.12; 174.7 *Pseudotsuga menziesii*.

Introduction

Time is a critical factor in the genetic improvement of commercial traits for long-lived species. Tree breeding programs are usually designed to maximize genetic gain per unit time, within the limits imposed by other constraints. For this reason, juvenile-mature correlations and the efficiency of selection before full commercial rotation are important considerations for tree breeders.

Most studies of early selection estimate selection efficiencies and correlations based on comparisons between data from various ages of the same progeny test or set of tests (COTTERILL and DEAN, 1988; FOSTER, 1986; GILL, 1987; KING and BURDON, 1991; LAMBETH et al., 1983). These tests generally represent environments and site conditions commonly found in operational plantations and efficiency values are usually moderate to high for stem yield traits. LAMBETH (1980) summarized age correlations in the *Pinaceae* and found consistent relationships. MAGNUSSEN (1988) further developed the concept with computational procedures that determine minimum age-age correlations above which early selection is a better alternative.

Other early selection tests screen trees in environments which differ from operational plantations. These may include nursery studies (LI et al., 1992; RITTERS and PERRY, 1987) or

growth chamber studies (JONSSON et al., 1990). Results from such trials vary, reflecting genotype by environment interactions resulting from testing under conditions which are very different from operational plantations.

Operational breeding programs are rarely concerned with only yield traits. Other traits such as stem form and wood density, or adaptive traits such as frost hardiness, may also be considered important. For Douglas-fir (*Pseudotsuga menziesii* [MIRB.] FRANCO), age correlations for wood density are generally high (GONZALEZ and RICHARDS, 1988; MCKIMMY and CAMPBELL, 1982; VARGAS-HERNANDEZ and ADAMS, 1992), and stem form traits appear to be most strongly exhibited at younger ages (KING et al., 1990). Adaptive traits such as frost or drought hardiness may be more difficult to screen. Adverse correlations among yield and period of shoot elongation in many species of the *Pinaceae* (BRIDGEWATER, 1990; MAGNUSSEN and YEATMAN, 1989; REHFELDT, 1983, 1985 and 1992) may result in increased risk of frost damage with selection for yield traits. For coastal Douglas-fir, LI and ADAMS (1993) have shown that selection for height will delay both budburst and budset, reducing risk from spring frost but possibly increasing fall frost risk, although the impact appears to be small. They also found early testing was effective for estimating growth timing effects, such as bud burst date. These studies indicate early selection shows promise for a variety of traits.

Increased genetic gain is likely with early selection methods if generation intervals are shortened and if error variances associated with the test are decreased. Control of progeny test environments to minimize heterogeneity caused by soil, drainage and non-crop plant competition is expected to increase precision and gain. The potential for early selection suggests Douglas-fir progeny tests could be established at closer spacing with the objective of using data from young trees; this would also reduce test size and heterogeneity.

Genotype by environment interactions for yield traits estimated from extensive Douglas-fir progeny test data in coastal British Columbia support the use of a single breeding zone within the coastal area (British Columbia Forest Service, unpublished data). The stability of families across test sites established in very different environments suggests that family performance can be estimated in a range of conditions. By selecting sites with soils and climate similar to those found in operational plantations, and by controlling environmental heterogeneity through site preparation and the control of competing vegetation, test precision and early selection potential may be enhanced.

This project investigates the use of farm-field progeny tests (CARLSON, 1990) for coastal Douglas-fir to estimate breeding values and selection efficiencies for yield and wood density traits. These estimates are compared with older progeny tests with the same families established under conditions more similar to operational planting.

Materials and Method

Genetic Material

Material for this study came from a farm-field test of 70 full-sib families from 6 6-tree half-diallels (some reciprocals and

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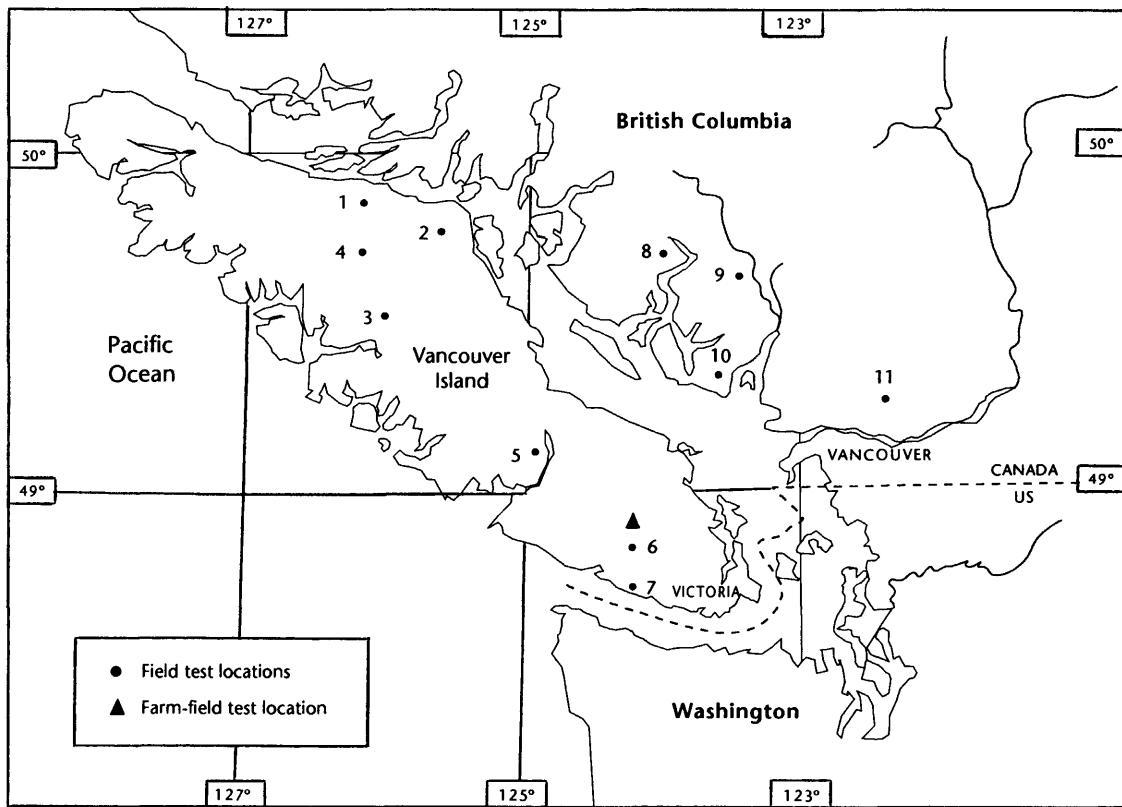


Figure 1. – Field trial and farm-field test locations.

missing crosses) without selfs. Parent trees are from natural stand selections in the coastal area of British Columbia at latitudes of 48.05° to 50.42° and elevations of 30 m to 823 m. The test is located at the Cowichan Lake Research Station on southern Vancouver Island, at an elevation of 160 m (Lat. 47.50°, Long. 124.08° – Figure 1). It was prepared to agricultural standards with complete stump removal, plowing and harrowing. The experimental design is a modification of the single-tree non-contiguous plot design of LIBBY and COCKERHAM (1980). The test contains 12 blocks and 4 independently randomized replications with single-tree plots at 1 m x 1 m spacing. Diallel sets are randomly mixed in the plantation.

Seedlings were grown for 1 year in 6 cm diameter by 15 cm deep containers in 2 randomly located family blocks of 45 seedlings each. Stock was planted in the spring of 1986. Weeds were controlled with herbicides to ensure no competition to the trees.

Progeny from the same families used in the farm-field test were previously outplanted in 1978 on 11 tests (Figure 1). These represent the range of sites used for Douglas-fir plantation forestry within the coastal breeding zone, and are part of the Douglas-fir breeding program in British Columbia (HEAMAN and WOODS, 1989). They range in elevation from 135 m to 576 m. In these plantations, all half-diallels were complete (15 crosses per 6-tree diallel). Full-sib families were planted in 4-tree row plots at 3 m x 3 m spacing with 4 replications per location. Site preparation was typical of that in operational plantations, with stumps and logging debris left intact. Brush and herbaceous growth were controlled with manual cutting to prevent excessive overtopping of the seedlings.

Data Collection

Measurements in the farm-field test included height at ages 1 to 7, root collar diameter at ages 3 and 5 and diameter at

1.3 m (DBH) at age 7. Volume at age 7 was estimated using the equations from OMULE *et al.* (1987). Wood specific gravity was determined for trees thinned from 8 blocks in 1990, using 3 of the 6 diallels. Ten centimetre long sections were cut from near the base of each thinned tree, bark was removed and density estimated using wet volume (measured by displacement) and oven-dry weight. These samples formed part of a related study (KOLOTELO and WOODS, in prep.).

For the field sites, which are 8 years older than the farm-field test, data were available for height at age 6 and 13 from seed and diameter at 1.3 m height (DBH) at age 13. Volume at age 13 was estimated using the equations of OMULE *et al.* (1987) (expected commercial rotation on these sites ranges from 40 years to 70 years). Only undamaged trees were included in the analyses. For specific gravity, information was available from 4 of the 11 sites (numbers 1, 6, 10 and 11 on Figure 1) based on pilodyn sampling. Two pilodyn measures were taken from each tree and their mean put into a regression equation to estimate specific gravity. This equation was derived by comparing pilodyn and whole core data (maximum-moisture-content method, SMITH, 1954) from a larger study to determine the effectiveness of the pilodyn method (KING *et al.*, 1988; British Columbia Forest Service, unpublished data).

Statistical Analysis

Analyses were performed using a version of the computer program DIALL (SCHAFER and USANIS, 1969) modified to include diallel-set effects (PARK and FOWLER, 1982). Least squares solutions, including expected mean squares and cross products coefficients, were obtained. The linear model for the individual site analysis of the farm-field site was;

[1]

$$Y_{ijk1m} = u + B_i + D_j + G_{jk} + G_{j1} + S_{jk1} + E_{ijk1m}$$

where

- Y_{ijklm} – is the performance of the tree m of parents k and l in diallel j and block i ;
 μ – is the overall mean;
 B_i – is the effect of the block i ;
 D_j – is the effect of diallel set j ;
 G_{jk} and G_{jl} – are the effects of the general combining abilities (GCA) of parents k and l in diallel j ;
 S_{jkl} – is the effect of the specific combining ability (SCA) of parents k and l in diallel j ;
 E_{ijklm} – is the residual error term.

For analyses across sites a location term L_m is incorporated into the model. Available computing facilities did not allow inclusion of interaction effects in the model. Consequently these are pooled in the residual error term and heritability estimates are conservative.

Family heritabilities (h^2_f) were calculated as described in BECKER (1984). Standard errors of heritability estimates were approximated using methods derived from KENDALL and STUART (1958). For the single farm-field site, genotype by environment variance (σ^2_{ge}) cannot be separated from GCA variance (σ^2_{gca}). Other analyses have shown σ^2_{ge} to be approximately one third of σ^2_{gca} (B. C. Ministry of Forests, unpublished data). Within this range, family heritability estimates will be slightly inflated for the farm-field site relative to the field sites. This confounding of σ^2_{ge} and σ^2_{gca} may seriously inflate individual-tree heritabilities and they are not reported.

Breeding values were calculated as follows;

[2]

$$BV_j = (2 * GCA_j * CT * h^2_F) + D_k$$

where BV_j is the breeding value of the j th parent, GCA_j is the general combining ability of the j th parent, CT is the bias correction term for GCA estimates from diallel analysis (FALCONER, 1981, p. 251) and D_k is the difference between the mean for diallel k and the mean across all diallels [$D_k - D$]. CT equals 1.25 for a 6-tree diallel.

Genetic correlations (r_g) (FALCONER, 1981) were estimated using variance and covariance components from the diallel analysis. Correlations of parental breeding values (r_{bv}) were also calculated among farm-field traits and for farm-field vs. field-site traits (BURDON, 1977).

Efficiencies from indirect selection were calculated for logical combinations of farm-field traits relative to 13-year volume and wood density in the field sites. Both family and within family selection was considered. From WHITE and HODGE (1989, p. 222), gain g in the response trait (volume at age 13) is calculated as;

[3]
$$g = \frac{iC'b}{\sqrt{b'Vb}}$$

where i is the selection intensity (held at 1 for comparison), C' is the transpose of a $n \times 1$ matrix of genetic covariances between n farm-field traits used for selection and field volume 13, V is a matrix of phenotypic variances and covariances among farm-field traits, and b is a column vector of index weights equal to C'/V . For selection of one trait (e. g. volume 13) using another trait (e. g. farm-field height 3), this formula reduces to that for correlated gain as shown by FALCONER (1981).

For family selection efficiency estimates, family phenotypic variance components (V_{pf}) in the V matrix were calculated as follows;

[4]
$$V_{P_f} = \sigma_G^2 + \frac{C_5 \sigma_S^2}{C_6} + \frac{\sigma_E^2}{C_6}$$

where σ_G^2 is the GCA variance component from DIALL, σ_s^2 is the SCA variance, σ_E^2 is the error variance and C_5 and C_6 are coefficients associated with the analysis of variance. For within-family selection efficiency estimates, V matrix within-family phenotypic variances were estimated as σ^2_E from the analysis of variance. Covariances (cov) were estimated in a similar way using cross products from the DIALL analysis.

Gain values from equation 3 were expressed as a percentage of mean tree volume at age 13. Gain per generation is the estimated gain from a single round of selection with a selection intensity (i) of 1. Gain per year was calculated as the gain per generation divided by the farm-field trait age plus 5 years for a breeding delay (time between selection and sowing). Actual gains would likely be greater as higher selection intensities would normally be used.

For both family and within-family selections, correlations between true and predicted genetic worths were estimated (WHITE and HODGE, 1989, p. 220) as follows;

[5]
$$Corr(w, \hat{w}) = \frac{c'V^{-1}c}{G}$$

where G is a scalar with the additive genetic value for volume 13.

Results

Heritabilities

Family heritabilities are high for most traits in both the farm-field and field tests, with the exception of first year height in the farm-field test (Table 1). Field-site heritabilities are high

Table 1. – Family heritabilities for farm-field and field test traits at various ages from seed (standard errors).

TRAIT	HERITABILITY
Farm Field	
HEIGHT 1	0.65 (0.14)
HEIGHT 2	0.86 (0.05)
HEIGHT 3	0.91 (0.04)
HEIGHT 4	0.90 (0.04)
HEIGHT 5	0.90 (0.04)
HEIGHT 6	0.90 (0.04)
HEIGHT 7	0.89 (0.05)
DIAMETER 3	0.87 (0.05)
DIAMETER 5	0.91 (0.04)
DBH 7	0.83 (0.07)
VOLUME 7	0.85 (0.06)
SPECIFIC GRAVITY 6 ^A	0.93 (0.04)
Field Sites^B	
HEIGHT 6	0.91 (0.03)
HEIGHT 13	0.89 (0.04)
DBH 13	0.87 (0.05)
VOLUME 13	0.88 (0.04)
PILODYN 13 ^C	0.92 (0.03)

^A) Based on 3 diallel sets

^B) Based on data from 11 field sites

^C) Based on data from 4 field sites

Table 2. – Correlations of parental breeding values (n = 36) among farm-field performance variables (above diagonal), and genetic correlations (below diagonal) based on individual trees (all significant at $\alpha = 0.05$).

	<u>HT1</u>	<u>HT2</u>	<u>HT3</u>	<u>HT4</u>	<u>HT5</u>	<u>HT6</u>	<u>HT7</u>	<u>DIA3</u>	<u>DIA5</u>	<u>DBH7</u>	<u>VOL7</u>	<u>SPGR^B</u>
<u>HT1^A</u>		.89	.83	.82	.82	.80	.81	.61	.65	.72	.50	-.64
<u>HT2</u>	.90		.96	.93	.88	.82	.83	.73	.81	.81	.58	-.59
<u>HT3</u>	.90	.95		.98	.93	.89	.88	.72	.82	.85	.64	-.55
<u>HT4</u>	.93	.93	.98		.97	.93	.92	.67	.79	.86	.65	-.55
<u>HT5</u>	.98	.86	.90	.96		.97	.96	.60	.72	.82	.64	-.57
<u>HT6</u>	.94	.80	.85	.91	.98		.99	.64	.74	.85	.67	-.57
<u>HT7</u>	.95	.77	.82	.89	.97	.99		.64	.74	.85	.65	-.59
<u>DIA3</u>	.58	.65	.62	.54	.46	.54	.51		.94	.81	.70	-.53
<u>DIA5</u>	.61	.76	.73	.67	.61	.65	.64	.93		.88	.72	-.68
<u>DBH7</u>	.81	.78	.80	.80	.80	.78	.79	.80	.86		.82	-.61
<u>VOL7</u>	.81	.78	.81	.82	.81	.79	.80	.78	.84	1.0		-.38
<u>SPGR^B</u>	-.51	-.50	-.49	-.49	-.57	-.49	---	-.42	-.56	---	---	

A) Trait abbreviations: HTx – height at age x from seed; DIAx – root-collar diameter; DBH7 – diameter at 1.3 m at age 7; VOL7 – volume at age 7; SPGR – specific gravity at age 6.

B) SPGR correlations are based on 18 parents from 3 diallel sets.

Table 3. – Parental breeding value correlations between farm-field test variables (top), and field test variables for 36 parents (underlined correlations are not significant at $\alpha = 0.05$).

	<u>HT1^A</u>	<u>HT2</u>	<u>HT3</u>	<u>HT4</u>	<u>HT5</u>	<u>HT6</u>	<u>HT7</u>	<u>DIA3</u>	<u>DIA5</u>	<u>DBH7</u>	<u>VOL7</u>	<u>SPGR^B</u>
<u>HT6</u>	.56	.63	.86	.87	.87	.87	.86	.58	.71	.81	.64	-.52
<u>HT13</u>	.60	.50	.75	.73	.78	.82	.80	.53	.62	.74	.60	-.49
<u>DBH13</u>	.54	.52	.64	.64	.60	.60	.59	.62	.70	.80	.71	-.66
<u>VOL13</u>	.50	.56	.71	.72	.69	.69	.67	.61	.71	.82	.68	-.60
<u>PIN13</u>	<u>-.30</u>	<u>-.19</u>	<u>-.30</u>	<u>-.29</u>	<u>-.27</u>	-.39	-.44	<u>-.26</u>	-.34	-.51	-.40	.83

A) Trait abbreviations: HTx – Height at age x from seed; DIAx – root-collar diameter; DBHx – diameter at 1.3 m; VOLx – stem volume; SPGR – specific gravity at age 6; PIN13 – specific gravity predicted from two pilodyn measures.

B) SPGR correlations are based on 18 parents from 3 diallel sets.

for all traits due to large sample sizes (up to 880 trees per half-sib family). In the farm-field site, equivalent heritabilities were achieved with a smaller sample size (up to 240 trees per half-sib family). This reflects the reduction in residual variance attributable to increased site homogeneity achieved with the farm-field site preparation and weed control relative to the field sites. Specific gravity heritability is very high in the farm-field test, as is typical for this trait (VARGAS-HERNANDEZ and ADAMS, 1992).

Correlations

Genetic correlations among all height and diameter traits in the farm-field test are high, ranging from 0.46 to 0.99 (Table 2). Breeding-value correlations agree closely with genetic correlations. Genetic correlations vary from -0.42 to -0.57 between growth traits and age-6 wood density; the breeding-value correlation between density and age-7 volume is -0.38 . These correlations among density and growth traits are in agreement with other studies (KING et al., 1988; British Columbia Forest Service, unpublished data).

Breeding-value correlations between farm-field traits and the 11 field tests are shown in table 3. These correlations are all positive and generally high among growth traits, ranging from 0.50 to 0.87. Correlations among pilodyn estimated wood

density values in the field sites and maximum-moisture content estimates in the farm-field test are very high, at 0.83.

Thirteen-year volume is the field trait of most interest for which data are available. Breeding-value correlations between volume 13 and farm-field heights increase from age 1 (0.50) to age 3 (0.71) then remain stable. Farm-field diameter correlations with volume 13 also increase with age and reach a higher level (0.82) than for height. Farm-field age-7 volume correlations are intermediate between those for 7-year height and diameter.

Breeding-value correlations between farm-field growth traits and volume 13 on individual field sites are all positive (Table 4). Some sites show higher average correlations than others, but few large differences are evident. Trends towards larger correlations with increasing farm-field test age are also evident for individual sites, but the trend is generally less well defined than for all sites combined.

Correlations between true and estimated genetic worths ($\text{corr}(w, \hat{w})$) provide a measure of the precision of selections. Table 5 shows $\text{corr}(w, \hat{w})$ values for selection of field volume or wood density at age 13, using various farm-field traits. Farm-field $\text{corr}(w, \hat{w})$ values increase quickly to 0.46 for height at ages 3 and 4, then decline slightly. For diameter and the combi-

Table 4. – Correlations estimated using individual field site (top-see Figure 1) volume 13 breeding values and breeding values for farm-field height, diameter and volume at various ages. Thirty-six parents are represented (underlined correlations are not significant at $\alpha = 0.05$).

	<u>ALL</u> ^A	<u>1</u>	<u>2</u>	<u>3</u>	<u>4</u>	<u>5</u>	<u>6</u>	<u>7</u>	<u>8</u>	<u>9</u>	<u>10</u>	<u>11</u>
<u>HT1</u> ^B	.50	.40	.41	.34	.33	.55	.53	<u>.06</u>	.33	.59	.40	.33
<u>HT2</u>	.56	.46	.49	.42	<u>.24</u>	.37	.50	<u>.16</u>	<u>.12</u>	.48	.56	.62
<u>HT3</u>	.71	.49	.56	.47	.42	.52	.60	.37	.39	.69	.65	.60
<u>HT4</u>	.72	.49	.56	.51	.44	.54	.60	.40	.45	.71	.66	.60
<u>HT5</u>	.69	.48	.51	.49	.44	.59	.58	.43	.48	.68	.65	.54
<u>HT6</u>	.69	.51	.51	.45	.45	.61	.57	.39	.50	.66	.64	.51
<u>HT7</u>	.67	.50	.48	.43	.45	.60	.55	.39	.49	.64	.62	.49
<u>DIA3</u>	.61	.43	.45	<u>.30</u>	.34	.40	.46	<u>.24</u>	<u>.19</u>	.48	.54	.53
<u>DIA5</u>	.71	.47	.54	.45	.43	.49	.54	.36	.34	.59	.67	.64
<u>DBH7</u>	.82	.55	.58	.55	.51	.56	.70	.46	.44	.74	.76	.65
<u>VOL7</u>	.68	.59	.47	.50	.39	.48	.64	.35	.30	.57	.66	.62

^A) Combined analysis for all field sites.

^B) Trait abbreviations: HTx – height at age x from seed; DIAx – root collar diameter; DBH7 – diameter at 1.3 m; VOL7 – stem volume.

nation of height and diameter, $\text{corr}(w, \hat{w})$ is highest at age 7 (0.56).

$\text{Corr}(w, \hat{w})$ values for within-family selections show a different trend. Values decline for selections based on farm-field height to about age 5, then stabilize. Diameter has the opposite trend, with values increasing from age 3 to age 5, then remaining stable to age 7. The combined index $\text{corr}(w, \hat{w})$ values are initially high, then stabilize at age 5. For both stem yield and density traits, within-family genetic worth correlations are higher for selections in the farm-field test than in field tests (Table 5).

Selection Efficiency

For selection in the farm-field test, efficiency estimates are based on expected gains in field volume at age 13. These gains are then expressed as a percentage of expected gains based on direct selection for field volume-13 using combined data from the 11 field sites and assuming a single generation (cycle) of testing and selection.

Table 5. – Correlations between true and predicted genetic worths for indirect and direct selection of families and trees within families.

SELECTION TRAIT	RESPONSE TRAIT	CORR(w, \hat{w})	
		FAMILY	WITHIN FAMILY
HT1	VOL13	0.16	0.105
HT2	VOL13	0.27	0.095
HT3	VOL13	0.46	0.090
HT4	VOL13	0.46	0.068
HT5	VOL13	0.43	0.053
HT6	VOL13	0.43	0.051
HT7	VOL13	0.40	0.047
DIA3	VOL13	0.32	0.021
DIA5	VOL13	0.46	0.049
DBH7	VOL13	0.56	0.052
HT3 DIA3	VOL13	0.49	0.097
HT5 DIA5	VOL13	0.55	0.059
HT7 DIA7	VOL13	0.56	0.053
VOL13	VOL13	0.88	0.026
RD6	PIN13	0.64	0.311
PIN13	PIN13	0.92	0.202

^A) When selection and response traits are the same, $\text{corr}(w, \hat{w})$ equals the family or within-family heritability.

Per-generation efficiencies for family selection, based on farm-field height, increase from 43% at age 1 to 72% at age 3 (Figure 2a). Efficiencies then stabilize at about 70% to age 7. Selection efficiency based on farm-field diameter increases from 61% at age 3 to 80% at age 7. Family selection using an index of height and diameter shows an efficiency of 75% at age 3, increasing slightly to 80% at age 7. Selection for wood density using farm-field data at age 6 is 84% as efficient as direct selection at age 13 in the field.

Per-generation efficiencies for within-family selection show a different pattern than for family selection (Figure 2b). High early within-family heritabilities for farm-field height result in a selection efficiency of 200% for first year height, dropping to 134% by age 7. Efficiencies for diameter are lower initially, but increase and stabilize at age 5 at about 140%. Selection on farm-field height and diameter combined follows the pattern for height, with efficiencies dropping from 192% at age 3 to 142% by age 7. Wood density selection efficiency based on age 6 is 185%.

The primary objective of early selection is to reduce generation intervals and increase gain-per-year. Selection efficiencies shown in figures 3a and 3b express gain on an annual basis as a percentage of direct selection for volume 13 on field sites. These gain estimates are based on the number of years in test plus a 5 year delay for breeding.

Family-selection efficiency per year based on farm-field height, diameter, and height and diameter combined are all highest at age 3, reaching values of 162%, 137% and 169% respectively (Figure 3a). Selection efficiency for specific gravity at age 6 is 137%. Family selection efficiency values for the farm-field test are over 100% for all ages.

Within-family selection efficiency values (Figure 3b) for height are very high at age 1 (600%), but drop quickly and begin to stabilize at about age 5. Selection efficiency values for diameter are more stable, at just over 200% from ages 3 to 7. Efficiency values based on height and diameter show a large drop from age 3 (432%) to age 7 (213%). Within-family selection efficiency for wood density is 303% at age 6.

Discussion

This study investigates a progeny test method that is intermediate between growth chamber tests (JONSSON et al., 1990)

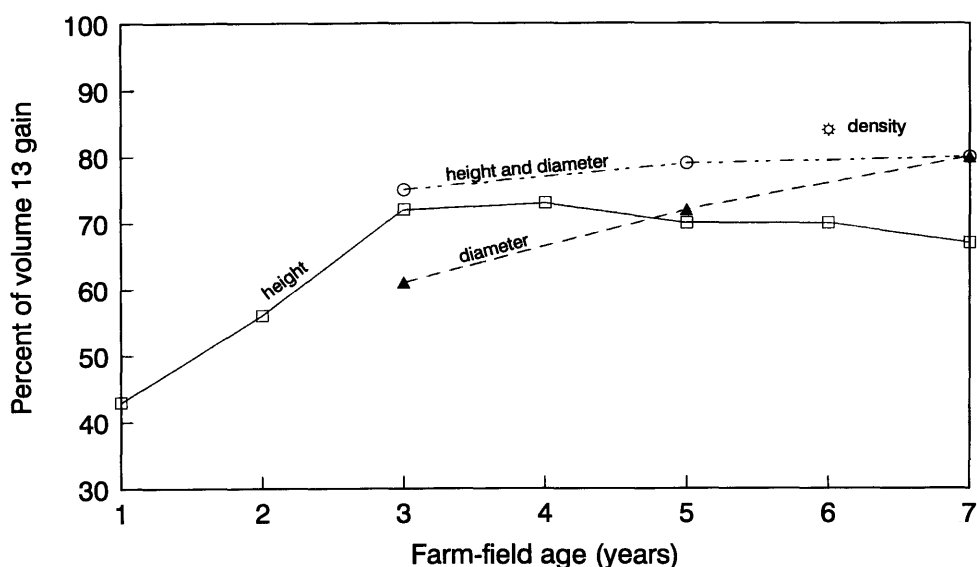
or short-term nursery tests of up to 3 years (FINS et al., 1990; RITERS and PERRY, 1987) and longer term field trials which may last to $1/2$ or full commercial rotation. Results indicate farm-field testing is a good intermediate alternative for estimating genetic effects of yield and wood density traits for coastal Douglas-fir. Site preparation and weed control appear to have effectively removed much of the microsite variability present in standard field trials, allowing trees growing under a homogeneous and non-competitive environment to express their genetic potential at an earlier age. High family heritabilities achieved at a young age and with a much smaller sample than in the field sites reflect the successful removal of environmental heterogeneity.

In contrast to nursery studies, farm-field tests are established in soils and climates similar to operational plantations. This

is expected to result in high correlations with operational plantations, as were found here. The increase in breeding-value correlations between field tests and the farm-field test from ages 1 to 4, and the subsequent levelling off of these correlations, suggests several years are needed for trees to demonstrate their longer-term growth potential. This is also reflected in the genetic worth correlations ($\text{corr}(w, \hat{w})$) for family selections, as values rose with test age for combined index selection, but stabilized at age 4 for selection on height only.

A strength of this study is the number of field sites and the large sample sizes for generating breeding values. These sites sample a variety of environments within the coastal breeding zone, and provide reliable breeding-value estimates for 13-year volume. The farm-field test also provides large sample sizes for

(A) Family selection per generation



(B) Within-family selection per generation

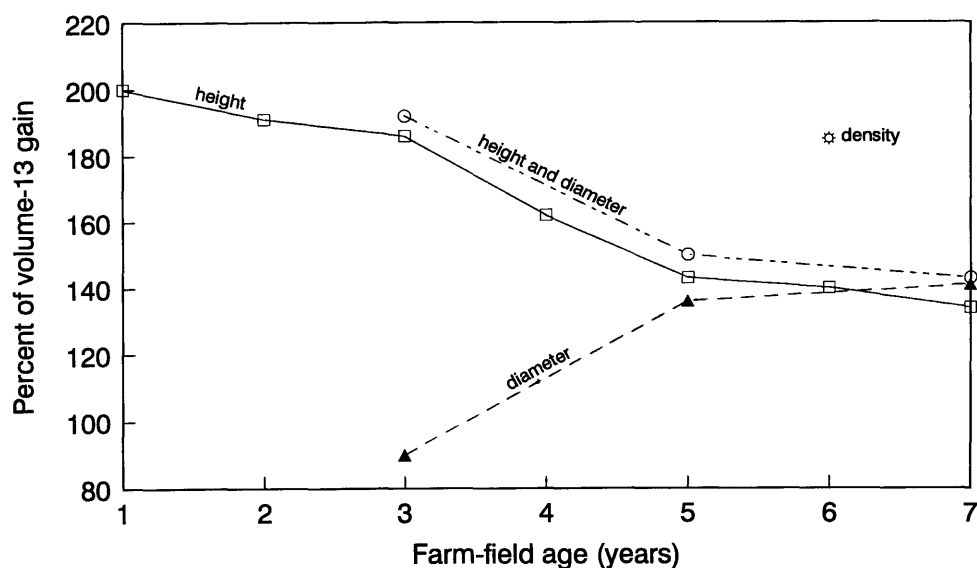
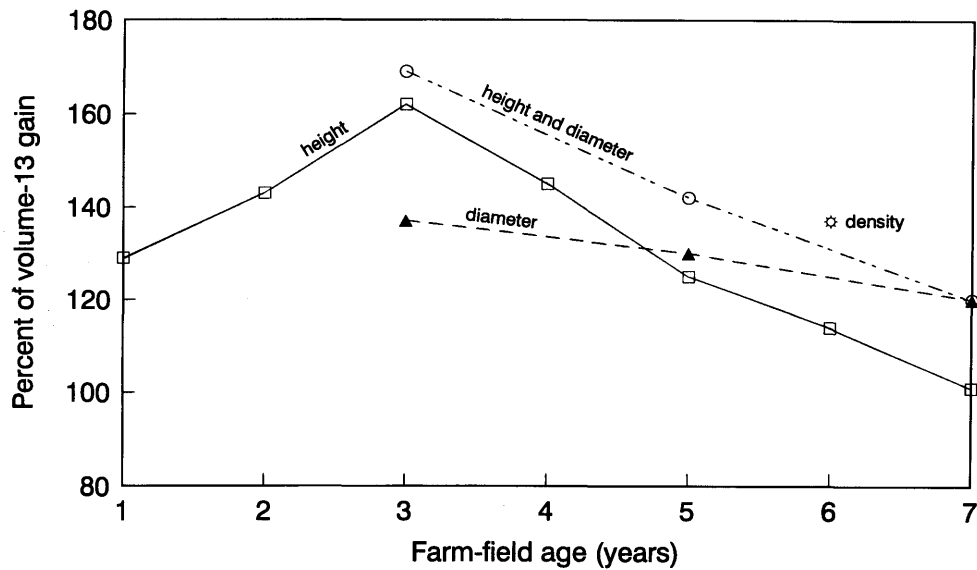


Figure 2. - Selection efficiencies expressed as a percent per breeding generation relative to direct selection on 13-year volume; (A) family selection, (B) within family selection.

(A) Family selection per year



(B) Within-family selection per year

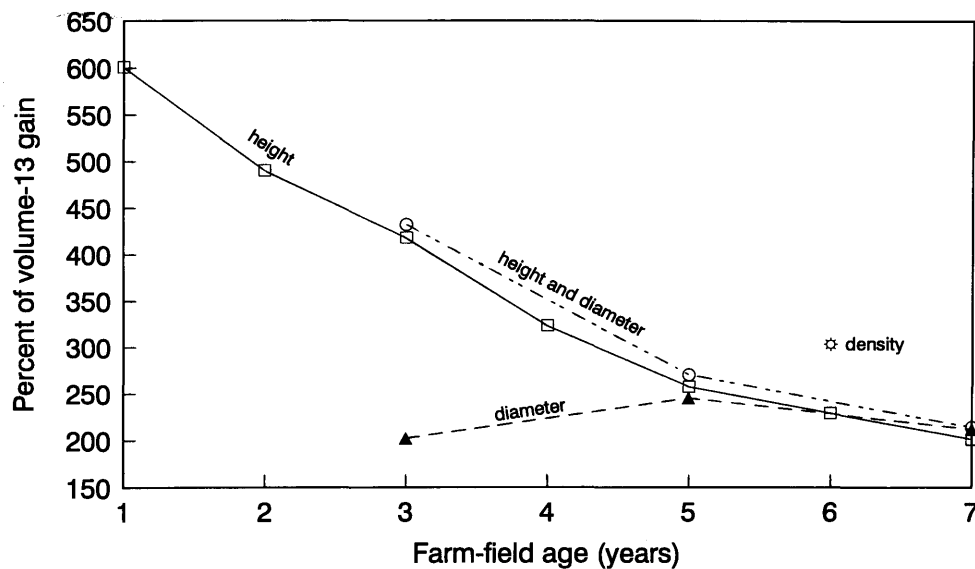


Figure 3. - Selection efficiencies expressed as a percent of gain per year relative to direct selection on 13-year volume (5-year breeding delay per generation assumed); (A) family selection, (B) within-family selection.

estimating parental breeding values, but this part of the study suffers from having data from only one site. However, consistent and positive breeding value correlations between the farm-field site and individual field sites provides confidence that family by site interactions are not overly large and the single site accurately reflects genetic potential over the coastal breeding zone.

The primary objective of early selection is to increase genetic gains achieved per year. Accurate prediction of parental breeding values is necessary, but in a recurrent selection program, the ability to select within families to establish a new generation (forward selection) is also important. Small error variance, large additive variance and a shortened generation interval in the farm-field test resulted in high within-family

selection efficiencies relative to the older field sites. On an annual gain basis, the farm-field test appears to have substantial advantages over field tests for forward selection on growth and wood density traits. Within-family genetic worth correlations were also higher for all farm-field yield and density traits than for the older field sites.

Field data in this study are limited to 13 years of age (about 20% to 25% of normal commercial rotation). No attempt was made to extrapolate selection efficiencies to rotation using correlations derived from a procedure such as that described by LAMBETH (1980), as was done by KING and BURDON (1991), as reliable data on phenotypic variances and heritabilities at rotation are not available. Use of derived figures would be pure speculation, and would contribute little to the decision to use

farm-field testing as part of an operational breeding program. It is recognized that predictions of genetic effects based on 13-year field data are subject to error, and will have a correlation of less than one with selections hypothetically made at rotation. Strategies relying on selection at any age before rotation are subject to risk associated with imperfect correlations. Tracking this risk as field tests age will provide data on the efficiency of early selection gains, but unless correlations become very small or negative, it is unlikely that early selections will provide less gain on an annual basis than older field selections due to the long generation interval of field selections (MAGNUSSEN, 1988).

Family selection efficiencies in the farm-field test were initially highest for height, but became higher for diameter after age 4. This change may reflect the period at which early root competition began. Crown competition at age 4 was probably insufficient to cause trees to modify their growth behaviour at that time. To survive in a stand, individual trees must maintain height growth relative to their neighbours. In comparison with fast-growing genotypes, slow growing genotypes may allocate a greater proportion of their resources to height growth, at the expense of diameter growth, once competition begins. In a fully stocked stand which has strong early expression of genetic potential, this strategy may be responsible for the quickly rising per generation selection efficiency seen for diameter.

The observed trend may be less of a reflection of diameter growth potential under open grown conditions than of a correlated response of diameter to the early height superiority. However, both traits contribute to stem-wood yield, and correlate well with stem volume in older tests. Uncertainty over which variable is most efficient at selection age is not of concern, as an index selection procedure will capture at least as much gain as is provided by the most efficient variable.

Wood density in Douglas-fir has previously been shown to have high heritabilities, age-age correlations and selection efficiency (VARGAS-HERNANDEZ and ADAMS, 1991, 1992). The high breeding-value correlation (0.83) between density estimated from stem samples in the farm-field test and density estimated from pilodyn pin penetration in the field tests provides confidence in both the value of farm-field estimates and the accuracy of pilodyn estimates.

The data presented here show that farm-field progeny tests are feasible and desirable for estimating the expected genetic values of families and individuals for yield and wood density traits up to field ages of about 25 percent of rotation. Experience with this and other farm-field tests shows that successful early selection is dependant on the following; 1. selection of sites on which intensive site preparation is feasible, 2. site preparation using low pressure tracked machines when soils are dry, 3. top quality seedlings and planting procedures which minimize stress associated with planting, and 4. careful weed control using herbicides or manual methods to ensure there is no competition to the seedlings. Quality control problems in any of these areas will reduce test precision and delay the time to which reliable results can be obtained.

The short generation interval used for farm-field testing does not allow thorough screening of families for longer-term adaptive traits such as frost or drought hardiness. In the first-generation of a breeding program, breeding zone delineation through understanding genotype by environment interactions is often one of the priorities. Short-term farm-field tests with narrow spacing may not provide this information, and should not be used until advanced generations, or until sufficient testing is done under operational planting conditions to address genotype by environment and stability concerns.

Acknowledgements

The authors gratefully acknowledge CHRIS HEAMAN for providing pedigreed seed and for many types of support during the project. Thanks are extended to BOB HATTIE, CHIO WOON and NORM POMEROY for technical assistance, LISA HAYTON for data management and TINA OGG for typing and manuscript preparation. All staff at the Cowichan Lake Research Station are thanked for ongoing support and practical help.

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Pinus halepensis x *Pinus brutia* subsp. *brutia* Hybrids? Identification Using Morphological and Biochemical Traits¹⁾

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(Received 8th May 1995)

Summary

The aim of this study was to verify whether trees which exhibit very vigorous growth are F₁-hybrids of *Pinus halepensis* X *Pinus brutia*, and to what extent they differ from typical *P. brutia* subsp. *brutia* trees growing in the same plantations and from typical native *P. halepensis* MILL. trees.

Comparison of data regarding morphological traits and isoenzyme analysis of biological material taken from *P. halepensis*, *P. brutia* and the very vigorously growing trees, provided evidence that the trees targeted are F₁-hybrids. The results indicate that the seed used to establish these *P. brutia* forest plantations was probably imported from sites in Greece where *P. halepensis* and *P. brutia* grow in geographic proximity.

Key words: Isozymes electrophoresis, morphological traits.

FDC: 165.3; 165.51; 165.7; 174.7 *Pinus halepensis* x *Pinus brutia* subsp. *brutia*.

Introduction

Recently, attention was drawn to few trees in 2 plantations due to their morphological traits and vigorous growth which separate them from the other trees in these plantations. These plantations were planted in Israel 19 years ago with *Pinus brutia* subsp. *brutia* a introduced species. One plantation was planted on the Mt. Carmel range near the Muchraka peak (32° 42' lat. N., 35° 04' long E., alt. of 425 m a. s. l.), the second in the Judean foothills near Beqoa (31° 51' lat. N., 35° 04' long. E., alt. 185 m a.s.l.). The seed used for planting was registered as imported from Greece in 1975. HETH (1990) suggested that these trees might be hybrids, probably F₁-hybrids of *P. halepensis* X *P. brutia* which exhibit heterosis as their growth rate is 160% of the largest *P. brutia* tree in these plantations. These trees are also less susceptible to the pine bast scale, *Matsu-*

coccus josephi BODENH. et HARPAZ, the most noxious insect of planted Aleppo pine (*P. halepensis* MILL.) in Israel (MENDEL, 1984).

The aim of this study was to verify whether these trees are F₁-hybrids, and to what extent they differ from *P. brutia* subsp. *brutia* trees growing in the same plantations and from *P. halepensis* MILL. trees.

Material and Methods

Two different methods were used to analyze the trees thought to be hybrids in comparison with *P. brutia* subsp. *brutia* trees growing in the 2 plantations and native Israeli *P. halepensis* MILL. trees growing on the Mt. Carmel range.

1. Morphological-anatomical method and traits measured

Morphological traits were analyzed using methods described by CALAMASSI *et al.* (1988), CALAMASSI (1986), DEBAZAC and TOMASSONE (1965), PANETSOS (1975) and RIVA and VENDRAMIN (1983).

a. Two-year-old healthy needles were taken at random from 10 branches at the upper part of the canopy. Twenty needles selected at random from these branches were used to measure the length, width and number of stomata rows per needle. Fresh and dry weights were determined on 50 needles selected at random. Dry weight was measured after 36 hours at 70 °C.

b. Cone length and the largest diameter, petiole length and angle between cone length axis and the branch bearing it were measured on 10 cones selected at random from the last year crop.

c. Seed weight, and seed and wing length were measured on 20 seeds selected at random from approximately 800 seeds, the seed yield of 10 cones per tree.

d. Anatomical slides of radial, tangential longitudinal and cross-sections of xylem wood were prepared from each of the 28 hybrid trees and of some of the 22 *P. brutia* and 10 *P. halepensis* trees to evaluate differences in number of resin ducts and their dispersal within the year-ring, number and shape of cross-field pits.

¹⁾ Contribution from the Agricultural Research Organization, The Volcani Center, Bet Dagan 50250, Israel. No. 1603-E, 1995 series

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