# LOCATION DIFFERENCES AND THEIR INFLUENCE ON HERITABILITY ESTIMATES AND GAIN PREDICTIONS FOR TEN-YEAR-OLD LOBLOLLY PINE

James A. Barker[1/]

Abstract.--Heritability estimates and predictions of gain from simple mass selection among 75 ten-year-old, open-pollinated families of loblolly pine growing in two locations indicated that the influence of location differences varied according to the trait under consideration. Values differed between locations, but no more than would have been expected from published reports. Estimates and predictions from combined data, however, indicated substantial upward bias arising from interactions between locations and families in some of the separate location values. Biases were apparently more serious for tracheid length, diameter, volume, and dry weight than for specific gravity and "cronartium score" (an index of fusiform rust infection).

The existence of substantial bias for some traits emphasizes the fact that heritability estimates and gain predictions from single location tests must be used with caution since they may be too high for valid application to a broad range of locations. Estimates of realized gain from single locations should also be liable to this same type of bias.

Numerous published values for heritability and gain exist for a wide variety of traits in a number of forest tree species. Many of these reports, however, are from tests planted in only one location. Values derived from single location tests are biased upwards because estimates of genetic effects from these tests also contain the effect of interactions between the genotypes and the particular location involved. Estimation and removal of these interaction effects can only be accomplished by evaluating the genotypes in more than one location (Comstock and Moll, 1963; Namkoong et al., 1966). The magnitude of this bias will vary according to the trait, genotypes, and location involved and may, in some instances, be mall enough to have no practical influence.

Similar biases result from the failure to adequately sample year effects. However, as Squillace (1969) has hypothesized, interactions between year effects and forest tree genotypes can be expected to be smaller than interactions with location effects, especially for those traits evaluated late in the life of an individual. The long span of time involved for the expression of these traits should cause year-to-year influences to average out for plantings made in different years. Year effects may, of course, be more important for traits such as survival which are more strongly influenced by extreme environmental fluctuations.

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[1/] Biometrician, International Paper Company, Southlands Experiment Forest, Bainbridge, Georgia.

The current study was designed to investigate one facet of this problem by examining the nature and relative magnitude of the influence of differences between two locations on estimates of heritability and predictions of gain from simple mass selection for merchantable ten-year-old loblolly pine (*Pinus taeda* L.) from unselected parents.

## MATERIALS AND METHODS

The trees evaluated for this study were from a portion of the Loblolly Pine Heritability Study, a cooperative venture of International Paper Company and North Carolina State University. Details of the objectives, design, and implementation of the heritability study have been given by Stonecypher (1966); therefore, only a brief description of that portion directly involved in the current investigation viz., the open-pollinated study, will be given here.

## OPEN-POLLINATED HERITABILITY STUDY

The open-pollinated study was initiated in the fall of 1959 by collecting wind-pollinated cones from 387 of the 390 parent trees originally selected as a basis for the heritability study. These parent trees were chosen at random from a natural stand of loblolly and shortleaf (Pinus echinata Mill.) pine resulting from seedfall onto abandoned agricultural land. Two restrictions were imposed on the completely random selection of parents: trees which were not producing female strobili or which were judged unsafe to climb were rejected. The chief danger to climbers was the presence of severe bole galls caused by fusiform rust (Cronartium fusiforme Hedc. and Hunt ex Grimm.) . Biases in favor of fecundity and against susceptibility to fusiform rust were thereby introduced, but were slight since less than one percent of the original random selections were rejected.

Of the 387 seed lots originally collected, 280 yielded sufficient seedlings for field planting. These 280 families were divided at random into ten sets, each with 28 families, to reduce field block size. Field plantings consisted of two replications at each of two locations. The two planting locations were only five to six miles apart, but were comprised of quite different soil types. Sets were randomly located within each replication and the positions of 25-tree square family plots within sets were also randomly assigned. A map detailing the location of the various portions of the heritability study, including the plantings investigated in the present study was presented by Stonecypher et al. (1973).

## SAMPLING PROCEDURES

In the summer of 1970, five sets were randomly selected for thinning with a modified mechanical -selection thinning regime. The entire fifth row in each plot was marked for removal to serve as an access row. Additional trees were marked on each plot so as to leave 12 trees by first marking all individuals which appeared unlikely to survive or make a useable tree at maturity, forked, broken, suppressed, and severely infected trees were marked. Any additional trees were chosen for removal on the basis of spacing considerations.

After marking was completed, 15 families per set from one replication at each location were chosen at random from among those families having at least five "crop" trees marked for removal in both locations. Crop trees were individuals which would normally be utilized for pulpwood during an operational thinning, i.e., all forked, broken, excessively diseased, or extremely mall individuals were rejected. These five crop trees from each plot comprised the sample from which estimates of heritability and predictions of gain were made. Sample trees were therefore better than the average individual removed during thinning, but were more representative of the merchantable component of each plot.

Each sample tree was evaluated for diameter at breast height, fusiform rust infection, unextracted specific gravity, tracheid length, total inside-bark volume, and total inside-bark dry weight. Fusiform rust infection was assessed through application of a subjective scoring system, ("cronartium score"), which assigns to each tree a score ranging from 1 to 10 with increasing severity of rust infection. Determinations of specific gravity and tracheid length were performed by the laboratory staff of the North Carolina State University-Industry Cooperative Tree Improvement Program. Volumes were calculated using prediction equations developed separately for each location from downed-tree measurements of an independent sample of trees. Dry weights were calculated for each tree from these volumes and their associated specific gravity. Measurement procedures have been described in greater detail by Barker (1973).

## STATISTICAL PROCEDURES

Analyses of variance and covariance were conducted for each of the six traits under consideration. Analyses were performed for each location and also for data combined from both locations. Expected mean squares for the analyses were derived assuming a random effects model (Eisenhart's (1947) Model II).

Components of variance from these analyses were used to calculate estimates of narrow-sense heritability (on an individual plant basis) for each trait in each location and for combined locations. Each heritability estimate was combined with its associated estimate of phenotypic standard deviation and an arbitrarily chosen intensity of selection to yield predictions of the progress to be expected from simple mass selection among the parent trees. An intensity of selection corresponding to selecting one percent of the population ($i = 2.6652$) (Namkoong and Snyder, 1969) was employed for all traits except cronartium score. Predictions for this trait were derived for the case where only 50 percent of the population was selected ($i = 0.7979$) since, in most cases, only about one-half of the trees in a given family will be infected and selection for resistance consequently cannot be more intense.

## RESULTS AND DISCUSSION

Single location estimates of narrow-sense heritability indicated that cronartium score is under moderate additive genetic control and that dry weight, volume, diameter, and tracheid length are under moderate to strong control while specific gravity is under relatively strong control. Predictions of genetic response to selection did not exactly reflect the relative magnitudes of the heritability estimates since, in some cases, greater levels of phenotypic variability tended to overcome lower heritability estimates. Gain predictions were generally of sufficient size to indicate worthwhile progress from selection directed towards improvement of these traits.

Results from the separate location analyses and estimations were, therefore very much as would be expected. Some heritability estimates and gain predictions did exhibit a rather wide divergence from location to location for the same trait, but these differences were not much larger than those reported in the literature and could be expected from the different levels of environmental variation existing in each location.

Many of the published reports of heritabilities and gains were based on information from populations which had undergone at least one cycle of selection for various traits. Estimates reported here are from an unselected population with the restriction of merchantability placed on those trees included in the analyses. This restriction undoubtedly had an influence on the resultant variation both within and among families, especially for cronartium score where a definite bias was introduced by discarding all severely infected trees. Similar biases for diameter, volume, and dry weight can also be expected from the omission of extremely small individuals. Lack of perfect correspondence with other reports can therefore be expected. What is surprising is that the estimates agreed with these reports as closely as they did.

The most interesting implications from the current study center upon the results obtained from the combined analyses and their lack of agreement with separate location estimates. For several traits, evidence was found for the existence of a substantial degree of location influence on estimates of heritability and response to selection. The nature and magnitude of these influences were not constant, but varied according to the trait under consideration.

Two general situations were found to exist with regard to the influence of location differences. For the first group of traits, heritability estimates and gain predictions were different between locations, some more so than other but estimates from the combined data were intermediate, both for gain and heritability. For the other group, location differences were still evident, but combined location estimates were substantially lower for these traits.

Location differences in the first situation arose from the existence of differential levels of phenotypic variability in each of the locations. Family components of variance remained relatively constant from location to location with the larger environmental variation for one location resulting in a lower estimate of heritability for this location. When data were combined from both locations, family variation remained relatively unchanged and phenotypic variation tended to average out, resulting in an intermediate heritability estimate. That location differences can be expected to occur has been pointed out by Falconer (1960) and many other authors when they caution that heritability estimates are the property not only of a character, but also of the genetic sample and the environment to which it has been subjected.

Implications from the second situation are far more important, for it is in these instances that the existence of a substantial degree of family by location interaction is indicated. Separate location estimates for these traits differed for the same reason indicated above, but the lower estimates from the combined data were due not to a greatly increased level of environmental variation but to a reduction in the magnitude of the genetic variation. This reduction in genetic variation resulted from separate location estimates being biased upwards because they contained the variation due to interactions between those particular families and that particular location under consideration. Interaction variation is inextricably bound to the genetic variation estimated from single location tests. Its estimation and removal can only be accomplished by evaluating those families involved in more than one location.

For the families and locations investigated in the current study, two traits, unextracted specific gravity and cronartium score, typified the situation where combined results were intermediate to separate location estimates. Estimates of heritabilities exhibited noticeable differences between locations with estimates of 0.67 and 0.98 for specific gravity and 0.11 and 0.35 for cronartium score. Combined location estimates for these traits, 0.76 and 0.23, respectively, were both intermediate to the separate location estimates (Figure 1). Gain predictions were similarly affected with predictions of 12 and 17 percent of mean specific gravity and 21 and 75 percent of mean cronartium score. Combined predictions of gain (13 and 48 percent of the mean, respectively) were also intermediate to their corresponding separate location estimates (Figure 2). Interactions between families in sets and locations were found to be statistically nonsignificant for the analyses of variance for both of these traits.

The other four traits (tracheid length, diameter, total volume, and total dry weight) yielded combined estimates which were considerably lower than separate location estimates. Heritabilities for these traits were also different from location to location with diameter (0.36 and 0.60), volume (0.40 and 0.56), and dry weight (0.39 and 0.55) yielding estimates agreeing more with each other than with those for tracheid length (0.31 and 0.99). Combined location estimates for these traits were not intermediate, but were substantially mailer than either separate location estimate. Combined location heritability estimates were 0.21 for diameter, 0.20 for volume, 0.19 for dry weight, and -0.06 for tracheid length (Figure 1). The negative estimate for tracheid length was due to the existence of a negative estimate for the family component of variance (-0.0009) from the combined analysis for this trait. In light of the relatively large standard error (0.002)x.) associated with this estimate, it is reasonable to assume that neither the component nor the heritability differed significantly from zero.

Gain predictions from the combined data were also considerably smaller than separate location predictions. Predictions from separate locations did not follow the same patterns exhibited by heritabilities from these locations, with gain for volume (48 and 45 percent of mean volume) and dry weight (48 and 45 percent) much larger than that for diameter (20 and 22 percent). Heritabilities for these three traits were of essentially the same magnitude. The larger gain predicted for volume and dry weight resulted from a higher level of phenotypic variability for these traits relative to that for diameter. In addition, gain predictions for these three traits agreed much more closely

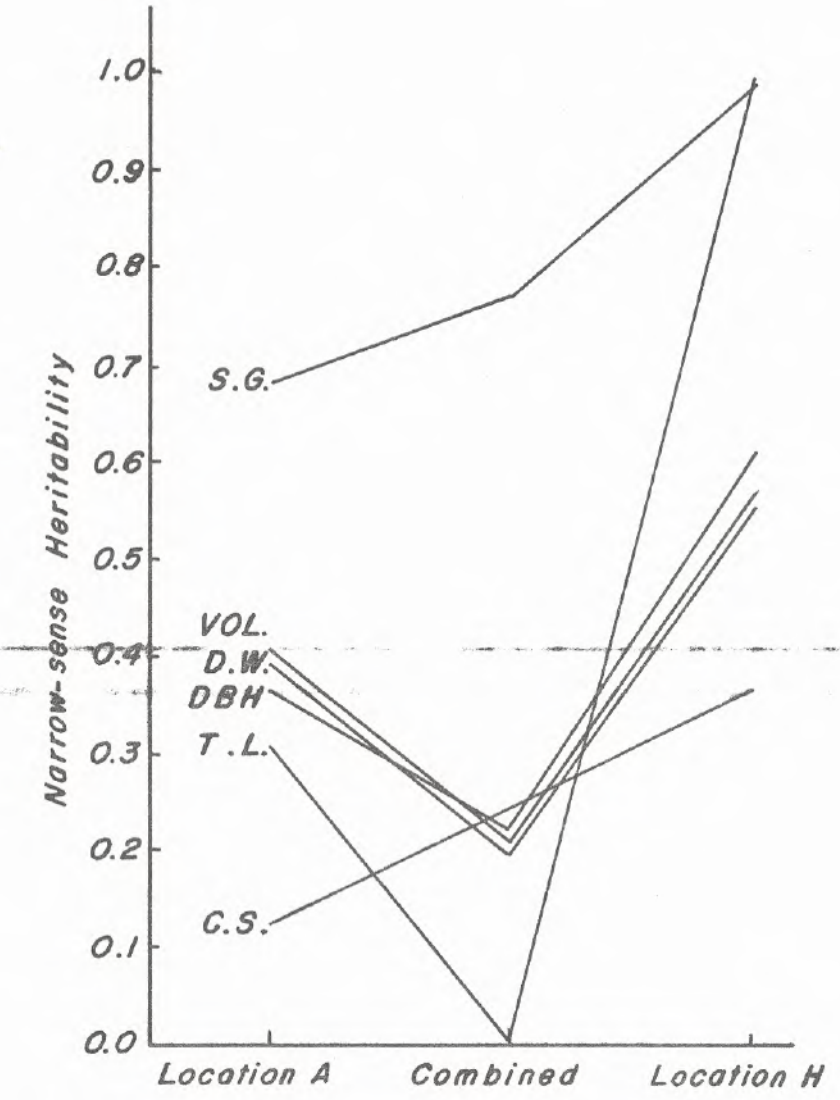

Figure 1. Narrow-sense heritability estimates for separate and combined locations.

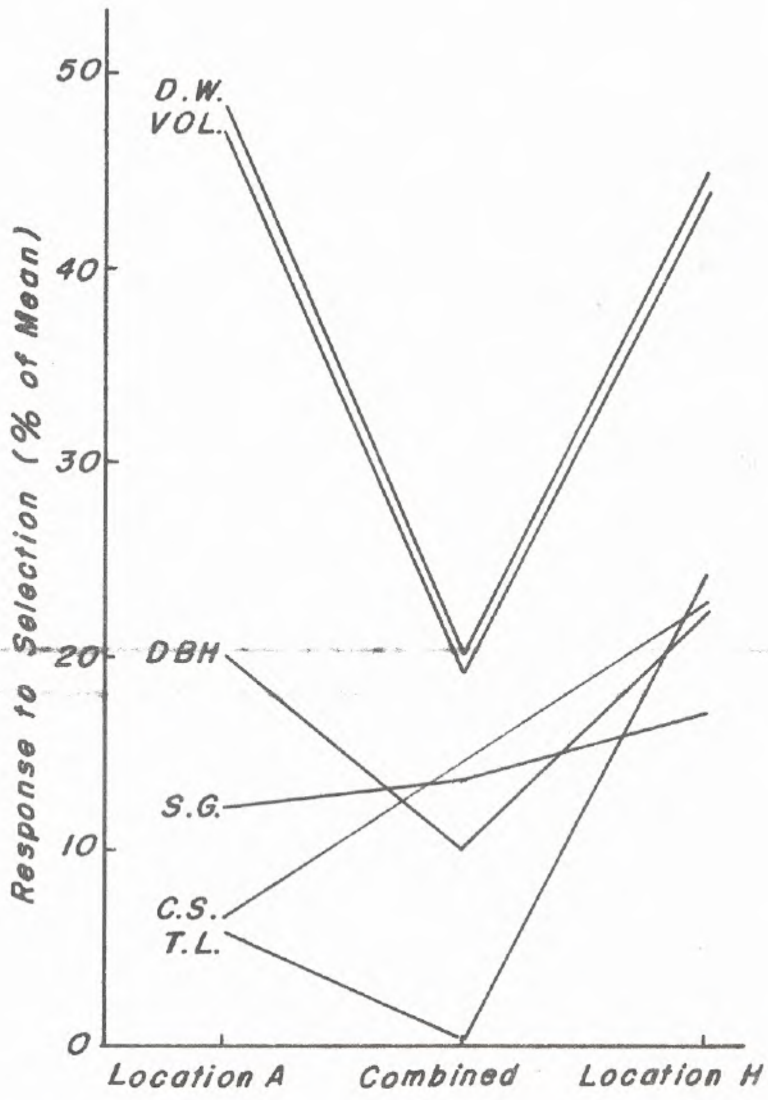

Figure 2. Predictions of gain from simple mass selection for separate and combined locations.

between locations than their heritabilities would indicate. This closer agreement was due to locations with lower heritabilities having a relatively higher phenotypic variation. Separate location gain predictions for tracheid length (five and 26 percent of mean tracheid length) were in closer agreement to their corresponding heritability estimates.

Predictions of gain for these traits from the combined data, like combined heritability estimates, were substantially smaller than either of their separate location predictions. These combined predictions were 20 percent of mean volume, 19 percent of mean dry weight, 10 percent of mean diameter, and minus one percent of mean tracheid length (Figure 2). The negative prediction for tracheid length is again probably not significantly different from zero. For the first three traits, gain predictions were approximately one-half of that predicted for each location. Interactions between families in sets and locations were found to be statistically significant for all four traits.

## CONCLUSIONS

It is apparent from the current study that location differences can have considerable influence on the magnitude of heritability estimates and gain predictions. Estimates from single location tests, while applicable to the particular location tested, are biased upwards to the extent that an interaction between the genotypes and the location actually occurs. This interaction will cause a similar bias in estimates of mean performance and will thereby result in estimates of realized gain which are also biased.

If enhanced family differences arising from this interaction are to be utilized for increased genetic gains, planting zones must be delineated so as to include those locations favorable for the selected genotypes. If, on the other hand, a group of genotypes with broad adaptability for several locations is to be selected, the interaction variance can no longer be "captured" and must be removed from heritability estimates and gain predictions by including all locations of interest in tests designed to provide these estimates. The amount of this bias varies depending on the trait under consideration and gain predictions may be less drastically influenced than heritability estimates.

If similar location effects exist for other populations, many of the heritability estimates and gain predictions which have been reported from single location tests can be expected to be too high for valid application to a broad range of locations. Future studies designed to provide similar estimates should include an adequate sample of locations of interest as well as genotypes if these estimates are to have broad applicability. The importance of including all locations of interest in these tests or the delineation of planting zones is apparently more crucial for some traits than for others.

Results from the current study are admittedly based on a biased sample. Further investigations on the effects of location (and year) differences should be made involving genotypes which more closely represent actual situations. A more extensive evaluation of location effects on the inheritance of non-destructively sampled traits is currently planned for the entire heritability study. The large number of progeny tests which include both year and location replication should yield much valuable information on interaction influences as they reach a meaningful age, even though they were not designed specifically for variance component estimation.

Until estimates based on adequate samples of years and locations become available, separate location and year estimates will, of course, have to serve. They should, however, be used with caution since realized gain for a broader range of locations and years can be expected to be somewhat less than that predicted from these single location estimates.

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