Time Trend of Genetic Parameters in Growth Traits of *Pinus taeda* L.

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Abstract

Annual measurements on growth traits from a total of 275 parents and 690 full-sib families from 23 diallel tests of loblolly pine (*Pinus taeda* L.) in the Northern, Coastal and Piedmont test regions of the southeastern U.S. were used to reveal the time trend of genetic parameters through age 8. Variance components were estimated from mixed model analyses on growth traits (height, DBH and volume) and were used to calculate genetic variance components, heritabilities and age-age genetic correlations. In three test regions, the dominance variance was found to be less than the additive variance. The range of the dominance variance fell within 20%~40% of the total genetic variance for all traits. Different trends of heritability estimates were found for three test regions, but the general trend was that heritability increased over time. The magnitude of heritabilities for DBH and volume was found to be comparable with the corresponding heritability for height. Age-age genetic correlations of early height with 8-year volume increased significantly in the first 3–4 years, and then leveled off after that. DBH and volume had higher age-age correlations than height. The trends of heritabilities and age-age correlations indicated that the optimum selection age could be as early as 3 for height and as early as 4 for DBH or volume. Early selection for volume at age 4–5 could maximize genetic gain.

Key words: Diallel mating design, heritability, Type B genetic correlation, age-age correlation, loblolly pine.

Introduction

Reliable time trend of genetic parameter estimations is essential for choosing appropriate selection and breeding strategies in tree breeding programs. Many studies have been done for estimation of genetic parameters and early selection for growth traits of loblolly pine (*Pinus taeda* L.) (LI *et al.,* 1992; LI *et al.,* 1991; LI *et al.,* 1997; *Li et al.,* 1996; BALOCCHI *et al.,* 1993; FOSTER, 1986; LAMBETH *et al.,* 1983; FRANKLIN, 1979). Most published results were from unimproved, first-generation progeny tests or based on rather small sample sizes of families with limited reliability and precision. The genetic variation and parameters over time for improved populations of loblolly pine is still unclear. How do genetic parameters change after one generation of improvement in a breeding program? Would the time trend be different from that of the unimproved populations on well-tested sites? How do test series and breeding regions differ in genetic parameters? On what traits, and when, should selection be made to maximize genetic gain? Even with high quality and uniform progeny tests, a large family sample size is critical for obtaining reliable estimates of genetic parameters. In addition, knowing the time trend of genetic parameters is very useful in developing optimal breeding strategies for future selection.

The North Carolina State University - Industry Cooperative Tree Improvement Program (NCSU-ICTIP) has completed 48 years of loblolly pine tree improvement in the Southeastern United States. Through the first 2 cycles of breeding, testing and selection substantial genetic gains have been achieved (LI *et al.,* 1999). The Cooperative's tree improvement program for loblolly pine has now moved into its third generation (LI *et al.,* 1996; MCKEAND *et al.,* 1997). To properly implement the third generation, and future breeding plans, it is necessary to thoroughly analyze and evaluate the data accumulated from the second-generation progeny tests of NCSU-ICTIP. In this study, twenty-three test series from three test regions were used in the analysis. Annual measurements from a total of 275 parents and 690 full-sib families were used to estimate a comprehensive range of genetic parameters: additive and dominance genetic variance, appropriate heritabilities for various selection methods and age-age genetic correlation for growth traits, as well as to reveal the time trend, through age 8, of each parameter. The results obtained were then used to determine whether or not these particular loblolly pine populations show significant differences in either the magnitude or time trend of the genetic parameters..

Materials and Methods

Mating design and field design

A disconnected-half-diallel mating design was used to generate progenies for the second-cycle breeding program at NCSU-ICTIP (*Table 1*). Each half diallel consisted of 6 parents and 15 full-sib crosses, without self and reciprocal crosses. Parent

Table 1. – Disconnected diallel mating design used for loblolly pine in the southeastern U.S.

F \ M	Diallel 1						Diallel 2					
	1	2	3	4	5	6	7	8	9	10	11	12
1		×	×	×	×	×						
2			×	×	×	×						
3				×	×	×						
4					×	×						
5						×						
6												
7								×	×	×	×	×
8									×	×	×	×
9										×	×	×
10											×	×
11												×
12												

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trees were assigned randomly to different diallels. To keep number of crosses per test in a manageable size, two diallels with a total of 30 full-sib crosses were tested together over four test sites in each test series. In each test, full-sib crosses were replicated over 6 blocks and planted in 6-tree row plots in each replication (Li *et al.,* 1996). Four check lots were also included in each test with two row plots in each replication.

A total of 65 loblolly pine progeny tests in 23 test series with annual growth measurements were used for analysis. These tests can be grouped into the following three areas: 1) Virginia and northern North Carolina; 2) Atlantic Coastal Plains, Georgia and Lower Gulf; 3) Piedmont of Georgia, South Carolina and North Carolina and Upper Gulf. They are referred to as the Northern, Coastal and Piedmont region, respectively. The above grouping of geographic areas was also adopted for the 3rd cycle breeding plan of the loblolly pine breeding program at NCSU-ICTIP (Annual Report, 1999). Each test region included 4, 8, 11 test series for Northern, Coastal and Piedmont region, respectively. Each test series included 4 tests, which were planted over two years on two different sites (MCKEAND, 1988).

Data collection and growth curve correction

All progeny tests were measured annually up to age 8 for height (HT), and measurement for diameter at breast height (DBH) started at age 4. Tree height was measured to the nearest centimeter, while DBH was measured to the nearest millimeter. Volume (VOL) was calculated following the formula for young loblolly pine (GOEBEL and WARNER, 1966):

$$VOL = 0.03371 + (0.00196128*DBH^2*HT) \qquad \text{(Eq. 1)}$$

RICHARDS' function was used to correct irregularities in the data, such as leaders broken by adverse weather, damaged by insects or diseases and measurement or data recording errors. This flexible growth model permits each individual tree to have its own growth curve (RICHARDS, 1959; BALOCCHI, *et al.* 1993). The form of this equation is shown as follows:

$$Y=A(1-e^{-bX})^c \qquad \text{(Eq. 2)}$$

where Y is the measurement of a certain character (e.g. height); A is the upper limiting value for the character; *e* is the base of natural logarithms; *b* and *c* are the shape parameters, which determine the shape of the curve along the time axis; X is age in years. All further analysis was performed based on the predicted values of this nonlinear model.

Linear model and statistical analysis

For each test series, the following linear model is used to estimate variance components.

$$Y_{ijoklm} = \mu + T_i + B_{j(i)} + D_o + G_{k(o)} + G_{l(o)} + S_{kl(o)} + TG_{ik(o)} + TG_{il(o)} + TS_{ikl(o)} + P_{ijokl} + E_{ijoklm} \quad \text{(Eq. 3)}$$

where,

Y_{ijoklm} is the *m*th observation of the *j*th block for the *kl*th cross in the *o*th diallel in the *i*th test;

μ is the overall mean;

T_i is the *i*th fixed test environment (location) effect, $i=1$ to t;

$B_{j(i)}$ is the fixed effect of the *j*th block within the *i*th test, $j=1$ to b;

D_o is the *o*th fixed diallel effect, $o=1, 2$;

$G_{k(o)}$ or $G_{l(o)}$ is the random general combining ability (GCA) effect of the *k*th female or the *l*th male within the *o*th diallel ~Normally and Independently Distributed (NID) $(0, \sigma^2_g)$, $k, l=1$ to p and $k<l$;

$S_{kl(o)}$ is the random specific combining ability (SCA) effect of the *k*th and the *l*th parents within the *o*th diallel $(k \neq l)$ ~NID $(0, \sigma^2_s)$;

$TG_{ik(o)}$ or $TG_{il(o)}$ is the random interaction effect of the *i*th test by the *k*th female or the *l*th male GCA ~NID $(0, \sigma^2_{gt})$;

$TS_{ikl(o)}$ is the random interaction effect of the *i*th test by the *kl*th SCA ~NID $(0, \sigma^2_{st})$;

P_{ijokl} is the random plot effect for the *kl*th cross within the *o*th diallel in the *i*th block ~NID $(0, \sigma^2_p)$, $l=1$ to n;

E_{ijoklm} is the random within plot error term ~NID $(0, \sigma^2_e)$

All random effects were assumed to be independent of each other. As a typical mixed model, the model can be analyzed with the SAS MIXED procedure by creating dummy variables for GCA effects (XIANG and LI, 2001; LITTLE *et al.,* 1996). The variance components of random effects were estimated using the default REML model fitting option.

Genetic variance and heritability estimation

Genetic and other parameters were defined and calculated using the variance estimates. Additive and nonadditive (dominance) genetic variances were calculated as $\sigma^2_A = 4\sigma^2_g$ and $\sigma^2_D = 4\sigma^2_s$, respectively. Values for the different types of heritability were calculated as follows (XIANG *et al.,* 2003):

Narrow sense individual heritability:

$$h^2=4\sigma^2_g/(2\sigma^2_g+\sigma^2_s+2\sigma^2_{gt}+\sigma^2_{st}+\sigma^2_p+\sigma^2_e) \qquad \text{(Eq. 4)}$$

Broad sense individual heritability:

$$H^2=4(\sigma^2_g+\sigma^2_s)/(2\sigma^2_g+\sigma^2_s+2\sigma^2_{gt}+\sigma^2_{st}+\sigma^2_p+\sigma^2_e) \qquad \text{(Eq. 5)}$$

Half-sib family mean heritability:

$$h^2_{HS} = \frac{\sigma^2_g}{\sigma^2_d+\frac{p\sigma^2_g}{p-1}+\frac{\sigma^2_s}{p-1}+\frac{p\sigma^2_{gt}}{t(p-1)}+\frac{\sigma^2_{st}}{t(p-1)}+\frac{\sigma^2_p}{bt(p-1)}+\frac{\sigma^2_e}{bnt(p-1)}} \qquad \text{(Eq. 6)}$$

Narrow-sense full-sib family mean heritability:

$$h^2_{FS} = \frac{2\sigma^2_g}{\sigma^2_d+2\sigma^2_g+\sigma^2_s+\frac{2\sigma^2_{gt}}{t}+\frac{\sigma^2_{st}}{t}+\frac{\sigma^2_p}{bt}+\frac{\sigma^2_e}{bnt}} \qquad \text{(Eq. 7)}$$

Broad sense full-sib family mean heritability:

$$H^2_{FS} = \frac{2\sigma^2_g+\sigma^2_s}{\sigma^2_d+2\sigma^2_g+\sigma^2_s+\frac{2\sigma^2_{gt}}{t}+\frac{\sigma^2_{st}}{t}+\frac{\sigma^2_p}{bt}+\frac{\sigma^2_e}{bnt}} \qquad \text{(Eq. 8)}$$

where, σ^2_g is genetic variance due to general combining ability (GCA), σ^2_s is genetic variance due to specific combining ability (SCA), σ^2_{gt} is GCA by test interaction variance, σ^2_{st} is SCA by test site interaction variance, σ^2_p is plot to plot variance, σ^2_e is within plot error variance, σ^2_d is variance due to diallel effect, p is number of parents in the diallel set, t is the number of test sites within each series, b is number of blocks at each test site, n is the number of trees within each plot for each cross. The estimates of variance components and genetic parameters were averaged across all test series in each test region to compare among traits and regions.

Genetic correlation and type B genetic correlation

Using the same variance estimation procedure, genetic correlations between a pair of traits were estimated using the following formula:

$$r_{Gxy} = \frac{\sigma_{gxgy}}{\sqrt{\sigma^2_{gx} \cdot \sigma^2_{gy}}} = \frac{\left[\sigma^2_{gx+gy}-\sigma^2_{gx}-\sigma^2_{gy}\right]/2}{\sqrt{\sigma^2_{gx} \cdot \sigma^2_{gy}}} \qquad \text{(Eq. 9)}$$

where X, Y are two traits of interest (e.g. height or volume at any age); σ^2_{gx} or σ^2_{gy} is the GCA variance of trait X or Y; σ_{gxgy} is the GCA covariance, i.e. $\frac{1}{4}$ of the additive genetic covariance

between two traits; σ^2_{gx+gy} is the GCA variance, i.e. $\frac{1}{4}$ of the additive genetic variance for the dummy variable obtained by the sum of values of two traits. Since the data were generally well balanced in terms of crosses and missing plots and the estimation of σ^2_e was not of particular interest, plot means were used to obtain σ^2_{gx+gy}.

The type B genetic correlation was calculated following the formula given by YAMADA (1962), which is a well-accepted measurement of genetic by environmental interaction (BURDON, 1977).

$$r_B = \sigma^2_A/(\sigma^2_A + \sigma^2_{AE}) = \sigma^2_g/(\sigma^2_g + \sigma^2_{gt}) \qquad \text{(Eq. 10)}$$

Results

Time trend of genetic parameters

Genetic variance estimates

The genetic variance of the three growth traits generally increased over time and had similar trends for all three regions (*Fig. 1*). Additive genetic variances (σ^2_A) were small but increased in a linear fashion for HT and DBH over time. Exponential increases were observed for additive genetic variances of VOL. Dominance genetic variances (σ^2_D) also increased over time similar to additive genetic variances, but they were less predictable than the additive component in the Coastal and Piedmont regions.

The three test regions differed in magnitude of genetic variance components. The Coastal region had the highest variance component estimates. For HT at age 8, the additive genetic variance was higher (1.88) in the Coastal region than in the Northern and Piedmont region (0.67 and 1.03 respectively). The same order in regional differences of genetic variance components was observed for both DBH and VOL.

Heritability

Narrow-sense individual heritability estimates ranged within 0.06~0.20. Non-additive variance added about 30% to the broad sense heritability, resulting in a range of 0.08~0.27 (*Fig. 2*). The family heritabilities ranged from 0.5 to 0.89 (*Fig. 3*).

While the general trend of heritability estimates was increasing over time and were similar for all three growth traits, the shape of the curves varied for different heritabilities and test region. In the Northern region all heritability estimates did not vary significantly with increasing age for all three traits. Slight increases were observed over time for individual heritabilities, while family heritabilities were rather stable over ages (*Fig. 2, 3*).

In the Coastal and Piedmont test regions, individual heritabilities for HT increased over time until age 4 or 5, then plateaued in the Piedmont region and slightly declined in the Coastal region (*Fig. 2*). The corresponding family heritability of the same trait followed similar but less marked changes as the individual heritabilities (*Fig. 3*). Individual heritability for DBH increased in the Northern region, but did not change appreciably in the Coastal region. There was no a general trend in the Piedmont region. The trends of heritabilities for volume were similar to the trends of DBH heritability.
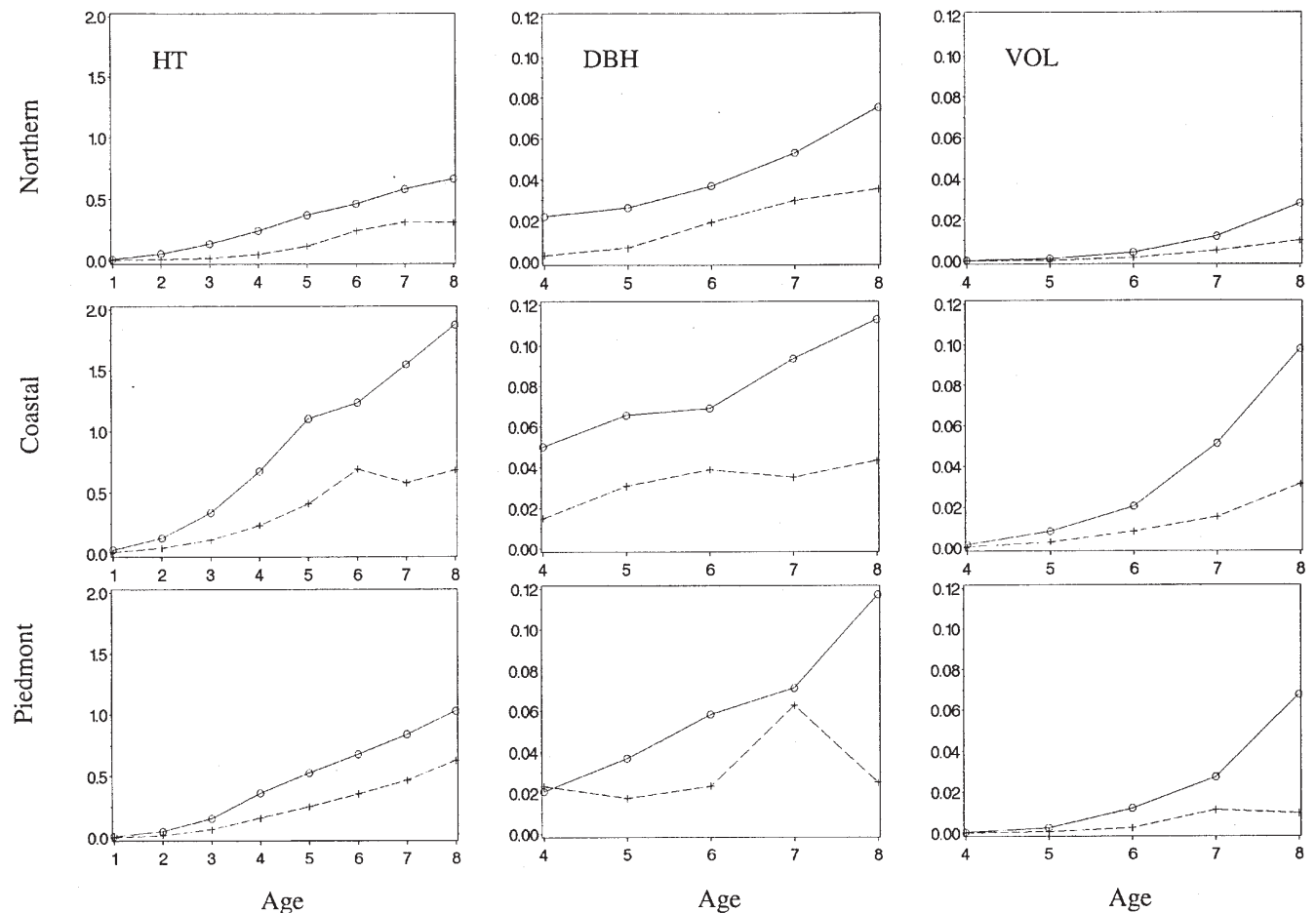

Figure 1. – Time trend of additive (σ^2_A) (circles, solid line) and dominance (σ^2_D) (plus sign, dashed line) variance component estimates for trait height (HT), diameter at breast height (DBH) and Volume (VOL) during early growth period in 3 test regions (Northern, Coastal and Piedmont).
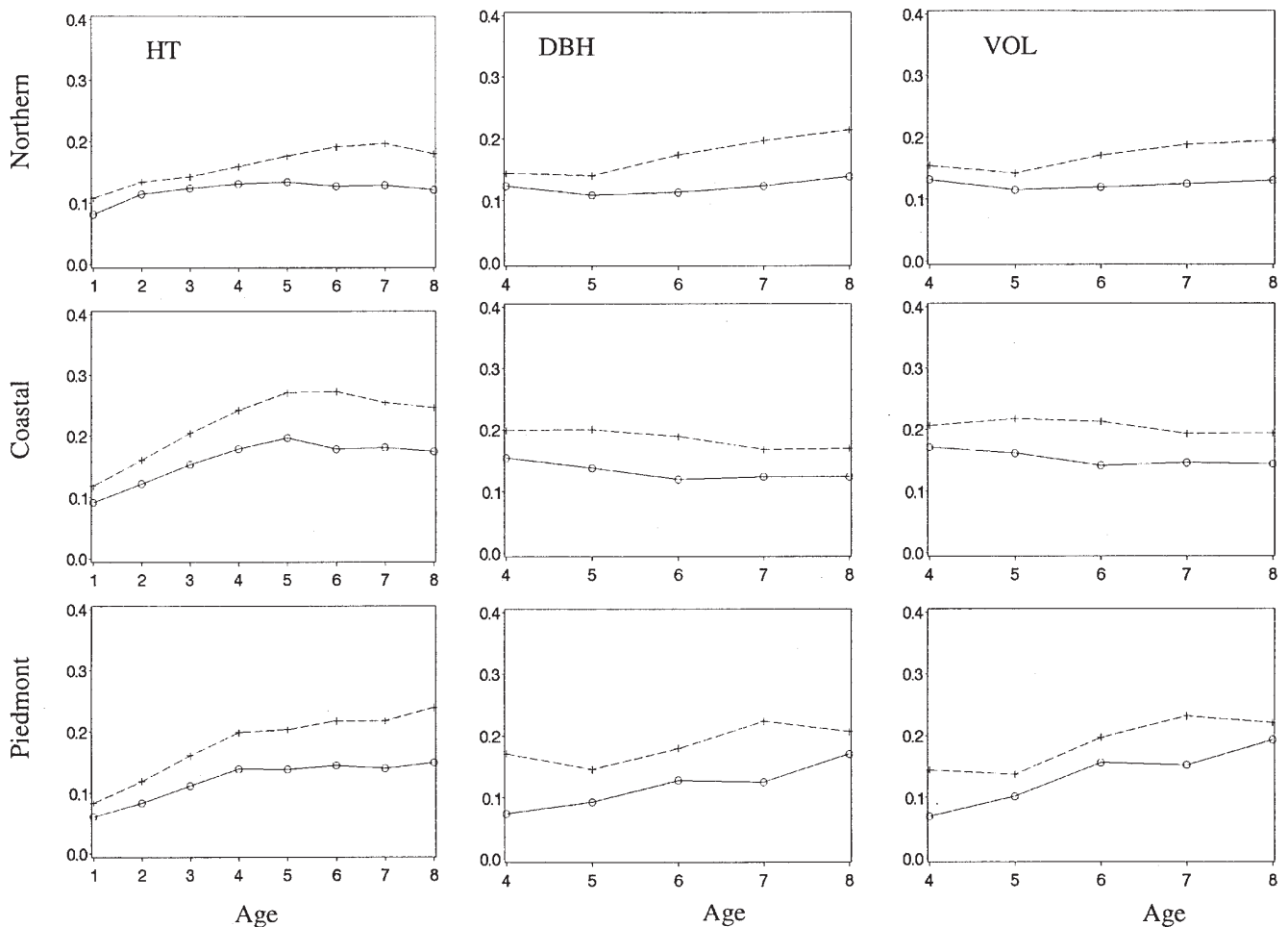
Figure 2. – Time trend of narrow-sense (h^2) (circles, solid line) and broad-sense (H^2) (plus sign, dashed line) individual heritabilities for trait height (HT), diameter at breast height (DBH) and Volume (VOL) during early growth period in 3 test regions (Northern, Coastal and Piedmont).

Type B genetic correlation

The type B genetic correlation for HT ranged from 0.65 to 0.93, with most values between 0.70 and 0.85. Similarly, DBH had high type B correlations across test regions and ages, ranging from 0.68 to 0.83. VOL had slightly lower type B correlations, with its range from 0.62 to 0.79 (*Table 2*).

In the Northern region, the type B genetic correlation was consistently high (larger than 0.70) across all ages for HT and DBH, showing a weak genetic by environment interaction effect within the test series for all ages. Correlation for VOL was relatively low (0.62) then increased gradually to 0.71 at age 8. In other two test regions, type B correlation for HT was high for most ages, except at age one. Correlation for DBH was slightly lower than 0.7 after age 5 in the Coastal region. Similar to the Northern region, the Piedmont region had constant high correlation (larger than 0.70) across ages for DBH. Unlike the Northern region, VOL correlation for the Coastal region started as high as 0.73 then went down slightly to 0.67 at age 8, while in the Piedmont region VOL correlation maintained a high level (larger than 0.7) across ages except for 0.64 at age 5.

The type B correlation increased slightly over time for HT. But for DBH and VOL, the general trend over time was not clear, partly because of the short time period from age 4 to 8. Overall though, the type B genetic correlation was fairly stable over time and test region for all three traits within the measurement time frame.

Genetic correlations

Age-age genetic correlation for the same trait

The genetic correlations between age 8 and previous ages of the same trait are shown in *Fig 4*. As expected, all correlations increased over time and approached unity at age 8. The range for correlation of HT was from 0.30 at age 1 in the Northern region and went up to 0.90 at age 5. The lowest correlation for DBH and VOL was around 0.60 at age 4 in the Coastal region. High correlations were observed at the very early growth stage for all three regions.

For common ages of all three traits, early height had the highest genetic correlation among the three traits in the Northern and Piedmont region, followed by VOL and DBH. On the contrary, in the Coastal region the genetic correlation for VOL slightly exceeded that for HT, which in turn was slightly higher than DBH.

In the Northern and Coastal regions, the age-age genetic correlation for early height (HT) rose rapidly from age 1 to age 3. At age 3, the correlation exceeded or was close to 0.80 and continued to increase gradually. The age-age genetic correlation for DBH and VOL in the Northern region started relatively low at early ages then increased to the same level as HT by age 7, while in the Coastal region, the DBH and VOL correlations were as high (0.90) as HT by age 4 and stayed at this high level through age 8. In the Piedmont region, the correlation for HT
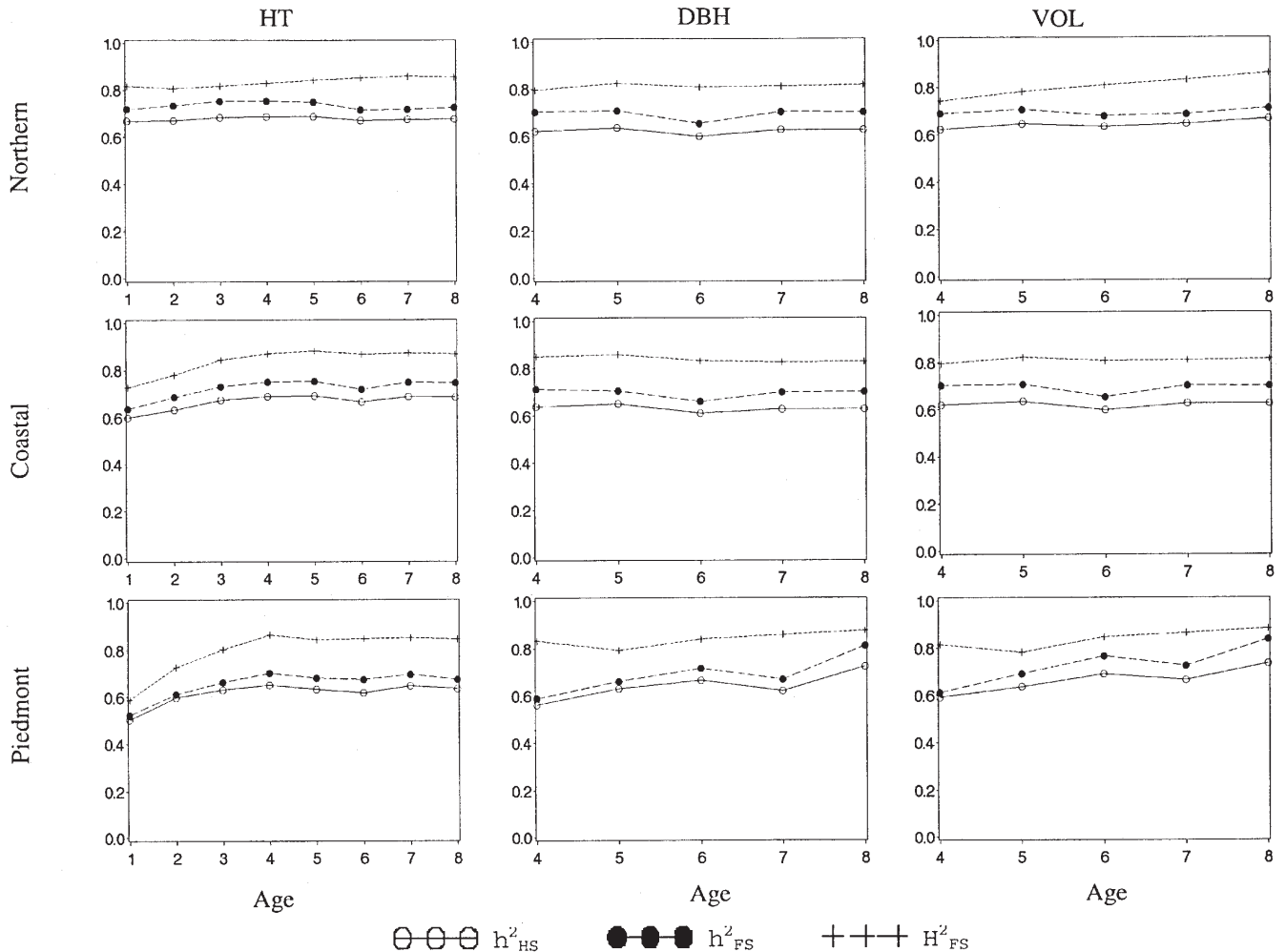
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Figure 3. – Time trend of family mean heritabilities for height (HT), diameter at breast height (DBH) and Volume (VOL) during early growth period in 3 test regions (Northern, Coastal and Piedmont).

was high (0.90) at age 2 and stayed high through age 8. DBH had slightly lower correlations than VOL, and both were below the correlations for HT through ages 4 and 5.

Age-age genetic correlation with volume at age 8

The genetic correlations of early height, DBH and volume with age-8 volume (VOL8) were presented in *Fig 5*. Correlations generally increased with time for all traits. The correlation for trait HT increased from 0.23 to 0.74 in the Northern region, from 0.55 to 0.85 in the Coastal region and from 0.74 to 0.88 in the Piedmont region. For trait DBH, correlations with

Table 2. – Averaged type B genetic correlations for growth traits of loblolly pine in three test regions in the southeastern U.S.

AGE	Northern region			Coastal region			Piedmont region		
	HT	DBH	VOL	HT	DBH	VOL	HT	DBH	VOL
1	0.74	-	-	0.69	-	-	0.65	-	-
2	0.71	-	-	0.69	-	-	0.75	-	-
3	0.74	-	-	0.79	-	-	0.84	-	-
4	0.76	0.76	0.62	0.82	0.80	0.73	0.93	0.72	0.78
5	0.77	0.76	0.64	0.82	0.83	0.74	0.84	0.74	0.64
6	0.79	0.77	0.67	0.77	0.71	0.68	0.83	0.78	0.73
7	0.81	0.79	0.71	0.80	0.68	0.67	0.82	0.78	0.74
8	0.79	0.83	0.78	0.79	0.68	0.67	0.79	0.80	0.79

VOL8 were higher than those for HT in all three regions. Juvenile volume had the highest correlations with VOL8 as expected in all three regions.

In the Coastal and Piedmont regions, the difference between the average genetic correlation of HT and either DBH or VOL was smaller than that observed for the Northern region. Particularly in the Piedmont region, the correlation at age 4 for HT was even higher than DBH. However, it must be noted that genetic correlation of HT with VOL8 showed more variation among test series. It exceeded 1 in some test series in the Piedmont region, which resulted in a slightly higher average correlation than for the other two regions. The shape of the trend curve over time for trait HT was also different than the corresponding curve for either of the other two traits, in that it had higher correlation in the middle of the measurement time duration. It peaked at age 5 for both Northern and Coastal region, and had two modes, age 3 and 5, for the Piedmont region.

VOL had the highest correlation among the three traits in the Northern and Coastal region, followed by DBH and HT. VOL still had its best correlation in the Piedmont region, but HT seemed to have higher genetic correlation in earlier years. Visibly, it exceeded DBH at age 4, when measurements first became available for comparison among all three traits. The three test regions also differed in the shape of the trend curves (*Fig. 5*). The increasing rate of genetic correlation in early ages was larger in the Northern region than in other two regions.
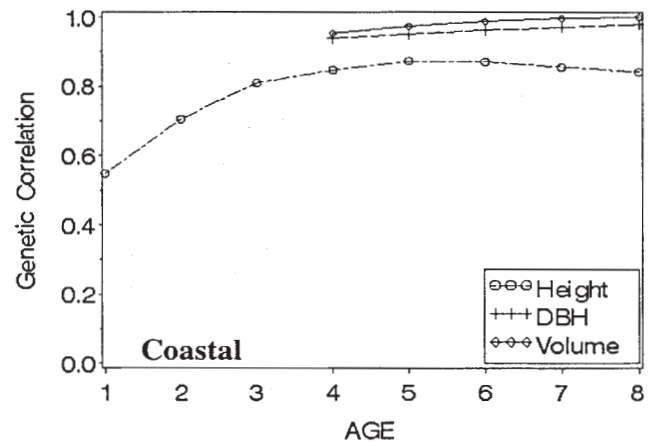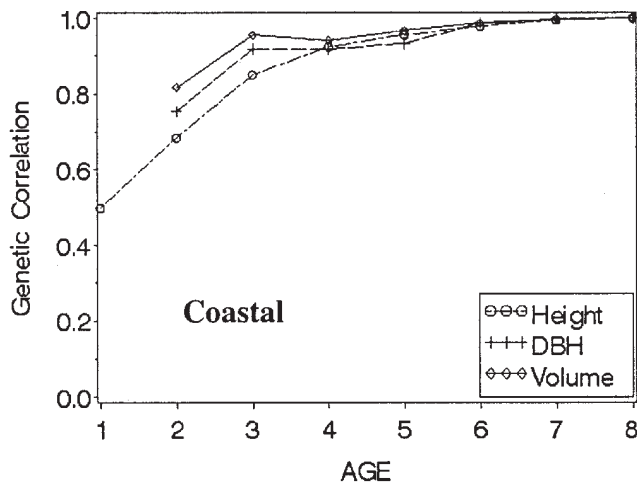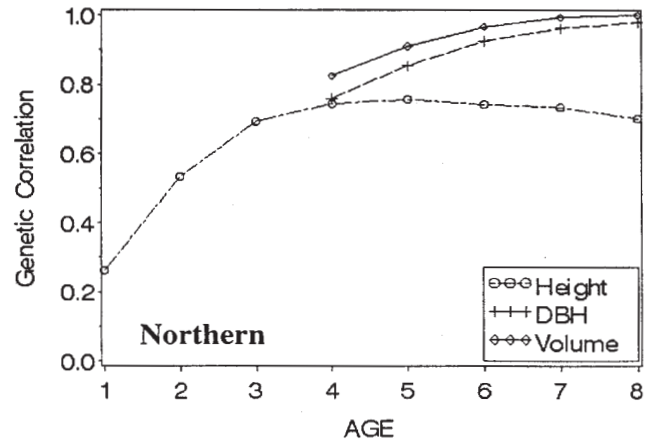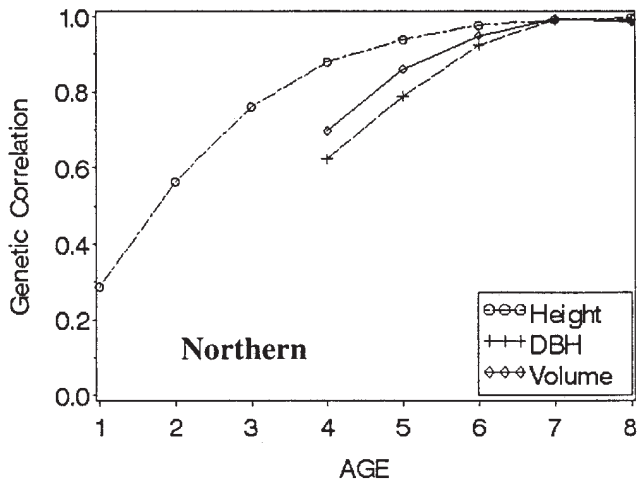
Figure 4. – Comparison of age-age genetic correlations of growth traits for 3 test regions: Northern, Coastal and Piedmont.

Figure 5. – Comparison of genetic correlations with age-8 volume of growth traits for 3 test regions: Northern, Coastal and Piedmont.

The later two regions differed in that HT had larger changes over time in the Coastal region while DBH and VOL had larger age-age difference in the Piedmont region.

Discussion

The genetic variance components generally increased over time and the trends were similar for all test regions. The increase for both height and DBH was almost linear with age, while the increase for volume was exponential. The three test regions differed in the magnitude of the variance components, however. The Coastal population showed the highest variance components, followed by the Piedmont and Northern sources. This may be due to the difference in growth rate observed between the different regions. Loblolly pine trees grow faster in the Coastal region than in the Northern and Piedmont regions. The Northern population is known to be cold-hardy but with a relatively slow growth rate. The Piedmont source is also cold-hardy, but has better stem form and its growth rate is in the middle of other two regions (Annual Report 1999). This region-

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al difference could also be due to the number of test series in each region.

Unlike the results from BALOCCHI *et al.* (1993), which showed that dominance variance exceeded additive variance at ages before 12, we found that the percentage of dominance variance within the total genetic variance varied from 10% to 40% for all three growth traits across the test regions, with the average around 30%. In addition, the percentage of dominance variance was the highest at around age 6 or 7 for the Northern and Coastal populations. In the Piedmont region, however, no clear pattern was observed. This difference might be due to the different population structures of the two studies. This time trend of genetic variances generally agrees with the results from an earlier study on the similar diallel tests (LI, *et al.*, 1996). The magnitude and the time trend of genetic variance components were also supported by another study of loblolly pine (ISIK, *et al.*, 2003).

Typical heritability estimates for growth traits were observed in this study. Heritability estimates showed different time trends for different test regions. Although large variation of heritability existed among test series, when averaged over the entire region, we found a general increase pattern for tree height in all three regions: heritabilities increased from age 1 to age 4 and then stabilized after that. For DBH and volume, heritabilities increased in the Piedmont region from age 4 to age 8. However, the time trends were different in the Coastal and Piedmont regions where the average estimates remained the same. Unlike other studies (LAMBETH, 1980), the magnitude of heritabilities for DBH and volume were found to be comparable with the corresponding heritabilities for height.

The type B genetic correlations were generally high across all test regions. This confirms early results, which showed that loblolly pine has little genotype by environment interaction and has high family stability performance across a wide geographic area (LI and MCKEAND, 1989; MCKEAND, *et al.,* 1990).

Genetic correlation is subject to large sample errors. In our study, the number of parents are fairly large, 48 parents (Northern region), 96 parents (Coastal region), 132 parents (Piedmont region). Hence we would expect that estimated age-age genetic correlations for growth traits are relatively reliable compared to most estimates in the literature.

Although the time trends of genetic parameters were similar to the first generation data (LI *et al.,* 1996), parameter estimates from these diallel progeny tests were generally higher, and the genetic correlations were higher at younger ages than the first generation data. This may be due to any change in genetic variation for the selected loblolly pine populations. However, it is difficult to separate the selection from the effects of population sizes (number of parents involved) and different age measurements between the two data sets. In addition, it is expected that the generally well-balanced diallel tests on uniform test sites should have improved parameter estimates. Nevertheless, the genetic parameter estimates obtained in this study should help to make selection decisions for next cycle breeding.

A generally high age-age correlation for height indicates that if our goal is to improve 8-year height, early selection can be considered at age 4, or even at age 3 in the case of the Coastal region. This also confirms the results from LI *et al.* (1996) that early height is a good prediction of 8-yr height growth. If our selection is for 8-yr volume, correlation for DBH and volume were better than height in all regions, with the exception of early ages for the Piedmont population. The 8-year volume has been determined to be a reliable measurement for rotation volume in loblolly pine (MCKEAND, 1988; XIANG, *et al.,* 2003).

These results indicate that although height performance at age 3–4 is a good indicator of performance at age 8, selecting on height alone might not be the most efficient for maximizing volume. Considering DBH and volume at age 4–5 might be advisable in order to achieve maximum genetic gain.

Conclusions

In all test regions, additive genetic variance from the second-generation progeny tests was found to be more important than dominance variance. The relative proportion changed slightly over time but fell within 10%~40% of total genetic variance for all traits. This result, together with earlier analysis on similar diallel tests (LI *et al.,* 1996), indicate that selected loblolly pine populations may have different genetic structure and time trends than those found in unselected populations (BALOCCHI *et al.,* 1993) and first generation populations.

Age-age genetic correlations of early height with 8-year volume increased significantly in the first 3-4 years and then leveled off. DBH and volume had higher age-age correlation than height. The trends of heritabilities and age-age correlations indicate that the optimum selection age could be as early as 3 for height and as early as 4 for DBH or volume. Early selection that includes volume at age 4-5 could maximize genetic gain.

Reference

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Trends in Variances and Heritabilities with Age for Growth Traits in Eucalyptus Spacing Experiments

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Abstract

Three experimental designs were carried out in the Congo to analyse the impact of spacing on trends in variance and heri-tability with age and to assess the genotype by spacing interac-tion in a eucalyptus breeding programme. Three populations of eucalyptus hybrids encompassing respectively 12 clones, 12 and 16 full sib families were established in square or rectangu-lar plots of 30, 36 and 36 trees respectively, at spacings of 625, 1111 and 2500 trees/ha. Height and circumference were mea-sured at different ages, from the juvenile stage up to the adult size of the trees.

Results showed that genetic effect was significant from the juvenile stage for the three experiments. Family by spacing interaction was not significant throughout the growth period but, for the clonal population, the interaction was highly signif-icant after age 3, with changes in clone ranking. Trends in between or within family or clone coefficient of variation with age exhibited two main phases. During the first phase the coef-ficient of variation decreased and during the second phases it was constant for the genetic effect and strongly increases in the case of within clone and within family effect. This two phases could correspond to a juvenile and a mature phase. In the case of these three experiments some results showed that the juve-nile phase could be reduced with closer spacing, as suggested by the Franklin's model.

Heritabilities based on the clone and family mean were very high for the three experiments due to the sample size and the high control of the environment in the design. Heritabilities based on individual trees were smaller because of the high within plot variance. These two parameters rapidly reached a plateau and the two phases mentioned for variances were not observed. Although heritability at close spacing decreased with age for the family experiments, due to the strong increase of the within clone and family variance, the impact of spacing was not statistically significant. The high heritability on the family means basis and the absence of family by spacing inter-action permits the family selection at close spacing with a good efficiency specially during the juvenile phase.

Key words: Spacing by genotype interaction, phase of growth, coefficient of variation, family, clone.

Introduction

Forest trees are long-lived organisms and the expression of genes in relation to age and competitive environment is likely one of the most important features to consider in tree genetics and tree breeding.

Numerous studies have been conducted in an attempt to understand the variation in genetic and environmental vari-ances with tree age in the most widely planted species like pines (WHITE and HODGE, 1992; KUSNANDER *et al.,* 1998) and eucalyptus (BORRALHO *et al.,* 1992; BOUVET and VIGNERON, 1995; WEI and BORRALHO, 1998). These studies have especially facilitated the development of methods to predict the optimal age of selection (SATO, 1994; BOUVET and VIGNERON, 1995; JOHNSON *et al.,* 1997). Several studies have also been imple-mented to test some models of stand development (NAMKOONG and CONKLE, 1972; NAMKOONG *et al.,* 1976) and specially the FRANKLIN's model (LAMBETH, 1983; FOSTER, 1986; BALOCCHI *et al.,* 1993). In his model, FRANKLIN (1979) compares the magni-tude of genetic versus environmental variances at different stages of the stand development for two pine species. In the model, stand development was divided into three phases: the juvenile-genotypic, the mature genotypic and the suppression co-dominance phase. FRANKLIN suggested that by hastening the onset of the mature-genotypic phase by inducing fast growth at close spacing and "perhaps by manipulating other environmen-tal factors" one could improve the prediction of ranking at mature age.

Very few studies, crossing genetic entries and spacing, have been carried out to test these hypotheses. This is mainly due to the large effort needed to carry out such experiments in the field. Some have tried to analyse the effect of competition at the nursery stage (ADAMS *et al.,* 1973; TAUER, 1975; TUSKAN and VAN BUIJTENEN, 1986) or through retrospective tests with seedlings tested in the nursery at different spacings and adult trees in the field (JANSSON *et al.,* 1998). The conclusions remain

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