GENETIC PARAMETER ESTIMATES FOR GROWTH AND WOOD DENSITY IN LOBLOLLY PINE (*PINUS TAEDA* L.)

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ReceivedAugust 14, 2000; accepted February 22, 2001

ABSTRACT

Phenotypic and genetic parameters for height, diameter and wood density of loblolly pine (*Pinus taeda* L.) established at four different years between 1967 and 1974 in the Western Gulf area of the United States were estimated using an individual tree model. The trees were assessed for height and diameter at 5-year intervals from 5 to 25 years. Unextracted wood density for each tree was determined for 0 to 5-year core, 6 to 20-year core and the total core. The parents were phenotypic selections from natural stands in Arkansas, Louisiana and Mississippi in the United States. Estimates of individual tree heritabilities suggested that wood density and height were strongly inherited (h^2 = 0.15–0.78) and that diameter was less strongly inherited (h^2 = 0.04–0.61). Age-age correlations indicated that all traits were highly correlated at both the phenotypic and genetic levels, particularly the latter. Trait-trait correlations indicated that genetic correlations between height and diameter were generally positive and varied from low to high, but those between growth and wood density traits were consistently unfavorable. Efficiencies of early selection indicated that growth at maturity could be improved by early selection of same growth trait, and similarly wood density at maturity could be improved by selecting for juvenile wood density. However, early selection for growth may result in a decline in wood density at maturity or the converse. To improve both the quantity and quality of wood, selection schemes that include both growth and wood density traits will need to be developed or growth and wood density may need to be improved in separate populations depending on the breeding objectives.

Keywords: heritability, genetic correlation, efficiency of selection, REML, *Pinus taeda* L.

INTRODUCTION

Loblolly pine (*Pinus taeda* L.) is one of the major commercial conifer species in the USA, where it occurs naturally, comprising more than 50% of the standing volume of pine (BAKER & LANGDON 1990). It is the most important commercial timber species in the southeastern United States. Genetic improvement of the species began in the 1950's with selections initially from natural stands and plantations, and thereafter from well-designed progeny tests (DORMAN 1976).

Phenotypic and genetic parameters are needed to estimate accurate breeding values, to combine different traits in selection, to predict genetic response to selection and to develop efficient breeding plans. Heritability estimates for height reported in *P. taeda* in the USA are moderate to high (BALOCCHI *et al.* 1993, FRANKLIN 1979), those for diameter are low to moderate and lower than those for height (FOSTER 1986). The most widely measured trait related to wood properties is wood density or specific gravity, because it is well correlated with major strength properties of sawn timber and with pulp and paper properties (VAN BUIJTENEN 1969). Heritability estimates for wood density in *P. taeda* are reported to be high (LOO *et al.*1984, TALBERT *et al.* 1983, WILLIAMS & MEGRAW 1994).

Reports on genetic correlations of *P. taeda* indicate that those between height and diameter are positive and moderate to high (BRIDGWATER *et al.* 1983, FOSTER 1986). Those between growth and wood density range from slightly negative (LOO *et al.* 1984) to slightly positive (WILLIAMS & MEGRAW 1994). In other conifers both negative genetic correlations between density and diameter or volume (BURDON & LOW 1992, VARGAS-HERNANDEZ & ADAMS 1991), and positive genetic correlations between density and height, have been reported (BURDON & LOW 1992). According to ZOBEL & TALBERT (1984), both positive and negative genetic correlations between growth traits and wood density are common in forest tree species. These reports indicate that the relationship between growth and wood density may be population specific, and hence cannot be extrapolated across populations.

This paper reports the variance components, heritabilities and correlations for height, diameter and wood density for *P. taeda* grown in the Western Gulf area of the United States using an individual tree model. In tree breeding programs there are limited numbers of reports of data analysed using an individual model – a model of choice in animal breeding – despite its desirable properties of incorporating all known information of the genetic relationships of all trees in a genetic test. 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. This model is particularly important for full-sib mating designs and in advanced generation breeding where information on relatives (both parents, grandparents, etc.) may be available and needs to be considered in the analysis.

General and specific combining abilities for growth traits were presented by BYRAM & LOWE (1986) and family heritability estimates and coefficients of genetic prediction for wood density by LOWE & BYRAM (1995) for *P. taeda* grown in the Western Gulf area. The present study reports the relationship between growth traits and wood density, and estimates individual tree phenotypic and genetic parameters. Potential breeding implications of the above mentioned relationships are considered.

MATERIALS

The data were from a mixture of half and full-sib families involving a total of 33 first-generation parents selected for good growth. The parents were selected phenotypically from natural stands in Arkansas, Louisiana and Mississippi in the United States of America. Georgia-Pacific Corporation, a member of the Western Gulf Forest Tree Improvement Program, established four tests, each having a different set of families, in Ashley County over a period of 7 years from 1967 to 1974. Ashley County is located in southeastern Arkansas, USA, which receives a mean annual rainfall of about 1300 mm per annum and with average temperature of 28 °C in July and 7 °C in January (USDA FOREST SERVICE 1969). Trees were assessed for height and diameter at 5, 10, 15, 20 and 25 years of age (Table 1). At 20 years of age, 9 mm cores of wood were extracted at breast height (1.4 meters) from randomly selected trees within a plot using an increment borer. Wood density estimates at breast height are known to be a reliable predictor of average wood density of a tree (MAGNUSSEN *et al.* 1985). About 20 trees were sampled per family in each test. Each of the extracted cores was divided into 2 parts: first five years from pith to assess juvenile wood density and 6–20 years to assess mature wood density. Age 5 years was selected as the age to assess juvenile density because selections for growth are made at 5 years in the Western Gulf Forest Tree Improvement Program (WGFTIP), and correlations between 5-year density and total core wood density were of major interest. Unextracted basic density was determined for the 0–5-year core, the 6–20-year core and for the total core using the maximum moisture content method described by SMITH (1954). All the tests were thinned at ages 15 and 20 years, except GP103 that was not thinned. Trees were planted at 2.4 × 2.4 metres spacing and each plot comprised 9–64 trees. The tests comprised 3–10 replicates in a randomised complete block design.

METHODS

The least square means were estimated using general linear model (GLM) procedure of SAS® (SAS INSTITUTE INC. 1985). Genetic parameters were estimated using the individual tree model ASREML (GILMOUR 1996). Individual-tree heritabilities and their standard errors were estimated using a univariate model. Genetic correlations and their standard errors were estimated using a bivariate individual tree model. Variance components for individual sites were estimated using the following individual tree model:

$$Y_{ij} = \mu + R_i + A_j + \epsilon_{ij} \qquad [1]$$

where: Y_{ij} = is the observation on the jth tree in the ith replication, μ = overall test mean, R_i = fixed effect of the ith replication, A_j = additive genetic effect of the jth tree, and ϵ_{ij} = residual term, assumed to be normally distributed with mean 0 and variance σ^2.

Data were not pooled across years to improve the precision of the parameter estimates because different sets of families were planted at each of the planting

Table 1. Details of genetic tests used in the analyses.

Test	Year planted	Reps	Plot size	No. of families	Age of assessment (years)				
					5	10	15	20	25
GP065	1974/5	10	10	47	■	■	■	■	
GP102	1967/8	3	64	38		■	■	■	■
GP103	1967/8	6	9	22			■	■	
GP258	1968/9	5	36	28		■	■	■	■

years.

The efficiency of early selection per generation was estimated using the method of FALCONER (1989). Assuming the selection intensities at the young age at mature ages are equal, the efficiency of early selection can be expressed as:

$$E = h_J . r_A . h_M^{-1} \quad [1]$$

where r_A is the additive genetic correlation between juvenile and the mature traits and h_J and h_M are the square roots of the narrow-sense heritabilities of juvenile and mature traits, respectively. These efficiencies indicate the relative genetic gain from indirect selection on a juvenile trait to achieve gain in a mature trait compared to direct selection on the mature trait itself. The juvenile traits were 5 and 10-year growth and juvenile wood density, and mature traits were 20 and 25-year growth and total wood density. Equation [1] gives a conservative estimate of efficiency of early selection since in practice the selection intensity at the mature age will be less than that at juvenile age (COTTERILL & DEAN 1988). Efficiency of selection per year was calculated as follows:

$$E = h_j . r_A . h_m^{-1} . T_m . T_j^{-1} \quad [2]$$

where T_j and T_m are the generation interval for juvenile and mature selection (assumed to be 20 years), respectively. The generation interval was the selection age plus 10 years. Ten years is the breeding phase for *Pinus taeda* in the USA (MCKEAND 1988), and is the time from making selection to progeny testing.

RESULTS AND DISCUSSION

Means

The total number of trees at each of the assessment ages depended on the number of families, number of replications, plot sizes, thinning, mortality and whether or not all trees per plot were assessed (Appendix 1). For example, the number of trees assessed at age 10 years in GP258 was lower than those assessed at 15 years because only the inner 16 trees per plot were assessed at age 10 years. Survival varied among the trials, being lowest at GP103 (72%), moderate at GP102 (79 %) and GP065 (82 %) and high at GP258 (90 %) at 15 years of age. At 10 years of age, trees at GP102 were largest both in height and diameter followed by those at GP258, and they maintained their superiority at 20 years of age (Appendix 1). Although the fastest growing tests did not necessarily have the lowest wood densities, the slowest growing test (GP103) had the highest wood density. The mean values for wood density were higher than those reported by TALBERT *et al.* (1983) (0.353 $g \cdot cm^{-3}$ at 7 years and 0.402 $g \cdot cm^{-3}$ at 20 years of age). The difference between the means from our study and those from TALBERT *et al.* (1983) study may be due to the relatively large sample size of 280 half-sib families in the latter study or may be due to environmental differences between the two studies.

Variance components and heritability estimates

In general, the additive and residual variance for growth traits increased with age, particularly for diameter, due mainly to scale effects (Appendix 2). Residual variances for growth traits were much larger than the corresponding additive variances, but not for wood density traits, and in particular those for mature and total wood densities. There were no apparent differences between additive variances from thinned tests and the unthinned test. This result is not consistent with that of COTTERILL & DEAN (1988) who found the additive variances were higher in unthinned populations. This is probably due to low survival in the unthinned test in our study.

Heritability estimates for height were moderate to high (0.15–0.63), and those for diameter were low to high (0.04–0.61) (Table 2). Despite the fact that most previous *P. taeda* studies were based on family models, heritability estimates for height reported here were within the range reported in these studies (range, 0.10–0.69) (BALOCCHI *et al.* 1993, FRANKLIN 1979, GWAZE *et al.* 1997, WILLIAMS & MEGRAW 1994). However, the estimates in the upper part of the range in these previous studies were obtained mainly from short-term tests planted at close spacing (e.g. WILLIAMS & MEGRAW 1994). Short-term tests accelerate stand development and hence lead to different changes in variances with age compared to conventional tests (FRANKLIN 1989). Heritability estimates for diameter were generally lower than those for height, as observed by BRIDGWATER *et al.* (1983) and FOSTER (1986), but heritability estimates for diameter reported here were higher. There was no detectable trend for heritability estimates with age for height, but those of diameter appeared to increase with age. Heritability estimates from unthinned test (GP103) were generally lower than those from thinned tests as observed by COTTERRILL & DEAN (1988). While the low heritability estimates in Cotterill and Dean's study were attributed to high phenotypic variances due to competition, in this study it is attributed to differential spacing caused by uneven survival.

Heritability estimates for wood density were generally higher than those for growth traits. Heritabi-

Table 2. Heritability estimates for growth and wood density at four tests and five ages.

Trait	h^2 (standard error)			
	GP065	GP102	GP103	GP258
H05	0.15 (0.05)	-	-	-
H10	0.16 (0.05)	0.63 (0.11)	-	0.41 (0.15)
H15	0.21(0.06)	0.52 (0.12)	0.23 (0.12)	0.39 (0.12)
H20	0.24 (0.08)	0.33 (0.11)	0.19 (0.10)	0.51 (0.14)
H25	-	0.35 (0.12)	-	0.43 (0.15)
D05	0.11 (0.04)	-	-	-
D10	0.17 (0.05)	0.07 (0.04)	-	0.61 (0.18)
D15	0.24 (0.07)	0.07 (0.03)	0.04 (0.03)	0.28 (0.11)
D20	0.34 (0.10)	0.12 (0.06)	0.07 (0.05)	0.39 (0.14)
D25	-	0.30 (0.12)	-	0.48 (0.16)
DenJ	0.43 (0.16)	0.38 (0.15)	0.18 (0.14)	0.39 (0.17)
DenM	0.48 (0.14)	0.54 (0.17)	0.78 (0.24)	0.62 (0.20)
DenT	0.48 (0.14)	0.55 (0.17)	0.69 (0.24)	0.63 (0.21)

Table 3. Age- age genetic and phenotypic correlations for growth.

Trait	Age, Age	Genetic correlations (se)				Phenotypic correlations			
		GP065	GP102	GP103	GP258	GP065	GP102	GP103	GP258
Height	5,10	0.90 (0.05)	-	-	-	0.81	-	-	-
	5,15	0.90 (0.06)	-	-	-	0.71	-	-	-
	5,20	0.89 (0.07)	-	-	-	0.57	-	-	-
	10,15	0.93 (0.04)	0.99 (0.00)	-	0.90 (0.05)	0.89	0.94	-	0.88
	10,20	0.93 (0.04)	0.95 (0.03)	-	0.85 (0.08)	0.75	0.85	-	0.78
	10,25	-	0.94 (0.04)	-	0.90 (0.07)	-	0.75	-	0.73
	15,20	1.00	0.98 (0.01)	0.95 (0.04)	0.98 (0.01)	0.90	0.92	0.93	0.93
	15,25	-	0.98 (0.01)	-	0.99 (0.01)	-	0.88	-	0.90
	20,25	-	0.96 (0.03)	-	1.00	-	0.89	-	0.95
DBH	5,10	0.85 (0.07)	-	-	-	0.81	-	-	-
	5,15	0.87 (0.07)	-	-	-	0.70	-	-	-
	5,20	0.80 (0.11)	-	-	-	0.61	-	-	-
	10,15	0.97 (0.02)	0.94 (0.04)	-	0.97 (0.02)	0.96	0.96	-	0.95
	10,20	0.92 (0.04)	0.89 (0.08)	-	0.96 (0.02)	0.90	0.91	-	0.90
	10,25	-	0.89 (0.08)	-	0.92 (0.05)	-	0.83	-	0.82
	15,20	0.99 (0.01)	0.98 (0.01)	0.98 (0.03)	0.99 (0.01)	0.98	0.98	0.98	0.98
	15,25	-	0.93 (0.05)	-	0.97 (0.02)	-	0.94	-	0.96
	20,25	-	0.98 (0.00)	-	1.00	-	0.96	-	0.98

lity estimates for juvenile density (range, 0.18–0.43) were less than those for mature density and total density (range, 0.48–0.78). Apart from the rather low estimate of 0.18, the results reported here were consistent with those reported in other studies in *P. taeda* (LOO *et al.* 1984, TALBERT *et al.* 1983, WILLIAMS & MEGRAW 1994). GWAZE (1997) summarized heritability estimates of wood density of *P. taeda* from various studies and found that it ranged from 0.42 to 1. Heritability estimates for mature and total wood densities were highest in the test with the lowest growth rate and highest mean wood densities (GP103).

Despite the relatively lower heritability estimates for diameter than height and wood density, the potential to improve diameter is good since the phenotypic variance of diameter was greater than that of height or wood density. For example, the coefficients of variation at 20 years were 14–24 % for diameter, 7–11 % for height and 5.5–6.2 % for wood density. Furthermore, diameter is easier and less costly to assess than height, particularly after canopy closure and on tall trees.

Genetic and phenotypic correlations of growth traits

Age-age correlations

Age-age genetic correlations were high for both height and diameter in all the four tests, being greater than 0.8 (Table 3). This indicates that early selection for height or diameter may be efficient. Generally, the age-age genetic correlations for height were higher than those for diameter, especially for GP065 and GP102, but not for GP258. In all the tests genetic correlations were higher than the corresponding phenotypic correlations, a result also observed by (GWAZE *et al.* 1997, MCKEAND 1988). NEWMAN & WILLIAMS (1991) carried out a literature survey of genetic and phenotypic correlations in *P. taeda* and found that genetic correlations were higher than phenotypic correlations, an observation reported also in other conifer species (PSWARAYI *et al.* 1996) and in animals (KOCH *et al.* 1982).

Correlations between height and diameter

Genetic correlations between height and diameter were moderate to high for GP065 and GP258 (>0.7), but were low for GP102 and GP103 (Table 4). Genetic correlations were higher than the corresponding phenotypic correlations for GP065 and GP258, but not for GP102 and GP103. The poor relationship between height and diameter in GP103 and GP102 is difficult to explain but may be attributed to lack of thinning in the former and low survival in both tests. Low survival may have resulted in a large proportion of trees having a large growing space that gave rise to short trees with relatively large diameters. The results, therefore, show that early height selection may not always be a good predictor of diameter at maturity, and vice versa.

Genetic and phenotypic correlations between wood density traits, and wood density and growth traits

Genetic and phenotypic correlations between juvenile wood density and mature wood density were moderate to high (0.36–0.95; Table 5). Genetic correlations between juvenile and mature wood density were generally lower (0.52–0.95) than those between juvenile or mature wood density and total wood density (>0.8). These results are consistent with those of TALBERT *et al.* (1983) who found that the genetic correlations between juvenile and mature wood density in *P. taeda* were high (>0.88). The high genetic correlations between juvenile or mature wood densities and total wood density are

Table 4. Trait–trait genetic and phenotypic correlations for growth.

Trait–trait	Genetic correlations (se)				Phenotypic correlations			
	GP065	GP102	GP103	GP258	GP065	GP102	GP103	GP258
H05 - D05	0.97 (0.02)	–	–	–	0.94	–	–	–
H05 - D10	0.86 (0.07)	–	–	–	0.83	–	–	–
H05 - D15	0.87 (0.07)	–	–	–	0.73	–	–	–
H05 - D20	0.79 (0.10)	–	–	–	0.65	–	–	–
H10 - D05	0.81 (0.09)	–	–	–	0.76	–	–	–
H10 - D10	0.84 (0.07)	0.75 (0.13)	–	0.92 (0.03)	0.87	0.76	–	0.85
H10 - D15	0.83 (0.08)	0.55 (0.21)	–	0.75 (0.11)	0.81	0.69	–	0.78
H10 - D20	0.80 (0.09)	0.08 (0.33)	–	0.75 (0.12)	0.75	0.52	–	0.71
H10 - D25	–	0.04 (0.32)	–	0.74 (0.13)	–	0.43	–	0.62
H15 - D05	0.84 (0.08)	–	–	–	0.65	–	–	–
H15 - D10	0.84 (0.07)	0.74 (0.14)	–	0.80 (0.11)	0.83	0.75	–	0.75
H15 - D15	0.91 (0.04)	0.31 (0.31)	-0.21(0.51)	0.82 (0.09)	0.84	0.70	0.69	0.76
H15 - D20	0.91 (0.05)	0.14 (0.33)	0.28 (0.42)	0.88 (0.06)	0.85	0.61	0.79	0.67
H15 - D25	–	0.20 (0.31)	–	0.85 (0.08)	–	0.56	–	0.57
H20 - D05	0.84 (0.10)	–	–	–	0.49	–	–	–
H20 - D10	0.87 (0.07)	0.40 (0.29)	–	0.82 (0.09)	0.73	0.66	–	0.68
H20 - D15	0.93 (0.04)	-0.03 (0.33)	0.29 (0.45)	0.75 (0.13)	0.76	0.64	0.76	0.70
H20 - D20	0.94 (0.03)	-0.07 (0.32)	0.52 (0.32)	0.82 (0.09)	0.77	0.55	0.79	0.62
H20 - D25	–	0.16 (0.30)	–	0.83 (0.09)	–	0.54	–	0.58
H25 - D10	–	0.47 (0.27)	–	0.84 (0.10)	–	0.57	–	0.61
H25 - D15	–	0.06 (0.34)	–	0.72 (0.17)	–	0.58	–	0.64
H25 - D20	–	-0.07 (0.34)	–	0.72 (0.15)	–	0.51	–	0.52
H25 - D25	–	0.34 (0.27)	–	0.75 (0.13)	–	0.52	–	0.51

expected given the autocorrelations involved since juvenile and mature cores are parts of the total core. Phenotypic correlations were always lower than the genetic correlations, and lowest between juvenile and mature wood density. These results indicate that juvenile wood density is a good predictor of total wood density but may not necessarily be an efficient predictor of mature wood density. Since the selections for growth traits are being made at 5 years in the WGFTIP it appears that selections for wood density could be made at the same time. It should, however, be noted that cores in this study were taken at breast height on 20-year old trees and trees varied in rate of growth. The cores in this study were measured at cambial age, and the cambial age may differ from calendar age. Therefore, results from this study might differ slightly from studies where wood density was determined on 5 and 20-year old trees.

Genetic correlations between growth traits and wood density traits were highly negative to slightly

Table 5. Genetic and phenotypic correlations between wood density traits, and height and wood density traits.

Trait–trait	Genetic correlations (se)				Phenotypic correlations			
	GP065	GP102	GP103	GP258	GP065	GP102	GP103	GP258
DenJ - DenM	0.60 (0.20)	0.52 (0.24)	0.95 (0.07)	0.76 (0.15)	0.54	0.36	0.49	0.52
DenJ - DenT	0.84 (0.09)	0.85 (0.09)	0.99 (0.04)	0.92 (0.05)	0.85	0.81	0.82	0.85
DenM - DenT	0.96 (0.03)	0.90 (0.06)	0.99 (0.01)	0.94 (0.04)	0.86	0.81	0.87	0.87
H05 - DenJ	-0.24 (0.30)	-	-	-	-0.02	-	-	-
H05 - DenM	-0.43 (0.24)	-	-	-	-0.27	-	-	-
H05 - DenT	-0.33 (0.26)	-	-	-	-0.13	-	-	-
H10 - DenJ	-0.27 (0.28)	0.08 (0.38)	-	0.18 (0.39)	-0.02	0.06	-	-0.02
H10 - DenM	-0.33 (0.24)	-0.05 (0.35)	-	0.06 (0.38)	-0.26	0.01	-	-0.13
H10 - DenT	-0.29 (0.25)	0.01 (0.36)	-	0.29 (0.33)	-0.14	0.01	-	-0.06
H15 - DenJ	-0.37 (0.27)	-0.25 (0.36)	-0.55 (0.48)	-0.31 (0.37)	-0.07	0.01	0.03	-0.22
H15 - DenM	-0.49 (0.21)	-0.32 (0.33)	0.07 (0.47)	-0.08 (0.38)	-0.29	-0.01	-0.09	-0.19
H15 - DenT	-0.41 (0.24)	-0.31 (0.33)	0.07 (0.49)	-0.13 (0.39)	-0.14	-0.01	0.03	-0.24
H20 - DenJ	-0.48 (0.26)	-0.07 (0.33)	-0.94 (0.18)	-0.39 (0.33)	-0.11	0.05	0.02	-0.18
H20 - DenM	-0.55 (0.21)	-0.14 (0.31)	-0.21 (0.46)	-0.16 (0.35)	-0.25	-0.01	-0.16	-0.17
H20 - DenT	-0.50 (0.23)	-0.07 (0.32)	-0.22 (0.49)	-0.29 (0.34)	-0.13	0.04	0.00	-0.21
H25 - DenJ	-	-0.02 (0.33)	-	-0.30 (0.35)	-	0.02	-	-0.18
H25 - DenM	-	-0.05 (0.31)	-	-0.11 (0.35)	-	0.01	-	-0.15
H25 - DenT	-	0.02 (0.31)	-	-0.22 (0.35)	-	0.05	-	-0.20

Table 6. Genetic and phenotypic correlations between diameter and wood density traits.

Trait–Trait	Genetic correlations (se)				Phenotypic correlations			
	GP065	GP102	GP103	GP258	GP065	GP102	GP103	GP258
D05 - DenJ	-0.02 (0.32)	-	-	-	-0.04	-	-	-
D05 - DenM	-0.45 (0.23)	-	-	-	-0.25	-	-	-
D05 - DenT	-0.27 (0.27)	-	-	-	-0.13	-	-	-
D10 - DenJ	-0.28 (0.26)	-0.08 (0.39)	-	0.03 (0.43)	-0.06	0.01	-	-0.08
D10 - DenM	-0.50 (0.20)	-0.66 (0.22)	-	0.06 (0.38)	-0.47	-0.31	-	-0.13
D10 - DenT	-0.43 (0.22)	-0.42 (0.32)	-	0.22 (0.39)	-0.28	-0.23	-	-0.11
D15 - DenJ	-0.35 (0.27)	-0.07 (0.37)	-0.95 (0.28)	-0.65 (0.25)	-0.02	0.09	-0.01	-0.27
D15 - DenM	-0.62 (0.17)	-0.60 (0.24)	-0.61 (0.37)	0.19 (0.35)	-0.50	-0.37	-0.39	-0.33
D15 - DenT	-0.50 (0.21)	-0.40 (0.32)	-0.65 (0.37)	-0.27 (0.42)	-0.22	-0.18	-0.20	-0.35
D20 - DenJ	-0.36 (0.27)	-0.10 (0.35)	-0.82 (0.31)	-0.54 (0.29)	-0.02	0.10	0.03	-0.17
D20 - DenM	-0.69 (0.15)	-0.40 (0.29)	-0.53 (0.37)	0.12 (0.32)	-0.47	-0.29	-0.37	-0.22
D20 - DenT	-0.53 (0.21)	-0.26 (0.33)	-0.54 (0.38)	-0.23 (0.38)	-0.16	-0.09	-0.14	-0.22
D25 - DenJ	-	0.04 (0.35)	-	-0.56 (0.28)	-	0.10	-	-0.18
D25 - DenM	-	-0.37 (0.29)	-	0.09 (0.31)	-	-0.25	-	-0.21
D25 - DenT	-	-0.14 (0.33)	-	-0.27 (0.36)	-	-0.04	-	-0.22

positive (Tables 5 and 6). The results support the observation of ZOBEL & TALBERT (1984) that genetic correlations between growth traits and wood density in forest tree species can be positive or negative. The generally unfavorable correlations between growth and wood density suggest that selection for increased growth alone may result in decreased wood density in this population. Therefore, index selection will be required to prevent further losses in wood density. Such an index will be a trade-off between quantity and quality of the wood, and will result in less than optimal genetic progress in each individual trait. Alternatively, multiple populations or sublines (BURDON & NAMKOONG 1983) in which one population or line is improved for growth and the other for wood density may be considered if simultaneous improvement in both traits is required.

Phenotypic correlations between wood density and growth traits were generally higher than the corresponding genetic correlations. This result differs from age-age correlations where genetic correlations were consistently higher than phenotypic correlations. It appears that the relationship between genetic and phenotypic correlations depends on whether the correlations are age-age or trait-trait.

The standard errors of genetic correlations between wood density and growth traits were substantially large due to the low values of the genetic correlations. Hence caution should be exercised in the interpretation of these estimates. Such large standard errors reflect the relatively small number of families used in the study. For low estimates of genetic correlations to be estimated with high precision large sample sizes are required (KLEIN *et al.* 1973).

Efficiency of early selection

Early selection per unit of time based on one trait to improve the same trait at maturity was efficient due to the high age-age genetic correlations (Table 7). The average efficiency of selection between juvenile and total wood density was 1.36. This result corresponds to efficiency of selection per generation of 0.68 and is consistent with the result of LOWE and BYRAM (1995) who found that selecting for juvenile wood density was about 68% as efficient as direct selection using coefficients of prediction. In fact in all cases indirect early selection resulted in higher gain per unit of time at maturity than direct selection at maturity if selection is carried out on the same trait. Early selection based on one of the growth traits to improve an alternative growth trait at maturity was fairly efficient in all the tests, except in GP102. Early selection for growth was not a generally efficient predictor of wood density at maturity due to the adverse genetic correlations between growth and wood density. Given that the correlations between growth traits and wood density were sometimes positive, the selection efficiencies for growth traits to improve wood density at maturity were sometimes positive but small (Table 7).

CONCLUSION

Heritability estimates for wood density and height were moderate to high and those for diameter were relatively lower. For wood density traits, juvenile wood density had lower heritability estimates than mature and total wood densities.

Early selection within each of the traits was effi-

Table 7. Efficiencies of selection per year for a mature trait (*M*) based on indirect early selection on a juvenile trait (*J*) relative to direct selection on mature trait (*M*).

Traits (J–M)		GP065	GP102	GP103	GP258	Mean
Age–Age	H05–H20	1.40	–	–	–	1.40
	H10–H20	1.14	1.97	–	1.14	1.42
	D05–D20	0.92	–	–	–	0.92
	D10–D20	0.98	1.02	–	1.80	1.27
	DenJ–DenT	1.60	1.42	0.96	1.44	1.36
Trait–trait	H05–D20	1.04	–	–	–	1.04
	H10–D20	0.83	0.27	–	1.16	0.75
	D05–H20	1.14	–	–	–	1.14
	D10–H20	1.10	0.27	–	1.35	0.91
	H05–DenT	-0.36	–	–	–	-0.36
	D05–DenT	-0.26	–	–	–	-0.26
	H10–DenT	-0.26	0.15	–	0.35	0.24
	D10–DenT	-0.39	-0.23	–	0.33	-0.29

cient due to the high age-age genetic correlations. Early selection across growth traits was not always efficient due to the genetic correlations between height and diameter that varied from low to high. Juvenile wood density was a good predictor of total wood density. The results indicated that early selections would give a correlated increase in total wood density. The lower heritability estimates for juvenile density (0.18–0.43) than for total wood density (0.48–0.69) slightly compromised the efficiency of early selection. The poor association between growth and wood density traits resulted in low positive to low negative efficiencies of selection. This indicates that selection on growth traits alone will result in low positive or negative genetic progress in wood density. To achieve optimum progress in both quantity and quality of wood produced, both growth and wood density traits should be included in the selection schemes. The relative emphasis on growth and wood density will depend on the particular breeding program. For programs with multiple breeding objectives, a multiple population or sub-line breeding strategy may be considered as an alternative to simultaneous improvement within a single population.

ACKNOWLEDGEMENTS

We thank Georgia-Pacific for maintaining the genetic tests used in this study. We also thank Boise Cascade Corporation, Champion International Corporation, Georgia-Pacific Corporation, International Paper Company and Temple-Inland Forest Products for financial support for this project.

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Appendix 1. Number of trees, least square means and standard deviations (SD) for height (m), diameter (cm) and density (g cm^{-3}) for the four tests.

Trait	Number of trees				Least square means (SD)			
	GP065	GP102	GP103	GP258	GP065	GP102	GP103	GP258
H05*	4246	–	–	–	2.24 (0.71)	–		–
H10	4035	5852	–	2035	7.55 (1.38)	9.92 (1.47)	–	8.40 (1.18)
H15	3874	5745	850	4538	13.13 (1.62)	13.89 (1.50)	12.94 (1.37)	13.23 (1.32)
H20	2575	2380	836	2062	17.05 (1.96)	18.41 (1.28)	16.31 (1.66)	17.88 (1.23)
H25	–	1523	–	1142	–	22.57 (1.41)	–	20.88 (1.24)
D05	3743	–	–	–	2.8 (1.44)	–	–	–
D10	4035	5852	–	2035	12.53 (3.32)	14.7 (3.12)	–	12.9 (2.48)
D15	3874	5745	850	4538	17.4 (4.18)	18.2 (3.79)	18.0 (3.59)	17.6 (3.31)
D20	2575	2380	836	2062	21.2 (5.09)	24.5 (3.57)	21.1 (4.33)	23.4 (3.28)
D25	–	1523	–	1142	–	30.5 (3.97)	–	27.6 (3.63)
DenJ	847	887	306	597	0.394 (0.026)	0.431 (0.042)	0.435 (0.033)	0.427 (0.035)
DenM	847	887	306	597	0.502 (0.033)	0.520 (0.032)	0.529 (0.029)	0.513 (0.029)
DenT	847	887	306	597	0.449 (0.026)	0.483 (0.030)	0.489 (0.027)	0.477 (0.026)

*H = height, D = Diameter at breast height, the numbers indicate the age of assessment, DenJ = juvenile wood density (0–5 years), DenM = mature wood density (6–20 years), DenT = total wood density (whole core density).

Appendix 2. Estimates of additive and residual variances for growth and wood density at four tests and five ages. Variances for DenJ, DenM and DenT×10^{-4}.

Trait	σ_a^2 (se)				σ_e^2 (se)			
	GP065	GP102	GP103	GP258	GP065	GP102	GP103	GP258
H05	0.068 (0.024)	–	–	–	0.395 (0.016)	–	–	–
H10	0.277 (0.089)	1.678 (0.416)	–	0.547 (0.253)	1.486 (0.061)	0.972 (0.222)	–	0.800 (0.143)
H15	0.517 (0.168)	1.367 (0.411)	0.369 (0.213)	0.698 (0.254)	2.001 (0.107)	1.284 (0.222)	1.260 (0.139)	1.099 (0.142)
H20	0.921 (0.338)	0.524 (0.209)	0.484 (0.279)	0.800 (0.291)	2.867 (0.210)	1.067 (0.118)	2.004 (0.192)	0.755 (0.163)
H25	–	0.681 (0.284)	–	0.657 (0.283)	–	1.240 (0.162)	–	0.883 (0.162)
D05	0.276 (0.098)	–	–	–	2.173 (0.074)	–	–	–
D10	1.847 (0.580)	0.649 (0.363)	–	4.691 (1.885)	8.792 (0.387)	9.123 (0.263)	–	2.885 (1.048)
D15	4.139 (1.325)	0.979 (0.508)	0.520 (0.442)	3.337 (1.491)	12.971 (0.810)	13.336 (0.377)	11.958 (0.656)	8.404 (0.844)
D20	8.723 (2.854)	1.521 (0.752)	1.262 (0.882)	4.234 (1.788)	16.815 (1.685)	11.081 (0.530)	17.113 (1.016)	6.713 (1.018)
D25	–	4.76 (2.23)	–	6.371 (2.672)	–	11.277 (1.298)	–	6.967 (1.515)
DenJ	3.06 (1.39)	6.51 (3.07)	1.98 (1.62)	4.95 (2.63)	3.98 (0.83)	10.57 (1.77)	9.11 (1.26)	7.78 (1.58)
DenM	4.65 (1.65)	5.14 (2.13)	7.84 (3.67)	5.51 (2.50)	5.01 (0.97)	4.31 (1.18)	2.20 (2.03)	3.44 (1.42)
DenT	3.07 (1.15)	4.64 (1.97)	5.67 (2.89)	4.90 (2.26)	3.33 (0.68)	3.83 (1.09)	2.54 (1.61)	2.87 (1.28)