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Optimum Selection Age for Height in *Pinus taeda* L. in Zimbabwe

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Summary

Four progeny tests of *P. taeda* L. planted in the Eastern Highlands of Zimbabwe were assessed for height at 1.5, 9.5, 13.5, and 22.5 years. Age-age genetic correlations were all positive and high (0.76 to 0.97), with low to moderate standard errors (0.01 to 0.10). Genetic correlations were always higher than corresponding phenotypic correlations. Two linear models were fitted, by regressing genetic correlation on (1) the natural logarithm of the ratio of the younger age to the older age (LAR), and on (2) age difference. The age difference model fitted the data better than LAR model, indicating that the commonly used logarithm models are not necessarily the most appropriate. Predictions of genetic correlations by models based on genetic correlation were more accurate than those estimated using the common model based on phenotypic correlation. Where flowering age was assumed to be 10 years, either genetic or phenotypic models predicted annual genetic gain to be greatest at 10 years. However, the phenotypic model underestimated genetic gain at all ages-particularly at very young ages, for which the potential gain was less than a quarter of that predicted by the other models. When flowering age was reducing to 3 years, optimum selection age under the phenotypic model was 6 years, but was reduced to 3 years using the genetic models. Reducing flowering age to 3 years increased annual genetic gain by 100%, indicating the potential of artificially inducing flowering for enhancing genetic progress with *P. taeda* in Zimbabwe.

Key words: Genetic correlation, phenotypic correlation, genetic gain, optimum selection age, *Pinus taeda*.

FDC: 165.3; 165.6; 174.7 *Pinus taeda*; (689.1).

Introduction

Pinus taeda Linnaeus is a major exotic plantation species in Zimbabwe and other southern African countries. Breeding of *P. taeda* in Zimbabwe began in 1958 (BARRET and MULLIN, 1968) and the most comprehensive progeny tests were established in the 1970s.

Forest trees have long generation intervals. Early selection is preferred, as it results in an increased gain per unit of time through reduced generation intervals and may lead to reduced testing costs (MAGNUSSEN, 1988). Such early selection is necessarily indirect and offers the means for quicker incorporation of gains into production as parents to be used for multiplication can be selected early and seed orchards or propagation hedges can be culled early.

Optimum selection age is usually defined as the age at which annual genetic gain of breeding cycle is maximized and it is critical to the efficiency of any tree breeding program. Thus, identification of the optimum age for early indirect selection has been of major interest to tree breeders (e.g. BALLOCHI *et al.*, 1993; KING and BURDON, 1991; MCKEAND, 1988; RIEMEN-

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Schneider, 1988; Xie and Ying, 1996). Unfortunately, traits are rarely measured at all ages up to harvest. Therefore, optimum selection age can only be estimated using models which make it possible to predict genetic correlations between ages other than those at which assessments were made. This has resulted in the development of predictive models for genetic correlations. Lambeth (1980) used phenotypic correlations as an approximation to genetic correlations and showed that such correlations between heights at different ages were predictable, based on the natural logarithm of the ratio of the younger and the mature age (LAR). He suggested that age-age genetic correlations were approximately equal to corresponding phenotypic correlations and therefore that phenotypic correlations could be used in place of corresponding genetic correlations. These logarithm-based models have been widely used by tree breeders to make decisions on optimum selection age (e.g. King and Burdon, 1991; McKeand, 1988; Riemenschneider, 1988; Xie and Ying, 1996). There is increasing evidence to demonstrate that genetic correlations are much higher than corresponding phenotypic correlations (Barnes *et al.*, 1992a and b; Lambeth *et al.*, 1983; Pswarayi *et al.*, 1996; Riemenschneider, 1988), implying that the phenotypic model underestimates genetic correlations and hence genetic gain. The economic consequences of not estimating optimum ages efficiently may be high in long rotation forest trees, and the phenotypic model has not been tested using data from pines grown in tropical regions. Therefore, choice of model for predicting genetic correlations is critical for efficiently predicting gain and optimum selection age.

One of the problems with estimates of age-age genetic correlations for growth traits is that assessments of genetic tests are carried out before maturity (harvest age) and mostly at less than half harvest age. For example, Riemenschneider (1988) used age-age genetic correlations from tests assessed up to 7 years in *P. banksiana*, Matheson *et al.* (1994) used correlations for up to 14 years of age in *P. radiata*, and McKeand (1988) used correlations for up to 16 years in *P. taeda*. Therefore, the genetic correlations involving mature age trait are extrapolations. The assumption that a linear relationship holds outside the range of the data may not be true; therefore, data that involve the trait at harvest age is preferred.

A constant heritability has been used in predicting the optimum age for selection in *P. taeda* (Lambeth, 1980; Gonzalez and Richards, 1988), but evidence suggests that heritability estimates for tree height in *P. taeda* increase with age, at least up to half mature age (Balocchi *et al.*, 1993; Franklin, 1979). Therefore, erroneously assuming heritability is constant could overestimate gain from early selections and may also affect estimates of the optimum age for selection.

One of the major factors that influences the generation interval, and hence optimum selection age, is the age at which the species becomes sexually mature and produces seed. For example, *P. taeda* in Zimbabwe flowers at 10 years of age (Barnes[4]), personal communication). Artificial induction of flowering in *P. taeda* has been successful in the USA, with flowering achieved at less than 3 years of age (Burris *et al.*, 1991; Bramlett *et al.*, 1995).

Although there are estimates of optimum selection age in *P. taeda* (Newman and Williams, 1991; Ballochi *et al.*, 1993), there appear to be no estimates of genetic gain and optimum selection age for height in *P. taeda* grown in the tropics. This is an issue of concern, as fast-growing tree crops do not exhibit the same genetic correlations as those that are slower growing at similar ages (Magnussen, 1988). Given that growth rates of *P. taeda* in the tropics can be substantially higher than those achieved in temperate regions, potential genetic gain and the optimum selection age may differ between these regions.

The objective of this paper is to estimate annual genetic gain and optimum selection age for height in *P. taeda* in the tropics using tests assessed up to near-harvest age. The effects of using different models for predicting age-age genetic correlations, taking into account age-related changes of heritability and of reducing the flowering age (and hence generation interval), were also explored here. Selection was based on height because it is a good predictor of volume at rotation age (Foster, 1986; Lambeth *et al.*, 1983), because heritability for height is higher than that for diameter in *P. taeda* (Foster, 1986) and because height is more easily and more accurately assessed at young ages than are diameter or volume. Furthermore, models exist for predicting age trends of age-age genetic correlations for height.

Materials and Methods

Data

The data arise from four progeny tests planted in 1972 in the Eastern Highlands of Zimbabwe. Full details of the tests are described by Gwaze *et al.* (in press). Briefly, the tests consisted of 140 full-sib families derived from an incomplete factorial mating design involving 8 male and 15 female parents. The 23 parents were selected from unimproved plantations in Zimbabwe and South Africa. Trees were planted at 2.4 m x 2.4 m spacing and each plot comprised ten trees. Each test 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 randomly with respect to measured traits.

The tests were assessed for height (HT) at 1.5, 9.5, 13.5 and 22.5 years (harvest age = 25 years). Assessments at 1.5, 13.5, and 22.5 years were made on standing trees; that at 9.5 years was made on the trees removed in thinning.

Statistical analyses

The heritabilities were estimated as described by Gwaze *et al.* (in press). Briefly, they ranged from 0.22 to 0.50, and peaked at 9.5 years. Genetic and phenotypic correlations were estimated using an individual tree bivariate model DFREML (Meyer, 1989). The general bivariate model was:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \end{bmatrix} + \begin{bmatrix} W_1 & 0 \\ 0 & W_2 \end{bmatrix} \begin{bmatrix} c_1 \\ c_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix} \tag{1}$$

where: y_1, y_2 = the vector of observations for traits 1 and 2, respectively,

b_1, b_2 = the vector of fixed effects for traits 1 and 2, respectively,
a_1, a_2 = the vector of random tree (additive genetic) effects for traits 1 and 2, respectively,
c_1, c_2 = the vector of additional uncorrelated random effects for traits 1 and 2, respectively,
X_1, X_2 = the incidence matrix for fixed effects for traits 1 and 2 respectively,
W_1, W_2 = the incidence matrix for additional random effects for traits 1 and 2, respectively.
Z_1, Z_2 = the incidence matrix for additive direct effects for traits 1 and 2, respectively,
e_1, e_2 = the vector of residual effects for traits 1 and 2, respectively.

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Site and replicate were considered as fixed effects, and full-sib family as the uncorrelated random effect. For reasons of software restrictions, preadjusted data for block effects were used for the analyses. Sampling errors of the genetic correlations were derived using the formula of ROBERTSON (1959) after verification using likelihoods of a subset,

$$se(r_A) = \frac{(1-r_A^2)}{\sqrt{2}} \times \frac{\sqrt{se(h_x^2)se(h_y^2)}}{h_x h_y} \qquad (2)$$

where:

$se(r_A)$, $se(h^2_x)$, $se(h^2_y)$ are standard errors of the genetic correlation and heritability estimates for traits x and y, respectively,
h_x, h_y = square root of the heritability estimates for traits x and y, respectively. Several results from using this formula were compared to confidence intervals obtained from the likelihood surface and were found to give reasonable values (GWAZE *et al.*, in press). Age-age genetic correlations for height were modelled using three models. Model 1 is that derived by LAMBETH (1980), in which r_p is assumed to equal r_g, and r_p predicted by:

$$r_P = 1.02 + 0.308 \log_e(\text{younger age/older age}). \qquad (3)$$

The equality of r_p and r_g was removed to derive Model 2:

$$r_g = \beta_0 + \beta_1 \log_e(\text{younger age/older age}) \qquad (4)$$

where β_0, β_1 were derived from estimates of r_g at 1.5, 9.5, 13.5 and 22.5 years. Model 3 was derived as for Model 2, but age difference was used as predictor:

$$r_g = \beta_0 + \beta_1 (\text{Age difference}). \qquad (5)$$

Rather than deriving a prediction model for heritability (e.g. WEI and BORRALHO, 1996), or predicting heritability estimates for ages at which assessments were not taken through linear interpolation between two assessment ages (e.g. MCKEAND, 1988), smoothing was carried out using cubic splines available in Genstat (Genstat 5 Committee, 1987). Deriving a model with only four points in this study was considered impractical; linear interpolation was not used because the age-trend of heritability estimates in our data was non-linear.

Annual genetic gain from mass selection was calculated for direct selection at rotation age (assumed to be 22.5 years) and for indirect selection at younger ages. Annual gain from direct selection for trait y was given by (FALCONER, 1989):

$$Gain_y = i_y h_y^2 \sigma_{py} L_y^{-1} \qquad (6)$$

and annual gain of trait y from indirect selection on trait x is given by:

$$Gain_y = i_x h_x h_y r_A \sigma_{py} L_x^{-1} \qquad (7)$$

where:

Gain_y = annual gain for trait y,
r_A = genetic correlation,
h_x, h_y = square root of individual tree heritability for traits x and y, respectively,
i_x, i_y = selection intensity for traits x and y, respectively, where selection intensity at 1 to 9 years was 2.665 (1:100), at 10 to 14 years 2.421 (1:50) and that at 15 and older 2.154 (1:25) in all traits,
σ_{py} = phenotypic standard deviation for trait y (1.732 m for height, and 0.650 m for straightness; GWAZE, *in prep.*),
L_x, L_y = generation interval for selection on traits x and y, respectively.

It was assumed that it takes three years to establish genetic tests for the next generation once the trees are in flower. Since *P. taeda* flowers at age 10 in Zimbabwe, the generation interval for selecting at ten years or younger was flowering age + 3 years (13 years), while that for selection at older ages was selection age + 3 years. Gain and optimum selection age were also estimated assuming that selected trees could be induced to flower at 3 years of age, as has been achieved for *P. taeda* in the USA (BURRIS *et al.*, 1991; BRAMLETT *et al.*, 1995). In this case, the generation interval for selecting at 3 years or younger was 6 years, while those at older ages were selection age + 3. Initially, heritability was assumed to be constant with age (0.2); subsequently, changes in heritabilities estimated using smoothing cubic splines were taken into account in calculating gain and estimating optimum selection age.

Results

Data parameters

Heritability estimates were similar at all ages (0.22 to 0.26), apart from that at age 9.5 which was substantially higher (0.50). Age-age genetic correlations for height were high, ranging from 0.76 to 0.97 (*Table 1*) and their standard errors were low (0.01 to 0.10). Low standard errors were associated with high genetic correlations. Phenotypic correlations were lower than corresponding genetic correlations (range, 0.31 to 0.80). As the age differential increased, both the genetic and phenotypic correlations decreased. Phenotypic correlations between height at age 9.5 years and the two older ages were not available since height was assessed on thinned trees at age 9.5 years.

Table 1. – Genetic and phenotypic parameter estimates for height assessed at 4 different ages, from bivariate individual tree models fitted using DFREML on data pooled across sites. Genetic correlations below diagonal, phenotypic correlations above diagonal, and heritability estimates on diagonal. Standard errors of the genetic correlations are in parentheses.

Age (years)	1.5	9.5	13.5	22.5
1.5	**0.22**	0.48	0.31	0.21
9.5	0.93 (0.03)	**0.50**	–	–
13.5	0.85 (0.07)	0.96 (0.01)	**0.22**	0.80
22.5	0.76 (0.10)	0.85 (0.05)	0.97 (0.01)	**0.26**

Comparison of models and prediction of heritability trend

Details of the results of fitting age-age genetic and phenotypic models are presented in *table 2*. The intercepts for Model 2 and 3 were not one and this might be attributed to random measurement errors. Since the genetic correlations between

Table 2. – Summary of results of fitting age-age genetic correlation linear models for height in *P. taeda*.

Type of Model	Regression coefficient		Residual	df	R^2
	Intercept±sd	Slope±sd	mean square		
Model 1	1.02	0.308			
Model 2	0.98±0.044	0.065±0.026	0.0032	4	0.61
Model 2 (constrained)	1	0.076±0.013	0.0028	5	
Model 3	1.03±0.031	-0.013±0.003	0.0011	4	0.87
Model 3 (constrained)	1	-0.011±0.001	0.0011	5	

height assessed at the same age can be expected, on statistical grounds, to be one, the regression models were forced to have a constant equal to 1, and the constrained models are also given in *table 2*.

For Model 2, constraining the genetic correlations between height assessed at the same age to be 1 resulted in a fit which was not significantly different from the unconstrained one (i. e. $\beta_0 = 1$, $P > 0.05$). The estimated regression slope for Model 2 was flatter than that of Model 1. As a result, predictions of the genetic correlations from Model 1 declined more rapidly than those from Model 2 as age differential increased (*Figure 1*). The good fit with Model 2 would be expected as it is obtained from the data presented, but the large divergence between the observed and predictions from the Model 1 is clear, particularly for genetic correlations involving 1.5-year height assessment (*Figure 1* and *Table 3*).

Model 3, in which the age difference is the predictor of genetic correlation, fitted the data better than when using logs of age ratio (Model 2), with a lower residual mean square and a higher R^2 (*Table 2* and *Figure 2*). For model 3, constraining the genetic correlations between height assessed at the same age to be 1 resulted in a fit which was not significantly different from the unconstrained one (i. e. $\beta_0 = 1$, $P > 0.05$).

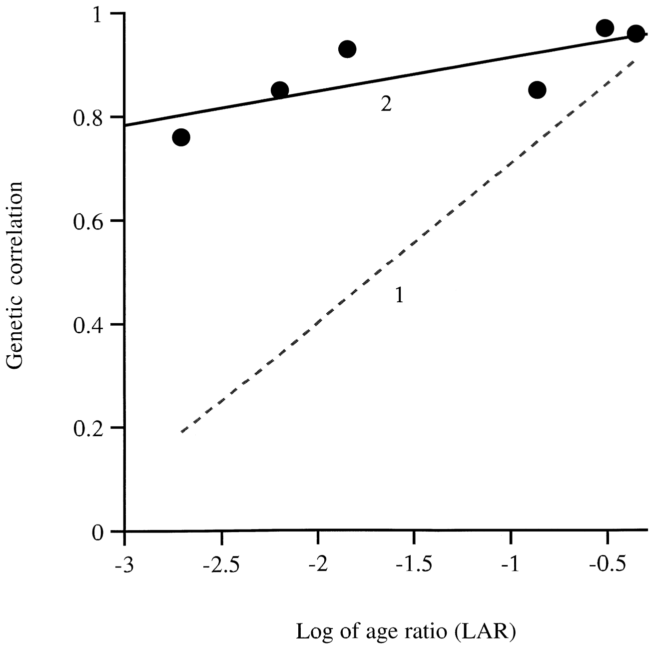

Figure 1. – Actual relationship between age-age genetic correlations for height and natural logarithm of the ratio of the younger to the older age, and predictions for Models 1 and 2.

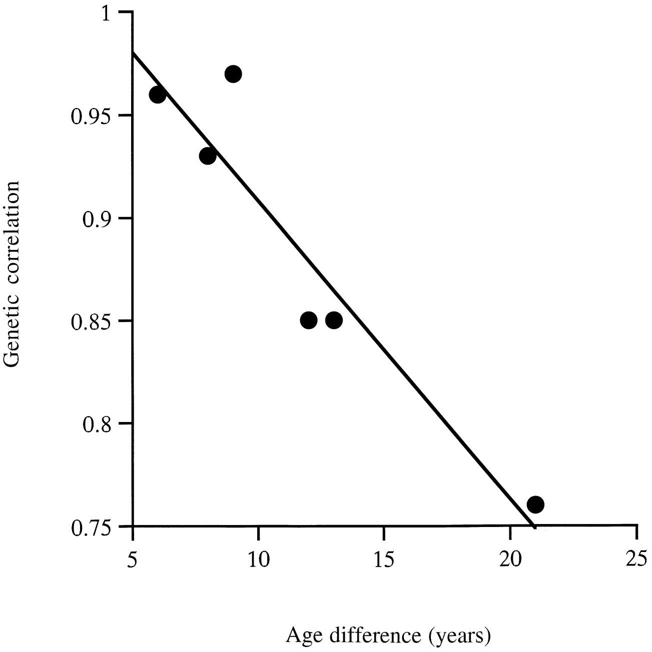

Figure 2. – Actual relationship between age-age genetic correlations for height and the age differences, and predictions for Model 3.

The estimated genetic correlations calculated using all the four models and the difference between them and those observed are shown in *table 3*. The genetic correlations predicted by Models 2 and 3 were more consistent with the observed values than those estimated by Model 1.

Smoothing with one degree of freedom gave a linear trend which was inconsistent with the data, and that with three degrees of freedom were not smooth as the smoothed trend reproduced the heritability estimates at ages that were assessed. We, therefore, selected two degrees of smoothing which was a compromise and conservative in its variation with age (*Figure 3*).

Gain and optimum selection age predictions

Assumption of constant heritability

The model used for estimating the age-age genetic correlations affected the magnitude of the expected gain and the optimum selection age. Genetic gain predicted using genetic correlations estimated by Model 1 was always lower than those predicted by the other 2 models. It was least at very young ages, where the potential gain was less than a quarter of those predicted by the other models. This can be attributed to lower genetic correlations, and the more rapid decline in genetic

Table 3. – Predicted age-age genetic correlations for height using Models 1 to 3, and the percentage difference between them and the observed estimates.

Age-age (years)	Observed	Model 1		Model 2		Model 3	
		Pred.	Diff.	Pred.	Diff.	Pred.	Diff.
1.5 - 9.5	0.93	0.45	52	0.86	8	0.91	2
1.5 - 13.5	0.85	0.34	60	0.83	2	0.87	-2
1.5 - 22.5	0.76	0.19	75	0.79	-4	0.77	-1
9.5 - 13.5	0.96	0.91	5	0.97	-1	0.96	0
9.5 - 22.5	0.85	0.75	12	0.93	-9	0.86	-1
13.5 - 22.5	0.97	0.86	11	0.96	1	0.90	7

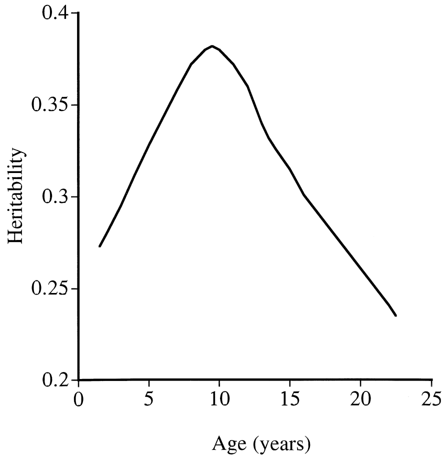

Figure 3. – Smoothed age-trends of heritability estimates using cubic splines.

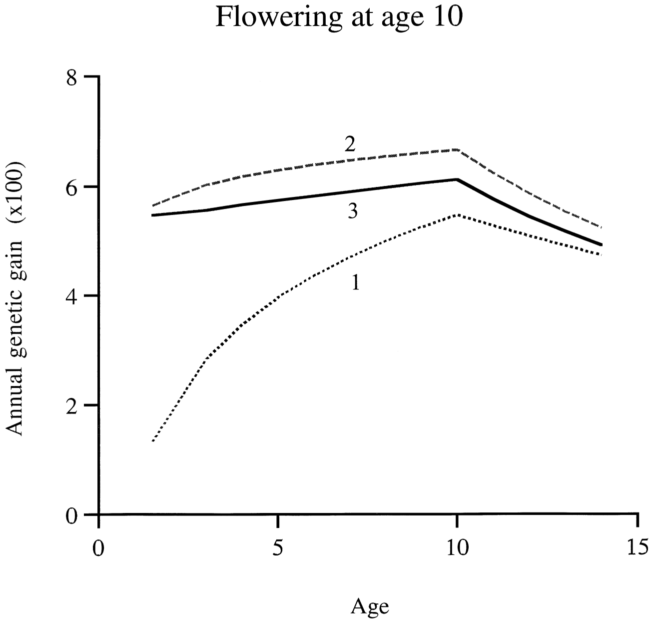

Figure 4. – Predictions of annual genetic gain from Models 1 to 3, when heritability is assumed constant, and flowering is assumed to be 10 years. Numbers 1 to 3 refer to Model 1 to 3, respectively.

correlations with age predicted by the Model 1 than by the other models. Where the flowering age was assumed to be 10 years, genetic gain was greatest for selection at 10 years (*Figure 4*), irrespective of the model for predicting genetic correlations. Reducing the flowering age to 3 years reduced the optimum selection age to 3 years under genetic correlation models, and 4 years under Model 1 (*Figure 5*).

Flowering age had a strong influence on the genetic gain expected and also on the optimum age for selection. Gain at optimum selection age increased with reduced flowering age, by as much as 100% when flowering was reduced from 10 to 3 years, with a corresponding reduction in optimum selection age using Models 2 and 3 (*Figures 4* and *5*).

Annual genetic gains for height from selection at ages between 3 and 14 years were greater than those at near-harvest age, confirming the efficiency of early selection. The genetic correlation predicted by Model 1 between heights at 3 and 22.5 years was 0.4, indicating that the genetic correlation for height between young ages and rotation age does not have to be high for early selection to be more efficient than selection at rotation age.

Assumption of variable heritability

The genetic gains predicted under the assumption of variable heritability were higher than those based on a constant heritability (*Figures 4* and *6*). This is attributed to higher heritability estimates than the assumed constant value at all ages.

Where flowering age was either 10 or 3 years, and age-age genetic correlations were estimated by Models 2 and 3, the optimum selection ages for the respective flowering ages were similar to those estimated assuming constant heritability. However, when the age-age genetic correlations were estimated using Model 1, the optimum selection age was 6 years after flowering age was reduced from 10 to 3 years (*Figure 6*). When flowering age was assumed to be 3 years, the difference between optimum selection ages predicted by Model 1 and the other two models was 3 years. This is attributed to a combination of low age-age genetic correlations involving young ages with Model 1 (*Table 2*), and the low heritability estimates at young ages.

Discussion

Age-age genetic correlations for height were high and are in a close agreement with estimates for *P. taeda* from USA genetic tests reported by LAMBETH *et al.* (1983) and MCKEAND (1988), and for pine species planted in Zimbabwe by BARNES (1992a and b) and PSWARAYI *et al.* (1996). However, for *P. taeda* in other USA genetic tests, FOSTER (1986) and WILLIAMS and MEGRAW (1994) reported weak genetic correlations (less than 0.4)

Figure 5. – Predictions of annual genetic gain from Models 1 to 3, when heritability is assumed constant, and flowering is assumed to be 3 years. Numbers 1 to 3 refer to Model 1 to 3, respectively.

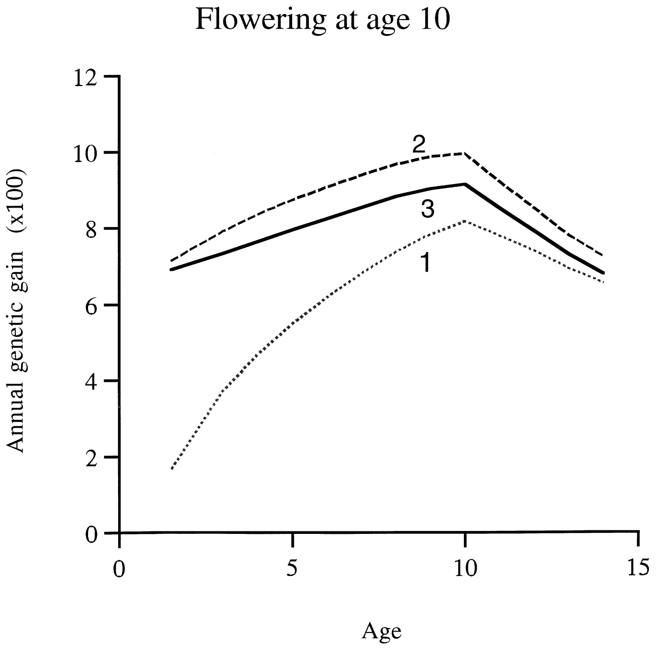

Figure 6. – Predictions of annual genetic gain from Models 1 to 3, when changes in heritability are considered, and flowering is assumed to be 10 years. Numbers 1 to 3 refer to Model 1 to 3, respectively.

between height at ages three or less with ages older than 12 years. In contrast, the results of this study demonstrate an opportunity for selecting at very young ages, as the genetic correlation between height at 1.5 and 22.5 years was strong (0.76). The differences between age-age genetic correlations from this study and those from USA genetic tests may be a consequence of management and methodological differences, since the USA tests were unthinned and family correlations were used as approximations of genetic correlations (GWAZE *et al.*, in press).

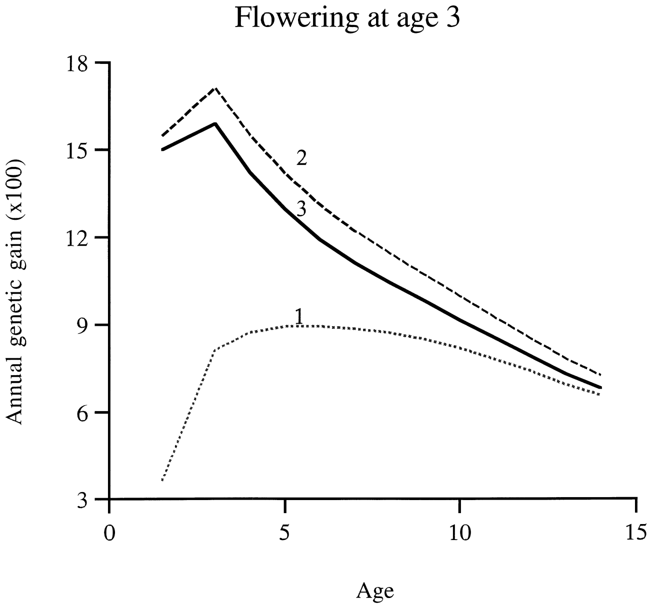

Figure 7. – Predictions of annual genetic gain from Models 1 to 3, when changes in heritability are considered, and flowering is assumed to be 3 years. Numbers 1 to 3 refer to Model 1 to 3, respectively.

The evidence is now substantial that age-age genetic correlations are higher than their phenotypic counterparts and, consequently, that models based on phenotypic correlations will underestimate genetic progress and needlessly delay selection. In this study, genetic correlations for height were higher than corresponding phenotypic correlations, which is consistent with the results of other studies of *P. taeda* (LAMBETH *et al.*, 1983) and with other pine species (BARNES, 1992a and b; PSWARAYI *et al.*, 1996; RIEMENSCHNEIDER, 1988). The results also support the findings of NEWMAN and WILLIAMS (1991), who surveyed available experimental data on *P. taeda* post-1980 and found that, in almost cases, a phenotypic model underpredicted genetic correlations. The observation that age-age genetic correlations are generally higher that corresponding phenotypic correlations has also been reported for morphometric traits in animals (BISHOP, 1992; FIMLAND, 1973; KOCH *et al.*, 1982). Since similar genes are likely to influence a trait assessed at different ages, age-age genetic correlations can be expected to be high. However, age-age phenotyic correlations can be expected to be reduced due to measurement errors and other environmental factors which accumulate as the time differences increases. The consequences of using the phenotypic model here was more than four-fold reduction in gain compared to those predicted by the genetic correlation models, and an overestimation of the optimum selection age by as much as 3 years.

When heritability was assumed to be constant, flowering age, and hence breeding interval, had a strong effect on the genetic gain and optimum selection age: as the breeding interval was reduced, gain increased and optimum selection age decreased. In contrast, when heritability was varied according to the pattern observed, changing the breeding interval had less impact on the optimum selection age in the presence of low genetic correlations predicted by the phenotypic model. MAGNUSSEN (1989) also found that the effect of the genetic correlations depended on the size and variation of the heritability estimates. Therefore, modelling of the heritability itself, as suggested by WEI and BORRALHO (1996), model may be based on covariance functions (KIRKPATRICK *et al.*, 1990), or on the direct 'coefficient of genetic prediction' ($h_x r_A h_y$, standardised genetic covariance or coheritability) as proposed by BARADAT (1976) will ensure more accurate predictions of gain and optimum selection age. This study highlights the need to assess genetic tests more frequently in order to improve prediction models for heritability.

The strength of this study is that assessments at near-harvest age were available, thus allowing realistic predictions of rotation age gains. Most studies suffer from the problem of not having assessments at maturity, and therefore of relying on extrapolations which may be inaccurate or have large errors (e.g. RIEMENSCHNEIDER, 1988 MCKEAND, 1988; MATEHSON *et al.*, 1994). However, the study also suffers from the problem of having few point estimates, a problem in many other forestry studies (e.g. 3 points, KING and BURDON, 1991; 4 points, MCKEAND, 1988).

This study indicates that the logarithmic model of age-age genetic correlations is not necessarily the best even though BURDON *et al.* (1992) found that the logarithmic model represented a valid framework for describing age-age genetic correlations for height. The best fit for the genetic correlations in this study was provided by the model involving age difference. The regression models assume consistent and predictable changes of age-age correlations with time, an assumption that has not been verified, and may not be valid in some cases. Therefore, alternative methods such as covariance functions (KIRKPATRICK *et al.*, 1990) might be more efficient, as they make fewer prior assumptions about the shape of the curve, and hence are more flexible.

The reproductive biology of *P. taeda* is a barrier to juvenile breeding of the species in Zimbabwe. Nevertheless, this study has demonstrated that, were early flowering to be induced, optimum selection age would be reduced from 10 to 3 years, and annual genetic gain increased by more than 100%. Therefore, effort could well be directed into reducing the flowering age of *P. taeda* in Zimbabwe.

Conclusion

This study demonstrates the disadvantages of phenotypic correlation models, such as LAMBETH's, for predicting gain and making decisions on optimum selection age. When the phenotypic model was used, gain was only a quarter of that predicted by the genetic correlation models, and optimum selection age was overestimated by up to three years. One important consequence of inaccurate models is that tree breeding programmes will operate inefficiently. Other related consequences are that the benefits from tree breeding will be undervalued, leading to less favourable appraisal of investment in tree breeding programmes, and misidentification of research priorities (e.g. the importance of identifying methods which induce early flowering). Genetic correlation models were robust in predicting optimum selection age for *P. taeda* data.

The effect of the genetic correlations on predictions of gain and optimum selection age depended on the size and variation of the heritability estimates, implying that heritabilities also need to be modelled over time.

With the current flowering age optimum selection age for *P. taeda* was 10 years in the tropics, but reducing flowering age to 3 years improved annual gain by 100% and reduced optimum selection age 3 years. Methods of artificially inducing flowering in *P. taeda* are available, and tree breeders in Zimbabwe should investigate the economics of promoting early flowering. Other options, such as selection of sites with early flowering potential, should also be explored in order to reduce the breeding interval.

Finally, given that *P. taeda* can be induced to flower at 3 years, and that there is accumulation of information on age-age genetic correlations, particularly in USA, the results highlight the need to develop a general prediction model for age-age genetic correlations in long rotation plantation species.

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The Genetics of Resistance to *Phoracantha semipunctata* Attack in *Eucalyptus globulus* in Spain

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Abstract

A study of the inheritance of resistance to *Phorancantha semipunctata* (eucalypt longhorn borer) was conducted in a progeny trial established in southern Spain, from a large *Eucalyptus globulus* base population, a commercial control seedlot and 2 previously selected clones. The results showed small race effects and a low heritability ($h^2 = 0.19$) for resistance to PHORACANTHA attack. The commercial seedlot was not significantly different from the mean of the Australian seedlots, but the 2 selected clones were significantly more resistant and faster growing. The level of PHORACANTHA attack was positively correlated with growth at the race ($r = 0.17$) but not at the genetic within race level (r-0.05).

Key words: Heritability, genetic correlation, drought, Eucalypt longhorn borer, Spain.

FDC: 165.3; 165.53; 232.1; 450; 453; 145.7 x 19.88 *Phoracantha semipunctata*; 176.1 *Eucalyptus globulus*; (46).

Introduction

In many areas of Iberia and the Mediterranean Basin, which is characterized by low rainfall and extended dry summers, the productivity of eucalypt plantation can be considerably reduced because low survival following attack by *Phoracantha semipunctata*, a cerambycide beetle native from Australia.

So far the main control measure used has been burning of trap log piles, but this is costly and only partially effective. There has been differences reported in resistance to *Phoracantha* attack between different eucalypt species (HANKS et al., 1993, 1995), but the magnitude of genetic variation within *Eucalyptus globulus*, the most important eucalypt species in Spain, has not been previously described. This papers looks at the level of genetic control of resistance to *Phoracantha* attack and its relationship with growth on a large *E. globulus* base population trial established in a severely infected area of the planting of Empresa Nacional de Celulosa (ENCE), in the South of Spain.

Material and Methods

Genetic material

The study includes a range-wide collection of 256 open-pollinated families covering the entire natural range of *Eucalyptus globulus* ssp. *globulus* in Australia. Collection details are given in GARDINER and CRAWFORD (1988) and published in JORDAN et al. (1994). Cuttings of 2 plus-trees from ENCE breeding program, and 1 commercial seedlot were also included in the trial. The plus-trees were selected for their superior growth and health and were amongst the very few survivors in highly affected plantations.

Trial site and design

The trial is located in the SW of Spain, in the province of Andaluzia, near Huelva (latitude 37°34'N; longitude 6°50'W; altitude 70 m). Climatic conditions are typically Mediterranean: mean annual rainfall of 500 mm, a mean annual temperature of 17.5 °C, and less than 10 days per year of frost. However, the climatic conditions prevalent during most of the life of the trial were generally drier than average: the total rainfall in the second year of the trial, was a record low of 250 mm. The soil is a distric cambisoil, with a hard-pan horizon at around 50 cm of depth. The soil was cultivated prior to planting to 60 cm using a mul-board plough. Plants were established at a 3 m x 3.5 m spacing, and fertilized at planting. For the commercial seedlings, a slow release fertiliser was also applied to the paper-pot medium. Weeds were controlled one year after planting by disc ploughing.

Families were nested in 5 sub-lines, but allowing for some crossover of races across different sublines (*Table 1*). The 2 clones, propagated from stem cuttings, and the commercial seedlot were included in all blocks across the 5 sublines. There were 4 blocks per subline. Each family or clone were represented in each block by 3 non-contiguous plots, each plot having 2 trees, which were randomly allocated within a block. DUTKOWSKI et al. (1998) race classification was used as a basis

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