

## GENETIC PARAMETERS FOR HEIGHT AND STEM STRAIGHTNESS IN *PINUS TAEDA* LINNAEUS IN ZIMBABWE

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### ABSTRACT

Genetic and phenotypic parameters for height and stem straightness were estimated for *Pinus taeda* L. in Zimbabwe using the individual tree model DFREML. The data were from 4 progeny tests comprising 140 full-sib families assessed at 1.5, 9.5, 13.5 and 22.5 years. Dominance variance tended to be lower than additive variance for both traits, except for straightness at 1.5 years. Heritability estimates for height were moderate to high (0.14 to 0.73) and peaked at 9.5 years; those for straightness were low at 1.5 years and increased to moderate levels with age (0.01 to 0.33). Individual site heritability estimates were higher than those using data pooled across sites, indicating presence of genotype × environment interactions and/or heterogeneity of variances. It is suggested that combining data as in the pooled analyses was not appropriate for this study. Genetic correlations were higher than their phenotypic counterparts in both traits. Age-age genetic correlations for height were high indicating opportunity for early selection (0.76 to 0.97). Age-age genetic correlations for straightness ranged from –0.05 to 0.94. Genetic correlations between height and straightness were low.

**Keywords:** Individual tree model, DFREML, heritability, age-age genetic correlation, *Pinus taeda*.

### INTRODUCTION

*Pinus taeda* L. is a major exotic plantation species in Zimbabwe and other southern African countries. Its success as an exotic is due to its fast growth rate and wide adaptability, although it is limited on some sites by problems such as susceptibility to drought and damage from pests such as *Pinus pine*, *Cinara cro-nartii* and baboons. With the increasing demand for wood products globally (SHARMA *et al.* 1992), maximising wood production on available land resources is of major importance. The high growth rate of *P. taeda*, the variation evident in natural stands and plantations in Zimbabwe and South Africa, and the need to increase production per unit area led to the establishment of a breeding programme in Zimbabwe in 1958 (BARRET & MULLIN 1968). The most comprehensive progeny tests in this programme were established in the 1970s. The major constraint to the efficient breeding of this species in Zimbabwe has been the lack of genetic parameter information to guide decisions on the most appropriate breeding strategy and, more generally, to monitor genetic progress.

Genetic parameter estimates available for *P. taeda* are predominantly from studies in the USA. Heritability estimates for height from these studies were high (BALOCCHI *et al.* 1993; FOSTER 1986; LAMBETH *et al.*

1983; FRANKLIN 1979) and age-age genetic correlations for height were positive and high (FOSTER 1986; LAMBETH *et al.* 1983). There are few reports of heritability estimates for stem straightness from studies in the USA, probably reflecting the fact that this trait is relatively difficult and costly to measure. The few estimates that are available indicate that the heritability for stem straightness is weak to moderate (WILLIAMS & LAMBETH 1989; BRIDGWATER & STONECYPHER 1979), and depends on the method of assessment. Whereas in Zimbabwe an absolute scale is used for assessing stem straightness, in the USA a relative score is commonly used.

There appear to be no estimates of genetic parameters for height and straightness in *P. taeda* grown in the tropics, an issue of concern as fast-growing tree crops are likely to exhibit different genetic parameters than slower growing ones (MAGNUSSEN 1988). Given the fact that growth rates of *P. taeda* in the tropics can be substantially higher than that achieved in the temperate regions, genetic parameters may differ between these regions. This lack of genetic parameter estimates for these economically important traits has potentially adverse consequences for realizing genetic progress in *P. taeda* breeding programmes in the tropics.

Traditionally, genetic parameters in forest tree breeding programmes have been estimated using sib

covariance genetic models. Unfortunately, these models do not allow use of covariances of other relatives, a particularly important aspect as breeding programmes advance to second and subsequent generations. Also, where information is available from both the male and female parents, such as in controlled cross mating designs, a problem is encountered as to how best pool the two resultant heritability estimates, especially when the two estimates are not of equal reliability and are correlated. The model which appropriately incorporates information on genetic relationships between trees is the individual tree model, which can be fitted in REML using derivative-free algorithms (DFREML, MEYER 1989). The individual model includes a random effect for the additive genetic merit or breeding value of each tree, both for trees with records and those that are represented as parents, and incorporates all known relationship information in the analysis. The additive genetic variance is then estimated as the variance of trees' additive genetic merit instead of estimating it from the variance between parents. The individual model has become the method of choice in animal breeding because of its desirable properties, and has recently been applied to tree breeding (*Eucalyptus* – BORRALHO *et al.* 1995).

The aim of the study was to estimate genetic parameters: variance components, heritability, genetic and phenotypic correlations, using individual tree model DFREML, for height and stem straightness. This is the first application of an individual tree model to estimate variance components for *Pinus taeda*.

## MATERIALS

The 140 full-sib families originated from an incomplete factorial mating design involving 8 male and 15 female parents. The 23 parents were selected phenotypically from unimproved plantations in Zimbabwe and South Africa.

Four progeny tests were planted in 1972 in the

Eastern Highlands of Zimbabwe. Details of the tests are given in Table 1. Trees were planted at 2.4 x 2.4 m spacing and each plot comprised ten trees. The tests comprised three replicates and ten to twelve blocks per replicate, in a triple lattice design. Systematic thinning was carried out by removing every other tree in each plot at ages 9.5 and 13.5 years, therefore removing 50% of the trees on each occasion. At age 9.5 years, height was assessed on trees that were felled after thinning.

The tests were assessed for height (HT) and straightness (ST) at 1.5, 9.5, 13.5 and 22.5 years. Stem straightness was assessed using a 7-point absolute visual scale (1 = crooked to 7 = very straight) outlined by BARRETT & MULLIN (1968). The total number of trees assessed for both traits was 13424, 5111, 5770 and 1973 at 1.5, 9.5, 13.5 and 22.5 years, respectively.

## METHODS

Variance components for individual sites were estimated using the following individual tree models:

$$Y_{ijkl} = \mu + R_i + B_{ij} + FM_{ijk} + A_l + \varepsilon_{ijkl} \quad [1]$$

$$Y_{ijklm} = \mu + R_i + B_{ij} + FM_{ijk} + Pt_m + A_l + \varepsilon_{ijklm} \quad [2]$$

– where:  $Y_{ijkl}$  is the observation on the  $l^{\text{th}}$  tree in the  $i^{\text{th}}$  replicate and  $j^{\text{th}}$  block and in the  $k^{\text{th}}$  family,  $\mu$  is the overall test mean,  $R_i$  is the fixed effect of the  $i^{\text{th}}$  replicate,  $B_{ij}$  is the random effect of the  $j^{\text{th}}$  block in the  $i^{\text{th}}$  replicate,  $FM_{ijk}$  is the random effect of the  $k^{\text{th}}$  family (female x male parent interaction),  $A_l$  is the additive genetic effect of the  $l^{\text{th}}$  tree, and  $\varepsilon_{ijkl}$  is the within plot error (residual), assumed to be normally distributed with mean 0 and variance  $\sigma^2$ .

The full-sib family variance component ( $\sigma_{FM}^2$ ) was interpreted as  $1/4\sigma_D^2$  where  $\sigma_D^2$  is the dominance genetic variance. The difference between the two models is that model 2 fitted plot ( $Pt_m$ ) as an additional random effect in order to measure common environ

**Table 1. Synopsis of progeny tests established in 1972 in Zimbabwe**

| Site (name)   | Tarka (A)  | Stapleford (B)  | Martin (C)  | Nyangui (D)   |
|---------------|--|---|---|---|
| Region        | Chimanimani  | Penalonga   | Chimanimani   | Nyanga  |
| Latitude      | 19°59'S  | 18°44'S   | 19°59'S   | 17°58'S   |
| Longitude     | 32°56'E  | 32°49'E   | 32°56'E   | 32°47'E   |
| Altitude (m)  | 1005   | 1745  | 1250  | 1882  |
| Rainfall (mm) | 2156   | 1836  | 1016  | 2364  |
| Soils         | Dolerite/alluvial<br>-derived; reddish<br>brown clays; well<br>drained | Dolerite-derived;<br>brown red clays;<br>well drained | Dolerite/siltstone<br>-derived; reddish<br>brown clays; well<br>drained | Dolerite-derived;<br>red-reddish brown<br>clays; well drained |

ment effect. For analyses of pooled data across the four sites, site was fitted as an additional fixed effect.

Comparisons between the individual tree models were made by likelihood ratio tests (MEYER 1993), which consist of subtracting the maximum log likelihood for the model with fewer parameters from the value corresponding to the model with more parameters, and then multiplying the difference by 2. The test statistic is distributed asymptotically as a  $\chi^2$  random variable with degrees of freedom equal to the difference in the number of parameters estimated for the two models. The test is appropriate where parameters in one model are a subset of parameters in the other.

The appropriateness of pooling data across sites was determined using the joint likelihood of the four independent analyses. Joint likelihood of the four analyses is simply the sum of the individual log likelihoods, asymptotically distributed as  $\chi^2$  with degrees of freedom equal to the sum of the parameters (*i.e.*  $df = 12$  for model 1 and  $df = 16$  for model 2). The difference between the joint likelihood and the analyses of pooled data is compared with  $\chi^2$  distribution with degrees of freedom equal to the differences in the number of parameters between them.

The additive genetic coefficient of variation ( $CV_A$ ) was calculated as:

$$CV_A = 100(\sigma_A/\mu)$$

where:  $\sigma_A$  is the additive genetic standard deviation, and  $\mu$  is the phenotypic mean for the trait.

The importance of the dominance variance was presented in two ways:

(i) dominance as a proportion of additive variance:

$$D_A = \sigma_D^2/\sigma_A^2, \text{ and}$$

(ii) dominance as a proportion of phenotypic variance:

$$D_p = \sigma_D^2/\sigma_p^2.$$

$D_A$  was used to assess the relative size of dominance to additive variance, and hence its contribution to the genetic variance. However, a high  $D_A$  may be inconsequential to a trait if the dominance variance is small compared with the phenotypic variance. Therefore,  $D_p$  was also calculated.

The standard errors of the heritability estimates were calculated using DFREML. At convergence, DFREML attempts to estimate the standard errors of heritability estimates by fitting a quadratic function to the likelihood surface using points evaluated during the search for the likelihood. As pointed out by MEYER (1993), little is known about the likelihood surface and the quadratic surface may not provide a good fit. Therefore, in order to get accurate confidence intervals for the heritability estimates from the pooled data, likelihood profiles were plotted by fixing the herita-

bility to different values, and the likelihood maximised with respect to all the other parameters. The 95% confidence interval was obtained by dropping 1.92 ( $0.5\chi^2_{1,0.05}$ ) from the maximum log likelihood (WETTERILL 1981).

Data pooled across sites were used for estimating genetic and phenotypic correlations. While for univariate analyses blocks were fitted as additional random effect, it was not possible to do so in the bivariate analyses because the programme restrictions allowed fitting only one extra random effect. This problem was overcome by pre-adjusting the data for the block effects before each bivariate analysis. The sampling errors of the genetic correlations were derived using the method of ROBERTSON (1959):

$$se(r_A) = \frac{(1-r_A^2)}{\sqrt{2}} \times \frac{\sqrt{se(h_1^2)se(h_2^2)}}{h_1 h_2}$$

where:  $se(r_A)$ ,  $se(h_1^2)$ ,  $se(h_2^2)$  are standard errors of the genetic correlation and heritability estimates for traits 1 and 2, respectively,  $h_1, h_2$  = square root of the heritability estimates for traits 1 and 2, respectively.

The formula by Robertson gives an approximate estimate of the standard error of the genetic correlation. Therefore, in order to get accurate confidence intervals for the genetic correlation estimates from the pooled data, likelihood profiles were plotted by fixing the genetic correlation to different values, and the likelihood maximised with respect to all the other parameters. Estimation of standard errors of genetic correlations in this way is computationally demanding, and therefore only a few likelihood profiles were plotted to verify the estimates from Robertson's formula.

## RESULTS

The overall means, standard deviation, coefficient of variation for height and straightness, and the number of trees at each site at each of the four ages are shown in Table 2.

### Variance components and heritability estimates

#### Individual sites analyses

The loglikelihood ratios (not presented) indicated that differences between models incorporating or omitting a common environment effect ( $Pt$ ) were not significant consequently, only results of the models for which the common environment effect was not fitted are reported for the individual site analyses.

The results from individual site analyses are represented in Tables 3 and 4 for height and stem straightness, respectively. For height, there was a large increase in all variances from age 1.5 to 9.5 years, with the additive variance peaking between 9.5 and 13.5 years, and the environment and dominance variances peaking at 13.5 years (Table 3). The additive variance for stem straightness peaked at 9.5 years at sites A and B, and that at C and D continued to increase with age (Table 4). For height, dominance variance (estimated from family variance component) was less than the corresponding additive variance ( $D_A < 1$ ), except at age 13.5 years in site D, indicating that additive variance was more important than dominance variance for this trait. In contrast, dominance was more important than additive variance for straightness, particularly at age 1.5 in three of the tests, where dominance was as much as 7 times greater than the additive variance. However, at this age  $D_p$  was less than 0.10, indicating that environmental effects were the major determinant of straightness at this age. The parameter  $D_p$  ranged from 0.002 to 0.30 for height and 0 to 0.45 for straightness, and there was no relationship between its magnitude and age for either trait.

The heritability estimates for height ranged from 0.14 to 0.73. Those for straightness generally ranged from 0.01 to 0.33, except for an unusually high estimate of 0.85 obtained at site C at 22.5 years of age

(Table 4). For each trait, estimates across the four sites at each assessment age are unlikely to be significantly different from each other, since their differences are less than two standard deviations, other than in the case of straightness at 22.5 years.

#### Analyses of data pooled across sites

Results of analyses of data pooled across the four sites are shown in Tables 5 and 6 for height and straightness, respectively. For height, additive variance and heritability peaked at 9.5 years, and the environment and dominance variances peaked at 13.5 years (Table 5). For straightness, the additive variance continued to increase with age (Table 6). Dominance variance was less than the corresponding additive variance ( $D_A < 1$ ) at all ages for height, and higher than additive variance at 1.5 years for straightness. The proportion of dominance to phenotypic variance was less than 0.12 for both traits.

The dominance and error variances estimated from fitting model 2 were lower than those estimated from fitting model 1, indicating that some of the common environment effects were confounded with the dominance and error variances. The additive variances

**Table 2. Overall means, standard deviations, coefficients of variation and numbers of trees for height and straightness at four sites and four ages.**

| Age (years) | Site | Height (m) |       |      | Straightness (score) |       |      | No of trees |
|-------------|------|------------|-------|------|----------------------|-------|------|-------------|
|             |      | Mean       | SD    | CV%  | Mean                 | SD    | CV%  |             |
| 1.5         | A    | 0.997      | 0.255 | 25.6 | 4.00                 | 0.600 | 15.0 | 4162        |
|             | B    | 1.13       | 0.291 | 25.8 | 3.85                 | 0.484 | 12.6 | 3557        |
|             | C    | 1.01       | 0.296 | 29.3 | 3.95                 | 0.540 | 13.7 | 2878        |
|             | D    | 0.704      | 0.227 | 32.2 | 3.59                 | 0.755 | 21.0 | 2907        |
| 9.5         | A    | 14.7       | 1.60  | 10.9 | 4.51                 | 0.682 | 15.1 | 1862        |
|             | B    | 12.1       | 1.68  | 13.9 | 4.64                 | 0.866 | 23.8 | 460         |
|             | C    | 14.8       | 1.73  | 11.7 | 4.42                 | 0.640 | 14.5 | 1381        |
|             | D    | 13.2       | 1.50  | 11.4 | 4.49                 | 0.740 | 16.5 | 1419        |
| 13.5        | A    | 19.4       | 2.68  | 13.8 | 3.91                 | 0.678 | 17.3 | 2101        |
|             | B    | 17.2       | 2.37  | 13.8 | 3.54                 | 0.746 | 21.1 | 1042        |
|             | C    | 19.9       | 2.01  | 10.1 | 4.68                 | 1.04  | 22.2 | 1260        |
|             | D    | 19.1       | 2.01  | 10.5 | 4.17                 | 0.800 | 19.2 | 1392        |
| 22.5        | A    | 22.5       | 1.92  | 8.53 | 4.27                 | 0.645 | 15.1 | 427         |
|             | B    | 24.2       | 2.00  | 8.26 | 6.66                 | 0.513 | 7.75 | 708         |
|             | C    | 24.5       | 1.42  | 5.80 | 4.75                 | 0.693 | 14.6 | 257         |
|             | D    | 25.1       | 1.49  | 5.94 | 5.89                 | 0.764 | 13.0 | 589         |

**Table 3. Estimates of variance components ( $m^2 \times 10^3$ ), importance of dominance variance and heritability (standard error) for height at four sites and four ages.**

| Age (years) | Site | $\sigma^2_A$ | $\sigma^2_D$ | $\sigma^2_E$ | $D_A$ | $D_P$ | $h^2$ (se) |
|-------------|------|--------------|--------------|--------------|-------|-------|------------|
| 1.5         | A    | 1.48         | 1.32         | 4.13         | 0.89  | 0.20  | 0.23(0.08) |
|             | B    | 2.68         | 0.751        | 4.54         | 0.28  | 0.09  | 0.32(0.09) |
|             | C    | 3.10         | 1.67         | 4.64         | 0.54  | 0.19  | 0.35(0.12) |
|             | D    | 0.729        | 0.290        | 4.10         | 0.40  | 0.06  | 0.14(0.05) |
| 9.5         | A    | 200          | 16.6         | 59.7         | 0.08  | 0.06  | 0.73(0.27) |
|             | B    | 116          | 49.1         | 138          | 0.42  | 0.17  | 0.41(0.14) |
|             | C    | 190          | 20.1         | 119          | 0.11  | 0.06  | 0.59(0.12) |
|             | D    | 93.7         | 51.1         | 121          | 0.55  | 0.22  | 0.39(0.13) |
| 13.5        | A    | 173          | 87.7         | 508          | 0.51  | 0.12  | 0.24(0.08) |
|             | B    | 173          | 60.6         | 296          | 0.35  | 0.11  | 0.32(0.11) |
|             | C    | 205          | 14.0         | 195          | 0.07  | 0.03  | 0.49(0.13) |
|             | D    | 93.2         | 122          | 268          | 1.31  | 0.30  | 0.23(0.11) |
| 22.5        | A    | 153          | 5.07         | 191          | 0.03  | 0.01  | 0.42(0.16) |
|             | B    | 105          | 65.19        | 209          | 0.62  | 0.16  | 0.26(0.11) |
|             | C    | 77.0         | 0.601        | 95.2         | 0.01  | 0.002 | 0.39(0.19) |
|             | D    | 86.7         | 16.4         | 90.6         | 0.19  | 0.08  | 0.40(0.13) |

**Table 4. Estimates of variance components ( $score^2 \times 10^3$ ), importance of dominance variance and heritability (standard error) for stem straightness at four sites and four ages.**

| Age (years) | Site | $\sigma^2_A$ | $\sigma^2_D$ | $\sigma^2_E$ | $D_A$ | $D_P$ | $h^2$ (se)  |
|-------------|------|--------------|--------------|--------------|-------|-------|-------------|
| 1.5         | A    | 0.540        | 0.790        | 32.6         | 1.46  | 0.02  | 0.02 (0.02) |
|             | B    | 0.260        | 2.04         | 22.1         | 7.85  | 0.09  | 0.01 (0.02) |
|             | C    | 2.22         | 0.550        | 25.5         | 0.25  | 0.02  | 0.08 (0.03) |
|             | D    | 1.17         | 1.50         | 53.6         | 1.28  | 0.03  | 0.02 (0.02) |
| 9.5         | A    | 11.6         | 1.76         | 30.9         | 0.15  | 0.04  | 0.25 (0.08) |
|             | B    | 16.2         | 0            | 54.0         | 0     | 0     | 0.22 (0.17) |
|             | C    | 6.49         | 0.720        | 32.5         | 0.11  | 0.02  | 0.16 (0.14) |
|             | D    | 9.80         | 15.9         | 40.5         | 1.62  | 0.29  | 0.18 (0.08) |
| 13.5        | A    | 7.51         | 0            | 38.5         | 0     | 0     | 0.16 (0.05) |
|             | B    | 9.78         | 11.2         | 36.6         | 1.15  | 0.20  | 0.18 (0.07) |
|             | C    | 30.3         | 0.080        | 78.6         | 0     | 0     | 0.27 (0.15) |
|             | D    | 15.3         | 7.09         | 48.5         | 0.46  | 0.11  | 0.23 (0.12) |
| 22.5        | A    | 6.77         | 18.8         | 28.6         | 2.78  | 0.45  | 0.16 (0.13) |
|             | B    | 8.67         | 4.46         | 15.1         | 0.51  | 0.17  | 0.33 (0.12) |
|             | C    | 50.0         | 20.2         | 1.12         | 0.40  | 0.34  | 0.83 (0.19) |
|             | D    | 18.9         | 5.72         | 34.1         | 0.30  | 0.10  | 0.32 (0.11) |

estimated by the two models were similar, as expected. This resulted in lower ratios of dominance and additive variance ( $D_A$ ) when model 2 was fitted.

The additive genetic coefficient of variation ( $CV_A$ ) for height decreased with age (Table 5), while that for straightness peaked at 13.5 years and appeared to remain constant thereafter (Table 6).

The heritability estimates for height peaked at 9.5 years. At 13.5 years, they decreased to the same level as that at 1.5 years and remained constant thereafter. The peak coincides with a peak in additive genetic variance and the low in dominance variance. The heritability estimates for straightness increased sharply between 1.5 and 9.5 years and again between 13.5 and 22.5 years,

**Table 5.** Estimates of variance components ( $m^2 \times 10^2$ ), importance of dominance variance, additive genetic coefficient of variation ( $CV_A$ ), and heritability (standard error) for height using data pooled across sites at each of the four ages.

| Age  | Model | $\sigma^2_A$ | $\sigma^2_D$ | $\sigma^2_E$ | $D_A$ | $D_p$ | AGCV | $h^2$ (se) |
|------|-------|--------------|--------------|--------------|-------|-------|------|------------|
| 1.5  | 1     | 1.73         | 0.540        | 4.98         | 0.31  | 0.07  | 14.0 | 0.24(0.07) |
|      | 2     | 1.74         | 0.239        | 4.47         | 0.14  | 0.07  | 14.0 | 0.24(0.11) |
| 9.5  | 1     | 139          | 29.0         | 121          | 0.21  | 0.10  | 8.62 | 0.50(0.15) |
|      | 2     | 140          | 23.3         | 112          | 0.17  | 0.08  | 8.66 | 0.50(0.12) |
| 13.5 | 1     | 130          | 55.1         | 380          | 0.42  | 0.10  | 6.04 | 0.24(0.06) |
|      | 2     | 128          | 45.4         | 364          | 0.35  | 0.08  | 6.00 | 0.24(0.08) |
| 22.5 | 1     | 73.5         | 37.5         | 195          | 0.51  | 0.12  | 2.98 | 0.24(0.08) |
|      | 2     | 71.5         | 28.6         | 168          | 0.40  | 0.09  | 2.94 | 0.23(0.07) |

**Table 6.** Estimates of variance components ( $score^2 \times 10^2$ ), importance of dominance variance, additive genetic coefficient of variation ( $CV_A$ ), and heritability (standard error) for stem straightness using data pooled across sites at each of the four ages.

| Age  | Model | $\sigma^2_A$ | $\sigma^2_D$ | $\sigma^2_E$ | $D_A$ | $D_p$ | AGCV | $h^2$ (se) |
|------|-------|--------------|--------------|--------------|-------|-------|------|------------|
| 1.5  | 1     | 0.345        | 1.29         | 34.00        | 3.74  | 0.04  | 1.53 | 0.01(0.01) |
|      | 2     | 0.341        | 0.86         | 33.13        | 2.53  | 0.02  | 1.51 | 0.01(0.01) |
| 9.5  | 1     | 5.43         | 5.80         | 41.80        | 1.07  | 0.12  | 5.46 | 0.11(0.04) |
|      | 2     | 5.31         | 4.30         | 38.56        | 0.76  | 0.08  | 5.40 | 0.11(0.04) |
| 13.5 | 1     | 5.98         | 1.89         | 58.20        | 0.32  | 0.03  | 5.99 | 0.09(0.01) |
|      | 2     | 5.94         | 0.95         | 55.76        | 0.16  | 0.01  | 5.97 | 0.09(0.03) |
| 22.5 | 1     | 9.52         | 3.63         | 30.40        | 0.38  | 0.09  | 5.74 | 0.21(0.07) |
|      | 2     | 9.43         | 2.97         | 26.46        | 0.31  | 0.07  | 5.71 | 0.21(0.08) |

but were comparable at 9.5 and 13.5 years. The results show no relationship between heritability and  $CV_A$  in either trait.

Heritability estimates for both traits from data pooled across sites were much lower than those estimated from individual sites. For example, heritability estimated for height from data pooled across sites at 22.5 years was 0.24, whereas that from individual sites ranged from 0.26–0.42. Similarly, heritability estimated from pooled data for straightness at 13.5 years was 0.09, while that from individual sites ranged from 0.16–0.27.

The log likelihood ratios (not presented) indicated that pooling data over sites at each age resulted in highly significant differences between the models, indicating that model 2, which included the common environment effect, better fitted the data.

All the log likelihood ratio tests for the difference between the joint likelihood and analyses of pooled

data across sites were significant (not presented), indicating heterogeneity of variance components or/and genotype  $\times$  environment interactions across sites.

In general, the likelihood profiles were not symmetrical, as assumed by the DFREML approximation, but their departure from symmetry was not great. This resulted in the confidence intervals from the loglikelihood profile being only slightly different from those estimated using DFREML which are presented in the standard errors.

### Genetic and phenotypic correlations

Results of analyses of pooled data over sites are shown in Table 7. Age-age genetic correlations for height were high, ranging from 0.76 to 0.97 with that between height assessed at very young age (1.5 years) and that assessed at near-maturity (22.5 years) being 0.76. As the age interval increased, the genetic correlations for

height decreased. The phenotypic correlations were lower than the genetic correlations (range, 0.21 to 0.80). In general, age-age genetic correlations for straightness were lower than those for height (range, –0.05 to 0.94) with those involving 1.5 years being lowest (range, –0.05 to 0.21). Phenotypic correlations for straightness were low to moderate (range, 0.02 to 0.55), and lower than genetic correlations. Genetic correlations between height and straightness were low to moderate (range, –0.28 to 0.66) with those involving straightness at 1.5 years being mostly negative. The highest correlation between height and straightness assessed at the same age was at 22.5 years (0.52); the highest correlation between ages was between height at 22.5 and straightness at 13.5 years (0.66). The other genetic correlations were below 0.45. Phenotypic correlations between height and straightness were also low (range, –0.19 to 0.48).

Two loglikelihood profiles were plotted for genetic correlations and, for both cases, the standard errors of the genetic correlations estimated using Robertson's formula were very similar to those estimated using the 2nd derivative of the loglikelihood. For example, the difference between the standard errors of the genetic correlation between straightness at 13.5 years and height at 22.5 years was only 0.02, with that estimated

using the Robertson's formula being lower. The loglikelihood profile was not symmetrical, although its departure from symmetry was not great. This resulted in the confidence interval from the loglikelihood profile being slightly different from that estimated using Robertson's formula.

## DISCUSSION

Despite the fact that this was the first reported use of the individual tree model in *P. taeda*, the heritability estimates for height were within the range reported previously for this species and consistent with those reported for other pine species (BARNES 1992a and b; COTTERILL *et al.* 1987; PSWARAYI *et al.* 1996). However, this is to be expected from results in early generations, and in the absence of information to correct for the effects of selection of parents. Here, heritability and additive variance for height increased with age from 1.5 years to 9.5 years, and then decreased with age. Although the trend differed from those observed by FRANKLIN (1979) and FOSTER (1986) in *P. taeda*, it agreed well with that reported by BALOCCHI *et al.* (1993), who found heritability peaking at 14 years of age in a slower growing *P. taeda* progeny test. While this study and that of BALOCCHI *et al.* (1993) differ in

**Table 7. Estimated genotypic and phenotypic correlations and heritability estimates for height and straightness, from data pooled across sites and based on analysis by bivariate individual tree model DFRML. (Genetic correlations are below the diagonal, phenotypic correlations are above diagonal, and heritability estimates on the diagonal. Standard errors of the genetic correlations are in the parentheses.)**

|         | HT 1.5          | HT 9.5          | HT 13.5         | HT 22.5        | ST 1.5          | ST 9.5         | ST 13.5        | ST 22.5     |
|---------|-----------------|-----------------|-----------------|----------------|-----------------|----------------|----------------|-------------|
| HT 1.5  | <b>0.22</b>     | 0.48            | 0.31            | 0.21           | 0.27            | 0.06           | 0.12           | 0.06        |
| HT 9.5  | 0.93<br>(0.03)  | <b>0.50</b>     | –               | –              | 0.09            | 0.01           | 0.48           | –0.19       |
| HT 13.5 | 0.85<br>(0.07)  | 0.96<br>(0.01)  | <b>0.22</b>     | 0.80           | 0.09            | 0.35           | 0.33           | 0.19        |
| HT 22.5 | 0.76<br>(0.10)  | 0.85<br>(0.05)  | 0.97<br>(0.01)  | <b>0.26</b>    | 0.05            | –0.04          | 0.16           | 0.21        |
| ST 1.5  | –0.08<br>(0.48) | –0.28<br>(0.32) | –0.17<br>(0.34) | 0.04<br>(0.36) | <b>0.01</b>     | 0.06           | 0.06           | 0.02        |
| ST 9.5  | 0.14<br>(0.28)  | 0.13<br>(0.21)  | 0.17<br>(0.21)  | 0.36<br>(0.19) | 0.20<br>(0.41)  | <b>0.12</b>    | –              | –           |
| ST 13.5 | 0.38<br>(0.24)  | 0.45<br>(0.16)  | 0.25<br>(0.19)  | 0.66<br>(0.12) | 0.11<br>(0.40)  | 0.94<br>(0.03) | <b>0.09</b>    | 0.55        |
| ST 22.5 | 0.14<br>(0.28)  | 0.22<br>(0.20)  | 0.28<br>(0.20)  | 0.52<br>(0.16) | –0.05<br>(0.43) | 0.66<br>(0.15) | 0.92<br>(0.04) | <b>0.20</b> |

the age of maximum heritability, the estimates were maximum at the same mean height, suggesting a possible link between mean height and heritability estimate. This is consistent with findings of BORRALHO *et al.* (1992a), but contrasts with results reported by BORRALHO *et al.* (1992b) who found no relationship between trends in heritability estimates for height and growth rate in *Eucalyptus globulus*. The change in heritability in long rotation crops such as tree is not surprising since genes involved in growth may change with age (NAMKOONG *et al.* 1988), and these changes may be related to different growth phases (FRANKLIN 1979). In animals, this change in heritability with age was also attributed to the fact that the trait may change genetically with age (VISSCHER *et al.* 1991), and is probably related to different growth phases as reported for trees. These growth phases might be due to changing influences of maternal effects in animals and to a lesser extent in trees and to nursery or competition effects in trees. Changes in heritability with age here may also be attributed to thinning and other management practices.

There are few published estimates of variance components and heritability for straightness in conifers, and it appears that this is the first time that trends of heritability for straightness up to near-rotation age in *P. taeda* has been reported. The results from this study indicated that there was very little evidence of additive or dominance variance for straightness at 1.5 years, suggesting that environment effects were the major determinant of straightness at this age. This can be attributed to large measurement error because straightness is difficult to score at a young age. Also, trees at this young age are likely to be more affected by environmental variation, resulting in lower heritability estimates than at older ages. The high heritability estimates for straightness at 22.5 years, and the low estimates at 1.5 years, appear to indicate that stem straightness might be easier to measure on large trees than on small ones, an observation also made by DEAN (1990). Heritability estimates for straightness in this study increased with age, a trend also reported by SHELBORNE & STONECYPHER (1971) in *P. taeda*, although their estimates were much higher. In general, the estimates of heritability of stem straightness were lower than those of height. Parameter estimates for stem straightness in the literature are variable: some heritability estimates for straightness in conifers have been higher than those for height (eg. MATZIRIS & ZOBEL 1973), whereas others have been lower (COTTERILL *et al.* 1987; BARNES 1992a and b; PSWARAYI *et al.* 1996; RAYMOND & COTTERILL 1990) or equivalent (BURDON *et al.* 1992). Estimates depend on how straightness was measured COTTERILL *et al.* 1987;

RAYMOND & COTTERILL 1990), with those originating from use of an absolute scale, as in this study, lower than those originating from a site specific scale. The low estimates reported in this study are consistent with those reported by BARNES (1992a and b) and PSWARAYI *et al.* (1996) using the same absolute scale with *P. patula* and *P. elliottii*, respectively. Major problems related to the use of the relative scale are that if a trait is poorly expressed at a site this method will indicate large genetic differences, when in fact they are absent, as reported by WILLIAMS and LAMBETH (1989), and results are not comparable across sites adversely affecting deployment decisions. The relative scale has not been used in Zimbabwe, and its use needs investigation especially because heritabilities originating from it are reported to be higher. The relative scale could be modified, possibly using controls over sites, so that results across sites are comparable.

The variance components and heritability estimates presented from data pooled over sites showed evidence of heterogeneity of variance over sites. Heritability estimates were more accurately estimated from pooled data because they were estimated from a larger sample, as evidenced by the smaller standard errors associated with them. The lower heritability estimates from pooled data imply that predicted gain would be less than that from the individual site estimates. Therefore, estimates from the pooled data will only be used subsequently in BLUP evaluation after correcting for heterogeneity of variances if there are no genotype  $\times$  environment interactions (GE) using appropriate methods such as that described by VISSCHER *et al.* (1991). However, if GE is present, and it is due to rank changes as preliminary results on these data indicate (GWAZE unpublished), combining the data as in the pooled analyses will remain inappropriate. However, even within a region, one should expect GE and the heritability estimated from data pooled across sites may yield results that are appropriate for commercial progress within a region. Furthermore, breeding values estimated from a single site are not as precise as those from the pooled data.

The ratio of dominance to additive variance for height was less than one at all ages in the pooled analysis, indicating that dominance variance was of lesser importance. These ratios differed from those of BALOCCHI *et al.* (1993) and FOSTER & BRIDGWATER (1986), who reported dominance variance to be considerably higher than additive variance at young ages (less than 6 years) in *P. taeda*. The ratios were consistent with those reported for *P. elliottii* grown in Zimbabwe (PSWARAY *et al.* 1996). For straightness, dominance variance was much greater than additive variance at 1.5 years; thereafter the relationship was reversed. The

pattern of the ratios in straightness differed from those reported by PSWARAY *et al.* (1996), who found dominance to be less than additive variance at 5 and 15 years of age but more than the additive variance at 8 years of age. Excluding the plot term from the model resulted in inflated estimates of dominance variance, but the heritability estimates and their standard errors were not sensitive to inclusion of plot effects in the model. This is because family groups were planted within single plots at each site.

All age-age genetic correlations estimated for height using pooled data were high indicating that early selection in *P. taeda* in Zimbabwe will be effective. Age-age genetic correlations estimated for height are in close agreement with estimates reported by LAMBETH *et al.* (1983) and MCKEAND (1988) for *P. taeda*, and BARNES (1992a and b) and PSWARAY *et al.* (1996) for other pine species in Zimbabwe. FOSTER (1986), FRANKLIN (1979) and WILLIAMS & MEGRAW (1994) reported weak genetic correlations (less than 0.4) between height at ages younger than three years and ages older than 12 years from *P. taeda* genetic tests in the USA. The results of the present study show an opportunity for selecting at a very young age (1.5 years). However, it may not be possible to take advantage of early selection because the species only starts flowering at age 10 years in Zimbabwe (GWAZE *et al.* 1996). However, if *P. taeda* were to be induced to flower at 3 years, selections could be carried out at 3 years of age (GWAZE *et al.* 1996). The difference between age-age genetic correlations from this study and those from USA genetic tests may be a consequence of management and methodological differences.

In some reports, family mean correlations were used as approximations of genetic correlations (e.g. MCKEAND 1988). Family mean correlations are likely to underestimate genetic correlations because the components of family mean correlation are (NAMKOONG *et al.* 1988):

$$r_{F1,F2} = \frac{COV_{A(1,2)} + COV_{e1,e2}}{\sqrt{\sigma_{A1}^2 + \sigma_{e1}^2} \sqrt{\sigma_{A2}^2 + \sigma_{e2}^2}}$$

where  $\sigma_A^2$  = additive variance and  $\sigma_e^2$  = error variance of family means,  $COV_{A(1,2)}$  = additive covariance and  $COV_{e1,e2}$  = error covariances. While the error covariance can be zero, the error variance is rarely zero, thereby biasing the genetic correlation downwards. Also, the error variance may contain dominance effects in the case of full sib-families, thereby increasing the bias in the genetic correlation estimate. For example, LAMBETH *et al.* (1983) found that the family mean correlations were less than corresponding genetic correlations by as much as 35%. In other studies, genetic tests were not thinned

at random (i.e. the best trees were retained; e.g. LAMBETH *et al.* 1983), while the Zimbabwe tests received a systematic thinning. This non-random thinning could also lead to biased estimates of genetic parameters. It has also been suggested that growth rates might affect the genetic correlations, with lower genetic correlations between any two ages in fast growing material (MAGNUSSEN 1988), perhaps as a consequence of slower physiological changes in slower growing trees leading to the expression of more similar genes at any two ages than for faster growing trees. The growth rates of trees in the Zimbabwe tests were higher than those in the USA tests. Under this hypothesis, genetic correlations from the Zimbabwe tests may be expected to be lower, but the opposite was true. Hence, differences in growth rates are unlikely to explain the differences in the genetic correlations reported here and those reported for *P. taeda* grown in USA.

Age-age genetic correlations for height were higher than their corresponding phenotypic correlations, which is consistent with other studies in *P. taeda* (LAMBETH *et al.* 1983) and in other pine species (BARNES 1992a and b; PSWARAY *et al.* 1996; RIEMENSCHNEIDER 1988). Therefore, assuming genetic correlations are similar to their corresponding phenotypic correlations as suggested by LAMBETH (1980) would result in less predicted gain and conservative prediction on optimum selection age in *P. taeda* (GWAZE *et al.* 1996).

Age-age genetic correlations for straightness between 1.5 years and older ages were very low, which could partly be explained by the fact that this trait is difficult to measure at a young age. Genetic correlations between straightness at older ages were moderate to high, indicating that early selection at ages 9.5 or older in this trait will result in improvement in straightness at rotation age. Results of this study are consistent with those reported by PSWARAY *et al.* (1996), and suggest that it might not be appropriate to consider straightness scores at different ages as repeated records; rather, they should be considered as different traits. The repeatability model assumes that the traits are genetically similar, and that variances across ages are equal and heritabilities are equal, which appears not to have been the case here.

Genetic correlations between height and straightness were generally low and positive, except those involving straightness at 1.5 years, presumably for reasons discussed above. Selection on height alone should result in improvement in straightness at rotation age. There appear to be no reports in the literature of genetic correlations between height and straightness in *P. taeda*. Those reported here were lower than those reported by COTTERRILL *et al.* (1987) and PSWARAY *et al.* (1996), and higher than those reported by BARNES

et al. (1992a, b), for other pine species in Southern Africa.

## CONCLUSION

The study has indicated that height is under moderate genetic influence, which peaked at 9.5 years, while straightness is under very weak genetic influence at very young ages, increasing to moderate levels with age. Dominance variance was less than additive variance for either height or straightness. The variance components and heritability estimates estimated from data pooled over sites showed evidence of heterogeneity of variances over sites.

High genetic correlations between heights at young ages and that at mature age indicate an opportunity for early selection in *P. taeda* in Zimbabwe. However, late flowering may pose a critical barrier to breeding of this species at an early age in Zimbabwe.

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## REFERENCES

- BALOCCHI, C. E., BRIDGWATER, F. E., ZOBEL, B. J. & JAHROMI, S. 1993: Age trends in genetic parameters for tree height in a nonselected population of loblolly pine. *For. Sci.* **39**:231–251.
- BARNES, R. D., MULLIN, L. J. & BATTLE, G. 1992A: Genetic control of fifth year traits in *Pinus patula* Schiede and Deppe. *Silvae Genetica* **41**:242–248.
- BARNES, R. D., MULLIN, L. J. & BATTLE, G. (1992B): Genetic control of eighth year traits in *Pinus patula* Schiede and Deppe. *Silvae Genetica* **41**:318–325.
- BARRETT, R. L. & MULLIN, L. J. 1968: A review of introductions of forest trees in Rhodesia. Rhodesia Bulletin of Forestry Research no. 1, 227pp.
- BORRALHO, N. M. G., COTTERILL, P. P. & KANOWSKI, P. J. 1992a: Genetic control of growth of *Eucalyptus globulus* in Portugal. II. Efficiencies of early selection. *Silvae Genetica* **41**:70–77.
- BORRALHO, N. M. G., KANOWSKI, P. J. & COTTERILL, P. P. 1992b: Genetic control of growth of *Eucalyptus globulus* in Portugal. 1. Genetic and phenotypic parameters. *Silvae Genetica* **41**:39–45.
- BORRALHO, N. M. G., JARVIS, S. F. & POTTS, B. M. 1995: Multivariate restricted maximum likelihood estimation of genetic parameters for diameter at 3 to 5 years in *Eucalyptus globulus* base population in Australia. In: Eucalypt plantations: Improving fibre yield and quality. (eds. B. M. Potts, N. M. G. Borralho, J. B. Reid, R. N. Cromer, W. N. Tibbits and C. A. Raymond: pp. 230–232. Proc. CRC-IUFRO Conf., Hobart, 19–24 Feb. CRC for Temperate Hardwood Forestry: Hobart.
- BRIDGWATER, F. E. & STONECYPHER, R. W. 1979: Index selection for volume and straightness in a loblolly pine population. In: Proceedings of the 15th Southern Conference on Forest Tree Improvement, Mississippi State University, pp. 132–139.
- BURDON, R. D., BANNISTER, M. H. & LOW C. B. 1992: Genetic survey of *Pinus radiata*. 3. Variance structures and narrow-sense heritabilities for growth variables and morphological traits in seedlings. *N. Z. J. For. Sci.* **22**:160–186.
- COTTERILL, P. P., DEAN, C. A. & WYK, VAN G. 1987: Additive and dominance genetic effects in *Pinus pinaster*, *P. radiata* and *P. elliotii* and some implications for breeding strategy. *Silvae Genetica* **36**:221–232.
- DEAN, C. A. 1990: Genetics of growth and wood density in radiata pine. Unpublished PhD thesis, University of Queensland, Australia, 78 pp.
- FOSTER, G. S. 1986: Trends in genetic parameters with stand development and their influence on early selection for volume growth in loblolly pine. *Forest Science* **32**:944–959.
- FOSTER, G. S. & BRIDGWATER, F. E. 1986: Genetic analysis of fifth-year data from a seventeen parent partial diallel of loblolly pine. *Silvae Genetica* **35**:118–122.
- FRANKLIN, E. C. 1979: Model relating levels of development of four north American conifers. *Silvae Genetica* **28**:207–212.
- GWAZE, D. P., WOOLLIAMS, J. A. AND KANOWSKI, P. J. 1996: Predicted genetic gain in height in 23-year old progeny tests of *Pinus taeda* L. in Zimbabwe, and inferences for the optimum age of selection. In: Tree Improvement for Sustainable Tropical Forestry, (eds. Dieters, M. J., Matheson, A. C., Nikles, D. G., Harwood, C. E. and Walker, S. M.: pp. 133–137. Proc. QFRI-IUFRO Conf., Caloundra, Queensland, Australia, 27 October – 1 November, 1996 (Queensland Forestry Research Institute, Gympie).
- LAMBETH, C., VAN BUIJTENEN, J. P., MCCOLLOUGH, R. B. & DUKE, S. D. 1983: Early selection is effective in 20-year-old genetic tests of loblolly pine. *Silvae Genetica* **32**:210–215.
- MAGNUSSEN, S. 1988: Minimum age-to-age correlations in early selections. *For. Sci.* **34**:928–938.
- MATZIRIS, D. I. & ZOBEL, B. J. 1973: Inheritance and correlations of juvenile characteristics in loblolly pine (*Pinus taeda* L.: *Silvae Genetica* **22**:38–45.
- MCKEAND, S. E. 1988: Optimum age for family selection for growth in genetic tests of loblolly pine. *For. Sci.* **34**:400–411.
- MEYER, K. 1989: Restricted maximum likelihood to estimate variance components for animal models with several random effects using a derivative-free algorithm. *Genet. Sel. Evol.* **21**:317–340.
- MEYER, K. 1993: DFREML version 2.1. Programs to estimate variance component by restricted maximum likelihood using a derivative free algorithm. User notes. Animal genetics and breeding unit, University of New England, Armidale, NSW, Australia (Mimeo), 101pp.
- NAMKOONG, G., KANG, H. C. & BROUARD, J. S. 1988: Tree breeding: principles and strategies, Springer-Verlag, New

- York, 180pp.
- PSWARAYI, I. Z., BARNES, R. D., BIRKS, J. S. & KANOWSKI, P. J. 1996: Genetic parameter estimates for production and quality traits of *Pinus elliottii* Engelm. var. *elliottii* in Zimbabwe. *Silvae Genetica* **45**:216-222.
- RAYMOND, C. A. & COTTERILL, P. P. 1990: Methods of assessing crown form in *Pinus radiata*. *Silvae Genetica* **39**:67-71.
- RIEMENSCHNEIDER, D. E. 1988: Heritability, age-age correlations, and inferences regarding juvenile selection in jack pine. *For. Sci.* **34**:1076-1082.
- ROBERTSON, A. 1959: The sampling variance of the genetic correlation coefficient. *Biometrics* **15**:469-485.
- SHARMA, N. P., ROWE, R., OPENSHAW, K. & JACOBSON, M. 1992: World forests in perspective. In: *Managing the world's forests: Looking for balance between conservation and development.* (ed. N. P. Sharma: pp. 17-31. Kendall/Hunt publishing company, Iowa.
- SHELBOURNE, C. J. A. & STONECYPHER, R. W. 1971: The inheritance of bole straightness in young loblolly-pine. *Silvae Genetica* **20**:151-156.
- VISSCHER, P. M., THOMPSON, R. & HILL, W. G. 1991: Estimation of genetic and environmental variances for fat yield in individual herds and an investigation into heterogeneity of variance between herds. *Livestock Production Science* **78**:273-290.
- WETHERILL, G. B. 1981: *Intermediate Statistical Methods.* Chapman and Hall Ltd, London, 390 pp.
- WILLIAMS, C. G. & LAMBETH, C. C. 1989: Bole straightness measurement for advanced-generation loblolly pine genetic tests: 20 years of results. *Silvae Genetica* **38**:212-217.
- WILLIAMS, C. G. & MEGRAW, R. A. 1994: Juvenile-mature relationships for wood density in *Pinus taeda*. *Can. J. For. Res.* **24**:714-722.