

Genetic Variation and Correlation in Growth, Biomass, and Phenology of Douglas-fir Diallel Progeny at Different Spacings

By Y. A. EL-KASSABY¹⁾²⁾ and Y. S. PARK³⁾

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Abstract

A genetic test of 104 full-sib families of low elevation, coastal Douglas-fir (*Pseudotsuga menziesii* (MIRB.) FRANCO) was evaluated 3 years after germination. The full-sib families were produced by a disconnected diallel mating scheme, consisting of 7 sets of 6-parent partial diallels, grown under 2 spacing treatments in a nursery. The objectives of the study were to determine the extent of genetic control of growth traits, biomass distribution and allocation strategies, and vegetative phenology. Spacing had a significant effect on 6 of the 11 traits studied. Significant general combining ability variance was found for all traits except 1-year height. Individual tree narrow-sense heritability varied from 0.06 to 0.69 for root-dry-weight to vegetative phenology, respectively. Spacing x family interaction variance was significant for only 2 traits. Two harvest indices, based on total and above ground dry weights, were used to assess dry matter allocation strategy and to explore potential usefulness in tree breeding. Both indices had similar heritability estimates and their genetic correlation was high (0.91), indicating that use of an index based on above ground dry weight is a good surrogate for that based on total dry weight. Genetic correlations among growth and biomass traits were generally high, while those correlations with harvest indices were variable.

Key words: Disconnected diallels, variance components, genetic correlation, harvest index.

Introduction

The main concern of tree breeding is to change populations genetically to increase forest productivity; however, it is likely that there are limits to biomass productivity per unit area (LIBBY, 1987; VELLING and TIGERSTEDT, 1984). LIBBY (1987) suggests that such limits may be related to adaptation and, in a well-adapted population, the domestication process will be increasingly concerned with reallocation of biomass among various parts of the tree. He indicated that possible strategies for such reallocation include breeding for shorter, fatter trees, deploying trees with little allocation to reproductive activity, changing branch form, and relative amount of roots.

VELLING and TIGERSTEDT (1984) indicated that partitioning of the phytomass to different parts or organs has been a major cause of yield increase in many agricultural and horticultural plants and that breeding has in many cases caused a change in allometric growth of plants. Furthermore, to increase the proportion of useful wood, they suggested that harvest index or tree ideotypes should be a basis for selection in cultivated trees. The concept of harvest index (HI) was first introduced by DONALD (1962), and it refers to the proportion of the total dry matter

produced that is harvested, relating reallocation of useful biomass. Despite its potential usefulness, calculation of harvest index in forest trees is a cumbersome task although the useful part of a tree is easily defined and measured. Nevertheless, VELLING and TIGERSTEDT (1984) indicated that a useful approximation is either the ratio of harvested volume to total volume or harvested fresh weight to total weight and that harvest index may become as important in tree breeding as it has been in many agricultural crops.

In this paper, we report on growth and biomass traits and vegetative phenology of Douglas-fir (*Pseudotsuga menziesii* (MIRB.) FRANCO) grown in a short-term (3-year-old) nursery test conducted under 2 different spacings. In particular, we were interested in biomass traits and their relationship with other traits because several early testing studies indicated total dry weight correlated well with later field heights. For example, LAMBETH et al. (1982) demonstrated in their Douglas-fir early testing study (11 months old) that total dry weight correlations with 6-year field height were better than those with earlier height measurements. Furthermore, they reported that the family rankings in total dry weight were consistent over 12 phytotron environments. Similar conclusions were also reported by RIJTERS and PERRY (1987) for 4-month-old dry weight and 6-year field height in Douglas-fir, and by MULLIN (1990) for 25-week-old total dry weight with 5-year field height in black spruce (*Picea mariana* (MILL.) B.S.P.). These results suggest that total dry weight of seedlings may be used for predicting field performance or used as juvenile traits in early testing and selection. If seedling dry weight traits are to be used for early selection, then it is prudent to understand how dry matter is being distributed and how much the dry matter allocation strategy is affected by the testing environment.

The objectives of this study were to examine the magnitude of genetic and environmental variance in seedling growth and biomass traits, to estimate the genetic correlations among the traits, and to elucidate biomass allocation strategy as affected by spacing. In addition, we examined the extent of genetic control in allometric growth using calculated harvest indices. A comparison between two harvest indices, one based on total dry weight and the other on above ground dry weight, is also presented.

Materials and Methods

Seeds used in this study originated from controlled-pollination made among clones of 4 Pacific Forest Products' low elevation Douglas-fir breeding population. The parents were selected from natural stands on sites ranging from sea level to 450 m in Vancouver Island and southeastern British Columbia. A disconnected diallel mating scheme consisting of seven sets of six-parent half diallels was used to produce a total of 104 full-sib families with one missing cross. Parents were assigned to the sets

¹⁾ Pacific Forest Products Limited, Saanich Forestry Centre, 8067 East Saanich Road, R. R.# 1, Saanichton, B. C., V0S 1M0, Canada

²⁾ Faculty of Forestry, University of British Columbia, Vancouver, B. C., V6T 1Z4, Canada

³⁾ Canadian Forest Service P. O. Box 4000, Fredericton, N. B., E3B 5P7, Canada

based on flowering phenology, i. e., availability and readiness of pollen and female strobili.

In the spring of 1985, seedlings were grown at Pacific Forest Products' commercial nursery in 415A styroblocs (80 cavities, 133 cm³) following standard nursery culture regimes. Each full-sib family was sown in four styroblocs. The styroblocs were laid out in the nursery in a randomized design. At the end of the growing season (fall 1985), seedlings were extracted and kept in cold storage (1 °C) until planting.

In the spring of 1986, the short-term test was planted on a uniform nursery bed. Two spacings were used: the narrow spacing was 15 cm between seedlings within rows with 15 cm between rows (15 cm x 15 cm), while the wide spacing had 30 cm between rows (15 cm x 30 cm). Each spacing was replicated twice (blocks), and seedlings were planted in 5-tree-row plots per full-sib family. Each block was surrounded by a buffer row to eliminate the edge effect. Maintenance during the 1986 and 1987 growing seasons consisted of hand weed control. The trial was irrigated when required, but no fertilizer was applied. In addition, conventional field tests were also established at 2 different locations in 1986.

Vegetative bud burst phenology (PHE) was determined, using the Julian calendar day, for every seedling during the third growing season. In the fall of 1987, after 3 growing seasons, the seedlings were lifted and data on height for each on the 3 years (HT1, HT2, and HT3), and root collar diameter (DIA) were obtained. The seedlings were dried in an oven at 70 °C for 48 hours, and root (RDW), stem (SDW), branch (BDW) and total dry weights (TDW) were determined. Two harvest indices were determined. The first, total harvest index (HIT), was determined by dividing the SDW by the TDW and multiplying by 100 for each seedling. The second harvest index (HIA) was determined by dividing the SDW by the total of above ground dry weights, i.e., the sum of SDW and BDW, and multiplying by 100.

The analyses of variance and covariance for the studied traits were based on individual seedling data following the additive linear model:

$$Y_{ijklmn} = \mu + T_i + R_j + D_k + G_{kl} + G_{km} + S_{klm} + TF_{iklm} + RF_{ijkm} + e_{ijklmn}$$

where:

- Y_{ijklmn} is the n th observation of the lm th family in the k th diallel set grown in the j th replication within the i th spacing, $n = 1, \dots, 5$;
- μ is the overall mean;
- T_i is the spacing effect, $i = 1, 2$;
- R_j is the j th replicate (block) effect within the i th spacing, $j = 1, 2$;
- D_k is the k th diallel set effect, $k = 1, \dots, 7$;
- G_{kl} (G_{km}) is the l th(m)th general combining ability effect within the k th diallel set, $l = m = 1, \dots, 6$;
- S_{klm} is the lm th specific combining ability effect within the k th diallel set;
- TF_{iklm} is the interaction effect between the i th spacing and the klm th family;
- RF_{ijkm} is the interaction effect between the j th block within the i th spacing effect and the klm th family (plot error); and
- e_{ijklmn} is the random error term (within-plot error).

Table 1. — Analysis of variance (covariance) form for disconnected diallel cross).

Source	d.f.	Expected Mean Squares ²
Spacing (T)	1	$\sigma_e^2 + 4.831\sigma_{RF}^2 + 9.581\sigma_{TF}^2 + 0.129\sigma_{SCA}^2 + 0.207\sigma_{GCA}^2 + 0.081\sigma_{SET}^2 + 491.403\sigma_R^2 + 982.755\sigma_T^2$
Reps/T (R)	2	$\sigma_e^2 + 4.834\sigma_{RF}^2 + 0.079\sigma_{TF}^2 + 0.079\sigma_{SCA}^2 + 0.150\sigma_{GCA}^2 + 0.079\sigma_{SET}^2 + 491.975\sigma_R^2$
Diallel set (D)	6	$\sigma_e^2 + 4.826\sigma_{RF}^2 + 9.594\sigma_{TF}^2 + 19.040\sigma_{SCA}^2 + 187.890\sigma_{GCA}^2 + 281.052\sigma_{SET}^2$
GCA/D	35	$\sigma_e^2 + 4.826\sigma_{RF}^2 + 9.581\sigma_{TF}^2 + 18.995\sigma_{SCA}^2 + 74.858\sigma_{GCA}^2$
SCA/D	62	$\sigma_e^2 + 4.826\sigma_{RF}^2 + 9.552\sigma_{TF}^2 + 18.865\sigma_{SCA}^2$
T x Family	102	$\sigma_e^2 + 4.791\sigma_{RF}^2 + 9.447\sigma_{TF}^2$
R x Family	203	$\sigma_e^2 + 4.743\sigma_{RF}^2$
Error	1556	σ_e^2

¹ For analysis of covariance, the variance components are replaced by respective covariance components, e. g., the GCA covariance between diameter (x) and harvest index (Y) is $\sigma_{GCA(xy)}$.

² σ_e^2 , σ_{RF}^2 , σ_{TF}^2 , σ_{SCA}^2 , σ_{GCA}^2 , σ_{SET}^2 , σ_R^2 , and σ_T^2 are variance components due to within-plot error, blocks within spacing x family interaction (plot error), spacing x family interaction, specific combining ability, general combining ability, diallel set, blocks within spacing, and spacing, respectively.

All the terms in the model were considered as random effects. The computer program DIALL (SCHAFER and USANIS, 1969) was modified to analyze the disconnected diallel mating scheme, and a least squares solution, including expected mean squares and cross-products coefficients, was obtained (Table 1). Subsequently, variance

Table 2. — Mean (standard error) of the studied traits for the narrow and wide spacing

Traits	Spacing	
	15 x 15 cm	15 x 30 cm
HT1: 1-year height (cm)	28.55 (0.15)	28.03 (0.16)
HT2: 2-year height (cm)	46.84 (0.22)	43.51 (0.23)
HT3: 3-year height (cm)	98.84 (0.55)	101.13 (0.57)
DIA: Diameter (mm)	10.62 (0.06)	13.33 (0.07)
RDW: Root dry weight (g)	15.17 (0.19)	28.66 (0.34)
SDW: Stem dry weight (g)	21.99 (0.32)	35.36 (0.47)
BDW: Branch dry weight (g)	27.00 (0.33)	48.37 (0.53)
TDW: Total dry weight (g)	64.17 (0.77)	112.39 (1.23)
HIT: Harvest index - total	33.60 (0.19)	30.99 (0.15)
HIA: Harvest index - above ground	44.16 (0.20)	41.70 (0.17)
PHE: Phenology (days)	114.35 (0.16)	112.30 (0.17)
Survival (%)	97.98 (0.53)	91.25 (1.16)

and covariance components were estimated, and the standard deviations of the estimated components were computed as shown by ANDERSON and BANCROFT (1952). Significance of the estimated variance components at the 5% probability level was determined by conventional F-test and SATTERTHWAIT (1946) approximation after comparing expected mean square coefficients (TIETJEN, 1974). Narrow-sense heritability based on individual seedlings were calculated as:

$$h^2 = \frac{4\sigma^2_{GCA}}{\sigma^2_P}$$

where σ^2_P is the total phenotypic variance, i.e.,

$$\sigma^2_P = \sigma^2_{SET} + 2\sigma^2_{GCA} + \sigma^2_{SCA} + \sigma^2_{TF} + \sigma^2_{RF} + \sigma^2_e$$

(see explanation of symbols in Table 1). The standard errors of the estimated heritabilities were determined as in BECKER (1984).

To examine relationships among traits, genetic correlations were computed. The formula for the genetic correlation ($r_{g(xy)}$) was:

$$r_{g(xy)} = \frac{\sigma_{GCA(xy)}}{\sqrt{\sigma^2_{GCA(x)}\sigma^2_{GCA(y)}}$$

where $\sigma_{GCA(xy)}$ is the additive covariance component between the traits x and y and $\sigma^2_{GCA(x)}$ and $\sigma^2_{GCA(y)}$ are the variances due to GCA for traits x and y, respectively. Approximate standard errors of the genetic correlation were determined following FALCONER (1981).

Results

Effects of spacing

Overall survival at the end of the third growing season was 95%, with better survival for the narrow (98%) than the wide (91%) spacing (Table 2). Survival varied among diallel sets (93% to 97%) and among diallel sets within spacings ranging between 95% to 99% and 89% to 97% for the narrow and wide spacings, respectively.

Although significant variances between the 2 spacings for HT1 and HT2 were found, the actual differences in mean heights (HT1, HT2 and HT3) were small (Tables 2 and 3). Spacing, however, had a strong influence on the distribution of the dry matter traits. The seedlings from the wide spacing allocated more energy towards roots and branches, producing larger diameter and heavier total dry weight than those from narrow spacing (Table 3). Consequently, wide spacing produced larger seedlings on average. Harvest index values (HIT and HIA) for narrow spacing, however, were higher than those for the wide spacing (33.60 vs. 30.99 and 44.16 vs. 41.70 for HIT and HIA, respectively) but the variances were not statistically significant (Tables 2 and 3). As expected, vegetative bud burst (PHE) was not influenced by spacing effect (Table 2).

Variance components and heritabilities

Growth traits

The largest genetic variance component for HT1 was due to SCA effects accounting for a significant 13.1% of the total phenotypic variance, while the variance components due to diallel sets and GCA were not significant and accounted for 2.5% and 3.4%, respectively (Table 3 and Figure 1). By ages 2 and 3, with the exception of σ^2_{TF} , all

Table 3. — Estimates of variance components (standard deviation) and their percentage of total phenotypic variation and individual tree heritability for the studied traits.

Variance Component	HT1 ^{1/2}		HT2		HT3		DIA		RDW	
	Estimate	%	Estimate	%	Estimate	%	Estimate	%	Estimate	%
σ^2_T	0.1(0.1)*	-	5.5(4.5)*	-	-36.3(27.5)ns	-	3.53(3.00)*	-	89.3(74.4)*	-
σ^2_R	-0.0(0.0)ns	-	-0.1(0.0)ns	-	76.7(54.9)*	-	0.24(0.18)*	-	3.4(2.5)*	-
σ^2_{SET}	0.6(0.8)ns	2.5	3.3(2.6)*	6.7	15.7(12.6)*	5.9	0.35(0.24)*	9.0	3.2(2.1)*	4.6
σ^2_{GCA}	0.8(0.5)ns	3.4	1.9(0.8)*	3.9	9.5(4.7)*	3.6	0.16(0.06)*	4.2	1.1(0.6)*	1.6
σ^2_{SCA}	3.0(1.0)*	13.1	2.5(1.1)*	5.1	12.1(7.3)*	4.5	0.11(0.07)*	2.8	0.2(1.0)ns	0.3
σ^2_{TF}	2.6(0.6)*	11.4	1.3(1.0)ns	2.6	6.3(8.0)ns	2.4	0.11(0.07)ns	2.7	2.1(1.4)ns	3.0
σ^2_{RF}	0.3(0.4)ns	1.1	1.0(1.0)ns	1.9	47.5(8.4)*	17.9	0.08(0.08)ns	2.0	0.0(1.4)ns	0.0
σ^2_e	15.8(0.6)	68.5	39.7(1.4)	79.8	175.1(6.3)	65.7	3.08(0.11)	79.3	62.6(2.2)	90.5
σ^2_P	23.9		51.7		275.7		4.03		70.3	
h^2	0.13 (0.09)		0.15(0.06)		0.14(0.07)		0.16(0.06)		0.06(0.03)	

variance components for height due to genetic effects, i.e., σ^2_{SET} , σ^2_{GCA} , and σ^2_{SCA} , were significant (Table 3). The variance component due to GCA represents 1/4 of additive

genetic variance, and the proportion was constant over the 3-year period, amounting to an average of 3.6% of total phenotypic variance (Figure 1). As a result, the

Variance Component	SDW		BDW		TDW		HIT		HIA		PHE	
	Estimate	%	Estimate	%	Estimate	%	Estimate	%	Estimate	%	Estimate	%
σ^2_T	82.3(73.1)ns	-	226.2(186.4)*	-	1144.4(949.5)*	-	-1.2(4.3)ns	-	-0.6(3.5)ns	-	1.6(1.8)ns	-
σ^2_R	13.7(9.9)*	-	3.6(2.8)*	-	34.7(25.8)*	-	9.1(6.5)*	-	7.1(5.1)*	-	1.0(0.7)*	-
σ^2_{SET}	14.5(9.8)*	10.0	10.8(8.5)*	6.0	79.5(53.4)*	8.1	1.5(1.3)*	6.4	1.9(1.5)*	6.0	-0.6(1.6)ns	0.0
σ^2_{GCA}	5.6(2.3)*	3.8	7.1(2.7)*	3.9	31.0(12.4)*	3.2	1.1(0.4)*	4.8	1.5(0.5)*	4.7	4.9(1.3)*	20.9
σ^2_{SCA}	4.3(3.0)ns	3.0	4.0(3.4)ns	2.2	20.7(16.2)ns	2.1	0.5(0.5)ns	2.3	0.2(0.5)ns	0.7	1.0(0.4)*	4.3
σ^2_{TF}	4.3(3.4)ns	3.0	7.2(3.9)*	4.0	22.4(18.7)ns	2.3	-0.3(0.6)ns	0.0	-1.0(0.7)ns	0.0	-0.4(0.4)ns	0.0
σ^2_{RF}	11.4(3.4)*	7.8	4.8(3.7)ns	2.7	16.8(19.5)ns	1.7	4.4(0.8)*	18.7	4.5(1.0)*	14.0	1.3(0.5)*	5.4
σ^2_e	105.8(3.8)	72.4	146.0(5.2)	81.2	808.2(29.0)	82.6	16.1(0.6)	67.8	23.7(0.9)	74.6	16.2(0.6)	69.4
σ^2_P	151.6		186.9		1009.7		24.8		33.2		28.2	
h^2	0.15(0.06)		0.15(0.05)		0.12(0.05)		0.18(0.07)		0.18(0.06)		0.69(0.18)	

1) See table 1 for abbreviations of traits.

2) $\sigma^2_P = \sigma^2_{SET} + 2\sigma^2_{GCA} + \sigma^2_{SCA} + \sigma^2_{TF} + \sigma^2_{RF} + \sigma^2_e$

* Significant at $P < 0.05$

narrow-sense heritability estimates remain similar for the 3 years, ranging from 0.13 to 0.15. The variance component due to SCA, representing the non-additive variance,

was sharply reduced from 13.1% for HT1 to 5.1% and 4.5% for HT2 and HT3, respectively (Figure 1). The SCA variance component for each of the 3 years was larger

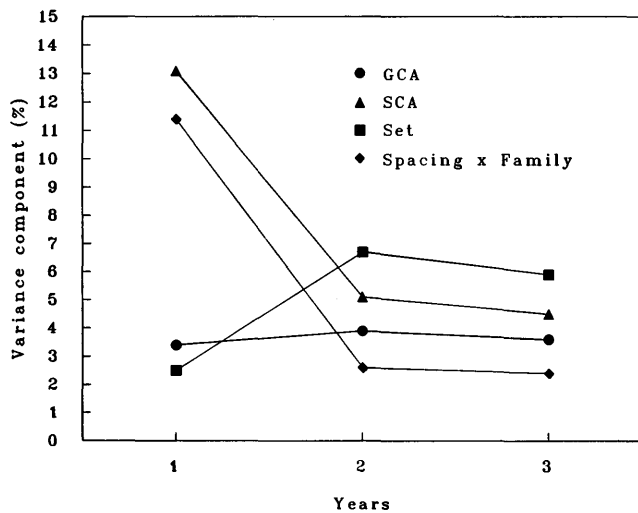


Figure 1. — Changes in GCA, SCA, diallel set, and spacing x family interaction variances for height over 3 years.

than that for GCA (Table 3 and Figure 1). Variance due to diallel set was not significant for HT1 but increased significantly to 6.7% and then decreased to 5.9% for HT2 and HT3, respectively (Table 3 and Figure 1). The proportion of variance due to diallel sets was larger than that due to the GCA or to SCA effect for HT2 and HT3 (Table 3).

All the variance components due to genetic effects for diameter were significant (Table 3). With the exception of the within-plot error component, the diallel set component was the largest variance component (9.0%). The GCA variance accounted for 4.2% of the total phenotypic variance and was higher than SCA variance (2.8%). Spacing x family interaction variance was small and non-significant (2.7%) with a lower percentage than that of the GCA but similar to that of the SCA (Table 3). Narrow-sense heritability for diameter was 0.16, which was slightly higher than those of HT1 and HT3 but comparable with HT2, and similar to that reported by CAMPBELL and WILSON (1973) for a 3-year-old Douglas-fir spacing trial.

Biomass and Harvest indices

With the exception of both plot and within-plot error components, the diallel set variance component was the largest for all dry weight measurements (RDW, SDW, BDW, and TDW) and ranged between 4.6% and 10.0%. The GCA variance for all dry weights was significant and larger than the non-significant SCA counterparts (Table 3). Spacing x family interaction was significant for BDW amounting to 4.0% (Table 3). Narrow-sense heritability estimates for dry weights ranged from 0.06 to 0.15 (Table 3).

Variance components for harvest indices (HIT and HIA) were similarly partitioned with the major part of the variance residing in the within-plot error (67.8% for HIT and 74.6% for HIA) (Table 3). The diallel set component accounted for 6.4% and 6.0% for HIA and HIT, respectively. Significant GCA and non-significant SCA variance components were obtained for both harvest indices, yielding narrow-sense heritability of 0.18 for both HIT and HIA (Table 3). Except for PHE, these estimates were the highest of all the traits studied, indicating that these traits may be more useful than the other size measurements for early selection. The inclusion of the root system

in the calculation of harvest index (HIT) did not affect the variance components or the heritability estimates. Although spacing x family interactions components for both indices were zero (negative), there were significant blocks within spacing x family interactions (plot error) (Table 3).

Vegetative phenology

The variation of vegetative bud burst (PHE) was largely explained by GCA effects that accounted for a significant 20.9% of the total phenotypic variance. Variances due to diallel sets and spacing x family interaction were not significant. The variance component due to SCA was small (4.3%). PHE gave the highest narrow-sense heritability and was not affected by spacing or spacing x family interactions. Bud flush is known to be heat and photoperiod dependent, neither of which are influenced by spacing (KRAMER and KOZLOWSKI, 1979).

Genetic correlations

The genetic correlations among heights for all pairs of ages were high and positive (Table 4). HT1 was more highly correlated with both HT2 and HT3 than was HT2 with HT3 (Table 4). Height-diameter genetic correlations were high and equalled or exceeded 0.50 (range: 0.50 to 0.74) (Table 4). Height-harvest index correlations were higher for HIT (0.49 to 0.71) than for their HIA (0.42 to 0.66) counterparts (Table 4). The correlations among heights with HIA tended to decline with age, from 0.66 to 0.46 and to 0.42 for HT1, HT2 and HT3, respectively (Table 4). Correlations among heights with PHE were negative and low (range: -0.02 to -0.11). Although these correlations may be zero judging by their standard errors, the apparent negative relationships were consistent with our expectations, as late flushing is usually associated with reduction of the growing season, consequently yielding shorter height increments.

Genetic correlations among diameter (DIA), dry weights, and harvest indices are very revealing. High correlations were obtained between DIA and all dry weight measurements (range: 0.75 to 0.89) supporting the use of DIA as a surrogate trait for dry weight estimation. On the other hand, correlations between DIA and harvest indices were low (0.29 and 0.22 for HIT and HIA, respectively) indicating that the dry matter allocation strategy is not strongly dependent on size or dry weights (Table 4). A low and negative correlation (-0.08) was obtained between DIA and PHE similar to those obtained for heights and PHE.

Genetic correlations among dry weight measurements (RDW, SDW, BDW and TDW) were positive and high (range: 0.61 to 0.96) (Table 4). These high correlations also indicate the presence of a balance between seedling parts. In other words, large seedlings are usually characterized by large stems that are needed to support their large root systems and branches. Conversely, small seedlings are characterized by their small stems, branches, and roots.

For genetic correlations between dry weights and harvest indices, low correlations were obtained for RDW (0.02 to 0.04), BDW (-0.10 to 0.19) and TDW (0.16 to 0.39) (Table 4). BDW and HIA were negatively correlated (-0.10), in contrast to the positive correlation obtained for HIT (0.19), indicating that the BDW effect on harvest index estimation could be masked when RDW is included in the calculation. Since SDW represents the most important factor in harvest index calculation, high and

Table 4. — Genetic correlation (standard error) coefficients among the studied traits. All traits except heights were measured during or after the third growing season.

	HT2	HT3	DIA	RDW	SDW	BDW	TDW	HIT	HIA	PHE
1-year height (HT1)	1.07 (-0.05)	0.91 (0.06)	0.60 (0.22)	0.58 (0.28)	0.83 (0.11)	0.58 (0.23)	0.74 (0.16)	0.71 (0.17)	0.66 (0.18)	-0.11 (0.29)
2-year height (HT2)		0.73 (0.15)	0.74 (0.13)	0.75 (0.15)	0.74 (0.13)	0.62 (0.17)	0.71 (0.14)	0.49 (0.21)	0.46 (0.21)	-0.02 (0.23)
3-year height (HT3)			0.50 (0.22)	0.58 (0.25)	0.82 (0.10)	0.67 (0.17)	0.78 (0.12)	0.58 (0.12)	0.42 (0.23)	-0.05 (0.25)
Diameter (DIA)				0.89 (0.07)	0.77 (0.11)	0.75 (0.12)	0.89 (0.06)	0.29 (0.24)	0.22 (0.24)	-0.08 (0.22)
Root dry weight (RDW)					0.61 (0.21)	0.68 (0.18)	0.77 (0.13)	0.02 (0.32)	0.04 (0.31)	-0.10 (0.27)
Stem dry weight (SDW)						0.82 (0.09)	0.93 (0.04)	0.69 (0.14)	0.47 (0.20)	-0.30 (0.21)
Branch dry weight (BDW)							0.96 (0.02)	0.19 (0.26)	-0.10 (0.25)	0.34 (0.20)
Total dry weight (TDW)								0.39 (0.23)	0.16 (0.25)	-0.31 (0.21)
Harvest index-total (HIT)									0.91 (0.04)	-0.06 (0.22)
Harvest index-above ground (HIA)										0.09 (0.21)
Phenology (PHE)										

positive correlations were expected between SDW and HIT (0.69) and HIA (0.47) (Table 4). The lower SDW correlation between HIA than HIT supports the root system masking effect on harvest index calculations. PHE and dry weights correlations were low, ranging between -0.10 and 0.34 for RDW and BDW, respectively. These results were similar to those obtained for height and DIA (Table 4).

The genetic correlation between HIT and HIA is of practical importance. A high and positive correlation was observed between the two harvest indices (0.91) (Table 4), indicating that the use of the above ground harvest index

(HIA) is an excellent predictor of total harvest index (HIT).

Discussion

Significant genetic variation due to GCA was found for all the studied traits except HT1. The pattern for height suggests that the importance of SCA, although greater than GCA, decreases with age while GCA remains unchanged, indicating that exploitation of GCA is possible. The relative magnitude of the GCA variance component for this early test period was very similar to that reported by YEH and HEAMAN (1987) for 7-year-old height of a con-

ventional Douglas-fir progeny test that consisted of 10 sets of six-parent disconnected diallels planted on 11 sites. If the rank changes among families over time were mainly among intermediate families and the GCA variance remains constant, as was the case in YEH and HEAMAN (1987), selection based on early evaluations is likely to be effective provided that selection intensity is not too high.

In this study, SCA variance representing the non-additive variation was larger than GCA variance for height in each of the three measurement years but declined over the 3-year test period, while GCA variance remained unchanged. The percentage contribution of SCA relative to GCA cannot be extrapolated beyond the 3 years studied. However, YEH and HEAMAN (1987) reported significantly lower SCA than GCA in 7-year height of Douglas-fir progeny testing. Such a change in the non-additive and additive variances over time is predicted by FRANKLIN'S (1979) model and was empirically demonstrated by several studies (BOYLE, 1987; NAMKOONG et al., 1972; LAMBETH et al., 1983).

Except for HT1 and PHE, variance due to diallel set was significant and often large. For example, it was larger than GCA or SCA variances for most traits studied. Similar results were reported for 7-year-old height of Douglas-fir progeny test where diallel set effect was 76% as large as the GCA variance component (YEH and HEAMAN, 1987). Since the diallel sets both in this study and, to a large extent, in YEH and HEAMAN'S study, were formed according to the availability of pollen and receptive strobili, the set effect may reflect genetic stratification caused by such grouping. Alternatively, the set effect may be due to sampling by the chance clustering of high or low GCA clones in one or more sets. Although the data were not presented, the means for diallel sets in this study differed, with sets 7 and 6 producing the highest and lowest height, diameter, and root, shoot and branch dry weights, respectively.

The strong influence of spacing was demonstrated on most growth (HT1, HT2 and DIA) and biomass traits (RDW, BDW and TDW). Generally, the wide spacing produced larger seedlings and greater dry weight than narrow spacing. This result is in general agreement with that reported for 3-year-old and 25-year-old Douglas-fir spacing trials by CAMPBELL and WILSON (1973) and SMITH and EL-KASSABY (1985), respectively.

As mentioned earlier, we were interested in genetic relationships and allocation strategies of early dry weight traits, since they related better with field performance relative to other juvenile traits in several studies. All the genetic correlations among growth and dry weight traits were large. The relatively large genetic correlations of DIA with the dry weight traits indicate the potential usefulness of DIA in predicting biomass production if dry weight data are not available.

We suggest using harvest index as a component for improving yield in tree breeding programs. Reallocation of photosynthate or biomass from branches and roots to increased growth of useful stem wood can be an important factor in forest productivity. Although our harvest indices were based on dry weights, there were no spacing effects. In addition, low but positive, genetic correlations indicate that harvest indices were not strongly dependent on dry matter production or size. Perhaps it indicates that harvest indices calculated from progeny tests with different spacing or cultural regimes can be equally useful; however,

actual biomass production is affected by such silvicultural practices.

Relatively high heritability estimates for harvest indices may indicate selection response is likely to be substantial in changing crop tree ideotypes. The high harvest index values, however, represent "stem-heavy-type" plants, but do not necessarily relate to growth traits or yield. Therefore, selection for harvest index alone will relate to allocation strategy, and smaller plants may be produced. VELLING and TIGERSTEDT (1984), presented a classic case where the small selfed trees produced higher harvest index than their outbred counterparts. When harvest index is considered as a selection criterion, we suggest the use of selection indices that include yield traits such as diameter and height. The positive but relatively low genetic correlations obtained among DIA, dry weights and both harvest indices support this notion.

For practical reasons, most studies of harvest index in trees have ignored the below ground parts (PULKKINEN et al., 1989), introducing what was perceived as a major error as the root systems are expected to be highly influenced by the environment. The high genetic correlation (0.91) obtained between HIT and HIA in our study supports the use of HIA if HIT is not available and calls for similar studies on other species.

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Foliage Resin Composition of *Cupressus sempervirens* L. as Affected by Environmental Factors¹⁾

By G. SCHILLER²⁾

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Abstract

Effects of some environmental factors on the relative amounts (%) of *Cupressus sempervirens* L. foliage resin compounds were examined in a partial factorial experiment. The results presented show that environmental factors, such as soil, water availability and radiation intensity, affect to a certain degree the foliage resin composition of clonal plants of *Cupressus sempervirens* L. cv. *stricta* and var. *horizontalis*.

Key words: *Cupressus sempervirens*, Italian cypress, monoterpenes.

Introduction

In earlier studies of the foliage resin composition of *Cupressus sempervirens* L. (SCHILLER, 1990; SCHILLER and MADAR, 1991) significant differences were detected in different environments between populations and between diseased and visually nondiseased trees. Differences in the development of cankers caused by the fungi *Seiridium* sp. or *Diploida* sp. were attributed to differences in soil properties (MADAR, personal communication) and water availability (MADAR *et al.*, 1989). Autecological studies of cypress have shown differences in growth patterns on different soils of *Cupressus sempervirens* cv. *stricta* and var. *horizontalis* (ZOHAR, 1984). Numerous studies, *e.g.*, BRIDGEN and HANOVER (1982), ENNOS and SWALES (1988), FRANICH *et al.* (1982), MICHELOZZI *et al.* (1990), ROCKWOOD (1974), SCHUCK (1982), have shown relations between resin composition and resistance to fungi.

The hypothesis that underlays the use of coniferous resin composition as a genetic indicator is that the composition is strongly inherited and subject to only minor environmental influences (SQUILLACE, 1976; VON RUDOLFF and REHFELDT, 1980). This premise was critically reviewed by BIRKS and KANOWSKY (1988) who concluded that the evidence for this assumption is not conclusive.

The present study was undertaken to determine whether, and to what extend, environmental factors affect the foliage resin composition of *Cupressus sempervirens* L. and hence, the reliability of the technique as a genetic indicator and as an indicator for disease resistance.

Materials and Methods

a) Plant material

Cuttings were taken from 2 different 70-year-old trees

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²⁾ Department of Natural Resources, Agricultural Research Organization, The Volcani Center, P.O. Box 6, Bet Dagan 50250, Israel.



Figure 1. — Italian cypress (*Cupressus sempervirens* L.) trees at Bet Dagan.

(A) Var. *horizontalis* (MILL.) GORDON;

(B) cv. *stricta* AIT. (= var. *stricta* AIT. = var. *pyramidalis* NYMAN).

of *C. sempervirens* L. (Fig. 1) growing at the Volcani Center at Bet Dagan, Israel (32°00' lat. N; 34°49' long. E). Tree A was of var. *horizontalis* (MILL.) GORDON, and tree B was of cv. *stricta* (var. *stricta* AIT. = var. *pyramidalis* NYMAN). Both trees are not irrigated and grow on a calcareous sandstone at 50 m' a.s.l. In October 1989, 5-cm-long cuttings of the 2 trees were taken from a few main branches at a similar height above ground. Cuttings were rooted using the method developed by CHEMLA (1986). In December, the rooted cuttings were transplanted into 5-liter plastic nursery bags.

b) Experimental design

The treatments applied were as follow: