

# Estimates of Components of Variance and Covariance in Root and Shoot Characteristics of Loblolly Pine After One Growing Season<sup>1/</sup>

ROY W. STONECYPHER, FRANKLIN C. CECH, AND BRUCE J. ZOBEL

## INTRODUCTION

Although a considerable amount of effort has been expended on delineating various types of root systems within and between tree species, there is practically no knowledge of the variation patterns in root development within a local population, or of the inheritance of such growth patterns. This information would be extremely valuable to the tree breeder. It would serve as a guide for improving such characteristics as ability to withstand transplanting shock, drought resistance, resistance to wind throw, as well as growth rate. Such information would also be very useful in tree improvement programs which might be aimed at providing genotypes for problem sites where specialized root systems would be advantageous.

Nearly all the attention of foresters has been focused on crown growth and resultant competition, and the patterns of tree to tree variation of root systems have been largely ignored. It seems logical that root development, efficiency, and competition might play a very large role in the performance of a tree. It is, therefore, essential to have some idea of the magnitudes of genetic and environmental variances for root characteristics.

The study reported here was designed to estimate genetic and environmental components of variance and covariance for several root and shoot characteristics of young loblolly pine from a single geographic source.

## LITERATURE REVIEW

There is abundant evidence that various environmental factors affect the form and growth rate of tree roots. Lodgepole pine root form varies widely with soil conditions and between individuals in the same soil (Horton, 1958). Root and shoot growth of loblolly pine was significantly affected by scalping, shading, and mulching in Texas (Bilan, 1960). Redmond (1954) demonstrated the fact that birch roots made their optimum development in loam as compared to sand, while Meyer (1961) found relative root length (root length per square centimeter of leaf area) in beech decreased with increasing soil fertility. Several investigators have noted that the general growth pattern of roots within a species is inherently controlled, but just as for top development, environmental influence will modify this pattern (Lenhart, 1934; Ogievskij, 1958; Merritt, 1960).

Growth patterns generally differ between species, and in the case of shortleaf and loblolly pine, the quantitative differences were maintained under differing environmental conditions (Reed, 1939). *Quercus* species also evidenced form and growth differences which were modified by different soils, and Carpenter and Guard (1954) were able to recommend transplanting certain species on the basis of root branching.

Genetically, little is known about root development and morphology. As early as 1949, Righter and Duffield demonstrated differences between the root system of ponderosa pine and the ponderosa - apache pine hybrid (*P. ponderosa* x *latifolia*). This hybrid has a more vigorous root system with a well developed tap root while the ponderosa pine seedling has a less vigorous root system with a poorly defined tap root. Similar differences were found in Willow hybrids by Ortman (1958).

Selection of tree and shrub willow forms was expedited by root type (Ortman, 1961), and drought resistance of *Acer saccharum* from west of the Appalachian mountains was attributed to the extensive, vigorous fibrous root system of that ecotype (Kriebel, 1961).

Racial variation in root form was noted by Snyder (1961) with longleaf pine (*Pinus palustris*) where the root systems of seedlings from the Southeast Georgia seed source were more fibrous than those from further west. The number of lateral roots was also greater for the Eastern form. Successful clonal selection for growth rate of hybrid poplar was based on bark thickness of roots of equal size (Anonymous, 1959) and Ruggeri (1963), also noted

<sup>1/</sup> Silviculturist, Southlands Experiment Forest, International Paper Company, Associate Professor of Forest Genetics, West Virginia University, and Professor of Forest Genetics, North Carolina State University.

anatomical differences in the roots of certain hybrid poplars involving bark thickness. In a study of blue and green races of douglas fir, Hengst (1958) noted that the influence of race on most root characteristics was negative but tree class and soil difference were important.

From this information it might be postulated that there are differences in root form due to environmental influence, but superimposed on these differences various species and sub-species possess unique root types. Within a species there are racial differences which have arisen because of differences in environment. For example, there is some indication that pines growing on the deep peat lands in the Coastal Carolinas have a stilt-like root form rather than the typical tap root usually found in the species. When trees with tap roots are planted in the deep peat soils they will grow for several years and then fall over while native trees of the same species are wind-firm even through hurricanes.

More recently Ledig (1965), has reported differences in shoot-root ratios between progenies of one-year-old loblolly pine, and further concluded that shoot-root ratios are only suitable for comparison of material which is the same age and has been grown under similar conditions.

## MATERIALS AND METHODS

### Experimental Design

The seedlings used in this study were from control pollinated crosses made as a part of the overall International Paper - North Carolina State University Cooperative Heritability Study. The mating design used and objectives of the study were described by Cech et. al. (1962). For the control pollination phase, Design I developed by Comstock and Robinson (1948, 1952), was used. Using this mating design, one tree was arbitrarily designated as male and mated to four different females; the four crosses with each male is termed a male group. One male and four females were used because of considerations of statistical efficiency, but as often happens when making controlled pollinations on forest trees, some crosses failed to produce viable seed. Because of such failures, fewer than four crosses were frequently obtained for a male group. Although the necessity of using fewer than four females for each male group decreases the statistical efficiency, the three and even two female "male groups" can be used to make estimates of the genetic and environmental parameters desired with very little computational difficulty.

The root study reported here was initiated with 50 full-sib families from excess seed remaining after the planting of the main study. Because this was excess seed, it was possible to use only one male group with four females present; the remainder had either three or two females per male. Sixty stratified seed from each family were divided equally and sown on April 19, 1963, in six metal pots which were eight inches in diameter and approximately seven inches deep. The seeds of each cross were weighed to the nearest 0.001 gm. prior to stratification and sowing.

Soils used were obtained from two locations and were placed in the pots with as little disturbance of the soil profiles as possible. The soils were obtained from the east and west properties of the Southlands Experiment Forest. The U.S.D.A, soil texture classification of the west property, hereafter referred to as soil A, was sand. The east property soil, hereafter referred to as soil B, was classified as loamy sand. Although fairly detailed laboratory analyses showed soils A and B to be quite similar, the natural vegetation growing on the east and west properties is definitely different. The east property supports stands of loblolly and shortleaf pines and is typical of the Southeastern Piedmont, while the west property has extensive stands of longleaf pine and scrub oak. The specific locality from which soil A was obtained has been under cultivation and now supports a slash pine plantation. Soil B was obtained from an area, which as far as is known, was never under agricultural cultivation.

Where necessary, the seedlings were thinned on June 26, 1963, so that no more than five seedlings were growing in each pot. Seed of some crosses had poor germination or survival which resulted in fewer than five seedlings in each pot.

### Measurements

Starting September 17, 1963, the seedlings were lifted from the pots and soil was carefully removed from the roots by a low-pressure stream of water. The group of seedlings from each pot were then placed in polyethylene bags and stored in a refrigerator until measure-

Table 1. Correlations between seed weight and seedling variables and ratios of seedlings approximately 150 days old.

Trait	r values
Shoot length	0.34*
Root length	0.08
Shoot weight	0.35*
Root weight	0.23
Number of lateral roots	0.27
Shoot length/root length	0.08
Shoot weight/root weight	0.11
Root length/number of lateral roots	-0.24

\* Significant at 0.05 level.

ments could be made. The measurements were made over a period of approximately sixty days.

At the time of measurement, the seedlings were removed from the bags, and the root systems were further cleaned by gentle agitation in water. Shoot and root length were then measured to the nearest cm. and the number of lateral roots greater than ten cm. in length were counted. Following these measurements, the seedling were cut at the root collar and both the roots and shoots were oven dried at 105 °C for 48 hours. Upon removal from the oven, the root and shoot of each seedling was weighed to the nearest 0.001 gm.

### Statistical Analyses

Because of poor germination and survival, only 39 of the original 50 full-sib families were complete enough to be included in the analyses. Because of the unequal numbers of seedlings in some pots, all analyses of variance and covariance were performed on plot means and the within plot variances were calculated separately for each plot. Robinson et.al.(1949) used a similar method for estimating the within plot variances in corn. Although, as Snedecor (1946) points out, this method is not exact, it was felt that reasonably accurate estimates of the parameters desired could be obtained for this root study.

In addition to the five traits measured (see Table 1), ratios of shoot weight to root weight, shoot length to root length, and root length to number of lateral roots were included in the analyses. Plot means and within plot variances were calculated for each trait as well as for the three ratios. Prior to performing the analyses of variance and covariance, correlations between seed weight and the eight variables were computed. It is commonly believed that size of seed has a direct effect upon size of shoot of the seedling and perhaps on the root characteristics. If this effect were large, it could result in an upward bias of the variance due to female differences. Therefore, seed size of the various crosses were measured, and the correlations of the traits are presented in Table 1.

It is obvious that because of the general low correlation between seedling size and seed size relationships, no adjustment for seed weight was necessary in the subsequent analyses.

Analyses of variance and covariance were performed on plot means first separately for soil A and B followed by the pooled analyses for both soils as illustrated in Tables 2 and 3.

1/

All analyses and computations were performed on an IBM computer with machine programs which were specifically designed by the senior author for the analyses of data for all phases of the control pollinated heritability study.

### Estimation of Genetic and Environmental Components of Variance and Covariance.

The mean squares for the analyses of the eight traits were determined by separate soils and combined for both soils. The pooled error terms were obtained by combining the replication by males and replications by females in males interactions. In addition to the analyses of variance, analyses of covariance for the 28 relationships among the traits were performed.

Estimates of components of variance and covariance were obtained from the means squares and mean cross products of the analyses of variance and covariance. In the case of the components of variance, difficulties arose because in several cases the estimates obtained were

1/ Grateful acknowledgement is made to Messrs. L. W. Brown and Graham E. Abbott of International Paper Company's Southern Kraft Division's Engineering Computer Facility, who provided computer time and helped in "debugging" the program used to analyze the data of this study.

Table 2. Form of analysis of variance and covariance used for analyses by separate locations.

Source	d.f.	m.s.	Expected mean squares <sup>a</sup>
Replications	2	m.s.1	$\frac{\sigma^2_w}{k} + \sigma^2_p + 39\sigma^2_b$
Males	15	m.s.2	$\frac{\sigma^2_w}{k} + \sigma^2_p + 3\sigma^2_f + 7.28\sigma^2_m$
Females/males	23 <sup>c</sup>	m.s.3	$\frac{\sigma^2_w}{k} + \sigma^2_p + 3\sigma^2_f$
Pooled error	76	m.s.4	$\frac{\sigma^2_w}{k} + \sigma^2_p$

---

Within plot                      b                      m.s.5                       $\frac{\sigma^2_w}{k}$

<sup>a</sup>    k = Harmonic mean of plants per plot = 4.13 for soil A and 4.25 for soil B.

$\sigma^2_w$  = Variance due to differences among plants in plots.

$\sigma^2_p$  = Variance due to differences among plots.

$\sigma^2_f$  = Variance due to differences among progenies from females mated to the same male.

$\sigma^2_m$  = Variance due to differences among progenies from the same male.

$\sigma^2_b$  = Variance due to differences among replications.

<sup>b</sup>    Within plot degrees of freedom for soil A and soil B was 396 and 407, respectively.

<sup>c</sup>    Ten male groups had two females per male, five had three, and one had four.

negative. Anderson (1960) discusses this problem and gives two alternative methods for estimating components from expected mean squares which contain negative component estimates. He points out that the biased procedure of pooling the sums of squares, assuming the true value of the component which had a negative estimate of zero, gives more precise estimates. This biased procedure was followed in estimating the components of variance from the mean squares (see Tables 4 and 5). The genetic correlations were estimated from the male components for the relationships between four of the five traits which had non-negative male components in the pooled analyses (Data are shown in Table 6).

#### Genetic Interpretation of the Components of Variance and Covariance.

The necessary assumptions for the genetic interpretation of components of variance estimated from Design I have been presented by Comstock and Robinson (1948). These authors further show that the male component ( $\sigma^2_m$  or  $\hat{\sigma}^2_m$  in Table 5) estimates one-quarter of the additive genetic variance, and the female component ( $\hat{\sigma}^2_f$  or  $\hat{\sigma}^2_f'$  in Table 5) estimates one-quarter of the additive plus one-quarter of the dominance variance. Similarly, the components of covariance have the same genetic interpretation as the components of variance (Falconer, 1960). For example, the component of covariance for males estimates one-fourth of the covariance of the additive values of two traits.

Heritabilities, such as those reported in Table 6, were estimated from the following formula:

$$h^2 = \frac{4(\hat{\sigma}^2_{m'})}{k' \left( \frac{\hat{\sigma}^2_{w'}}{k'} + \hat{\sigma}^2_{p'} + \hat{\sigma}^2_{fs} + \hat{\sigma}^2_{ms} + \hat{\sigma}^2_{f'} + \hat{\sigma}^2_{m'} \right)}$$

The genetic correlations, which are reported in Table 6, were estimated by the following formula:

$$\hat{r}_g = \frac{\hat{\sigma}_{mxy}}{(\hat{\sigma}^2_{mx'} \hat{\sigma}^2_{my'})^{1/2}}$$

Where:

$\hat{r}_g$  = genetic correlation estimate

$\hat{\sigma}_{mxy}$  = additive genetic covariance for traits x and y

$\hat{\sigma}^2_{mx'}$  = additive genetic variance for trait x

$\hat{\sigma}^2_{my'}$  = additive genetic variance for trait y

Table 3. Form of analysis of variance and covariance used for analyses which were pooled over soils.

Source	d.f.	m.s.	Expected mean squares <sup>a</sup>
Soils	1	m.s.1'	$\frac{\sigma^2_{w'}}{k'} + \sigma^2_{p'} + 3\sigma^2_{fs} + 7.77\sigma^2_{ms} + 39\sigma^2_{b'} + 117\sigma^2_s$
Replications/soils	4	m.s.2'	$\frac{\sigma^2_{w'}}{k'} + \sigma^2_{p'} + 39\sigma^2_{b'}$
Males	15	m.s.3'	$\frac{\sigma^2_{w'}}{k'} + \sigma^2_{p'} + 3\sigma^2_{fs} + 7.28\sigma^2_{ms} + 6\sigma^2_{f'} + 14.56\sigma^2_{m'}$
Females/males	23	m.s.4'	$\frac{\sigma^2_{w'}}{k'} + \sigma^2_{p'} + 3\sigma^2_{fs} + 6\sigma^2_{f'}$
M x S	15	m.s.5'	$\frac{\sigma^2_{w'}}{k'} + \sigma^2_{p'} + 3\sigma^2_{fs} + 7.28\sigma^2_{ms}$
F/M x S	23	m.s.6'	$\frac{\sigma^2_{w'}}{k'} + \sigma^2_{p'} + 3\sigma^2_{fs}$
Pooled error	152	m.s.7'	$\frac{\sigma^2_{w'}}{k'} + \sigma^2_{p'}$
Within plot	803	m.s.8'	$\frac{\sigma^2_{w'}}{k'} + \sigma^2_{p'}$

<sup>a</sup> k' = Harmonic mean of plants per plot = 4.19

$\sigma^2_{w'}$ ,  $\sigma^2_{p'}$ ,  $\sigma^2_{f'}$ , and  $\sigma^2_{m'}$  are due to the same sources as indicated in Table 3.

$\sigma^2_{fs}$  = Variance due to the interaction between paternal half-sibs and soils.

$\sigma^2_{ms}$  = Variance due to the interaction between progenies from the same male and soils.

$\sigma^2_s$  = Variance due to differences among soils.



TABLE 4. Mean squares for the analyses of variance by separate soils and combined for soils

SOIL A:

Source	d.f.	Shoot Length		Shoot Weight		No.Laterals	Shoot Length	Shoot Weight	Root Length
		Root Length	Root Length	Root Length	Root Weight		No.Laterals		
Replications	2	18.08250	412.71500	0.12340	0.00850	55.31975	0.05957	2.76295	166.19400
Males	15	20.25040	30.40333	0.01178	0.00149	3.11790	0.06972	1.12195	20.85806
Females/males	23	27.03691	43.62608	0.00829	0.00082	2.27847	0.09649	0.58949	15.36526
Pooled error	76	2.89643	24.14683	0.00940	0.00075	1.39883	0.02192	0.45248	11.90062
Within plot	396	40.05710	76.21543	0.01610	0.00141	3.24310	0.22359	0.74775	35.18589

SOIL B:

Replications	2	68.04000	740.03000	0.47190	0.03986	23.70740	0.04339	0.69855	55.00650
Males	15	11.78473	103.27733	0.05278	0.00421	3.79877	0.05717	0.58986	12.54226
Females/males	23	13.34130	106.31043	0.05717	0.00461	2.83559	0.02267	0.40910	3.94652
Pooled error	76	8.17396	45.50302	0.04295	0.00368	1.84585	0.01306	0.44511	5.68951
Within plot	407	20.50335	113.40839	0.05098	0.00387	3.38304	0.08147	0.87080	17.11010

COMBINED:

Soils	1	788.39900	579.36000	3.36600	0.25654	20.07220	0.29333	0.20510	117.10000
Reps/soils	4	43.06125	576.37000	0.29765	0.02418	39.51355	0.05148	1.73072	110.60025
Males	15	19.56193	72.52733	0.02818	0.00350	4.86603	0.08170	1.19634	16.54073
Females/males	23	17.18491	92.35608	0.02919	0.00230	1.77164	0.07803	0.67352	8.88713
Males x soils	15	12.47320	61.15266	0.03638	0.00220	2.05063	0.04519	0.51546	16.85960
Females/males x soils		23.19330	57.58043	0.03626	0.00313	3.34242	0.04113	0.32506	10.42465
Pooled error	152	5.53520	34.82499	0.02617	0.00222	1.62235	0.01750	0.44880	8.79506
Within plot	803	30.14630	95.06666	0.03378	0.00266	3.31403	0.15156	0.81012	26.02419

TABLE 5. Estimates of components of variance by separate soils and combined for soils

SOIL A	Shoot Length		Shoot Weight	Root Weight	No.Laterals	Shoot Length	Shoot Weight	Shoot Length	
	Root Length	Root Length				Root Length	Root Weight	No.Laterals	
$\hat{\sigma}_m^2$	N.C.	N.C.	0.00036	0.00009	0.26360	N.C.	0.07314	0.75450	
$\hat{\sigma}_f^2$	6.14440	6.49308	N.C.	0.00002	0.29321	0.01585	0.04567	1.15488	
$\hat{\sigma}_p^2$	N.C.	5.69274	0.00551	0.00041	0.61358	N.C.	0.27143	3.38104	
$\frac{\hat{\sigma}_w^2}{k}$	9.69905	18.45409	0.00389	0.00034	0.78525	0.05413	0.18105	8.51958	
SOIL B									
$\hat{\sigma}_m^2$	N.C.	N.C.	N.C.	N.C.	0.13230	0.00473	0.02103	0.99693	
$\hat{\sigma}_f^2$	1.72244	20.26913	0.00474	0.00031	0.32991	0.00143	N.C.	N.C.	
$\hat{\sigma}_p^2$	3.34964	18.81871	0.03096	0.00277	1.04984	N.C.	0.08007	1.66361	
$\frac{\hat{\sigma}_w^2}{k}$	4.82432	26.68131	0.01199	0.00091	0.79601	0.01917	0.20489	4.02591	
COMBINED									
$\hat{\sigma}_m^2$	.08723	N.C.	N.C.	0.00006	0.16713	N.C.	0.03021	0.30951	
$\hat{\sigma}_f^2$	N.C.	5.79594	N.C.	N.C.	N.C.	0.00615	0.04016	N.C.	
$\hat{\sigma}_{ms}^2$	N.C.	0.49069	0.00001	N.C.	N.C.	0.00055	0.01139	0.88392	
$\hat{\sigma}_{fs}^2$	4.71899	7.58514	0.00336	0.00030	0.57335	0.00264	N.C.	0.51349	
$\hat{\sigma}_{p'}^2$	N.C.	12.13605	0.01811	0.00158	0.83141	N.C.	0.25545	2.58404	
$\frac{\hat{\sigma}_w^2}{k'}$	7.19482	22.68894	0.00806	0.00064	0.79037	0.03617	0.19334	6.21102	

1/ N.C. = negative estimate of component

TABLE 6. Estimates of heritability and genetic correlations

<u>Estimates of Heritabilities</u> <sup>1/</sup>					
<u>Trait</u>	<u>Shoot Length</u>	<u>Root Weight</u>	<u>No. Laterals</u>	<u>Shoot Weight</u> <u>Root Weight</u>	<u>Shoot Length</u> <u>No. Laterals</u>
Heritability:	0.01	0.05	0.14	0.11	0.04

Estimates of Genetic Correlations

<u>Traits</u>	<u>Root Weight</u>	<u>No. Laterals</u>	<u>Shoot Weight/Root Weight</u>
Shoot Length	3.18	2.97	0.36
Root Weight		2.37	-0.78
No. Laterals			-0.50

1/  $\hat{\sigma}_m^2$  for shoot weight, root length, and shoot length - root length ratio, were negative and, therefore, no additive variance was indicated for these traits.

RESULTS AND DISCUSSION

A total of 1,037 seedlings were measured in this study. Considerable within plot differences were found as can be seen from the estimates of the within plot components of Table 5. In the case of two traits (shoot length-root length ratio, and shoot length) the estimate of the within plot component was larger than the plot to plot component.

Male group mean values for the eight traits analyzed are given in Table 7. Also in

TABLE 7. Male group means averaged over both soils and means for both soils for the eight variables used in analyses

Male #	No. of Female	Shoot Length CM.	Root Length CM.	Shoot Weight GMS	Root Weight CMS	No. of Lateral Roots	<u>Shoot Length</u>	<u>Shoot Weight</u>	<u>Root Length</u>
							Root Length	Root Weight	No. Lateral Roots
10	2	15.4	34.8	0.45	0.13	4.8	0.46	3.5	8.3
12	3	17.8	35.4	0.50	0.14	4.7	0.56	3.4	9.0
14	3	18.3	32.0	0.41	0.11	3.6	0.34	3.6	10.0
16	3	16.6	30.3	0.43	0.11	4.2	0.61	4.0	9.8
19	2	15.4	37.8	0.48	0.14	4.7	0.45	3.4	10.3
20	4	15.9	37.1	0.45	0.14	4.8	0.45	3.3	9.5
28	2	15.0	32.6	0.40	0.10	3.3	0.51	3.9	12.4
30	2	16.6	33.9	0.43	0.11	3.7	0.52	3.7	11.1
34	2	15.6	34.3	0.42	0.11	3.8	0.50	3.8	10.5
37	2	16.7	33.0	0.38	0.11	3.8	0.56	3.5	10.0
39	2	17.3	30.7	0.46	0.11	3.2	0.59	4.4	12.0
40	2	15.6	33.0	0.44	0.12	3.9	0.49	3.9	9.8
43	3	17.5	36.0	0.52	0.13	4.8	0.50	3.9	9.5
46	2	15.9	34.9	0.43	0.13	4.7	0.52	3.7	9.4
49	2	16.2	36.5	0.53	0.16	5.2	0.48	3.5	8.3
50	3	13.9	35.1	0.40	0.11	3.9	0.41	3.4	10.6
TOTAL	39								
<u>Averages:</u>									
Soil A		14.4	32.7	0.33	0.10	4.0	0.49	3.6	10.7
Soil B		18.1	35.9	0.57	0.16	4.6	0.56	3.7	9.3
Both Soils		16.2	34.3	0.45	0.13	4.3	0.52	3.6	10.0

Table 7 are the average values for each of the traits by soils. As mentioned earlier, laboratory analyses of the physical and chemical properties of the two soils used showed the soils to be quite similar. However, it is obvious from the mean values presented in Table 7, that the growth response of the seedlings was quite different in the two soils. The F test of soil effects was significant at the five percent level for three of the eight traits analyzed, viz., shoot length, and shoot weight, and root weight.

Of the eight traits presented in Table 7, the greatest difference among male group means is for number of lateral roots greater than ten cm., followed by root weight and the ratio of shoot weight to root weight in order. Only one of the traits analyzed (number of lateral roots) showed a significant difference for male effects.

Although there was no evidence for differences among male groups in the case of root length, there was evidence for differences among females mated to the same male. Even more striking in the case of root length, is the evidence for a large female by soil interaction effect. If an F test for females effect on root length is applied to the mean squares of separate soils in Table 5, we find that there are significant differences among females mated to the same male. If, however, we apply an F test to the combined mean squares, we find that the test for root length difference among females is non-significant if the female by soils interaction is used as the denominator for the test.

Such genotype by environment interaction effects are of great importance to the tree breeder. For example, the breeder who wanted to increase root length would be forced to decide whether to concentrate on producing types with an increased root length for a specific soil and thereby possibly obtain greater improvement, or to concentrate on producing types which had longer roots in a variety of soils with a possible resultant lesser degree of improvement. It would seem, at the present time, that the forest tree breeder is more interested in producing types which are fairly widely adapted to a variety of site conditions. However, the possibility of selecting genotypes for specific environmental and cultural situations should not be overlooked by the forest geneticist. More important, tests of superior tree progeny as well as experiments designed to estimate genetic variances in forest trees should be planned so that some measure of the magnitudes of genotype-environment interactions can be obtained.

The F test for the presence of a significant female by soil interaction effect showed that shoot length, number of lateral roots, and the ratio of shoot length to root length were significant at the 0.01. level, and root length was significant at the 0.05 level (see Table 4).

The estimates of narrow sense heritability reported in Table 6 are on an individual basis, and were obtained from the components of variance derived from the combined analyses.

As can be seen in Table 6, the heritability estimates are generally low. It is encouraging, however, that root weight, shoot weight-root weight ratio, and number of lateral roots, show some evidence for presence of additive variance in these young seedlings. It appears that some gains could be obtained by selecting within a population for more fibrous or spreading root systems resulting in a production of seedling types which have a greater ability to survive outplanting as well as to more fully utilize soil nutrients.

In order to examine the possible relationships between these three root traits and ability to survive outplanting, an examination of values obtained from the field planting of 31 full-sibs, which were common to both the large field study and the root study, was made. There were no significant correlations between number of laterals or root weight and survival, but there was a small but significant negative correlation between the shoot weight-root weight ratio and first year survival. Since the seedlings of the field planting were carefully handled and environmental conditions were such as to maximize survival, the value of the correlation obtained could be conservative. More rigid tests of survival ability might possibly show much better relationships to root traits.

Of the traits analyzed in this study, three (root length, shoot length/root length, and root weight/root weight) show evidence of dominance variance. This is particularly strong in the case of root length as can be seen by the estimates of the female components in the combined analyses of Table 5. As mentioned above, the estimates of the female in male components of variance  $S_{14}^2$  contain one-fourth of the additive plus one-fourth of the dominance variance if the assumption of no epistasis is made. Therefore, - if the estimate of the female component of variance is larger than the male component there is evidence for the presence of dominance variance.



If an appreciable portion of the genetic variance of a characteristic is the result of dominance variance, then methods of selection used should be altered in order to make maximum gains. A simple selection system will not give maximum gain and only specific crosses, progeny tested under proper conditions, would enable the breeder to take advantage of dominance variance.

Estimates of genetic correlations, which are reported in Table 6, are of interest to the breeder for the following two reasons: 1. They indicate how selection for one trait will change another trait, and 2. They indicate if a secondary trait which might be relatively easy to evaluate can be used to select for a primary trait which might be more difficult to evaluate. For example, if an above ground seedling characteristic had a high genetic correlation with a root characteristic, the former more easily measured trait could be used to select for the root trait.

The genetic correlations in Table 6 were estimated from the combined covariance analyses and the variance analyses for four traits which contained non-negative male components. Theoretically, these genetic correlations should be less than or equal to one. The fact that the correlations were estimated from components of variance and covariance which had rather large standard errors resulted in values greater than one. The exact values of the correlations reported in Table 8 should not receive great emphasis. However, it is of interest to examine the sign and general degree of relationship between the traits.

The two correlations of most interest are those which show the relationships between shoot length and the root characteristics of weight and number of lateral roots. The indication from the correlations calculated is that selection for increased shoot length would also result in an increase of root number and size.

It is important to emphasize that this study used families which were derived from randomly selected parent trees which were growing in the same locality under quite similar environmental conditions. Whether the estimates obtained in this study are similar to natural loblolly pine growing under more varied environmental conditions is debatable. However, it seems logical that the heritability estimates obtained in this study are conservative when compared to estimates which might be obtained from populations growing under more varied environmental conditions which, for example, exist over an area serviced by a loblolly pine seed orchard.

#### Summary

The estimates of additive variance and, therefore, the narrow sense heritabilities obtained from the characteristics observed in this study were generally quite low. Of the five root and shoot traits and three ratios analyzed, number of lateral roots greater than 10 cm., root weight, and the ratio of shoot weight to root weight gave the highest estimates of narrow sense heritability. Although the heritability estimates were fairly low for number of laterals and root weight, their values indicate that there is usable genetic variance present in a local population for these two root traits.

The results indicated that the genetic variances of three traits analyzed in this population are the result of dominance variance. Although dominance variance can be utilized in a breeding program, the evaluation of specific crosses becomes necessary.

Four characteristics and ratios analyzed showed evidence of quite large variances caused by genotype by environment interactions. These interaction estimates were particularly strong in the case of the female by soils effects. The possibility of presence of such genotype by environment interactions should be strongly considered in planning progeny tests as well as experiments designed to estimate genetic variances in forest trees. If such effects are ignored, serious over estimates of gains or poor evaluations of genotypes could result.

The standard errors of the estimates of the components of variance, particularly the male components, were disappointingly high. It appears that if reliable estimates of genetic and environmental components of variance for forest tree population grown under field conditions are to be made, large amount of experimental material will have to be used.

The standard errors of estimates of components of variance, obtained from traits measured in the extensive field plantings involving 51 male groups at Southlands, are of acceptable magnitudes. These larger studies are yielding reliable estimates of genetic variances for many important tree characteristics.

## LITERATURE CITED

- Anderson, R. L., 1960. Uses of variance component analysis in the interpretation of biological experiments. Bulletin of the International Statistical Institute 31st Session, Vol. 37.
- Anonymous, 1959. U.S.D.A., N.E. Forest Experiment Station Annual Report, p. 18.
- Bilan, V. M., 1960. Root development of loblolly pine seedlings in modified environments. Bulletin 4, Dept. For., S. F. Austin State College, Nacagdoches, Texas.
- Carpenter, I. W. and Guard, A. T., 1954. Anatomy and morphology of the seedling roots of four species of the genus Quercus - Journal of Forestry 52(4):269-274.
- Cech, F. C., Stonecypher, R. W., and Zobel, B. J., 1962. Early results from the cooperative loblolly pine heritability study. Proc. of a Forest Genetics Workshop., Publ. No. 22 of the SFTIC, 64-68.
- Comstock, R. E. and Robinson, H. F., 1948. The components of genetic variance in populations of biparental progenies and their use in estimating the average degree of dominance. Biometrics 4:254-266.
- \_\_\_\_\_ 1952. Estimation of average dominance of genes. Heterosis. Iowa State College Press: 494-516.
- Falconer, D. S., 1960. Introduction to quantitative genetics. The Ronald Press Company, New York, 365 p.
- Hengst, E., 1958. Wurzelstockuntersuchungen an der Douglasie (The root system of douglas fir) Arch. Forstw. 7(4/5):338-351.
- Kriebel, H. B., 1963. Selection for drought resistance in sugar maple. World Consultation on Forest Genetics and Tree Improvement, Section 3 FAO, Stockholm, Sweden.
- Ledig, F. T., 1964. Genetic differences in relative growth of shoot and root systems in Pinus taeda seedlings as measured by the shoot-root ratio and the allometric formula. M. S. Thesis, North Carolina State University, Raleigh, North Carolina.
- Lenhart, D. Y., 1934. Initial root development of longleaf pine. Journal of Forestry 32:459-461.
- Merritt, C., 1959. Studies in the root growth of red pine (Pinus resinosa). Forestry Abstracts 21(3):2858, July 1960. (Thesis Abstract).
- Meyer, F. H., 1961. Die Entinicklung von Buchenjungopflanzen in unterschiedlichen Bodenmilieu ( The development of young beech plants in different soil conditions) Ber. Dtsch. Bot. Ges 74(7):292-299.
- Ogievskij, V. V., 1958. Vljanie uslovij mestoproizrastanija na stroenie kornevyh system v 17-20 letnih kulturah sosny (Pinus silvestris L.) Lenigradskoj oblasti (The effect of site factors in the form of the root system of 17-20 year old Pinus sylvestris L. in plantations in Leningrad Province). Bot. Z. 43(11):1613-1618.
- Ortmann, C., 1958. Kurzer Beitrag zur Frage arteignener Wurzeltypen bei Salix (Specific variation in root systems of Willows) Arch. Forstw. 7(10/11):888-910.
- \_\_\_\_\_ 1961. Vorlaufige Untersuchungsergebnisse zur Frage der Selektionstypen fur die Fruhdiagnose von Salix alba-populationen (Preliminary investigations into the selection of types for the early diagnosis of Salix Alba populations) Silvae Genetica 10(2):43-48.
- Redmond, D. R., 1954. Variations in development of yellow birch roots in two soil types. For Chron. 30(4):401-406.
- Reed, J. F., 1939. Root and shoot growth of shortleaf and loblolly pines in relation to certain environmental conditions. Bulletin 4, School of Forestry, Duke University, 52 p.
- Righter, F. I. and Duffield, J. W., 1951. Hybrids between ponderosa and apache pine. Journal of Forestry 49:345-349.
- Ruggeri, C., 1963. Anatomical differences in the roots of some Euramerican popular hybrids. Publ. Cent. Sper. Agric. For. Roma 6:131-140.
- Snyder, E. B., 1961. Racial variation in the root form of longleaf pine seedlings. Proc. 6th South. Conf. For. Tree. Imp., June 1961., Gainesville, Fla.