Trends in Genetic and Environmental Parameters for Height, Diameter, and Volume in a Multilocation Clonal Study with Loblolly Pine

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ABSTRACT. Seedlings from 30 full-sib families (contained in 2, 4 x 4 factorials) of loblolly pine (*Pinus* taeda L.) were cloned and planted in three test sites in Georgia. Analyses were conducted on total height at ages 1 to 5 yr in the field, dbh at age 5, and individual tree volume at age 5. Four sources of genetic control were tested: male parent, female parent, male x female parent interaction, and clone within family. Differential growth responses due to test sites were present. Significant differences were detected among male parents for only one (age 5 height) of the seven traits in only one factorial. However, variation for height among female parents was found at ages 1 to 5 in only one of the two factorials accounting for 1% to 9% of the total variation. Significant effects of clone within family were found at all ages in one factorial and at ages 1, 3, and 4 in the other factorial for height but not for dbh or individual tree volume. None of the parental sources (male, female, or male x female) were interactive with test sites except one isolated case at age 2 in one factorial. However, the clone within family source of variation interacted significantly with site for height at ages 3 to 5 in factorial 1. Differences due to male or female parent effects were somewhat lower than has been found in other similar studies, possibly due to the relatively low number of parents in both factorials and hence, sampling effects. Future genetic studies should include more parents in the mating design but with approximately the same number of cloned individuals per cross in order to provide a better test of sources of variation.

Trends in genetic and environmental variances and heritabilities were examined. Additive genetic variance (V_A') for tree height displayed a steady increase from age 1 to 5. Dominance genetic variance (V_D jfor height also increased steadily over the same age range. The relationship between V_A' and V_D', differed between the two factorials. In factorial 1, V_A' was larger than V_D' for ages 1 to 4, then V_D' became larger for age 5. The reverse pattern occurred in factorial 2. Epistatic genetic variance was detected only at age 1 for height in factorial 1 and at ages 1 and 3 in factorial 2. Dominance variance equaled or exceeded additive genetic variance for dbh and individual tree volume at age 5. Narrow-sense and broad-sense heritabilities for height were low to intermediate (0.05 to 0.37) from ages 1 to 5 and were more or less stable over ages. The importance of dominance genetic variance, at least to age 5, underscores the likelihood of additional geneticgains through a clonal tree improvement and deployment program beyond the gains achieved in a seed orchard/seedling based program. FOR. SCI. 42(1):87–98.

Additional Key Words: *Pinus taeda,* genetic variance, clone, heritability.

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ACCEPTANCE AND USE OF CLONAL REFORESTATION depends on efficient production and selection of appropriate clones. Understanding patterns of genetic and phenotypic control of tree height, diameter, and volume is essential for efficient clonal tree improvement programs. In addition, the knowledge of genotype by environment interactions is crucial to such programs to guide establishment of breeding and deployment zones for a species.

Traditional tree improvement programs which practice recurrent selection and seed orchard/seedling propagation can utilize only additive genetic variation, whereas a clonal development and selection approach capitalizes on the total genetic variation. The potential advantages of the use of clonal methods have been reviewed by several researchers (Thulin and Faulds 1968, Burdon and Shelbourne 1974, Kleinschmit 1974, Libby et al. 1972, Brix and van den Driessche 1977, Foster and Shaw 1987, Park and Fowler 1987, Mullin and Park 1992, Mullin et al. 1992). Three clonal trials with loblolly pine (*Pinus taeda* L.) have been reported (Foster et al. 1986, Foster 1988, McRae et al. 1993) which have demonstrated considerable variation among clones for height, dbh, root collar diameter, number of growth cycles, and crown width. However, in only one of these trials (McRae et al. 1993) was the replication extended to more than one site. The lack of information on the magnitude of sources of variation leading to additive and nonadditive genetic variation greatly hampers the development of efficient tree improvement programs using clones.

Models are needed that predict changes in variance over stand age and also predict correlations between traits at different ages, which is useful for calculating correlated response from indirect selection. Once these models are developed, forest geneticists and tree breeders can use them to compare different tree improvement strategies (e.g., clonal versus seed orchard/seedlings), and also to optimize the chosen strategy (e.g., selection age). Empirical results are available from a few studies (LaFarge 1972, Franklin 1979, Lambeth et al. 1983, Byram and Lowe 1986, Foster 1986, McKeand et al. 1986, Balocchi et al. 1993) but more conclusive information is needed throughout stand establishment and especially for the first 10 yr for relatively short rotation species. Establishment of a single pattern is still lacking. Most previous studies lack annual or biennial measurements and the common practice of only measuring forest genetic studies every 4 or 5 yr is not informative enough and important parts of the trends are unavailable. In addition, many of the studies in the literature are located on a single site, hence, genetic variances and genotype *x* environmental effects are confounded. Regardless, most studies have concluded that changes in variance are most pronounced prior to, during, and shortly after crown closure. Cannel1 et al. (1978) hypothesized that genotype performance before crown closure, when plants have reduced tree to tree competition, may not be related to performance during post crown closure. Franklin (1979) suggested that heritability of growth traits may be high initially and then decrease possibly to zero at crown closure. Balocchi et al. (1993), reported values less than 0.05 for heritability from ages 1 to 5. Selection at earlier than normal ages has been shown to be economically efficient (Lambeth et al. 1983, Byram and Lowe 1986, Foster 1986, and Balocchi et al. 1993), but a more complete model is needed to optimize selection efficiency .

Genotype x environment interactions involve the differential responses of specific genotypes to environmental conditions. This interaction complicates testing and selection in tree improvement programs and results in reduced genetic gains. Studies of genotype *x* environment interaction can be used to (1) define breeding zones that best fit groups of genotypes with similar growth and phenological patterns and (2) define genotypes that show little interaction and consequently can be used over a wider range of environments (Bentzer et al. 1988). If the design includes several sites, the estimation of clone-site interactions will enable one to: (1) partition variance due to genotype *x* environment interaction, thus allowing for a more reliable and conservative estimation of genetic effects and (2) help to ascertain the range of sites over which a selection of clonal stock might maximize its potential. The literature on genotype *x* environment interaction is extensive for forest trees in general (Squillace 1970, Shelbourne 1972, Shelbourne and Campbell 1976, Morgenstem 1982) but relatively limited for clonal studies (Burdon 1971, St. Clair and Kleinschmit 1986, Park and Fowler 1987, Bentzer et al. 1988, Mullin et al. 1992, McRae et al. 1993). Clones would be expected to be more interactive with differing environments than either families or seed sources due to the lack of genetic homeostasis with clones (Bentzer et al. 1988).

Variance among clones provides an estimate of total genetic variance and has been widely studied. However, genetic variances have been estimated from only three clonal trials with loblolly pine (Foster et al. 1986, Foster 1988, McRae et al. 1993) of which only one was planted on more than one site (McRae et al. 1993).

In this study, we present results from a design that includes multiple locations, clonal replicates, and a family structure which provides information for genetic parameter estimation. This design allows estimation of additive and nonadditive genetic variance and subsequent partial separation of nonadditive variance into dominance and epistatic components.

The objectives of the study were: (1) to delineate sources of genetic and phenotypic control of height at field ages 1 to 5, and diameter (dbh) and volume at field age 5; (2) to determine the contribution of various types of gene action (additive, dominance, and epistasis) to height, diameter and volume growth to field age five years; (3) to assess the pattern of narrow-sense and broad-sense heritabilities of height at ages 1 to 5, diameter and volume at age 5, and (4) to compare genotype x environment interaction at the half-sib family, full-sib family, and clone level.

Material and Methods

Population Structure

The parent population for this study contained 3 1 first-generation selections of loblolly pine from a larger popu-

lation managed by International Forest Seed Company, Odenville, AL. The initial population consisted of 127 trees that were chosen from a pool of tested, first-generation selections from a combination of the North Carolina State University-Industry Cooperative Tree Improvement Program and the Cooperative Program between the USDA Forest Service and the Georgia Forestry Commission. Parental selection from this population was based on resistance to fusiform rust *(Cronartium quercuum* [Berk.] Miyabe ex f. sp. *fusiforme*) as well as superior height growth as evidenced by field progeny test results (Foster and Shaw 1987).

These 127 trees were mated in small factorials (usually 4 x 4). Seedlings from each of the full-sib families were screened for resistance to fusiform rust using standard inoculation techniques at the USDA Forest Service Bent Creek Resistance Screening Center (Anderson et al. 1983). Seedlings that emerged from this screening process with no rust galls at 6 months of age were then planted in a cutting orchard at International Forest Seed Company.

Two of the earliest 4 x 4 factorials were selected for this study, based on completeness of the potential crosses. Each factorial lacked 1 cross, resulting in 15 families per factorial for a total of 30 full-sib families.

Vegetative Propagation System

Each tree in the cutting orchard was hedged to maintain height at approximately 1 ft in order to (1) retard maturation (e.g., Libby et al. 1972) and (2) increase the number of potential cuttings (Foster et al. 1981). Seedlings were hedged three times per year (twice in the summer and once in the winter).

Shoots of approximately 3 in. length were collected from the hedged material. A 0.1 in. basal cut was made on the excised end of the shoot and the exposed area dipped into a propriety modification (held by International Forest Seed Company) of Hare's (1974) rooting powder that consisted of half of Hare's recommended indole-3-butyric acid (Greenwood et al. 1980) plus other modifications. Cuttings from each hedged ortet were placed in multiple five-cutting plots in a completely random design (Foster 1990) in the greenhouse for rooting. At the time of cutting collection (May 1986) for these subsequent trials, the seedling ortets were approximately 1 1/2 yr old. The cuttings rooted and grew approximately 6 in. in height over the period of May to October 1986, at which time they set resting buds. They were moved outside from the greenhouse in September to acclimate to outside growing conditions. The rooted cuttings were grown in 5.5 $in.^3$ plastic containers with a 1:1 peat:perlite media.

Planting

Rooted cuttings emerging from the propagation system were planted at 8 *x* 10 ft spacing on three test sites, during the winter of 1986–1987 at sites in Georgia: Claxton (December 1986), Dublin (January 1987), and Blakely (June 1987). Claxton and Blakely were old field sites, and Dublin was a clearcut forest site. The sites are widely separated across southern Georgia.

Experimental Design

The function of a mating design is to create a specific genetic structure among individuals in a population for estimating genetic parameters. A factorial mating design (N.C. State Design II factorial design, Cockerham 1961) was used where *m* males are mated to *f* females to produce c cloned individuals (Shaw and Hood 1985).

The field tests were planted at each site in a randomized complete block design with six blocks per site. All families were represented in each block, with one ramet per clone in each of two blocks per site totaling six ramets per clone (three sites x two ramets per site). Trees from the two factorials were comingled in each block. This field design provides the method for partitioning the components of genetic and environmental variance.

The following traits were measured or derived, as in the case of volume:

total height (ft) at field ages 1 to 5 (HT1-HT5),

diameter at breast height (in.) at field age 5 (DBH5), and

individual tree volume (ft^3) at age 5 (VOL5), where

$$VOL5(ib) = 0.01182 + 0.00199894\ (DBH5^2\ HT5)$$

(Smalley and Bower 1968).

All trees that died during any of the 5 yr were excluded from analyses.

The specific genetic model can be equated to variance components in the analysis of variance. Inherent in the translation of the experimental components of variance (Table 1) are the following assumptions (Comstock et al. 1958):

1. regular diploid behavior at meiosis;
2. no cytoplasmic or maternal effects;
3. no correlation of genotypes at separate loci which implies no linkage among genes affecting any single character or that, where linkage existed, the distribution of genotypes was as expected in the absence of linkage;
4. that the distribution of genotypes in the parents was of the nature to be expected in a random sample from a random breeding population.

When these assumptions are fulfilled, the variance components for our factorial experiment have the following genetic expectation (Becker 1984):

σ^2_M = variance among male parents = $1/4V_A + 1/16V_{AA} + \ldots$

σ^2_F = variance among female parents = $1/4V_A + 1/16V_{AA} + \ldots$

σ^2_{FM} = variance due to interaction of male and female parents = $1/4V_D + 1/8V_{AA} + 1/8V_{AD} + 1/16V_{DD} + \ldots$

Table 1. Form oftheanalysisofvariancefor heightatages 1 to 5, dbh at age 5 (DBH5), and volume at age 5 (VOL5) of loblolly pine clones.

Source	EMS
TEST(T)	$\sigma^2_E + k_{29}\sigma^2_{TC(FM)} + k_{30}\sigma^2_{TFM} + k_{31}\sigma^2_{TF} + k_{32}\sigma^2_{TM} + k_{33}\sigma^2_{R(T)} + k_{34}\sigma^2_T$
BLOCK(R)/T	$\sigma^2_E + k_{28}\sigma^2_{R(T)}$
MALE(M)	$\sigma^2_E + k_{22}\sigma^2_{TC(FM)} + k_{23}\sigma^2_{TFM} + k_{24}\sigma^2_{TM} + k_{25}\sigma^2_{C(FM)} + k_{26}\sigma^2_{FM} + k_{27}\sigma^2_M$
FEMALE(F)	$\sigma^2_E + k_{16}\sigma^2_{TC(FM)} + k_{17}\sigma^2_{TFM} + k_{18}\sigma^2_{TF} + k_{19}\sigma^2_{C(FM)} + k_{20}\sigma^2_{FM} + k_{21}\sigma^2_F$
$F \times M$	$\sigma^2_E + k_{12}\sigma^2_{TC(FM)} + k_{13}\sigma^2_{TFM} + k_{14}\sigma^2_{C(FM)} + k_{15}\sigma^2_{FM}$
CLONE(C)/(FM)	$\sigma^2_E + k_{10}\sigma^2_{TC(FM)} + k_{11}\sigma^2_{C(FM)}$
$T \times M$	$\sigma^2_E + k_7\sigma^2_{TC(FM)} + k_8\sigma^2_{TFM} + k_9\sigma^2_{TM}$
$T \times F$	$\sigma^2_E + k_4\sigma^2_{TC(FM)} + k_5\sigma^2_{TFM} + k_6\sigma^2_{TF}$
$T \times F \times M$	$\sigma^2_E + k_2\sigma^2_{TC(FM)} + k_3\sigma^2_{TFM}$
T x C/(FM)	$\sigma^2_E + k_1\sigma^2_{TC(FM)}$
ERROR	σ^2_E

NOTE: Where σ^2_T = variance among test sites; $\sigma^2_{R(T)}$ = varianceamong blocks within test sites; σ^2_M = varianceamong maleparents; σ^2_F = variance among female parents. σ^2_{FM} = variance due to the interaction of female and male parents; $\sigma^2_{C(FM)}$ = variance among clones within families; σ^2_{TM} = variance due to interaction of test sites and male parents; σ^2_{TF} = variance due to the interaction of test sites and female parents; σ^2_{TFM} = variance due to the interaction of test sites, male parents and female parents; $\sigma^2_{TC(FM)}$ = varianceduetothe interaction of test sites and clones within families; σ^2_E = errorvariance. Forfactorials 1 or2 respectively: k_1 = 1.55 or 1.55; k_2 = 1.38 or 1.36; k_3 = 8.36 or 10.19; k_4 = 1.38 or 1.33; k_5 = 8.37 or8.32; k_6 = 27.70 or28.85; k_7 = 3.40 or 1.23; k_8 = *6.92 or* 8.81; k_9 = 24.03 or 31.03; k_{10} = 1.54 or 1.56; k_{11} = 3.43 or 2.61; k_{12} = 1.34 or1.29; k_{13} = *9.32* or 12.81; k_{14} = 2.66 or 1.96; k_{15} = *25.49 or 37.79*; k_{16} = 1.30 or 1.05; k_{17} = 8.69 or 7.63; k_{18} = 28.72 or 27.73; k_{19} = 2.59 or 1.57; k_{20} = 24.66 or 22.26; k_{21} = 36.04 or 83.13, k_{22} = 1.33 or 1.21; k_{23} = 6.86 or 11.92; k_{24} = 24.01 or 41.33; k_{25} = 2.65 or 1.82; k_{26} = 19.38 or 35.31; k_{27} = 71.92 *or 123.96*; k_{28} = 21.26 or 29.27; k_{29} = 1.38 or 1.24; k_{30} = *6.09* or 6.59; k_{31} = 21.25 or 23.62; k_{32} = 21.27 or 23.66; k_{33} = 14.14 or 15.72; k_{34} = 84.85 or 94.32.

$\sigma^2_{C(FM)}$ = variance among cloned individuals within a cross = $1/2V_A + 3/4V_D + 3/4V_{AA} + 7/8V_{AD} + 15/16V_{DD} + ..$

where

V_A = additive genetic variance

V_D = dominance genetic variance

V_{AA}, V_{AD}, V_{DD} = epistatic genetic variance due to additive by additive effects, additive by dominance effects, and dominance by dominance effects, with similar notation for higher order interaction.

Estimates of genetic parameters are then calculated as follows:

$$V_A' = 2(\sigma^2_M + \sigma^2_F) = V_A + 1/4V_{AA} + \ldots$$

$$V_D = 4(\sigma^2_{FM}) = v_D + 1/2V_{AA} + 1/2V_{AD} + 1/4V_{DD} + \ldots$$

$$V_I' = \sigma^2_{C(FM)} - (\sigma^2_M + \sigma^2_F) - \sigma^2_{FM} = 1/4V_{AA} + 1/2V_{AD} + 3/4V_{DD} + \ldots$$

Primes on V_A' and V_D' indicate that the estimates of additive and dominance variance contain fractions of epistasis, and epistasis (V_I') is underestimated.

The total genetic variance (V_G) and phenotypic variance (V_P) *are* then calculated as:

$$V_G = \sigma^2_M + \sigma^2_F + \sigma^2_{FM} + \sigma^2_{C(FM)}$$

$$V_P = V_G + \sigma^2_{TM} + \sigma^2_{TF} + \sigma^2_{TFM} + \sigma^2_{TC(FM)} + \sigma^2_E$$

where

σ^2_{TM} = variance due to the interaction of site and male parents,

σ^2_{TF} = variance due to the interaction of site and female parents,

σ^2_{TFM} = variance due to the interaction of site, male, and female parents,

$\sigma^2_{TC(FM)}$ = variance due to the interaction of site and cloned individuals within a cross,

σ^2_E = variance due to error.

Analysis of Variance

The form of the analysis of variance and expected mean squares is presented in Table 1. All interactions with blocks were pooled in the Error term to simplify the model. Family effects were considered random because parent trees were chosen at random from a pool of tested, first-generation selections from a combination of North Carolina State University-Industry Cooperative Tree Improvement Program and the Cooperative Program between the USDA Forest Service and the Georgia Forest Commission. This genetically improved population is the one to which future inference would be made.

Prior to conducting the analysis of variance, the data were checked to determine whether the assumptions for the analysis of variance were fulfilled (Sokal and Rohlf 1969). The test for homogeneity of variance (Sokal and Rohlf 1969) among the three test sites was found to be statistically significant (P = 0.05). The data were transformed using either logarithm to base 10 or square root, but the heterogeneity of variance among tests remained significant. The results in this study are therefore based on the untransformed data, hence, results of the F- test among sites may be slightly biased.

Imbalance occurred in the data for the number of clones per families (Table 2) due to differential: numbers of seeds produced per cross, number of gall-free seedlings arising from the fusiform rust screening, rooting percent of the cuttings, and tree survival in the field trials. The first three factors appeared to be more influential toward final imbalance than survival. Therefore, a least-squares analysis was used to calculate the sums of squares. Coefficients of the variance components were adjusted to compensate for unequal sample size (Hartley 1967, Goodnight and Speed 1978). Standard errors of the variance components were calculated according to Anderson and Bancroft (1952). Variance components were calculated by equating the mean squares with expected mean squares (Kempthome 1969) (Type III sums of squares, PROC GLM; SAS Institute Inc. 1985).

The magnitude of genetic variances is related to the mean of the trait in this study. This is a particular problem when examining the changes in genetic parameters associated with growth (ontogeny) for a trait. For this reason, the genetic variances are also expressed as the genetic coefficient of variation (Comstock and Robinson 1958), which is simply the square root of the genetic variance divided by the mean of the trait.

Heritabilities

Heritabilities were determined on broad- and narrow-sense, and on family-mean and clone-mean basis. These determinations can be used in developing contrasting tree improvement strategies. The formulas for estimation of heritabilities are presented below. Broad-sense heritability was calculated for each trait on an individual ramet basis (H^2):

$$H^2 = V_G/V_P$$

Broad-sense heritability on a clone-mean basis $H^2_{\bar{x}}$ was calculated as follows:

$$H_{\bar{x}^2} = V_G /(V_G + \sigma^2_{TM} / t + \sigma^2_{TF} / t + \sigma^2_{TFM} / t + \sigma^2_{TC(FM))} / t + \sigma^2_E / rt)$$

where

t = number of test sites

r = number of blocks per clone per site

Narrow-sense heritability on an individual basis (h^2)was calculated as follows:

$$h^2 = 2(\sigma^2_M + \sigma^2_F) / V_P$$

Narrow-sense heritability on a family-mean basis $H^2_{\bar{x}}$ was calculated using the following formula:

$$h_{\bar{x}^2} = (\sigma^2_M + \sigma^2_F)/(\sigma^2_M + \sigma^2_F + \sigma^2_{FM} + \sigma^2_{C(FM)} / c) + \sigma^2_{TM} / t + \sigma^2_{TF} / t + \sigma^2_{TFM} / t + \sigma^2_{TC(FM)} / tc + \sigma^2_E / rct)$$

where c = number of clones per full-sib family.

Results and Discussion

Survival of the trees in the Blakely and Dublin, Georgia test sites, at age 5, was 81 and 88%, respectively. Trees in the Claxton test site suffered a higher mortality, resulting in a 68% survival at age 5. Although representative of major soil types in that area, the sandier soil may have contributed to the added mortality of trees at that site.

Growth of the trees was good, averaging 3.6 ft/yr. Height development varied among tests. Height growth at Blakely and Dublin demonstrated a larger percent increase from age

Table 2. Number of cloned individuals per full-sib family from two factorials of loblolly pine grown at three locations

	Male parents							
	Factorial 1				Factorial 2			
Female parents	5	6	7	8	13	14	1.5	16
1	2	7	2	2				
2	0	21	17	12				
3	22	18	1.5	18				
4	3	13	8	18				
9					28	3	25	19
10					0	3	25	27
11					32	17	30	32
12					32	6	27	30

Table 3. Mean height (ages 1 to 5, HT1–HT5), diameter (age 5, DBH5), and volume (age 5, VOL5) of cloned families of loblolly pine grown in three locations in Georgia.

Traits	Claxton	Dublin	Blakely
HT1 (ft)	1.52	2.29	0.86
HT2 (ft)	2.42	4.21	2.27
HT3 (fi)	5.51	7.88	6.66
HT4 (ft)	9.18	11.52	11.99
HT5 (ft)	13.65	15.36	18.32
DBH5 (in.)	2.71	2.65	3.51
VOL5 (ft^3)	0.24	0.25	0.51

1 through age 5 than did height growth at Claxton (Table 3). In addition, height at age 5 was considerably greater at Blakely (18.32 ft) than at Claxton (13.65 ft) and at Dublin (15.36 ft) (Table 3). When compared with the average overall test sites, height, dbh, and volume performance at the Blakely test site exceeded that of Dublin and Claxton at ages 4 and 5 (Table 3). The mean dbh at age 5 was 2.71 in. for Claxton, 2.65 in. for Dublin, and 3.51 in. for Blakely (Table 3).

Genetic Effects

Few clonal studies with forest tree species have examined the separate contribution to genetic effects of male and female parents and cloned offspring. In this study in general, male parents' effects for height, dbh, and volume was a nonsignificant effect in the model except height at age 5 in factorial 2. A steady increase in percentage of total variation for height accounted for by male parents was observed as the study progressed from ages 1 (0.3%) through 5 (2.9%), in the average of factorials 1 and 2. This trend in half-sib family variations as an increasing percentage of total variance with age found in this study agreed with the findings of Foster (1986), except that, in his study, the percentage of variation was found to be significant at all measurements.

While male parents did not contribute significantly to the total variation in the model for either factorial, female parents appeared to be a source of significant variation with respect to height in factorial 1 but not in factorial 2. In factorial 1, this source of variation accounted for 1.0 to 8.6% of the total variation across ages 1 to 5 (Table 4). In factorial 2, female parents accounted for 3% or less of the total variation (Table 5). On average, this pattern agrees with the report published by Franklin (1979). The first stage, from ages 1 to 5, exhibits family variance which was low and increased slowly over that period, a phase during which young trees overcome interspecific competition to establish themselves in the stand. The lack of statistically significant effects, in factorial 2, may be an artifact of the use of a relatively insensitive synthetic F-test (after Cochran 1951). The size of the standard error for female parents reveals that the effects of male and female parents may be equal, and the difference in significance level displayed may be as a result of the sensitivity of the F-test. Family variance was nonsignificant for either DBH5 or VOL5 except for variance among female parents in factorial 1 for DBH5 (Table 6). Foster (1986) also reported that family variance for fifth-year volume and diameter reflected nonsignificant effects and accounted for no more than 1% of the total variation in loblolly pine.

It has been suggested by Foster (1986) that the pattern of family effects over stand age diminishes as internee competition increases, and the shift for family differences, from significant to nonsignificant, could be due to declining variability among families or to increasing error variance. Foster and Shaw (1988), in a *Populus deltoides* L. study, reported female parents to be nonsignificant ($P > 0.05$) for height at ages 1 through 8, diameter at ages 3 and 4, and volume at ages 4 and 8. Male parents however, were reported to be significant for the same traits. Foster and Shaw (1988) were able to rationalize this finding, considering the small number of parents (seven) in the factorial design. Small sample sizes (three or four) for either male or female parent effects in the current study or that by Foster and Shaw (1988) may affect the chances for significant variance among parents.

Male and female parent interaction, as a source of variation for height, was detected at age 5 in factorial 1 and ages 2 and 4 in factorial 2, accounting for 5% and 1 to 3% of total variation, respectively (Tables 4 and 5). However, there was

Table 4. F-value and variance components (±SE) for height at ages I-5 (HT1–HT5), in factorial 1 of a loblolly pine study grown in three test sites.

Source of variation	DF	Var. Components				
		HTI	HT2	HT3	HT4	HT5
TEST(T)	2	0.7898 ± 0.5819***	1.4748 ± 1.0956***	1.7284 ± 1.3125***	1.9812 ± 1.5155***	4.5348 ± 3.4302***
BLK/(T)	13	0.0005 ± 0.0028 ns	0.0654 ± 0.0036***	0.2654 ± 0.1216***	0.3849 ± 0.1780***	0.5449 ± 0.2637***
MALE(M)	3	< 0.0000 ± 0.0033 ns	0.0092 ± 0.0200 ns	0.0559 ± 0.0793 ns	0.2116 ± 0.2193 ns	0.3016 ± 0.3980 ns
FEMALE(F)	3	*0.0098* ± 0.0088*	*0.0903* ± 0.0686**	*0.2878* ± 0.2287*	*0.5611* ± 0.4570**	0.5589 ± 0.5244*
$F \times M$	8	*0.0034* ± .0044 ns	0.0319 ± 0.0270 ns	0.1071 ± 0.0808 ns	0.2298 ± 0.1820 ns	0.5914 ± 0.3774*
CLONE(C)/(FM)	163	0.0175 ± 0.0076*	0.0611 ± 0.0290*	0.2085 ± 0.0981*	0.4432 ± 0.1677*	0.8371 ± 0.2754***
$T \times M$	6	0.0030 ± 0.0057 ns	< 0.0000 ± 0.0290 ns	< 0.0000 ± 0.0858 ns	< 0.0000 ± 0.1890 ns	< 0.0000 ± 0.4002 ns
$T \times F$	6	0.0018 ± 0.0046 ns	0.0018 ± 0.0046 ns	0.0050 ± 0.0758 ns	< 0.0000 ± 0.1644 ns	< 0.0000 ± 0.3412 ns
$T \times F \times M$	15	*< 0.0000 ± 0.0044* ns	*< 0.0000 ± 0.0216* ns	< 0.0000 ± 0.0547 ns	< 0.0000 ± 0.1270 ns	< 0.0000 ± 0.1698 ns
T x C/FM	203	< 0.0000 ± 0.0089 ns	< 0.0000 ± 0.0350 ns	0.2645 ± 0.1185*	0.5096 ± 0.1905*	0.5613 ± 0.2969*
Error	265	*0.1470 ± 0.0130*	*0.5667 ± 0.0493*	*1.4483 ± 0.1254*	*2.2050 ± 0.1904*	*3.7906 ± 0.3280*

NOTE: A synthetic F-test, after Cochran (1951), was used to test the following sources of variation: Test, Male, Female, and Female × Male. ns = nonsignficant; * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$; HT1, C.V. = 0.48; HT2, C.V. = 0.40; HT3, C.V. = 0.28; HT4, C.V. = 0.23; HT5, C.V. = 0.21.

Table 5. F-value and variance components (±SE) for height at age l-5 (HT1–HT5), in factorial 2 of a loblolly pine study grown in three test sites.

Source of variation	DF	Var. Components HTI	HT2	HT3	HT4	HT5
TEST(T)	2	0.5741 ± 0.3845***	1.7630 ± 1.1959***	2.5929 ± 1.7947***	2.5012 ± 1.7941***	2.5988 ± 1.8896**
BLK/(T)	13	0.0002 ± 0.0028 ns	0.0527 ± 0.0288***	0.2549 ± 0.1169***	0.5161 ± 0.2240***	0.5782 ± 0.2691***
MALE(M)	3	0.0039 ± 0.0053 ns	0.0223 ± 0.0209 ns	0.1009 ± 0.0813 ns	0.1605 ± 0.1310 ns	0.2912 ± 0.2014*
FEMALE(F)	3	0.0025 ± 0.0071 ns	0.0155 ± 0.0313 ns	0.0442 ± 0.0833 ns	0.0925 ± 0.1458 ns	0.1984 ± 0.2139 ns
F × M	8	*0.0061 ± 0.0070* ns	0.0308 ± 0.0199*	0.0787 ± 0.0701 ns	0.1556 ± 0.1106*	0.1096 ± 0.1074 ns
CLONE(C)/(FM)	321	*0.0315* ± 0.0121***	0.0381 ± 0.0363 ns	0.3100 ± 0.1120**	0.3394 ± 0.1766*	0.3578 ± 0.2763 ns
T × M	6	*< 0.0000* ± .0043 ns	0.0033 ± 0.0088 ns	< 0.0000 ± 0.0307 ns	< 0.0000 ± 0.0398 ns	< 0.0000 ± 0.0662 ns
T × F	6	*0.0006 ± 0.0054* ns	0.0281 ± 0.0210*	0.0126 ± 0.0457 ns	0.0233 ± 0.0593 ns	0.0546 ± 0.0962 ns
T x F x M	15	*0.0027 ± 0.0086* ns	< 0.0000 ± 0.0144 ns	< 0.0000 ± 0.0674 ns	< 0.0000 ± 0.0852 ns	< 0.0000 ± 0.1269 ns
T × C/FM	219	*0.0030 ± 0.0164* ns	*< 0.0000 ± 0.0579* ns	*0.0238* ± 0.1542 ns	0.2419 ± 0.2487 ns	0.4260 ± 0.4032 ns
Error	372	*0.2137 ± 0.0141*	*0.7787 ± 0.0566*	1.9677 ± 0.1442	2.9719 ± 0.2173	4.7828 ± 0.3499

NOTE: A synthetic F-test, after Cochran (1951). was used to test the following sources of variation: Test, Male, Female, and FemalexMale. ns = nonsignficant; * = P < 0.05, ** = *P< 0.01,* *** = *P< 0.001;* HT1, C.V. = 0.47; HT2, C.V. = 0.41; HT3, C.V. = 0.27; HT4, C.V. = 0.21; HT5, C.V. = 0.19.

a consistent increase in percent of total variation contributed by male and female parent interaction from age 1 through age 5 (Tables 4 and 5). The male x female parent interaction was responsible for an average of 2% of the total variation in height across ages. This interaction was found to be significant for DBH5 and VOL5 in both factorials (Table 6). Mullin et al. (1992) detected no significant variance due to this source for height at ages 4 or 5 yr but did find significant variance for survival in their black spruce (*Picea mariana* [Mill.] B.S.P.) study.

The clone within family source of variation was significant for nearly all height traits. The effect of clones, expressed as a percentage of total variation for height, ranged on the average over both factorials, from 3% at age 1 to 5% at age 5 (Tables 4 and 5). This finding coincided with that of Shaw et al. (1988) where 7% of total variation was found at age 5 in Norway spruce *(Picea ubies* [L.] Karst.). With black spruce, Mullin et al. (1992) had a similar finding for height at ages 4 and 5 where this source accounted for 5 to 6% of the total variation. Averaged across both factorials in the current study, the clone within family variation for height was approximately the same magnitude as the variation due to male or female parents. Clonal effects for volume were nonsignificant (0 to 3% of total variation) in both factorials (Table 6). Diameter (DBH5) was not significantly affected by clone within family, registering 2 and 3% of total variation for factorials 1 and 2, respectively (Table 6). In a study of loblolly pine by Foster (1988), variances among clones within family for height at ages 1, 2, and 3 and diameter at age 3 were found to be significant. Burdon (197 1) conducted a

Table 6. F-values and variance components (±SE) for dbh at age 5 (DBH5) and volume at age 5 (VOL5) in factorials 1 and 2 of a loblolly pine study grown in three test sites.

Source of variation	Var. Components Factorial 1 DBH5	Factorial 1 VOL5	Factorial 2 DBH5	Factorial 2 VOL5
TEST(T)	*0.2255* ± 0.1716***	*0.0174* ± 0.0132***	*0.0906* ± 0.0679*	*0.0075* ± 0.0057**
BLK/(T)	0.0400 ± 0.0194***	0.0019 ± 0.0009***	0.0234 ± 0.0134***	0.0021 ± 0.0010***
MALE(M)	*< 0.0000 ± 0.0006* ns	< 0.0000 ± 0.0006 ns	0.0002 ± 0.0068 ns	0.0007 ± 0.0008 ns
FEMALE(F)	*0.0296* ± 0.0267*	*0.0015 ± 0.0015* ns	0.0149 f0.0204 ns	0.0013 ± 0.0015 ns
F × M	*0.0265* ± 0.0174*	*< 0.0016 ± 0.001* 1*	*0.0234* ± 0.0151*	0.0011 ± 0.0007*
CLONE(C)/(FM)	*0.0150 ± 0.0184* ns	< 0.0000 ± 0.0009 ns	< 0.0000 ± 0.0230 ns	0.0013 ± 0.0012 ns
T × M	*< 0.0000* ± 0.0181 ns	< 0.0000 ± 0.0009 ns	< 0.0000 ± 0.0074 ns	0.0004 ± 0.0005 ns
T × F	*< 0.0000 ± 0.0157* ns	0.0000 ± 0.0010 ns	< 0.0000 ± 0.0084 ns	0.0005 ± 0.0004 ns
T x F x M	*< 0.0000 ± 0.0117* ns	0.0001 ± 0.0009 ns	< 0.0000 ± 0.0146 ns	< 0.0000 ± 0.0007 ns
T x C/FM	*0.0774* ± 0.0255**	*0.0064* ± 0.0013***	*0.0728* ± 0.0367**	*0.0031* ± 0.0019*
Error	*0.2812 ± 0.0243*	*0.0122 ± 0.0009*	*0.3938 ± 0.0283*	*0.0204 ± 0.0014*

NOTE: ns = nonsignficant; * = *P* < 0.05, ** = *P< 0.01,* *** = *P < 0.001;* Factorial 1: DBH5, C.V. = 0.28; Vol5, C.V. = 0.68; Factorial 2: DBH5, C.V. = 0.26; VOL5, C.V. = 0.61. A synthetic F-test, after Cochran (1951), was used to test the following sources of variation: Test, Male, Female, and Female × Male.

similar study, using *Pinus radiata* D. Don where he also reported clonal variance for height to be generally higher than that for diameter.

The additive genetic variance demonstrated a consistent rise from ages 1 through 5, 0.02 at age 1 to 1.72 at age 5 in factorial 1, and 0.01 at age 1 to 0.98 at age 5 in factorial 2 (Table 7). By age 5, dominance genetic variance for height surpassed that of additive variance in Factorial 1. In Factorial 2, dominance variance for height exceeded that of additive variance at ages one to four but then fell to about half the size of additive variance at age five. Dominance genetic variance for diameter at age 5 (DBH5) was two to three times greater and for VOL5 was one to two times greater than additive genetic variance in the two factorials (Table 7). Epistatic variance was present at age 1 for height in factorial 1 only and at ages 1 and 3 in factorial 2. There was no detectable evidence for epistasis regarding height and volume at age 5 in either factorial. The true value for epistasis is actually larger than the value derived in our model (V_I'), since our value contains only fractional components of each type of epistasis.

Previous reports on time trends for additive and nonadditive variances for tree height and volume in loblolly pine are inconclusive. Consistent among the reports are that the nonadditive and additive variances are present at most ages. In the current study, V_A' for height increased rapidly from year to year. The age trend for additive genetic variation in tree height in this study was different than that reported by Franklin (1979). He reported that from ages 3 to 5, the additive genetic variance was quite low, but began to increase about the time of crown closure. Foster (1986) showed that additive variance rose steadily from age 1 through 5 and then declined during the years 6 and 7. Foster (1986) also showed rapid increase in phenotypic variance through the study. In this current study, the ratio of nonadditive to additive genetic variance ranged from 0.0 to 3.4 over all traits in factorials 1 and 2, respectively. In anotherloblolly pine study, Byram and Lowe (1986) concluded that additive genetic variance was the major portion of the genetic variation from ages 5 to 20 in several tests; however, they reported the presence of nonadditive and additive genetic variance at all ages. The nonadditive genetic variance in Byram and Lowe's (1986) study only represented 0.12 to 0.40 of the additive genetic variance. McKeand et al. (1986) found that for total height at age 5, the ratio of nonadditive to additive genetic variance ranged from 0 to 2.5, while the ratio was 0 for dbh at age 5. Stonecypher and McCullough (1986) found that the ratio of nonadditive to additive variance in their Douglas-fir study was 0.9 to 1.6 for height and 0.6 to 0.7 for dbh. Epistasis was equal to V_A and double V_D for height at age 2, but it then diminished quickly at older ages. With *Populus deltoides*, Foster and Shaw (1988) found that height at ages 1 to 8 as well as dbh at ages 3 and 4 and volume at age 4 were controlled mainly by additive genetic variance. Epistatic variance was 2.4 and 1.1 the size of additive genetic variance for dbh and volume, respectively, at age 8. Balocchi et al. (1993) found low additive variance for height from age 1 (.0089) through age 5 (0.1259), but a more dramatic increase in the nonadditive variance. The ratio of nonadditive to additive variance ranged from 0.20 at age 1 to 4.05 at age 5. With black spruce (*Picea muriunu* [Mill.] B.S.P.) Mullin et al. (1992) found the ratio of epistatic variance to additive variance for height at ages 4 and 5 to be 0.71 and 0.56, respectively, but with dominance variance virtually nonexistent.

Inconsistent patterns in time trends for genetic variances may have several causes. The scales may differ among studies and expressing variances as coefficients of variation (C.V.) will minimize this effect. Differences in test design and quality may also affect the absolute values and significance level of variances. Several of the studies cited earlier are only planted at a single site thereby confounding genetic variances with their interaction with location. Scale effects can explain differences in absolute value but not in direction of time trends (i.e., decreasing versus increasing time trend or flat versus increasing trend). Differences in the presence and frequency of various alleles among species, populations

Table 7. Genotypic (VG), phenotypic (V_P), additive (V_A'), dominance (V_D') and epistatic (V_I') variance for height at ages 1 to 5 (HTI-HT5) and dbh (DBH5) and volume (VOL5) at age 5 from two factorials in a loblolly pine study.

Genetic parameter	HT1	HT2	HT3	HT4	HT5	DBH5	VOL5
				Factorial 1			
V_G	**0.0307**	0.1925	**0.6593**	1.4457	2.2890	0.0711	0.003 1
V_P	**0.1825**	0.7610	**2.3771**	4.1603	6.6409	0.4297	0.0218
V_A'	**0.0196**	0.1990	**0.6874**	**1**.5454	1.7210	0.0592	0.0030
V_D'	**0.0136**	0.1276	**0.4284**	**0.9192**	2.3656	0.1060	0.0064
V_I'	**0.0043**	0.0000	**0.0000**	**0.0000**	0.0000	0.0000	0.0000
				Factorial 2			
V_G	**0.0440**	**0.1067**	**0.5338**	0.7480	0.9570	0.0385	0.0044
V_P	**0.2640**	**0.9168**	**2.5379**	3.9851	6.2204	0.505 1	0.0288
V_A'	**0.0128**	**0.0756**	**0.2902**	0.5060	0.9792	0.0302	0.0040
V_D'	**0.0244**	**0.1232**	**0.3 148**	0.6224	0.4384	0.0936	0.0044
V_I'	**0.0190**	**0.0000**	**0.0862**	0.0000	0.0000	0.0000	0.0000

within species, and individuals within populations may be much of the source of variation in time trends and ratios of nonadditive to additive genetic variance that is apparent in the scientific literature. Molecular level studies will offer the solution to this question.

The presence of additive genetic variance in populations of forest trees is supported by the current study as well as virtually every other genetic study. Evidence for the presence of nonadditive (dominance and epistasis) genetic variance in populations of forest trees appears to be less certain and seems to vary by trait, age, and species. Most studies, designed to do so, seem to detect its presence for some trait-age combination. Tree improvement strategies for using both additive and nonadditive genetic variation are well known (for example, Kleinschmit 1974, Foster and Shaw 1987, McKeand et al. 1986, Foster 1993, Lambeth et al. 1994, Mullin and Park 1992). The question remains of whether to breed for enhanced nonadditive variation as well as additive variation (McKeand et al. 1986) or just to breed for enhanced additive variation and utilize any nonadditive variation that is present (Foster and Shaw 1987). Based on the results from this paper and others in the literature, it appears best to practice the latter. Additional genetic gain will accrue, especially from clonal programs, but its magnitude will vary depending on trait, age, and species.

Environmental Effects

Test location effects were present for height at all ages; however, there was a decline in the percentage of total variance accounted for by this source as the study age advanced. Differences among test locations accounted for most of the total variation (Tables 4, 5, and 6). In factorial 1, variation in height at age 1 accounted for by this source of variation was ***8 1%*** and declined to 39% of total variation at age 5 (Table 4). The average percentages (between factorials) of total variation explained by location effect for diameter and volume were 23% and 31%, respectively (Table 6). Bentzer et al.(1988) found a much lower location effect (< 1% of total variation) in a Norway spruce clonal trial. Huehn et al. (1987) also reported results from a Norway spruce study which corroborated Bentzer et al.'s (1988) study. Because Claxton and Blakely were old agriculture field sites while Dublin was a cutover forest site, it is possible that the magnified location effects in this study could be attributed to different edaphic conditions. In addition, the importance of location effects declined with advancing age for HT while the importance of the error term increased (Tables 4 and 5).

Genotype × Environment Interaction Effects

For both factorials, there was only a single case of significant variation in height at any age resulting from female parent or male parent x test site interaction. The percentage of total variation contributed by these sources was less than 1% on average. Female or male parent x site interaction as a source of variation for diameter and volume was almost nonexistent; the percentage of total variation for this source remained near zero and was nonsignificant for both factorials. These results indicate a stable ranking of both male and female parent families among the three test sites, even though the sites differed significantly in their productivity (Table 3).

Clone within family x test site interaction was significant for HT3, HT4, and HT5 (5–8% of total variation), DBH5 (11% of variation), and VOL5 (16% of variation) in factorial 1 and for DBH5 (12%) and VOL5 (15%) in factorial 2 (Tables 4 and 6). There were no predictable trends in the direction of percentage of variation in these factorials. The results in factorial 1 were different from that of factorial 2 and indicated either (1) unstable ranking of clones among test sites for factorial 1 while the clonal ranks were stable in factorial 2 or (2) that variances were different among the test sites which can lead falsely to significant interactions. These two hypotheses were not tested in this study, but the latter seems likely since there was significant heterogeneity of variance among test sites.

Burdon's (197 1) results supported the significant test by clone effects found in our study in factorial 1. In that study Burdon surmised that the ability of certain clones to access minerals, particularly phosphates, may have contributed to the clone by test interaction. Mullin et al. (1992) found significant family x test site and clone within family x test site interactions for height at ages 4 and 5 yr. The family x test site effect was smaller (average of 1.5% of total variance) than the clone within family x test site effect (average of 2.3% of total variance). Clonal performance for diameter and volume in the current study appears to be more sensitive to environmental influence than for height. Since the average height and dbh was greater at some test sites (Table 3), the trees may have been more crowded on the better sites, hence under more competition, especially by age 5. Tree height is less susceptible to the influence of crowding than dbh or volume. Therefore, even though HT3-5, DBH5, and VOL5 all had significant clone x site interaction, total variation accounted for was always greater for DBH and VOL than HT at any age. McRae et al. (1993) published the results of a study with loblolly pine in which they used the same population and tests as in the current study, plus they added two more test sites. They used a simpler design with no family structure and only 61 clones. They found a significant clone x test site interaction for height, dbh, and volume at age 5, accounting for 9 to 15% of total variation. They did note that removing one test site (Claxton, Georgia) from the analysis reduced the level of statistical significance of the interaction.

For height in the current study, the clone by test interaction was, at most, 127% of the clone within family effect with an average of 52% across ages. As stated earlier, this interaction either could be an artifact of the unequal variances at each site or could represent a true rank change of clones among sites. This potential disparity in clone ranking among test sites may indicate that clone superiority in factorial 1 depended somewhat on site type, and superior subsets of clones may be chosen for specific site types. The disparity is even greater for diameter and volume in factorial 1. Interestingly, the clones in factorial 2 were much more stable across sites. Implicit here is that selection for height, volume, or diameter at this stage of stand development could be compromised if a single set of superior clones were chosen from factorial 1. The

confounding effect of the clone by test interaction relative to diameter and volume at age 5 in this study agrees with a report on Norway spruce published by Bentzer et al. (1988). In that study the clone by test interaction effects for diameter were 50% of the clonal effect and that of volume to be equal to that of the clone effects. Further investigation of the cause of clone *x* test site interaction is needed to determine its true cause and how widespread it is for the species.

The error component of variance for height traits rose gradually with increasing age. The error variance for HT averaged 20% of the total variation at age 1. For age 5 (HT5), the error variance component increased to 42% of the total variation (Tables 4 and 5). The error variance for diameter and volume were an average of 52% and 41% of total variance for factorial 1 and 2, respectively.

Heritability

During early stand development, trees are highly sensitive to environmental influences. Large error terms contribute to low estimates of heritability via substantial levels of phenotypic variance. Heritability values in this study ranged from 0.05 to 0.62, depending on type of heritability, between factorials. The pattern of change in advancing age for the factorials in our study was different from that of Franklin (1979) in that there was no steady decline in he&abilities with advancement through the early ages of 1 through 5.

The trend for narrow-sense heritability for height in both factorials 1 and 2 was relatively stable from 0.11 to 0.26 and 0.05 to 0.16 in factorials 1 and 2, respectively, with slight annual fluctuations (Table 8). In factorial 1, h^2 increased from age 1 to 4, then dropped a bit; however, in factoral 2, h^2 increased steadily from age 1 to 5. Foster (1986) reported narrow-sense heritability to double from age 1 (0.09) to age 2 (0.15) and then plateau until age 6. In their study of height in loblolly pine, Balocchi et al. (1993) found narrow-sense heritability to be stable at 0.04 for ages 1 to 5. Narrow-sense heritability for VOL5 at age 5, in our study, was equal (0.14) in both factorials and also equal to that for DBH5 in factorial 1. Narrow-sense heritability for DBH5 in factorial 2 was about half the value in factorial 1.

The pattern for narrow-sense heritability on a family-mean basis was very similar to that for narrow-sense heritability in both factorials (Table 8), except that the former was approximately double the latter heritability in factorial 1 and three to four times in factorial 2. Balocchi et al. (1993) found a range of 0.27 to 0.16 for narrow-sense heritability on a family-mean basis for height at ages 1 to 5. Like that of narrow-sense heritability, the narrow-sense heritability on a family-mean basis for VOL5 in the current study was greater than or equal to that of DBH5 (Table 8).

The broad-sense heritability pattern was slightly different than the narrow-sense heritability pattern. In factorial 1, broad-sense heritability for HT increased steadily from age 1 (0.17) to 4 (0.35) then remained stable at age 5 (Table 8). In factorial 2, it was flat, fluctuating between 0.12 and 0.21. Broad-sense heritability in Balocchi et al.'s (1993) study was somewhat lower for height ranging from 0.06 to 0.19. Broad-sense heritability for VOL5 was approximately the same size as for DBH5 in factorials 1, but double the size in factorial 2 in the current study.

Broad-sense heritability on a clone-mean basis was moderate throughout all traits, ages, and factorials. The pattern in both factorials was similar to, but double, that for broad-sense heritability on a ramet basis (Table 8). The pattern for the broad-sense heritability on a clone-mean basis for DBH5 and VOL5 was similar to that for the other types of heritability.

Heritability in the current study was comparable to earlier loblolly pine studies and was sufficiently large in all cases to indicate significant genetic advance from selection is possible. In addition for a particular trait-age combination, the order of magnitude of the various heritability types was as expected (i.e., $h^2 \le h_{\bar{x}}^2, H^2 \le H_{\bar{x}}^2, h_{\bar{x}}^2 \le H_{\bar{x}}^2$) in most cases. Heritability on a clone-mean basis was often the largest value and underscores the value of using clonal replicates to enhance the reliability of selection for genetic value.

Table 8. Narrow-sense heritabilities (h^2), narrow-sense heritabilities on a family-mean basis $H_{\bar{x}}^2$, broad-sense heritabilities (H^2) and broad-sense heritabilities on clone-mean basis $H_{\bar{x}}^2$ for height at ages 1 to 5 (HT1–HT5) and dbh (DBH5) and volume (VOL5) at age 5 from two factorials in a loblolly pine study.

	Traits						
Heritability	HT1	HT2	HT3	HT4	HT5	DBH5	VOL5
Factorial 1							
h^2	0.11	**0.26**	**0.29**	**0.37**	**0.26**	0.14	**0.14**
$h_{\bar{x}}^2$	0.36	**0.57**	**0.58**	**0.62**	**0.46**	**0.37**	**0.34**
H^2	0.17	**0.25**	**0.28**	**0.35**	**0.35**	**0.17**	**0.14**
$H_{\bar{x}}^2$	0.40	**0.53**	**0.54**	**0.62**	**0.62**	**0.37**	**0.32**
Factorial 2							
h^2	0.05	0.08	0.11	0.13	0.16	**0.06**	**0.14**
$h_{\bar{x}}^2$	**0.25**	**0.35**	0.45	0.49	0.55	**0.34**	**0.48**
H^2	**0.17**	**0.12**	0.21	**0.19**	0.15	**0.08**	**0.15**
$H_{\bar{x}}^2$	**0.33**	**0.24**	0.40	**0.36**	0.30	**0.16**	**0.29**

NOTE: **For factorials 1 or 2, respectively: r = 1.5 or 1.5; t = 2.2 or 1.7, c = 5.4 or 6.6.**

Conclusions

This study is one of the first, at least for southern pines, to fully partition sources of phenotypic variation for height, dbh, and volume into both additive and nonadditive sources of genetic variation. The variance components were used to estimate additive, dominance, and epistatic genetic variance as well as heritabilities. This paper provides information that can guide development of future genetic trials as well as tree improvement programs.

Family level (female parent, male parent, and female x male parent interaction) sources of genetic variation for height appeared to be of minor to moderate importance (0 to 9% of total variation) depending on the trait. There was an indication that the importance of either the female or male parent source increased from ages 1 to 5 yr in the field. Other studies with loblolly pine have indicated similar magnitudes of total variance for this source, but usually it was statistically significant. Small numbers of parents involved and the fact that the parents resulted from selection in a tree improvement program undoubtedly contributed to the lack of statistical significance in the current study.

For height, the variation among clones within families was approximately equivalent to that among families. This result varied between the factorials but on average was equivalent. For fifth-year dbh and individual-tree volume, this source of variation was somewhat smaller than the family level, generally, and was nonsignificant. The results for height indicate that combined selection for both superior families and clones within families will be effective. It also indicates the potential for added genetic gain from clonal selection and development for the production population.

Genetic variation was found at all ages in both factorials for height and for dbh and volume at age 5. Additive and dominance genetic variance for height had opposite patterns, as far as relative size, in the two factorials. Averaged between the factorials, additive and dominance genetic variance were essentially the same magnitude. Heritabilities for height tended to be lowest at age 1 and increase steadily to age 5. This trend indicates that selection for genetic improvement of these traits should probably be postponed at least until age 4. Additional genetic gain should be available by practicing clonal selection and reforestation as opposed to just recurrent selection and seedling/seed orchard based tree improvement. Detailed information as given in this study should be published for older stand ages in order to follow the same type of trends and verify the potential gain from tree improvement.

The lack of interaction between families and test sites indicates the possibility of including these site types, represented by the test sites, and the population, represented by the selected parents, in a single breeding zone. This result is supported by previous test results (Li and McKeand 1989) with loblolly pine. Clones were more interactive with test sites, as anticipated, but the nature (scale effect or true rank change) of the interaction needs to be explored more fully. Results from McRae et al. (1993) with more test sites indicate very little interaction at the clone level; hence, these early results are tentative yet appear to point toward the use of broadly adapted clones of loblolly pine.

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