Estimates of the Heritability of Height Growth in Western White Pine Based on Parent-Progeny Relationships

By R. J. Steinhoff and R. J. Hoff[1]

Introduction

The long period of time required to produce a crop of merchantable trees imposes many restrictions on the planning and execution of tree improvement programs. A major area of concern is the reliability of heritability estimates based on juvenile materials. If these estimates are less than the true value, one might either abandon efforts to improve a given trait or begin an overly complex selection-and-testing program to achieve a desirable gain. Conversely, if the estimates are inflated, a given breeding program will yield less than the expected gain.

Frey and Horner (1957) have cautioned that heritability estimates obtained from regression analyses of some characteristics can fluctuate greatly if the parents and progeny are grown under different environmental conditions which may influence relative yields (scale effects). It appears that an analogous situation occurs in evaluating height growth in trees. It is desirable to get early estimates of the heritability of height growth. These estimates may be obtained through parent-offspring regression, but one complicating feature is that the growth rate of the progenies is much less than that of the parents. Because of this complication, the upper limit for the heritability estimate probably will be considerably less than 1.0. Conversely, if the progeny either produce greater yield or grow at a faster rate than the parents, the limit for the heritability estimate may be greater than 1.0 (Frey and Horner 1957); these authors recommended coding the data in terms of standard deviation units to compensate for such differences between the parents and progeny. Such a procedure yields a regression coefficient identical to the correlation coefficient which is based on the original data (Frey and Horner 1957).

Some workers believe that the differences between a trait measured on young progeny and the same trait measured on mature parents may be of such magnitude that it would be better to consider these traits as separate ones (Stonecypher 1966; Squillace, A. E., personal communication). If that should be the case, analysis by correlation techniques may be more appropriate than analysis by regression techniques. In originally proposing methods for calculating heritability estimates by relating progeny values to female parent values within sire groups (intra-sire correlations or regressions of offspring on dam), Lush (1940) stated that correlation and regression could be interchanged if the dams were an unselected group.

In this paper we will present information on changes in heritability estimates of tree height growth that have occurred as progeny growth rate increased during two periods. During the first period the progeny grew at a rate approximately one-third that of the parents while in the second period they grew at a rate two-thirds that of the parents. We will also compare estimates obtained by regression and correlation techniques.

Materials and Methods

During the course of work at this Station to produce western white pine resistant to blister rust, periodic growth measurements have been recorded for a number of progenies of known parents. Since there are many independent resistant factors within western white pine, the parent trees can probably be considered as random members of the rust resistant population with regard to height growth. The progeny were artificially inoculated with blister rust fungus in the nursery and naturally inoculated in field transplant beds. After natural inoculation the survivors were transplanted to an arboretum in Moscow, Idaho, for future breeding efforts.

A paper by Squillace, Bingham, Namkoong and Robinson (1967) used data taken when the seedlings were 4 years old and still located in three widely separated field plantings. In the present report we have used data for two periods of growth in the arboretum. The progeny were first measured in 1963 when they ranged in age from 9 to 12 years. We subjectively rated them for year of recovery from transplanting shock and included only those which showed at least 3 years of growth following recovery. On some of the trees as many as 5 years growth were included. The second period covers the 4 years from 1964 through 1967. These data represent the periodic annual growth (PAG) computed by measuring the total amount of growth during the observation period divided by the number of years in the period.

The parents were measured in 1953 for another study (Squillace and Bingham 1954) and the PAG values computed for the 10-year period 1943 to 1952. The PAG values so obtained were further adjusted for age and site differences by Squillace, Bingham, Namkoong and Robinson (1967). These adjusted PAG values were used as the independent variables in the present analyses.

The study included 19 trees used as parents to produce the 60 progenies indicated in *Table* 1. The number of offspring per cross ranged from 1 to 10 and averaged 3.9. The average for all the offspring of a cross was the value used in the computations.

Regression and correlation coefficients between the parental and progeny PAG values for the two growth periods were calculated with the data grouped in the following five ways:

1. Progeny on female parents without regard to male parent;

2. Progeny on female parents mated to a common male (intra-sire regression or correlation);

3. Progeny on male parents without regard to female parent;

4. Progeny on male parents mated to a common female (intra-dam regression or correlation);

5. Progeny on midparent, i. e., the average of male and female values.

Regression and correlation coefficients were calculated using standard statistical procedures. Intrasire and intra-dam calculations followed the procedures of Becker (1967, pages 64—68). Heritability estimates were obtained by doubling the correlation or regression coefficients based on single parent values or by using the midparent coefficients directly.

Results and Discussion

The heritability estimates we obtained for the two periods of growth with the various parent-progeny groupings are presented in *Table 2*. The data of *Table 2* form

[1] Research Geneticists, USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah 84401; stationed in Moscow, Idaho, at Forestry Sciences Laboratory, maintained in cooperation with the University of Idaho.

Table 1. — Average periodic annual height growth (PAG) of progenies and parents used in the heritability analyses.

Female parent	Progenies Periodic Annual Growth — Male parent														Ave.	Female parent PAG
	1	10	16	17	18	21	22	24	25	29	30	58	59	65		
									Feet							
15					0.69')				0.82		0.66		0.43		0.65	2.62
					1.64				1.38		.95		1.12		1.27	
16				0.66					.92		.66				.75	1.69
				1.41					1.48		1.57				1.49	
17									.85		.72		.72		.76	2.99
									1.54		1.38		1.64		1.52	
19	0.69	0.72	0.69	0.75	.85	.72	0.62	0.66	.49	0.75	.98	0.69	.66	0.88	.72	1.60
	1.48	1.34	.98	1.64	1.38	1.02	1.34	1.15	.75	.75	1.74	1.38	.88	.95	1.20	
20		.56	.66			.56	.66	.69	.72			.62		.56	.63	1.75
		1.44	1.12			1.05	1.31	.85	.95			1.38		1.21	1.16	
22	.62			.75	.69				.72	.33	.75		.36		.60	1.84
	1.41			1.80	1.15				1.67	.56	1.41		.72		1.25	
25		.56			.75						.69		.92		.73	1.89
		1.02			1.08						1.25		1.64		1.25	
37	.46			.82					.82						.70	1.84
	1.12			1.67					1.57						1.45	
58			.95	.98	.79	.56	.85	.66	.82	.79	.79			.72	.79	2.62
			1.41	1.67	1.56	1.12	1.74	1.37	1.61	1.21	1.41			1.21	1.43	
62	.85		.49			.89						.95			.80	2.16
	1.38		1.34			1.05						1.61			1.34	
Ave.	.66	.61	.70	.82	.75	.68	.71	.67	.77	.62	.75	.75	.62	.72	.71	
	1.35	1.27	1.21	1.70	1.36	1.13	1.46	1.12	1.37	0.84	1.39	1.46	1.20	1.12	1.30	
Male parent PAG	2.42	2.44	1.69	2.99	2.23	1.75	1.84	2.71	1.89	1.75	2.13	2.62	1.97	2.26		

') Upper value in the pair refers to the period from 1959 to 1963.
Lower value in the pair refers to the period from 1964 to 1967.

the basis for several interesting comparisons. First, the estimates based on correlation coefficients are usually larger than those based on regression coefficients. Second, while the estimates based on regressions doubled, or more than doubled, from the first period to the second (average from 0.14 to 0.36) the estimates based on correlations increased only slightly (average from 0.42 to 0.49). Third, it made little difference in the estimates based on the female parent-offspring relationship whether the females were grouped within males or left ungrouped; but grouping substantially increased the estimates based on the male parent relationship.

The correlation coefficients are larger than the regression coefficients because the variance of the parental measurements is larger, for both periods, than the variance of the progeny measurements. Therefore, dividing the covariance of the two measurements by the larger (parental) variance (i. e., for regression) will yield a smaller value than dividing by the geometric mean of the variances to obtain the correlation coefficient. However, inclusion of the progeny variance in the denominator also tends to cancel the scaling effects; so use of the correlation coefficient should yield more precise and more consistent results.

The increase in the estimates based on regression coefficients from one period to the next is primarily the result of the increased growth rate of the progeny. The periodic annual growth approximately doubled from the

Table 2. — Estimates of the heritability of periodic annual height growth for western white pine.

Progeny-parent relationship	Heritability equations	Periods of progeny growth	
		1959—1963	1964—1967
		Heritability estimates	
Progeny and female parent — ungrouped	$h^2 = 2b$	0.13 ± 0.16	0.22 ± 0.36
	$h^2 = 2r$	.42[1])	0.32
Progeny and females within males	$h^2 = 2b$	$.13 \pm .09$	$.23 \pm .16$
	$h^2 = 2r$	.43	.41
Progeny and male parent — ungrouped	$h^2 = 2b$	$.11 \pm .20$	$.45 \pm .42$
	$h^2 = 2r$	.28	.53
Progeny and males within females	$h^2 = 2b$	$.21 \pm .08$	$.57 \pm .16$
	$h^2 = 2r$	.72	.89
Progeny and midparent	$h^2 = b$	$.14 \pm .13$	$.35 \pm .28$
	$h^2 = r$	.27	.31
Means	$h^2 = 2b$ or b	.14	.36
	$h^2 = 2r$ or r	.42	.49
Grand mean		.28	.43

[1]) Standard errors for correlation coefficients are not symmetrical but approximate ± 0.24 or 0.48 for r and 2r respectively for most of the values presented here.

first period to the second and resulted in an almost three-fold increase in the covariance. Since the same parental measurements were used for both growth periods, the increase in covariance leads to a direct increase in the regression coefficients. On the other hand, the correlation coefficients increased only slightly because the variance of the progeny measurements increased nearly in proportion to the increase in the measurements themselves and the resulting covariance. The estimate of the correlation coefficient would also increase if the variances were to decrease while the covariance remained constant.

Grouping of the females within males or males within females gave variable results probably because of the small numbers of crosses involved. The same is very likely true for much of the overall variation in the estimates.

Although the heritability estimates based on correlation coefficients should be more precise than those based on regression coefficients where scaling effects are present, we decided to use the mean of the various estimates to calculate the predicted response to selection in a breeding program because all of the estimates have large standard errors due to the low numbers of parent-offspring groups represented.

The common formula for response to selection (R) is:

$$R = i \times \sigma_p \times h^2$$

where

i = Selection intensity in standard deviation units,

σ_p = Phenotypic standard deviation of the population in which selection is practiced,

h^2 = Heritability (Falconer 1960, page 231).

If selection intensity is restricted to the parents used in this study, it would have to be very low to avoid inbreeding losses in future generations. Also, to have a reasonable number of progeny for comparison of predicted and actual response, we needed to retain a large portion of the parents because only a few of the possible crosses have been made *(Table 1)*. For example, only 3 crosses have been made among the top 7 parents and only 10 among the top 10 parents. For these reasons we chose to retain the top 10 of the 19 parents for use in the following calculations. This gives a selection intensity of 0.726 standard deviation units (Becker 1967, *Table 2*). The standard deviation of the parental measurement was 0.426 foot. The mean heritability estimates as shown in *Table 2* are 0.28 for the period from 1959 to 1963 and 0.43 for 1964 to 1967. Substitution of these values in the selection response formula yields the following results:

For 1959 to 1963: R = 0.726 × 0.426 foot × 0.28 = 0.09 foot.
For 1964 to 1967: R = 0.726 × 0.426 foot × 0.43 = 0.13 foot.
For comparative purposes we found the mean value for the progenies of crosses among the 10 selected parents for each period and substracted the mean for all progenies for the period from each. The mean actual increase for the 1959 to 1963 period was 0.07 foot compared to the predicted value of 0.09 foot. For the 1964 to 1967 period the actual increase was 0.12 foot compared to the predicted value of 0.13 foot. These increases are approximately 10 percent

of the mean for each period. Again, these results should be viewed with caution since only a small portion of the possible crosses among the 10 selected parents are represented. However, the close agreement between predicted and actual values is encouraging.

These heritability values are considerably above most of the published estimates for height growth in trees. Squillace, Bingham, Namkoong and Robinson (1967) measured many of the same seedlings included in this report at 4 years of age and computed an average heritability of 0.07 on the basis of an analysis of variance. In summarizing the work in several species for predicting progress in a Douglas-fir breeding program, Campbell (1964) settled on a heritability of 0.10 for periodic height growth as a figure which could likely be attained.

The heritability estimates based on regression coefficients presented here may be higher than would be obtained in regular field plantings if conditions in the irrigated arboretum allowed more growth than would occur in the field. The estimates based on correlation coefficients, however, should be little affected unless the families respond differentially to the arboretum and field environments. It would be desirable to take similar measurements in other environmental conditions, preferably in a test where heritability estimates could also be obtained through analysis of variance procedures.

Summary

Heritability estimates for periodic annual height growth were computed from regression and correlation coefficients of progeny growth on male parent, female parent, and mid-parent. The average for the various estimates increased by 1-½ times as the growth rate of the progenies approximately doubled. It appears that most of the increase in the estimates is due to the scaling effect of the increased growth rather than to shifts among the individual progenies. Actual growth increases calculated for a hypothetical selection and breeding program compared closely to predicted values.

Literature Cited

Becker, W. A.: Manual of procedures in quantitative genetics. Second Edition. The Program in Genetics, Wash. State Univ., Pullman, 130 + XI p. (1967). — Campbell, R. K.: Recommended traits to be improved in a breeding program for Douglas fir. Weyerhaeuser Co. Forestry Res. Note No. 57, 19 p. (1964). — Falconer, D. A.: Introduction to quantitative genetics. The Ronald Press Co., New York, 365 + IX p. (1960). — Frey, K. J., and T. Horner: Heritability in standard units. Agron. J. 49: 59—62 (1957). — Lush, J. L.: Intra-sire correlations or regressions of offspring on dam as a method of estimating heritability of characteristics. Proc. Amer. Soc. Animal Production 33: 293—301 (1940). — Squillace, A. E., and R. T. Bingham: Breeding for improved growth rate and timber quality in western white pine. J. Forest. 52: 956—961 (1954). — Squillace, A. E., R. T. Bingham, Gene Namkoong, and H. F. Robinson: Heritability of juvenile growth rate and expected gain from selection in western white pine. Silvae Genet. 16: 1—6 (1967). — Stonecypher, R. W.: The loblolly pine heritability study. International Paper Co., Southlands Exp. Forest Tech. Bull. No. 5, XIV + 128 p. (1966).