Aug. 1969, Raleigh, N. C., USA. — Nilsson, B., und Wiman, S.: Om Köttsättning på ymper och ursprungsträd av gran. Föreningen skogsträdsförädling och Institut för Skogsförbättring årsbok 1967, 59-68. — Ppipperling: Erfahrungen über die Nachzucht der Fichte durch Steckreiser. Neue Jahrbücher der Forstkunde. Herausg. von G. W. Freiherr von Wedekind, 1830, 7, S. 54-62. — Plinius, G. S.: Naturgeschichte, 76 n. Chr. Ubers. von Chr. Leb. Strack XVII. Buch Abs. 13 Pkt. 21. — Rieger, R., Michaelis, A., and Green, M. M.: A Glossary of Genetics and Cytogenetics. Springer-Verlag, Berlin — Heidelberg — New York, 1968, 507 S. — Roulund, H.: Experiments with cuttings of Picea abies, Picea sitchensis and the Hybrid Picea omorica × Picea sitchensis. Forest tree Improvement 3, 25—27 (1971). — Ruden, T.: Stecklingsvermehrung von Fichten. — Methodik und Anwendungsmöglichkeiten in Wissenschaft und Praxis. Vortragsreihe des 2. Symposiums für industriellen Pflanzenbau, Wien, 1965, S. 133—137. — Ruden, T.: Avdelning for plantefordedling. Meddel. frå det Norske Skogsforsksoven, 1967, S. 213—247. — Schreiner, E. J.: Forest Tree Breeding Technique. Journal of Forestry 36, 712—715 (1938). — Schreiner, E. J.: Genetics of Eastern Cottonwood. Forest Serv. Research Papers, USDept. of Agriculture, WO-11, 1970, 32 S. — Snow, A. G.: Use of Indolebutyric Acid to stimulate the rooting of dormant aspen cuttings. Journal of Forestry 36, 582—587 (1938). — Speidel, G.: Forstliche Betriebswirtschaftslehre. Verlag Paul Parey, Berlin 1967, S. 1544 ff. — Thiemann, K. V., and Delisle, A. L.: The vegetative propagation of difficult plants. Journal Arnold Arboretum 20, 116—231 (1939). — Thulin, I., and Faulds, T.: The use of cuttings in the breeding and afforestation of Pinus radiata. New Zealand J. Forestry 13, 66—77 (1968). — Webber, H. J.: New Horticultural and agricultural terms. Science 18, 1903, S. 501, zit. Rieger, R., Michaelis, A., and Green, M. M., A Glossary of Genetics and Cytogenetics. Springer-Verlag, Berlin, 1968. — Weber, E.: Mathematische Grundlagen der Genetik. VEB Gust. Fischer Verlag, Jena, 1967, 464 S. — Wright, J. W.: Species crossability in spruce in relation to distribution and taxonomy. Forest Sci. 1, 319—349 (1955). — Yanagisawa, T.: F_1 hybrids between Picea jezoensis and P. glauca. Bull. Government Forest Exp. Sta. Meguro, Tokyo, 70, 1954, 55—70, ref. Silvae·Genetica 6, 127 (1957).

Spacing-Genotype Interaction in Douglas-Fir

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Introduction

Spacing-genotype interaction is a potential problem for tree breeders in forest regions that have not yet settled on standard plantation spacings. In these regions, spacing could be incorporated as an additional factor in family evaluation plantations if benefits were likely to offset costs. Unfortunately, a cost-benefit analysis requires information that will be expensive, especially in terms of time — 30 to 50 years, perhaps, for most species. In the Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) region, we lack even the information needed to categorize the problem as serious or trivial.

Spacing-genotype interactions are troublesome to breeders because interactions tend to camouflage the "value" of genotypes (Allard and Bradshaw 1964). In this context, the important aspect of interaction is the relative size of its camouflaging effect, which may be expected to vary depending on its type. Evans et al. (1966) proposed that statistically significant interactions may be an expression of: (1) changes in rank of genotypes over different spacings, (2) changes in variance among genotypes at different spacings, or (3) a combination of changes in rank and variance. Interaction (1) would appear to have the greater effect, followed in order by (3) and (2).

Reports of spacing-genotype interactions are non-existent for forest species, to our knowledge, but occur frequently in perennial-forage-crop literature (e. g., Nissen 1960, timothy grass; Lazenby 1957, and Wright 1960, ryegrass; Rumbaugh 1963, Evans et al. 1966 alfalfa) and in agricultural-crop literature (Hinson and Hanson 1962, soybeans; Russell 1968, corn). If the trait being studied is vegetative yield, i. e., forage production, plant dry weight, or plant volume, there are few instances of rank changes. In density trials incorporating greatly different spacings, occasional important rank changes have occurred at the widest spacings, presumably caused by differences in the ability of genotypes to use unrestricted space (Hinson and Hanson 1962, Lazenby and Rogers 1964). In spacing trials combining two or more species, rank changes are associated with competition between relatively unrelated genotypes, such as grass and clover (Nissen 1960, Wright 1960), grown under sward conditions. In contrast, rank changes for vegetative traits are lacking or minor in mixtures of varieties, which are closely related (Lazenby 1957, Wright 1960, England 1967, Evans et al. 1966). Hinson and Hanson (1962) demonstrated competitive ability differences among soybean varieties selected for diversity of height and maturity, yet rank changes were negligible in traits related to vegetative yield, such as height and number of branches and nodes. In a test of two sets of genotypes, one relatively more diverse than the other, Evans et al. (1966) found high positive correlations between genotypic effects (i. e., consistent genotypic ranking) at different spacings, regardless of genetic diversity in the set.

Many reported spacing-genotype interactions appear to be associated with changes in trait variance at different spacings — the (2) interaction. Kempthokne (1957, page 194) pointed out that statistically significant interactions of this type could result from non-additive properties of growth under different levels of fertilizer. He suggested removing it by choosing an appropriate scale of observation. Type (2) interactions are usually accompanied by heterogeneity of error variance which is often a feature of reports of significant spacing-genotype interaction (Wright 1960, Russell 1968, Hinson and Hanson 1962, Evans et al. 1966). The use of appropriate scales of observation successfully eliminated interactions of genetic effects and spacings, or years, for vegetative yield traits (Evans et al. 1966) but not for seed yield (Hinson and Hanson 1962). In addition, transformations often normalize data which, in original scale, tend to give skewed distributions at the closer spacings (Obeid et al. 1967).

If type (1) interactions usually occur in spacing trials that include greatly different plot densities or widely divergent genotypes, spacing-genotype interactions in Douglas-fir tests will probably be of type (2). The range of potential spacings for commercial plantations of forest trees is usually small. Also, genetic evaluation plantations will usually be made up of fairly closely related entities, for example, a set of families from a single physiographic region.

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Our purpose was to make a preliminary test of the hypothesis that spacing-genotype interaction, if present, is of type (2). For this, we used 3-year-old Douglas-fir seedlings of 30 families growing at four spacings in a nursery. Since the main interest of breeders in spacing-genotype interaction is in older trees, we also subjectively compared seedling responses to spacing with responses of 43-year-old Douglas-fir of unidentifiable parentage grown at six spacings.

Materials and Methods

Thirty families were constructed according to Comstock and Robinson's (1952) design 1. Crosses used 36 parents, six as females, 30 as males — five crossed to each female. Seedlings were started in the greenhouse in April 1966 and transplanted into spaced plantings in the nursery in June after radicles had reached 3 to 7 cm. in length. The nursery design was a split-plot with four replicates — whole plots being square spacings (1, 3, 5, and 7 inches) and subplots being families. Subplots consisted of a row of seven seedlings from a full-sib family, but analyses were restricted to data from three randomly chosen interior seedlings. Subplots were randomized within whole plots and whole plots were randomized within blocks. Borders of whole plots were planted at appropriate spacing with one row of seedlings from a common woods-collected seed source.

Analyses were based on measurements of 3-year heights, 3-year root-collar diameters, and the compound variable (3-year heights) $\times$ (3-year diameters squared) = (D^2H). The phenotypic value of the lth progeny in the kth family in the ith block at the jth spacing is:

$$X_{ijkl} = \mu + B_i + S_j + a_{ij} + G_k + SG_{jk} + b_{ijk} + c_{ijkl}$$

where:

μ = population mean
B_i = ith block effect
S_j = jth spacing effect
G_k = kth family effect
SG_{jk} = interaction of jth spacing with kth family
a_{ij}, b_{ijk} = random error effects associated with whole and subplots, respectively, and
c_{ijkl} = environmental error effects between plants within subplots plus genetic variance between full sibs.

Sums of squares for families were further partitioned into female (F) and male within female (M/F) effects.

Performance of 3-year and 43-year plants cannot be statistically compared because the two experiments include sampling units of greatly different makeup. However, their performance can be subjectively compared on several bases. One is to examine response to density. To do this we separately fitted data for seedlings and older trees to the reciprocal yield law using the Shinozaki-Kira (1956) model, which states:

$$w^{-1} = a + bx$$

where:

w = mean plant yield and
x = stand density

Thus, for each age class this provided a linear regression analysis, to be used in testing fit of data to the model. For seedlings, the 16 means of D^2H for spacings (density classes) by blocks were used as observations in calculating the regression equation. Error for testing deviations from the model was calculated as the within-spacing sums of squares

minus the block sums of squares with (s-1) (b-1) degrees of freedom (Li 1964, pp. 223 and 348). For 43-year trees, data were from a Douglas-fir spacing trial recently described by Reukema (1970). In part, the trial consists of five 2.8-acre blocks with trees at square spacings of 4, 5, 6, 8, and 10 feet. Three ¼-acre subplots were nested within each 2.8-acre block. Observations used in calculating the regression equation were the 15 means of subplots expressed as cubic-foot-volume per tree of all trees 1.5 inches in d.b.h. and larger. Error for testing deviations from the model was the mean within-spacings sums of squares with 10 degrees of freedom.

Results and Discussion

Fewer than 3 percent of the seedlings died during the first two growing seasons, and loss was distributed about equally among the four spacings. In the third year, mortality (9 percent) occurred mainly in the narrowest spacing, with no significant differences among half-sib or full-sib families. Other traits, height (H), diameter (D), and volume-index (D^2H), did differ significantly among families, and effects were not exclusively a function of seed size, as shown by significant differences among males (Table 1). Thus, genetic variation can be inferred as an important component of family differences.

For data in the observed scale, family-spacing interactions appeared in analyses of D and D^2H but not in H. In each instance, error variances were also heterogeneous. For example, for D^2H, within-spacing error mean squares, based on subplot averages, were 18, 335, 531, and 1,331 for 1-, 3-, 5-, and 7-inch spacings, respectively. Diameters were transformed to $(x + 0.5)^{1/2}$ and D^2H to $\log_{10}\underline{x}$ on recommendation (Snedecor and Cochran 1967) that observations be transformed to their square roots or to logarithms, depending on whether variances or standard deviations are proportional to treatment means. After transformations, variances were less heterogeneous, as indicated by within-spacing error mean squares of 4.4, 3.7, 2.3, and 1.5 for analyses of $\log_{10}D^2H$.

In analyses of transformed data, spacing-family interactions were no longer significant (Table 1). To provide an even more sensitive test, the interaction term of the $\log_{10}(D^2H)$ analysis was partitioned into its linear, quadratic and cubic components, each with 29 degrees of freedom (mean squares: spacing-linear $\times$ families 0.11; spacing-quadratic $\times$ families, 0.12; spacing-cubic $\times$ families, 0.14). None contributed significantly to explanation of variance. In this analysis, the performance of each family is described by a separate regression line. Lack of a significant interaction indicated that the configuration of regression lines did not differ among families. However, elevation of lines did differ, as shown by the highly significant family effects (last column, Table 1).

To visually illustrate the interaction in D^2H and its correction by transformation, two response surfaces were constructed. The objective was to provide a general picture of family performance, at each of the four spacings, of families of different growth capabilities. As an index of growth capability, we used mean-family-D^2H, averaged over all experimental units. Consequently, prediction equations were expressed in terms of spacing (X_2) and family means for D^2H. For the first surface mean D^2H's were in the observed scale (X_1) and for the second, in log scale [$X_3 = \log_{10}(X_1)$]. Multiple linear regression analyses of subplot means were used to select models for each surface and to develop prediction equations. The parameters tested in

analyses were X_1 or X_3, depending on the surface being constructed, and X_2, $(X_2)^2$, $(X_2)^3$, and all first order interactions, e. g., $X_1X_2, \ldots, X_1(X_2)^3$. Only parameters which were shown to be significant by regression analyses are included in the following models:

1) for observed data, $Y = a + b_1X_1X_2 + b_2X_1(X_2)^2$

and

2) for transformed data, $Y = a + b_3X_3 + b_4X_2 + b_5(X_2)^2 + b_6(X_2)^3$

The surfaces that resulted from fitting data to above models are given in *Figures 1-A and 1-B*.

The average D^2H's in original scale of the 30 families over the whole experiment ranged from 36 to 83. Families with a mean experimental D^2H of 45 cc per seedling average 25 D^2H at the 3-inch spacing and 94 D^2H at the 7-inch spacing. By comparison, families with a mean D^2H of 75 averaged 41 in the 3-inch spacing and 156 in the 7-inch spacing; so, in this example, differences in mean seedling D^2H were 16 and 62 at the 3-inch and 7-inch spacing, respectively. In general, family effects were proportional rather than additive. For example, families with an average D^2H of 85 were about 50 percent larger than families with an average D^2H of 55, over all spacings. This nonadditivity of effects appeared in the analysis of observed data as a statistically significant spacing-family interaction. With transformed data, differences among families were not proportional to size of seedlings *(Figure 1-B)*, and interactions were not significant *(Table 1)*.

Spacing-genotype interactions in this test are reducible by change in scale. Had families differed in rank from spacing to spacing, we would have expected the interaction term based on transformed data to be significant. Since interaction could not be shown in appropriately scaled data, we conclude that rank changes have been small and due to chance. The spacing-genotype interaction therefore conforms to the type 2 of EVANS et al. (1966).

When a component of variance can be estimated for interaction, it may be subtracted from genetic variance.

Table 1.—Expected and observed mean squares for spacing and family effects on 3-0 seedling traits of Douglas-fir

	d.f.	Expected mean squares	1969 height H	1969 diameter D	(Diameter + 0.5)$^{1/2}$	D^2H	$\log_{10}(D^2H)$
Blocks	(r-1)	$\sigma_1^2 + p\sigma_2^2 + gp\sigma_3^2 + sgp\sigma_R^2$	9875*	44	1.12	32688	1.88*
Spacing	(s-1)[1/]	$\sigma_1^2 + p\sigma_2^2 + gp\sigma_3^2 + rp\frac{s}{s-1}\sigma_{SG}^2 + rgp\frac{\Sigma S^2}{s-1}$	74438**	5066**	167.89**	804278**	134.64**
Linear	1		171268**	15124**	493.77**	2333257**	370.03**
Quadratic	1		28676**	18	7.31**	58674*	26.62**
Cubic	1		23371**	58	2.62*	20752	7.28**
Whole plot error (a_{ij})	(r-1)(s-1)	$\sigma_1^2 + p\sigma_2^2 + gp\sigma_3^2$	1518	12	0.32	8805	0.39
Families	(g-1)[1/]	$\sigma_1^2 + p\sigma_2^2 + rsp\sigma_G^2$	770**	16**	0.49**	5636**	0.42**
Females	(f-1)	$\sigma_1^2 + p\sigma_2^2 + rsp\sigma_{M(F)}^2 + rsmp\sigma_F^2$	1737*	60**	1.81**	14021*	1.36**
Males/female	f(m-1)	$\sigma_1^2 + p\sigma_2^2 + rsp\sigma_{M(F)}^2$	569**	7**	0.22**	3889**	0.23**
Spacing x families	(s-1)(g-1)	$\sigma_1^2 + p\sigma_2^2 + rp\frac{s}{s-1}\sigma_{SG}^2$	168	5*	0.13	1966**	0.12
Spacing x females	(s-1)(f-1)	$\sigma_1^2 + p\sigma_2^2 + rp\frac{s}{s-1}\sigma_{SM(F)}^2 + rmp\frac{s}{s-1}\sigma_{SF}^2$	173	5	0.13	2428	0.13
Spacing x males/female	f(s-1)(m-1)	$\sigma_1^2 + p\sigma_2^2 + rp\frac{s}{s-1}\sigma_{SM(F)}^2$	166	5*	0.14	1870*	0.12
Subplot error (b_{ijk})	r(s-1)(g-1)	$\sigma_1^2 + p\sigma_2^2$	152	4	0.11	1304	0.10
Within-plot error (c_{ijkl})	Σ(p-1)	σ_1^2	116	3	0.09	1273	0.08

Where:

r = replications = 4

s = spacings = 4

g = families = 30

f = females = 6

m = males per female = 5

p = number of plants in ith plot = 3

σ_1^2 = sum of within-plot environmental variance and genetic variance among full sibs

σ_2^2 = variance of sub-plot effects

σ_3^2 = variance of main-plot effects

σ_{SF}^2, $\sigma_{SM(F)}^2$, σ_{SG}^2 = interaction variance among female or male or family effects and spacings

σ_F^2 = variance of female effects

$\sigma_{M(F)}^2$ = variance of male within female effects

σ_G^2 = variance of family effects

[1/] The (s-1) = 3 d.f. for spacing are partitioned into linear, quadratic and cubic components; the (g-1) = 29 d.f. for families are partitioned into female and male per female components, etc.
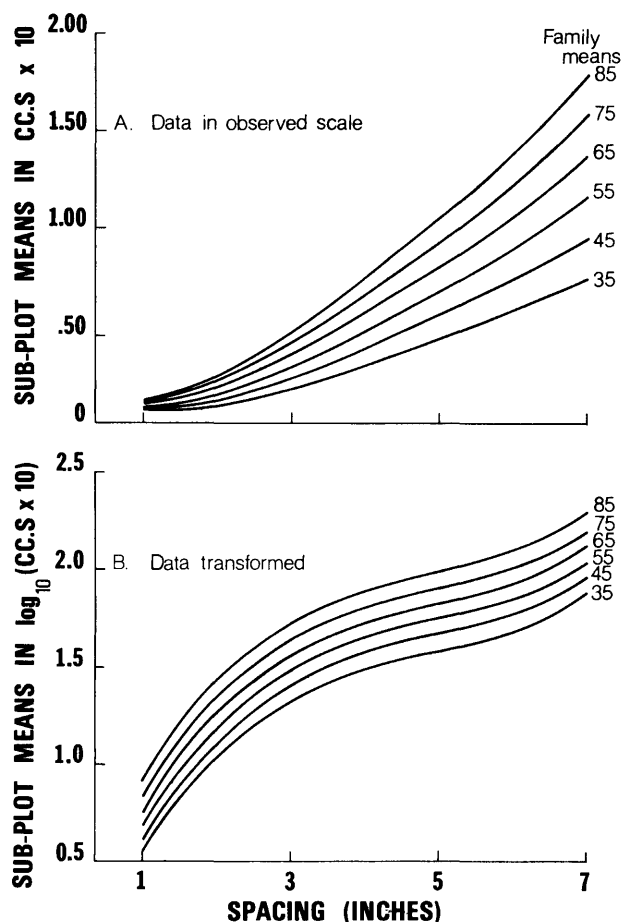
* = p <0.05

** = p <0.01

Figure 1. — Overall family means related to performance of families at each spacing in (A) observed scale, and (B) transformed to common logarithms.

The result is a smaller heritability estimate, but one which is applicable to a larger set of environments. The biasing effect of interaction on genotype estimation is sometimes examined (e. g., SQUILLACE et al. 1967) by comparing a heritability that takes interaction into account with one that does not. In this study, components of variance attributable to spacing-family interactions were not a large part of total variances in the original scales. When total variances were calculated excluding spacing and block effects, interactions accounted for 2.2 or 3.1 percent of totals in diameter and D²H analyses, respectively. The ratio of spacing-genotype interaction to genetic variability, as measured by the ratio of components of variance σ_{SG}^2/σ_G^2, was substantially decreased by transformation. For diameter, the decrease was from $.08/.26 = .31$ to $.0017/.0079 = .22$, and for D²H, from $44.2/90.3 = .49$ to $.0013/.0067 = .19$. But transformations also changed plot and within-plot errors. Consequently, when heritability of an individual seedling was calculated as:

$$h = \frac{2(\sigma_F^2 + \sigma_{M(F)}^2)}{\sigma_F^2 + \sigma_{M(F)}^2 + \sigma_{SF}^2 + \sigma_{SM(F)}^2 + \sigma_2^2 + \sigma_1^2}.$$

heritabilities for diameter and its transformation were 0.165 and 0.166, respectively, and for D²H and its transformation, 0.135 and 0.153, respectively. Thus, heritabilities were not changed appreciably by correction of interaction, because error estimates changed concurrently with genetic variance and because within-plot error (σ_1^2) constituted the majority of total variance. QUARTERMAIN and FREEMAN (1967), reporting similar results, concluded that effects of transformation on

heritability and genetic correlation were insufficient to make any practical difference in applied breeding.

Experimental plants were much younger than trees in tests for which experimental results might have application. In a practical sense, the current experiment is simulation, and its value rests on the assumption that seedlings and older trees respond similarly to density. An adequate test of this would take several decades, so it will be necessary to examine supplementary evidence. The most convincing would be if plants of many species, growth habits, and ages respond identically to density. In the following section, we compare density responses of Douglas-fir seedlings, trees, and other species of similar or contrasting growth habits.

Seedling and mature (43-year-old) trees developed physical attributes remarkably alike in response to spacing. Height/diameter ratios for seedlings ranged from 15 to 4; for mature trees, from 10 to 6. Spacing effects on the frequency distributions of individual plant volumes were also similar (Figure 2). Comparable responses have been reported in Pinus resinosa (MAEGLIN 1967), in Pinus densiflora and several crop species (KOYAMA and KIRA 1956), and in fibre flax (OBEID et al. 1967).

Plant-to-plant variability was greater at the wider spacings both with seedlings and with 43-year-old trees (Figure 2). This pattern has been reported in several pines (ADAM and CHAPMAN 1942). Similar density-variability effects in crop and forage species have been reported in the form of variance estimates (HINSON and HANSON 1962, soybean; RUSSELL 1968, corn), or are evident in the data (STERN 1965, subterranean clover; SAKAI 1965, barley; EVANS et al. 1966, alfalfa), or are implied in statements of relative variability (LAZENBY 1957, ryegrass).

Density strongly influenced Douglas-fir seedling heights, diameters, and volume-indexes, which were consistently smaller at the greater densities (Table 2). For vegetative yield, i. e., mean plant-dry-weight or volume, the SHINOZAKI-KIRA yield law has effectually described response of plants to density (Pinus densiflora, subterranean clover, Azuki beans, soybeans, carrots — SHINOZAKI and KIRA 1956; beets — DEWIT 1959. as cited in DONALD 1963; rape — HOLLIDAY 1960). Further, COOPER (1961) successfully fitted the yield model to stem basal area per tree for ponderosa pine at three ages ranging from 29 to 49 years. The biological support for the model assumes that: (1) plant-dry-weight growth is logistic, (2) initial growth rate is independent of plant size, (3) final yield per unit area is constant at high density, and (4) sowing time is common to all densities. As a first approximation the assumptions seem reasonable for the Douglas-fir tests; and although several yield models have been proposed, we think the SHINOZAKI-KIRA model has the better biological foundation. Also, it has been satisfactory in practice (WILLEY and HEATH 1969).

We tested the fit of D²H to the S-K model using two sets of seedling data. The first included all densities; the second discarded data from the narrowest spacing, which produced a density markedly greater than remaining spacing — hence data at this relatively high density might have excessive "weight" in a regression equation. However, both tests revealed highly significant linear regressions, the first with an r² of 0.96 and the second, 0.73. The model applied to mean volumes of 43-year-old trees also gave a highly significant regression mean square with an r² of 0.96. In any test, deviations from the model were not significantly larger than error.
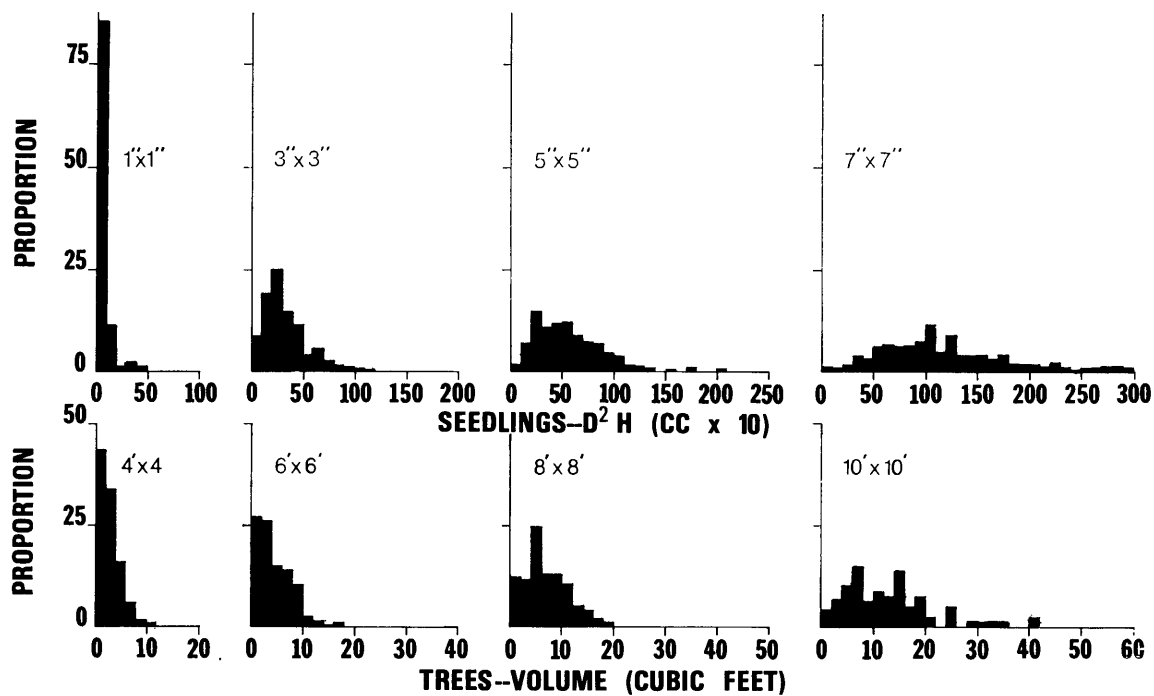
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Figure 2. — Distribution of individual plant volumes as affected by spacing in seedlings and 43-year-old Douglas-fir. Note that true distributions in 1" × 1" seedlings, 4' × 4' and 6' × 6' trees are not L-shaped as they appear in the figure. Rather, they are extreme examples of the skewed distribution shown in 3" × 3" spacing. Skewness at close spacing has been masked by the coarseness of class intervals. For seedlings, the histogram for each spacing is based on 360 seedlings. For 43-year trees, n ranged from 317 at 4' × 4' spacing to 78 at 10' × 10' spacing.

In summary, seedlings and mature Douglas-fir trees react similarly in terms of size-space relationships, frequency distributions, and variances, and fit to a yield law equation. Furthermore, the same patterns have been discovered in other species as diverse as root vegetables, grass, and alfalfa. By analogy, older trees might be expected to have the same interaction patterns that have been discovered in tree seedlings and in crop and forage species. It should be

Table 2.—Density of live plants at time of measurement related

to average height, diameter, and volume per plant

3-0 seedlings				43-year trees	
Plants per square meter	Height cm	Diameter mm	Volume index D²H in cc x 10	Plants per hectare	Volume in cubic meters
1,259	35.3	3.1	4.45	4,319	.06
1,302	41.6	3.3	5.75	3,064	.09
1,313	43.5	3.6	7.19	3,155	.08
1,323	35.7	3.4	5.50	3,116	.07
166	71.2	7.1	42.23	3,116	.09
164	67.8	6.9	37.25	2,891	.08
166	63.7	7.0	37.78	2,181	.13
164	57.0	6.4	25.74	2,031	.10
62	73.7	10.0	83.27	2,100	.14
60	65.4	9.3	64.93	1,263	.20
60	52.0	8.3	39.56	1,364	.18
58	64.3	9.1	58.51	1,223	.24
31	79.2	12.9	139.74	959	.36
30	70.9	12.3	118.52	895	.45
30	70.2	12.0	109.58	840	.37
29	67.4	11.7	100.66		

emphasized that this must remain an assumption, considering the indirect and fragmentary nature of the evidence. The practical question remains as to whether spacing should be included as a variable in genetic test plantations. We suggest that it be relegated low priority in comparison to, say, sampling of additional plantation environments. Based on evidence from this preliminary test, exclusion of spacing is not likely to appreciably affect selection accuracy in Douglas-fir. At any common spacing, a transformation normalizing individual tree data is likely to eliminate significant spacing-genotype interactions. Even if transformations are not used, genotype-spacing interaction will probably account for a trifling part of total variance. Exceptions might occur if: (1) entries being evaluated are genetically diverse (e. g., races or extreme ecotypes) and the experimental design encourages competition among entries, or (2) something other than vegetative yield is being scored.

Although this experiment did not show spacing-genotype interaction as having a significant potential for camouflaging breeding values, we do not recommend discontinuing experimental long-term spacing-genotype interaction tests. On the contrary, this test points out several spacing-related problems that deserve study in rotation age trees. One of the more interesting would be an evaluation of the response of individual families or clones to competition, as well as to density. This could be done by comparing parameters of suitable yield-law models fitted to families of presumably different yield potential. If families were grown both in the presence and absence of competition from other families, comparisons should add considerably to our knowledge of genotype and site-productivity relationships.

Summary

This paper reports that a spacing-genotype interaction, present in a Douglas-fir seedling test, does not involve

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rank changes of family performance at different spacings. The significant interaction can be attributed to changes in trait variance at different spacings and is eliminated by an appropriate transformation. Test materials were 3-year-old seedlings of 30 families from a 5-males-within-6-females Design I mating grown at four spacings (1, 3, 5, and 7 inches apart) in a nursery.

Growth response of seedlings to spacings was subjectively compared (i. e., no statements of statistical reliability were possible) to responses in 43-year-old Douglas-fir and to responses in several crop and forage species. In terms of effect of spacing on relative variability, on shapes of frequency distributions, and on vegetative yield, seedlings and mature trees performed similarly to one another and to several agricultural species. On the assumption that similar responses to density imply similar types of genotype-spacing interaction, spacing-genotype interaction in Douglas-fir is not likely to appreciably affect selection accuracy, particularly if individual tree data are transformed to a scale which normalizes their distribution.

Key words: Douglas-fir, seedling growth, heritability, spacing-genotype interaction.

References

ADAMS, W. R., and CHAPMAN, G. L.: Competition in some coniferous plantations. Vermont Agr. Exp. Sta. Bull. 489, 26 p. (1942). — ALLARD, R. W., and BRADSHAW, A. D.: Implications of genotype-environmental interactions in applied plant breeding. Crop Sci. 4, 503—508 (1964). — COMSTOCK, R. E., and ROBINSON, H. F.: Estimation of average dominance of genes. In Heterosis, J. GOWEN (Ed.), Iowa State College Press, Ames, p. 494—516 (1952). — COOPER, C. F.: Equations for the description of past growth in even-aged stands of ponderosa pine. Forest Sci. 7, 72—80 (1961). — DONALD, C. M.: Competition among crop and pasture plants. Advances in Agronomy 15, 1—118 (1963). — ENGLAND, F.: Non-sward densities for the assessment of yield in Italian ryegrass. I. Comparison between sward and non-sward densities. J. Agr. Sci., Camb., 68, 235—241 (1967). — EVANS, K .H., DAVIS, R. L., and NYQUIST, W. E.: Interaction of plant spacing and combining ability in an eight-clone diallel of Medicago sativa L. Crop Sci. 6, 451—454 (1966). — HINSON, K., and HANSON, W. D.: Competition studies in soybeans. Crop Sci. 2, 117—123 (1962). — HOLLIDAY, R.: Plant population and crop yield. Nature, Lond., 186, 22—24 (1960). — KEMPTHORNE, O.: The contribution of statistics to agronomy. Advan. Agron. 9, 177—204 (1957). — KOYAMA, H., and KIRA, T.: Intraspecific competition among higher plants. VIII. Frequency distribution of individual plant weight as affected by interaction between plants. J. Inst. Polytech., Osaka City Univ. Ser. D, 7, 73—94 (1956). — LAZENBY, A.: The problem of assessing strains — a study in grass-breeding technique. J. Agr. Sci. 48, 294—304 (1957). — LAZENBY, A., and ROGERS, H. H.: Selection criteria in grass breeding. II. Effect, on Lolium perenne, of differences in population density, variety and available moisture. J. Agr. Sci. 62, 323 (1964). — LI, J. C. R.: Statistical Inference II. Edward Brothers, Inc. Ann Arbor, Mich. p. 575 (1964). — MAEGLIN, R. R.: Effect of tree spacing on weight yields for red pine and jack pine. J. Forest. 65, 647—650 (1967). — NISSEN, O.: Testing hay varieties of grasses as spaced plants, in a pure stand or in a mixture with a legume. Proc. Eighth Int. Grasslands Congr. 310—313 (1960). — OBEID, M., MACHIN, D., and HARPER, J. L.: Influence of density on plant-to-plant variation in fiber flax, Linum usitatissimum L. Crop Sci. 7, 471—473 (1967). — QUARTERMAIN, A. R., and FREEMAN, A. E.: Some transformations of scale and the estimation of genetic parameters from daughter-dam regression. Biometrics 23, 823—833 (1967). — REUKEMA, D. L.: Forty-year development of Douglas-fir stands planted at various spacings. U. S. Dept. Agr. Forest Serv. Res. Pap. PNW-100, 21 p. (1970). — RUMBAUGH, M. D.: Effects of population density on some components of yield in alfalfa. Crop Sci. 3, 423—424 (1963). — RUSSELL, W. A.: Testcrosses of one- and two-ear types of corn belt maize inbreds. I. Performance at four plant stand densities. Crop Sci. 8, 244—247 (1968). — SAKAI, K.: Contributions to the problem of species colonization from the viewpoint of competition and migration. In The Genetics of Colonizing Species, Proc. First Int. Union Biol. Sci. Symp. General Biol., H. G. BAKER and G. L. STEBBINS (Eds.), Academic Press, New York, p. 215—239 (1965). — SHINOZAKI, K., and KIRA, T.: Intraspecific competition among higher plants. VIII. Logistics theory of the C-D effect. J. Inst. Polytech. Osaka City Univ., Ser. D, 7, 35—72 (1956). — SNEDECOR, G. W., and COCHRAN, W. G.: Statistical Methods. Iowa State Univ. Press, Ames, p. 593 (1967). — SQUILLACE, A. E., BINGHAM, R. T., NAMKOONG, G., and ROBINSON, H. F.: Heritability of juvenile growth rate and expected gain from selection in western white pine. Silvae Genet. 16, 1—6 (1967). — STERN, W. R.: The effect of density on the performance of individual plants in subterranean clover swards. Aust. J. Agr. Res. 16, 541—555 (1965). — WILLEY, R. W., and HEATH, S. B.: The quantitative relationships between plant population and crop yield. Advan. Agron. 21, 281—321 (1969). — WRIGHT, C. E.: The introduction of an associated legume at the progeny testing stage in perennial ryegrass breeding. Proc. Eighth Int. Grasslands Congr., p. 313—317 (1967).

Frequency of Seedlings from Natural Self-Fertilization in Coastal Douglas-fir

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Introduction

Because forest trees frequently become established in family groups, and because there appear to be no phenological or physiological barriers to self-fertilization or to cross-fertilization between related individuals, some inbreeding can be expected in the wind-pollinated progenies of naturally occurring trees. Published information about the natural inbreeding in conifers comes primarily from the genus *Pinus*.

SARVAS (1962) estimated that about 7% of all filled seed in *Pinus sylvestris* resulted from self-fertilizations and that self-pollination in the top one-third of the crown appeared to be only about 60% as frequent as in the lower two-thirds. He also reported that in more open mature pine stands, in seed tree stands, and in mixed stands, the share of self-fertilized full seed could rise to 10 to 20% of the total full-seed crop.

SQUILLACE and KRAUS (1963) estimated the degree of natural selfing in *Pinus elliottii* var. *elliottii*. They defined natural selfing as the production of viable seedlings by self-fertilization and obtained natural selfing estimates ranging from 0 to 27% for 11 trees. Nine of the trees showed 5% or less selfing, and two showed 23 and 27%, respectively.