VARIANCE COMPONENT AND GENETIC GAIN ESTIMATES FROM 6-YEAR-OLD DIALLEL TESTS OF LOBLOLLY PINE

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Abstract. In the North Carolina State University - Industry Cooperative Tree Improvement Program with loblolly pine *(Pinus taeda L.),* data from 21 test series (two 6-tree diallels planted in 4 test locations per series) at age 6 years from throughout the Southeast were analyzed for height, straightness, and fusiform rust incidence. Individual-tree and family-mean heritabilities, genetic correlations, and genetic gains were estimated for all three traits. Individual-tree heritabilities for height were $h^2_{Ns} = 0.22$ and $h^2_{Bs} = 0.30$. Half-sib family mean heritabilities (narrow-sense) were 0.72, 0.78, and 0.73 for height, rust infection, and straightness score, respectively. On average, genetic correlations were essentially zero among the traits, but ranged between -1 and 1 for different diallels.

Gains from family selection were compared for height, straightness, and fusiform rust incidence. For selection intensities of i = 1.00, percent gain estimates were 2.5, 4.4, 7.7, respectively. The economic impact from gains of this magnitude are discussed for each trait.

Keywords: Breeding, genetic correlations, heritability, *Pinus taeda* L., selection

Cooperators in the NCSU Tree Improvement Program have been actively breeding and testing over 3000 plantation selections and over 700 second generation selections since the early 1980's. The breeding is complete and by 1996 all progeny tests will be planted. Selections were bred in 6-parent disconnected half-diallels and the resulting progeny were planted in balanced test series (4 tests per series) each comprised of progeny from two or on occasion three diallels. Each full-sib family is planted in a 6-tree plot and is replicated 6 times in each of the 4 tests (see Talbert et al. 1981 for details). As of March 1995, measurement and analyses have been completed in 21 test series at age 6 years, with 44 separate diallels represented (Table 1). As the analyses of the diallel tests have proceeded and we gained some experience with the selection procedure some interesting and useful trends and relationships have developed. Highlights of analyses and interpretations are summarized.

Relationships Between Genetic Parameters and Test Characteristics

Several informative relationships among progeny test characteristics and estimates of genetic parameters have been identified. The estimates of individual-tree heritabilities (both narrow-sense and broad-sense) appear to be in line with other estimates for height (Cornelius 1994). The average narrow-sense heritability (individual basis) was .22, while the comparable broad-sense heritability average was .30. The average narrow-sense family mean heritability estimates for height, fusiform rust infection, and straightness score were 0.72, 0.73 and 0.78 respectively (Table 1).

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Table 1. Average height, % fusiform rust infection, and % survival and heritability estimates for different traits in the 8 Test Areas within the Cooperative.

Test Area[1]	# Test Series	# Diallels	Averages			Individual Tree Heritabilities for Height		Family Mean Heritabilities		
			Height	Rust	Survival	h^2_{NS}	h^2_{BS}	Ht.	Rust	Strt
1	3	6	17.9′	1.7%	95%	.31	.38	.85	.	.84
2	0	0								
3	4	9	20.8	12.7	82	.08	.12	.46	.72	.58
4	4	8	19.6	31.9	88	.22	.34	.72	.81	.89
5	6	13	21.3	23.3	93	.31	.39	.85	.87	.76
6	2	4	17.4	3.0	87	.12	.25	.57	.	.49
7	2	4	17.5	44.2	81	.18	.24	.84	.85	.76
8	0	0								
Total	21	44	19.7	19.8	89	.22	.30	.72	.73	.78

[1] Test Areas are: 1 = VA, 2 = Coastal NC, 3 = Coastal SC, 4 = Coastal GA & FL, 5 = Lower Gulf, 6 = Upper Gulf, 7 = Piedmont GA & SC, 8 = Piedmont NC.

The estimates for narrow sense heritability (individual basis) ranged between 0 and 0.93. Reasons for this large range of estimates include: 1) Genetic sampling, there were real differences in the genetic variance included in the 44 samples of 6 parents comprising the diallel mating groups. 2) The variation in heritability estimates were at least partially explained by variation in test precision (as measured by the coefficient of variation (CV) based on rep x family effects) and by average test survival. If test precision was relatively low (CV > 8%) then the likelihood of having a high heritability was relatively low (Figure 1). Likewise if survival was below 85%, there were very few estimates of heritability greater than 0.20 (Figure 2).

Although these relationships are not extremely strong, they illustrate the value of maintaining minimum standards for survival and environmental uniformity in a progeny testing program. While high survival and good test precision do not guarantee that heritability estimates will be high, (the effect of genetic sampling in the small diallels can always be influential - sometimes there are no genetic differences among the six parents, and $h^2 = 0$), in tests that have large environmental variance and/or poor survival, genetic effects will very often be masked, and heritability will be low.

There was no relationship between average height and any estimate of heritability (Figure 3). This is an important "non-relationship". From this, we conclude that we are just as likely to see strong genetic effects on low site index sites as on high site index sites. The average height for a test series varied by almost 25% (from 15.6 feet to 19.2 feet) at age 6

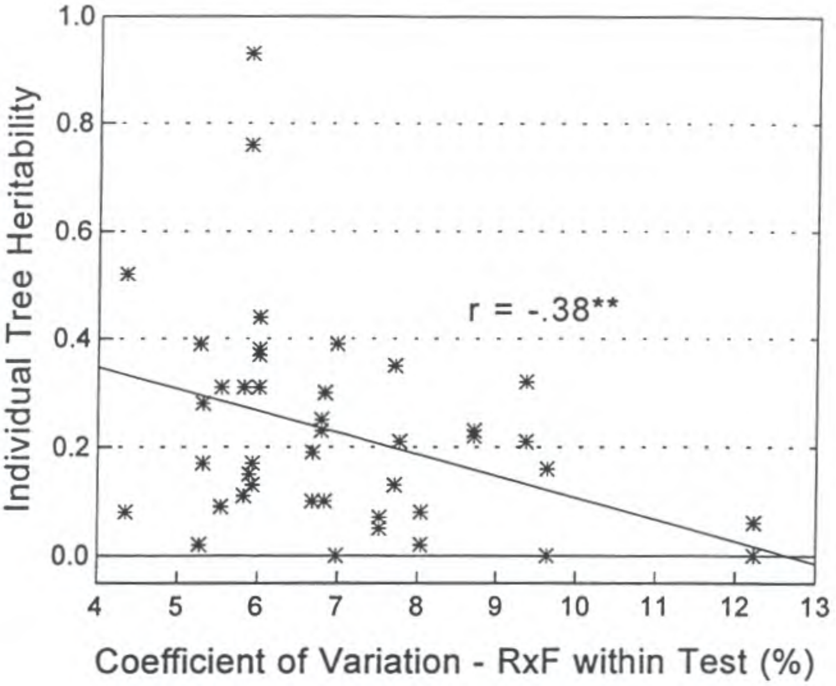

Figure 1. Relationship between estimates of individual-tree narrow-sense heritabilities for height at age 6 years and estimates of pooled coefficients of variation (rep x family mean basis) for height.

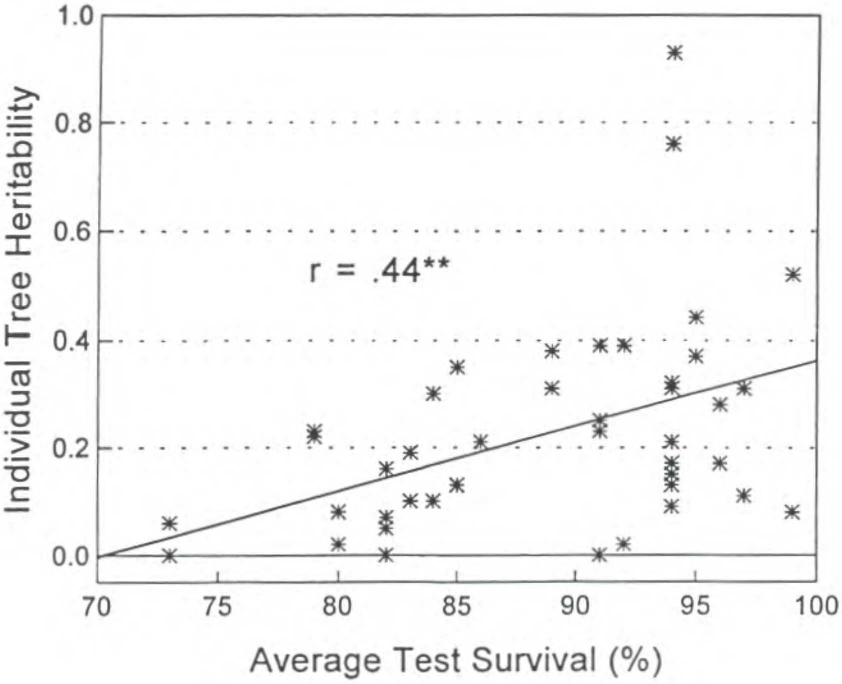

Figure 2. Relationship between estimates of individual-tree narrow-sense heritabilities for height and average test survival at 6 years.

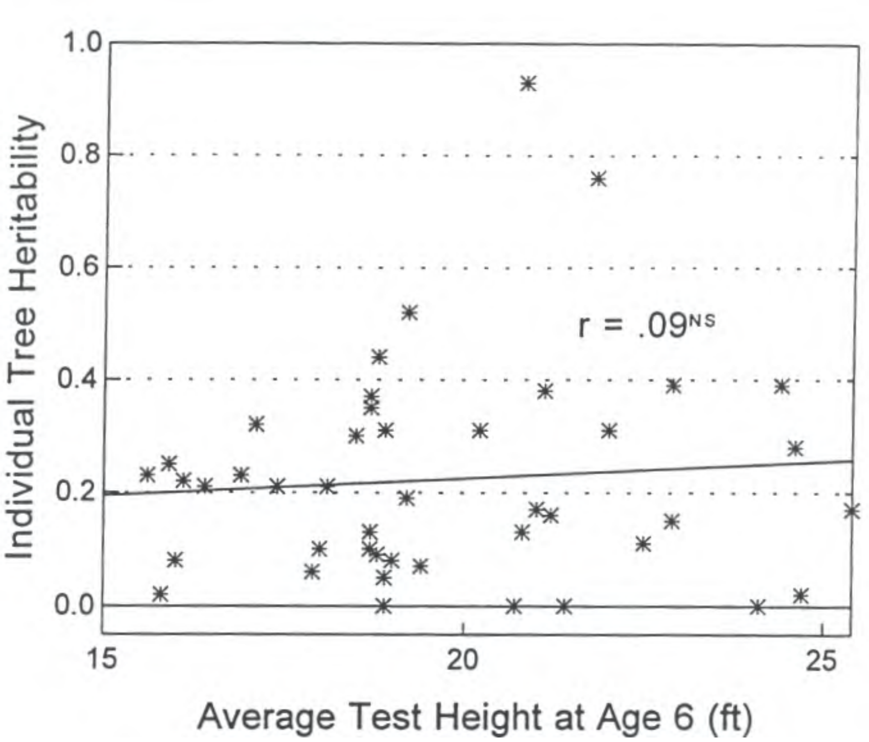

Figure 3. Relationship between estimates of individual-tree narrow-sense heritabilities for height and average test height at age 6 years.

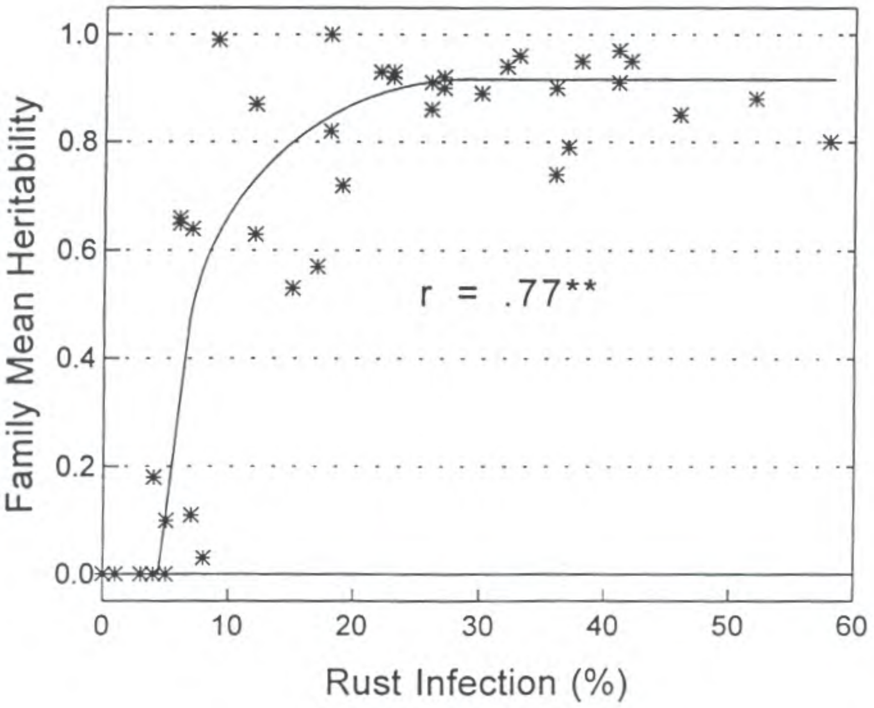

Figure 4. Relationship between estimates of family-mean narrow-sense heritabilities for percent fusiform rust infection and average rust infection level at the test at 6 years.

years. When establishing progeny tests, the use of agricultural fields was encouraged, not because of the potential for fast growth, but because in general the site uniformity on agricultural fields is much better than what is routinely encountered on cut over sites.

The most useful relationship between heritability and site factors was for fusiform rust infection (Figure 4). When rust levels were very low (< 5%) there was very little chance of detecting significant family differences (h^2 based on family means usually near 0). With rust levels of 5% - 20%, the estimates of h^2_F were much more variable than at levels of rust above 20%. The consistency of heritability estimates when rust was above 20% is cause for confidence in these estimates. For routine analyses of diallel tests and OP tests in the Cooperative, rust performance is estimated only when average fusiform rust infection equals or exceeds 20%.

Genetic Correlations Among Traits

In a multi-trait selection index, the relationships or associations among the traits included in the index have a major impact on the gains for any individual trait of interest. For example if there is a strong, unfavorable relationship between height and straightness, selecting for height would degrade stem quality. Across the different diallels, the genetic correlations varied widely:

Genetic Correlation for:	Low	High	Average
Height - Rust Infection	-0.93	0.96	-0.20
Height - Straightness	-1.08	0.98	0.05
Rust - Straightness	-0.93	0.93	0.08

When there is a favorable correlation between height and rust infection or between height and straightness (i.e., negative correlation is favorable since high values for rust and straightness score are bad), selecting trees has been relatively easy. When there is a strong unfavorable genetic correlation, it has been difficult to find tall, straight, rust-free trees. Fortunately the average genetic correlations were either slightly favorable (i.e., r = -0.20 for height and rust infection) or were essentially zero for height and straightness. Again, with the small genetic samples included in each diallel, the correlation can vary widely, but the expectation for the average of all correlations is about zero.

Genotype by Environment Interactions

In past studies, we have seen very little evidence for important genotype by environment interaction (GxE) at the half-sib family level. For example, in the Good General Combiner trial, half-sib families were remarkably stable across a wide range of sites that encompass large differences in site productivity (Li and McKeand 1989, McKeand et al. 1990). In the diallel tests, we have the opportunity to assess GxE for both half-sib and full-sib families. Full-sib families might be expected to display a higher degree of interaction with the environment than half-sib families since there is less genetic variance within each family (i.e., a lower level of buffering to environmental variations) and more of the genetic variance exists among families. Additionally, since GxE at the full-sib family level is caused by both additive and non-additive effects.

One way to evaluate the importance of G x E is to relate its magnitude to the magnitude of genetic variance. The ratio of the genotype x environment variance over the genetic variance may be referred to as the K-statistic:

For half-sib families: $K = \frac{1}{4}\sigma^2_{AxE} / \frac{1}{4}\sigma^2_A$

For full-sib families: $K = (\frac{1}{2}\sigma^2_{AxE} + \frac{1}{4}\sigma^2_{NAxE}) / (\frac{1}{2}\sigma^2_A + \frac{1}{4}\sigma^2_{NA})$

This is a useful measure of genotype by environment interaction when the environments are considered to be a random sample from a larger set. For this case, the K-statistic may be interpreted as the proportional amount by which the expected genetic variance within environments exceeds the genetic variance measured over environments.

The average K-statistic for half-sibs was 0.31 meaning that the GxE variance was only about one-third the genetic variance. As we have found in other trials, the family by environment or specifically the additive genetic by environment variance is of little practical concern. On the other hand, the GxE for full-sibs is higher (K = 0.54), apparently this is due to the contribution of non-additive effects to the GxE. Never the less, the magnitude of GxE variance for full-sibs is still only about half the magnitude of the genetic variance, and it appears to be of small practical importance. More analyses will be conducted to determine if any significant rank changes occur for full-sib families.

Gain Estimates

Genetic gains from family selection for height, % fusiform rust, and straightness score were estimated using the average family mean heritabilities (h^2_F) and average phenotypic standard deviations of family means *(cr$_F$)* for each trait:

$$\text{Gain} = i\, h^2_F\, \sigma_F$$

For a selection intensity of i = 1.0, the expected means of progeny from selected parents (e.g. deployment of the best open-pollinated families from a seed orchard of these clones) would be:

Trait	Current Family Mean	Mean After Selection
Height	19.73'	20.17'
% Rust	34.8%	24.6%
Straightness'	51.0%	57.5%

[1] Straightness is percentage of trees above average for straightness.

Larger gains are possible with higher selection intensities, but these gains illustrate the relative gains possible in the three traits used in selection. These gains do not reflect the gain over unselected populations or over the previous generation. When more tests are available from more Test Areas, and family means can be compared to the same check seedlots, we will estimate gains over unselected populations and the previous generation.

In summary, the analyses of 44 diallels in 21 test series and the initial third-cycle selection work has led to several conclusions:

1. Planting tests on uniform sites is essential if reasonable levels of heritability and genetic gains are to be achieved.
2. Test survival below 85% usually results in low heritability estimates.
3. Genetic differences in height are not related to site index, but genetic differences in rust resistance can only be detected if rust infection exceeds 20%.
4. Genetic correlations among traits vary because of the sampling effect with small diallels, however, on average the correlations are near zero, which indicates that the traits are inherited independently.
5. Genotype by environment interaction effects are relatively minor.

As more diallel data become available, these estimates of variance components and gains will be updated on a regular basis. Ultimately an excellent data base for each of the Test Areas in the Cooperative will be available for us to fine-tune testing and selection procedures.

LITERATURE CITED

Cornelius, J. 1994. Heritabilities and additive genetic coefficients of variation in forest trees. Can. J. For. Res. 24:372-379.

Li, Bailian and S.E. McKeand. 1989. Stability of loblolly pine families in the southeastern U.S. Silvae Genetica. 38:96-101.

McKeand, S.E., B. Li, A.V. Hatcher and R.J. Weir. 1990. Stability parameter estimates for stem volume for loblolly pine families growing in different regions in the southeastern United States. For. Sci. 36:10-17.

Talbert, J.T., F.E. Bridgwater and C.C. Lambeth. 1981. Genetic testing manual. N.C. State University-Industry Cooperative Tree Improvement Program. 37 p.