Optimum selection age for wood density in loblolly pine

D.P. Gwaze, K.J. Harding, R.C. Purnell, and F.E. Bridgwater

Abstract: Genetic and phenotypic parameters for core wood density of *Pinus taeda* L. were estimated for ages ranging from 5 to 25 years at two sites in southern United States. Heritability estimates on an individual-tree basis for core density were lower than expected (0.20–0.31). Age–age genetic correlations were higher than phenotypic correlations, particularly those involving young ages. Age–age genetic correlations were high, being greater than 0.75. Age–age genetic correlations had a moderately linear relationship, while age–age phenotypic correlations had a strong linear relationship with natural logarithm of age ratio. Optimum selection age for core density was estimated to be 5 years when calculations were based on both genetic and phenotypic correlations. However, age 5 was the youngest examined in this study and optimum selection age may be younger than 5. Generally, the optimum selection age was robust to changes in breeding phase and assumptions concerning age-related variation in heritability estimates. Early selection for core density would result in a correlated increase in earlywood density but little progress in latewood density or latewood proportion at maturity.

Résumé : Les auteurs ont estimé les paramètres génétiques et phénotypiques de la densité du bois juvénile de *Pinus taeda* L. pour les âges de 5 à 25 ans à partir d'arbres situés sur deux sites dans le Sud des États-Unis. Les estimés d'héritabilité au sens strict pour la densité du bois sont plus faibles que prévu (0,20–0,31). Les corrélations génétiques entre différents âges sont plus fortes que les corrélations phénotypiques, particulièrement au stade juvénile. Les corrélations génétiques entre différents âges sont élevées et supérieures à 0,75. Elles démontrent une relation linéaire modérée, alors que les corrélations phénotypiques entre différents âges démontrent une forte relation linéaire avec le logarithme naturel du rapport des âges. L'âge optimal de sélection pour la densité du bois juvénile est estimé à 5 ans lorsque les calculs sont basés à la fois sur les corrélations génétiques et phénotypiques. Toutefois, 5 ans est l'âge le plus précoce qui a été étudié et l'âge optimal de sélection pourrait être inférieur à 5 ans. Généralement, l'âge optimal de sélection est peu affecté par les changements de stades d'amélioration et par les hypothèses concernant la variation des estimés d'héritabilité liée à l'âge. La sélection en bas âge pour la densité du bois juvénile devrait se traduire par une augmentation correspondante de la densité du bois initial, mais peu d'augmentation de la densité du bois final ou de la proportion de bois final à maturité.

[Traduit par la Rédaction]

Introduction

The importance of including wood properties in genetic improvement programmes has long been recognized in forestry (Lowe et al. 1999; van Buijtenen 1969; Zobel and van Buijtenen 1989). Wood density or specific gravity is the most important wood-quality trait because it is well correlated with major strength properties of sawn timber and with pulp and paper properties (van Buijtenen 1969). To improve wood density through selection, knowledge of genetic parameters for wood-density traits is essential.

There are numerous reports on genetic parameters for age-specific wood density in loblolly pine (*Pinus taeda* L.) (Zobel and van Buijtenen 1989; Loo et al. 1984; Talbert et al. 1983; Williams and Megraw 1994). These reports indicate that heritabilities and age–age genetic correlations for wood-density traits are generally high. These results imply that selection for wood properties may yield greater genetic response and may be made earlier than for growth traits. Loo et al. (1984) and Williams and Megraw (1994) suggested that wood density could be selected as early as 2 years in ordinary tests and short-term tests, respectively. A major limitation of these studies is that the age at which genetic gain is maximized (optimum selection age) was not estimated. Wood properties are currently not a selection criterion in loblolly breeding populations in the Western Gulf area (Lowe and van Buijtenen 1986). However, given the adverse correlations between growth and wood properties, speciality populations for wood-quality improvement may be established (Namkoong et al. 1988) or selecting for wood density may be done when establishing some deployment populations (Lowe et al. 1999).

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Knowledge of age trends of age–age genetic correlations and heritalibilities is critical for determining the optimum selection age. Wood density is difficult and more expensive to assess than growth traits, and hence, data on all ages up to harvest is rare. Inferences on early selection of wood density have been based on observations of genetic correlations on very few landmark ages. In growth traits, particularly height, models have been developed to enable predictions of genetic correlations at all ages including at ages where assessments were not made (e.g., Lambeth 1980), allowing predictions of optimum selection age to be made. To date, there are no models for predicting age trends of age–age genetic correlations of wood density in *Pinus* species thereby compromising decisions on early selection for wood density. Greaves et al. (1997) found that core density was well described by the Lambeth model in *Eucalyptus nitens*. Optimum selection age for wood density traits has not been determined in *P. taeda*. That determined for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) with a rotation age of 50 years was estimated to be 15 years using phenotypic correlations and assuming constant heritability across ages (Gonzalez and Richards 1988).

Wood density is strongly influenced by the relative proportions of earlywood and latewood (Zobel and van Buijtenen 1989). Earlywood is formed in the first part of the growth season and has low density, while latewood is produced later and has higher density, and therefore, latewood has greater strength, greater dimensional stability, and higher pulp yields (Zobel and van Buijtenen 1989; Zobel and Jett 1995). While early selection may be practiced on mean core density, knowledge of the effect of early selection for core density on the other wood-density traits is important in tree-breeding programs.

The objectives of this study were to estimate the age trends of genetic parameters of wood density and to determine the potential for early selection for wood density in *P. taeda*.

Materials and methods

The International Paper Company in southern Georgia, U.S.A., established the two genetic tests. Details of these tests are provided by Balocchi et al. (1993). The number of full-sib families was 180, and these originated from a nested mating design involving 65 male parents mated to between 2 and 4 different female parents. The parents were randomly selected from a 6475-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 replicates and 12-tree row plots. The tests were established in 1963, 1964, and 1965, and different sets of families were planted in the 3 years. Random thinning was carried out at age 10 years, removing about half of the trees per plot.

The data used for density determinations were described in detail by Harding (1995). Briefly, in 1992 at ages 27, 28, and 29 years, pith-to-bark 12-mm cores of wood were extracted from the midwhorl closest to breast height (1.3 m) from randomly selected trees within a plot using an increment borer. The increment cores contained between 25 and 27 growth rings from pith reflecting their age and the sampling height. Wood density is dependent on height position of the tree (Megraw 2001). However, wood-density estimates at breast height are known to be a reliable predictor of mean wood density of a tree (Zobel et al. 1960). Six trees were sampled per family in each test. Intraring density information was obtained using a direct scanning X-ray densitometer. Within each growth ring, data were partitioned into earlywood and latewood using a density criterion of 480 kg/m^3. This value was determined empirically by separating earlywood and latewood by ocular examination and determining the density for each segment. This demarcation value may not correspond precisely to traditional definitions of earlywood and latewood, such as Mork's definition of latewood quoted by Zobel and Talbert (1984), but it describes the within-ring density and cell wall width variation, which approximates ocular patterns of earlywood and latewood. Hodge and Purnell (1993) also used this density criterion in a study of slash pine. Latewood proportion was calculated by dividing the latewood width with the ring width. The mean core density was obtained by weighting the mean ring density with the respective ring width. Rings affected by compression wood, heartwood, or resin streaks were removed prior to analyses. Rings 1–4 had large numbers either missing or partially sampled as core samples had missed the pith. For these reasons, rings 1 to 4 from pith were omitted from the analyses. Therefore, core density at 5 years was mean ring density for the fifth ring from the pith, while core densities for subsequent ages were weighted ring densities for that year and younger ages. The weighting used was the basal area of each growth ring using ring-width data and assuming that each growth ring after the first ring was perfectly circular. Thus, the final core density was the weighted mean of rings 5–25 from the pith. Wood from rings at the same age in the three plantings made in different years was laid down in different years but was the same age from the pith. The data were highly unbalanced, and only families represented in at least two replications on each site were included in the analyses. The total number of trees included in the analyses was 605 comprising 63 families from 83 parents.

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:

$$[1] \qquad Y_{ijklm} = \mu + S_i + \mathrm{Set}_j + R_k + F_l + A_m + \varepsilon_{ijklm}$$

where Y_{ijklm} is the observation on the mth tree in the ith site in the jth set in the kth replicate and lth family, μ is the overall mean, S_i is the random effect of the ith site, Set_j is the random effect of the jth set (i.e., set of families), R_k is the random effect of the kth replicate, F_l is the random effect of the lth family, A_m is the additive genetic effect of the mth tree, and ε_{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^2_F) was in-

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terpreted as $1/4\sigma_D^2$, 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 (Dungey et al. 2000; Gwaze et al. 1997).

Preliminary analysis indicated that heritability estimates for earlywood, latewood, and ringwood varied inconsistently with ages. Also, early selection in tree breeding programs is more likely to be based on core density than on earlywood, latewood, or ringwood so as to lessen the effect of abnormal seasons due to drought or flood that may significantly decrease or increase the ring based density values in a single season. Core density is by far the most important wood trait for most wood products, since it is a composite trait of several important wood traits, e.g., percentage of latewood, cell size, and cell wall thickness (Zobel and Talbert 1984). Hence, trends in variances, trends in heritability, and inferences on early selection were all based on core density.

The following equation was fitted to age–age genetic correlations between core density at younger age and core density at 25 years (Lambeth 1980):

$$[2] \qquad r_g = \beta_0 + \beta_1 \times \log_e\left(\frac{\text{younger age}}{25}\right)$$

The regression equation was fitted to extrapolate correlations at ages not assessed and to generally correct for irregularities in the correlations. The same model was fitted to age–age phenotypic correlations. To predict heritability estimates for ages at which no assessments were taken, linear and nonlinear regression equations were fitted to heritability estimates and 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):

$$[3] \qquad E_{gen} = \frac{h_j r_g}{h_m}$$

where E_{gen} is the gain efficiency, r_g is the genetic correlation between the juvenile trait and mature trait, and h_j and h_m are the square roots of individual tree heritability at juvenile and mature ages, respectively.

The gain efficiency per generation is the ratio of predicted genetic gain at maturity from indirect selection based upon early selection, relative to the predicted gain at maturity from direct selection at maturity. Gain efficiency per year (E_{year}) was calculated as follows:

$$[4] \qquad E_{year} = \frac{h_j r_g T_m}{h_m T_j}$$

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 phase for *P. taeda* in the United States and is the time from making selection to progeny testing. Previously, the breeding phase was 10 years for *P. taeda* (McKeand 1988), but this has been reduced to less than 5 years because of the widespread use of the top grafting technology (Bramlett et al. 1995). Optimum selection age was also determined assuming a breeding phase of 10 years to test the effect of the different breeding phases on optimum selection age.

Results and discussion

Means

Core density increased with age from 0.396 at 5 years, peaking at age 11 years at 0.490 and remained fairly constant thereafter. The mean values for core wood density at 20 years were consistent with those reported by Talbert et al. (1983) for *P. taeda*. Analyses of variance indicated that families differed in core density at all ages.

Variance components and heritability estimates

The phenotypic variance was slightly low at 5 and 6 years of age and remained fairly constant thereafter (Fig. 1). Additive variance decreased with age from 5 to 7 years, remained constant between 7 and 10 years, and then increased again with age until age 12 when it levelled off. On the other hand, nonadditive variance was very low at 5 years and increased with age until age 7 years then remained constant. Additive variance was higher than nonadditive variance at ages younger than 7 years but was about equal to nonadditive at 7 years or older ages. Heritability for core density was high at early ages (0.31 at age 5), declined slightly to minimum of 0.2 at 10 years before increasing to 0.28 at 13 years, and remaining constant thereafter (Fig. 2). The high standard errors of the heritability estimates (0.16–0.20) were due to the small number of progeny (605). The standard errors increased with an increase in the heritability estimate. The high heritability estimates at early ages are due to high additive variance and low phenotypic variances. Previous studies have reported heritability estimates for core density for *P. taeda* to be greater than 0.4 (Loo et al. 1984; Talbert et al. 1983). Furthermore, Gwaze (1997) summarized heritability estimates of wood density of *P. taeda* from various studies and found that it ranged from 0.42 to 1. Therefore, heritability estimates from this study were much lower than the previous estimates in *P. taeda* but were very comparable with those found by Hodge and Purnell (1993) for slash pine. The difference between the heritability estimates from this study and those from previous studies may partly be due to different models used in estimating the heritabilities (Mohiuddin 1993). This study used an individual-tree model that takes into account all relationships present in the pedigree, and previous studies have used parental models. Phenotypic variance may be larger than other studies for two reasons. First, the random thinning done at age 10 may have created differential growing space and, thus, diameter growth. Second, the wood produced at a given age from pith was, in fact, laid down in three successive years because of the successive annual plantings. The low heritability might also be attributed to the fact that the parent trees were 35-year-old natural stand trees from one geographic area with limited genetic variation. All these factors in combination might be viewed quite positively as providing a realistic estimate of heritability more relevant to real world forestry practice than those obtained from genetic trails where these factors are more tightly controlled.

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Fig. 1. Age trends in additive, nonadditive, and phenotypic variances for core density.

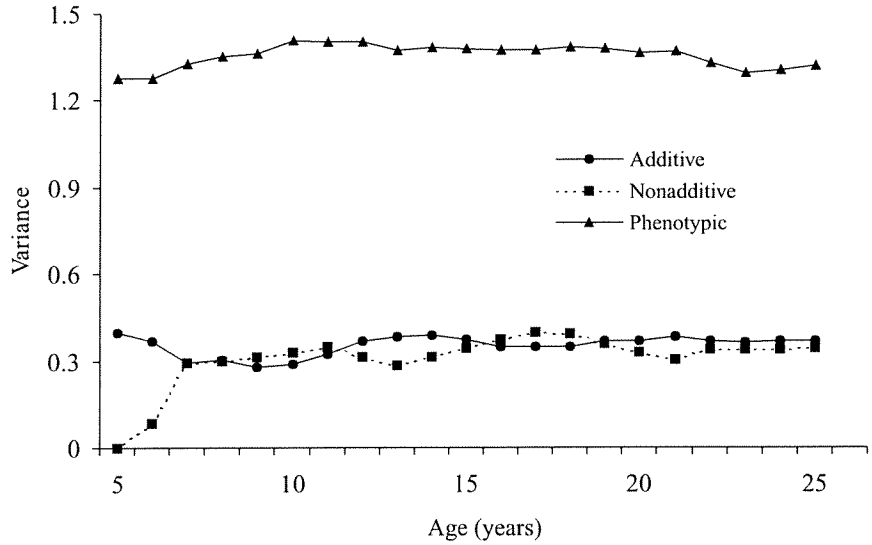
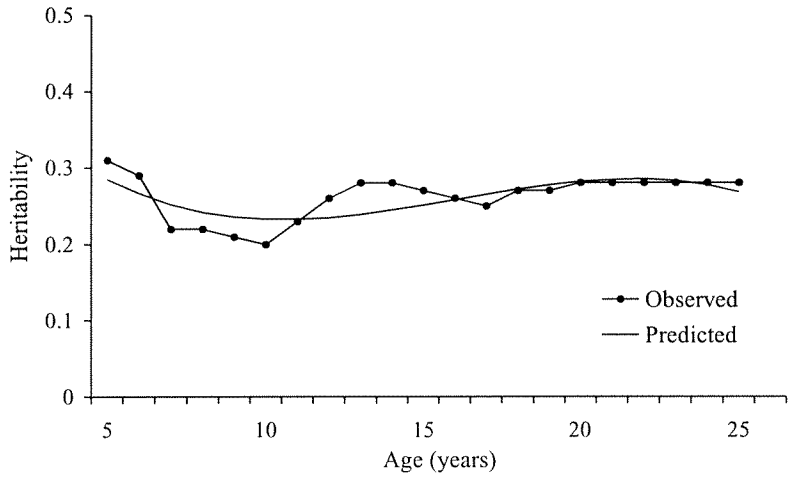


Fig. 2. Age trends in heritability estimates of overall core density. The range of the standard errors of the heritability estimates was 0.16–0.20.



The relationship between heritability estimates for core density and age was essentially nonlinear (h^2 = 0.465 – 0.0525 × age + 0.000 370 × age^2 – 0.000 076 4 × age^3, R^2 = 0.44; Fig. 2). Although the R^2 was low the above relationship was significant (P = 0.018). Since the linear model was not significant (P = 0.10; R^2 = 0.14) and given the relatively low R^2 for the nonlinear model and the biological difficulties to explain this model, a constant heritability with age was appropriate for estimating the optimum selection age.

Age–age correlations

Age–age genetic and phenotypic correlations for core densities were positive and strong (Fig. 3). The high correlations between early core densities and core density at 25 years is expected given the autocorrelations involved, since early core densities are included in the core at 25 years. To remove effects of autocorrelations, correlations should be estimated using ring densities. Vargas-Hernandez and Adams (1992) observed that the age–age genetic correlations for core density were similar to those of individual rings suggesting that age–age genetic correlation of core densities were unlikely to be influenced by autocorrelations. Similarly, Borralho et al. (1992) observed little difference between genetic parameters for absolute and incremental growth traits suggesting little inflation due to autocorrelation.

Phenotypic and genetic correlations between core density at each age and core density at 25 years increased as the age differential decreased. Genetic and phenotypic correlations were similar at older ages, but at younger ages, genetic correlations were much higher than their phenotypic counterparts, indicating that phenotypic correlations decreased more rapidly as age difference increased (Fig. 3). Therefore, assuming the phenotypic correlations are equal to genetic correlations is likely to underestimate potential gain from early selection and lead to conservative estimates of optimum selection ages for core density, as has been observed in growth traits (e.g., Gwaze et al. 1997). Standard errors of genetic correlations decreased with an increase in the genetic corre-

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Fig. 3. Trends in age–age genetic (r_g) and phenotypic (r_p) correlations between core density from 5 to 24 years and core density at 25 years. The range of the standard errors of r_g was 0–0.11 and that for r_p was 0–0.03.

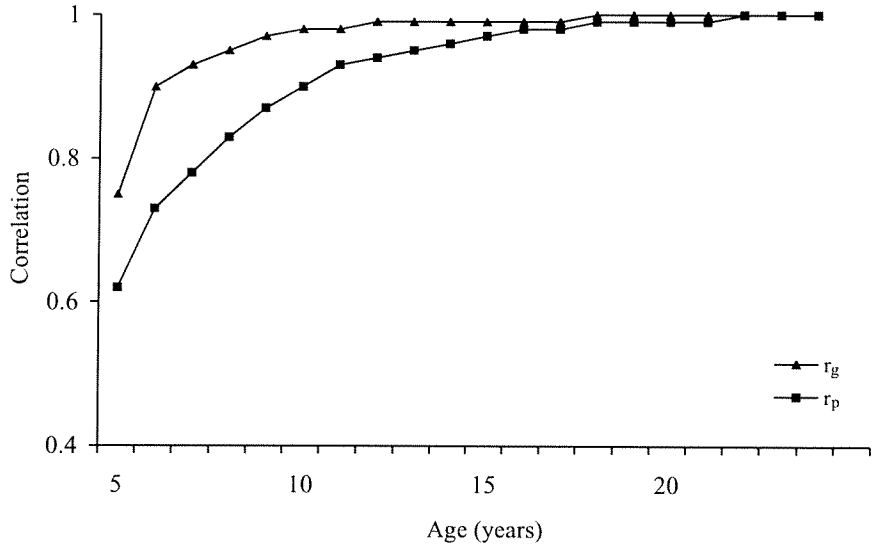

Table 1. Results of fitting age–age correlation linear models for core density.

	Regression coefficient				
Independent variable	Intercept	Slope	Residual MS	df	R^2
Genetic correlation	1.03 (0.014)	0.098 (0.018)	0.0014	18	0.62
Phenotypic correlation	1.05 (0.014)	0.210 (0.018)	0.0014	18	0.88

Note: Standard errors of coefficients are given in parentheses.

lation itself. They varied from 0.11 when the genetic correlation was 0.75 to between 0 and 0.07 when the genetic correlation was higher than 0.90. Genetic correlations involving core density at a very young age were slightly lower than those reported by Loo et al. (1984) in *P. taeda* who found genetic correlations to be 0.96 between core density at 2 years and core density at 25 years.

The estimated regression slope for the genetic correlations was significantly lower than that of phenotypic correlations ($P < 0.05$) (Table 1), indicating that predictions of phenotypic correlations declined more rapidly than genetic correlations as age differential increased. Age–age genetic correlations for core density were moderately described by the logarithm model ($r^2 = 0.62$), while the phenotypic correlations were well described by the same model ($r^2 = 0.88$) (Table 1). The slope of the age–age genetic correlations was smaller than that obtained in growth traits using older genetic tests but similar to slope derived from advanced generation tests (Gwaze et al. 2000). This implies that density might be selected earlier than growth traits as suggested by Loo et al. (1984) and Williams and Megraw (1994), particularly when selection decisions are based on older genetic tests.

Efficiency of early selection

The optimum selection age for core density was estimated to be 5 years when calculations were based on genetic correlations, and the optimum selection age was robust to changes in breeding phase (Figs. 4 and 5). Optimum selection age derived assuming a constant heritability across ages was similar to that derived taking into account the age-related heritability trends. Optimum selection age based on phenotypic correlations was 1 or 2 years higher than that based on genetic correlations. The study confirms that selecting at very young age is effective for wood density as suggested by Loo et al. (1984) and Williams and Megraw (1994). Extrapolating to ages younger than 5 (the youngest age measured in the current study) suggested that selecting at 1 or 2 years may be effective for core density. However, these ages were outside the range of our data, and further studies would be necessary to determine if optimum selection ages younger than 5 are feasible.

It should be noted that the cores in this study were measured at breast height, and hence, age 5 cores might actually be 8 years from seed (Williams and Megraw 1994). Therefore, the optimum selection age for tree density may be slightly older than that predicted in this study. Gain from early selection was higher when genetic correlations were used than when phenotypic correlations were used. Early selection for core density would result in correlated increase in early wood density but little progress in latewood density or latewood proportion at 25 years (Table 2).

Conclusion

Heritability estimates for core density were moderate and lower than expected. Age–age correlations were high and higher than corresponding phenotypic correlations. The study showed that age–age genetic correlations were moderately described by the logarithm prediction model developed

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Fig. 4. Efficiencies of selection for core density at different ages, different breeding phases and assuming variable heritability. Values are the breeding phase in years. The arrow indicates the youngest age measured in the current study. r_g, genetic correlation; r_p, phenotypic correlation.

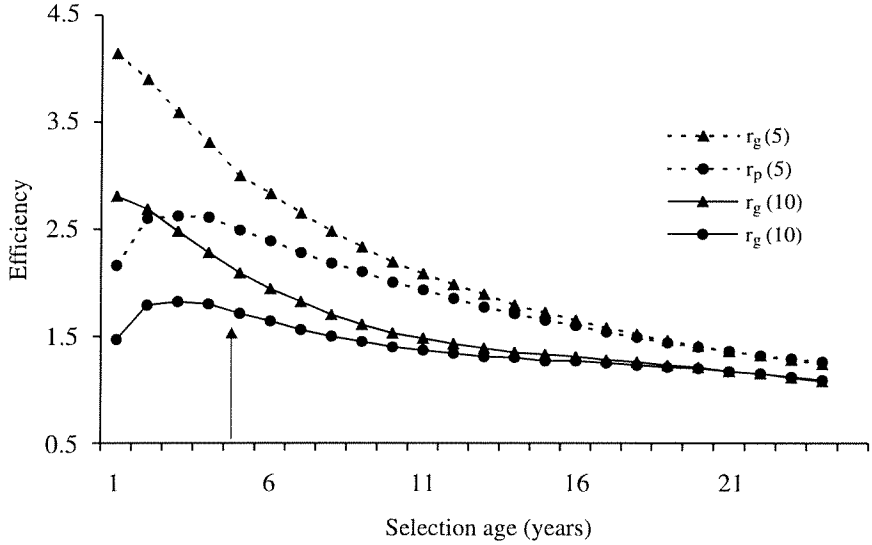

Fig. 5. Efficiencies of selection for core density at different ages, using different breeding phases and assuming constant heritability. Values are the breeding phase in years. The arrow indicates the youngest age measured in the current study. r_g, genetic correlation; r_p, phenotypic correlation.

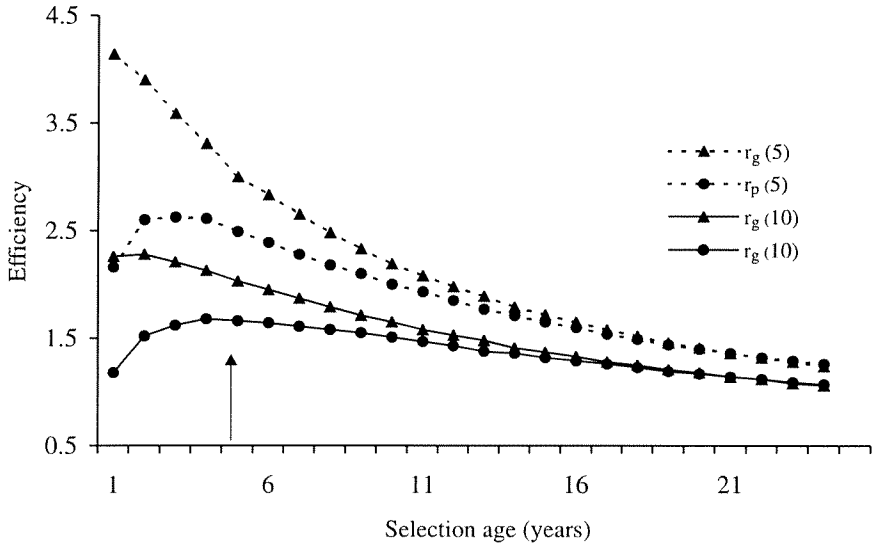

Table 2. Genetic and phenotypic correlations between core density (core) at ages 5–7 years and earlywood density (EW), latewood density (LW), ringwood density (ring) and latewood proportion at 25 years.

	Genetic correlations					Phenotypic correlations				
Age (years)	EW	LW	Ring	Core	LW proportion	EW	LW	Ring	Core	LW proportion
5	0.81 (0.25)	0.15 (0.35)	0.59 (0.32)	0.75 (0.11)	0.54 (0.37)	0.16	0.21	0.20	0.62	0.10
6	0.80 (0.22)	0.25 (0.32)	0.62 (0.29)	0.90 (0.06)	0.48 (0.35)	0.20	0.22	0.23	0.73	0.12
7	0.87 (0.20)	0.33 (0.30)	0.67 (0.25)	0.93 (0.04)	0.48 (0.34)	0.22	0.25	0.27	0.78	0.15

Note: Standard errors of genetic correlations are given in parentheses.

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by Lambeth. As demonstrated in growth traits, genetic gain predicted using phenotypic correlation model was less that that predicted using genetic correlation model.

Optimum selection age for core density in our study was estimated to be 5 years when calculations were based on genetic correlations or phenotypic correlations. However, age 5 data were the youngest reported and optimum selection age could be less than 5. Optimum selection ages were robust to changes in breeding phase and assumptions concerning age-related variation in heritability estimates. Early selection for core density would result in correlated increase in earlywood density, but little progress in latewood density or latewood proportion at maturity. In the future, possibilities of early selection for wood density at ages younger than 5 should be explored.

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