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Genetic variances and interactions in 9-year-old Douglas-fir grown at narrow spacings

By R. K. Campbell, R. M. Echols and R. W. Stonecypher[1])

Summary

The variance structure (additive-genetic, plot, within plot, and interactions) in a population of unselected Douglas-fir was studied; 54 control-pollinated families grown at three close spacings (30, 60, 90 cm) in two plantations were used. Significant genotype × spacing interaction occurred only for height of 5-year- and volume of 9-year-old Douglas-fir and could be attributed to measurement scale. Plantation × genotype interactions occurred in diameter, height, height increment, branch length, volume, and dry weight of stem. Traits fell roughly into three individual-tree heritability (h^2) classes. The lowest group ($h^2 \approx 0.15$) included total height at younger ages, height increment and branch length; the medium group ($h^2 \approx 0.20$), 9-year height, diameter, volume, and dry weight of stem; and the highest group ($h^2 \approx 0.48$), specific gravity.

Close spacing appears to have the potential for improving effectiveness of early selection for total height by increasing the age-age correlation as hypothesized by Franklin (1979). Close spacing, however, apparently did not shift the genetic variance structure from the juvenile to the mature phase. Coefficients of variation for additive-genetic, plot, and within-plot effects were similar to corresponding coefficients calculated for tests in young loblolly pine, ponderosa pine, and Douglas-fir grown at much wider spacing.

Key words: Genetic variations, plantation spacing, growth, growth rate, Douglas-fir, *Pseudotsuga menziesii.*

Zusammenfassung

Es wurde die Varianzstruktur (additiv-genetische, Parzellen-, innerhalb der Parzellen und Interaktions-Varianz) in einer Population unselektierter *Pseudotsuga menziesii* studiert. Hierzu wurden 54 kontrolliert bestäubte Familien, die in 3 engen Pflanzen-Abständen (30, 60, 90 cm) auf zwei Versuchsflächen herangewachsen waren, benutzt. Signifikante Genotyp × Standraum Interaktionen gab es nur für die Höhe im Alter 5 und das Volumen im Alter 9 der Douglasien und konnten der Meßskala zugeschrieben werden.

Versuchsfläche × Genotyp Interaktionen traten beim Durchmesser, bei der Höhe, dem Höhenzuwachs, der Astlänge, dem Volumen und dem Stammtrockengewicht auf. Die Merkmale fielen grob in 3 Einzelbaum-Heritabilitäts-(h^2)-Klassen. Die niedrigste Gruppe ($h^2 \approx 0.15$) enthielt die Gesamthöhe im jüngeren Alter, den Höhenzuwachs und die Astlänge; die mittlere Gruppe ($h^2 \approx 0,20$) die Höhe im Alter 9, den Durchmesser, das Volumen und das Stammtrockengewicht, die höchste Gruppe ($h^2 \approx 0,48$) das spezifische Gewicht.

Der enge Abstand schien die Fähigkeit zu besitzen, die Effektivität für eine Frühselektion auf die Gesamthöhe durch Erhöhung der Alter zu Alter Korrelation zu verbessern, wie *Franklin* 1979 hypothetisch angenommen hat. Ein geringer Pflanzenabstand verschob jedoch augenscheinlich nicht die genetische Varianzstruktur von der Jugend- zur Altersphase. Additiv genetische Variationskoeffizienten und Parzellen-Variationseffekte, sowie die innerhalb von Parzellen waren entsprechenden Koeffizienten ähnlich, die in Tests mit jungen *Pinus taeda*, *Pinus ponderosa* und *Pseudotsuga menziesii* errechnet wurden, die mit viel größerem Abstand aufgewachsen waren.

Introduction

In a previous study of 3-year-old, nursery-grown Douglas-fir *(Pseudotsuga menziesii* [Mirb.] Franco var. *menziesii)* seedlings with a widest spacing of 18 cm × 18 cm, spacing-genotype interactions in stem diameter and volume were attributed to effects of measurement scale (Campbell and Wilson 1973). In this paper, we report an experiment involving 9-year-old cross-pollinated families grown in two plantations at square spacings ranging from 30 to 90 cm.

The experiment tested interaction but also provided information on genetic and environmental variances for several traits, and on age-age correlations for stem height. Variance structures for stem height have been shown to change with age in Douglas-fir (Namkoong *et al.* 1972), ponderosa pine *(Pinus ponderosa* Laws.) (Namkoong and Conkle 1976), loblolly and slash pines *(P. taeda* L., *P. elliotii* Engelm.) (Franklin 1979). These changes apparently give rise to characteristic time trends in variances, heritabilities, and age-age correlations (Franklin 1979). Franklin suggested that trends might be manipulated by silviculture, one factor being close spacing, to increase the age-age correlation and thereby make early selection more

Table 1. — Expected mean squares for analyses of traits.

Variation source	df	σ_w^2	σ_p^2	$\sigma_{1sm(f)}^2$	$\sigma_{sm(f)}^2$	$\sigma_{1m(f)}^2$	$\sigma_{m(f)}^2$	σ_{1sf}^2	σ_{sf}^2	σ_{1f}^2	σ_f^2
						Expected mean square[a]					
Plantations (L)	1										
Replications in plantations (R(L))	6										
Spacings (S)	1										
L x S	1										
Females (F)	8	1/k	1[b]			12(8)	24(6)			72(48)	144(96)
L x F	8	1/k	1			12(8)				72(48)	
S x F	16(8)[c]	1/k	1	4	8			24	48		
L x S x F	16(8)	1/k	1	4				24			
Males in females M(F)	45	1/k	1			12(8)	24(6)				
L x M(F)	45	1/k	1			12(8)					
S x M(F)	90(45)	1/k	1	4	8						
L x S x M(F)	90(45)	1/k	1	4							
Pooled error	966(642)	1/k	1								
Within plot		1									

a/ σ_w^2 = sum of within-plot environmental effects and variance among full-sib progeny

σ_p^2 = variance of plot effects

$\sigma_{1sm(f)}^2$, $\sigma_{sm(f)}^2$, $\sigma_{1m(f)}^2$ = interaction variance of males in females with plantation and spacing

$\sigma_{m(f)}^2$ = variance of male effects averaged over females

σ_{1sf}^2, σ_{sf}^2, σ_{1f}^2 = interaction variance of females with plantation and spacing

σ_f^2 = variance of females.

b/ Coefficients of variance components--coefficients in parentheses are for analyses on two spacings only--k = harmonic mean of plants per plot, 4.23 and 4.27 for 3- and 2-spacings analyses, respectively.

c/ Degrees of freedom in parentheses for analyses at two spacings; e.g., for specific gravity and dry weight.

effective. If FRANKLIN's proposal is correct, stand treatment for controlling trends could become an important aspect of tree breeding.

We report that close spacing in this experiment has not changed the variance structure of Douglas-fir; our variance structure was similar to structures from other tests of Douglas-fir and of other species in which young plants were grown at much wider spacing. Close spacing, however, has affected age-age correlations; whether this effect is likely to be beneficial for early selection appears to depend partly on the spacing at younger and older ages.

Materials and Methods

Families came from crosses made according to the Design I crossing scheme (COMSTOCK and ROBINSON 1952). The 63 parents, 9 used as females, 54 as males--6 males nested in each female--were chosen randomly from reproductive trees in a small, naturally regenerated stand in Pack Demonstration Forest near La Grande, Washington (elevation, 335 m). Stratified seeds of each cross were planted in the nursery in four randomized blocks. After two growing seasons in the nursery, bare-root seedlings were outplanted in two plantations near Centralia, 50 km west of La Grande. Plantations were 25 kilometers apart and at low elevation (less than 200 meters). Plantation 1 had clay-loam soil; plantation 2, sandy soil with a large component of gravel and cobbles. After planting, plantation 1 was watered once. Plantation 2 was watered several times in the first two growing seasons; it was also kept essentially free of weeds.

At each plantation, seedlings were planted at three square spacings (30 cm, 60 cm, 90 cm) in 20 replications of single-tree plots (54 seedlings per plot--one from each family--randomly allocated to a spot within the plot) at each spacing. A maximum of 40 seedlings was available for each full-sib family in each spacing (20 replications × 2 plantations). The three spacing plots in each of the 20 replications were systematically placed for efficient blocking and were surrounded by border trees not included in the study.

Because of mortality, data for seedlings from five juxtaposed replications were combined and the resulting two to five observations per spacing and family were treated as one plot in a randomized block. This not only solved the problem of missing plots but also ensured that areas sampled by the surviving seedlings in each family plot were of roughly comparable size, regardless of spacing.

All trees were harvested after the ninth growing season. Except for wood specific gravity, which was measured only for trees in the two widest spacings, the following data were taken for each tree: (1) stem height at ages 5, 7, and 9 years; (2) stem diameter measured by caliper at 30 cm above ground line, (3) length of longest branch in the second whorl from the apex; and((4) wood specific gravity determined from a disk 1—4 cm wide taken from the stem about 30 cm above ground line.

From these data we constructed additional traits: (1) stem volume calculated from simple volume equations based on a 10-percent sample of half-height diameters, (2) an index of stem dry weight calculated as stem volume × wood specific gravity, and (3) stem height increments for the years 5—7 and 7—9.

Standard analyses of variance based on the following model were performed on plot means for each trait (Y). Locations, replications in locations, families, and individuals in families are considered random samples from infinite populations and spacing is considered a fixed effect. The model is:

$$Y = \mu + L_l + R_{r/l} + S_s + (LS)_{ls} + F_f + (LF)_{lf} + (SF)_{sf} + (LSF)_{lsf} + M_{m/f} + (LM)_{lm/f} + (SM)_{sm/f} + (LSM)_{lsm/f} + e_p + e_w$$

where

L_l = lth location effect

$R_{r/l}$ = rth replication effect in the lth location

S_s = sth level effect of spacing

$(LS)_{ls}$ = interaction deviation of lth location with sth spacing level

F_f = fth female effect

$M_{m/f}$ = effect of the mth male mated to fth female

(LF), (SF), (LFS), (LM), (SM), (LMS) = interaction effects of designated main effects

e_p = plot error

e_w = within plot error including variance among full sibs

Table 2. — Trait means at two plantations and three spacings.

Plantation and spacing (cm)	Diameter age 9 (cm)	Total ht., age 5 (cm)	Height increment, 5-7 yr (cm)	Total ht., age 7 (cm)	Height increment, 7-9 yr (cm)	Total ht., age 9 (cm)	Stem volume (1)	Specific gravity	Stem dry weight (gm)	Branch length (cm)
Plantation 1:										
30	2.47	158.2	123.6	281.8	69.5	351.3	1.022	--	--	46.1
60	4.00	182.1	159.7	341.8	134.3	476.1	3.057	.406	1227.8	70.1
90	5.51	201.0	171.6	372.6	156.8	529.4	5.896	.394	2316.1	80.5
Plantation 2:										
30	2.72	178.2	112.5	290.7	66.5	357.2	1.168	--	--	43.9
60	4.29	183.2	141.2	324.4	109.9	434.4	3.047	.399	1221.0	57.2
90	5.92	193.0	133.6	326.6	145.1	472.7	5.724	.382	2184.1	68.8

Table 3. — Significance of F-tests applied to mean squares, and error coefficients of variability (CV) for 10 traits.

Sources of variation	Diameter, age 9	Total ht., age 5	Height increment, 5-7 yr	Total ht., age 7	Height increment, 7-9 yr	Total ht., age 9	Stem volume	Specific gravity	Stem dry weight	Branch length
Females	***	**	***	***	--	***	***	***	***	**
Plantation x females	--	*	--	--	**	--	--	+	--	*
Spacing x females	--	*	+	+	--	--	***	--	+	+
Plantation x spacing x females	--	--	--	--	--	--	--	--	--	--
Males/females	***	***	**	***	***	***	***	***	***	***
Plantation x males/females	**	--	--	--	--	--	**	--	**	--
Spacing x males/females	--	--	--	--	+	--	+	--	--	--
Plantation x spacing x males/females	--	--	--	--	--	--	--	--	--	+
Error mean squares (EMS)	0.35080	505.084	392.495	853.651	680.555	1495.562	1.35233	0.0001254	252892.0	63.4349
CV = $\sqrt{EMS}/\bar{X}$	14.3	12.3	14.1	9.0	22.9	8.9	35.0	2.8	28.9	13.0

+ = significant at probability < 0.10.
* = significant at probability < 0.05.
** = significant at probability < 0.01.
*** = significant at probability < 0.001.

To obtain estimates of components of variance, mean squares were equated to their expectations (Table 1), and the resulting equations were solved. Analyses of covariance and estimates of components of covariance followed the same form as for variances (Table 1) except that all calculations involved mean cross-products.

Calculations of standard errors for genetic correlations and variance components were based, respectively, on procedures developed by McCullough (1972) and explained by Kempthorne (1957, page 246). Reported individual tree heritabilities (h²) are based on the relationship $h^2 = \sigma_A^2/$

σ_t^2 where the additive genetic variation was calculated as $\sigma_A^2 = 2\sigma_f^2 + 2\sigma_{m(f)}^2$ and phenotypic variation was calculated as $\sigma_t^2 = \sigma_f^2 + \sigma_{lf}^2 + \sigma_{sf}^2 + \sigma_{lsf}^2 + \sigma_{m(f)}^2 + \sigma_{lm(f)}^2 + \sigma_{ms(f)}^2 + \sigma_{lsm(f)}^2 + \sigma_p^2 + \sigma_w^2$.

To compare variance structures in our test with the structures reported in other tests, the relative magnitudes of variance components were calculated for different traits and species. For these comparisons, we transformed the ith component (σ_{ij}^2) for trait j to its coefficient of variation ($\sigma_{ij}/\bar{X}$).

To provide information for evaluating Franklin's (1979) proposal that close spacing might increase age-age correlations, correlations were calculated among the mean heights of the 54 full-sib families. The nine combinations

Table 4. — Components of variance and standard errors (in parentheses) for 10 traits.

Components of variance[a]	Diameter, age 9	Total ht., age 5	Height increment, 5-7 yr	Total ht., age 7	Height increment, 7-9 yr	Total ht., age 9	Stem volume	Specific gravity	Stem dry weight	Branch length
σ_f	0.08952	65.45741	35.1476	176.9697	9.4725	312.196	0.29477	9.9760-04	57797.01	5.31481
	(0.04899)	(39.8025)	(17.2148)	(93.8441)	(15.8076)	(173.760)	(0.15712)	(0.5098-04)	(32593.12)	(3.47677)
σ_{lf}	-0.00376	10.3975	-3.2687	5.2563	15.2128	11.883	-0.00783	0.2911-05	-2078.53	0.86740
	(0.00257)	(8.1166)	(1.0004)	(9.3394)	(9.7772)	(15.005)	(0.01192)	(0.2741-05)	(3729.60)	(0.69381)
σ_{sf}	0.00230	10.3525	6.2473	14.2186	-4.2895	2.817	0.09762	-0.2606-06	6260.41	1.13180
	(0.00482)	(5.7566)	(4.7334)	(9.2393)	(5.9952)	(15.418)	(0.04439)	(0.1761-05)	(4517.59)	(0.79165)
σ_{lsf}	0.00290	-7.4729	1.8163	-9.1876	-1.0716	5.372	-0.01142	-0.1880-09	-4461.49	-1.20960
	(0.00562)	(5.8952)	(4.9257)	(10.6117)	(8.0762)	(20.621)	(0.01698)	(0.2219-05)	(2696.79)	(0.81807)
$\sigma_{m(f)}$	0.10417	82.7944	16.3993	133.6585	75.1097	344.959	0.26340	0.8216-04	66131.37	9.64870
	(0.2698)	(22.1564)	(6.6054)	(37.7418)	(19.8876)	(84.683)	(0.07562)	(0.1893-04)	(20190.97)	(2.42932)
$\sigma_{lm(f)}$	0.01942	2.4638	-6.8964	16.7532	-18.0339	-0.630	0.07050	0.4762-06	23860.51	-1.36010
	(0.01012)	(9.1908)	(5.3245)	(18.4166)	(7.9789)	(50.333)	(0.03813)	(0.3780-06)	(11443.00)	(1.61980)
$\sigma_{sm(f)}$	0.00612	-19.6973	-7.2200	-35.4306	27.2163	30.702	0.05861	0.4424-07	5125.94	-1.18170
	(0.00877)	(12.0017)	(6.7815)	(19.5526)	(17.4883)	(35.902)	(0.04155)	(0.4647-06)	(8556.45)	(1.88946)
$\sigma_{lsm(f)}$	-0.00989	6.8446	-23.3137	6.1829	-31.8356	-61.602	-0.00250	-0.4224-06	-9913.27	3.40750
	(0.01147)	(19.6268)	(10.5958)	(33.7996)	(20.3917)	(46.044)	(0.04947)	(0.5597-05)	(10996.96)	(2.84065)
σ_p	0.01757	-23.3014	-80.3924	89.660	349.327	201.115	0.12980	0.1077-03	14806.14	2.50040
σ_w	1.40957	2235.0724	2000.3128	3231.6836	1401.0931	5475.385	5.17131	0.4600-03	1,016,626.58	237.03516

a/ Components defined as in Table 1.

Traits	X̄	h²	σ_t
9-year diameter (cm)	4.16	0.24	1.28
5-year height (cm)	182.6	.13	48.6
5- to 7-year height growth (cm)	140.4	.05	44.0
7-year height (cm)	323.0	.17	60.2
7- to 9-year height growth (cm)	113.9	.09	42.7
9-year height (cm)	436.8	.21	79.5
9-year volume (l)	3.32	.18	2.46
Specific gravity	.396	.48	.027
Dry weight (gm)	1737.0	.21	1084.0
Branch length (cm)	61.1	.12	16.0

of total height measured at three ages in three spacings gave 36 correlation coefficients dissociable into three types: (1) age-age correlations among the three ages when heights were measured in the same individuals within a spacing, (2) correlations between two spacings of full siblings of the same age, and (3) age-age correlation among the full siblings measured in different spacings.

Coefficients were analyzed in an analysis of variance for each type of coefficient, in classification models with age and spacing contrasts and interactions. Because coefficients were not replicated, error was estimated with sums of squares and degrees of freedom derived from the nonlinear interactions terms in the model (Lı 1964). Untransformed correlation coefficients were used only in one analysis that compared type 1 correlations with LAMBETH's (1980) model. In all other analyses coefficients were transformed to FISHER's z scale (KEMPTHORNE 1957). Each of the average correlations reported later in the text is a backtransformation of an average z.

Results

Tree size was greatly affected by spacing. For both plantations, the widest spacing produced trees larger than did the narrowest spacing: 1.4 times larger in height; 2.2, in diameter; and 5.2 in volume (Table 2). The average stem volume of trees in the two plantations was almost identical, but trees in plantation 1 were taller and slimmer and had longer branches than trees in plantation 2.

Genetic variability occurred in all traits as is indicated by highly significant mean squares for females and males (Tables 3, 4).

Traits fell roughly into three heritability classes. The trait group showing lowest heritability (≈ 0.15) included total height at younger ages, height increments, and branch lengths (Table 5). Heritabilities for height at 9 years, diameter, volume, and stem dry weight clustered around h² =

0.20. The trait with the strongest additive genetic control was wood specific gravity (h² = 0.48, Table 5).

Strong genetic correlations occurred among yield traits, height, diameter, volume, and dry weight (Table 6). Correlations among yield traits and other traits, especially wood specific gravity, were smaller. Also, for specific gravity and branch length, calculations based on male components appeared to give rise to coefficients indicating correlations that were fundamentally different from those based on female components. For example, although none of the coefficients involving specific gravity were significant, those derived from male components were consistently more positive than those from female components. For branch length, the situation was reversed--coefficients from male components were consistently less positive than those from female components.

Genotype × plantation interactions were also inconsistent among estimates for females and males and were sometimes large. Components of variance for genotype × plantation interaction as a percentage of family variance ranged from 16 percent for 5-year height and branch length to 36 percent for dry weight, except for 7- to 9-year height increment which was 160 percent (Table 4). The size of this latter interaction implies striking changes in rank among female families at the two plantations. Female × plantation interactions occurred primarily in traits involving axial extension; e.g., stem height and branch length (Table 3). In contrast, male × plantation interactions occurred in traits more strongly influenced by radial expansion--diameter, volume, and dry weight. Also, size of interactions did not appear to be related to differences in trait means between plantations. The largest interactions occurred in 5-year height, volume, and dry weight--traits for which the plantation means differed by less than 5 percent (Table 2).

For most traits, family genotypes did not interact significantly with spacing. The significant spacing × female interaction for 9-year volume (Table 3) apparently resulted mainly from scale effects associated with the taller families at wider spacings (Fig. 1). Even so, the component of variance for interaction was small-about one-third of the variance among females (σ_{fs}^2/σ_f^2 = 0.33). Female × spacing effects for 5-year height were comparatively smaller, 16 percent of the female effect. Male × spacing interactions were not significant for total height at any age; only the 7- to 9-year height increment approached significance, P ≤ 0.06 (Table 3).

Components of variance for interactions decreased or increased with tree age, depending on whether effects were measured in male or female families. Coefficients of variation (CV) for female × spacing effects in total height

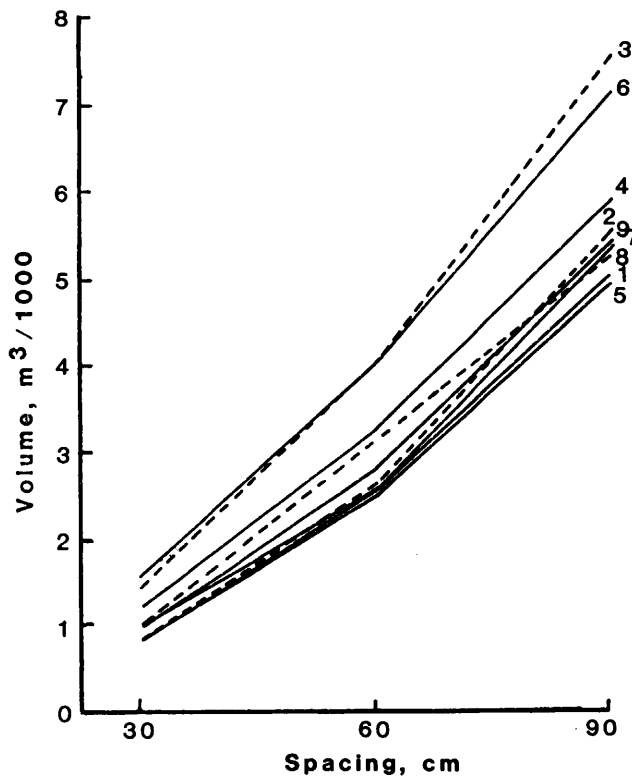|	Height	Branch length	Diameter	Specific gravity	Volume	Dry weight
Height	1	0.90(0.12)	0.81(0.16)	-0.14(0.37)	0.88(0.22)	0.92(0.24)
Branch length	0.63(0.12)	1	0.73(0.23)	-0.24(0.38)	0.83(0.14)	0.87(0.17)
Diameter	0.85(0.10)	0.53.(0.14)	1	-0.45(0.32)	0.99(1.10)	0.97(1.08)
Specific gravity	0.08(0.18)	0.23(0.17)	-0.01(0.18)	1	-0.46(0.31)	-0.30(10.90)
Volume	0.88(0.11)	0.51(0.15)	0.99(0.70)	-0.01(0.19)	1	0.99(0.01)
Dry weight	0.91(0.11)	0.57(0.13)	0.98(0.69)	0.16(4.19)	0.98(0.01)	1

Figure 1. — Female family mean-volumes averaged over two plantations. The dashed lines for families 2, 3, and 8 highlight the possible changes in rank.

decreased with measurement age 5, 7, and 9 years (from data in *Tables 4* and *5,* 100 $\sigma_{fs}/\overline{X}$ = 1.8 percent, 1.2 percent, and 0.4 percent). For male $\times$ spacing effects, coefficients increased with measurement age (CV = -2.4 percent, -1.8 percent, and 1.2 percent--the negative sign indicates a negative estimate of $\sigma_{sm(f)}^2$, *Table 4).*

Close spacing apparently has not shifted the variance structure in our experiment into a pattern inappropriate to young trees. The estimates of additive genetic variability in 9-year height in our test closely resembled estimates from young trees measured in other tests of Douglas-fir in families planted at much wider spacing than in our test. In one of these tests, the older one, heights were measured several times spanning six decades. In the other, heights were measured once at 6 years. In the older test, conditions varied considerably from those in our test. Estimates of additive genetic variances were derived as an average of sets of families within provenances (Namkoong *et al.* 1972). Some provenances originated quite distant from the plantation sites and may have been poorly adapted. Also, variances were based on measurement of surviving trees after mortality (average 40 percent) which differed among provenances.

In the older experiment, additive-genetic coefficients of variation, calculated as $(3\sigma_{f(p)}^2)^{0.5}/\overline{X}$, decreased from 0.14 at age 5 to 0.08 at age 12. From age 12 to age 23, coefficients remained constant and then decreased again to zero at age 40. Thus, in spite of the different conditions in the two tests, our estimate (0.08, *Table 7*) corresponded to estimates in the 12- to 23-year measurements in the older test. Our data also closely paralleled the pattern provided by

Table 7. — Coefficients of variation for additive genetic variation ($\sigma_A/\overline{X}$), plot variation ($\sigma_p/\overline{X}$), and within plot variation ($\sigma_w/\overline{X}$) for several species and traits.

Species and age	Data source[a]	Spacing (m)	Coefficients		
			$\sigma_A/\overline{X}$	$\sigma_p/\overline{X}$	$\sigma_w/\overline{X}$
Total height					
Wind-pollinated loblolly pine; 6-yr	1	2.4	0.11	0.10	0.18
Control-pollinated loblolly pine; 5-yr	1	2.4	.09	.06	.15
Wind-pollinated Douglas-fir; 10-yr	2	2.1	.12	.20	--
Wind-pollinated ponderosa pine; 8-yr	3	2.4	.07	.04	.14
Control-pollinated Douglas-fir; 9-yr	4	0.6	.08	.03	.17
Control-pollinated Douglas-fir; 5-yr	4	0.6	.09	-.03	.26
Control-pollinated Douglas-fir; 6-yr	5	3.0	.09	.12	.25
Diameter					
Wind-pollinated loblolly pine; 6-yr	1	2.4	.20	.21	.33
Control-pollinated loblolly pine; 5-yr	1	2.4	.14	.16	.42
Control-pollinated Douglas-fir; 9-yr	4	0.6	.15	.03	.29
Control-pollinated Douglas-fir; 6-yr	5	3.0	.11	.13	.25
Volume					
Wind-pollinated loblolly pine; 6-yr	1	2.4	.24	.26	.56
Control-pollinated loblolly pine; 5-yr	1	2.4	.14	.17	.46
Control-pollinated Douglas-fir; 9-yr	4	0.6	.32	.11	.69
Wood specific gravity					
Wind-pollinated loblolly pine; 6-yr	1	2.4	.05	.02	.06
Control-pollinated loblolly pine; 5-yr	1	2.4	.06	.03	.06
Control-pollinated Douglas-fir; 9-yr	4	0.6	.05	.03	.05
Stem dry weight					
Wind-pollinated loblolly pine; 6-yr	1	2.4	.23	.25	.45
Control-pollinated Douglas-fir; 9-yr	4	0.6	.29	.07	.58

a/ 1 = Stonecypher *et al.* (1973).
    2 = Namkoong *et al.* (1972).
    3 = Namkoong and Conkle (1976).
    4 = this experiment.
    5 = Yeh and Heaman (1982).

data from YEH and HEAMAN's (1982) control-pollinated test of Douglas-fir measured at 6 years (Table 7).

Our variance patterns also seemed to correspond to patterns found in tests of young trees of other species. Coefficients of variation for additive genetic variability ($\sigma_A/\overline{X}$) and within-plot variability ($\sigma_w/\overline{X}$) in our experiment were remarkably similar to coefficients derived from data for other species grown to similar ages (Table 7). Spacing did not appear to have affected patterns appreciably. Trees in other experiments have been provided with from 12 to 16 times more growing space than in our experiment. For some traits, notably wood specific gravity, coefficients of variation were virtually identical for 6-year loblolly pine and 9-year-old Douglas-fir. Other traits showed major differences among species only in plot variability ($\sigma_p/\overline{X}$), which is mainly a function of site heterogeneity and blocking, items unique to each experiment.

Spacing affected the correlations among means of 54 full-sib families in several ways, depending on the type of correlation involved. Nine of the correlations among the nine combinations of three ages and three spacings described correlations among heights measured at three ages on the same individuals within the same spacing (Table 8, type I). Conceptually, there are also nine other correlations in this set, those among individuals measured at the same age in each of the three spacings; these latter coefficients (not shown) are, by definition, r = 1.0. This set of coefficients represents correlations of type I, the age-age correlation in the sense of LAMBETH's (1980) model. The coefficients of the first nine correlations increased with larger ratios of younger age to older age, in a nonsignificant (Table 9--A_L, P ≤ 0.103), but indicative, linear trend. Spacing apparently had no influence on coefficients of this type (Table 9). The relationship between type I coefficients and logn X, where X = youngest age/oldest age, was similar to that shown by LAMBETH (1980) for other data (our equation, Y = 0.998 + 0.284 logn X, r² = 0.86; LAMBETH's equation, = 1.020 + 0.308 logn X, r² = 0.93).

A second set of nine coefficients describes correlations of individuals of the same age between two spacings (Ta-

Table 9. — Analysis of variance of type 1 correlations. Contrasts are coded (Roman and Arabic numerals) to classifications in Table 8.

Source of variation	d.f.	M.S.	P ≤ ....
Total	8		
Age-age contrasts	(2)	0.3075	
(A_L) I vs III	1		0.103
(A_Q) II vs I + III	1		0.865
Spacing contrasts	(2)	0.0777	
(S_L) 1 vs 3	1		0.573
(S_Q) 2 vs 1 + 3	1		0.398
Interaction	(1)	0.0597	
A_L x S_L	1		0.381
Residual	3	0.0569	

ble 8, type II). In this set and in the following set, the individuals representing a family in different spacings are full sibs. The correlations are therefore not of measurements on the same individuals at three ages, as in the above set. When correlations of type II were averaged over the three spacings-combinations, age of measurement apparently did not influence the correlations (Table 10). Spacing did affect correlations, however; correlations between 30 and 90 cm spacing were smaller than for the other two spacing combinations (Table 10--C_Q, P ≤ 0.037).

The final set, of 18 coefficients, represents age-age correlations among families measured in different spacings. The influence of spacing on these correlations was examined by comparing the correlation observed when the youngest age was measured at the narrower of two spacings with the correlations observed when the youngest age was measured at the widest of two spacings (Table 8, type III). If close spacing improves prediction of family ranks at older ages, the correlation should be larger when measurements on younger trees are measured at the narrower spacing.

Coefficients were slightly larger on the average, but not always, when heights of younger trees were measured at the narrower spacing (Table 8--r = 0.766 vs 0.726; Ta-

Table 8. — Three types of correlations of stem height among 54 full-sib famililies measured at 5, 7, and 9 years (yr) and grown at three spacings (sp). 1/

	Type 1; age-age correlations within spacings	Type 2; spacing-spacing correlations within ages	Type 3; age-age correlations between spacings		

I.

	5 yr with 9 yr at:	5 yr with 5 yr at:	5 yr with 9 yr at:		
(1)	30 cm sp, 0.80	30 and 60 cm sp, 0.77	30 and 60 cm sp, 0.65	or	60 and 30 cm sp, 0.77
(2)	60 cm sp, 0.88	30 and 90 cm sp, 0.69	30 and 90 cm sp, 0.70	or	90 and 30 cm sp, 0.62
(3)	90 cm sp, 0.83	60 and 90 cm sp, 0.78	60 and 90 cm sp, 0.83	or	90 and 60 cm sp, 0.66

II.

	5 yr with 7 yr at:	7 yr with 7 yr at:	5 yr with 7 yr at:		
(1)	30 cm sp, 0.92	30 and 60 cm sp, 0.77	30 and 60 cm sp, 0.69	or	60 and 30 cm sp, 0.79
(2)	60 cm sp, 0.92	30 and 90 cm sp, 0.77	30 and 90 cm sp, 0.77	or	90 and 30 cm sp, 0.63
(3)	90 cm sp, 0.85	60 and 90 cm sp, 0.86	60 and 90 cm sp, 0.86	or	90 and 60 cm sp, 0.69

III.

	7 yr with 9 yr at:	9 yr with 9 yr at:	7 yr with 9 yr at:		
(1)	30 cm sp, 0.87	30 and 60 cm sp, 0.78	30 and 60 cm sp, 0.73	or	60 and 30 cm sp, 0.75
(2)	60 cm sp, 0.94	30 and 90 cm sp, 0.74	30 and 90 cm sp, 0.72	or	90 and 30 cm sp, 0.75
(3)	90 cm sp, 0.96	60 and 90 cm sp, 0.83	60 and 90 cm sp, 0.85	or	90 and 60 cm sp, 0.80

1/ Roman and Arabic numerals in parentheses indicate the classes used in contrasts that were tested in analyses of variance (Tables 9, 10, 11).

ble 11--0, P ≤ 0.019). The size of the correlation depended strongly on the specific spacing of younger and older trees (*Table 11--C_L × 0, P ≤ 0.001*). If the comparison was between spacings of 30 and 60 cm, correlations were consistently larger when the younger age was measured at 60 cm (*Table 8, Figure 2a, b*). If the comparison was between 60 and 90 cm, correlations were larger when the younger age was measured at 60 cm. The difference in correlation coefficients was largest when the age-age difference was largest (*Table 8*).

On the average, correlations also differed between the spacing combinations (*Table 11--C_L, P ≤ 0.013, C_Q, P ≤ 0.019*). Coefficients were smallest when the correlations were between spacings of 30 and 90 cm (*Table 8--$\bar{r}$ = 0.729*) and largest when between spacings of 60 and 90 cm (*Ta-*

ble 8--r = 0.790). Correlations also increased as the age-age ratio increased (*Table 11--A_L, P ≤ 0.021; Table 8--5 yr/9 yr, $\bar{r}$ = 0.713; 5 yr/7 yr, $\bar{r}$ = 0.740; 7 yr/9 yr, $\bar{r}$ = 0.771*).

Discussion

Tree breeders need information about two kinds of genotype × spacing interactions. The first kind embodies the interaction of genotype with spacing at harvest age. Such interaction is usually considered detrimental. It complicates selection because choosing superior parents may be conditioned by spacing at harvest age. The second kind involves the modification of spacing and genotype effects by age at measurement. It may be beneficial if, by controlling spacing in tests of young material, the breeder can improve the ability to predict ranking of families at harvest age. Whether our results facilitate tree-breeding decisions in either of these respects hinges on their applicability to trees at harvest age, usually 50 years or older in Douglas-fir.

If we assume a harvest age of 9 years (putting aside, for the moment, the question of applicability) spacing × genotype interaction of the first kind appears to be negligible in Douglas-fir. In stem height, it was significant only at 5 years. In stem volume, it consisted mainly of scale effects and only small rank changes, confirming previous results with nursery age seedlings (CAMPBELL and WILSON 1973). Spacing at harvest age, therefore, may not be a complicating factor in selection.
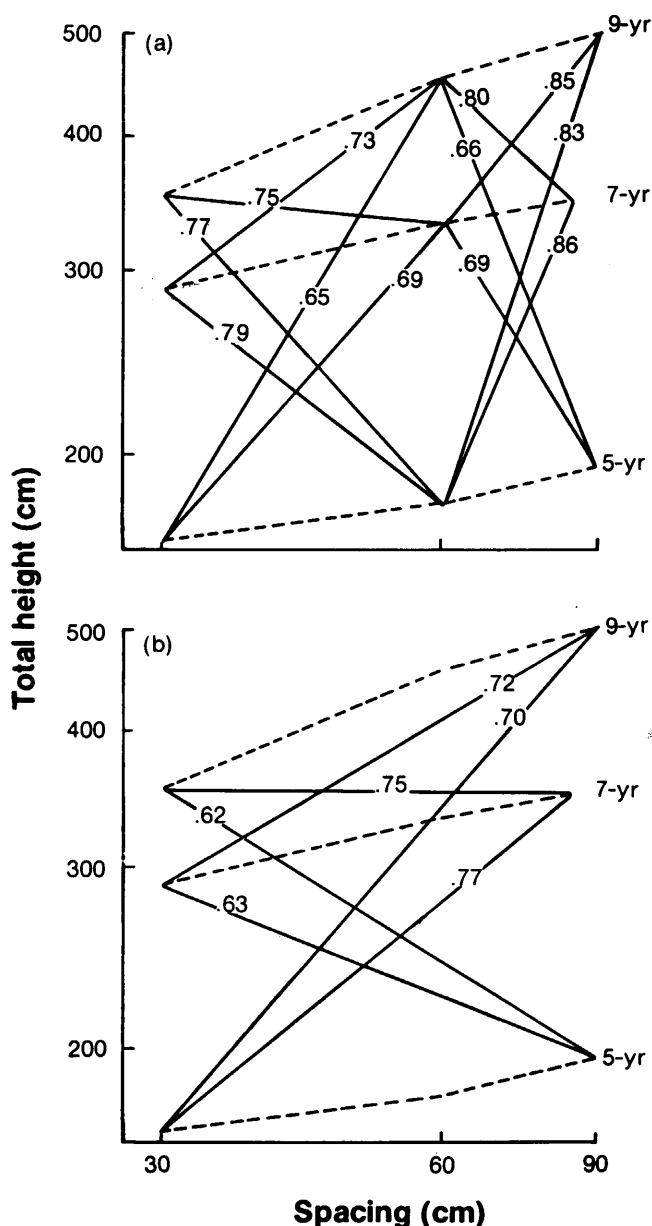

Figure 2a, b. — Correlations of stem heights at 5, 7, and 9 years (yr) among the means of 54 full-sib families grown at three spacings. The dashed lines are the mean total heights averaged over all families grown in two plantations. Axes are in log intervals. Subfigures are to reduce complexity of the graph: (a) correlations between spacings of 30 and 60 cm or of 60 and 90 cm, (b) correlations between spacings of 30 and 90 cm.

Table 10. — Analysis of variance of type 2 correlations. Contrasts are coded to classifications in *Table 8*.

Source of variation	d.f.	M.S.	P ≤ ....
Total	8		
Ages	(2)	0.0302	
(A_L) I vs III	1		0.179
(A_Q) II vs I + III	1		0.130
Spacing combinations	(2)	0.0352	
(C_L) 1 vs 3	1		0.068
(C_Q) 2 vs 1 + 3	1		0.037
Interaction	(1)	0.0038	
A_L × C_L	1		0.409
Residual	3	0.0041	

Table 11. — Analysis of variance of type 3 correlations. Contrasts are coded to classification in *Table 8*.

Source of variation	d.f.	M.S.	P ≤ ....
Total	17		
Main effects	(5)	0.0459	
Age-age contrasts	(2)		
(A_L) I vs III	1		0.020
(A_Q) II vs I + III	1		0.822
Spacing combinations	(2)		
(C_L) 1 vs 3	1		0.013
(C_Q) 2 vs 1 + 3	1		0.010
Younger at narrower spacing vs younger at wider spacing (0)	1		0.019
Interactions	(4)	0.0572	
A_L × C_L	1		0.257
A_L × 0	1		0.390
C_L × 0	1		0.001
A_L × C_L × 0	1		0.080
Residual	8	0.0060	

There were also positive aspects in the evidence about the second kind of spacing × genotype interactions. Part of our data indicated that spacing modified trends of height growth with increasing age. Generally, correlations between younger and older measurements were improved slightly by closer spacing at younger age.

It is difficult to account for interactions of the second kind. Age-related trends of genetic variation in total height have been hypothesized as accompanying transitions between juvenile and mature phases, the latter being determined either reproductively (NAMKOONG et al. 1972) or vegetatively (FRANKLIN 1979). Based on an analysis of genetic variation in total height, FRANKLIN suggested that intense competition may foster an early shift to the mature phase and consequently may be the means for providing an early evaluation of mature performance. Close spacing in our experiment apparently did not change the variance structure from that found at young ages in other tests of Douglas-fir and of other species. This creates a question whether the spacing in our experiment has had any influence on maturity. An alternative speculation is that spacing effects are one aspect of an adaptive strategy for optimally allocating photosynthates to the materials adding to stem height (for maintaining competitive position within a stand) or to diameter and wood density (for maintaining support). The tactical use of materials probably varies genetically from family to family or even tree to tree (McKIMMY and CAMPBELL 1982). Depending on its growing space and its evolved strategy, a growing tree may change its dimensions to favor height or support. Within limits, therefore, age may be incidental in age-related trends of height variability. The important determinant may be only the dimensions of the tree in relation to its growing space.

If spacing effects do, in fact, reflect the allocation of resources within the tree, the relationship of spacing and age-age correlations may be complex. Families in this experiment differed in genetically correlated components that determine size (Tables 4 and 6, height, diameter, wood specific-gravity). Size, in turn, is likely to be associated with competitive ability. Individuals in some families may therefore react more strongly to competition at a younger age than do individuals in other families. If so, spacing effects on age-age correlations are likely to depend on the specific ages, spacings, and genotypes involved in any comparison. Except for two of the nine comparisons, age-age correlations in our experiment were larger when the younger age was measured at the narrower spacing. These two comparisons involved measurements at two ages in 60 cm spacing, however, and were therefore not completely independent. The deviations from the general trend may not be as consistent as they appear to be (Figure 2a, b). Formal hypotheses about causes of spacing effects on age-age correlations are therefore premature. Similar interactions must first be demonstrated in other experiments.

Whatever the reason for the effect of spacing on age-age correlations, in this experiment it had only a transitory influence on spacing-genotype interactions (of the first kind, in stem height). Interaction, though significant at 5 years (Table 3) disappeared at later ages. There is no evidence that the interaction was simply a scale effect--at 5 years the variance of mean family heights at 30 cm spacing was only 10 percent larger than the variance at 90 cm spacing. The interaction probably reflects a difference in ranking at 30 and 90 cm spacing--the correlation among families is lower in this spacing combination than in the others (Table 8, Type 2). By 7 years, the interaction was no longer significant. The ranking of family means that occurred at 5 years in 30 cm spacing was therefore not established at 90 cm spacing until after 5 years, but before 7 years. The interaction in stem height did not carry over into other traits. A significant spacing × genotype interaction in stem volume still existed at 9 years, but it appeared to be mainly a scale effect.

Although close spacing in this experiment apparently did not shift the variance structure into the mature pattern as hypothesized by FRANKLIN (1979), results did support his suggestion that close spacing might make early selection more effective for stem height. Unfortunately, whether the same results can be expected for other traits could not be tested--the measurements at intermediate ages needed for calculating age-age correlations were available only for height. Also, whether young spacing tests can be used to predict mature interactions cannot be evaluated confidently until spacing-genotype interaction in young trees can be compared with spacing-genotype interactions in mature trees. Older spacing-family trials are not available in Douglas-fir. Consequently, direct evidence for confirming the applicability of our results awaits spacing trials carried to standard rotation ages. We therefore suggest caution in extrapolating our variance estimates, including estimates of interaction, to older trees.

We also recommend establishment of spacing-family trials involving a much greater range, than we had, of spacings and measurement ages. There may be combinations of spacing and age that will optimize results of early selection. In designing such studies we foresee the need to consider at least one question arising from this experiment. Did close spacing foster plantation × genotype interactions that would not have appeared, or would have appeared later, had the experiment been established at a conventional spacing? We could not verify FRANKLIN'S (1979) suggested effect of increased stand density on time trends of genetic variance. If such an effect does exist, however, stand density may also influence time trends in plantation × genotype interactions. Our plantation × genotype interactions were surprisingly large considering the apparent environmental similarity of the two plantations and the reported lack of such interactions in other experiments (YEH and HEAMAN 1982).

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Provenance Variation of Eastern Cottonwood in the Lower Mississippi Valley

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Abstract

Variation patterns were analyzed for eleven traits in a provenance study of eastern cottonwood (Populus deltoides Bartr.) planted in Mississippi. Two models of variation patterns were used to analyze the data: 1) stands and clones-within-stands and 2) clones pooled across stands.

Stand level variation declined with age of the test while the level of variation among clones-within-stands increased with advancing test age. Variation levels for the stand effect were smaller than clones-within-stands effects for all traits except beetle damage. At the stand level, volume (age seven) appeared to have an ecotypic distribution with no evidence for clines.

Broad-sense heritabilities were larger for stands (range of 0.29 to 0.91) than clones-within-stands (range of 0.19 to 0.77); and using the second model, the heritabilities for clones were generally intermediate as compared to stands and clones-within-stands. Comparing predicted gain between the two models, clonal selection, irrespective of stand origin, was superior to stand and clone-within-stand selection for all traits but beetle damage.

Genetic correlations between height, d.b.h., and volume were large (greater than 0.50) among the various ages with the correlation between volume at age four and volume at age seven equal to 0.96. This almost perfect correlation provided opportunities for correlated response in age seven volume, based on selection for volume at age four, which was 89 percent that of direct selection for age seven volume.

Key words: clone, heritability, gain, selection, correlations.

Zusammenfassung

In einer Provenienzstudie bei Populus deltoides Bartr. in Mississippi wurden die Variationsmuster von 11 Merkmalen analysiert. Um die Daten zu analysieren, wurden für die Variationsmuster 2 Modelle benutzt: 1) Bestände und Klone innerhalb der Bestände, 2) Klongruppen quer durch die Bestände. Die Variation im Bestandesniveau nahm mit dem Testalter ab, während die Variation zwischen den Klonen innerhalb der Bestände mit zunehmendem Testalter anstieg. Die Variationsniveaus für Bestandeseinflüsse waren geringer als die der Klone innerhalb der Bestände, und zwar für alle Merkmale, außer den Schäden durch Käfer. Auf dem Bestandesniveau schien das Volumen im Alter 7 eine ökotypische Verteilung zu haben, ohne den Beweis für das Vorhandensein eines Klines. Die Heritabilitäten im weiteren Sinne waren für die Bestände größer (Rang von 0,29—0,91) als für Klone innerhalb der Bestände (Rang von 0,19—0,77). Bei Benutzung des 2. Modelles waren die Heritabilitäten für Klone generell intermediär, verglichen mit den Beständen und den Klonen innerhalb der Bestände. Vergleicht man den vorausgesagten genetischen Gewinn der beiden Modelle, so war die Klonselektion ohne Rücksicht auf die Bestandesherkunft, der Bestandes-Selektion und der Selektion von Klonen innerhalb von Beständen für alle Merkmale, außer dem Käferschaden, überlegen. Die genetischen Korrelationen zwischen Höhe, BHD und Volumen waren hoch (größer als 0,50); bei den verschiedenen Altersstufen, d. h. zwischen den Volumen im Alter 4 und 7, betrug die Korrelation 0,96. Diese insgesamt perfekte Korrelation zeigt, daß bei einer Selektion auf das Volumen im Alter 4 bereits 89% der Pflanzen selektiert worden wären, die im Alter 7 durch direkte Selektion ausgelesen wurden.

Introduction

The ability to vegetatively propagate eastern cottonwood (Populus deltoides Bartr.) (hereafter referred to as cottonwood) using stem cuttings provides the avenue for clonal selection. The magnitude of genetic gain through clonal selection depends both on the heritability of the trait and the amount and distribution of the variation. Previous studies demonstrated substantial heritabilities for most growth traits as well as large clonal variances (Mohn and Randall, 1971; Randall and Cooper, 1973).

Despite the extensive natural range of cottonwood, few provenance studies have been established to study variation patterns for the species. Bridgwater (1972) studied variation patterns for six growth and wood traits along three major rivers extending from eastern Oklahoma westward. He found significant variation among stands and clones within stands for all six traits. Ying and Bagley (1976) investigated variation patterns in cottonwood, including provenances located over much of the natural range. Variation among provenances, families in provenances, and clones in families was significant for all 13 traits studied. In 1971, Cooper sampled stands of cottonwood along the Mississippi River from Memphis, TN to Baton Rouge, LA. Variability in resistance to Septoria leaf spot (Cooper and Filer, 1976), Melampsora rust (Cooper and Filer, 1977), and cottonwood leaf beetle (Chrysomela scripta F.) (Oliveria and Cooper, 1977) have been reported from this study. The following report describes genetic and environmental variability for growth traits expressed in a genetic test of clones from Cooper's original collection. The objectives of