43. Discussion

431. Pollination method. — Making allowance for conditions in the isolation bags being not quite natural the results as presented in table **3** suggest that insects are the main agents of pollination. Wind plays only a minor role.

432. Regeneration method. — The figures in respect of fruit formation (tables 1 *and 3)*, fruit diameter (fig. *3)*, and germination (table 4) all point to teak being mainly a crosspollinating species.

The fact that insects succeeded in producing a relatively great number of fruits in bags where only selfpollination was possible suggests that a normal batch of fruits will contain many selfings. Calculating by the germination percentages (table 4) the element of selfpollination in the fruit lot deriving from open pollination amounts to c. 30%. The fruits from double bags are likely to contain a high number of selfings because the flowering periods of the two inflorescences did not completely coincide.

Judging from table 1 ("control") fruits will not develop without preceding pollination.

Acknowledgement

The authors are indebted to HENRIK KEIDING, the Arboretum, Hørsholm, Denmark, who initiated the flowering studies on teak in Thailand in **1965** and who has kindly read the manuscript.

Summary

Studies at the Thai-Danish Teak Improvement Center in Thailand were intended to give information about the flowering habit of teak (Tectona grandis L.), to find a technic of controlled pollination, and to establish the natural ways of pollination and generative reproduction.

It appears that the flowering period of the individual flower is one day. Emasculation and isolation may be carried out for approx. one hour after the flower has fully opened. The early afternoon is the best time for pollination.

Insects were found the principal agents of natural pollination although some windpollination may take place.

Teak is mainly a crosspollinating species, but fruits after selfpollination occur. The germination of these fruits is poor compared to that of fruits resulting from crosspollination. Apomixis has not been observed.

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Heritability of Height Growth in Western White Pine Seedlings

By JAMES W. HANOVER and BURTON V. BARNES[1])

(Received for publication November **28, 1967)**

The use of heritability estimates to predict genetic gain in tree breeding programs may be seriously restricted by the fact that combined environmental and nonadditive genetic effects may exert a stronger, less predictable influence than additive gene action on quantitatively inherited traits of tree species. Such an influence almost certainly operates on the trait of growth rate of western white pine (Pinus monticola DOUGL.). Genotypic reaction to the environment is of course maximized under varying natural conditions, but for some species it is probably also substantial under the relatively controlled conditions of a nursery, greenhouse, or growth chamber, even if simulation of natural conditions, and not stress, is the imposed environment.

Naturally outcrossing tree species are highly heterozygous and commonly show patterns of natural variation that include varying degrees of genotype-environment interaction and phenotypic plasticity. These phenomena certainly have a genetic basis (BRADSHAW 1965), but they nevertheless represent nonadditivity in the derivation of narrow-sense heritability estimates. Hence, breeders are cautioned that a heritability value applies only to the population, trait, and environment for which the value was determined.

Under such restrictions, heritability values having much general usefulness are difficult to obtain. Published values are useful simply as gross indicators of the feasibility of selection for one or more traits (HANSON 1963; CAMPBELL 1964; NAMKOONG et *al.* 1966).

Information about the relative amounts of additive and nonadditive genetic variances and environmental variance for tree characteristics is rather meager (NAMKOONG et al. 1966). Nevertheless, even this is potentially useful and is interesting from the theoretical standpoint. Such information can be made more meaningful by analysis of the heritability concept itself, using actual data. Answers are needed to such questions as these: How do the components of variance for a given population vary over typical site or age gradients? What changes in variance components can be expected from use of realistically different populations for their derivation? — from use of male and female parents from different populations? — from use of different males and females from the same population? — from variation in the number of male or female parents within practical limitations for forest trees? Some answers may be available from investigations of growth rate of progenies of western white pine.

Breeding for blister rust resistance in western white pine in the Intermountain region requires investigations of growth and quality traits to assure that rust resistant progenies are not inferior from these standpoints. Because of the wide variety of macro- and micro-environments to which this species is apparently adapted, we are continually seeking knowledge about genetic control over white pine traits other than resistance.

This study presents the components of variation in juvenile height growth of 1- and 2-year-old progenies from a new experiment and compares the results with those from

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[1]) Formerly Geneticist and Research Forester, respectively, U. S. Department of Agriculture, Intermountain Forest and Range Experiment Station, Ogden, Utah, and who were stationed at Moscow, Idaho; study was made in cooperation with University of Idaho. Presently, Dr. HANOVER is Associate Professor, Department of Forestry, Michigan State University, East Lansing, and Dr. BARNES is Associate Professor, School of Natural Resources, University of Michigan, Ann Arbor.

a previous experiment (Hanover and Barnes 1963). Also, a comparison is made of variance and heritability estimates based on mating of two different sets of females with the same set of males.

Materials and Methods

The factorial crossing scheme adopted is identical to one used previously by Hanover and Barnes (1963) and is similar to the standard North Carolina Design II. Seeds were obtained from controlled crosses of four male parents and seven female parents. The pollen parents were growing in a single low-elevation natural stand near Fernwood, Idaho, and the seed parents were located in four different drainages in northern Idaho, ranging from low-elevation stream bottom (3,140 ft) to subalpine habitats (5,400 ft) *(Table 1,* Set 2). All the parents are blister rust resistant selections used in the Intermountain Station's white pine breeding program.

Table 1. — Elevation and location of female parents used to estimate heritabilities of height growth of 1- and 2-year-old progenies.

Set 1 matings [1]			Set 2 matings [2]		
Female parent	Elevation	Location	Female parent	Elevation	Location
	Feet			*Feet*	
193	3,875	Lower Long Creek	103	4,240	Rainy Creek
195	3,950	Lower Long Creek	118	3,880	Rainy Creek
197	3,875	Lower Long Creek	140	3,140	Placer Creek
201	4,100	Lower Long Creek	150	3,520	Placer Creek
203	4,100	Lower Long Creek	181	5,400	Upper Long Creek
204	4,100	Lower Long Creek	195	3,950	Lower Long Creek
205	4,100	Lower Long Creek	214	3,750	Lower Long Creek

[1] Results reported in Hanover and Barnes 1963.

[2] Results reported in the present paper.

Seeds from the 28 crosses were sown in 3- by 3- by 8-inch tarpaper plant bands in the nursery at Moscow, Idaho. Five seeds were sown in each plant band, and seedlings were thinned after one growing season to two per container. After thinning, there were about 120 seedlings per cross, located in five randomly placed eight-tree rows in each of three blocks. Because some crosses produced fewer seedlings than the others, first- and second-year height measurements, to the nearest millimeter, for only the first 30 seedlings measured in each block were used in the analyses.

Height growth was analyzed in two steps to derive variance components. First, individual seedling and plot mean values were used to estimate within-plot or individual-tree variance. Then plot means were used to compute mean squares for males, females, male-female interaction, and the product of male-female combinations and replicate interaction. Details of the analysis, computational formulae, and genetic interpretations were given in the earlier report (Hanover and Barnes 1963).

Results and Discussion

The mean height of each family at 1 and 2 years of age is shown in *Table 2,* and the results of variance analyses are given in *Table 3.* Heritability estimates for 1-year and 2-year height growth, respectively, on the bases of male, female, and male-plus-female variances were 15.3 and 21.8 percent, 52.4 and 50.0 percent, and 33.9 and 35.9 percent, respectively.[2] These estimates are based upon individual-tree data rather than family means. The correspondence of estimates for the two ages of materials is high, indicating that no radical change in relative progeny performance occurred over the short time interval of 1 year. An unusually high mean square for replications was obtained for the 1-year measurements. Possibly there were unknown differences in potting soil preparation procedure or in post-germination treatment of the beds, as in watering and fertilizing. There were no such responses between replications at 2 years *(Table 3).*

Table 2. — Mean total heights[1] of white pine progenies at 1 and 2 years of age.

Female parent	Male parent									
	17		19		22		58		Mean	
	1 yr	2 yr	1 yr	2 yr	1 yr	2 yr	1 yr	2 yr	1 yr	2 yr
	Millimeters									
103	41	65	37	59	43	67	37	58	39	62
118	36	57	35	54	38	56	39	60	37	57
140	45	70	42	64	44	68	43	70	44	68
150	42	62	42	59	44	61	41	60	42	60
181	42	66	38	59	42	62	42	69	41	64
195	39	62	37	57	40	61	36	62	38	61
214	43	69	39	60	40	64	41	69	41	66
Mean	41	65	39	59	42	63	40	64	40	63

[1] Each value represents the mean of 90 seedlings except for progenies 103×19 and 118×22 which had 51 and 41 seedlings, respectively.

Table 3. — Analyses of variance.

Source of variation	Degrees of freedom	Mean square		Variance component	
		1 yr	2 yr	1 yr	2 yr
Replications	2	5364	90		
Male parents	3	3524	13576	143±106	571±410
Female parents	6	6399	17262	490±266	1306±721
Males ×females	18	525	1584	110± 57	339±171
Male-female combinations × replications	54	194	568		
Within plots	2342	2837	7782		

The estimate of heritability based upon female parent variance was considerably greater than that based upon male parent variance at both ages *(Table 3).* In young seedlings, where seed weight may be an influencing factor, one would expect the female parent variance to be greater than the male. In fact, if a large number of both male and female parents are used in deriving heritability estimates, the difference between male and female variances should give an estimate of maternal effects. However, in the present study the difference is probably a reflection of the small sample of female parents. In fact, our previous computations (Hanover and Barnes 1963) showed a higher variance for males than for females in 1-year height data.

The previous study and the present one involved the same mating design and the same male parents but different female parents. Thus, the two sets of matings may be compared to discover the effects of different female parents on variance estimates. In contrast to those in Set 2 (present paper), the female parents in Set 1 (previous paper) all came from a single middle-elevation drainage

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[2] Heritability estimates include a component, σ^2_e = error variance associated with plots, which is 1.54 and 4.59 for the 1- and 2-year data, respectively.

Table 4. — Effect of different male and female parent sets on heritability estimates for western white pine height growth.

Matings	Heritability estimates	
	Male parents	Female parents
	Percent	
Set 1 (1 yr)	19.7	8.4
Set 2		
1 yr	15.3	52.4
2 yr	21.8	50.0

(Table 1). Microenvironments in the two tests also differed, although the tests were made in the same nursery. The heritability estimates from both experiments are summarized in *Table 4*. Both studies gave reasonably similar heritability values for height growth based on the male parent data. The change in female parents obviously had a large effect on the heritability values derived from the female parent data: 8.4 versus 52.4 percent for 1-year-old trees. It should be emphasized that the Set 2 female parents represented a greater diversity of habitats than the Set 1 female parents. This difference may be responsible for a corresponding wide discrepancy in estimates derived from the two sets. However, the results do illustrate the desirability of using as many parents as possible and choosing parents at random from a natural population, so as to get unbiased heritability estimates. Even the male parent estimates, although similar in magnitude and free from maternal effects, do not necessarily give a true estimate of heritability because of the small number of male parents used. The relatively high standard errors for the male variance compared with those for the female variance *(Table 3)* also indicate the desirability of using more than four parents for deriving components of genetic variation.

The relative ranking of progenies for mean height growth was similar for both the previous and present experiments. This is evidence for the relatively small but repeatable additive genetic component of white pine seedling height growth. As indicated earlier, any increase in environmental diversity, such as that encountered under plantation and natural conditions, lowers the heritability estimate in both magnitude and usefulness, not uncommonly to zero.

Within-plot variance is by far the largest source of variability in both of our experiments and probably in most other tests of forest tree species. Individual-tree variation within families and variation due to male-female interaction both have at least a partial genetic basis. Individual-tree variation is undoubtedly one mechanism that allows the species to adapt to changes in environment or to new environments. We know little about the genetics of male-female interaction (specific combining ability), but it can lead to substantial genetic gain, judging from the results in *Table 2* and in our previous experiment. Hence, in the future we should see an increased use of the phenomenon for rapid, predictable improvement of certain species when the use of a relatively narrow genetic base seems allowable.

Some additive gene effects on growth rate have been demonstrated in these and other studies. For practical purposes, however, the present great need is for measures of the relative stability of growth rates of known populations over a reasonable range of environments. Information of this type will allow the concept of heritability to contribute more to accurate prediction of genetic gain in long-term tree breeding programs.

Summary

The inheritance of height growth of 1- and 2-year-old western white pine nursery seedlings was studied using a factorial design similar to the standard North Carolina Design II. Variation in 1- and 2-year heights due to additive gene effects was estimated to account for 15.3 and 21.8 percent, respectively, of total variation based upon male parent variance; 52.4 and 50.0 percent based upon female parent variance; and 33.9 and 35.9 percent based upon the combined parental variances. Individual-tree variation within progenies was the major source of variability in height growth. The results from this study and an earlier but comparable one demonstrate that choice of individual parents or parental population can greatly influence heritability estimates derived from progeny analyses. Heritability values computed from the male variance components were similar in both studies (19.7 vs. 15.3 percent). This was not unexpected because the same male parents were used in both tests. Heritabilities computed from female variances were markedly divergent (8.4 vs. 52.4 percent). Part of this difference may be due simply to the use of small numbers of different females, but much of it is probably caused by the habitat diversity and resultant genetic diversity within each group. For the improvement of western white pine, as many parents as possible, chosen at random from a natural population, should be used in heritability estimates. There is also need for new measures of progeny performance over reasonable ranges of site conditions.

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