through provenance selection (JOHNSON *et al.*, 1955). It has therefore been suggested that high heritability coupled with high genetic advance is the true index for effective selection (JOHNSON et al., 1955; SWARUP and CHAUGALE, 1962). The genetic advance estimated for the first generation from provenance selection ranged from 0.075 for taper to 5.568 for tree height (*Table 4*). When expressed as percent of mean, the values obtained ranged from 7.14% for taper to 58.14% for number of forks. High provenance heritability was not in most cases associated with high genetic advance, which is very much in agreement with the observation of SWARUP and CHAUGALE (1962). The provenance heritability estimated for any one characteristic is useful when high selection gain in that characteristic is also feasible (KAUL and BAHN, 1974). In the present study, a genetic advance as percent of mean of 15.00 would be considered high. For instance, a 10% increase in DBH will, in strict mathematical terms, result in approximately a 20% increase in basal area, hence in volume (LAURIDSEN *et al.*, 1987). Even small improvements become economically important in large planting programmes (ZOBEL, 1977). Over 15% genetic gain was recorded for all the characteristics except taper. Coupled with their high provenance heritability estimates, a reasonable level of genetic improvement can be achieved through provenance selection for each of the characteristics. Although taper had a fairly high provenance heritability, its genetic advance was low.

Acknowledgements

The first author thanks the Director, Forestry Research Institute of Nigeria for providing the funds for this project.

References

BURLEY, J. and WOOD, P. J.: A manual on species and provenance research with particular reference to the tropics. Tropical Forestry Papers, No 10. Department of Forestry, Commonwealth Forestry Institute, University of Oxford. 226 pp. (1976). — BURTON, G. W. and DEVANE, E. W.: Estimating heritability in tall fescue (*Festuca arundinaceae*) from replicated clonal material. Agronomy Journal **45**: 478—487 (1953). — HANSON, C. H., ROBINSON, H. F. and COMSTOCK, R. E.: Biometrical studies of yield in segregating population of Korean Lespedeza. Agronomy Journal **48**: 268—272 (1956). — JOHNSON, H. W.., ROBINSON, H. F. and COMSTOCK, R. E.: Estimate of genetic and environmental variability in soybeans. Agronomy Journal **47**: 314—318 (1955). — KAUL, M. L. H. and BAHN, A. K.: Studies on some genetic parameters of rice (*Oryza sativa* L.). Theoretical and Applied Genetics **44**: 178—183 (1974). — LAURIDSEN, E. B., WELLENDORF, H. and KEIDING, H.: Evaluation of an international series of *Gmelina* provenance trials. Danida Forest Seed Centre, Humlebeck, Denmark. 110 pp. (1987). — LEDIG, F. T. and WHITMORE, J. L.: Heritability and genetic correlation for volume, foxtails, and other characteristics of Caribbean pine in Puerto Rico. Silvae Genetica **30**: 88—92 (1981). — OTEGBEYE, G. O.: Provenance productivity in *Eucalyptus camaldulensis* DEHNH. and its implications to genetic improvement in the savanna region of Nigeria. Silvae Genetica **34**: 121—126 (1985). — OTEGBEYE, G. O. and SAMARAWIRA, I.: Growth and form of *Eucalyptus camaldulensis* DEHNH. provenances in Northern Nigeria. Forest Ecology and Management **42** (3—4): 219—229 (1991). — SWARUP, V. and CHAUGALE, D. S.: Studies on genetic variability in sorghum. I. Phenotypic variation and its heritability component in some important characters contributing towards yield. Indian Journal of Genetics and Plant Breeding **22**: 31—36 (1962). — ZOBEL, B. J.: Increasing southern pine timber production through tree improvement. Southern Journal of Applied Forestry **1**: 3—10 (1977).

Genetic Parameter Estimates for Growth Traits at Different Ages in Slash Pine and Some Implications for Breeding[1])

By G. R. HODGE and T. L. WHITE

Department of Forestry, Institute of Food and Agricultural Sciences, University of Florida, Gainesville FL, 32611, USA

(Received 6th December 1991)

Abstract

Data from 57 slash pine open-pollinated progeny tests, 585 different families and approximately 70,000 trees were used to estimate genetic parameters (heritabilities, Type B genetic correlations between measures of a trait on two sites, and genetic correlations between two different traits) for cumulative growth traits at ages 5, 10 and 15, and incremental and relative growth rates between ages. A modification of an analytical approach discussed by BURDON (1977) made use of all possible pairs of progeny tests with common families to estimate parameters. Heritabilities for cumulative growth traits (height, DBH, volume) in slash pine at age 5 are low, on the order of 0.05 to 0.10, and increase to 0.12 to 0.16 by ages 10 and 15. Genetic correlations of age 5 growth traits with the same trait at age 10 or 15 were moderate (0.5 to 0.7), while age 10 and 15 growth had extremely high correlations (approximately 1). Finally, Type B genetic correlations were higher between pairs of locations of similar site indices (< 2.6 m different) than between pairs of locations with very different site indices (≥ 2.6 m different). This indicates that genotype x environment interaction arises from differences in site quality, and suggests that large site index differences between progeny test sites and commercial production land will decrease the reliability of progeny test data in predicting breeding values.

Key words: Heritability, genetic correlation, Type B genetic correlation, genotype x environment interaction, juvenile-mature correlation, *Pinus elliottii* ENGELM. var. *elliottii*.

Introduction

Precise and accurate genetic parameter estimates are crucial for making sound decisions in many stages of a tree

[1]) This is Journal Series No. R-02357 of the Institute of Food and Agricultural Sciences, University of Florida, Gainesville FL, 32611. We gratefully acknowledge the efforts of GREG POWELL, HARM KOK, and the CFGRP cooperators whose efforts in collecting and managing the data made these analyses possible. Thanks are also due to TONY SHELBOURNE and ROWLAND BURDON for their thorough and helpful reviews.

improvement program. For example, the degree and type of genetic control over important traits affect both strategies for breeding and for commercial propagation (WHITE, 1987; NAMKOONG et al., 1988, p. 45). Also, knowledge of genetic and environmental parameters is used to design efficient progeny testing strategies (NAMKOONG, 1979, p. 234; BRIDGWATER et al., 1983), and to calculate gain from selection (NAMKOONG et al., 1966; SHELBOURNE, 1969). Additionally, genetic and phenotypic relationships among different traits or ages of measurement are used in progeny test analysis to develop selection indices (Best Linear Prediction) or Best Linear Unbiased Predictions (BLUP) to maximize gain from selection (BAKER, 1986; WHITE and HODGE, 1989; COTTERILL and DEAN, 1990), and to evaluate the efficiency of indirect selection (BINET, 1965). Further, heritabilities and juvenile-mature genetic correlations are essential to determination of optimal selection age (LAMBETH, 1980; LAMBETH et al., 1983; FOSTER, 1986; MATHESON, 1988; BURDON, 1989). Finally, knowledge of genetic correlations between growth traits during different time intervals may be of use to researchers attempting to identify physiological mechanisms associated with superior performance in the field. Since genetic parameters are used in so many ways in breeding programs, much research effort has gone into genetic tests aimed at obtaining estimates.

Often genetic parameter estimates are made using small experiments, frequently even based on a single progeny test. Genetic parameter estimates based on a single test are biased by the presence of genotype x environment interaction (COMSTOCK and MOLL, 1963). Further, precise estimates of genetic parameters require large experiments sampling many families (NAMKOONG and ROBERDS, 1974). To give a quantitative sense of the size of experiments necessary, KLEIN et al. (1973) determined that for a heritability (h^2) = 0.20, nearly 800 half-sib families of size 4 are needed to estimate h^2 with a standard error of 0.10. To reduce the standard error to 0.05 required nearly 1600 families of size 4. Similar results indicating a need for large numbers of families were obtained from a simulation study using models and genetic parameters more representative of forest trees[2]). Assuming $h^2 = 0.25$, and a mating and testing design of six-parent disconnected partial half-diallels (planted on two sites, 4 blocks, 6 trees/family/block), a total of 99 diallels (494 parents) were needed to estimate h^2 with a standard error of 0.05.

Perhaps even more so than heritabilities, genetic correlations are often estimated with relatively large errors. Heritabilities are estimated as functions of two parameter estimates, additive and phenotypic variance, with phenotypic variance generally being very precisely estimated. In contrast, genetic correlations are estimated as functions of three parameter estimates, two variance components and a covariance component, with all three being difficult to estimate precisely. Furthermore, when working with multiple traits or ages we are often interested in estimating a matrix of many genetic variances and covariances (NAMKOONG et al., 1988, p. 83). In a manner analogous to estimating 'experiment-wide' error rates in multiple comparison tests, when estimating many parameters simultaneously we are interested in 'experiment-wide' precision; precise estimates of all parameters are needed to ensure a precise estimate of the matrix of relationships. The difficulty in obtaining these precise 'experiment-wide' estimates is discussed by HILL and THOMPSON (1978), and this further illustrates the need for large amounts of data for genetic experiments.

The Cooperative Forest Genetics Research Program (CFGRP) consists of 14 members including both forest industry and state agency members working to improve slash pine (*Pinus elliottii* ENGELM. var. *elliotti*). The CFGRP is currently planning advanced-generation breeding and progeny testing strategies. In this study, the overall goal was to estimate genetic parameters for slash pine using data from a large number of tests and families so that resulting estimates could be used with confidence in all facets of program planning and implementation. Specifically, the objectives were 1) to estimate genetic parameters (heritabilities, genetic correlations between different traits, and Type B genetic correlations calculated for the same trait expressed in two different environments - a measure of genotype x environment interaction) for growth traits at three ages (5, 10, 15), and for relative and absolute growth rates during three intervals (5 to 10, 10 to 15, 5 to 15), and 2) to determine if these parameters vary according to site quality.

Materials and Methods

Progeny Test Data

From 1956 to 1963, members of the CFGRP made over two thousand first-generation selections of slash pine from natural stands. Each organization then grafted the selections it made into its own seed orchards. Open-pollinated seed from these selections were collected from the grafted seed orchards, and then planted in field progeny tests. On each individual tree, total height and diameter at breast height (DBH) were measured, and volume calculated (GODDARD and STRICKLAND, 1968) at ages 5, 10, and 15. In addition, the absolute growth increment, and relative growth rate $[(\ln g]_2 - \ln g_1)/(t_2 - t_1)$ from CAUSTON and VENUS, 1981, p. 25)] for each of the growth traits from ages 5 to 10, 10 to 15, and 5 to 15 were calculated. This was a total of 30 traits for which all genetic parameters were estimated. Site indices for all tests were calculated on the basis of 10-year height measurements using an equation developed by PIENAAR et al. (1990).

The primary objective of the CFGRP progeny tests was to rank parental selections for general combining ability. Each progeny test was planted in a randomized complete block design; however, family composition, number of families, number of blocks, and number of trees per plot all varied from test to test. A total of 57 progeny tests were identified which had measurements at multiple ages: 27 tests had been measured at ages 5, 10 and 15; 8 tests had been measured at ages 10 and 15; and 22 measured at ages 5 and 10. There were 585 different open-pollinated families and approximately 70,000 trees present in the 57 tests. The number of families present in any one test ranged from 5 to 150, and the number of common families in any pair of tests ranged from 5 to 150. In addition, there were no subsets of more than 3 tests that had the same common families. Because of the extreme unbalance, the available data were not extremely well-suited for classical variance component estimation approaches, and an alternative approach was devised.

General Approach to Parameter Estimation

The basic approach utilized in this study was to estimate parameters using all possible pairs of tests with common

[2]) DUDLEY HUBER, personal communication.

families, estimating family variances and covariances using a *Type B* correlation framework as outlined by BURDON (1977). This approach involves both single-site analyses of variance and analyses of all possible pairs of tests. When data are unbalanced, there are a number of analytical techniques available for variance component estimation (including HENDERSON's methods I, II and III, maximum likelihood, restricted maximum likelihood, and MINQUE), and there is no globally optimum method of analysis (MILLIKEN and JOHNSON, 1984, p. 260; SEARLE, 1987, p. 495). The approach in this study, adapted from BURDON (1977) and JOHNSON and BURDON (1990) for variance component estimation offers some important advantages over the classical approach. For example, heterogeneous variance structures among sites pose no problems in this approach, but violate an assumption of conventional analysis of variance (ANOVA). ANOVAs need only be conducted one site at a time, which simplifies computations and eliminates certain problems with family imbalance across tests, i. e. particular families represented in only a subset of the tests. In addition, the approach offers advantages when investigating age-age correlations. When measuring the same trees at different ages, the error terms may not be independent and thus genetic covariances may be confounded by environmental covariances. To eliminate this, measurements on the two traits should be made on independent trees (NAMKOONG et al., 1988, p. 81). In general, the paired test approach is more flexible and can be of particular use in unfavorable circumstances such as described above. Other aspects of the Type B approach and its relationship to classical ANOVA are discussed by YAMADA (1962) and DICKERSON (1962), while our use is described below.

Linear Model

The linear model used to represent the data for a given trait measured at a given age is:

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

where

μ = a fixed general mean,

t_i = random effect of i^{th} test environment, i = 1, 2, ... e, $E(t_i) = 0$, $Var(t_i) = \sigma^2_t$,

r_{ij} = random effect of j^{th} block within the i^{th} test, j = 1, 2, ... b_i, $E(r_{ij}) = 0$, $Var(r_{ij}) = \sigma^2_r$,

f_k = random effect of k^{th} family, k = 1, 2, ... s_i, $E(f_k) = 0$, $Var(f_k) = \sigma^2_f$,

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 k^{th} family in j^{th} block of i^{th} test, $E(p_{ijk}) = 0$, $Var(p_{ijk}) = \sigma^2_p$,

w_{ijkl} = random tree error of l^{th} tree in ijk^{th} plot, 1 = 1, 2, ... n_i, $E(w_{ijkl}) = 0$, $Var(w_{ijkl}) = \sigma^2_w$, and

the covariances between all pairs of factors are assumed zero.

The f_k effects are assumed random and are associated with the average genetic effects of the open-pollinated families planted in each test. When open-pollinated families are considered true half-sib families, and assuming no epistatic effects, f_k is the general combining ability of the k^{th} parent, so f_k is equal to ½ of the breeding value (BV) of the k^{th} parent. Thus, $Var(f_k) = Var(\frac{1}{2}BV) = \frac{1}{4}\sigma^2_A$ (i. e., ¼ of the additive genetic variance).

There are several conditions that must be met for open-pollinated families to approximate true half-sib families (SQUILLACE, 1974; SORENSON and WHITE, 1988), and detailed knowledge of the mating system is needed to assess how variance component estimates would be affected. Lacking that knowledge for slash pine, we assume that open-pollinated families are half-sib families.

Single Site Analyses and Biased Heritabilities

If variance components are estimated on a site-by-site basis (as is commonly done), family x environment interaction variance cannot be estimated, and in fact is added to the estimate of family variance on that site; thus, the estimate of variance among families includes both σ^2_f and σ^2_{fe}, and has been referred to as biased since it does not estimate only σ^2_f (COMSTOCK and MOLL, 1963). In effect, the linear model above is modified such that

$$y_{ijkl} = \mu_i + r_{ij} + F_{ik} + p_{ijk} + w_{ijkl},$$

where

$\mu_i = \mu + t_i$, the mean for the i^{th} test,

$F_{ik} = f_k + fe_{ik}$, random effect of k^{th} family on the i^{th} test, $E(F_{ik}) = 0$, $Var(F_{ik}) = \sigma^2_F = \sigma^2_f + \sigma^2_{fe}$.

This modified linear model was used to conduct an analysis of variance on a site-by-site basis, and variance components estimated by the method of moments (MILLIKEN and JOHNSON, 1984, p. 233), i. e., equating observed mean squares with their expectations. The data were nearly 100% balanced on the plot level, and ANOVAs were calculated using plot means. Estimates of within-plot variance for each trait were calculated separately, Biased heritability (h^2_B), and total phenotypic variance estimates (σ^2_P) were calculated for each trait for each of the 57 tests as below:

$$\sigma^2_P = (\sigma^2_F + \sigma^2_p + \sigma^2_w),$$

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

The biased heritability (equivalently called a single-site heritability), is referred to as biased because it estimates the sum of additive plus additive x environment variance relative to the total phenotypic variance, thus will be biased upward relative to the typical narrow-sense heritability.

Paired Site Analyses

Family means were calculated for each trait in every test. Then, for every pair of tests with at least 5 common families ,the covariance of family means for each growth trait in the two tests was calculated, yielding a direct estimate of family variance (σ^2_f). As family effects are the only terms in the model which can cause a covariance between family performance on two sites, the covariance of family means estimates only family variance, and not any family x environment interaction variance. The estimate of family variance is independent of differences in experimental design of the two test (BURDON, 1977). Similarly, the expected value of a family-mean covariance between different traits measured on two different sites equals the family covariance between those two traits (σ_{f,f^*}, the asterisk signifies effects associated with the second trait).

Thus, for every pair of tests, estimates were calculated

for σ^2_f for every trait, and for $\sigma_{f,f'}$ for every pair of traits; in addition, combined estimates of total phenotypic variance ($\sigma^2_{P'}$) and biased family variance ($\sigma^2_{F'}$) were calculated as geometric means of the two single-site estimates of phenotypic variance and biased family variance, respectively. Narrow-sense heritability (h^2), the Type B genetic correlation (r_B) and the genetic correlation between different traits (r_g) were then estimated for each pair of tests as:

$$h^2 = 4\,\sigma^2_f / \sigma^2_{P'}$$

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

$$r_g = \tfrac{1}{2}[\mathrm{Cov}(\bar{y}_{i\cdot k\cdot}, \bar{y}^*_{i'\cdot k\cdot}) + \mathrm{Cov}(\bar{y}^*_{i\cdot k\cdot}, \bar{y}_{i'\cdot k\cdot})] / (\sigma^2_f\,\sigma^2_{f^*})^{1/2}$$
$$= \sigma_{f,f^*} / (\sigma^2_f\,\sigma^2_{f^*})^{1/2}$$

The Type B genetic correlation (r_B) is for present purposes the genetic correlation between the same trait expressed on two different sites, and is essentially a measure of GxE (Burdon, 1977): $0 \leq r_B \leq 1$, and $r_B \approx 1$ indicates no GxE variance.

Average Parameter Estimates Across All Tests

The next step was to determine an average parameter estimate and a measure of standard error for both biased and unbiased heritabilities, and all genetic correlations. First, estimates for r_g and r_B were bounded at —1.3 and 1.3, and —0.3 and 1.3, respectively, before means were calculated. Next, to obtain means, one alternative would have been to assume that all estimates of a parameter had equal precision, and simply calculate the unweighted average and the variance. In this study, the single-test and pair-wise test estimates all were based on different amounts of data (different numbers of families, blocks, etc.), and therefore have different variances. Estimates based on large numbers of families (all other things being equal) are more precise (have lower variance) than estimates based on small numbers of families. When calculating a mean from observations with different variances, the best linear unbiased estimator (BLUE) is calculated by weighting each observation by the inverse of its variance. As the true variance of an estimate is never known, we calculated an approximate variance for each estimate in order to use these as weights to calculate overall averages (i.e. to approximate BLUE averages).

There are formulae available to approximate the variance of heritability ($\mathrm{Var}(h^2)$) or genetic correlation estimates ($\mathrm{Var}(r_g)$) from standard analysis of variance approaches utilizing a Taylor series expansion (e.g., Mode and Robinson, 1959; Becker, 1975; Namkoong, 1979); however, the accuracy of this approximation is not well known. In this study, this type of approximation could be used for the h^2_b estimates from Eq. 4; however, even if the approximation is good for a single test, it may not accurately reflect the variance of heritability estimates from test to test. In such a case it may be better to obtain a direct empirical estimate of variability from the actual data (Mosteller and Tukey, 1977, p.123). Further, the absence of approximate formulae for variances of h^2, r_B and r_g estimates from Eqs. 8 to 10 makes necessary a direct empirical estimate of the variances of the parameter estimates.

In formulae from the Taylor series expansion, the variance of these genetic parameter estimates is roughly inversely proportional to the degrees of freedom for family, and preliminary analyses did indeed show that estimates based on larger numbers of families had smaller empirical variances. For volume at age 10 (a trait for which the maximum amount of data was available), empirical variances of the heritability estimates were calculated for 5 subsets of the data representing estimates based on different numbers of families (5 to 7, 8 to 10, 11 to 20, 21 to 30, 31 and up). After plotting variance versus number of families, an appropriate curve form was determined (Jensen and Homeyer, 1971), and a regression developed to predict $\mathrm{Var}(h^2)$ for these two traits as a function of the number of families (f).

$$\mathrm{Var}(h^2) = -0.0059 + 0.0590\,[(f-4)]^{-1/2},\quad R^2 = 0.85$$

These weights appeared to hold for other traits and parameters, and thus, the inverse of the predicted variances from the above equation were used as weights in the calculation of mean values for h^2_b, h^2, r_g, and r_B for all traits and pairs of traits. Thus, as the number of families that were involved in a parameter estimate increased, more weight was placed on that estimate in the determination of the overall mean.

Using this approach we have defined the mean parameter estimate as the weighted average of the parameters, as opposed to the function of the average variance and/or covariance components which make up the parameters (e.g., see Itoh and Yamada, 1990, Eq. 31). This was done primarily because all the parameters are bounded, while variance and covariance components, which make up the parameters, are not. This made it easier derive the weights (approximating variances of the parameters) which are discussed above.

Results

Parameter Estimates

Narrow-sense heritability (h^2) estimates (unbiased, or across sites) for the three cumulative growth traits were all approximately 0.07 at age 5, and increased to approximately 0.12 for height and 0.16 for DBH and volume at ages 10 and 15 (*Figure 1*). Approximate standard errors for the mean h^2 estimates were low, all less than 0.02 (*Table 1*). For height, DBH, and volume, 10-year growth and 15-year growth appear to be under nearly identical genetic control. Narrow-sense heritability estimates are slightly higher at age 15, but the estimated 10 to 15 age-age correlations are 0.994±.033, 1.02±.018, and 1.03±.017 (mean ± standard error) for height, DBH, and volume, respectively (*Table 1*). The three estimated 5—15 age-age correlations for height, DBH, and volume are 0.794±.070, 0.614±.115, and 0.692±.062, respectively (*Table 1*).

There appears to be moderate GxE interaction present in slash pine growth traits. Type B genetic correlations between sites (r_B in *Table 1*) are approximately 0.50 to 0.65 for 10 and 15-year growth traits, and all biased (within-site) heritabilities (h^2_b) were approximately 1.5 to 2 times as high as narrow-sense (across-site) heritability estimates; this indicates the presence of genotype x environment interaction variance which is approximately 50% to 100% of the size of the additive genetic variance.

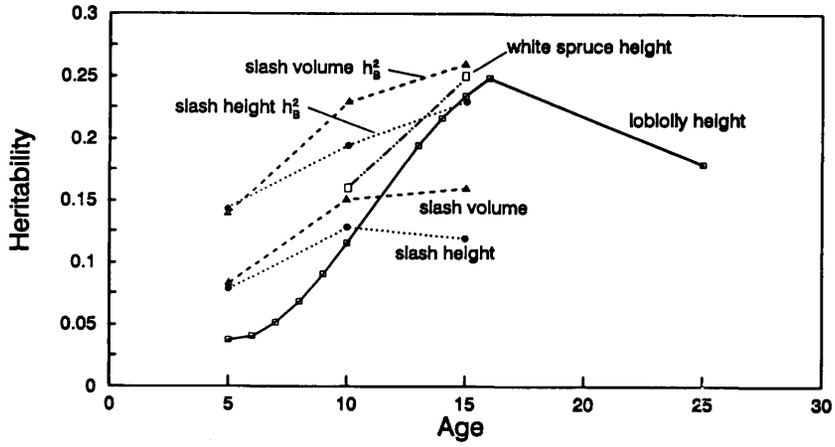

Figure 1. — Heritability of growth traits at various ages for some conifers. Data for loblolly adapted from BALOCCHI (1990), and for white spruce from NIENSTAEDT and RIEMENSCHNEIDER (1985). When lines are noted as h^2_B they represented biased (single-site) heritability estimates. All other lines represent typical narrow-sense heritability (h^2) estimates.

Absolute growth increments had slightly lower heritability estimates than cumulative growth traits, and were highly correlated to the cumulative traits (*Table 2*). The genetic correlation between cumulative growth to age 5 and subsequent incremental growth from age 5 to 10 is 0.828±.047 and 0.582±.072 for volume and height, respectively. Substantially less correlation is found between cumulative growth to age 5 and incremental growth from age 10 to 15: r_g = 0.615±.079 for volume, and r_g = 0.227 ±.189 for height. Thus, probably less than 50% of the variability in genetic effects for harvest volume can be accounted for by variability in cumulative 5-year field growth traits.

Relative growth rates for height, DBH, and volume were disappointing traits for all time periods. Narrow-sense heritabilities for all relative growth rates were less than 0.07, and the majority were less than 0.04; however, all were more than 2 approximate standard errors greater

Table 1. — Estimates of genetic parameters for a number of cumulative growth traits of slash pine. The estimated parameters are: 1) h^2_b, biased heritability from a single site ANOVA; 2) h^2, typical narrow sense heritability; 3) r_B, the Type B genetic correlation for same trait measured on two sites (see BURDON, 1977); and 4) r_g, the genetic correlation of different traits. Entries are sample mean with empirical standard errors in parentheses.

Trait	h^2_b	h^2	r_B	Genetic correlation (r_g)							
				H10	H15	D05	D10	D15	V05	V10	V15
Height, age 5 (H05)	.142 (.016)	.078 (.013)	.498 (.065)	.945 (.024)	.794 (.070)	.818 (.032)	.496 (.065)	.168 (.113)	.980 (.015)	.756 (.041)	.347 (.091)
Height, age 10 (H10)	.195 (.018)	.128 (.014)	.666 (.046)		.994 (.033)	.705 (.048)	.533 (.050)	.539 (.048)	.911 (.037)	.826 (.028)	.643 (.062)
Height, age 15 (H15)	.230 (.022)	.119 (.019)	.536 (.069)			.718 (.084)	.319 .082)	.344 (.074)	.842 (.082)	.691 (.047)	.461 (.084)
DBH, age 5 (D05)	.130 (.015)	.063 (.011)	.460 (.060)				.818 (.045)	.614 (.115)	.999 (.021)	.894 (.031)	.441 (.205)
DBH, age 10 (D10)	.225 (.014)	.149 (.011)	.665 (.042)					1.02 (.018)	.731 (.060)	.983 (.010)	.834 (.062)
DBH, age 15 (D15)	.237 (.020)	.158 (.016)	.671 (.056)						.431 (.093)	.990 (.020)	.972 (.007)
Volume, age 5 (V05)	.137 (.016)	.080 (.012)	.592 (.061)							.856 (.041)	.692 (.062)
Volume, age 10 (V10)	.232 (.017)	.156 (.013)	.665 (.043)								1.03 (.017)
Volume, age 15 (V15)	.260 (.022)	.161 (.016)	.628 (.052)								

Table 2. — Estimates of genetic parameters for a number of incremental growth traits of slash pine. The estimated parameters are: 1) h^2_b, biased heritability from a single site ANOVA; 2) h^2, typical narrow sense heritability; r_B, the Type B genetic correlation for same trait measured on two sites (see BURDON, 1977); and 4) r_g, the genetic correlation of different traits. Entries are sample means with empirical standard errors in parentheses.

Trait	h^2_b	h^2	r_B	Genetic correlation (r_g)				
				H05	**ΔH0510**	**H10**	**ΔH1015**	**H15**
Height increment, age 5-10 (**ΔH0510**)	.158 (.016)	.103 (.011)	.636 (.048)	.582 (.072)	x	1.00 (.022)	.773 (.124)	.969 (.103)
Height increment, age 10-15 (**ΔH1015**)	.138 (.016)	.054 (.013)	.491 (.078)	.227 (.189)	.773 (.124)	.592 (.088)	x	.898 (.051)
				D05	**ΔD0510**	**D10**	**ΔD1015**	**D15**
DBH increment, age 5-10 (**ΔD0510**)	.234 (.019)	.144 (.014)	.655 (.046)	.428 (.085)	x	.933 (.030)	.813 (.085)	.970 (.040)
DBH increment, age 10-15 (**ΔD1015**)	.161 (.022)	.113 (.014)	.719 (.067)	.272 (.140)	.813 (.085)	.840 (.071)	x	.991 (.025)
				V05	**ΔV0510**	**V10**	**ΔV1015**	**V15**
Volume increment, age 5-10 (**ΔV0510**)	.234 (.019)	.151 (.016)	.615 (.047)	.828 (.047)	x	1.00 (.001)	1.01 (.036)	1.05 (.028)
Volume increment, age 10-15 (**ΔV1015**)	.243 (.022)	.153 (.016)	.640 (.054)	.615 (.079)	1.01 (.036)	1.02 (.024)	x	1.00 (.000)

Table 3. — Estimates of genetic parameters for a number of relative growth rates of slash pine. The estimated parameters are: 1) h^2_b, biased heritability from a single site ANOVA; 2) h^2, typical narrow sense heritability; 3) r_B, the Type B genetic correlation for same trait measured on two sites (see BURDON, 1977); and 4) r_g, the genetic correlation of different traits. Entries are sample means with empirical standard errors in parentheses.

Trait	h^2_b	h^2	r_B	Genetic correlation (r_g)				
				H05	**RH0510**	**H10**	**RH1015**	**H15**
RGR Height, age 5-10 (**RH0510**)	.087 (.006)	.023 (.010)	.482 (.066)	-.619 (.064)	x	-.043 (.093)	.549 (.244)	.589 (.155)
RGR Height, age 10-15 (**RH1015**)	.095 (.011)	.024 (.011)	.406 (.095)	-.563 (.244)	.549 (.244)	-.275 (.101)	x	.208 (.135)
				D05	**RD0510**	**D10**	**RD1015**	**D15**
RGR DBH, age 5-10 (**RD0510**)	.084 (.005)	.036 (.009)	.519 (.072)	-.701 (.074)	x	.119 (.105)	.685 (.222)	.755 (.126)
RGR DBH, age 10-15 (**RD1015**)	.095 (.008)	.044 (.010)	.503 (.090)	-.068 (.165)	.685 (.222)	.162 (.124)	x	.432 (.101)
				V05	**RV0510**	**V10**	**RV1015**	**V15**
RGR Volume, age 5-10 (**RV0510**)	.092 (.006)	.033 (.008)	.491 (.064)	-.286 (.091)	x	.378 (.088)	.628 (.179)	.594 (.149)
RGR Volume, age 10-15 (**RV1015**)	.085 (.008)	.029 (.011)	.557 (.081)	-.121 (.183)	.628 (.179)	.350 (.117)	x	.508 (.108)

than zero (*Table 3*). Apparently, real genetic differences exist for these traits, but are relatively small. For all traits, the estimated genetic correlations between RGR from ages 5 to 10 and ages 10 to 15 are negative with cumulative 5-year traits, and positive with cumulative 15-year traits (*Table 4*).

Site Quality Effects

Site index for the 57 tests ranged from 14.5 m to 28.5 m (47 ft to 93 ft) using base age of 25. Estimated single-site heritabilities (h^2_B) showed no association with site index, suggesting that the degree of genetic control and site uniformity were apparently the same on sites of both high and low quality. To investigate the effect of site quality on GxE interaction, pairs of tests with site indices different by more than 2.6 m (8.5 ft) were classified as 'Different', while if the site index difference was less than 2.6 m, the pair was classified as 'Same'. The value of 2.6 meters was chosen to classify approximately half of all possible pairs as 'Different' and half as 'Same'; 2.6 m was approximately 1 standard deviation in site index for the 57 tests. The average site index difference was 4.7 m (15.3 ft) for pairs of 'Different' tests, and 1.3 m (4.3 ft) for 'Same' tests. Type B genetic correlations (r_B) measure the degree of commonality of gene effects for a trait (e.g.,, height growth) in two different environments. For every cumulative growth trait, a higher r_B was found for pairs of sites with similar site quality than for pairs of different site quality (*Table 4*). The lowest difference between r_B for 'Same' and 'Different' sites was 0.079 for age 5 height, and the highest was 0.378 for age 15 DBH. On average across all 9 cumulative growth traits, r_B = 0.71 for 'Same' sites, and r_B = 0.51 for 'Different' sites. Thus, at least a portion of GxE in slash pine results from different growth performances on sites of different quality.

There is also an interesting relationship between r_B and increasing age in the 'Same' and 'Different' classes (*Table 4*). At age 5, r_B for the 'Same' class is only slightly larger than for the 'Different' class. For the 'Same' class, estimated r_B increases as age increases, i. e., over time GxE interaction decreases and family performances become more alike on separate sites of similar site quality. In contrast, for the 'Different' class, estimated r_B decreases as age increases, thus family performances on sites of very disparate site qualities would become less and less alike over time.

Table 4. — Estimates of Type B genetic correlation (r_B) on pairs of sites of similar or different site quality. Pairs of tests with site indices differing by less than 2.6 m (8.5 ft) are classified as 'Same', otherwise are classified as 'Different'. Average site index difference for the 'Different' class was 4.7 m (15.3 ft), site index difference for the 'Same' class was 1.3 m (4.3 ft). Entries are sample means with empirical standard errors in parentheses.

Trait	r_B	
	Same	Different
Height, age 5 (H05)	.543 (.097)	.464 (.088)
Height, age 10 (H10)	.708 (.066)	.628 (.064)
Height, age 15 (H15)	.731 (.097)	.388 (.087)
DBH, age 5 (D05)	.513 (.082)	.422 (.086)
DBH, age 10 (D10)	.782 (.061)	.560 (.055)
DBH, age 15 (D15)	.888 (.060)	.510 (.075)
Volume, age 5 (V05)	.636 (.082)	.556 (.087)
Volume, age 10 (V10)	.738 (.066)	.602 (.055)
Volume, age 15 (V15)	.811 (.062)	.491 (.068)

Discussion

Time Trends in Genetic Parameters

Previous estimates of narrow-sense heritabilities for slash pine were summarized by Dorman and Squillace (1974) and ranged from h^2 = 0.03 to 0.37 for height, —0.22 to 0.58 for DBH, and 0.16 to 0.35 for volume. The current estimates tend to lie in the lower ends of the ranges of previously published estimates, and seem to be in th low ends of ranges reported for several conifers (e.g. see Zobel and Talbert, 1984, p.130). Since previous estimates for slash pine are comparable to those for other conifers, the lower estimates found in this study are probably not due to species differences. There are a number of other possible reasons for this result. Many previous estimates in the literature have been based on results from a single test, which would bias heritabilities upward. In addition, there may be some tendency for researchers not tc publish very low or negative heritability estimates. Finally, this study used a different methodology to estimate parameters, and this may be related to lower estimates.

There appear to be only small genetic differences for relative growth rates in slash pine. However, it is possible that heritabilities are somewhat reduced simply due to the log transformation used to calculate relative growth rates. For example, h^2 for cumulative height at age 5 (H05) is 0.071, while the h^2 for ln(H05) is 0.056. Similarly, for age 5 DBH, h^2 is 0.060 versus 0.045 for the cumulative versus the log transformed trait; and for age 5 volume, h^2 is 0.072 versus 0.041 for the cumulative versus the log transformed. Thus, lower heritabilities were, at least in part, simply a result of the transformation. It is possible that transformation of plot means rather than individual tree values would have mitigated this problem. It is also possible that some covariance adjustment for differences in initial starting size for each period would have improved the results for RGRs in this study. RGR has been generally observed to decline as plants get larger and depart from an exponential growth pattern (Caloin and Yu, 1982.) In this study, the negative correlations between RGR and cumulative 5-year growth variables correspond with this tendency. However, the correlations between cumulative 15-year growth and RGR from ages 5 to 10, and age 10 to 15, are positive. This could be an effect of competition accentuating size differences, although competition (i.e., having missing and/or variable size neighbors) does not seem to have a significant effect on individual tree size in slash pine progeny tests (White et al., 1988). One should note, however, that the genetic correlations involving RGR variables are extremely imprecise (compare standard errors in *Table 3* with those in *Tables 1* and *2*), making interpretation somewhat precarious.

NIENSTADT and RIEMENSCHNEIDER (1985) report heritabilities for *Picea glauca* (MOENCH) Voss (individual trees within provenances) that are strikingly similar to the heritabilities reported by BALOCCHI (1990) for loblolly pine (*Pinus taeda* L.). From age 9 to age 15, heritability for *P. glauca* increased from $h^2 = 0.16$ to $h^2 = 0.25$, and for loblolly pine from $h^2 = 0.09$ to $h^2 = 0.23$. In contrast, slash pine appears to have a higher heritability for height at early ages than these two species. In addition, for slash pine, a slight decline in height heritability begins at an earlier age (*Fig. 1*). Thus, the 'Mature Genotypic Phase' and 'Codominance-Suppression Phase' of FRANKLIN (1979) may occur earlier in slash than in some other conifers, and this may reflect the rapid early growth of slash pine.

LAMBETH (1980) developed an equation to predict age-age height correlations in *Pinaceae*, and found that in general there was linear relationship between the log of the age ratio (LAR) and the age-age correlation. However, the equation was developed with phenotypic age-age correlations, and may tend to underpredict genetic correlations (see LAMBETH et al., 1983). Comparing our age-age correlations with the LAMBETH equation, the genetic correlations for height in this study appear to follow a slope similar to the LAMBETH equation, but with a higher intercept, yielding higher correlations than predicted (*Fig. 2*). In other words, for given age-to-age combinations, slash pine has higher juvenile-mature genetic correlations than predicted by the LAMBETH equation. RIEMENSCHNEIDER (1988) has reported very similar results with jack pine (*Pinus banksiana* LAMB.). In this study, volume age-age genetic correlations appear to follow a steeper slope as LAR increases than do height age-age correlations.

Modification of Genetic Correlation Estimates

Genetic correlation estimates are subject to large errors, i.e., they can be very imprecise (NAMKOONG et al., 1988, p.83). When estimating a system of correlations in a matrix, the errors can be compounded such that the probability of obtaining a matrix that is non-positive definite (i.e., theoretically impossible) is extremely high even for relatively simple systems with large family sizes (THOMPSON and HILL, 1978). An example from this study is found for the matrix dealing with volume-volume correlations in *table 1* (r_g = 0.856, 0.692, and 1.03 for age 5 to 10, 5 to 15, and 10 to 15 correlations, respectively). This system is clearly inadmissable due to the estimated correlation of 1.03 between age 10 and age 15 volume. It is possible, however, for all elements of the matrix to be within theoretical bounds but for the overall system to be inadmissable. Even if the age 10 to 15 correlation is reduced to 1.00, 0.99, 0.98, or 0.97, the matrix still has a negative eigenvalue, and therefore the system is inadmissable. Thus, it is often necessary to examine the entire system of correlations and perhaps modify some or all of them to obtain the best 'system-wide' estimates.

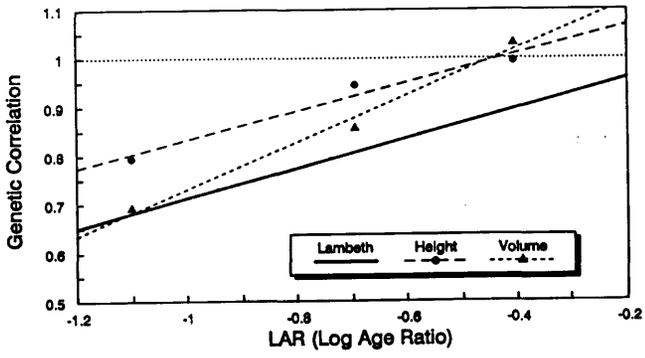

Figure 2. — Age-age genetic correlations observed for slash pine height and volume growth. Results for diameter at breast height (DBH) not shown, but are nearly identical to results for volume. Solid line indicates predicted age-age correlation for height in conifers as a function of the natural log of the age ratio (LAR) (LAMBETH, 1980).

One approach to refine the estimates is 'bending' suggested by HAYES and HILL (1981). They prove for a specific case ($P^{-1}G$, where P and G are the phenotypic and genetic variance and covariance matrices, respectively) that the eigenvalues of estimated genetic correlation matrices are typically too spread out relative to the eigenvalues of the true matrix. In simulation studies they showed selection indices developed after 'bending' could give substantially better results than indices using 'unbent' parameters. We used a similar approach to shrink all eigenvalues of the volume genetic correlation matrix toward their mean of one by a shrinkage factor γ, and then used the original eigenvectors and the shrunken eigen values to recreate the matrix of correlations. The HAYES and HILL approach effectively changes the estimated heritabilities simultaneously with changing the genetic correlations. Our approach did not change heritability estimates, which seems reasonable since they were estimated with substantially more precision than genetic correlations. Since there is no *a priori* way of choosing an optimum shrinkage factor (HAYES and HILL, 1981), we chose to find γ which gave the least shrinkage while still producing an admissible system of correlations. A γ = 0.05 resulted in an admissible system, with bent correlations of r_g = 0.81 0.66 and 0.97, for age 5 to 10, 5 to 15, and 10 to 15 correlations, respectively. As noted by BURDON (1989), with this approach all correlations between traits are reduced toward zero (negative estimates would also be reduced toward zero, i. e., become less negative), and this may not be intuitively pleasing.

As an alternate approach to modification, we reduced the 10 to 15 correlation (since by itself it was theoretically out of bounds) until we found an admissible system. Holding the 5 to 10 and 5 to 15 estimates constant at 0.856 and 0.692, a 10 to 15 correlation of 0.96 resulted in an admissible system. As a third approach, the age 5 to 10 correlation was left constant (since it was based on the most data), and the other two modified. This resulted in a system of correlations of r_g = 0.856, 0.72, and 0.97. As a compromise between the three approaches, we suggest r_g = 0.84, 0.67 and 0.96 as our best estimates of the age 5 to 10, 5 to 15 and 10 to 15 genetic correlations for volume. In general, it is important to examine and perhaps modify correlation estimates between other traits before using the system of correlations in planning or analysis.

Optimum Selection Age

The genes involved in 5-year growth appear to be somewhat different from those affecting 10-year growth, and substantially different from those affecting 15-year growth. It is interesting that these data indicate only a moderate 5 to 15 age-age genetic correlation (0.6 to 0.8), but an extremely high 10 to 15 age-age correlation (approaching 1). Characterizing the intermediate age-age correlations (6 to 15, 7 to 15, etc.) would be extremely valu-

able to help identify the optimum age of selection, but cannot be done with the current data set. One possible approach to adress the problem would be to develop an equation similar to LAMBETH (1980) to estimate the intermediate correlations. While determining optimum selection age is not the focus of this paper, some initial observations are possible, although the optimum age will depend on the type of selection (mass, family, within-family, or combined) and on economic assumptions, as well as the specific parameter estimates. NAMKOONG et al. (1988, p.84) have suggested that even correlations as low as 0.6 could be useful in early selection, thus even 5-year field performance in slash pine may still be of some utility. For the cumulative growth traits, age-10 measurements provide the same genetic information as age-15 traits: heritabilities are approximately equal, and for all practical purposes genetic correlations are one. Thus, there appears to be no point in prolonging field progeny tests past age 10.

Assuming an interest rate of 8%, half-sib progeny test data, and selection for additive effects in loblolly pine, BALOCCHI (1990) determined the optimum age of selection as 9 years for family selection, and 10 years for both within-family selection and combined family plus within-family selection. In that study, the estimated genetic correlation with the target trait (25-year height) was 0.73 at age 5 and reached 1.00 at age 7. For slash pine in this study, assuming selection for 15-year volume, the estimated genetic correlation with the target trait was 0.69 at age 5, and reached 1.00 by age 10, and may possibly have reached this level at earlier ages. Therefore, the comparable juvenile-mature genetic correlations, the higher heritability for slash pine at early ages, and lower peak heritability at later ages will probably drive the optimum selection age closer to age 5 than was calculated for loblolly pine.

GxE Interaction and the Effect of Site Quality

SHELBOURNE (1972) suggests that when GxE interaction variance is half the size of additive variance (i.e., when r_B = 0.67), effects on gains from selection may be serious, thus implying that testing or breeding strategies should be modified to address this. This is approximately the level of GxE interaction observed for cumulative growth traits in slash pine. Genotype x environment interaction can be classified as either *predictable* or *unpredictable* (ALLARD and BRADSHAW, 1964), with significantly different implications for an operational breeding program. With predictable variation, environments can be classified into types (e.g., on the basis of climatic or edaphic variables) such that GxE differences are primarily between types, not within types. Then families could be selected which would perform well in the specific environments. If, however, the environments cannot be so classified, GxE variation is unpredictable and breeding must aim at developing a population that performs well and is stable over a wide range of environments.

Soil type differences (volcanic pumice soils vs phosphorous-deficient clays) have been found to contribute to predictable GxE interaction in *Pinus radiata*. Type B genetic correlations between growth on sites with the same type soils was much higher (0.84 to 0.96) than between sites with different soil types (0.16 to 0.55), and establishment of separate breeding units for the two soil types would increase overall expected program gain from 22% to 25% (JOHNSON and BURDON, 1990). This 3% gain, although considered "small" by the authors, could be quite valuable. Percent genetic gains necessary to justify an entire tree improvement program have been estimated as low as 2.5% to 4% (DAVIS, 1967). Given that some tree improvement program will be conducted, and that many costs associated with the program would be fixed (salaries, equipment, etc.), the marginal benefit of the additional 3% genetic gain could probably justify the marginal costs associated with forming two breeding units.

For slash pine, two relatively simple approaches to classifying environments come to mind: 1) classification of sites based on their productivity or quality as measured by site index, and 2) based on their fusiform rust hazard. In this study, there was no increase in the biased (single-site) heritabilities on better quality sites, i.e., increased growth rate alone did not increase heritability. A similar result was found in *P. caribaea* MORELET var. *hondurensis* BARRET and GOLFARI (WOOLASTON et al., 1990). However, results from this study did indicate that genes affecting growth of slash pine differ to some extent depending on site quality. This result has implications for genetic testing strategies. In the past, progeny tests were generally planted on sites representative of commercial forest lands (ZOBEL and TALBERT, 1984, p.248). Recently, it has been suggested that progeny tests be planted on higher quality sites, such as old agricultural land, or that more intensive cultural practices be used in genetic tests. The intent is to increase environmental uniformity, allow genetic differences to be more readily observed, and increase heritability of the traits measured, thus making make more genetic gain possible (GATES, 1983; TOLIVER, 1983; Anonymous, 1990). However, if in addition to the increased uniformity, the test sites have increased fertility and site quality in comparison to representative commercial land, the increase in heritability may be offset by a decrease in correlation between the trait measured (growth on a high quality site) and the target trait which the breeder ultimately wants to improve (growth on commercial quality land). Note that as average site index difference went from 4.3 ft to 15.3 ft, r_B decreased by an average of 0.20 (from 0.71 to 0.51) for the growth traits in this study (see *Table 4* for trait by trait comparisons). Larger differences in site quality than those observed in this study may result in larger differences in Type B genetic correlation. Furthermore, the pattern of decreasing r_B (increasing GxE) with time for different site index classes could continue after age 15 until harvest age. If so, this would further increase the benefits of strategies in progeny testing or development of production populations designed to take advantage of predictable GxE interaction.

Currently, CFGRP volume breeding value predictions are made for an 'average' site ($SI_{25} \approx 64$), and account for differences in site quality. All other things being equal, less weight is given to data from progeny tests with increasing differences between the progeny test site quality and the 'average' site quality (WHITE and HODGE, 1988). If the target of breeding is the 'average' site, or good performance over the range of all sites, future progeny tests of slash pine should probably be replicated on sites with divergent site indices. Then, all clones will be tested across the range of sites they might experience in commercial plantations. No attempt was made to accomplish this with the bulk of progeny tests established from the early 1960s through the mid 1970s.

It is possible that selections for breeding and production populations be made using different criteria. If only one

breeding population is desired, selections for this population should be made for average sites. If progeny tests are established across a wide range of site qualities, data from high-quality sites could be used in conjunction with data from low-quality sites to predict breeding values for both high, average, and low-quality sites as long as appropriate weights are utilized. If the Type B correlations are well estimated, appropriate weights can be assigned through the use of selection index, BLP, or BLUP (WHITE and HODGE, 1989, p.157). With separate breeding value predictions for 'high' and 'low' quality sites, landowners with different commercial land bases could utilize different clones in their production populations. The changes associated with r_B over time also suggest that selections for the breeding and production populations could take place at different times. At young ages, GxE interaction is unpredictable, therefore selection (particularly forward selection) for a breeding population adapted for the average site seems reasonable. At older ages, GxE becomes more predictable, thus allowing further selection of clones for a production population (e.g., establishment or roguing of seed orchards, seed collection from specific clones for specific sites, vegetative propagation of specific crosses) in order to capture additional gain associated with performance on specific site types.

The effects of fusiform rust infection on growth performance in slash pine progeny tests have been investigated on a subset of the data (17 tests) utilized in the current study. Those results indicated that the family mean correlation between volume growth on two sites was higher when those sites experienced similar fusiform rust infection than when the two sites had widely different rust infection levels (HODGE and WHITE 1986). Site quality and soil differences do have an effect on the fusiform rust hazard (SMITH et al., 1977), so there may be some confounding of fusiform rust effects and site index effects on the genotype x environment interaction.

Physiological Mechanisms

Recently there has been growing interest in investigating the physiological mechanisms which lead to differences in field growth performances in forest trees (WILLIAMS, 1987; LI et al., 1989; PHARIS et al., 1991). Many of these investigations utilize seedling material (from 3 to 24 months old) to examine differences in physiology, and then study correlations between the physiological measures and long-term field growth. The genetic parameter estimates from this study provide evidence of significant changes in genetic mechanisms affecting growth over time. Only about 50% of the variance in 15-year breeding values can be accounted for by variance in 5-year breeding values. These results suggest that there are certain mechanisms which are important to early field survival and establishment that are not important to long-term field growth after succesful initial establishment. Since physiological mechanisms important to field growth seemingly change over time, physiological differences observed in seedling studies may correlate only with early field growth, or only with late field growth, or with both. To elucidate the temporal sequence and relative importance of particular physiological mechanisms, it is necessary to have field measures of both early (juvenile) and late (mature) field growth. Consequently, for slash pine we intend to predict breeding values for growth at age 5 using only 5-year-old data, and breeding values at age 15 using only 10- and 15-year-old data. These will be used for comparisons of performance in ongoing and future studies on early selection and physiological genetics.

The Type B Framework for Parameter Estimation

This study appears to be the first large scale use of the Type B framework to estimate genetic parameters. While not free of complications, this approach allowed estimation of unbiased narrow-sense heritabilities (across-sites) and genetic correlations between different traits. In addition, the use of the Type B genetic correlations (between the same trait on different sites) allowed straightforward investigation of genotype x environment interaction in a search for predictable patterns. For this data set, these tasks would have been substantially more difficult using a conventional analysis of variance approach.

Conclusions

Heritabilities for cumulative growth traits in slash pine at age 5 are low, on the order of 0.05 to 0.10, and increase to 0.12 to 0.16 by ages 10 and 15. Genetic correlation between cumulative growth to age 10 with growth to age 15 is very high (approaching 1), and heritabilities at the two ages are roughly equal, thus there appears to be little point in measuring progeny tests past age 10. Genetic correlations of cumulative growth up to age 5 with cumulative growth to age 15, and with incremental growth from age 5 to age 15 are low, and indicate that less than 50% of the variance in genetic effects for harvest volume can be accounted for by variance in 5-year field growth traits. There is moderate genotype x environment interaction for growth in slash pine, some of which is associated with site quality. Type B genetic correlations between pairs of test sites with similar site indices (differing by less than 2.6 m) are on the order of 0.70 versus 0.50 for pairs of sites with relatively different site indices. Thus, the utility of progeny test measurements to predict future sibling-family performance on commercial lands can be affected by the site quality of the progeny test. In future progeny tests, families should be tested over a range of site indices, and site quality should be considered when using data to predict breeding values.

Literature Cited

ALLARD, R. W. and BRADSHAW, A. D.: Implications of genotype-environmental interactions in applied plant breeding. Crop Sci. 4: 503—508 (1964). —— Anonymous: Thirty-fourth annual report: North Carolina State University - Industry Cooperative Tree. Impr. Program. Raleigh, NC. 20p (1990). —— BAKER, R. J.: Selection Indices in Plant Breeding. CRC Press, Boca Raton, FL. 218 p (1986). —— BALOCCHI, C.: Age trends of genetic parameters and selection efficiency for loblolly pine (*Pinus taeda* L.) Ph. D. Dissertation, N. C. State University, Raleigh, NC.. 93 p (1990). —— BECKER, W. A.: Manual of Quantitative Genetics. Washington State Univ. Press, Pullman, WA. 170p (1975). —— BINET, F. E.: On the construction of an index for indirect selection. Biometrics 21: 291—299 (1965). —— BRIDGWATER, F. E., TALBERT, J. T. and ROCKWOOD, D. L.: Field design for genetic tests of forest trees. p. 28—38. *In*: Progeny testing of forest trees. Proc. Workshop on Progeny Testing, June 15—16, 1982. Auburn, Alabama. South. Coop. Series Bull. No. 275 (1983). —— BURDON, R. D.: Genetic correlation as a concept for studying genotype-environment interaction in forest tree breeding. Silvae Genet. 26: 168—175 (1977). —— BURDON, R. D.: Early selection in tree breeding: principles for applying index selection and inferring input parameters. Can. J. For. Res. 19: 499—504 (1989). —— CALOIN, M. and YU, O.: An extension of the logistic model of plant growth. Ann. Bot 49: 599—560 (1982). —— CAUSTON, D. R. and VENUS, J. C.: The Biometry of Plant Growth.

Edward Arnold, Ltd, London (1981). — Comstock, R. E. and Moll, R. H.: Genotype-environment interactions. p. 169—194. *In*: Statistical Genetics and Plant Breeding. R. E. Hanson and H. F. Robinson (eds.). NAS-NRC Pub. 982, Washington, DC (1963). — Cotterill, P.P. and Dean, C. A.: Successful tree breeding with index selection. CSIRO, Melbourne, Victoria, Australia. 80 p. (1990). — Davis, L. S. Investments in loblolly pine clonal seed orchards: production costs and economic potential. J. For. 65: 882—887 (1967). — Dickerson, G. E.: Implications of genetic-environmental interaction in animal breeding. Anim. Prod. 4: 47—64 (1962). — Dorman, K. W. and Squillace, A. E., Genetics of Slash Pine. USDA For. Serv. Res. Pap. WO-20. 20p (1974). — Foster, G. S.: Trends in genetic parameters with stand development and their influence on early selection for volume growth in loblolly pine. Forest Sci. 32: 944—959 (1986). — Franklin, E. C.: Model relating levels of genetic variance to stand development in four North American conifers. Silvae Genet. 28: 207—212 (1979). — Gates, J. E.: Site selection, site preparation and test layout. p. 363—368. *In*: Progeny Testing - Proceedings of servicewide genetics workshop. USDA For. Serv. Timber Management. Dec. 5—9, 1983, Charleston, SC (1983). — Goddard, R. E. and Strickland, R. K.: Volume and weight tables for five-year-old plantation grown slash pine. School of Forestry Res. Rep. No. 14. University of Florida, Gainesville, FL. 8 p. (1968). — Hayes, J. F. and Hill, W. G.: Modification of estimates of parameters in the construction of genetic selection indices ('bending'). Biometrics 37: 483—493 (1981). — Hill, W. G. and Thompson, R.: Probabilities of non-positive definite between-group or genetic covariance matrices. Biometrics 34: 429—439 (1978). — Hodge, G. R. and White, T. L.: Relationship of fusiform rust and growth traits in open-pollinated slash pine progeny tests. P. 469—481: In: Proc. IUFRO Symp. on Breeding Theory, Progeny Testing, and Seed Orchards. Oct. 13—17, Williamsburg VA (1986). — Itoh, Y. and Yamada, Y.: Relationships between genotype x environment interaction and genetic correlation of the same trait measured in different environments. TAG 80: 11—16 (1990). — Jensen, C. E.: and Homeyer, J. W.: Matchacurve-2 for algebraic transforms to describe curves of the class x^n. USDA For. Ser. Res. Pap. INT-106. Intermnt. For. Range Exp. Stn., Ogden, UT, 84401 (1971). — Johnson, G. R. and Burdon, R. D.: Family-site interaction in *Pinus radiata:* Implications for progeny testing strategy and regionalised breeding in New Zealand. Silvae Genet. 39: 55—62 (1990). — Klein, T. W., DeFries, J. C. and Finkbeiner, C. T.: Heritability and genetic correlation: standard errors of estimates and sample size. Behavior Genetics 3: 355—364 (1973). — Lambeth, C. C.: Juvenile-mature correlations in Pinaceae and implications for early selection. Forest Sci. 26: 571—580 (1980). — Lambeth, C. C., van Buijtenen, J. P., Duke, S. D. and McCullough, R. B.: Early selection is effective in 20-year-old genetic tests of loblolly pine. Silvae Genet. 32: 210—215 (1983). — Li, B., McKeand, S. E. and Allen, H. L.: Early selection of loblolly pine families based on seedling shoot elongation characters. P. 228—234. In: Proc. Twentieth South. For. Tree Improve. Conf. June 26—30, Charleston, SC (1989). — Matheson, A. C., Spencer, D. J. and Magnussen, D.: Optimum age for selection in *Pinus radiata* using basal area under bark for age-age correlations. P. 213—217. In: Proc. Tenth Aust. For. Genet. Res. Work. Group 1. M. J. Dieters and D. G. Nikles (eds.). Oct. 30 to Nov. 04, Gympie, Queensland, Aust. (1988). — Milliken, G. A. and Johnson, D. E.: Analysis of Messy Data. I. Designed Experiments. Lifetime Learning Pub., Belmont, CA 473 p. (1984). — Mode, C. J. and Robinson, H. F. Pleiotropism and the genetic variance and covariance. Biometrics 15: 518—537 (1959). — Mosteller, F. and Tukey J. W.: Data Analysis and Multiple Regression. Addison-Wesley Pub., London, GB. 588 p (1977). — Namkoong, G.: Introduction to quantitative genetics in forestry. U. S. Dep. Agric., Tech. Bull. No. 1588, 342p (1979). — Namkoong, G., Kang, H. C. and Brouard, J. S.: Tree Breeding: Principles and Strategies. Springer-Verlag, New York. 180 p. (1988). — Namkoong, G. and Roberds, J. H.: Choosing mating designs to efficiently estimate genetic variance components for trees. Silvae Genet. 23: 43—53 (1974.) — Namkoong, G., Snyder, E. B. and Stonecypher, R. W.: Heritability and gain concepts for evaluating breeding systems such as seedling seed orchards. Silvae Genetica 15: 76—84 (1966). — 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) — Pharis, R. P., Yeh, F. C. and Dancik, B. P.: Superior growth potential in trees: What is its basis, and can it be tested for at an early age? Can. J. For. Res. 21: 368—374 (1991). — Pienaar, L. V., Page, H. H. and Rheney, J. W.: Yield prediction for mechanically site-prepared slash pine plantations. South J. Appl. For. 14: 104—109 (1990). — Riemenschneider, D. E.: Heritability, age-age correlations, and inferences regarding juvenile selection in jack pine. Forest Sci. 34: 1076—1082 (1988). — Searle, S. R.: Linear Models for Unbalanced Data. John Wiley and Sons, New York, NY 536p (1987). — Shelbourne, C. J. A.: Tree Breeding Methods. Forest Research Institute Technical Paper 55, New Zealand Forest Service. Wellington, New Zealand. 41p (1969). — Shelbourne. C. J. A.: Genotype-environment interaction: Its study and implications in forest tree improvement. P. 1—28 *In*: Proc. IUFRO Joint Genetics Symp. Jap. For. Exp. Station, Tokyo, Japan (1972). — Smith, W. H., Hollis, C. A. and Gooding, J. W.: Influence of soil factors on fusiform rust incidence. P. 81—88. *In*: Management of Fusiform Rust in Southern Pines. R. J. Dinus and R. A. Schmidt (eds.). Symposium Proceedings, University of Florida, Gainesville, FL, Dec. 7—8, 1976, 163p (1977). — Sorensen, F. C.: and White, T. L.: Effect of natural inbreeding on variance structure in tests of wind-pollination Douglas-fir progenies. Forest Sci. 34: 102—118 (1988). — Squillace, A. E.: Average genetic correlations among offspring from open-pollinated forest trees. Silvae Genet. 23: 149—156 (1974). — Toliver, J.: Discussion summary: progeny test methodology. P. 22—23. *In*: Progeny testing of forest trees. Proc. Workshop on Progeny Testing, June 15—16, 1982, Auburn, Alabama. South. Coop. Series Bull. No. 275 (1983). — White, T. L.: A conceptual framework for tree improvement programs. New Forests 4: 325—342 (1987). — White, T. L.: and Hodge, G. R.: Best linear prediction of breeding values in a forest tree improvement program. Theor. Appl. Genet. 76: 719—727 (1988). — White, T. L. and Hodge, G. R.: Predicting Breeding Values with Applications in Forest Tree Improvement. Kluwer Academic Pub., Dordrecht, The Netherlands. 367p. (1989). — White, T. L., Hodge, G. R., Powell, G., Kok, H., deSouza, S., Blakesley, G. and Rockwood, D.: Thirtieth progress report of the Cooperative Forest Genetics Research Program. Dept. of Forestry, IFAS, University of Florida, Gainesville, FL. 44p. (1988). — Williams, C. G.: The influence of shoot ontogeny on juvenile-mature correlations in loblolly pine. Forest Sci. 33: 411—422 (1987). — 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). Yamada, Y.: Genotype by environment interaction and genetic correlation of the same trait under different environments. Jap. J. Genet. 37: 498—509 (1962). — Zobel, B. J. and Talbert, J.: Applied Forest Tree Improvement. John Wiley and Sons, New York, NY. 505p (1984).