INHERITANCE OF GUM YIELD AND OTHER CHARACTERISTICS OF SLASH PINE

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The extensive amount of forest genetics and tree improvement work in the South requires that we learn something of the heritability of traits with which we are working. Admittedly, heritability estimates are beset with certain assumptions and the application of specific estimates is necessarily severely restricted. In spite of this, we need them to provide some sort of estimate of expected gains from our efforts and to help guide future programs.

Highly accurage estimates of heritability require extensive data and usually it is preferable to design experiments specifically for studying it. Unfortunately, few experiments in forest genetics have been set up specifically for this purpose. Where they have been, it will be some time before reliable data encompassing an appreciable portion of rotation age will become available. Meanwhile, we will have to make use of studies originally established for other purposes.

This report presents preliminary estimates of heritability for several economically important traits of slash pine. They are considered preliminary because the progeny trees are not yet mature, relatively few parent trees are involved, and finally, because the experiments involved were not designed specifically for estimating heritability. However, the study includes observations from what is believed to be the oldest progeny test in the country that involves an appreciable number of individual tree crosses, and we believe the results will be useful.

PROCEDURE

The heritability estimates presented here are based upon three plantations described below.

1. Progeny plantation 0-116. --This plantation was established from 1-year-old seedlings in June 1946. The parents of the trees had been selected for either

high, average, or low gum yielding ability. Both wind- and cross-pollinated progenies were included. The plot layout consisted of seven blocks, each containing from 2 to 6 individuals per progeny randomly positioned in each block. Spacing was 20 x 20 feet.

2. Progeny plantation 0-146. --This plantation was established from 1-year-old seedlings in January-February 1951. The parents had been selected for high or average gum yielding ability and both wind- and control-pollinated progenies were represented. The plot layout consisted of four randomized blocks. In these blocks the cross-pollinated progenies were represented by row plots of from 15 to 18 trees each and the wind-pollinated progenies were represented by row plots of 2 to 7 each. Spacing was 12 x 18 feet.

3. Clonal plantation 0-132.--This plantation was established from rooted cuttings which were planted at various times between 1945 and 1947. The cuttings had been taken from trees selected for high, average, or low gum yielding ability. The plantation contains from 2 to 8 trees from each clone, not arranged in any type of design. Spacing was 20 x 20 feet.

Gum yields were measured by a microchipping technique in progeny plantation 0-116 in the summer of 1956. Under this technique the flow of gum is measured from 1-inch--square punch wounds over a relatively small part of a season (Ostrom and True, 1946). It seems to be fairly satisfactory as a measure of relative yield capacity. Yields in clonal plantation 0-132 were measured in the summer of 1960. Progeny plantation 0-146 has not yet been tapped for gum, because the trees are a little undersize for that purpose.

Diameters, total heights, branch lengths, and bark thickness were measured in the late fall of 1959 or winter of 1959-1960. Average branch length was measured at a point 12 feet from the top of the tree. Bark thickness was measured at Breast height at 4 points uniformly spaced around the stem of the tree and averaged.

The statistical procedures used in estimating heritability were patterned largely after those employed by Robinson et al. (1949) and Falconer (1960). Time will not permit a full discussion of the statistics involved. One procedure is to run an analysis of variance on the progeny or clonal data and then estimate the genetic and environmental components of variance. Heritability is then computed as the proportion of genetic to total variance, expressed in percent. In another procedure the parent-progeny regression or correlation provides an estimate of heritability. In still another method called the "selection experiment method" the amount by which the selected parents exceed the population average. More details of the methods employed will be covered in another report.

In analyzing cross-pollination data, the matings were pared off into groups of two, each group containing a common female. In such a case the female component is the best estimate of additive genetic variance (or "breeding value") but where the male component is not appreciably larger both can be used (Falconer, 1960). Of course, larger groups having a common female (or common male parent) are preferable if available.

The wind-pollinations similarly provide an estimate of additive genetic variance. Ordinarily one assumes that the wind-borne pollen is genetically uniform and equally effective for all seed parents. Under this assumption one multiplies the additive genetic variance by 4 to estimate heritability (because the component of genetic variance estimated is 1/4 of the theoretical value under the assumption). However, the parents may be growing in different areas in which case the wind-borne pollen may be genetically different because of racial effects. A similar situation may be true even for trees within the same stand; that is, pollen in the immediate neighborhood of one selection may be genetically superior to that surrounding another selection. Finally, the selections may have different degrees of selfing or other types of inbreeding. All these factors tend to exaggerate the estimate of additive genetic differences. If one assumes that the wind-borne pollens effective on each tree are completely different, the computed additive genetic variance should be multiplied by 2 instead of 4 (because the genetic component estimated is 1/2 of the theoretical value under this assumption). In order to take into account these sources of error the estimates of heritability for wind-pollinations presented herein are given as a range between two values representing the two extreme cases discussed (that is, multiplying genetic variance by 2 and 4 respectively).

The estimates of heritability computed for clonal data include non-additive genetic effects (dominance and epistatic deviations) in addition to additive ones. Under most situations only the additive variance is considered pertinent. Therefore, estimates obtained from clonal data, which will usually be higher than those from progeny data, should be considered maximum estimates of heritability.

RESULTS

The progeny and clone means for each trait studied are presented in tables 1 and 2, to give an idea of the extent of presumably genetic variation in each trait. Note that the variation is much higher for gum yield than for other traits. This is largely because the parents were selected for high-gum-yielding ability only. In respect to the other traits, the trees can be considered random, although the possibility of linkage with gum yield exists. In any event, even the variation among these is fairly substantial. For example, the wind-pollinated progenies of plantation 0-116 varied from an average 7-9 inches d.b.h. to 9.1 inches, a spread of about 15 percent. A purposive selection for d.b.h. would likely have resulted in still greater variation.

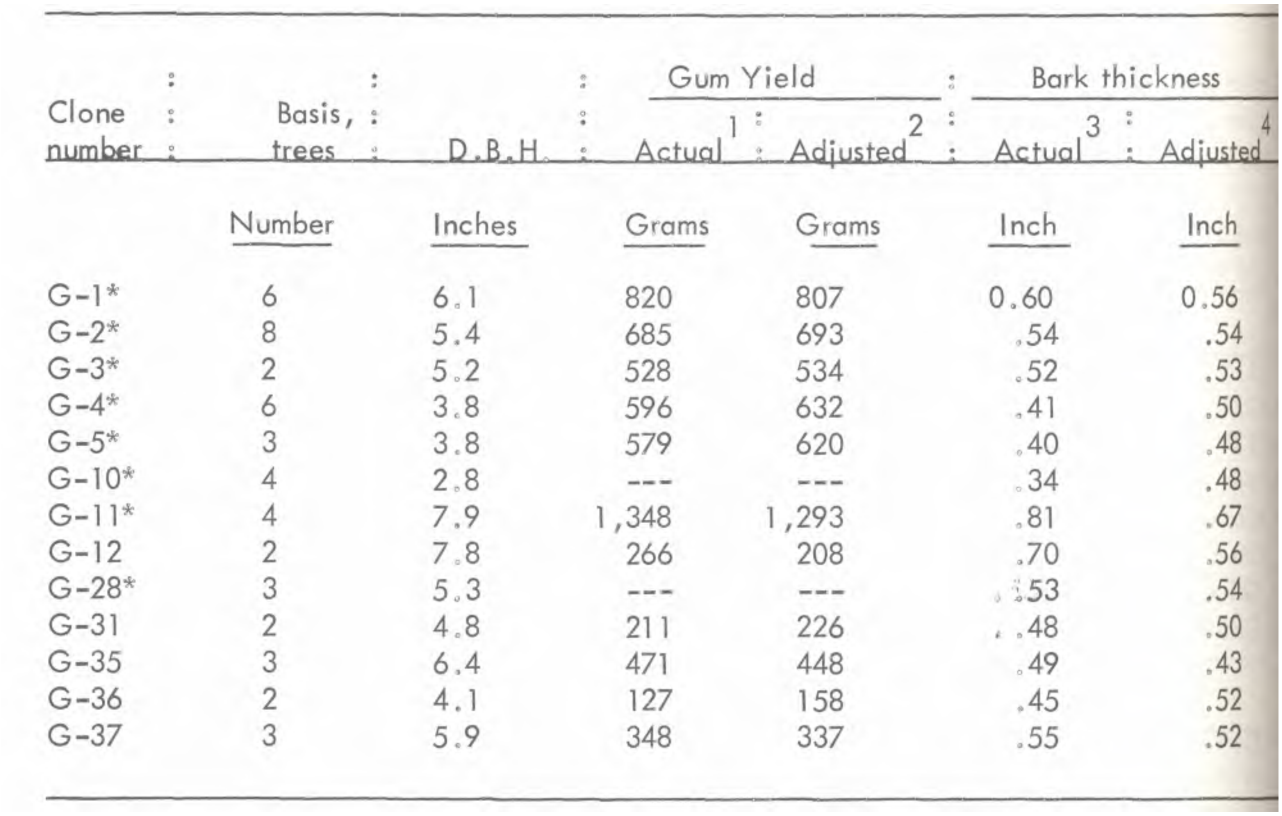
The estimates of heritability obtained from analyses of variance among progeny data are presented in table 3. Estimates obtained by other procedures will be discussed under the appropriate traits.

Table 1.--Progeny means of various traits for which estimates of heritability were made.

Progeny	Basis, trees	Gum yield[1]	d.b.h.	Stem volume	Total height	Branch length[2]	Bark thickness[3] Actual	Bark thickness[3] Adjusted[4]
	Number	Grams	Inches	Cu.ft.	Feet	Feet	Inch	Inch
PLANTATION 0-116--CROSS-POLLINATIONS								
G1* x G2*	27	260	8.7	7.9	40	7.9	.72	.72
G1* x G7*	27	195	9.3	9.1	40	8.8	.78	.76
G3* x G2*	27	195	9.0	8.2	40	8.4	.83	.82
G3* x G6	12	123	9.4	9.4	40	8.8	.88	.85
G6 x G3*	13	108	8.4	6.5	36	8.3	.81	.83
G6 x G8	27	109	8.6	7.7	40	8.2	.82	.83
PLANTATION 0-116 -- WIND-POLLINATIONS								
G1* x wind	38	166	8.8	8.0	39	8.6	.81	.80
G2* x wind	37	194	8.8	8.4	42	7.5	.75	.74
G3* x wind	36	154	8.9	8.0	39	8.4	.84	.83
G4* x wind	18	191	8.6	7.6	40	7.3	.80	.80
G6 x wind	34	91	7.9	6.0	38	8.0	.76	.79
G8 x wind	17	149	8.6	7.7	41	8.6	.84	.84
G23 x wind	33	123	8;1	6.6	40	8.3	.69	.73
G25 x wind	39	217	9.1	8.3	39	8.2	.86	.83
PLANTATION 0-146--CROSS-POLLINATIONS								
G1* x G5*	64	--	3.8	--	20	--	--	--
G1* x G9*	68	--	3.8	--	20	--	--	--
G10* x G5*	70	--	3.4	--	18	--	--	--
G10* x G11*	64	--	4.0	--	20	--	--	--
PLANTATION 0-146--WIND POLLINATIONS								
G3* x wind	25	--	3.7	--	19	--	--	--
G8 x wind	26	--	3.7	--	20	--	--	--
G10* x wind	26	--	3.8	--	20	--	--	--
G13 x wind	27	--	3.8	--	19	--	--	--
G31 x wind	22	--	3.8	--	20	--	--	--
G36 x wind	16	--	4.4	--	22	--	--	--
G37 x wind	24	--	3.9	--	20	--	--	--

*Phenotypically selected for high gum yield; all other parents were average or low gum yielders. [1] Yields were obtained from microchipping in the summer of 1945(4 biweekly streaks, 1-inch square, acid-treated). [2] Branch length was measured at a point 12 feet from top of tree. [3] Bark thickness was measured at 4 points uniformly spaced around stem of the tree at d.b.h. and averaged. [4] Adjusted for apparent effects of d.b.h. by covariance techniques, to a common d.b.h. of 8.9 (b=.058) for controlled pollinations and to a mean of 8.6 for wind pollinations (b-.047).

Table 2.--Clonal means for d.b.h., gum yield and bark thickness. (Rooted cutting plantation, 0-132)

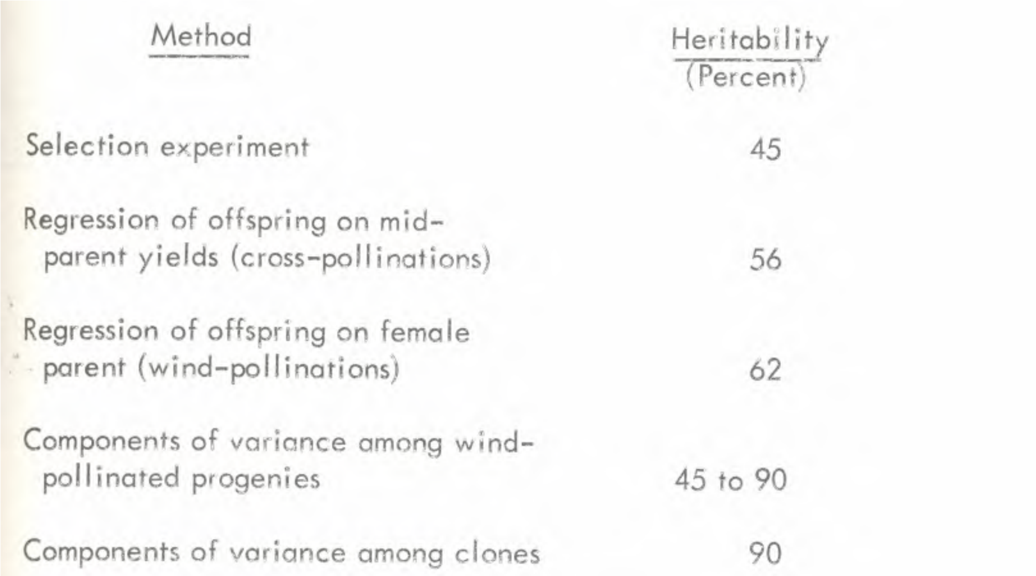


Clone number	Basis, trees	D.B.H.	Gum Yield		Bark thickness	
			Actual[1]	Adjusted[2]	Actual[3]	Adjusted[4]
	Number	Inches	Grams	Grams	Inch	Inch
G-1*	6	6.1	820	807	0.60	0.56
G-2*	8	5.4	685	693	.54	.54
G-3*	2	5.2	528	534	.52	.53
G-4*	6	3.8	596	632	.41	.50
G-5*	3	3.8	579	620	.40	.48
G-10*	4	2.8	---	---	.34	.48
G-11*	4	7.9	1,348	1,293	.81	.67
G-12	2	7.8	266	208	.70	.56
G-28*	3	5.3	---	---	.53	.54
G-31	2	4.8	211	226	.48	.50
G-35	3	6.4	471	448	.49	.43
G-36	2	4.1	127	158	.45	.52
G-37	3	5.9	348	337	.55	.52

*Phenotypically selected for high gum yield; all other parents were average or low gum yielders.

1. Yields were obtained from microchipping in the summer of 1960 (12 biweekly streaks, 1 -inch square, acid treated).
2. Adjusted for apparent effects of d.b.h. to a common d.b.h. of 6.0 inches (b=22.85).
3. Bark thickness was measured at 4 points uniformly spaced around stem of tree at d.b.h. and averaged.
4. Adjusted for apparent effects of d.b.h. to a common d.b.h. of 5.3 inches (b-.055).

The estimates of heritability given by Squillace and Doman (1959), plus an estimate made from recent data on the clonal plantation, indicate that the heritability of gum yield under the conditions tested is quite strong. The various estimates obtained are tabulated below:



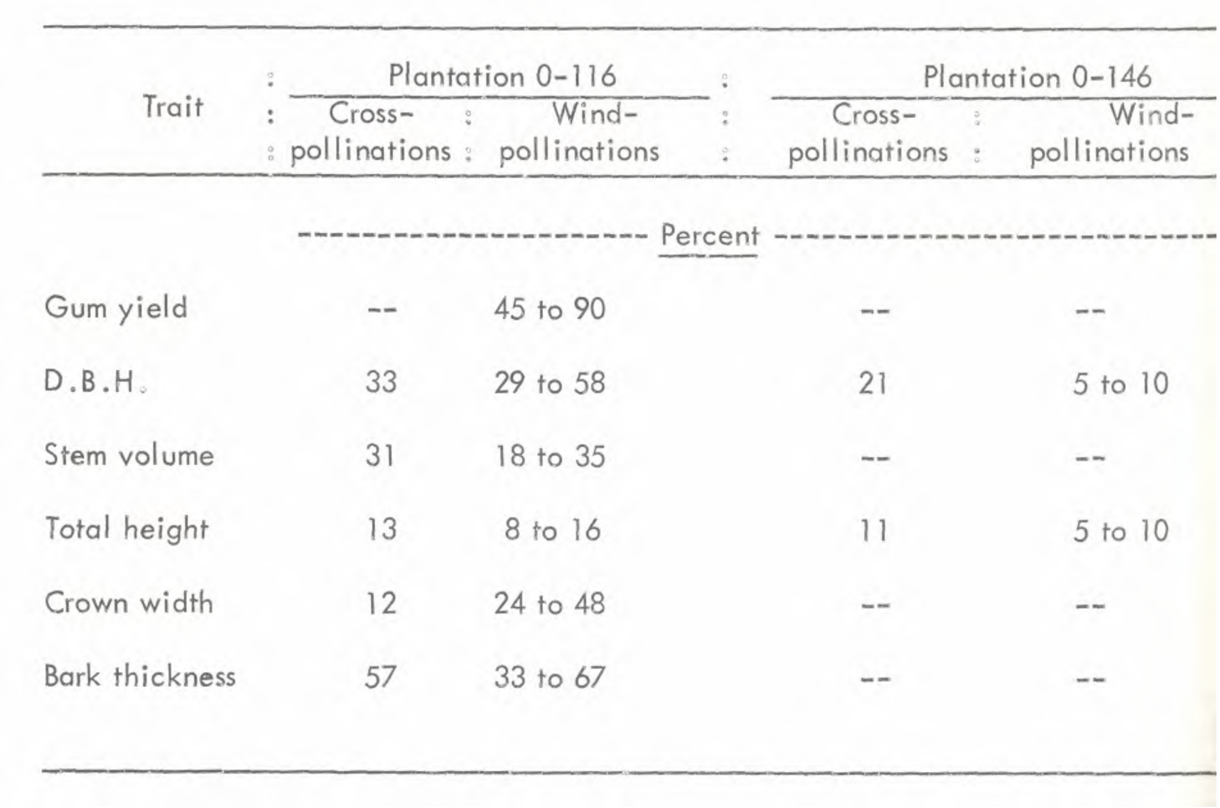
Method	Heritability (Percent)
Selection experiment	45
Regression of offspring on mid-parent yields (cross-pollinations)	56
Regression of offspring on female parent (wind-pollinations)	62
Components of variance among wind-pollinated progenies	45 to 90
Components of variance among clones	90

The actual estimate given by Squillace and Dorman for components of variance among wind-pollinated progenies was 90 percent. However, for reasons discussed earlier, all estimates based on components of variance in wind -pollinations are shown as a range of values as indicated.

The first three estimates listed are based upon both parental and progeny data and the heritabilities apply to selection under conditions existing for the parents. The latter two are based upon progeny and clonal data only, and the estimates apply to selection under conditions existing in the plantations. This probably partially explains the relatively lower estimates (45 to 62 percent) in the forme and the higher ones (45 to 90 percent) in the latter. This important point will he elaborated upon later.

In all of the foregoing estimates for heritability of gum yield, except possibly the "selection experiment" estimate, we most recognize that the parents were not randomly selected. Non-randomness, on the average, tends to exaggerate heritability. In computing the estimate only by components of variance for the wind-pollinated progenies we were able to take this difficulty into account. The parent trees were grouped into high and

Table 3.-- Estimates of heritability of various traits obtained for progeny data from Plantations 0-116 and 0-146 by components of variance methods.



Trait	Plantation 0-116		Plantation 0-146	
	Cross-pollinations	Wind-pollinations	Cross-pollinations	Wind-pollinations
	Percent			
Gum yield	--	45 to 90	--	--
D.B.H.	33	29 to 58	21	5 to 10
Stem volume	31	18 to 35	--	--
Total height	13	8 to 16	11	5 to 10
Crown width	12	24 to 48	--	--
Bark thickness	57	33 to 67	--	--

average gum yielders and the variances were computed within these groups separately. The estimate, therefore, is probably conservative and we still came up with 45 to 90 percent. Thus, we feel that the remaining values are fairly reliable. The cross-pollinated progenies could not be grouped in a similar manner, and hence no estimate was mode for them.

Prior to obtaining the estimate for the clonal plantation we found that gum yield from microchipping was significantly correlated with d.b.h. within clones. Therefore, actual yields were first adjusted for effects of d.b.h. Also, as indicated earlier, the estimate from clonal data includes non-additive genetic variance. This, coupled with non-randomness of the clonal plantation, reduces the reliability of the estimate based on these gum - yield data.

The estimates of heritability of d.b.h. were variable, ranging from 25 to 58 percent for the wind-pollinated progenies of plantation 0-116 to 5 to 10 percent for the wind-pollinated progenies of plantation 0-146. The variation is not surprising because, as pointed out earlier, the separate analyses are based upon relatively few parents.

Stem Volume

The two estimates of heritability for stem volume were 31 percent and 18 to 35 percent, no highly erratic and probably reasonable.

Height Total

The four estimates for total height were surprisingly consistent and low, varying from 5 to 16 percent. They are considerably lower than the estimates for d.b.h. or stem volume. We can only speculate as to the cause of this. A sig nificant point may be that the spacing was quite large in both plantations and crown corn petition has not yet been very severe Thus, it is possible that under such conditions genetic variability in height growth has not had an opportunity to become expressed. Under a normal, closer spacing results may have been different.

Crown Width

The two estimates of heritability for crown width were low (12 percent) to moderately high (24 to 48 percent).

Bark Thickness

The two estimates of heritability obtained for bark thickness from the progeny data were rather high and fairly consistent (57 and 33 to 67 percent). Bark thickness was found to be rather strongly related to d.b.h. and a covariance technique had to be used. Thus, the estimates of heritability of bark thickness are independent of d.b.h. In the same manner an estimate of 52 percent was obtained from the clonal data.

DISCUSSION

Heritability estimates provide a measure of the gains expected from phenotypic selection. However, a specific estimate applies to the conditions under which the experiment was conducted. This is because heritability depends on environmental as well as genetic effects. If two groups of trees are of identical genetic constitution, one could get different estimates of heritability if they are growing on different sites or if they are evaluated with different accuracies.

Thus, for example, parental selections in this study ate growing in diverse stands on different sites and they were of different ages. Their gum yielding ability was evaluated in comparison with surrounding trees, taking into account the effects of diameter. Now in applying heritability determined from such data one assumes that selection will be made under the same conditions. On the other hand, the progenies were growing in a nicely replicated plantation, with a large portion of the site effects accounted for by randomized blocks. When heritability is computed on the basis of progeny data alone the estimate will likely be higher, but such estimates then apply to plantation conditions, with selection to be made within small areas of uniform site in the plantation.

On the basis of gum yield results one might conclude tentatively that the heritability of gum yield among trees growing under natural conditions and evaluated in the manner described is about 55 percent. Thus, if one selects trees under these conditions and establishes orchards he can expect to gain about 55 percent of the selection differential (the difference between average yielding ability of selections and the average for the whole population).

Heritability of gum yield under plantation conditions is likely somewhat higher, possibly about 70 percent. Thus, if selections are made within small uniform areas in plantations one can expect to gain about 70 percent of the selection differential.

On the basis of the results presented for other traits, we can probably say that the heritability of d.b.h., stem volume, and branch length under plantation stand conditions was weak to moderately strong, in the neighborhood of about 25 percent. The heritability of total height was consistently weak, about 10 percent. For bark thickness it was rather strong, about 50 percent. Heritability of these traits under natural stand conditions would very likely be less.

As cautioned earlier, these results are not based upon ideal data for estimating heritability and the samples were small. Nevertheless they are our best estimates and probably have some merit.

Taking them at their face value it would appear that phenotypic selection for high gum yield, even in natural stands, would pay high dividends. In other words, if trees are selected in the manner done in this study, substantial gains could be made merely by phenotypic selection and establishment of clonal orchards or seeding orchards from crosses made among them, without progeny testing. Likewise, even seed -production areas with trees selected on basis of gum yield tests would likely pay off. Of course, progeny testing would provide even higher gains. The same would probably be said for bark thickness if it were advisable to select for such a trait. The high estimates for these traits also suggest that relatively few trees need be progeny tested to obtain a sufficient number of superior trees for orchards. Testing of about twice the number required for orchards would be adequate, although other considerations may affect one's decision here.

Heritability among the remaining traits, as they apply to selection in plantations, was weak to moderately strong. As indicated earlier, it would likely be even less under natural stand conditions. Therefore, it would appear that when selecting under natural stand conditions, progeny testing is necessary to ensure that we make appreciable gains. Under plantation conditions phenotypic selection within small areas of uniform site without progeny testing may be worthwhile. The relatively low heritabilities for these traits also suggest that relatively large numbers of trees should be progeny tested.

Irrespective of the type and intensity of selection required, the genetic variation found for all traits considered in this study suggests that we are getting somewhere with out tree improvement efforts.

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