

DETERMINING THE OPTIMUM SELECTION AGE FOR DIAMETER AND HEIGHT IN LOBLOLLY PINE

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ABSTRACT

Genetic and phenotypic correlations for diameter, height and volume were estimated for *Pinus taeda* L. in the southeastern USA using the individual tree model ASREML. The data were from two progeny tests comprising 191 full-sib families assessed at 1 to 25 years. The age-age genetic correlations ranged from 0.15 to 0.98. Height at young ages was more genetically correlated to volume at 25 years than diameter, but at older ages the reverse was true. At the phenotypic level, height was always less correlated to volume at 25 years than diameter. Age-age genetic and phenotypic correlations for diameter and height had a strong linear relationship with logarithm of age ratio ($R^2 > 0.90$). The slopes of the genetic correlation models for diameter were higher than those for height. Using a biological criterion (gain per year), calculated optimum selection ages for height and volume at 25 years based on height were 9 and 7 years respectively, and those for diameter and volume at 25 years based on diameter were 10 and 8 years respectively. Gain efficiency based on height was higher, suggesting that height is a better selection criterion than diameter.

Keywords: Genetic correlation, phenotypic correlation, early selection, optimisation, *Pinus taeda*.

INTRODUCTION

Optimum selection age is defined as the age at which genetic gain per year of breeding cycle is maximized, and is critical to the long-term efficiency of any tree-breeding program (ZOBEL & TALBERT 1984). Optimum selection age of *P. taeda* L. has been estimated to be between 6 and 10 years for family selection, based on height growth (BALLOCHI *et al.* 1993a, MCKEAN 1988). The justifications for making selections based on height are that height is a good predictor of volume at rotation age and is less affected by competition than diameter (FOSTER 1986, LAMBETH *et al.* 1983), and heritability for height is higher than that for diameter (BRIDGWATER *et al.* 1983, FOSTER 1986). Furthermore, height is more correlated with tree-form traits (BURDON *et al.* 1992) and wood density (BRIDGWATER *et al.* 1983) than diameter. Optimum selection age for diameter and volume may differ from that of height. LI *et al.* (1996) found that heritability estimates for height and diameter were comparable, and age-age genetic correlations for height were lower than those for diameter in 1st and 2nd generation *P. taeda* genetic tests in southeastern USA, indicating that diameter may be a better selection criterion than height. Since tree competition is

less of a concern in current *P. taeda* breeding programs if intensive thinning is conducted, diameter may be a desirable selection criterion for diameter or volume at rotation age.

Knowledge of genetic parameters and their age trends are critical for determining the optimum time of selection. Optimum selection age can only be estimated using models that make it possible to predict age-age genetic correlations involving ages not assessed. The most common model used is the model developed by LAMBETH (1980) which predicts phenotypic correlations for height given age ratios. There appear to be no models for diameter in *P. taeda* despite the fact that diameter is a good predictor of volume, is easier to assess than height, and has less measurement errors (LI *et al.* 1996) particularly after canopy closure and on tall trees. For *Pinus radiata* D. Don, optimum selection ages have been based on diameter (e.g. KING & BURDON 1991, MATHESON *et al.* 1994). Hence, age-age prediction models for diameter are required to determine potential for early selection on this trait in *P. taeda*.

Optimum selection ages have been determined using models that predict height at maturity in *P. taeda*. Volume is the primary breeding goal in *P. taeda*, hence

prediction models should be based on how well they predict volume at maturity rather than height. The lack of models for predicting volume at maturity may be due to unavailability of diameter measurements at maturity. Results from other studies indicate that age-age genetic correlations between early height and late volume are low to moderate, and differ from those between height assessments. For example, FOSTER (1986) reported a genetic correlation between height at 5 years and height at 15 years as 0.74 while that between height at 5 years and volume at 15 years was only 0.58. Therefore, optimum selection age based upon height-height prediction models may differ from that based on height-volume prediction models. Furthermore, genetic correlations between diameter at an early age and volume at 20 years of age was reported to be higher than those between height at an early age and volume at 20 years in *P. taeda* (LI *et al.* 1996), indicating that selections for volume based on diameter may be made earlier than those based on height.

Most of the previous reports on optimum selection age in *P. taeda* are based on young tests, or on tests assessed on very few landmark ages, or on data in which both diameter and volume are not available. The current study addresses these deficiencies by examining data from tests assessed regularly up to rotation age and having data on both diameter and volume. We hypothesized that optimum selection ages based on diameter is lower than that based on height since diameter is likely to be more correlated with volume than height. We further hypothesized that decisions on optimum selection age would differ when volume, rather than height or diameter, is used at the breeding goal. The objectives of this study were to (1) develop age-age genetic correlation predictive models for diameter and height (2) develop age-age genetic correlation predictive models for height and diameter with volume at maturity and (3) to evaluate implications of these models for decisions on early selection in *P. taeda*.

MATERIALS AND METHODS

Materials

The International Paper Company (IP) established the two genetic tests in southern Georgia, USA. Details of these tests and the parent material are provided by BALOCCHI *et al.* (1993b). The total number of full-sib families were 191, and these originated from a nested mating design involving 65 male parents each mated to 2–4 different female parents (i.e. a total of 191 female parents). The parents were randomly selected from a 6,475 ha forest containing large, uneven-aged, natural

stands of loblolly pine in Georgia. The parent trees were at least 15.2 m apart and had sufficient male or female strobili for crossing and were safe to climb. Each of the two tests comprised three complete replicates and 12-tree row-plots. The tests were established in 1962, 1963 and 1964. The families were grouped in 10 sets of about 20 full-sib families. Each set was planted in only one of the three planting years. Thinning was carried out at age 10 years, removing 50 % of the trees per plot. Thinned trees were selected at random. The tests were measured for height at ages 1–4 years and for both height and diameter at ages 5–10, 13–17, and at 25, 26 and 27 year, hereafter collectively referred to as 25 years. Volume at 25 years was calculated using a volume equation developed for International Paper by Clemson University for Georgia – source loblolly pine:

$$\text{Volume (m}^3\text{)} = [0.31995 + (0.00294 \cdot \text{DBH}^2 \cdot \text{Height})] \cdot 0.02832 \quad [1]$$

Where *DBH* is diameter at breast height in inches and height in feet. Only those trees assessed at 25 years were considered for analyses of growth at younger ages.

Methods

A univariate individual-tree model was used for estimating heritabilities and their standard errors, while correlations and their standard errors were estimated using a bivariate individual-tree model, ASREML (GILMOUR 1996). The following model was used:

$$Y_{ijklm} = m + S_i + Set_j + R_k + F_l + A_m + e_{ijklm} \quad [2]$$

where: Y_{ijklm} is the observation on the m^{th} tree in the i^{th} site in the j^{th} set in the k^{th} replicate and l^{th} family, m = overall mean, S_i = random effect of the i^{th} site, Set_j = random effect of the j^{th} set (i.e. set of families), R_k = random effect of the k^{th} replicate; F_l = random effect of the l^{th} family (male x female interaction); A_m = additive genetic effect of the m^{th} tree, and e_{ijklm} = is the within plot error (residual).

The individual tree model fits 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 relationship information in the analysis. Since the additive variance was estimated by A_m in the model, the full-sib family variance component (σ_F^2) was interpreted as $1/4 \cdot \sigma_D^2$ where σ_D^2 is the dominance genetic variance. Epistatic variance was assumed to be zero. The individual tree

model such as this has been used previously for estimating genetic parameters of tree species (GWAZE *et al.* 1997a). Heritability was calculated as:

$$h^2 = \sigma_A^2 / \sigma_P^2 \quad [3]$$

where: σ_A^2 is the additive variance and σ_P^2 is the phenotypic variance. The phenotypic variance was the sum of the additive variance (σ_A^2), the family variance (σ_F^2) and the residual variance (σ_e^2). Phenotypic correlations were estimated using individual-tree observations.

The following equation (LAMBETH 1980) was fitted to age-age genetic correlations between earlier heights and height at 25 years, earlier heights and volume at 25 years, earlier diameters and diameter at 25 years and earlier diameters and volume at 25 years:

$$r_g = \beta_0 + \beta_1 \cdot LAR \quad [4]$$

where r_g is genetic correlation between the early-age and mature-age trait expression and LAR is the log_e (younger age/25). It should be noted that rotation-age trait expression is of most interest, and therefore correlation of earlier age with 25-year trait expression were used. While some potential data points were not used, the study focuses on the most important dataset for early selection decision-making. The regression equations were fitted in order to interpolate correlations involving ages not assessed and to generally correct for year-to-year ‘noise’ variations in the correlation estimates. The same model was fitted to age-age phenotypic correlations (r_p). Regression equations were also fitted with LAR^2 as the independent predictive variable as suggested by LAMBETH & DILL (2001).

In order to interpolate heritability estimates for ages at which no assessments were taken, linear and non-linear regression equations were fitted to heritability estimates and age. A non-linear model may best fit the data but there are biological difficulties in explaining the model. Non-significant linear and non-linear models would suggest that a constant heritability with age is appropriate for estimating the optimum selection age.

Optimum age for selection was estimated using the gain efficiency per year. Assuming equal intensities of selection between mature and young ages, gain efficiency per generation is given by (FALCONER 1989):

$$E_{gen} = h_j r_g h_m^{-1} \quad [5]$$

where: E_{gen} = gain efficiency per generation, r_g = genetic correlation between the juvenile trait and mature trait, h_j , h_m = square roots of individual tree heritabilities at early and mature ages respectively.

Gain efficiency per year (E_{year}) was calculated as follows (FALCONER 1989):

$$E_{year} = h_j r_g h_m^{-1} T_m T_j^{-1} \quad [6]$$

Where T_j and T_m are the generation interval for juvenile and mature selection (assumed to be 25 years), respectively. The generation interval was the selection age plus 5 years. Five years is the current breeding lag time for *P. taeda* in the USA, and is the time from making selections to planting progeny tests. The lag-time breeding phase used to be 10 years for *P. taeda* (MC-KEAND 1988), but this has been reduced to less than 5 years through the widespread use of the top grafting technology (BRAMLETT *et al.* 1995).

RESULTS

Means and heritability estimates

The phenotypic means and individual-tree heritability estimates are shown in Table 1. Heritability estimates for height varied from a low 0.03 to 0.29. Generally, heritability estimates for height increased with age, peaking at age 15 years and decreasing thereafter. Heritability estimates for diameter varied from 0.09 to 0.2 being low between ages 5 and 7 years, increasing at age 8 years and remaining fairly constant thereafter (Table 1). Heritability estimates for height were higher than those for diameter.

The fitted relationship for heritability estimates for height on age was essentially non-linear [$h^2 = 0.024 + 0.030 \cdot \text{Age} - 0.001 \cdot \text{Age}^2$; $R^2 = 0.89$] and that for heritability estimates for diameter on age was linear [$h^2 = 0.108 + 0.004 \cdot \text{Age}$; $R^2 = 0.54$] (Figure 1). Both models were significant ($P < 0.05$).

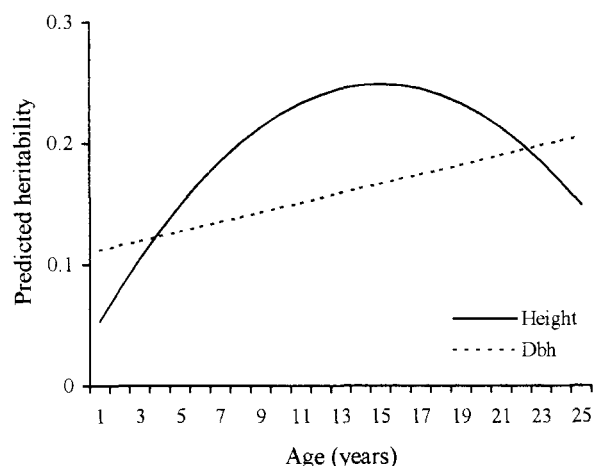


Figure 1. Predicted age-trends of individual-tree heritability estimates (fitted regressions).

Table 1. The mean, standard deviation (SD), estimated individual-tree heritability (h^2) and approximate standard error of h^2 (SE) for height and diameter.

Age (years)	Height (m)				Diameter (cm)			
	Mean	SD	h^2	SE	Mean	SD	h^2	SE
1	0.44	0.16	0.08	0.04	–	–	–	–
2	1.06	0.36	0.03	0.03	–	–	–	–
3	1.98	0.62	0.10	0.04	–	–	–	–
4	3.07	0.80	0.13	0.05	–	–	–	–
5	4.05	0.94	0.14	0.05	6.35	2.15	0.12	0.05
6	5.02	1.02	0.18	0.06	8.48	2.28	0.13	0.05
7	6.08	1.11	0.20	0.07	10.49	2.49	0.09	0.04
8	7.38	1.11	0.20	0.07	12.03	2.64	0.17	0.06
9	8.85	1.14	0.25	0.08	13.59	2.70	0.17	0.06
10	10.15	1.21	0.25	0.08	14.91	2.82	0.16	0.06
13	13.63	1.44	0.22	0.07	18.55	3.39	0.14	0.05
14	14.66	1.47	0.25	0.08	19.43	3.53	0.15	0.05
15	15.68	1.51	0.29	0.09	20.29	3.67	0.18	0.06
16	16.63	1.59	0.24	0.08	20.88	3.78	0.17	0.06
17	17.59	1.63	0.24	0.08	21.50	3.89	0.18	0.06
25	23.54	2.38	0.20	0.07	26.07	5.28	0.20	0.06

Genetic and phenotypic correlations

Estimated age-age genetic correlations between height at a young age and height at 25 years varied widely from 0.15 to 0.91 (Table 2). The corresponding estimated age-age phenotypic correlations were lower than the estimated genetic correlations and varied from 0.15 to 0.64. As the age difference increased, both the genetic and phenotypic correlations decreased. Age-age genetic correlations for diameter also varied widely from 0.45 to 0.97 (Table 2). At young ages (< 8 years) heights were more genetically correlated to height at 25 years than diameters to diameter at 25 years, and at older ages the reverse was true. Phenotypic correlations ranged from 0.48–0.95, and were generally lower than corresponding genetic correlation estimates for all ages except those involving ages 5 and 6.

Estimated genetic and phenotypic correlations involving volume at age 25 and height increased with age of the height measurement (0.19–0.74, Table 3). The same trend was observed for genetic and phenotypic correlations between volume at age 25 and diameter (range 0.45–0.98, Table 3). At young ages (< 7 years) height was more genetically correlated to volume than diameter, and at older ages height was less correlated to final volume than diameter. At the phenotypic level, height was always less correlated to volume than diameter.

The logarithm model using LAR as the independent variable fit the data well, with R^2 being greater than 0.90 (Table 4). The slopes of the regression equations

Table 2. Estimated genetic correlations (r_g), approximate standard errors of the r_g (SE), and phenotypic correlations (r_p), for height at 25 years with earlier heights, and diameter at 25 years with earlier diameters.

Age	Height		Diameter	
	r_g (SE)	r_p	r_g (SE)	r_p
1	0.15 (0.12)	0.15	–	–
2	0.30 (0.13)	0.20	–	–
3	0.46 (0.10)	0.25	–	–
4	0.54 (0.09)	0.32	–	–
5	0.58 (0.09)	0.36	0.45 (0.09)	0.48
6	0.63 (0.08)	0.39	0.48 (0.09)	0.54
7	0.67 (0.07)	0.40	0.66 (0.06)	0.62
8	0.71 (0.07)	0.42	0.74 (0.05)	0.67
9	0.73 (0.06)	0.45	0.79 (0.04)	0.73
10	0.78 (0.05)	0.49	0.81 (0.04)	0.77
13	0.81 (0.05)	0.55	0.90 (0.02)	0.88
14	0.82 (0.04)	0.61	0.92 (0.02)	0.90
15	0.87 (0.04)	0.63	0.94 (0.01)	0.92
16	0.94 (0.02)	0.63	0.95 (0.01)	0.93
17	0.91 (0.03)	0.64	0.97 (0.01)	0.95

for diameter were higher than those for height, indicating that correlations for diameter declined more rapidly than those for height as age difference increased. There was no evidence that the LAR² model provided a significantly better fit than LAR model (Tables 4 & 5). Thus, genetic gain was estimated using the LAR model.

Table 3. Estimated genetic correlations (r_g), approximate standard errors of the r_g s (SE) and phenotypic correlations (r_p), for heights or diameters with volume at 25 years.

Age	Height		Diameter	
	r_g (SE)	r_p	r_g (SE)	r_p
1	0.19 (0.12)	0.25	–	–
2	0.34 (0.12)	0.30	–	–
3	0.45 (0.10)	0.34	–	–
4	0.47 (0.10)	0.40	–	–
5	0.52 (0.09)	0.43	0.45 (0.09)	0.46
6	0.54 (0.09)	0.45	0.46 (0.09)	0.52
7	0.57 (0.08)	0.46	0.67 (0.06)	0.60
8	0.61 (0.08)	0.47	0.74 (0.05)	0.65
9	0.61 (0.07)	0.49	0.76 (0.05)	0.70
10	0.61 (0.07)	0.48	0.76 (0.05)	0.74
13	0.69 (0.07)	0.53	0.85 (0.03)	0.85
14	0.64 (0.07)	0.55	0.88 (0.03)	0.87
15	0.70 (0.06)	0.59	0.91 (0.02)	0.89
16	0.73 (0.06)	0.57	0.91 (0.02)	0.90
17	0.71 (0.06)	0.60	0.93 (0.02)	0.92
25	0.74 (0.06)	0.66	0.98 (0.00)	0.97

Genetic gain and optimum selection age

Genetic gain per year for height when selecting on height was maximized at 9 years (gain efficiency = 1.88), and that for volume based on height selection was maximized at 7 years (Table 5). Gain per year for diameter when selecting on diameter was maximized at 10 years (gain efficiency = 1.32), and that for volume based on diameter selection was maximized at 8 years. The maximum gain efficiency per year for volume

based on height (1.32) was higher than that based on diameter (1.26).

DISCUSSION

Heritability estimates for diameter in this study were generally lower than those for height as observed by BRIDGWATER *et al.* (1983) and FOSTER (1986). However, LI *et al.* (1996) obtained comparable heritability estimates for the respective traits in *P. taeda*. The low heritability estimates for diameter – a trait sensitive to differential competition – in our study and in other previous studies may be due to the less intensive silvicultural practices common in the older genetic tests (GWAZE *et al.* 2000). Age-trends of heritability estimates for height were non-linear, peaking at 15 years, while that for diameter were essentially linear, and increased with increase in age. In this study the plot term was not included in the model used for estimating heritability estimates. GWAZE *et al.* (1997b) found that exclusion of the plot term in the model did not have an effect on heritability estimates for height and their standard errors, but dominance variances were inflated. It would be desirable to study the impact of plot common environment effect on estimates of heritability and dominance variance for diameter.

Age-age genetic correlations for height are in close agreement with estimates published elsewhere for *P. taeda* (FOSTER 1986, LAMBETH *et al.* 1983, GWAZE *et al.* 2000). The age-age genetic correlations for diameter were not available for tests in the USA but were consistent with those of HAGEDORN (1994) using *P. taeda* tests in South Africa. Age-age genetic correlations

Table 4. Parameter estimates for age-age correlation regression using LAR as the independent variable and fit statistics, and estimated optimum selection age (Age).

Variables involved (X – Y)	Intercept ± SE	Slope ± SE	RMS ⁺	DF ⁺	R ²	Age
<i>r_g</i>						
HT – HT 25	1.01 ± 0.011	0.270 ± 0.007	0.0005	13	0.99	9
HT – VOL 25	0.78 ± 0.011	0.172 ± 0.007	0.0006	14	0.98	7
DBH – DBH 25	1.17 ± 0.034	0.426 ± 0.034	0.0020	9	0.95	10
DBH – VOL 25	1.06 ± 0.034	0.346 ± 0.036	0.0033	10	0.90	8
<i>r_p</i>						
HT – HT 25	0.68 ± 0.019	0.190 ± 0.012	0.0015	13	0.95	9
HT – VOL 25	0.63 ± 0.008	0.128 ± 0.006	0.0004	14	0.97	7
DBH – DBH 25	1.12 ± 0.010	0.396 ± 0.010	0.0002	9	0.99	10
DBH – VOL 25	1.04 ± 0.034	0.348 ± 0.020	0.0010	10	0.97	9

⁺ RMS = residual mean square and DF = degrees of freedom.

between the various heights and volume at 25 years were lower at older ages, but higher at younger ages, than those between diameters and volume at 25 years. Our results, particularly those involving early ages, differed from those of LI *et al.* (1996) who found that genetic correlations between the various heights and volume at 20 years were always lower than those between the various diameters and volume at 20 years. The weak correlations between early diameters and volume at 25 years may be due to the less intensive silvicultural practices that were prevalent in the older genetic tests.

The superiority of LAR^2 over LAR as a predictive independent variable for age-age correlations in *Pinus taeda* recently reported by LAMBETH & DILL (2001) was not evident in this study. The LAR model that has been used for predicting age-age correlations for height in *P. taeda* (LAMBETH 1980) was found to be appropriate for age-age genetic and phenotypic correlations for both height and diameter. Similarly, KING & BURDON (1991) found that age-age genetic and phenotypic correlations for diameter in *P. radiata* in New Zealand were well described by the LAR general predictive model, but MATHESON *et al.* (1994) found that a polynomial model was a better prediction model than a simple linear model using LAR for diameter in the same species in Australia. In this study, diameter models had higher slopes than height models, indicating that the correlations for diameter decreased more rapidly with increase in age difference. However, JOHNSON *et al.* (1997) found that the slopes of the age-age genetic correlation prediction models for height and diameter were similar in Douglas-fir (*Pseudotsuga menziesii*).

Using a biological criterion (gain per year), the optimum selection age for height or volume using height as selection criterion (7–9 years) was 1 year lower than those for diameter or volume using diameter as the selection criterion (8–10 years). Using volume as the breeding goal and early height or diameter growth as the selection criterion reduced the optimum selection age by 2 years, and gain efficiency based on height was higher. This suggested that height was a better early selection criterion than diameter for volume at maturity. In less intensively managed tests, as in this study, the optimum selection age for diameter might be expected to be higher than that for height due to the higher impact of competition on diameter than height. However, in equally non-intensively managed tests, LI *et al.* (1996) inferred that optimum selection age for diameter was likely to be lower than that of height given the higher age-age correlations and the comparable heritability estimates.

Optimum selection ages for height in this study were

consistent with those of BALOCCHI *et al.* (1993a) using the same data, but selections were at the family level and coefficients of genetic prediction were used instead of genetic correlations. However, the optimum selection ages for height were slightly higher than those estimated by LAMBETH *et al.* (1983) and MCKEAND (1988) (5–8 years for family selection), particularly the former. As pointed out by BALOCCHI *et al.* (1993a) the earlier studies used tests assessed at only four ages, hence they may have underestimated the optimum selection age. The optimum selection ages for height were also higher than those estimated more recently by LAMBETH & DILL (2001).

Although observed phenotypic correlations were always lower than genetic correlations, optimum selection ages based upon phenotypic correlations were similar to those derived using genetic correlations. Therefore, using phenotypic correlations rather than genetic correlations would underestimate genetic progress, but not delay selection. GWAZE *et al.* (1997a) found that using phenotypic correlations in place of genetic correlations not only underestimated gain but also delayed selection in *P. taeda* in Zimbabwe.

Economic factors were not considered in this study, and these are likely to reduce the optimum age of selection further (MCKEAND 1988). To determine the economic optimum, the present values or net present values of the gains could be calculated. The net present values which include the costs of more rapid turnover of generations and more frequent seed orchard establishment would be preferred, but information for such an analysis is unlikely to be available for many tree breeding programmes.

The strength of this study was that the population sample size was large (191 families) and assessments at rotation age were available, therefore allowed reasonably precise genetic statistics and realistic predictions of rotation age gains. However, the study was limited by the fact that it was established at only two sites. Age-age genetic correlations and models for predicting these correlations have been shown to differ among sites or geographic regions (GWAZE *et al.* 2000, LAMBETH & DILL 2001).

CONCLUSION

Age-age genetic correlations for diameter were well described by the linear model using LAR as the predictive variable, but the slopes were steeper than those for height. Thus, the age-age genetic correlations for diameter, though higher at older ages, decreased more rapidly with increase in age difference. At very young ages age-age genetic correlations for diameter were

lower than those for height.

Using volume as the breeding goal reduced the selection age by two years, particularly when gain per year was used to determine optimum selection age. The current practice of using height-height prediction models, rather than height-volume prediction models, needs review using data from more advanced-generation genetic tests.

This study demonstrates that height is a better selection criterion than diameter. Selections based on height were made one year earlier than those based on diameter when gain per year was used for determining the optimum selection age. Furthermore, efficiency of selection for volume was higher, irrespective of the method used for estimating gain efficiency, when selection was based on height rather than diameter. This superiority of height over diameter as selection criterion may be due, in part, to use of outdated silvicultural practices in tests from this study. Since silvicultural practices have improved substantially over time, heritability estimates and genetic correlations based upon newer tests may be higher than those from earlier tests.

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