variance had a local maximum at about 6 years of age and increased only slightly after that time.

Non-additive variance for cross-sectional area in this experiment was unimportant after about 6 years of age.

The assumption that trees are generally circular in cross-section would not lead to appreciable inaccuracy in selection in this experiment.

References

BECKER, W. A.: Manual of Quantitative Genetics. 4th ed.. Academic Enterprises, Pullman, WA, USA (1984). — BENTZER, B. G., FOSTER, G. S., HELLBERG, A. R. and PODZORSKI, A. C.: Trends in genetic and environmental parameters, genetic correlations, and response to indirect selection for 10-year volume in a Norway spruce clonal experiment. Canadian Journal of Forest Science 19, 897—903 (1989). — COTTERILL, P. P. and DEAN, C. A.: Changes in the genetic control of growth of radiata pine to 16 years and efficiencies of early selection. Silvae Genetica 37, 138—146 (1988). — COTTERILL, P. P. and ZED, P. G.: Estimates of genetic parameters for growth and form traits in four *Pinus radiata* D. DON progeny tests in South Australia. Australian Forest Research 10, 155—167 (1980). — FALCONER, D. S.: Introduction to Quantitative Genetics. 3rd ed. Longman, Harlow, UK (1989). — FOSTER, S.: Trends in genetic parameters with stand development and their influence on early selection for volume growth in loblolly pine. Forest Science 32, 944—959 (1986). — FRANKLIN, E. C.: Model relating levels of genetic variance to stand development of four North American conifers. Silvae Genetica 28, 207—212 (1979). — GRIFFING, B.: Concept of general and specific combining ability in relation to diallel crossing systems. Australian Journal of Biological Sciences 9, 463—493 (1956). — LAMBETH, C. L.: Juvenile-mature correlations in Pinaceae and implications for early selection. Forest Science 26, 571—580 (1980). — LOWE, W. J. and VAN BUIJTENEN, J. P.: Early testing procedures applied to tree improvement programs. Proc. 20th Southern Forest Tree Improvement Conference, Charleston, SC, 26 to 30/6/1989, pp 250—258 (1989). — MAGNUSSEN, S.: Determination of optimum selection ages: a simulation approach. Proc. 20th Southern Forest Tree Improvement Conference, Charleston, SC 26 to 30/6/1989, pp 269—285 (1989). — MATHESON, A. C. and RAYMOND, C. A.: Effects of thinning in progeny tests on estimates of genetic parameters in *Pinus radiata*. Silvae Genetica 33, 125—128 (1984). — MATHESON, A. C., SPENCER, D. J. and KRIEDEMANN, P. E.: Age-age correlation in radiata pine. I. Family x environment interactions in plantation and greenhouse. Australian Forestry, (in press) (1994). — NAMKOONG, G., USANIS, R. A. and SILEN, R. R.: Age-related variation in genetic control of height growth in Douglas-fir. Theoretical and Applied Genetics 42, 151—159 (1972). — ROUSSEAU, R. J.: Genetic performance and early-age selection within a ten-year-old mid-west sycamore progeny test. Proc. 20th Southern Forest Tree Improvement Conference, Charleston, SC, 26 to 30/6/1989, pp 294—301 (1989). — SCHAFFER, H. E. and USANIS, R. A.: General Least Squares analysis of diallel experiments. A computer program — DIALL. North Carolina State University, Genetics Department, Research Report No. 1. 61 pp. (1969).

Genetic Parameters for Bole Volume in Longleaf Pine: Large Sample Estimates and Influences of Test Characteristics[1])

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Abstract

Data from 17 progeny test/seedling seed orchard sites of longleaf pine (*Pinus palustris* MILL.) containing a total of 901 open-pollinated families and 40,801 trees were analyzed to obtain precise genetic parameter estimates for bole volume at age 8, to evaluate genetic gains in seedling seed orchards, and to determine relationships between genetic parameter estimates and the test characteristics of survival, site productivity, and statistical precision. Estimates of bole volume heritability based on individual-test analyses (biased heritability) averaged 0.311 (range 0.143 to 0.570 across the 17 tests). Thirty-four pairwise combinations of tests were also analyzed to estimate unbiased heritabilities and Type B genetic correlations (r_B). The mean estimates for these parameters were 0.205 and 0.675, respectively. In most cases, genetic parameter estimates were not significantly related to characteristics of the tests. Type B genetic correlations, however, were significantly larger (indicating less genotype x environment interaction) when test pairs were in the same geographical planting zone (r_B = 0.747), than when they were in different (east vs. west) zones (r_B = 0.610). Planting zone x family interaction will need to be considered in future selection and seed deployment decisions. Nevertheless, even if this interaction is ignored, genetic gain in eight-year volume from low intensity (50%) roguing of families and individuals in the seedling seed orchards is expected to average around 11%. Gain in a 1.5 generation clonal seed orchard containing the best individual in each of the top 25 (2.8%) of the families is expected to exceed 35%.

Key words: Heritability, Type B genetic correlation, genotype x environment interaction, seedling seed orchard, *Pinus palustris* MILL..

FDC: 165.3; 232.11; 232.311.3; 174.7 *Pinus palustris*.

Introduction

Longleaf pine (*Pinus palustris* MILL.) is a high quality timber tree known for straight, well-formed stems, high bolewood density, and resistance to fusiform rust (SNYDER et al., 1977; BOYER, 1990). Despite these attributes, longleaf pine is a low priority choice relative to slash (*Pinus elliotii* ENGELM.) or loblolly (*Pinus taeda* L.) pines, for planting within the longleaf native range in the southeastern United States. The main reason historically for this low priority status has been the difficulty experienced in adequately establishing longleaf pine plantations. In addition to low seedling survival, young longleaf pine typically

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remains in a stemless grass stage for several growing seasons after planting. During this time, longleaf is susceptible to brown-spot disease (*Scirrhia acicola* (DEARN.) SIGGERS) and competing vegetation, which may severely limit early growth (BOYER, 1990). However, recent advances in longleaf nursery culture and site preparation, including production of larger or containerized seedlings, effective fungicide application, and more through competition control, have greatly alleviated many of these problems and have increased interest in planting this species (LOVELESS et al., 1989; BARNETT et al., 1989; SIRMON and DENNINGTON, 1989).

The Cooperative Forest Genetics Research Program (CFGRP) began work with longleaf pine in 1963 with the traditional approach of intensive field selections, followed by the establishment of clonal seed orchards. It was soon realized than the limited planting of longleaf pine would not warrant the same intensity of breeding effort being applied to slash and loblolly pines. In addition, difficulties with grafting and control crossing, as well as the greater importance of juvenile traits such as seedling survival, emergence from the grass stage, and early stem growth in longleaf pine, suggested a different approach (GODDARD et al., 1976; SCHMIDTLING and WHITE, 1989). Thus, in the early 1970's, the CFGRP embarked on a seedling seed orchard (SSO) program for this species, in which open-pollinated progeny testing and seed orchard production activities were combined in the same plantings (WRIGHT, 1961; TODA, 1964). This program called for low intensity field selections followed by the establishment of their open-pollinated progenies on several sites.

To date, more than 1000 families have been established on 185 acres (75 ha) of progeny test/SSO sites, and 8-year measurements of stem height and diameter are available for most of these tests. This provided the opportunity to assess the genetic control of bole volume growth in longleaf pine based on a large sample of families and test sites.

The first objective of this analysis was to obtain precise estimates of the heritability (h^2) of bole volume and the magnitude of genotype x environment interaction (GxE) for this trait, and to utilize these estimates to evaluate potential genetic gains from the SSO program. Information on quantitative genetic parameters in longleaf pine is extremely limited. Although a number of reports are published showing a great deal of genetic variation for seedling survival, timing of emergence from the grass stage, resistance to brown-spot disease, and early stem growth (SNYDER, 1969; SNYDER and NAMKOONG, 1978; GODDARD and BRYANT, 1981; GODDARD et al., 1984; SLUDER, 1984 and 1986; BYRAM and LOWE, 1985), most of these are based on limited numbers of families from restricted geographical ranges. Thus, h^2 estimates for bole volume range widely, from 0.07 to 0.57. There is almost no published information on the importance of GxE interactions for stem growth in longleaf pine (GODDARD et al., 1984).

The second objective of our analysis was to examine the extent to which the test characteristics of survival, site productivity and statistical precision influence the magnitude of bole volume h^2 and GxE interaction for this trait. Such information would be useful when considering designs, numbers and locations of future progeny tests. For example, it has been suggested that the ability to distinguish progenies is greatest on high quality sites (WRIGHT, 1976; GODDARD et al., 1983). Nevertheless, recent results from studies in several conifer species indicate there is no consistent relationship between the magnitude of h^2 estimates and site productivity (NIENSTAEDT and RIEMENSCHNEIDER, 1985; JOHNSON and BURDON, 1990; WOOLASTON et al., 1990; HODGE and WHITE, 1992). Site factors promoting GxE interaction are also of interest. HODGE and WHITE (1992), for example, found that GxE interaction is greater when test sites differ in site quality.

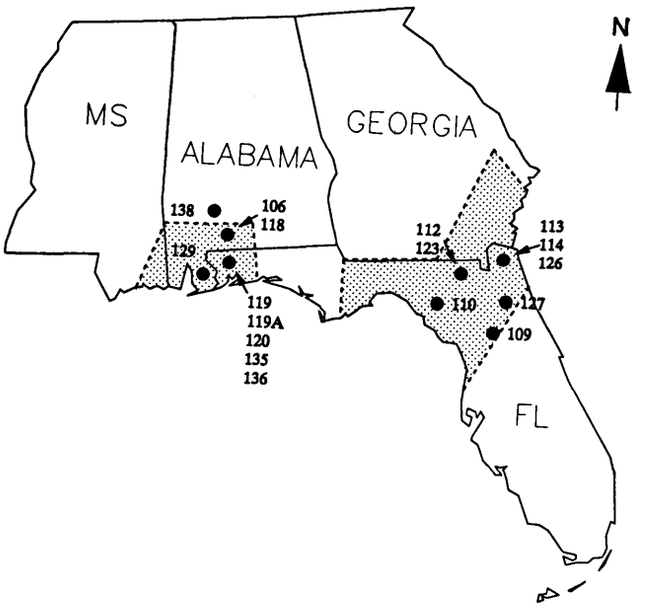


Figure 1. — Primary distributions of longleaf pine parent tree selections in 1977 (east zone) and in 1979 and 1983 (west zone), and locations of the progeny tests included in this study.

Materials and Methods

Progeny test data

Parent tree selections for the SSO program were made primarily in 3 excellent seed crop years, 1977, 1979, and 1983, with 371, 297 and 172 trees selected, respectively, each year. In addition, around 165 trees had been selected in other years. Although a few of the earlier trees were selected intensively using a baseline system, most only had to meet the criteria of acceptable form and growth, plus reasonable seed production. Selections were made in natural stands and older plantations in the southern distribution of the species range, with most selections concentrated either in a relatively restricted area in the central Gulf Coast ("west zone") or in a somewhat larger area in north Florida and southeast Georgia ("east zone") (*Figure 1*). Each main seed collection year was followed by test plantings consisting primarily (usually $>$ 70 %) of the open-pollinated progenies collected that year. Thus, there are three series of tests. Because the seed crop in 1977 was mostly in the east zone, the 1977 test series contains primarily east zone families. Likewise, the 1979 and 1983 series emphasize progenies from selections in the west zone. Provenance tests have shown that west zone seed sources grow exceptionally well throughout most of the southern coastal plain (LANTZ and KRAUS, 1987; SCHMIDTLING and WHITE, 1989).

Seeds were sown in bareroot nurseries in the spring at wide spacing (4 x 4 in) and outplanted the following winter. Tests were established by members of the CFGRP on their own land. Within each test, families were rep-

Table 1. — Statistics for individual test sites, including proportions of trees that emerged from the grass stage at age 2 (EGS), and estimated test means, phenotypic coefficients of variation (CV) and individual biased heritabilities (h^2_b) of bole volume at age 8.

Test	Year estab.	Total fams.	Trees/ family	Rep.[a] size	Age 1 surv.	EGS	Stem volume (ft^3)[b] Mean	CV	h^2_b[c]
1977 seed									
106	1979	176	13.0	0.12	0.74	0.67	0.419	0.44	0.282
109	1979	180	15.9	0.20	0.78	0.18	0.288	0.59	0.315
110	1979	165	15.8	0.19	0.61	0.29	0.481	0.42	0.570
112	1979	187	13.8	0.17	0.78	0.60	1.060	0.39	0.416
113	1979	63	15.8	0.57	0.72	0.18	0.573	0.55	0.385
114	1980	63	16.6	0.29	0.70	0.41	1.213	0.47	0.486
119A	1981	70	14.3	0.13	0.37	0.89	1.278	0.33	0.191
1979 seed									
118	1981	149	14.9	0.14	0.57	0.21	0.545	0.47	0.295
119	1981	153	18.2	0.22	0.73	0.92	1.204	0.31	0.407
120	1981	155	15.0	0.12	0.48	0.91	0.949	0.37	0.143
123	1981	158	17.2	0.84	0.70	0.83	0.903	0.45	0.332
126	1982	237	13.8	0.18	0.56	0.51	1.247	0.39	0.350
127	1982	171	16.3	0.19	0.70	0.23	0.273	0.55	0.155
129	1982	163	18.9	0.85	0.97	0.38	0.414	0.44	0.293
1983 seed									
135	1985	236	15.8	0.84	0.58	0.73	0.442	0.61	0.169
136	1985	181	9.8	1.02	0.48	0.49	0.994	0.50	0.323
138	1985	202	13.6	0.74	0.61	0.52	0.610	0.59	0.176
Means									
E zone		153	15.6	0.33	0.69	0.40	0.755	0.48	0.376
W zone		165	14.8	0.47	0.61	0.64	0.762	0.45	0.253
Overall		159	15.2	0.40	0.65	0.53	0.758	0.46	0.311

[a]) Size (in acres) of average sub-block (when families are subdivided into sets) or block (when families are not subdivided into sets).
[b]) Trees were measured at 9 years of age in tests 114 and 126, but at 8 years in all other tests.
[c]) Approximate standard errors of h^2_b estimates ranged from 0.039 to 0.134 (mean = 0.072) over tests. Empirical standard error of the overall mean estimate is 0.029.

resented by 4- or 5-tree row plots in each of 8 to 10 blocks. Tree spacing was 3 feet within rows and 12 to 15 feet between rows. Because of the large number of families in most tests (150 to 250), families were usually subdivided at lifting into 4 to 5 planting groups or sets, which were replicated as sub-blocks within whole blocks. Groupings were done independently by each cooperator, thus, the composition of sets differed in each test of a series. Seventeen tests were available for analysis of 8-year bole volumes, 7 from series 1977, 7 from 1979, and 3 from 1983 (*Table 1*, *Figure 1*). These tests include plantings by 11 different cooperators and are geographically clumped either within the east (8 tests) or west (9 tests) zones. The primary difference between the 2 geographical zones is in precipitation during the growing season (March until May). Over this time, the west zone receives 50% more rainfall (16 to 18 in) than the east (10 to 12 in) (NELSON and ZILLGITT, 1969).

Based on visual assessment of height growth, stem form and disease resistance, these tests were thinned at age 4 (i.e., after the 4th growing season in the field) to the best 2 out of the 4 or 5 trees in each family-row plot. Then at age 8, the bottom 50 % of the families in each block (based on performance across all tests) were rogued, and the remaining family plots thinned to the best single tree. From this point onwards the sites were managed for seed production. Although the tests were thinned to the best 2 trees per family row plot at age 4, the potential for exerting selection pressure at this age was very limited because mean survival one year after planting was only 65 % (*Table 1*). Based on height and diameter (at 4.5 ft) measurements at age 8 (age 9 for tests 114 and 126), individual tree bole volumes were estimated using the "total bole wood" equation in BALDWIN and SAUCIER (1983).

Adjustments to data sets

All individuals present prior to the roguing at age 8 (or 9) were included in the data set, with the following exceptions. First, all trees less than 5 feet tall were removed. These trees either emerged extremely late from the grass stage or were stump sprouts following thinning at age 4 and are not expected to reach merchantable size (DORMAN, 1976). On average, approximately 2 % of the trees in each test were removed for being too small (range 0 % to 17.6 %). Second, some families (mean 8.05 %) were removed

because of extremely low numbers of individuals. Despite these 2 adjustments, the total number of families (901) and trees (40,801) included in the analyses is considerable. Finally, because the composition of family sets differed on each test site in a series, family effects were confounded with sub-blocks. This made it very difficult to compare families across tests. Thus, sub-block effects were removed by adjusting individual-tree bole volumes by their sub-block means. Sets were then ignored in subsequent analyses. We assume, since sets were formed independently, that mean genetic differences between sets are essentially zero. Therefore, this adjustment is expected to remove only environmentally caused differences between sub-blocks.

Statistical analyses

Analyses of variance of individual tree bole volumes were conducted in 2 stages. First, the data for each test were analyzed separately. These analyses made it possible to estimate bole volume heritability individually for each test (h^2_b) and to examine relationships between h^2_b and characteristics of the tests. Heritabilities estimated from the data of a single site are upwardly biased in the sense that they are inflated by family x site interaction (HODGE and WHITE, 1992). To obtain unbiased estimates of heritability (h^2) and to examine GxE interaction, analyses of variance were also carried out on pairs of tests. Although 2 tests from 1977 were not included in the pair-wise analyses because they had few families in common with other tests, all other possible pairs within each series were analyzed, giving a total of 34 pairs of tests (10 in series 1977, 21 in 1979, 3 in 1983).

For the paired analyses the following linear model was used to represent bole volumes of individual trees:

$$Y_{ijkl} = \mu + t_i + r_{ij} + f_k + fe_{ik} + p_{ijk} + w_{ijkl}$$

where

μ = the overall mean;
t_i = random effect of i^{th} test site, $E(t_i) = 0$, $Var(t_i) = \sigma^2_t$;
r_{ij} = random effect of j^{th} block within the i^{th} test, $E(r_{ij}) = 0$, $Var(r_{ij}) = \sigma^2_r$;
f_k = random effect of k^{th} family, $E(f_k) = 0$, $Var(f_k) = \sigma^2_f$;
fe_{ik} = random interaction effect of k^{th} family with the i^{th} test, $E(fe_{ik}) = 0$, $Var(fe_{ik}) = \sigma^2_{fe}$;
p_{ijk} = random plot error of the k^{th} family in the j^{th} block of the i^{th} test, $E(p_{ijk}) = 0$, $Var(p_{ijk}) = \sigma^2_p$;
w_{ijkl} = random tree error of the l^{th} tree in the ijk^{th} plot, $E(w_{ijkl}) = 0$), $var(w_{ijkl}) = \sigma^2_w$, and the covariances between all pairs of factors are assumed to be zero. The linear model for individual test analyses is basically the same as above, after removing effects for test (t_i) and family x site interaction (fe_{ik}). Also, the random effect for the k^{th} family in the individual test analyses includes both f_k and fe_{ik}, which we designate as F_k ($Var(F_k) = \sigma^2_F = \sigma^2_f + \sigma^2_{fe}$.

Variance components in the above models were estimated by subjecting each data set (individual and test pairs) to the SAS Varcomp, restricted maximum likelihood (REML) procedure (SAS Institute Inc., 1989). This is one of a number of analytical techniques for variance component estimation when data are unbalanced (including HENDERSON's methods I, II, and III, maximum likelihood, and MINQUE). Although none of these methods is superior in all situations (MILLIKEN and JOHNSON, 1984, p. 260; SEARLE, 1987, p. 495), a recent computer simulation study of variance component estimation utilizing unbalanced forest-tree data sets similar to those in longleaf pine, revealed that the REML procedure was the most effective in providing estimates of variance components and derived genetic parameters (e.g., heritabilities) with minimum bias and minimum sampling variation (HUBER et al., 1994). In addition to providing direct estimates of variance components, REML provides large-sample variances and covariances of these estimates in the inverse of the information matrix.

Genetic parameter estimation

Heritabilities based on individual site analyses were estimated as

$$h^2_b = 4(\sigma^2_F)/(\sigma^2_P)$$

where

$$\sigma^2_P = \sigma^2_F + \sigma^2_p + \sigma^2_w .$$

Note that this equation assumes that tree volumes are corrected for block means and that open-pollinated families are true half-sibs.

Prior to analyses of test pairs, individual tree volumes in each test were transformed by dividing by the observed σ_w derived from the single site analysis of the test. Paired analyses were conducted on transformed data in order to more closely meet the assumption of homogeneous error variance structures (SEARLE, 1987, p. 8). Estimated variance components in the paired analyses were subsequently back transformed to the original scale prior to genetic parameter estimation. Unbiased heritabilities were estimated as

$$h^2 = 4(\sigma^2_f)/(\sigma^2_P).$$

Approximate (large sample) standard errors of both h^2_b and h^2 were calculated using the method of DICKERSON (1969).

The extent of family x site interaction in bole volume was quantified by estimating for each site pair the Type B genetic correlation (BURDON, 1977) as follows:

$$r_B = (\sigma^2_f)/(\sigma^2_f + \sigma^2_{fe}).$$

In this application, r_B is the genetic correlation between the same trait expressed in 2 different sites ($0 \leq r_B \leq 1$) When $r_B \approx 1$, no G x E interaction is indicated. An estimator for the approximate variance of r_B was derived using the formula in NAMKOONG (1979, p. 232).

Genetic gains estimates

We estimated genetic gains in 8-year bole volume for 2 situations. First, we calculated expected gains for an average SSO, from roguing at age 8. Gains in any one SSO are limited by the low selection intensities that are possible. Thus, we also addressed gains that could be expected if the best individual in each of the top 25 (2.8%) families across all tests were selected to form a "1.5 generation" clonal seed orchard. In both situations, we assumed that gains in bole volume from thinning at age 4 were negligible because many family plots already contained 2 or fewer trees due to poor survival.

Gains from roguing SSO's at age 8 are derived from 2 sources: gain due to selecting the best 50% of the families on each site, based on the performance of families across all sites tested (G_f), and gain from selecting the best individual in each family plot remaining after family selection (G_{wp}). We used the mean estimates of the variance components across all test pairs, as appropriate for an average site (i.e., where mean site bole volume was

average). Expected gain (% of mean volume) from family selection is

$$G_f = i\, h^2_f\, (\sigma_{Pf}/X)\, (100),$$

where

- i = 0.798 (50% of families selected, FALCONER, 1981, Appendix A);
- h^2_f = $(\sigma^2_f)/(\sigma^2_{Pf})$ (heritability of family means);
- σ^2_{Pf} = $\sigma^2_f + (\sigma^2_{fe}/e) + (\sigma^2_p/re) + (\sigma^2_w/nre)$ (phenotypic variance of family means);
- e = mean number of sites on which each family is tested (3);
- r = mean number of blocks in a test (9.1);
- n = mean number of trees per plot (1.67), and
- X = mean individual-tree bole volume for the average test site.

Gain from within plot selection is:

$$G_{wp} = i_{wp}\, h^2_{wp}\, (\sigma_w/X)\, (100)$$

where

- i_{wp} = 0.479 (1 out of every 1.67 trees, interpolated from FALCONER, 1981, Appendix B) and
- h^2_{wp} = $(3\sigma^2_f)/(\sigma^2_w)$ (heritability of individual tree deviations within plots).

Total expected gain from both sources is $G_T = G_f + G_{wp}$.

Gains in the 1.5 generation clonal seed orchard are also derived from family and within family selection. Gains from family selection were calculated using the equation for G_f above, but with i=2.295 (best 25 out of 901 families). Within family selection can now occur among all trees in a family, regardless of location within and across tests. We assumed, however, that individual-tree volumes are adjusted by both their family mean for the test site in which they are found, as well as their block mean, prior to ranking. Under this assumption, the expected gain from within family selection is

$$G_{wf} = i_{wf}\, h^2_{wf}\, (\sigma_{wf}/X)\, (100)$$

where

- i_{wf} = 2.210 (1 out of 45.6 (mean number of trees per family) selected, interpolated from FALCONER, 1981, Appendix B);
- h^2_{wf} = $(3\sigma^2_f)/(\sigma^2_{wf})$, and
- σ^2_{wf} = $\sigma^2_p + \sigma^2_w$.

Results

Individual test analyses

The individual tests differ greatly in the proportion of trees surviving at age 1, the proportion of trees that emerged from the grass stage at age 2 (EGS) and mean bole volume (*Table 1*). Mean bole volume was greatest in tests 114 and 126, but volumes in these tests were assessed one year later (age 9) than the others. Nevertheless, 8-year bole volumes still ranged more than 4-fold among the remaining tests. The tests also differed considerably in characteristics expected to influence the statistical precision of the tests: number of trees measured per family ranged from 9.8 to 18.9 and the mean size of a replication ranged from 0.12 acres to 1.02 acres (0.05 ha to 0.41 ha) (*Table 1*). Although tree spacing and number of trees per plot were influencing factors, most of the variation in replication size is due to whether or not families were planted in large blocks or subdivided into smaller sets, which then formed sub-blocks at planting.

Eight-year bole volumes varied widely among individual trees within tests with coefficients of phenotypic variation ranging 31 % to 61 % (*Table 1*). Genetic variation in bole volume was also considerable; ranges in family means were 2-fold to 4-fold at most test sites (average 2.8), and the ratio of the estimated family variance component to its standard error always exceeded 2 (mean 4.3). Biased heritability estimates ranged 0.143 to 0.570 over tests, averaging 0.311 (*Table 1*).

Because the test sites were localized into 2 discrete planting zones (east and west, *Figure 1*), we also examined mean parameter estimates for the zones separately. There is a significant ($p < 0.05$) difference in mean h^2_b between planting zones with h^2_b in the east zone nearly 50% greater than in the west. Inspection of variance components indicate that the primary reason for the larger h^2_b in the east tests, is that the mean family variance in the east (0.0138) is nearly twice that in the west (0.0072). Planting zone and geographical source of families are largely confounded. That is, 5 of the 8 tests in the east zone are from series 1977 which contains mostly east zone families, while

Table 2. — Correlation between mean test statistics.

	EGS[a]	Repl. size (A)	Trees/ family	Volume/ Tree (ft³)	CV[b]	h^2_b[c]
Survival at age 1	-0.344	0.119	0.570*	-0.073	0.170	0.306
EGS	-	0.018	-0.028	0.575*	-0.575*	-0.284
Repl. size		-	-0.052	-0.139	0.463	-0.143
Trees/family			-	-0.176	-0.094	0.153
Volume/tree				-	-0.682*	0.225
CV					-	-0.256

a) Proportion of trees per plot which emerged from the grass stage at age 2
b) Phenotypic coefficient of variation.
c) Estimate of biased heritability.
*) Significantly different from zero ($p<0.05$).

Table 3. — Matrices of estimated individual unbiased heritabilities (above) and Type B genetic correlations (below, bold) for pairwise combinations of tests[a)b)].

1977 seed

	109	110	112	119A	Test mean
106	0.103	0.215	0.171	0.145	0.158
	0.347	**0.483**	**0.482**	**0.550**	**0.466**
109	–	0.263	0.289	0.175	0.208
		0.605	**0.805**	**0.592**	**0.587**
110		–	0.399	0.349	0.306
			0.795	**0.702**	**0.646**
112			–	0.282	0.285
				0.754	**0.709**
119A				–	0.238
					0.650

1979 seed

	119	120	123	126	127	129	Test mean
118	0.299	0.134	0.193	0.194	0.122	0.215	0.193
	0.846	**0.602**	**0.614**	**0.587**	**0.593**	**0.727**	**0.662**
119	–	0.182	0.278	0.263	0.174	0.210	0.234
		0.623	**0.794**	**0.694**	**0.683**	**0.610**	**0.708**
120		–	0.181	0.168	0.094	0.181	0.157
			0.663	**0.611**	**0.610**	**0.773**	**0.647**
123			–	0.287	0.167	0.183	0.215
				0.875	**0.670**	**0.570**	**0.698**
126				–	0.183	0.203	0.216
					0.772	**0.618**	**0.693**
127					–	0.125	0.144
						0.583	**0.652**
129						–	0.186
							0.647

1981 seed

	136	138	Test mean
135	0.217	0.168	0.192
	0.984	**1.000**	**0.992**
136	–	0.173	0.195
		0.719	**0.852**
138		–	0.170
			0.860

Overall mean

0.205 ± 0.012[c]
0.675 ± 0.023[c]

[a)] The total number of families in each pair ranged from 183 to 301 (mean = 228), of which 92 to 184 (mean = 110) were common to both tests.
[b)] Expected standard errors of individual heritability and Type B genetic correlation estimates ranged 0.029 to 0.107 (mean = 0.058) and 0.096 to 0.273 (mean = 0.168), respectively.
[c)] Empirical standard errors of the mean estimates.

7 of 9 tests in the west zone are from series 1979 or 1983 plantings which contain mostly west zone families. Thus, although the larger family variance in the east may be due to environments that promote greater differentiation of families, it may also reflect the larger geographical area from which parent trees were selected in the east zone (*Figure 1*).

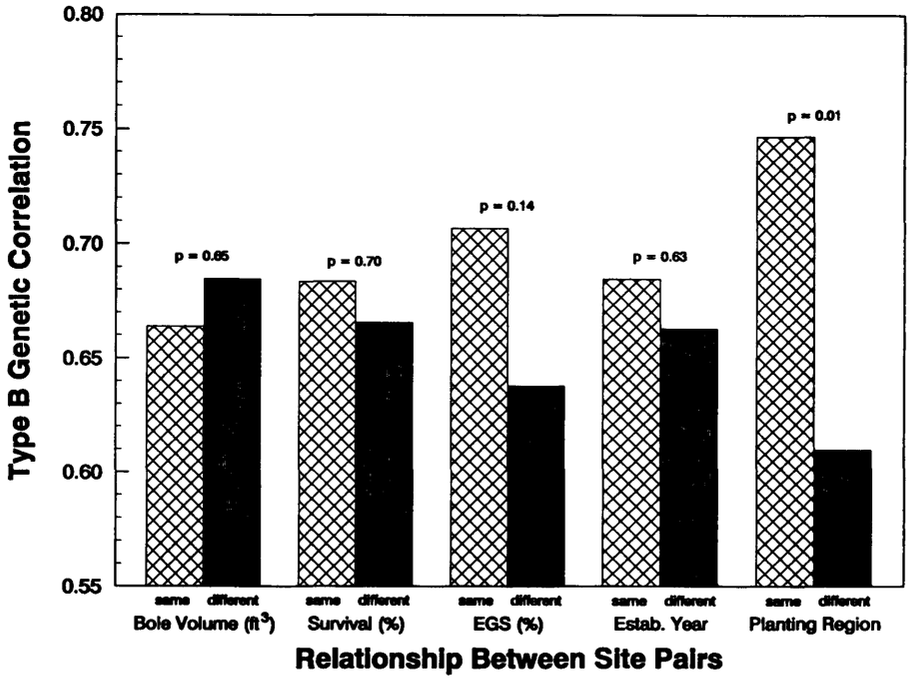
Mean statistics thought to be related to the productivity and statistical precision of the tests were correlated with h^2_b in an attempt to explain variation in h^2_b across test sites (*Table 2*). We expected, a priori, that h^2_b would increase with increasing first year survival, EGS, number of trees per family and mean bole volume, but would decrease with replication size and coefficient of phenotypic variation. With 1 exception (relationship with EGS), the sign of the estimated linear correlation coefficients were as expected, but they were all small and non-significant. This lack of significant relationships of h^2_b with test characteristics is perhaps not too surprising given the limited number of tests and the extent to which test characteristics were confounded (*Table 1*). It is interesting, however, that moderately strong associations were found between EGS and bole volume. With increasing EGS, mean bole volume increased and the coefficient of phenotypic variation decreased. Thus, timing of emergence from the grass stage has a profound influence on both the magnitude and uniformity of bole volume production (Snyder et al., 1977).

Paired site analyses

The mean estimated unbiased heritability across all test pairs (h^2 = 0.205, *Table 3*) is one-third less than mean h^2_b (*Table 1*). The lower unbiased heritability is due to the less than perfect genetic (Type B) correlation in bole volume between tests, which averaged 0.675 over all 34 pairs analyzed (*Table 3*). Multiplying mean h^2_b by mean r_B should give a value very close to mean h^2 (i.e., $h^2_b \times r_B = (4\,\sigma^2_F)/(\sigma^2_P) \times (\sigma^2_f)/(\sigma^2_F) = h^2$), which, in fact it does 0.311 x 0.675 = 0.210).

Type B genetic correlation estimates ranged widely among test pairs, from 0.37 (pair 106 — 109) to 1.00 (pair 135 — 138), although it was only in the 1977 series that r_B fell below 0.50, and test 106 was always involved in these pairs (*Table 3*). Differences between pairs of tests for 5 characteristics were investigated in order to try to explain

Figure 2. — Influence of the degree of difference between tests in mean bole volume (ft^3), percent survival at age 1, percent grass stage emergence at age 2 (EGS), year of establishment, and planting region, on the magnitude of Type B correlations. Same (different) group means are 0.22 ft^3 (0.73 ft^3) for bole volume, 7% (29%) for survival, and 17% (56%) for EGS. The probability of the t-statistic given the null hypothesis of no difference between group means is given above each pair of bars.



the variation in r_B. These were differences in mean bole volume (D_{vol}), mean survival at age 1 (D_{surv}) and mean EGS (D_{EGS}), and whether the tests were planted in the same or different years (D_{yr}), or in the same or different geographical zone (east vs. west, D_{zone}). Magnitudes of D_{vol}, D_{surv}, and D_{EGS} appear to have little influence on r_B, since the absolute value of their linear correlations with r_B were all less than 0.07. We also treated D_{vol}, D_{surv}, and D_{EGS} as qualitative traits by grouping test pairs into two classes (i.e., "same" vs. "different") for each factor. The classes were chosen to subdivide the test pairs into equal or nearly equal (16 vs. 18 pairs) groups. Test pairs where $D_{vol} \leq 0.45$, $D_{surv} \leq 0.14$ and $D_{EGS} \leq 0.35$ were classified as same for each factor, respectively, while those with larger differences were classified as different. Mean Type B correlations did not differ significantly between classes for any of these factors, although the difference approached significance for D_{EGS}, where mean r_B for different pairs was 10% less than for pairs where EGS was the same in both tests (*Figure 2*). Whether or not 2 tests in a pair were planted in the same year also seems to have little influence on r_B (*Figure 2*).

The magnitude of r_B, however, is substantially influenced by whether the 2 tests are located within the same or different planting zones. Mean r_B is greater when 2 tests are in the same zone (0.747) than when they are in different zones (0.610); and for tests in the same zone, it makes no difference whether both tests are in the east (6 pairs, mean $r_B = 0.754$) or in the west (10 pairs, mean $r_B = 0.743$). Thus, family x test interactions for bole volume are less when families are tested within the same region than when they are tested in different regions.

Because of the large influence of differences in planting zone on the magnitude of r_B, we also investigated the relationships between r_B and D_{surv}, D_{EGS}, and D_{vol} after first adjusting r_B for effects of planting zone. This was done by regressing r_B on each of these factors with planting zone included as a covariate in the model. Estimated regression coefficients for all 3 factors were essentially zero in these models; that is, after accounting for planting zone, D_{surv}, D_{EGS}, and D_{vol} explained almost none of the remaining variation in r_B.

Genetic gains

The heritability of family means ($h^2_f = 0.623$) was estimated to be about 3 times that for individual trees, and the expected gain in bole volume at age 8 from selecting the top 50% of the families in an average test site, was estimated as 6.7%. Gain from choosing the fastest growing tree within each family plot was based on a selection of 1 out of an average of 1.67 trees remaining at age 8 and was estimated as an additional 4.0%. Therefore, the overall gain due to both family and within plot selection is expected to be 10.7%. Additional gains might be anticipated in these orchards as they are subsequently thinned to keep crowns open-grown. These additional gains are likely to be limited, however, because spacing rather than genetics will play an increasingly important role in roguing decisions as the orchard ages.

As expected, estimated gains from selecting the best individual out of each of the top 25 families across all tests to form a 1.5 generation clonal seed orchard are considerably greater than in an average SSO. Gains are estimated as 19.2 % from family selection, and 16.4 % from within family selection; thus the combined gain is estimated as 35.6 %.

Discussion

All genetic parameter estimates apply specifically to the population from which the data was drawn, i.e., they apply

to a particular situation involving species, trait, measurement age, environment and silvicultural treatments. Since one of the primary objectives of this study was to predict gain from selection in the thinned seedling seed orchards, the appropriate genetic parameters are those developed from the thinned population. However, we believe that these genetic parameters would likely also apply to 8-year-old longleaf plantations which have not been thinned at age 4: first, there was little opportunity for within-family selection in the thinning at age 4 due to low survival, and second, the effectiveness of individual-tree selection at age 4 would probably be quite low due to low heritability. Thus, any bias of the 8-year genetic parameters caused by the age 4 thinning would probably be small. Supporting this assumption are the results of BARNES et al. (1992) with 8-year-old *P. patula*. They found that data from selectively thinned progeny tests gave essentially the same parameter estimates as systematically thinned tests.

Quantitative genetic parameters are notorious for the poor precision in which they are generally estimated (NAMKOONG, 1979). Despite the large sample sizes in this study, individual estimates of heritability ranged by as much as 0.415 (*Tables 1* and *2*) and individual estimates of r_B by as much as 0.653 (*Table* 2). Thus, it seems unwise to place a great deal of confidence on genetic parameter estimates derived from only one or a few test sites, especially if the number of unrelated families is small.

Given the large sample sizes and low empirical standard errors, we feel the precision of the overall estimates of h^2 and r_B in this study are quite good. Our h^2 estimates, however, may be upwardly biased due to violation of the assumption that families are true half-sibs (SQUILLACE, 1974). In an earlier study in longleaf pine, general combining ability variance based on open-pollinated progenies was, over many traits, nearly twice that based on controlled crosses (diallel mating design, SNYDER and NAMKOONG, 1978). These results lead the authors to conclude that the additive variance observed among open-pollinated families was more like that expected from full-sib families than from half-sibs. The degree to which sampling influenced these results, however, is unknown since only 13 parents were involved. The mean h^2 for bole volume in our study is close to the average (0.21) found for a large number of other tree species (primarily conifers, CORNELIUS, 1994), but is a little higher than recently reported for a large study of slash pine in the same region ($h^2 = 0.156$, at age 10, HODGE and WHITE, 1992).

It is somewhat surprising that, aside from planting zone, we found no significant relationships between h^2_b and characteristics of the tests. With so many factors varying among tests, detecting an association with any single factor would be difficult unless the influence of the individual factor was particularly large. Thus, we can at least conclude that none of the factors we investigated, other than planting zone, had a large influence on the magnitude of h^2_b. It has been suggested that the reason heritability does not consistently increase with increasing site productivity is because any advantage gained on better sites from increased separation of family means is counteracted by greater overall phenotypic variance, such that the magnitude of heritability remains unchanged (WOOLASTON et al., 1990). The lack of a significant increase in h^2_b with decreasing replication size is particularly interesting given the nearly 9-fold range in replication size among tests (*Table 1*). Recall that most of the variation in replication size was due to whether or not families were subdivided into sets prior to planting (i.e., whether replications were large blocks or sub-blocks). Subdivision of large numbers of families into smaller sets is commonly practiced in progeny testing of forest trees as a method to reduce environmental variation among families within replication units and thus, improve the precision of family separation. There is no evidence, however, that this practice greatly improved the ability to detect family differences in the longleaf tests in this study.

The relatively strong h^2 and large phenotypic variance observed for bole volume indicate the rapid progress can be made in improving this trait in longleaf pine breeding programs. Even genetic gains under the low selection intensities possible in SSO's are expected to be quite respectable; we estimated the average bole volume gain from roguing orchards at age 8 as approximately 11 %. With the formation of a 1.5 generation clonal orchard, selection intensities are no longer constrained to what is possible on any one SSO site; expected gains in our example were more than 3 times as great as in an average SSO. Whether or not such high gains would justify the expense of establishing a clonal orchard will depend on the longleaf pine planting needs of the particular organization.

A less expensive alternative to a 1·5 generation clonal orchard might be to establish a new SSO using open-pollinated seed collected from the same trees selected for the clonal orchard, i.e., the best individuals in the best 25 families. Expected gain from an orchard of this type is equivalent to the average of the gain from the female and male parents. The female parents of the new SSO are the best individuals in the best 25 families, with a gain = 35.6 %. The male parents are all trees in the original SSO (after roguing, and assuming no pollen contamination), with a gain = 10.7 %. Thus, the gain from the new SSO would be $0.5 \cdot (35.6\ \% + 10.7\ \%) = 23{\cdot}2\ \%$. Although there would be little opportunity for additional genetic gain from family selection (since there are only 25 families), there would be opportunity for some within-family selection. Assuming a similar planting design, gain from within-family selection would be on the order of an additional 4 %.

The above gains were calculated using heritabilities appropriate to the performance of individuals and families across all test sites, and thus, are the gains expected if G x E interaction is ignored in selection and seed deployment decisions. SHELBOURNE (1972) suggested that when G x E interaction variance exceeds half the size of additive variance (i.e., when $r_B < 0.67$), that gains from selection can be seriously impacted. The G x E interaction observed among tests within zones in this study ($r_B = 0.747$) is well below this threshold· In addition, there seem to be no obvious characteristics of the test sites themselves which might explain G x E interaction within zones. Thus, without more knowledge, there is nothing that can be done about this interaction, except to select for genotypes that perform well across all potential planting environments within a zone.

G x E interaction due to differences between planting zones is a different situation since it appears to be predictable. Although planting zones are somewhat confounded by differences in cooperators, seed sources, and planting years (*Table 1*, *Figure 1*), the most consistent factor which distinguishes them is their geographical location. The zones

differ in precipitation, especially in the growing season from March until May, when the west zone receives 50 % more rainfall (16 to 18 in) than the east (10 to 12 in) (NELSON and ZILLGITT, 1969). Thus, G x E interaction due to planting zones, may reflect differential responses of families to different precipitation regimes, and, there may be advantages to separately selecting genotypes that perform well in each regime. We intend to explore the significance of the genotype x planting zone interaction during the process of making breeding value predictions (WHITE and HODGE, 1989) for the families in the SSO's. Our approach will be to develop three sets of predictions: 1 for performance across test zones and 2 for performance within each zone separately. We will then compare the expected gains when selections are made on each set of breeding values. Preliminary analyses indicate, for this level of G x E interaction, that only at high selection intensities (e.g., 2% = the top 18 of 901 parents) would it be important for breeders to account for the G x E. However, it is clear that if the intended goal is to develop one broadly adapted breeding population of longleaf pine, it will be essential to establish future tests in both the east and west planting zones. A similar conclusion was reached for radiata pine (*Pinus radiata* D. DON) in New Zealand, where significant interactions were found among families tested on 2 contrasting soil types (JOHNSON and BURDON, 1980).

G x E interaction might also be expected when genotypes are raised under different cultural regimes. Longleaf pine is particularly sensitive to cultural conditions in the nursery and in the first several years after planting, which can substantially impact survival of seedlings, speed of emergence from the grass stage, and subsequent early growth. We found no evidence, however, that post-planting survival, speed of emergence from the grass stage, or site productivity significantly impacts G x E interaction in bole volume. Although r_B was lower (but not significantly so) when test pairs differed widely in survival or EGS (*Figure 2*), no relation was found between r_B and D_{surf} or D_{EGS} after adjusting for planting zone effects, despite the fact that survival and EGS differed by as much as 0.49 and 0.70, respectively, among sites within zones. Thus, the ranking of genotypes for individual-tree bole volume in longleaf pine does not appear to be strongly influenced by seedling survival or speed of grass stage emergence, both factors which are sometimes difficult to control in this species.

Conclusions

The seedling seed orchard strategy adopted for longleaf pine has been a cost-efficient approach and has resulted in reasonable genetic gains. Similar approaches may be useful for other species for which more intensive improvement programs cannot be justified due to small land bases or financial constraints. For longleaf pine, the success of the SSO approach is partially due to its moderately high heritability for 8-year volume (average $h^2 = 0.21$).

Genotype x environment interaction is moderate, and related to geographic regions. This predictable pattern of G x E will likely be too small to influence future breeding strategies, but should probably be considered in progeny testing and deployment decisions.

Literature Cited

BALDWIN jr., V. C. and SAUCIER, J. R.: Aboveground weight and volume of unthinned, planted longleaf pine on west Gulf forest sites. USDA Forest Service Res. Pap. SO—191, 35 p (1983). — BARNES, R. D., MULLIN, L. J. and BATTLE, G.: Genetic control of eight year traits in *Pinus patula* SCHEIDR and DEPPR. Silvae Genetica 41: 318—326 (1992). — BARNETT, J. P., LAUER, D. K. and BRISSETTE, J. C.: Regenerating longleaf pine with artificial methods. In: Proceedings of the Symposium on the management of longleaf pine. Ed. R. M. FARRAR jr.. USDA Forest Service Gen. Tech. Rep. SO—75, p. 72—93 (1989). — BOYER, W. D.: *Pinus palustris* MILL. longleaf pine. In: Silvics of North America: 1. Conifers. Tech. Coordinators R. M. BURNS and B. H. HONKALA. USDA Forest Service, Wash., DC., Agr. Handbook 654, p. 405—412 (1990). — BURDON, R. D.: Genetic correlation as a concept for studying genotype-environment interaction in forest tree breeding. Silvae Genet. 26, 168—175 (1977). — BYRAM, T. D. and LOWE, W. J.: Longleaf pine tree improvement in the Western Gulf region. Proc. 18th South. Forest Tree Improv. Conf. p. 78—87 (1985). — CORNELIUS, J.: Heritabilities and additive genetic coefficients of variation in forest trees. Can. J. For. Res. 24, 372—379 (1994). — DICKERSON, G. E.: Techniques for reseach in quantitative animal genetics. In: Techniques and Procedures in Animal Science Research. Amer. Soc. of Animal Research, Albany, NY, p. 36—79 (1969). — DORMAN, K. W.: The genetics and breeding of southern pines. USDA Forest Service, Wash., DC., Agr. Handbook No. 471, 407 p. (1976). — FALCONER, D. S.: Introduction to Quantitative Genetics. Second ed., Longman Group Limited, New York. 340 p. (1981). — GODDARD, R. E. and BRYANT, R.: Genetic variation in survival of longleaf pine. Proc. 16th South. Forest Tree Improv. Conf. p. 136—142 (1981). — GODDARD, R., LAND, S. and KOSSUTH, S.: Test establishment, maintenance, measurement. In: Progeny Testing of Forest Trees, Southern Cooperative Series Bulletin 275, Department of Agricultural Communications, Texas A&M University, College Station. p. 40—50 (1983). — GODDARD, R. E., ROCKWOOD, D. L., and KOK, H. R.: Cooperative forest genetics research program twenty-six progress report. School of Forest Resources and Conserv., Univ. of Florida, Gainesville, Res. Rep. No. 35, 26 p. (1984). — GODDARD, R. E. ROCKWOOD, D. L., KOK, H. R., HOLLIS, C. A. and HENDRICKSON, J. A.: Cooperative forest genetics research program eighteenth annual progress report. School of Forest Resources and Conserv., Univ. of Florida, Gainesville, Res. Rep. No. 25, 20 p. (1976). — HODGE, G. R. and WHITE, T. L.: Genetic parameter estimates for growth traits at different ages in slash pine and some implications for breeding. Silvae Genet. 41, 252—262 (1992). — HUBER, D. A., WHITE, T. L. and HODGE, G. R.: Variance component estimation techniques compared for two mating designs with forest genetic architecture through computer simulation. Theor. Appl. Genet., in press (1994). — JOHNSON, G. R. and BURDON, R. D.: Family-site interaction in *Pinus radiata*: implications for progeny testing strategy and regionalized breeding in New Zealand. Silvae Genet. 39, 55—62 (1990). — LANTZ, C. W. and KRAUS, J. F.: A guide to southern pine seed sources. USDA Forest Service Gen. Tech. Rep. SE-43, 34 p. (1987). — LOVELESS, R. W., PAIT, J. A., III and MCELWAIN, T.: Response of longleaf pine to varying intensity of silvicultural treatments. In: Proc. Fifth Biennial South. Silv. Res. Conf. Comp. J. H. MILLER. USDA Forest Service Gen. Tech. Rep. 50—74, p. 159—164 (1989). — MILLIKEN, G. and JOHNSON, D. E.: Analysis of messy Data. I. Designed Experiments. Lifetime Learning Pub., Belmont, CA. 473 p. (1984). — NAMKOONG, G.: Introduction to Quantitative Genetics in Forestry. U. S. Dept. Agric., Tech. Bull. No. 1588. 342 p. (1979). — NELSON, T. C. and ZILLGITT, W. M.: A forest atlas of the south. USDA Forest Service, South. Forest Exp. Sta. and Southeast. Forest Exp. Sta. 27 p. (1969). — NIENSTAEDT, H. and RIEMENSCHNEIDER, D. E.: Changes in heritability estimates with age and site in white spruce, *Picea glauca* (MOENCH) VOSS. Silvae Genet. 34, 34—41 (1985). — SAS Institute Inc.: SAS/STAT user's guide. Version 6. 4th ed., Vol. 2. SAS Institute Inc., Cary, NC. 846 pp. (1989). — SCHMIDTLING, R. C. and WHITE, T. L.: Genetics and tree improvement of longleaf pine. In: Proceedings of the symposium on the management of longleaf pine. Ed. R. M. FARRAR jr. USDA Forest Service Gen. Tech. Rep SO-75, p. 114—127 (1989). — SEARLE, S. R.: Linear Models for Unbalanced Data. John Wiley and Sons, New York. 536 p. (1987). — SHELBOURNE, C. J. A.: Genotype-environment interaction: its study and its implications in forest tree improvement. In: Proc. IUFRO Genetics — SABRAO Joint Symp., Jap. Forest Exp. Sta., Tokyo, Japan. p. 1—28 (1972). — SIRMON, G. A. and DENNINGTON, R. W.: Longleaf pine management on the De Soto National Forest — A case study. South. J. Appl. Forestry 13, 34—40 (1989). — SLUDER, E. R.: Selecting and progeny testing superior and aberrant phenotypes. Final report 4100 FS-SE-1403-24(4), USDA Forest Service, Southeast. For. Exp. Sta.. 40 p. (1984). — SLUDER, E. R. Gains from first-cycle selection in slash

and longleaf pines. Silvae Genet. 35, 155—159 (1986). —— SNYDER, E. B. Parental selection versus half-sib family selection of longleaf pine. Proc. Tenth South. Forest Tree Improv. Conf. p. 84—88 (1969). —— SNYDER, E. B., DINUS, R. J. and DERR, H. J.: Genetics of longleaf pine. USDA Forest Service Res. Pap. WO-33. 22 p. (1977). —— SNYDER, E. B. and NAMKOONG, G.: Inheritance in a diallel crossing experiment with longleaf pine. USDA Forest Service Res. Pap. SO-140. 31 p. (1978). —— SQUILLACE, A. E.: Average genetic correlations among offspring from open-pollinated forest trees. Silvae Genet. 23, 149—156 (1974). —— TODA, R.: A brief review and conclusions of the discussion on seed orchards. Silvae Genet. 13, 1—4 (1964). —— WHITE, T. L. and HODGE, G. R.: Predicting Breeding Values With Applications in Forest Tree Improvement. Kluwer Acad. Publ., Boston. 367 p. (1989). —— WOOLASTON, R. R., KANOWSKI, P. J. and NIKLES, D. G.: Genetic parameter estimates for *Pinus caribaea* var. *hondurensis* in coastal Queensland, Australia. Silvae Genet. 39, 21—28 (1990). —— WRIGHT, J. W.: Progeny tests or seed orchards? Recent Adv. Bot. 2, 1681—1687 (1961). —— WRIGHT, J. W.: Introduction to Forest Genetics. Academic Press, New York. 463 p. (1976).

Genetic Variances and Covariances for Frost Tolerance in Eucalyptus globulus and E. nitens

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Summary

Controlled- and open-pollinated families of *Eucalyptus globulus* subsp. *globulus* (referred to here as *E. globulus*) and *E. nitens*, were tested for frost resistance at 3 test temperatures (—5.5 °C, —7.0 °C and —8.5 °C) using the electrical conductivity method. Additive, dominance and error variance and covariances were estimated using a derivative-free restricted maximum likelihood (DFREML) procedure and heritabilities, genetic and phenotypic correlations were calculated. *E. nitens* was more frost tolerant than *E. globulus*, the former being largely undamaged at —8.5 °C. *E. globulus* control-pollinated material (GCP) was tolerant to —7.5 °C but was severely damaged at —8.5 °C. Open-pollinated *E. globulus* from both seed orchards (GSOP) and natural stands (GOP) was severely damaged at —7.0 °C with the 50 % damage criteria probably met at about —6.0 °C. Heritabilities were moderate to high for both species, ranging from 0.29 to 0.50 for GCP and 0.23 to 0.44 for *E. nitens* control-pollinated material (NCP). It is suggested that estimates of heritability from *E. globulus* open-pollinated families from native stands (GOP), with values ranging from 0.53 to 0.61, are over-estimated due to the effects of selfing and neighbourhood inbreeding. Estimates of heritability for open-pollinated families from seed orchards in both species (GSOP and NSOP) were similar to corresponding control-pollinated families (GCP and NCP, respectively) suggesting that removal of selfing and other inbreeding effects have occurred. Genetic correlations between relative conductivity at different temperatures were high, suggesting the same genes are involved despite differing levels of damage.

Key words: Relative conductivity, REML, provenances, heritability, genetic correlation.

FDC: 165.3; 165.53; 181.221.1; 422.1; 176.1 *Eucalyptus globulus;* 176.1 *Eucalyptus nitens.*

Introduction

Temperate eucalypts are widely used as a source of pulp and paper manufacture in the cool-temperate regions of the world but further extension of their planting is generally limited by seasonal low temperatures and occasional frosts. Temperate eucalypt species which have been shown to be relatively frost hardy such as *Eucalyptus nitens, E. gunnii, E. delegatensis, E. viminalis* and *E. dalrympleana* tolerate temperatures as low as —12 °C provided acclimation has taken place before the onset of frost (PATON, 1981; DAVIDSON and REID, 1987; TIBBITS and REID, 1987a). More sensitive temperate species include *E. globulus* and *E. regnans*, with critical temperatures around —7 °C (TURNBULL and PRYOR, 1978; HALLAM et al., 1989; ELDRIDGE et al., 1993).

E. globulus subsp. *globulus* (hereafter referred to as *E. globulus)* and *E. nitens* are 2 of the most important temperate eucalypt species, due to their excellent productivity, fibre characteristics and pulp yield. They are currently being established in large areas in Australia, South America and south-western Europa. *E. nitens*, the more frost tolerant of the 2, has become the preferred species for eucalypt plantation forestry in higher altitude areas, subject to frequent winter frosts, whereas *E. globulus* has been confined to milder sites.

Improvements in frost tolerance have the advantage if significantly increasing the area of land suitable for eucalypt plantations by reducing the risk of losses due to frost. Evidence of provenance differences in frost tolerance have been reported for *E. nitens* (TIBBITS and REID, 1987b; HALLAM and TIBBITS, 1988; RAYMOND et al., 1989), and for *E. globulus* (ALMEIDA, 1993) but studies on the magnitude of additive genetic variation have been limited. Frost damage in leaves and branches of field grown trees of open-pollinated origin has been shown to be highly heritable in *E. nitens* (TIBBITS and REID, 1987b) with h^2 above 0.6 but low to moderate in *E. grandis* (VAN WYK, 1976) and *E. gunnii* (CAUVIN et al., 1993) with h^2 between 0.10 and 0.29. More recently, indirect methods for frost tolerance assessment, based on electric resistance (or conductivity) of leaf exudates have been developed. They have the advantage of being non-destructive and provide a continuous variable, more suitable to statistical treatment and interpretation (see RAYMOND et al., 1992a for a review). Inheritance of electric conductivity measurements were carried out in *E. nitens* (TIBBITS and REID, 1987; RAYMOND et al., 1992b) and *E. regnans* (C. A. RAYMOND and J. V. OWEN, unpublished) and have shown a high heritability, with values usually above 0.6.

Although the economic importance of tolerance to frost damage is obvious, basic information on the genetic control of this trait in eucalypts, and in particular in *E. nitens* and

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