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Genetic Variability in Juvenile Height-Growth of Douglas-Fir

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(Received March 1971)

Introduction

In the Douglas-fir region of western North America, planting methods for establishing stands and cultural practices for maintaining them are in a state of evolution. Some seedlings are planted in areas so clean they approximate agricultural fields; others in jungles of slash and brush. In some Douglas-fir plantations, seedling growth is impeded for years by overtopping brush or by browsing of deer and hare. Because seedlings with rapid juvenile height-growth pass through the vulnerable stage more quickly, nursery and outplanting practices which increase seedling growth are being developed. Innovative practices are now undergoing extensive testing: the planting of seedlings grown in paper or plastic containers, machine planting on terraced slopes, and fertilizing, irrigating, or mulching of planted seedlings. Some of these practices are expensive and genetic improvement of juvenile growth rate has been suggested as an alternative. The suggestion is worth pursuing as long as negative correlations with mature growth, or other detrimental side effects, are not found.

As a first step, this paper examines genetic variability in seedling height increment of Douglas-fir. It reports estimates of additive genetic variances, dominance effects, and family-location interaction variances based on a sib analysis of 54 families grown in two plantations. An example of genetic gain from mass selection is used to illustrate effects of interaction on heritability and gain.

Materials and Methods

Families came from crosses made according to the Design I crossing scheme of COMSTOCK and ROBINSON (1952). The 63 parents, nine used as females, 54 as males — six crossed to each female — were chosen randomly from reproductive trees in a small, naturally regenerated stand in Pack Demonstration Forest near LaGrande, Washington (elevation 335 meters). Stratified seed of each cross were planted in four randomized blocks using procedures closely approximating those of forest nurseries in the Pacific Northwest. In February 1966, seedlings, then 2-0, were outplanted at two locations near Centralia, Washington. Location 1 is on a relatively fertile soil (Salkum series) having a clay-loam subsurface texture and a clay subsoil. Location 2 is on a droughty site, the soil (Spanaway series — gravelly, sandy loam) being excessively drained and of medium fertility. Locations are 25 kilometers apart and both are at low elevations (less than 200 meters).

At each location, 60 seedlings from each of the 54 families were planted in February 1966 in a randomized block design of 15 replications of 4-tree family plots. Both sites were cultivated prior to planting. After planting, location 1 was watered once, while location 2 was watered several times in the 1966 and 1967 growing seasons and kept essentially weed free.

Height increments from 1966 and 1967 growing seasons were measured and analyzed separately for effects due to location, replication, females, males, and their interactions, all effects being considered random. Because of differential mortality, between- and within-plot variances were analyzed in two steps: (1) an analysis of plot means ignoring differences in their reliabilities, and (2) an analysis of within-plot variability, estimated from random plots in each replication and location, then pooled (KEMPTHORNE 1957). Components of variance were estimated by equating mean squares to expectations (*Table* 1). Assuming the absence of effects due to inbreeding, epistasis, linkage, and maternal environment, variance among females estimates one quarter of the additive genetic variance. Variance among males in females estimates one quarter of the additive genetic variance plus one quarter of the dominance variance (COMSTOCK and ROBINSON 1948). See CAMPBELL and REDISKE (1966) for a discussion of the likelihood of violations of assumptions in this material.

Genetic gain (R) from mass selection is estimated by

$R = i\,h^2\,\sigma_{ph}$ where:

i = the selection differential expressed in phenotypic standard deviations (For this example, the assumption is that 1 percent of seedlings are selected as parents, so in large samples from a normally distributed population, $i = 2.67$.)

$$h^2 = \frac{4\hat{\sigma}_f^2}{\hat{\sigma}_f^2 + \hat{\sigma}_{s(f)}^2 + \hat{\sigma}_e^2 + \hat{\sigma}_w^2} \text{ for within-plantation, and}$$

$$= \frac{4\,\hat{\sigma}_f^2}{\hat{\sigma}_f^2 + \hat{\sigma}_{s(f)}^2 + \hat{\sigma}_{pf}^2 + \hat{\sigma}_{ps(f)}^2 + \hat{\sigma}_e^2 + \hat{\sigma}_w^2} \text{ for combined}$$

plantations (See *Table* 1 for description of symbols.)

σ_{ph} = phenotypic standard deviation from the denominator

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Table 1. — Forms of analyses of variance.

Source variation	Degrees of freedom	Mean square expectations
A. Analysis for data in one location:		
Replications	(r-1)	
Females	(f-1)	$\sigma_w^2/k + \sigma_e^2 + r\sigma_{s(f)}^2 + rs\sigma_f^2$
Males in females	f(s-1)	$\sigma_w^2/k + \sigma_e^2 + r\sigma_{s(f)}^2$
Plot error	(r-1)(fs-1)	$\sigma_w^2/k + \sigma_e^2$
Plants in plots	Σ(k´-1)	σ_w^2
B. Analysis for data in two locations:		
Locations	(p-1)	
Replications in locations	p(r-1)	
Females	(f-1)	$\sigma_w^2/k + \sigma_e^2 + r\sigma_{ps(f)}^2 + rs\sigma_{pf}^2 + rp\sigma_{s(f)}^2$ $+ rps\sigma_f^2$
Males in females	f(s-1)	$\sigma_w^2/k + \sigma_e^2 + r\sigma_{ps(f)}^2 + rp\sigma_{s(f)}^2$
Locations x females	(p-1)(f-1)	$\sigma_w^2/k + \sigma_e^2 + r\sigma_{ps(f)}^2 + rs\sigma_{pf}^2$
Locations x males/females	f(p-1)(s-1)	$\sigma_w^2/k + \sigma_e^2 + r\sigma_{ps(f)}^2$
Plot error	p(fs-1)(r-1)	$\sigma_w^2/k + \sigma_e^2$
Plants in plots	Σ(k´-1)	σ_w^2

Where:

p = locations = 2

r = replications per location = 12 or 15

f = females = 9

s = males per female = 6

k = number of plants measured in ith plot

k = harmonic mean of number of plants per plot

σ_e^2 = variance of plot effects

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

σ_{pf}^2, $\sigma_{ps(f)}^2$ = interaction variance among female or male effects and location environments

σ_f^2 = variance of female effects

$\sigma_{s(f)}^2$ = variance of male effects

of the appropriate heritability equation (either within- or combined-plantations) assuming selection is to be within replications.

Results

Variation among female and male/female portions of the nested families is statistically significant for 1966 and 1967 increments (*Table 2*). Family means are arranged graphically in *Figure 1*. On the average, full-sib mean is based on 59 and 51 plants in locations 1 and 2, respectively. In general, looking at variation in family means among locations and measurement years, the range in both types of family means is about 10 cm, or 25 to 30 percent of the experiment mean, although the range for families of males/females is usually larger, and especially so in location 1. Ranges for both types of families are consistently greater in location 2, by 1 to 2 cms for 1966 increment and by 3 to 5 cms for the 1967 increment. For the 1966 increment, the overall experiment mean is smaller by 16 percent at location 2, and for 1967 increment, equal at the two locations.

The differences in range between locations are reflected by the larger variance component estimates (*Table 3*) for female (σ_f^2) and male ($\sigma_{s(f)}^2$) effects in location 2 compared to location 1. Furthermore, variability among males/females ($\sigma_{s(f)}^2$) is consistently larger than among females (σ_f^2), and the difference over both measurement years is larger in location 1 compared to location 2. This implies that a proportion of total genetic variation for height increment is expressed as dominance variance since, by definition, dominance variance $= 4(\sigma_{s(f)}^2 - \sigma_f^2)$. Calculated by this equation, dominance variance in location 1 contributes 65, 54, and 63 percent to total genetic variance in 1966, 1967, and combined increments, respectively; in location 2, 46, 12, and 42 percent; in locations combined, 34, 47, and 42 percent.

Table 2 shows significant interactions for 1967 female × locations and for 1966, 1967 males/females × locations. Examples involving rank changes are apparent in *Figure 1:* maternal half-sib families A vs. H (1967) and full-sib families A10, G88, and G15 (1966); A20, B31, C5, etc., (1967). For the 1967 increment, components (*Table 3*) for location-genotype interactions (σ_{pf}^2, $\sigma_{ps(f)}^2$) contribute fully as much to variance as does the female component. Components for male/females × location effects are consistently larger than those for female × location.

For both traits, estimated genetic gains from mass selection (*Table 4*) are higher for location 2 than for location 1. Phenotypic standard deviations of increment are similar

Table 2. — Variance analyses of 1966 and 1967 height increments and of increments combined.

Source variation	Degrees of freedom[1]	Mean squares					
		1966		1967		1966 & 1967	
		Loc. 1	*Loc. 2*	*Loc. 1*	*Loc. 2*	*Loc. 1*	*Loc. 2*
Replications	14	2,681**	564**	5,766**	1,356**	15,832**	3,574**
Females	8	550*	825**	624**	1,577**	2,048*	3,864**
Males in females	45	219**	236**	203**	323**	769**	1,032**
Plot error	742	61	57	51	83	186	225
		Locations combined					
Locations	1	11,323**		383		14,150	
Replications in locations	22 (28)	1,623		3,561		9,703	
Females	8	1,238**		1,472**		5,386**	
Males in females	45	336*		368**		1,442**	
Locations × females	8	79		493**		526	
Locations × males/females	45	102**		134**		359**	
Plot error	1,166 (1,484)	59		67		206	

[1]) Degrees of freedom in parentheses refer to 1966 + 1967 increments only.

* Significant at probability 0.05.

** Significant at probability 0.01.

Table 3. — Components of variance and standard errors of estimates for 1966, 1967 and combined height increments.

Trait	Location	σ_f^2	$\sigma_{s(f)}^2$	σ_{pf}^2	$\sigma_{ps(f)}^2$	σ_e^2	σ_w^2
1966	1	3.677	10.570			19.963	144.815
height		(2.778)	(3.020)				
increment	2	6.543	11.948			16.450	131.210
		(4.136)	(3.256)				
	1 and 2	6.426	9.747	—0.322	3.628	16.912	138.566
		(3.885)	(3.021)	(0.572)	(1.772)		
1967	1	4.679	10.144			26.436	79.685
height		(3.137)	(2.801)				
increment	2	13.935	15.963			21.304	200.047
		(7.870)	(4.447)				
	1 and 2	5.174	9.743	4.984	5.566	26.087	135.912
		(4.853)	(3.364)	(3.085)	(2.314)		
1966 and 1967	1	14.211	38.908			44.475	503.795
height		(10.328)	(10.598)				
increment	2	31.466	53.784			60.825	531.867
		(19.345)	(14.218)				
	1 and 2	20.986	36.116	1.852	10.230	49.282	516.909
		(13.554)	(10.218)	(2.739)	(4.590)		

at the two locations; so, higher gains reflect the higher estimates of additive variance at location 2. Gains predicted from the 1967 increment analysis are appreciably affected by the genotype-location interaction. This is seen from the combined analysis, which includes effects of locations-family interactions. In it, predicted gain is approximately three quarters the average of predictions for locations analyzed individually.

Discussion

The potential for genetic improvement in seedling height-growth in Douglas-fir appears to be good. The impressive range in family means *(Fig. 1)* indicates considerable genetic variability. Some seems to be in the dominance form, but a substantial part is left in additive. Unfortunately, this separation into components has low reliability because the mating design used only nine of the 63 parents to estimate female (additive) effects. Heritability and genetic gain estimates are similarly limited. On the other hand, if we discount dominance as being due to underestimation of female effects, the estimator for additive variance becomes $2(\sigma_f^2 + \sigma_{s(f)}^2)$, based on 63 parents. Using this equation and components from *Table 3*, additive variances average 36 percent larger than estimates from female effects alone, and heritabilities are correspondingly larger than those in *Table 4*. In any case, if the stand that provided the 63 percent is typical, there appears to be a sizable component of genetic variability in juvenile height-growth of Douglas-fir.

However, it should be emphasized that the larger gains in *Table 4* probably cannot be obtained by using an identical breeding scheme in conjunction with commercial operations. Experimental plantations were not comparable to

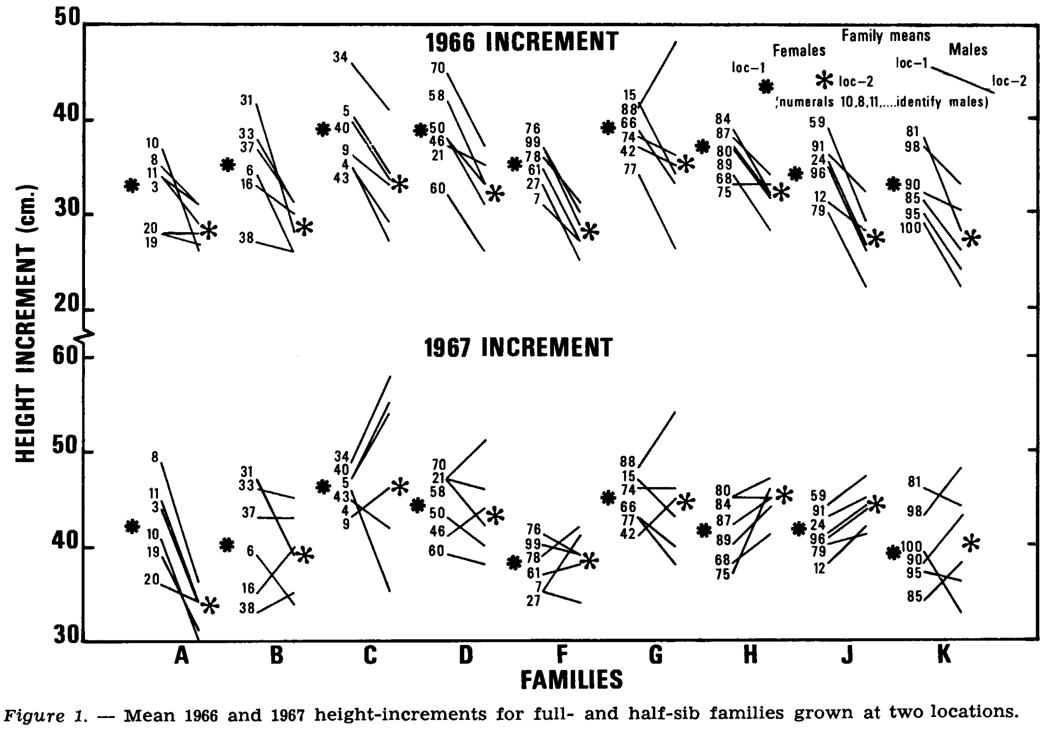

Figure 1. — Mean 1966 and 1967 height-increments for full- and half-sib families grown at two locations.

Table 4. — Heritabilities and genetic gains from mass selection (i = 2.67) within replications in the respective plantations.

Trait	Locations	$\bar{x}$ cm	σ_{ph}	h^2	Genetic gain in % of mean
1966 height increment	1	35.73	13.38	8.2	8.2
	2	30.15	12.89	15.8	18.0
	1 and 2	32.94	13.23	14.7	15.8
1967 height increment	1	41.97	11.00	15.5	10.8
	2	41.64	15.85	22.2	22.6
	1 and 2	41.80	13.69	11.0	9.6
1966 + 1967 height increment	1	77.70	24.52	9.5	8.0
	2	71.74	26.04	18.6	18.0
	1 and 2	74.74	25.21	13.2	11.9

the Douglas-fir region's commercial forest plantations. Indeed, it is unlikely that any experiment could sample an appreciable segment of the possibilities. When test and commercial plantation environments are not comparable, genotype-environment interactions may arise, genetic effects estimated in the test are not totally repeatable in forest plantations, and the test overestimates genetic gain in the field (Namkoong *et al.* 1966).

Family-location interactions are a significant part of the test's total variability even though only two locations were sampled. Striking and inexplicable rank changes occurred both in 1966, when the average height-increment differed significantly between localities, and in 1967, when increments were identical. Few of the families show consistently superior performances over growing seasons and locations, e. g., C34, D70, G88 *(Fig. 1)*. This suggests that in a breeding program to develop widely adapted strains, evaluation plantations should sample many locations. In such a program, gain in height-increment is likely to be considerably diminished by genotype-environment interactions, and the program's benefit-cost ratio to be reduced considerably in consequence.

On the other hand, needs for strains with increased juvenile height increment are often restricted to small areas. These may have relatively homogeneous sites and be amenable to uniform planting practices. If this restricted condition can be inexpensively sampled, say, by two or three evaluation plantations, there appears to be sufficient genetic variability to make it feasible to breed for increased seedling height-growth in Douglas-fir. Whether a breeder should concentrate on the first post-planting increment or on later ones apparently depends on economic considerations. Genetic variances and estimated gains are similar for the individual increments and their combination.

Acknowledgements

Financial assistance for producing families used here came by grant from the Institute of Forest Products, College of Forestry, University of Washington, while the author was employed by the College. The two plantations were installed and are being maintained by Weyerhaeuser Company's Forestry Research Center, Centralia, Washington. The author also gratefully acknowledges the many helpful comments by referees.

Summary

Height increments of the two growing seasons following planting were measured for 54 full-sib families planted at two locations. Sib-analyses indicate considerable total genetic variability and, though estimated with poor reliability, dominance variance apparently makes up a sizable proportion. The increment formed the second season after outplanting was especially affected by family-location interactions. As a result, heritabilities of average performance over both locations are low (10 to 16 percent).

Zusammenfassung

Der Höhenzuwachs in 2 Wachstumsperioden, die auf die Pflanzung folgten, wurde bei 54 Vollgeschwister-Familien gemessen. Diese waren auf 2 verschiedenen Flächen ausgepflanzt worden. Die Analysen zeigten beachtliche Variabilität. Dabei hatte die Dominanzvarianz einen großen Anteil. Der Zuwachs im 2. Jahre nach der Auspflanzung wirkte sich besonders auf die Familien-Standort-Interaktionen aus. Die Heritabilitäten der Durchschnittsleistungen über beide Flächen sind niedrig (10—16%).

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