Heritability of Juvenile Growth Rate and Expected Gain from Selection in Western White Pine

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(Received for publication March, 1966)

Estimates of heritability are valuable aids in planning tree improvement programs that involve selection. Probably their most important use is in predicting the amount of genetic improvement that might be attained under various breeding schemes. Such knowledge of expected gains helps in choosing the best approach and also suggests how much money can justifiably be spent in attaining them. Heritability estimates likewise help the tree breeder in judging the relative amount of effort he should expend on each of the traits he is seeking to improve. Finally, they provide insight into such questions as, "How many trees should be selected and progeny tested, and how intensive should each phase of the program be?"

This paper reports heritability estimates that were made for juvenile growth rate in western white pine (*Pinus monticola* DOUGL.) by analysis of variance of progenies and by parent-progeny regressions. In relying upon juvenile rates of growth, one assumes that relative rates of growth for different genotypes do not vary greatly with age. Admittedly, usefulness of juvenile growth rates has limitations because patterns of growth rate change as trees mature. However, we feel that estimates presented herein do have merit when used with due precaution.

The estimates of heritability published herein are "narrow sense" estimates (LUSH, 1940); that is, only the additive component of genetic variance is considered.

Material and Methods

The data used in this study were recorded from a western white pine breeding project being conducted at the U. S. Forest Service's Forestry Sciences Laboratory, Moscow, Idaho (BINGHAM et al., 1953). In this project trees in natural stands were selected for their demonstrated resistance to blister rust. For purpose of the present study, dealing only with rate of height growth, the trees were considered as random members of the population in respect to growth rate.

The breeding project began in 1950, and several hundred progenies are now in various stages of testing. In the present study only the progenies from first-year's breeding were used ("1952 Progeny Trial"). The controlled pollinations for these progenies were made in the spring of 1950. Twenty-one different parents were involved in a total of 61 matings (Table 1). Many of the crosses were made on three of the trees used as females; other matings were generally random, as several trees were used as both males and females.

Seeds were sown in plant bands filled with forest soil in a nursery at Spokane, Wachington, in the spring of 1952. Two years later the seedlings were outplanted in the bands at three locations: Fernwood, Idaho; Elk River, Idaho; and Randolph Creek near Haugan, Montana. The Randolph Creek plantation is at a relatively high elevation (4,320 feet) and is a rather severe site for western white pine. The Fernwood and Elk River plantations, at lower elevations

Table 1. — Average fourth-year height increment of progenies (on all planting sites) and periodic annual height growth (PAG) of parents used in the heritability analyses.

Female parent	Average height increments, by male parent																	Average	PAG of female parent
	1	10	16	17	18	19	20	21	22	24	25	28	29	30	37	39	58		
									Feet										
1													.242					.242	2.42
10																		—	2.44
15	.266										.239			.203				.236	2.62
16	.250							.253			.237			.226				.242	1.69
17											.260			.239				.250	2.99
18														.266				.266	2.23
19	.282	.237	.240	.248	.251		.222	.240	.218			.227	.221			.228	.240	.238	1.60
20	.275		.239						.201	.259				.211		.193		.230	1.75
21				.278											.254			.266	1.75
22	.217			.196							.219		.224	.194				.210	1.84
23			.216	.247														.232	1.91
24																		—	2.71
25		.236			.264			.267						.222				.246	1.89
27							.243											.243	1.99
28																		—	1.86
29																		—	1.75
30	.262							.288			.229				.255			.258	2.13
37				.243														.243	1.84
38						.217												.217	1.80
39										.223								.223	2.02
58			.253	.303	.246			.263	.204	.257	.254		.253	.227	.217	.213		.245	2.62
Averages	.259	.236	.237	.252	.254	.217	.232	.262	.208	.246	.240	.227	.235	.224	.242	.211	.240	.239	2.09

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(2,770 and 3,000 feet, respectively), were better sites; Elk River was the best of the three.

A randomized block design was used at each plantation. The trees were planted in row plots of 2 to 10 trees (average, about 7 trees per row), with 3 replicates. Rows were 1 foot apart and trees were 1 foot apart in the rows. The planting sites were completely cleared and cultivated prior to planting, and were weeded and cultivated at least once yearly after planting. These conditions are unusual and unnatural, and could well have influenced the results, as is discussed later.

Total heights and current growth were measured periodically, but only height increment during the fourth year from seed was used in the present analysis. The main reason for restricting analysis to fourth-year increment was that total heights at the end of each of the first 4 years from seed remained significantly correlated with seed weight, whereas fourth-year increment was not.

The original data from parent trees consisted of average rate of height growth per year, during the last 10 years ("PAG"). The parents' ages ranged from about 25 to 60 years, and all parent trees were in four stands in northern Idaho. Actual current growths were converted to "40-year equivalents" by using a set of curves representing the last 10-year PAG over age. These curves were adapted from site curves published by Haig (1932) and were extended to include young ages by using data filed at the Forestry Sciences Laboratory of the U. S. Forest Service, Moscow, Idaho.

Similar measurements were also made on "check trees," *i. e.*, comparable trees located near each designated parent tree. Preliminary examination showed that growth rates of each selected parent tree were rather closely related to those of the nearby check trees. This relationship undoubtedly was largely due to site effects. Therefore, a regression of growth of parent trees was run on average growth of respective check trees. The regression was highly significant, and accounted for about 69 percent of the variation among selections. Then the PAG values of selections were adjusted to the average check tree PAG using the regression ($b = .9741$ and mean check tree PAG = 2.01 feet per year) by the method outlined by Snedecor (1946, p. 114).

Results

Sib Analyses

The mating design used in the study involved 61 crosses in an irregular pattern — largely determined by the female flowering capacity of the parent trees. Twenty-one parent trees were involved in the crosses; 13 served as both males and females, four served only as males, and the other four served only as females. Thus, the design was an incomplete and unbalanced diallel with 60 degrees of freedom for crosses: 20 degrees of freedom for parent trees, 13 degrees of freedom for the comparison "maternal vs. paternal" effects, and 27 degrees of freedom for deviations from these effects (*i. e.*, specific combining ability).

The experimental design used was one of nested environments consisting of three locations and three replications within locations. Each replication had a fairly complete set of the above-mentioned 61 crosses. An analysis of variance was constructed using the following sources of variation: locations, replications in locations, crosses, locations by crosses, and error. In this analysis, the 60 degrees of freedom for crosses and the 120 degrees of freedom for locations by crosses were partitioned as described above.

In order to estimate various kinds of heritabilities discussed in the following sections, an analysis of variance of the genetic and environmental sources of variance listed above would normally suffice. From such an analysis, components of variance are estimable and the heritability ratios are easily computed. The extreme unbalance of the data we had to use precluded making a normal analysis of variance. However, unbiased estimators of the variance components could be and were obtained by computation of the sums of squares and their variance component expectations similar to that used by Kempthorne (1952, pp. 113—118). The yield model (applying to plot means) used was:

$$Y_{ijkl} = \mu + l_l + r_{k(l)} + g_i + g'_j + s_{ij} + m_i + m'_j + lg_{li} + lg'_{lj} + ls_{lij} + lm_{li} + lm'_{lj} + e_{ijk(l)}$$

Where: μ = general mean
l_l = an effect due to the location
$r_{k(l)}$ = an effect due to the replication in the location
g_i = an additive effect of the male parent i
g'_j = an additive effect of the female parent j
s_{ij} = a deviation effect of the $i \times j$ cross
m_i = an effect due to using the genotype i as a male
m'_j = an effect due to using the genotype j as a female
$l(g, s, m)$ = interaction of the genotypic effects with location
$e_{ijk(l)}$ = plot error

and where:

$g_i = g'_i$
$m_i = m'_i$

and all effects are assumed random.

Using estimators derived for balanced experiments on unbalanced data is admittedly highly inefficient. Also, the errors of the estimators and of any heritability values derived from them are unavailable. However, the estimates used are unbiased and can be readily calculated. Alternative approaches, such as the "fitting of constants" in an unbalanced diallel, are not as amenable to simple computation.

The formulae for the expectation of the sums of squares appear in *Tables 2 and 3*. These coefficients were derived by procedures outlined by Anderson and Bancroft (1952) for the sums of squares of the diallel using the above model. The estimation is complicated by the involved expectations of the general combining ability, specific combining ability, and maternal effects. The estimates of the variance components are given in *Table 4* for the analyses performed at each location separately, and for all locations combined.

The genetic interpretation of the variance components is most clearly explained if general combining ability is iden-

Table 2. — Expectations of sums of squares for within-location analyses.

Sum of squares due to:	Expectation coefficients for variance components					
	μ^2	$\sigma^2_{r(l)}$	σ^2_g	σ^2_s	σ^2_m	σ^2_l
General mean	183	61	27.344	13	18.098	11
Replications	183	183	27.344	13	18.098	13
General combining ability	366	122	366	63	146.196	21
Specific combining ability	183	61	366	183	366	61
Maternal effects	95.196	31.732	95.196	39	315	13
Plot error	183	183	366	183	366	183

Table 3. — Expectations of sums of squares for the combined analysis.

Sums of squares due to:	Expectation coefficients for variance components									
	μ^2	σ^2_l	$\sigma^2_{r/l}$	σ^2_g	σ^2_s	σ^2_m	σ^2_{lg}	σ^2_{ls}	σ^2_{lm}	σ^2_l
General mean	549	183	61	82.033	9	54.295	27.344	3	18.098	1
Locations (L)	549	549	183	82.033	9	54.295	82.033	9	54.295	3
Replications in locations	549	549	549	82.033	9	54.295	82.033	9	54.295	9
General combining ability (GCA)	1,098	366	122	1,098	189	438.588	366	63	146.196	21
Specific combining ability (SCA)	549	183	61	1,098	549	1,098	366	183	366	61
Maternal effects (M)	285.588	95.196	31.732	285.588	117	945	95.196	39	315	13
L × GCA	1,098	1,098	366	1,098	189	438.588	1,098	189	438.588	63
L × SCA	549	549	183	1,098	549	1,098	1,098	1,549	1,098	183
L × M	285.588	285.588	95.196	285.588	117	945	285.588	117	945	63
Plot error	549	549	549	1,098	549	1,098	1,098	549	1,098	549

Table 4. — Estimates of variance components (× 10,000).

Item	σ^2_g	σ^2_s	σ^2_m	σ^2_{lg}	σ^2_{ls}	σ^2_{lm}	σ^2_e	σ^2_w
Fernwood	0.597	—17.496	8.409				29.111	70 47
Elk River	3.262	—7.097	5.036				32.018	87.24
Randolph Creek	.752	1.702	—1.081				10.558	23.53
Average within location	1.537	—7.630	4.121				23.895	60.41
Combined analysis	1.419	—6.728	3.642	.117	.682	—0.400	23.895	61.12

tified with a half-sib covariance, specific combining ability with the covariance of full sibs minus twice the covariance of half-sibs, and the error term with environmental effects between plants within plots. Then, assuming that epistatic effects are of minor concern and that the parents and progenies are not inbred, the general combining ability can be identified with one-quarter of the additive genetic variance ($\frac{1}{4}\sigma^2_A$), and the specific combining ability variance can be identified with one-quarter of dominance genetic variance ($\frac{1}{4}\sigma^2_D$). Similarly, the location by general combining ability component can be identified with one-quarter of the additive by location interaction and the location by specific combining ability component can be identified with one-quarter of the dominance by environment interaction. Thus, heritability based on young *individual* trees can be calculated as follows:

$$h^2 = \frac{4\sigma^2_g}{\sigma^2_w + \sigma^2_e + \sigma^2_s + 2\,\sigma^2_g + \sigma^2_m} \text{ within locations and}$$

$$h^2 = \frac{4\sigma^2_g}{\sigma^2_w + \sigma^2_e + \sigma^2_s + 2\,\sigma^2_g + \sigma^2_m + \sigma^2_{ls} + 2\,\sigma^2_{lg} + \sigma^2_{lm}}$$

between locations, where the within plot variance is designated as: σ^2_w = environmental variation between plants within plots + genetic variance between full-sibs. Estimated from random plots in each cross in each replication and pooled.

Heritabilities computed from the estimates of variance components listed in *Table 4* are shown below.

	h^2
Fernwood	2.6
Elk River	10.5
Randolph Creek	8.3
Average	7.3
Combined	6.6

The above data show that the heritabilities are roughly equivalent and they indicate very low environmental interactions in height growth for these progenies. The average heritability pooled within locations is only slightly larger than the heritability when taken over all locations; this suggests that results from a limited number of locations can be extrapolated to many locations. However, one must take into account the unique conditions under which the plants were grown.

Parent-Offspring Covariance

The data available on growth rates of parent trees provide information on the correlation between juvenile and mature growth rates. In this and similar studies involving measurements on mature parent trees and their juvenile offspring, the usual correlation, regression, and covariance statistics apply to two distinct characters (Sakai, 1957). That is, there is a certain degree of independence between the characters of an individual tree when young in contrast to when mature. This independence is measurable by the nonperfect correlation between the juvenile and mature traits. Thus, the effectiveness of selection in the juvenile stages for mature character gain is diminished by the departure of this correlation from unity.

The covariances obtained in this study were between midparent (average PAG of the two parents mated) and progeny means, between male parents within females and their progeny means, and between female parents within males and their progeny means. These covariances are listed in *Table 5* for each location and for a combined analysis. The covariance between midparent and progeny means and the covariance between single parents and their progeny means estimates one-half of this additive covariance between juvenile and mature traits. These covariances are analogous to the additive genetic variance except that cross-products instead of sums of squares are used.

In applying the first method, we decided to group the progenies in such manner that no parent was used more than once as a mating partner within any one group, in order to avoid possible biases. Sixty crosses were thus made

Table 5. — Estimates of the additive covariance between juvenile and mature height growth.

Data source	Fern-wood	Elk River	Ran-dolph Creek	Aver-age	Com-bined analy-sis
Midparent	.0024	.0088	—.0004	.0036	.0042
Within males	.0048	.0072	.0026	.0048	.0049
Within females	.0090	.0128	.0020	.0080	.0074

in 12 groups, with five crosses per group. Covariances on progeny means were then run on midparent PAG's within groups and within plantations and, finally, on plantation averages.

We found that the covariances varied greatly among groups of progenies, among plantations, and among methods of computation. Much of this was probably due to small sizes of samples. The average additive covariance from all of the estimates is taken to be .0052. Its utility is discussed below in estimating genetic gains.

Estimates of Genetic Gains

Genetic gain (ΔG), or response to selection, from a generation of mass selection can be estimated from the formula $\Delta G = h^2S$, in which h^2 is heritability and S is the selection differential — or the difference between the mean of the selected population and the mean of the whole population (Falconer 1960, p. 189). Thus, for example, if a group of trees growing at the rate of 3 feet per year is selected from a population averaging 2 feet per year, and heritability is 20 percent, the selection differential is 1 foot and expected gain is .2 foot. That is, progenies produced by controlled pollinations among the selected trees theoretically would grow 2.2 feet per year.

The selection differential can be expressed in terms of standard deviations instead of actual units and is then called the "intensity of selection" (i). Thus, $i = \frac{S}{\sigma_p}$, in which σ_p is the phenotypic standard deviation. The formula for response then becomes

$$\Delta G = i\sigma_p h^2.$$

This response formula is useful when one does not know the selection differential but wishes to estimate response resulting from selecting ("saving") various proportions of the population. Assuming a normal population, one can obtain theoretical values of i for various percentages of the population to be saved (Lush, 1945, p. 148; and Falconer, 1960, p. 193). Thus, for example, if one plans to select 1 percent of a population, *i* is 2.67 standard deviations and the estimated gain for heritability of 20 percent is (2.67) σ_p (.20) = .53 standard deviation.

Statistics obtained in the present study will be used to estimate genetic gain for various types of tree improvement schemes. Estimates apply only to populations as prescribed in this study. It is assumed that the expected amount of additive genetic variance in the parents is relatively the same as that found in the progenies — in other words, that the heritability estimates computed apply to variation at advanced ages as well as at the juvenile stage.

The following population statistics are to be used:

h^2 = heritability = 7 percent

$\bar{p}$ = average PAG of parent trees = 2.10 feet

$\bar{x}$ = average growth of progenies = .239 foot

σ_p = estimated phenotypic standard deviation of parent trees = .82 foot.

This estimate was obtained as follows:

$$\sigma_p = \frac{\bar{p}}{\bar{x}}\left(\sqrt{\sigma_T^2}\right) = \frac{2.10}{.239}\left(\sqrt{.0088}\right),$$

in which σ_T^2 is equal to the denominator for h^2 (combined analysis) plus a small additional component, .0003, due to replications within location. It is preferred over the actual $\sigma_p = .40$, which is based on deviations from local averages.

σ_A = square root of additive genetic variance in terms of parental values = .21, estimated as follows:

$$\sigma_A = \frac{\bar{p}}{\bar{x}}\left(\sqrt{4\sigma_g^2}\right) = \frac{2.10}{.239}\left(\sqrt{4(.0001419)}\right)$$

Estimated gains from five types of tree improvement schemes follow.

1. Phenotypic selection of mother trees with no control over pollination (collection of wind-pollinated seed from selections in a forest).

Since there is no selection of pollen parents here, genetic gain will be half of that expected when pollination is controlled. The amount of gain will depend upon the intensity of selection. For example, if the best 1 percent of trees are selected ($i = 2.67$), the expected gain, $\Delta G = \frac{1}{2}(i\sigma_p h^2) = \frac{1}{2}(2.67)(.82)(.07) = .08$ foot. Expressed as a percent of the mean, the gain is $\frac{.08}{2.10} = 3.8$ percent.

2. Establishment of seed-production areas.

Here selection is practiced among both seed and pollen parents by providing isolation of the selections. Expected gain need not be halved as in *type 1*. Gain again depends upon the intensity of selection. If 10 percent ($i = 1.75$) of the trees are saved, $\Delta G = i\sigma_p h^2 = (1.75)(.82)(.07) = .10$ foot, or about 4.8 percent of the mean of the original population.

3. Phenotypic selection and establishment of clonal orchards without progeny testing.

This is similar to establishment of seed-production areas except that it enables a much higher intensity of selection. For a selection intensity of 1 in 100, gain would be 2.67 (.82) (.07) = .15 foot or 7.1 percent of the mean.

4. Phenotypic selection, progeny testing (genotypic selection), and establishment of orchards with clones of the parents proved to have general combining ability.

Here gain is expected not only from the original phenotypic selection in the parental population but also from genotypic selection based upon performance of progenies. The additional gain to be obtained from the progeny testing will depend upon what proportion of the originally selected trees is retained for the orchards. As an example, a situation representing the same overall selection intensity as in *type 3* will be chosen. If one selects phenotypically 1 in 20 ($i = 2.06$), and then 1 in 5 ($i = 1.40$) after progeny testing, the overall intensity would be 1 in 100 as before. Gain from phenotypic selection would be $i\sigma_p h^2 = (2.06)(.82)(.07) = .12$ or 5.7 percent of the mean.

Computation of additional gain from progeny (family) selection is complicated by the fact that heritability changes when one switches from mass selection to selection on a basis of replicated tests. Assume that progeny are tested at 3 locations with 3 replications, 7 trees per plot, and with, say, 5 top cross or tester parents. In such a case, if additive genetic variance remains constant, the heritability or regression of true parental value on mature progeny estimated value can be formulated as follows:

$$h^2 \text{ or } b = \frac{\text{Covariance (parental value and progeny measure)}}{\text{Variance of that progeny measurement}}$$

Assuming that measurements were made within blocks or that we adjusted for block differences:

$$h^2 \text{ or } b = \frac{\rho \sigma_A^2}{\frac{\sigma_w^2}{lrw} + \frac{\sigma_e^2}{lr} + \frac{\sigma_{ls}^2}{ls} + \frac{\sigma_{lm}^2}{l} + \frac{\sigma_{lg}^2}{l} + \frac{\sigma_s^2}{s} + \sigma_m^2 + \sigma_g^2}$$

where ρ = genetic correlation coefficient between the predicted individual (parent) and its predictor (progeny) = 1/2, in this case.

$\sigma_A^2 = 4\ \sigma_g^2$

s = number of crosses made to each parent = 5

r = number of replications/locations = 3

l = number of locations = 3

w = number of plants per plot = 7

Using the previously obtained estimates of the components for the combined analysis *(Table 4):*

$h^2 = .39$

and

$\sigma_{\bar{p}}$ adjusted to mature sizes $= \frac{2.10}{.239}\left(\sqrt{.000729}\right) = .237.$

Then,

$\Delta G = i\sigma_{\bar{p}}\, h^2 = (1.40)\ (.237)\ (.39) = .13$ foot or 6.2 percent.

Total gain would then be 6.2 percent plus the 5.7 percent for phenotypic selection in the parents, equaling 11.9 percent. This compares with the expected gain of 7.1 percent for phenotypic selection alone at the same overall intensity *(type 3* above). (Under actual practice one should, of course, use both the phenotypic and the progeny evaluations in making the final selections. This would complicate computations, but the likelihood of increasing gains further thereby should be recognized.)

The above computations assume that the progenies were mature at time of evaluation. If, on the other hand, the progenies are evaluated at the juvenile stage, the expected gain would be somewhat diminished, as indicated by the following analysis. The combination 1/20 phenotypic selection and 1/5 progeny selection is used again for an example.

ΔG = (Response to selection for juvenile growth) × (regression of mature genetic value on juvenile genetic value)

where this regression $= \frac{\sigma_{A_jA_m}}{\sigma_{A_j}^2} = r_{A_jA_m}\frac{\sigma_{A_m}}{\sigma_{A_j}}$

where A_m and A_j denote the additive genetic value of the mature and juvenile traits, respectively, and where response to selection for juvenile growth is:

$i\rho\frac{\sigma_{A_j}^2}{\sigma_{\bar{p}_j}}$, where $\sigma_{\bar{p}_j}^2$ = variance of the juvenile progeny means.

$$\text{Then, } \Delta G = i\rho\frac{\sigma_{A_j}^2}{\sigma_{\bar{p}_j}}\, r_{A_jA_m}\frac{\sigma_{A_m}}{\sigma_{A_j}}$$

$$= i\rho\frac{\sigma_{A_j}}{\sigma_{\bar{p}_j}}\, r_{A_jA_m}\,\sigma_{A_m}$$

$$= i\rho\frac{\sigma_{A_jA_m}}{\sigma_{\bar{p}_j}} \text{ analogous to } i\rho\frac{\sigma_A^2}{\sigma_{\bar{p}}}$$

Using the covariance estimate previously obtained for

$\sigma_{A_jA_m} = .0052$, and $\sigma_{\bar{p}_j} = \sqrt{.000729} = .027$,

$\Delta G = 1.40\ (1/2)\ \frac{(.0052)}{.027} = .13$ foot or 6.2 percent.

Total gain, then, would be 5.7 + 6.2 = 11.9 percent. Thus, it is apparent that, even if progenies are evaluated on the basis of juvenile performance, progeny testing results in gains appreciably greater than that obtained under phenotypic selection alone (7.1 percent), as obtained under *type 3* above.

5. Phenotypic selection in the original parental population, progeny testing, phenotypic selection within selected F_1 progenies, and establishment of clonal orchards.

Here clonal orchards would be established from F_1 individuals instead of from original parents; and seed collected for commercial planting would be F_2 seed.

Computation of gain here is difficult. Presumably if one cloned the "average" individuals in the selected progenies, the attainable gain would be approximately equivalent to that in *type 4.* By phenotypically selecting the best individuals within those families, an additional gain theoretically would be obtained. However, this additional gain is difficult to estimate and would depend upon the size and numbers of families tested, the amount of variance within them, and possibly other factors.

Discussion

Estimates of genetic gains computed for various types of tree improvement program shows that appreciable improvement in growth rate of western white pine is possible, even though heritability was found to be low. The percent improvement in growth rate could very well be less than the actual percent increase in economic value. However, it should be emphasized that the progenies were grown under rather unusual conditions and that under these conditions genetic gain by environment interaction was not great. Plantings under more nearly natural conditions may show greater interactions, with an attendant loss in genetic gain or a need for development of strains suitable for different environments.

For a given intensity of selection, selection of trees in the original population on the basis of progeny tests alone (that is, progeny testing of random members of the population and selection on the basis of tests) is more effective than phenotypic selection alone. For example, a progeny test of the type assumed earlier (3 locations, 3 replications, 7-tree plots, and 5 tester parents) and a selection intensity of 1/100 gives 11.8 percent gain. Phenotypic selection alone, with an intensity of 1/100 gives a gain of 7.1 percent. Thus, under the conditions assumed, "progeny selection" is more than half again as effective as phenotypic selection. Progeny selection can, of course, be made even more effective by manipulation of the progeny test design. For example, if the number of replications and the size of plots are doubled, heritability applicable to progeny selection would be 52 percent instead of 39 percent, with an attendant increase in expected gain.

However, in choosing a breeding method only the relative costs of progeny testing vs. phenotypic selection must be considered. Phenotypic selection is usually much cheaper than progeny testing, and high intensities of selection may be feasible. This suggests using some combination of the two techniques; then the problem becomes one of selecting the most profitable combination. For example, one might select very intensively and progeny test only, say, twice as many trees as would be required for the orchards. On the other hand, he might "lower his sights" a little and select 10 times as many as would be required for the orchard and progeny test. The latter procedure would give a little more gain. But would the increased gain resulting from expending more effort on progeny testing justify the additional work? To answer this question the breeder needs to consider such other factors as relative costs, availability of selection material, and others. Expected gain, important as it is, is only one factor.

Summary

Materials consisted of 61 4-year-old full-sib progenies produced from somewhat random matings among 21 parents. Progenies were grown at each of three localities in randomized blocks, using row plots and three replications. Parental data consisted of average height growth during the last 10 years, adjusted for differences in age, and local site conditions. Progeny data used was fourth-year height increment.

Narrow sense heritabilities, computed separately for each locality, averaged about 7 percent. For the combined analysis, they were only slightly less, indicating low environmental interaction in these data.

Expected genetic gains were computed for several hypothetical breeding programs by using statistics obtained from the experimental data. Results showed that appreciable genetic gains are possible in spite of the low heritability. Although other factors, not studied here, need to be considered in planning a breeding program, the results reported here suggest desirability of using a combination of phenotypic selection and progeny testing.

Literature Cited

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Einige Ergebnisse von Testanbauten mit Aspenhybriden

2. Kreuzungen der Jahre 1953 und 1958

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(Eingegangen am 1. 2. 1966)

Einleitung

Wie die im Teil 1 dieses Berichtes beschriebenen Versuche (Melchior und Seitz 1966) verfolgten auch die Kreuzungsarbeiten von J. Grehn im Jahre 1953 und die von F. W. Seitz im Jahre 1958 den Zweck, eine erste Orientierung über das Verhalten verschiedener Arthybriden in der Sektion *Leuce* zu erhalten und einen näherungsweisen Vergleich von reinen Aspen, Hybridaspen und Graupappeln zu führen. Entsprechend den Schwierigkeiten bei der Durchführung kompletter Kreuzungsexperimente mit den erwähnten Baumarten (Probleme der Kreuzung und der Pflanzenanzucht) als auch infolge Schwierigkeiten bei der Werbung von Blühreisern lieferten diese Kreuzungsversuche kein Material, das heutigen Anforderungen an die Züchtungsmethodik in allen Punkten entsprechen könnte. Nur an einem Teil der Sorten konnten methodische Fragen bearbeitet werden. Im Gegensatz zu den Feldversuchen mit den Nachkommenschaften aus dem Jahre 1951 enthalten die in den späteren Jahren angelegten Versuche Wiederholungen (Anlage in vollständigen Blocks oder Zweisatzgittern, die hier wie vollständige zufällige Blocks behandelt werden), wodurch die Auswertung kleiner im Material enthaltener dialleler Kreuzungen möglich wurde; ferner erlaubte in einigen Fällen der Anbau gleicher Nachkommenschaften auf mehreren Versuchsorten eine Einschätzung der eingetretenen Interaktionen zwischen Sorten und Anbauorten. Für die Methodik der Anlage und der Messung von Nachkommenschaftsprüfungen mögen schließlich Untersuchungen der Korrelationen der erhobenen Merkmale einige Bedeutung haben.

Jedoch — und die Wiedergabe dieser Ergebnisse wird hier als weitaus wichtiger erachtet — ergab sich aus den Experimenten eine gewisse Sortenmannigfaltigkeit, die auf den Versuchsflächen konserviert werden konnte und die zukünftig praktischen Zwecken nutzbar gemacht wird. Sie liefert bereits heute Ausgangsmaterial für die praxisnahe Erprobung von Klonen. Hierfür vorhandene Gegebenheiten, die den eigentlichen Wert der Testanbauten ausmachen, werden im letzten Abschnitt dieses Berichts beschrieben.

Material und Methoden

Jeweils zwei Vegetationsperioden nach der Saat wurden die Versuchspflanzen in quadratischen Parzellen zu je 9 im Verband 2 × 2 m oder 2,5 × 2,5 m ausgebracht (Lochpflanzung). Von den Feldversuchen mit den Kreuzungen aus dem Jahre 1953 wurden hier die Flächen As 9, 11 und 12 ausgewertet, von den Versuchen mit Nachkommenschaften aus dem Jahre 1958 die Flächen As 25 und 26.

As 9 im Bereich des Staatlichen Forstamts Syke bei Bremen (Höhenlage ca. 30 m, 9° ö. L., 53° n. Br.) stockt auf sandigem Lehm (Braunerde) mit guter Versorgung mit kalkhaltigem Grundwasser; dieser Versuch enthält 25 Sorten. As 11 im Bereich des Staatlichen Forstamts Trittau in Schleswig-Holstein enthält 16 Sorten, der Standort ist dort stark anmoorig mit Unterlagerung durch Fließsand; die Seehöhe beträgt etwa 20 m, die geographische Lage ist etwa 10° ö. L., 54° n. Br. Es mag interessieren, daß der unmittelbare Nachbarbestand auf dem gleichen Standortstyp aus etwa gleichaltriger *Populus × euramericana* cv. *'Regenerata Harff'* im Absterben begriffen ist. As 12 im Fürstl. Ysenburg'schen Forstamt Wächtersbach bei Frankfurt a. M. mit 35 verschiedenen Sorten wurde im Jahre nach der Pflanzung etwas durch Mäusefraß geschädigt, der teilweise

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