Theoretical and Applied Genetics 42, 151–159 (1972)

Age-Related Variation in Genetic Control of Height Growth in Douglas-fir *)

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Summary. The development of genetic variances in height growth of Douglas-fir over a 53-year period is analyzed and found to fall into three periods. In the juvenile period, variances in environmental error increase logarithmically, genetic variance within populations exists at moderate levels, and variance among populations is low but increasing. In the early reproductive period, the response to environmental sources of error variance is restricted, genetic variance within populations disappears, and populational differences strongly emerge but do not increase as expected. In the later period, environmental error again increases rapidly, but genetic variance within populations does not reappear and population differences are maintained at about the same level as established in the early reproductive period. The change between the juvenile and early reproductive periods is perhaps associated with the onset of ecological dominance and significant allocations of energy to reproduction.

Introduction

To reproduce successfully, forest trees must grow rapidly enough to avoid suppression by neighboring trees and to develop a large and durable seed-producing machinery. Trees must also produce seed for many years because the availability of sites for seedling growth is highly uncertain in any one year. Therefore, trees have the recurring strategic problem of allocating the proper amounts of photosynthate for the requirements of survival and for those of seed production.

For sub-climax species like Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) which form pure stands following large-scale disasters (Fowells, 1965), the nature of the vegetative competition, and hence the growth requirements, may change when trees reach sexual maturity. The main environmental influences upon seedlings are micro-climate and other micro-site factors and competition from herbs and shrubs. To establish a population, seedlings must be able to grow rapidly in a wide variety of habitats because extreme variations in habitat occur over very short distances (Franklin and Dyrness, 1969). This can be accomplished by a wide physiological homeostasis, (Lerner, 1954), which requires some appropriate level of genetic variance among trees (Levins, 1968). In 10 to 20 years, however, trees begin to dominate their own environment, and their severest competition comes from neighboring trees of similar age with the possible addition of older residual trees. Thereafter, a tree must maintain a growth rate and crown position sufficient for continued survival relative only to cohorts of the same population. It may then occur that a different balance between physiological and populational genetic homeostasis would be possible. In this paper we analyze the genetic control of height growth in Douglas-fir plantations established 53 years ago in western Washington.

In western Washington and northwestern Oregon, Douglas-fir grows in widely different environments even within the radius of freely interbreeding neighborhoods and expresses some intra-populational genestic variance in height growth in the juvenile stages (Campbell, 1964). Because Douglas-fir also grows over a wide geographic range, some isolation occurs among populations on areas which differ in soil, elevation, climate, and other macro-site factors. These conditions can be expected to lead to the development of differing growth patterns among populations when they are grown in a common environment. Thus, while height growth is expected to be an important component of fitness, an optimal growth strategy might require not only that genetic variation change with age but also that population differences change as the trees mature.

Materials and Methods

The trees measured were derived from a genetic study of Douglas-fir established in 1912 in western Washington and northwestern Oregon (Munger and Morris, 1936). The present paper concerns a small, tangential segment for which a special sample of the larger study was drawn. Because we wished to measure apical growth potential, our sample was restricted to those trees which survived without detectable mechanical damage to the central stem. Most of the original trees died before sampling or displayed some past history of stem damage. Thus, the means and variances are appropriately sampled only for living 53-year-old trees with whole stems and are not appropriate for commercial populations. In addition, the

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* This paper is published with the approval of the Director of Research, North Carolina Agricultural Experiment Station, as No. 3361 of the Journal Series. The computing services in this project were supported by NIH Grant GM-11546, held by the Institute of Statistics, North Carolina State University at Raleigh.

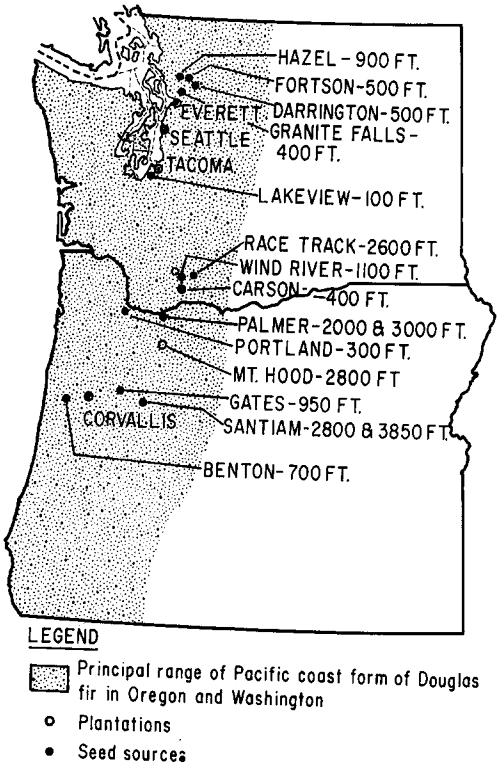

Fig. 1. Location of seed source populations and the Wind River and Mt. Hood plantations

trees were planted as 1-year-old seedlings in a spaced plantation; hence, their initial distribution over the site was much more uniform than would occur naturally. However, they were allowed to grow without human disturbance, and their environment for the subsequent 52 years was essentially a natural one.

Thirteen parental populations were sampled within the Willamett Valley east of the Coast Range and up the lower slopes of the western edge of the Cascades. The locations and elevations of the seed sources and of the plantings made from these sources at Wind River and lower Mt. Hood are shown in Figure 1. The populations came from areas with various soils, elevations, and climates. Within each population, open-pollinated seed (presumably representing half-sib families) was collected from 3 to 11 trees; total collection was 116 families from the 13 populations. The seedlings were raised in a nursery for 2 years and transplanted in 1915 into two replicate blocks in each of six locations.

Within each location, populations were randomly blocked together and families were randomly assigned to rows within their respective population blocks. Heights were measured by pole and tape measures when the trees were 5, 10, 12, 15, 23, and 28 years old. After age 28, the trees were generally too tall to measure conveniently and no further direct measurements were made. In 1966, it was found that the planting near Wind River at 335 m. elevation was the only one with a long growing season and enough survival and undamaged stems to provide accurate growth data for detailed analyses. However, the climate at this plantation is variable and has occasionally caused some selective damage and mortality as the stands developed. In contrast, the plantation on Mt. Hood at 260 m. elevation was exposed to a less variable climate but to more severe winters and shorter growing seasons; hence, it produced trees which grew much more slowly. Nevertheless, survival at Mt. Hood was good, and enough stems remained in good condition to give additional information on growth potentials in another climatic regime. Although it was not always possible to obtain growth records for each plot, we tried to measure two randomly chosen trees in each family plot with an Abney level for total height between the 53rd and 54th growing season. Variance resulting from measurement error was estimated by duplicating measurements on a sample of trees and was found to be around .3 m. Because Douglas-fir at Wind River and Mt. Hood consistently produced only one new nodal whorl of branches from the apical meristem each year, measurements of height at previous ages were easily made by locating whorls down the stem. Thus, heights were established for the trees at ages 40, 33, 28, 23, and 18. The standard error resulting from inconsistent measurement ranged from ±.15 m. at age 40 down to virtually zero at ages 28, 23, and 18 when the latter measurements were matched with the records of previous years.

Table 1. *Univariate analysis of variance for height of Douglas-fir in the Wind River plantation*

Source of variance	d. f.	Expected mean squares
Blocks	1	
Populations	12	$\sigma_e^2 + 1.80\ \sigma_f^2 + 7.46\ \sigma_r^2 + 14.47\ \sigma_p^2$
Block error	12	$\sigma_e^2 + .20\ \sigma_f^2 + 7.01\ \sigma_r^2$
Families	103	$\sigma_e^2 + 1.63\ \sigma_f^2$
Plot error	65	σ_e^2

The analysis of variance for measurements taken in any single year or for any single function of the measurements is listed in Table 1. The unequal and fractional coefficients in the expected mean squares result from imbalance in the data. The analysis on height (Y_{ij}) was constructed under the assumptions of random and independent sampling and plot location error effects from the split-plot linear model:

$$Y_{ij} = \mu + b_i + p_j + b\,p_{ij} + f/p_{k(j)} + e_{ijk}$$

where

μ = experimental mean

b_i = effect of planting block i, $i = 1,2$

p_j = effect of population j, $j = 1, 2, \ldots 13$

$b\,p_{ij}$ = major plot error deviation of population i in block j

$f/p_{k(j)}$ = family k deviation within population j, $k = 1, 2, \ldots 11$

e_{ijk} = family plot error deviation of family k within population in replication i.

A stepwise estimation of the adjusted mean squares was provided by programming a general least-squares analysis of variance.

In addition to several multivariate analyses, two sets of univariate analyses were run to determine the existence of significant genetic (*i. e.*, population and family within population) sources of variance. The first set of univariate analyses was on the parameters of a curve fitted to the height/age measurements of each sample tree. In the first set, our objective was to achieve economy in the number of parameters required to detect changing patterns in the genetic control of growth by finding a well-fitting function with a limited number of parameters. Six non-linear functions were examined for suitability on the basis of the size of the variance of residual error and the presence of systematic errors. A subsample of 30 trees was used to test the curve fittings. Each tree's measurements were fitted and its parameters estimated according to the algorithm and computer program developed by D. W. Marquardt (1966). The curves tested were the Gompertz, Logistic, and Richards' generalized function (Richards, 1959); a Generalized Logistic (Nelder, 1961 and 1962); and von Bertalanffy's generalized curve (Bertalanffy, 1957). In addition, a fifth-degree polynomial was tested to see if the advantages of maximum likelihood estimation and testing described by Grizzle and Allen (1968) could be used.

Despite the fact that curves with more parameters may have fitted the data better, Eisen *et al.* (1969) were able to detect differences in growth curves among selected lines of mice with Richards' generalized four-parameter curve. Beck (1969) was also able to fit height growth of eastern white pine with a three-parameter simplification of the same curve. Turnbull (1963) also found Richards' curve to give good fits for both height and volume growth of Douglas-fir. In our tests, Richards' curve gave small errors, lower residual variances, and less systematic error than any other curve. We, therefore, felt justified in using the parameters of the Richards' curve as the best available variables in testing whether any non-linear function with less than five parameters could mimic consistent growth trends and help our analyses. Because any function with fewer parameters than points to fit cannot be expected to predict perfectly each tree's growth, the lack of fit resulting from poor curve approximation contributes to errors in measuring true growth differences. Thus, our criterion of success in using Richards' curve is relative to the power of any other multivariate test of differences among families and populations.

The Richards' curve takes the form

$$Y_i = A\,(1 - b\,e^{-ct_i})^{\frac{1}{1-m}} \qquad \text{for } m < 1$$

or

$$Y_i = A\,(1 + b\,e^{-ct_i})^{\frac{1}{1-m}} \qquad \text{for } m > 1$$

where

Y_i = measurement at time t_i
A = upper asymptote
c = a rate-of-growth parameter
m = a shape-of-curve parameter
b = a function of initial values

and

e = the base of natural logarithm.

The growth data for each tree was fitted separately and the parameters A, c, and m derived in the fitting were used as measures of tree growth, while b was used as an arbitrary parameter of the curve fitting.

Results and Discussion

The mean heights of the source populations at ten ages are shown for the Wind River plantation in Table 2. The mean squares for the univariate analyses of variance of the heights at the ten ages are listed in Table 3, and the variance components derived from these mean squares are listed in Table 4. F-tests made for each age indicated no significant family component. An approximate F-test for the population mean squares was made by reconstructing an error mean square from the estimated variance components and EMS coefficients (Table 1) to provide a clean F-ratio. These results are given in Table 3.

Trends in Error Variances

In these analyses, the plot and block error variances, σ_e^2 and σ_r^2, reflected the cumulative effects

Table 2. *Mean heights (meters) of the source populations at ten ages in the Wind River plantation*

	Age (years)									
Population	5	10	12	15	18	23	28	33	40	53
Lakeview	.357	1.51	2.33	4.26	6.30	10.54	14.78	18.83	23.16	29.22
Portland	.369	1.55	2.20	4.08	6.17	10.19	14.28	18.15	22.47	28.27
Carson	.317	1.09	1.64	2.98	4.76	8.33	12.30	16.08	20.27	26.61
Granite Falls	.451	1.63	2.45	4.55	7.07	11.41	15.78	19.81	24.14	30.08
Darrington	.408	1.38	1.99	3.56	5.51	9.26	13.30	17.18	21.35	27.27
Fortson	.341	1.37	2.00	3.62	5.69	9.64	13.68	17.34	21.64	26.94
Hazel	.341	1.30	2.05	3.58	5.57	9.27	13.43	17.54	21.42	26.89
Benton	.369	1.26	2.02	3.46	5.74	9.68	14.01	17.99	22.46	28.33
Gates	.372	1.45	2.13	3.76	5.51	9.64	13.75	17.65	21.85	27.63
Wind River	.363	1.36	2.03	3.50	4.50	8.92	12.80	16.44	20.25	26.10
Palmer	.332	1.27	1.85	3.54	5.60	9.65	13.86	17.40	22.30	28.86
Race Track	.366	1.12	1.72	3.11	4.94	8.64	12.67	16.58	21.04	27.33
Santiam	.323	.963	1.44	4.18	6.67	10.90	15.09	19.00	23.28	29.39
Mean	.363	1.33	1.99	3.71	5.70	9.70	13.83	17.69	21.97	27.92

Table 3. *Mean squares for heights at ten ages in the Wind River plantation*

Source of variance	d.f.	Age (years)									
		5	10	12	15	18	23	28	33	40	53
Replication	1	.5034	9.2403	14.1291	22.6920	25.9439	18.3784	5.3640	.0732	.3492	5.4974
Population	12	.0251^{ns}	.4698^{ns}	1.0625^{ns}	2.9277^{ns}	6.3395^{ns}	10.9351^{ns}	14.0616*	16.1853*	19.2365*	20.6731*
Block error	12	.0153	.3274	.7437	2.4520	3.9612	5.7708	6.1129	6.0903	5.9528	9.9509
Families in populations	103	.0090^{ns}	.0841^{ns}	.1547^{ns}	.4911^{ns}	.8075^{ns}	1.2114^{ns}	1.5294^{ns}	1.9261^{ns}	2.8533^{ns}	5.7441^{ns}
Plot error	65	.0075	.0704	.1413	.4428	.6914	.9846	1.3345	1.7521	2.9909	6.3330

^{ns} = non-significant F-test at 5% level of testing. — * = significant F-test at 5% level of testing.

Table 4. *Variance components derived from mean squares for heights at ten ages in the Wind River plantation*

Variance components		Age (years)									
		5	10	12	15	18	23	28	33	40	53
Populations	σ_p^2	.0005	.0078	.0185	.0208	.1012	.3207	.5153	.6678	.9143	.7646
Block error	σ_r^2	.0011	.0364	.0857	.2858	.5439	.6787	.6781	.6157	.4250	.5265
Families in populations	σ_f^2	.0009	.0084	.0082	.0296	.0712	.1391	.1195	.1067	−.0844	−.3610
Plot error	σ_e^2	.0077	.0704	.1413	.4428	.6914	.9846	1.3345	1.7521	2.9909	6.3330
Intraclass correlation	$\frac{\sigma_f^2}{\sigma_f^2 + \sigma_e^2}$	.126	.119	.058	.067	.103	.141	.090	.061	—	—
Mean height		.36	1.33	1.99	3.71	5.70	9.70	13.83	17.87	21.97	27.92

of microsite and plot error differences. As expected, these random error components generally increased as the trees grew. Because height measurement in trees necessarily includes previous height growth, the absolute value of variances would not decrease unless there were strong negative correlations between different ages. Ordinarily, any random environmental effects would be expected to continually increase the error variances. However, if growth becomes constant for all trees, the error variances would stay at the same levels. Our analyses showed that this variance neither increased uniformly over the period measured nor did it randomly fluctuate. The change in the size of the sum of the error components, σ_r^2 and σ_e^2, is most clearly displayed in Figure 2 as a ratio of mean height. In the Wind River plantation, both the total and the error variances increased logarithmically in absolute value but increased linearly relative to mean heights up to around 18 years of age. After this juvenile period, a slump occurred and a decline in the relative size of the error variance persisted up through the 33rd year. A similar change occurred in the progress of the block effect, which increased in absolute size up to the 15th year and thereafter declined to small negative estimates after the 28th year. In Figure 2, the relative size of the block effect is seen to increase only until the 10th or 12th year, after which it declines to virtually zero.

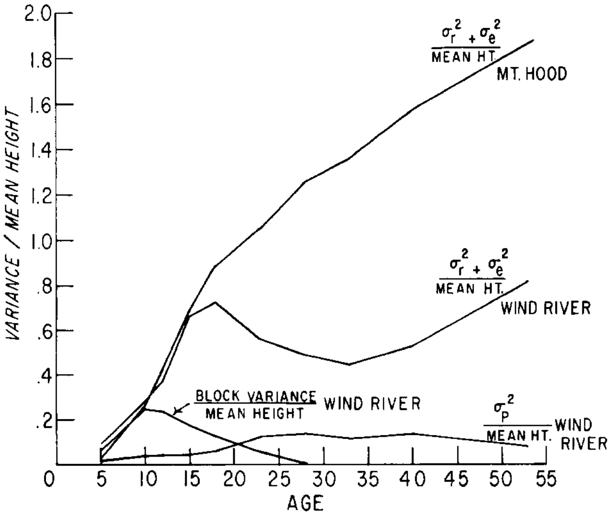

Fig. 2. Time trends in variance components as a ratio of mean height

By the 40th year, the error variances again appeared to be increasing and may be expected to continue increasing until selective mortality or some asymptotic maximum height is approached and more mature stands approach uniformity. At the present time, however, the error variances are increasing, but the block effects no longer exist. Because the contribution of increased measurement errors to the error variance is less than 2% of the size of the plot error component, this contribution could not account for the changes in the relative sizes of error. It appears that response to environmental effects between the 15th and 40th years was restricted by the trees' own growth mechanisms and that this control of response became more relaxed after around 40 years.

In contrast to this pattern of control of error variance exhibited at Wind River, far less control was exhibited in the shorter trees growing at Mt. Hood (Figure 2). The cooler environment at Mt. Hood permitted less expression of differences in growth potential. While there appears to have been some change in the rate of growth of the error variances, it seems clear that the relative size of the error was essentially identical in the two plantations during the first 15 years, but that it differed after that period. By the 33rd year, even the absolute size of the variance at Mt. Hood exceeded that at Wind River and did so with smaller trees. Thus, in the Mt. Hood environment no genetic control of error variation developed, allowing much more variation among trees of the same family to exist. The variance components and mean heights for the Mt. Hood planting are listed in Table 5.

Correlations among the deviations in plot error at Wind River are listed in Table 6 for ages 5 through 53. They were computed as the ratio of the pairwise covariance component for the deviations in plot error to the square root of the product of the respective components of error variance. As expected, correlations gradually declined for any given age when

Table 5. *Variance components derived from mean squares for heights at ten ages in the Mt. Hood plantation*

Variance component		Variance components at ages —									
		5	10	12	15	18	23	28	33	40	53
Populations	σ_p^2	.0001	.0035	.0056	−.0219	−.0673	−.0957	−.1310	−.1401	−.2591	−.2847
Block error	σ_r^2	.00007	.0204	.0411	.1535	.3221	.6919	1.2691	1.9036	2.9590	4.5541
Families in populations	σ_f^2	−.0001	−.0077	−.0222	−.0297	−.0462	−.0774	−.0632	−.1706	−.3107	--.4277
Plot error	σ_e^2	.0025	.0468	.1007	.1940	.3591	.8169	1.3722	2.0848	3.3548	5.7712
Mean height		.28	.814	1.146	1.707	2.31	4.36	6.90	9.54	13.12	18.28

Table 6. *Correlations of deviations in plot error at Wind River for ages 5 through 53*

Years	Correlations for ages —								
	10	12	15	18	23	28	33	40	53
5	.29	.29	.28	.25	.25	.21	.18	.17	.15
10		.87	.74	.68	.67	.59	.56	.52	.46
12			.89	.85	.82	.76	.71	.64	.56
15				.94	.90	.84	.78	.69	.62
18					.95	.88	.81	.71	.62
23						.95	.89	.78	.70
28							.97	.89	.82
33								.95	.88
40									.91

correlated with successively older or younger ages but never became negative. The correlations among older ages were larger than for a comparable year span at younger ages because heights of older trees necessarily shared a larger portion of their life's growth in common. Thus, after plot means were adjusted for replication, population, and family effects, the correlation among effects of residual error followed an orderly and expected declining progression, because juvenile differences among trees tended to accumulate random deviations.

Trends in Population Variances

The analyses of the height data at Wind River also clearly indicated the presence of inherited population differences in growth rate and age-dependent trends in the relative sizes of genetic versus environmental sources of error variance. In the early years, the differences among populations were insignificantly small. The population variance component, σ_p^2, accounted for less than 8% of all of the components (excluding the replication effect) during the juvenile period. However, there was a rise after the 15th year which stabilized at around 20% of the total variance through the 40th year. The ratio of σ_p^2 to mean height, which is traced in Figure 2, also showed that the rise in population differences was relatively stable with respect to increasing tree height during this period. At the 53rd year, a small, relative decline in σ_p^2 occurred. Because differences in the mean heights of populations did not diminish and σ_p^2 increased in absolute size, this decline was largely attributable to increases in error variances and total height, as already noted.

The establishment of population differences during the late juvenile period was also reflected in the correlations among population deviations (Table 7).

Table 7. *Correlations of deviations in populations at Wind River for ages 5 through 53*

Years	Correlations for ages —								
	10	12	15	18	23	28	33	40	53
5	1+[1]	1+	.36	.22	.22	.27	.31	.31	.24
10		1+	1+	.92	.75	.69	.72	.59	.58
12			1+	.90	.74	.75	.81	.68	.71
15				1+	1+	1+	1+	1+	1+
18					1+	1+	1+	1+	1+
23						1+	1+	1+	1+
28							1+	1+	1+
33								1+	1+
40									1+

[1] 1 + indicates a correlation estimate which exceeds 1.0.

Correlations involving ages of less than 15 years tended to follow the same declining progressions as did the correlations of error effects. The correlations of population effects of 5-year height with greater ages declined rapidly but appeared to stabilize at around 0.2 to 0.3. Similarly, the correlations of ages 10 and 12 with older ages also declined but also appeared to stabilize at around 0.6 to 0.7. Thus, any juvenile differences which may have existed and which were estimated by the small σ_p^2 in these ages were not entirely persistent, because population differences tended to accumulate independently of initial height differences. However, correlations of ages greater than 15 with older heights were all high (estimates exceeded 1.0) and remained so. It thus appears that population differences were not well established until around the 15th year and after that time relative performance was highly consistent. Because population differences tended to increase slowly after the 15th year, the coincidence of an emerging consistency of strong interpopulation differences with the reduction of response to random microsite variations suggested genetic canalization at the population level at 15 years and its possible relaxation after 40 years. This development of population differences was limited to the Wind River plantation; no population sources of variance developed in the Mt. Hood plantation (Table 5). At Mt. Hood, the environment permitted less expression of differences in growth potential. Neither error control nor genetic differences developed; hence, all families appeared to be about equal in their ability to grow under the shorter growing season. Growth differences among trees at Mt. Hood therefore seemed to be simply a cumulative response to effects of environmental deviation around a general mean capacity for growth, and no genetic differences in capacity for growth in this environment have developed.

Curve Function Analyses

The emergence of population differences in the early reproductive years and the increase of uniformity within populations, as made apparent in the univariate analyses, may be more clearly patterned by a unified analysis of all ten measurement ages.

Analyses of the parameters of the Richards' nonlinear function should provide simple interpretations of genetic differences — if simple functional differences among genotypes existed. However, because significant differences were found for population effects only in the later ages and the population variance did not increase at a constant rate, the differences in the overall pattern of the growth curve may not be easily detected. Nevertheless, if any curve with four or fewer parameters can detect these differences, Richards' curve parameters should. The mean squares for the analyses of variance on the parameters A, c, and m at Wind River are given in Table 8, and the variance components are listed in Table 9. Non-significance of all genetic sources of variance, and examination of the curves themselves, showed that the extra variation caused by the lack of fit was sufficient to obscure any differences. Some growth curves for individual trees, especially those in which the growth was irregular, showed that wide variations in parameters produced relatively small increase in the lack-of-fit error variance. Therefore, the parameters obtained for several such trees could vary widely even if the basic growth patterns were similar, and such estimation errors would increase the error in curve comparisons. Thus, although population differences in height growth existed, the deviations were not easily detected in the parameters of Richards' curve. Because univariate analyses of separate measurements showed significant population differences, the lack of significance in the curve parameters may have been due to the non-uniform response of populations to simple variations in the parameters of Richards' curve.

Table 8. *Mean squares for curve parameters at Wind River*

Source of variation	d.f.	Mean squares for parameters — A	c	m
Replication	1	170.7	.000827	.0118
Population	12	784.3^{ns}	.00358^{ns}	.1355^{ns}
Block error	12	782.2	.000885	.1839
Families in populations	103	771.3^{ns}	.000286^{ns}	.0476^{ns}
Plot error	65	851.3	.000241	.0343

Table 9. *Variance components for curve parameters at Wind River*

Variance component	Variance components for parameters — A	c	m
σ_p^2	5.8	−.000042	−.0049
σ_r^2	− 8.4	.000091	.0211
σ_f^2	−49.0	.000028	.0082
σ_e^2	851.3	.000241	.0343

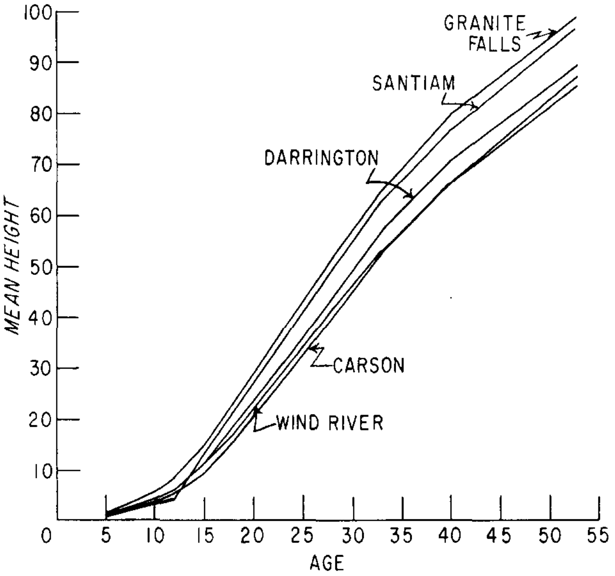

Fig. 3. Average height growth of five populations at Wind River

Unadjusted average heights for each population at Wind River are listed in Table 2, and curves for five of them are drawn in Figure 3. Some populations were consistently taller (*i. e.*, Granite Falls) and some usually were shorter (*i. e.*, Carson), as previously indicated on the basis of juvenile growth at Wind River by Munger and Morris (1936). There was also some variation in the shape of the growth curves and in relative ranking among populations, as seen in the decline of the local Wind River population and the relative escalation in rank of the Santiam, Race Track, and Palmer populations. This variation supports the evidence from analysis of the variance components that population differences do not uniformly increase. These observations on average growth curves indicate that the genetic differences among populations are not simply controlled by such mechanisms as consistently different abilities to utilize site resources. Moreover, if the differences were in the nature of the availability of site resources to the growing stem, then the differences among populations should be similar to differences in growth curves among plantings of the same population on sites of differing qualities. Such differences in growth curves as a result of site variations have been intensively studied for Douglas-fir, and tables of heights at various site indices have recently been constructed for western Washington by King (1966). After King's tables were adjusted by 10 years to conform to our measurement scale, our curve for the Darrington population fitted very closely with King's curve for site index 96. In Figure 4, the curves for the Darrington, Granite Falls, and Carson populations illustrate the variation among populations, and the curves for site indices 84, 100, and 116 illustrate the expected variation among sites. Although both sets of curves have small differentials at age 15, at age 53 the differentials for the site index curves are greater than those for the population curves. Population differences were therefore more consistent, and populations tended to generate parallel growth curves with a mean displacement around a general growth curve for the planting site.

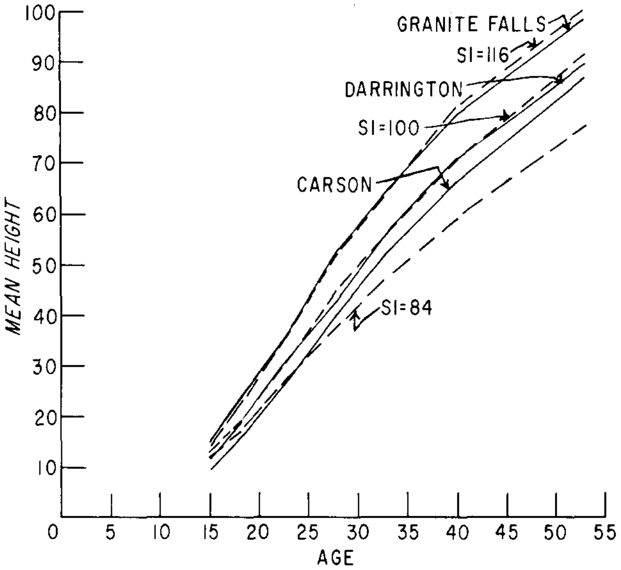

Fig. 4. Growth curves for three populations at Wind River and expected curves for three site indices

Trends in Family Variances

In the height analyses, the development of heritable variation among families within populations contrasted sharply with the development of heritable growth differences among populations. Whereas the magnitude of population differences rose to become a significant factor in the control of growth in the early reproductive years, family differences suffered an irregular decline. Family differences accounted for about 10% of the total variance at age 5 and declined to zero (small negative estimates of σ_f^2) after age 40. The intraclass correlation ratio of $\sigma_f^2/(\sigma_f^2+\sigma_e^2)$ is traced in Table 4. If the families are half-sibs, the ratios can be multiplied by 4 to obtain a "heritability" since σ_f^2 would contain at least 1/4 additive genetic variance. Moderate levels of genetic variance among families within populations of juvenile Douglas-fir have been indicated in other tests (Campbell, 1964), but no tests of older materials have been reported. In our material, the F-test for differences in height among families at age 5 was not significant at the 5% level of testing. Multivariate analyses of variance to test family differences over a series of years were then constructed, and the following statistic was computed:

$$-n \ln\left(\frac{|\sigma_e^{ij}| \cdot df\,(\text{error})}{|\sigma_e^{ij}+\sigma_f^{ij}| \cdot \sum_k df}\right)$$

where n = [total d. f. for family and error] + 1
$|\sigma_e^{ij}|$ = the determinant of the matrix of error variances and covariances, i, j = ages 5, 10, . . . , 53.
df (error) = d. f. for error = 65

$\sum_k df$ = total d. f. for family and error,

k = population 1, 2, . . . 13 .

and

σ_f^{ij} = matrix of family variances and covariances.

This statistic has an approximate χ^2 distribution with $p(q-1)$ degrees of freedom, where p = number of ages, and q = number of families (Kendall and Stuart, 1966). When tested for the first two age classes (5 and 10), the χ^2 = 423.6. This value gives a χ^2/d. f. ratio of 2.05. When tested for more inclusive age classes, the χ^2/d. f. ratio

for ages 5, 10, and 12 is	1.86,
for ages 5, 10, 12, and 15 is	1.82,
for ages 5, 10, 12, 15, and 18 is	1.72,
for ages 5, 10, 12, 15, 18, and 23 is	1.70,
for ages 5, 10, 12, 15, 18, 23, and 28 is	1.63,
for ages 5, 10, 12, 15, 18, 23, 28, and 33 is	1.58,
for ages 5, 10, 12, 15, 18, 23, 28, 33, and 40 is	1.51,
and	
for ages 5, 10, 12, 15, 18, 23, 28, 33, 40 and 53 is	1.56.

For 65 d. f., a χ^2 of 1.305 is significant at the 5% level of testing. The trend from an insignificant univariate F-test for the 5-year measurement alone to a significant χ^2/d. f. which thereafter declines is indicative of a declining trend in genetic variance. This trend may have resulted because genetic variation within populations which exists in the juvenile years was lost in the early reproductive years, when any height differences initially established were concealed by the accumulation of error or response to environmental effects. An alternative mechanism for this trend may have been the existence of a tendency towards a convergence in heights among members of the same population. Thus, negative estimates of the components of family variance for the 40- and 53-year data may have been due to a greater similarity, and hence to a positive correlation in heights among members of the same population, than would

Table 10. *Correlations of deviations in families within populations at Wind River for ages 5 through 33*

	Correlations for ages —						
Years	10	12	15	18	23	28	33
5	.60	.14	−.07	−.23	−.20	−.44	−.57
10		.60	.01	−.01	−.14	−.58	−.74
12			−.11	−.21	−.37	−.91	−1
15				1.00	.64	.26	.24
18					.85	.77	.93
23						.95	.97
28							.96

have been expected if only random deviations existed. If there was a tendency for heights to converge, the correlations of adjusted family deviations should have reflected a change towards negative values with increasing age. The 40- and 53-year data could not be used because their σ_f^2 was estimated as negative and none of the F-tests individually indicated a significant family effect; nevertheless, the pattern in the multivariate tests indicated that early genetic differences did exist. The correlation coefficients for ages 5 through 33 are listed in Table 10; they reflect a consistent pattern of shifting in relative height growth among families. The correlations for the early ages *inter se* were consistently positive and declined with age. Similarly, the correlations for the later ages were consistently positive and were higher than for the younger ages, as expected. In contrast, the period from 15 to 18 years indicated a clear disruption in growth pattern, as all earlier ages showed consistent negative correlations with all later ages. Thus, family differences tended to become less distinct as some form of compensatory growth occurred among the slower families. This tendency produced a relative convergence of average family heights which in turn resulted in a reduced component of family variance after the 15th year. Consequently, some evidence exists for a continuing control of variation among families of a kind which diminishes variation among phenotypes and genotypes within populations. Cumulative growth curves of five families in the Darrington population are illustrated in Figure 5. If any consistent family differences are re-emerging by a continued or reversed growth trend in later ages, they are masked by increasing error variances and may not ever again be strong enough to notice. Thus, genotypic differences within populations may exist as a significant source of variance only in the juvenile years.

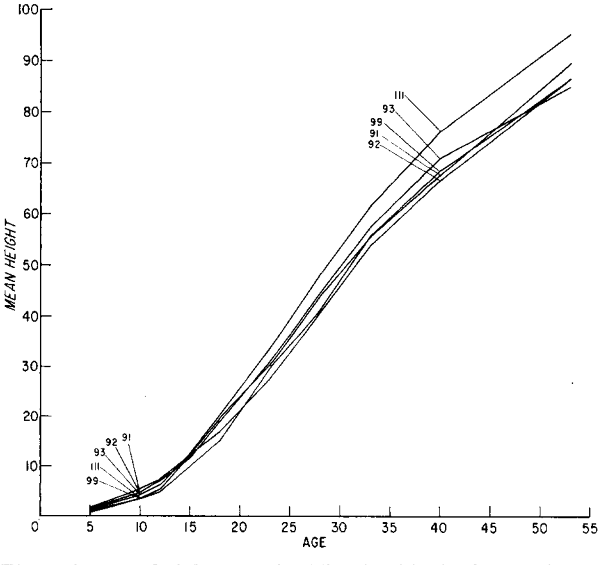

Fig. 5. Average height growth of five families in the Darrington population at Wind River

Conclusions

The results of the several analyses indicate that the genetic control of apical growth in Douglas-fir exists in certain expressive environments and that it changes during a tree's lifetime. It is strongest in the juvenile and early reproductive years and then declines. Because height is an important component of fitness, the relative decline of variance in environmental error during this period, accompanied by the loss of genetic variance within populations and the increase in variance among populations, indicates that means and variances in growth are selectively adaptive features of Douglas-fir populations.

In the juvenile period, the populations from the general region of western Washington established themselves in plantations with roughly comparable growth rates. At that time, some moderate levels of genetic variance within populations existed; this variance may have been a response to the requirement of populations to adapt to the variable soils and climates found within mating neighborhoods. As the trees emerged from the period of competition with low vegetation and began to dominate their own environment, differences in growth among populations appeared and genotypic differences within populations disappeared. Additive genetic variance, at least of the kind associated with the height of open-pollinated families, seemed to be limited to that part of the life cycle associated with adaptation to highly variable soil surface conditions and interspecific grass and brush competition; once an ecological dominance was achieved, the height growth became more uniform and genetic differences among trees in the population were reduced. Thus, it appears that several early growth strategies among seedling genotypes within populations may be followed, but these become relatively uniform when ecological dominance is achieved. This uniformity occurs long before any asymptotic height effects can be felt. However, populations develop growth differences which are genetically controlled and also probably adaptive.

When Douglas-fir begins to dominate the vegetation, differences among populations are established, but these differences do not become strongly intensified. Because tree growth is cumulative, trees can capitalize on early differences in size. However, the populations at Wind River which demonstrated early growth differences did not increase those differences as expected. In addition, the variances in environmental error did not increase as expected. Therefore, the genetically controlled differences in population growth and the control of environmental response indicate that the growth strategy in the period studied is not one which maximizes growth but one which limits response to environmental differences and produces a consistent growth pattern. Among genotypes within populations a tendency toward uniformity develops, and even among populations a tendency toward uniformity in new growth develops in the early reproductive years. At this stage, trees are the dominating vegetation and strongly influence their own environment, making it more predictable; consequently, populational homeostasis may be easier to achieve on an individual basis in this period than earlier.

There is some evidence to suggest that variation in plot error increases again after 40 years and that random environmental sources of variation thereafter have an increasing effect on growth differences. There is no evidence that genotypic variation within populations is reappearing at Wind River, but it may develop in older materials.

The coincidence of events around the 15th year, including the emergence of population differences and their stabilization, the decline of genetic variation within populations, and the relative decline of error variances, may be related to a single phenomenon. This phenomenon may well be the added physiological requirements for significant amounts of reproduction; in Douglas-fir, the period for such requirements usually begins at ages 15 through 20 and intensifies thereafter. Height growth may be subject to restrictions imposed by the need to maintain a competitive position in the canopy and the need to allocate energy to reproductive needs. Hence, height growth may be subject to a populational form of developmental canalization. It seems reasonable to hypothesize that seed production in Douglas-fir is postponed until an environmental dominance develops and that the genetic control of growth thereafter results in relatively uniform growth patterns. Older materials may again be subject to variations which have been more strictly controlled in the early reproductive years. Thus, it may be that other perennial organisms which eventually dominate their environment also undergo similar rhythms in genetic variance and populational homeostasis.

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Received June 15, 1971
Communicated by J. E. Legates

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