Age-Age Correlations and Early Selection for Wood Density in Young Coastal Douglas-Fir

JESUS VARGAS-HERNANDEZ

W.T. ADAMS

ABSTRACT. Age-age correlations and age-associated changes in the genetic control of wood density and its components (earlywood density, latewood density, and latewood proportion) were investigated in 15-yr-old trees of 60 open-pollinated families of coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco). The possibility of using wood density components as secondary traits to increase the efficiency of early selection for overall wood density was also explored. Heritability estimates for overall density and its components increased with age, mainly because of a decrease in the error variance as the number of rings in the core sample increased. Overall density and its components at age 15 had strong genetic correlations with their respective traits at all younger ages analyzed. Moreover, with few exceptions, age-age genetic correlations were greater than phenotypic correlations. Early selection to improve overall density at age 15 was quite efficient (relative efficiency above 79%), even when selection was based on core density at the youngest age (age 7). Using wood density components as secondary traits produced a slight increase in the efficiency of early selection only at the youngest ages, presumably because age-age correlations for overall core density were already strong, limiting the possibility of additional improvement. FOR. SCI. 38(2):467–478.

ADDITIONAL KEY WORDS. *Pseudotsuga menziesii*, heritability, genetic gains, correlated response, index selection.

D ETERMINING THE AGE AT WHICH TREES OR FAMILIES in genetic tests can be reliably selected for relative performance at a later age (often, rotation age) is critical to the efficiency of tree improvement programs, because age of selection determines, to a large extent, the length of the breeding cycle and the amount of genetic gain that can be achieved per unit of time (Lambeth 1980, McKeand 1988). Selection at an early age, with the goal of improving a trait expressed at a later age, is a particular case of indirect selection, in which response in the older trait is a correlated response of selection on the early trait (Nanson 1969).

The ratio of genetic gain in an older trait expected from indirect selection based on an early trait, relative to the gain expected when the older trait is selected directly, is called the relative efficiency (*RE*) of indirect (early) selection. Assuming equal intensity of selection at both ages, *RE* is expressed by the following equation (Falconer 1981):

$$RE = r_{Aeo} * (h_e/h_o) * 100 \tag{1}$$

where r_{Aeo} = the genetic correlation between the trait selected at the early age

and the trait of interest at an older age, and h_e and h_o are the square roots of the heritabilities of the early and older traits, respectively. Thus, the degree to which heritability of the selected trait and its genetic correlation with the older trait change with age is important in evaluating the feasibility of early selection. When the trait at both ages is the same, the correlation is called an "age-age genetic correlation." The appropriate heritabilities depend on the particular selection system involved (e.g., individual-tree heritabilities are used for mass selection, and family heritabilities for selection based on family means).

Previous studies on efficiency of early selection have primarily focused on growth traits (Lambeth et al. 1983, Foster 1986, Gill 1987, Cotterill and Dean 1988, Magnussen 1988, Riemenschneider 1988), and only limited information on age trends of heritability of wood density or age-age correlations for this trait is available (McKimmy 1966, Nicholls 1967). There is some evidence, however, that genetic variation for wood density can be large (Stonecypher and Zobel 1966, Cown 1976, Loo et al. 1984) and that early selection for both juvenile and mature wood density is feasible (Nebgen and Lowe 1985, Gonzalez and Richards 1988). In general, previous studies have emphasized early selection based on an individual trait, usually the same trait as the trait of interest at the older age. Information on multiple early traits, however, may improve the efficiency of early selection (Foster 1986, Cotterill and Dean 1988, Burdon 1989).

In this study, overall wood density of 60 open-pollinated families of coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* [Mirb.] Franco) at age 15 was estimated by X-ray densitometry of increment core samples (Vargas-Hernandez and Adams 1991). At this age, all wood is considered to be juvenile wood (Megraw 1985). From the X-ray data, average density of each annual ring outward from the pith was determined and used to calculate average core densities at various ages. In addition, average density of each ring, as well as average core density (CD) at a given age, were partitioned into three components: earlywood density, latewood density, and latewood proportion.

At present, many tree improvement programs in coastal Douglas-fir are planned to make final selections between 15–20 years of age (Silen and Wheat 1979). Can overall wood density at age 15 (i.e., CD-15) be reliably predicted at much younger ages? Being able to select earlier than age 15 is important for several reasons. First, if genetic improvement in juvenile wood density is desired, it might be possible to shorten the breeding cycle by making an earlier prediction of overall density at age 15. The effect of this early prediction on mature wood density depends on the genetic relationship between early age and mature wood density. Presumably, if the relationship between early age and age 15 is strong, selecting at an earlier age would produce a similar response in mature wood density than delaying selection to age 15. Determining the relative efficiency of early selection is also useful if an early culling of parents is necessary (e.g., roguing clones in a seed orchard or reducing the number of individuals in breeding programs prior to controlled mating). In addition to addressing the general question of early selection, this study had the following objectives: (1) to describe age trends in variance components and heritabilities for wood density and its components, (2) to describe age-age correlations for wood density and its components, and (3) to assess the utility of information on wood density components for the purposes of early selection of CD-15.

During the summer of 1988, one pith-to-bark (5 mm) increment core sample was taken at breast height (1.37 m) from each tree of two sets of 30 open-pollinated families (sets 2 and 4) established at the Coyote Creek progeny test site, near Eugene, OR. The parent trees, part of the Noti Breeding Unit in the Umpqua Tree Improvement Cooperative (Silen and Wheat 1979), were selected in natural stands located between 150 and 450 m elevation in the central Coast Range of Oregon. Each set of families was planted in 1974 as a separate randomized complete block design experiment with four replications. Four-tree noncontiguous family plots were established in each block, with trees in each plot assigned to planting spots at random. Cores were taken from all surviving trees (total 806) in the two sets (84% of those originally planted).

Intra-ring density information for each sample was obtained by using the direct scanning X-ray densitometry system described by Hoag and McKimmy (1988). The first and the last rings from every sample were excluded from further analysis because they were usually incomplete. For each of the remaining annual rings in the samples, earlywood density, latewood density, latewood proportion, and average ring density were obtained directly from the X-ray density profiles. The average of the minimum and maximum density in the ring was used as the criterion to separate earlywood from latewood (Green and Worrall 1954). This criterion assumes earlywood and latewood are present in all annual rings, and density of cells at the transition point may change from year to year.

The number of growth rings in each sample varied slightly as trees reached the breast-height sampling position at different ages. Annual rings were identified and numbered starting from the bark inward, to account for year-of-ring formation. When different numbers of growth rings are present in cores, counting the rings from the pith outwards introduces a confounding effect, since the growth rings at the same distance from the pith may not have been formed the same year. By identifying each ring by its year of formation, average values of core density and its components could be derived cumulatively from the earliest age of formation (age 7 in most samples) to age 15 (i.e., core ages 7 to 15). To obtain the averages for each core age, the mean values of annual growth rings present in the sample up to that age were weighted by their respective width. The averages for each core age, therefore, represent the values that would have been obtained if increment core samples had been taken every year at breast height, beginning at age 7.

Analyses of variance for all ages were performed according to the random effects model for individual-tree data (Table 1) using the SAS GLM procedure (SAS Institute 1987), and type III sums of squares. SAS type III sums of squares are partial sums of squares in which each effect is adjusted for all other effects in the model. This is one of many approaches used to estimate variance components from unbalanced data. Analyses of covariance between all pairs of traits at the same age, and between traits at different ages were also computed as in Table 1, using expected cross-products instead of expected mean squares. Early rings (ages 7 and 8) were not represented in some cores; thus, covariance analyses for age 7 ($n = 521$ cores and 19 missing plots) and age 8 ($n = 737$ cores and 5 missing plots) with all other ages included only individuals having these rings.

TABLE 1.

Form of the variance and covariance analyses for overall core density and its components measured at different ages.

Source of variation	Degrees of freedom	Expected mean squares[a]
Sets	$s - 1$	$\sigma_w^2 + k_6\sigma_e^2 + k_7\sigma_{f(s)}^2 + k_8\sigma_{b(s)}^2 + k_9\sigma_s^2$
Blocks/sets	$s(b - 1)$	$\sigma_w^2 + k_4\sigma_e^2 + k_5\sigma_{b(s)}^2$
Families/sets	$s(f - 1)$	$\sigma_w^2 + k_2\sigma_e^2 + k_3\sigma_{f(s)}^2$
Plot error	$s(b - 1)(f - 1)$[b]	$\sigma_w^2 + k_1\sigma_e^2$
Within-plot	$\displaystyle\sum_{i=1}^{t} (n_i - 1)$	σ_w^2

s = number of sets (2); b = number of blocks/set (4); f = number of families/set (30); k_j = coefficient associated with the jth variance component; n_i = number of trees in plot i; t = total number of plots; σ_w^2 = within-plot variance; σ_e^2 = plot-to-plot variance; $\sigma_{f(s)}^2$ = variance among families in sets; $\sigma_{b(s)}^2$ = variance among blocks in sets; σ_s^2 = variance among sets.

[a] For covariance analyses, cross products are used instead of mean squares.

[b] Actual degrees of freedom varied depending on the total number of missing plots (see text).

Covariance analyses involving all other ages included the full complement of core samples (n = 806 cores and 3 missing plots).

For each age, variance components of wood density traits were estimated by equating mean squares with their respective expectations from the model (Table 1), using the estimates of the k_j coefficients given by the SAS GLM procedure. Variance components were expressed in terms of coefficients of variation to avoid potentially confounding scale effects. Individual-tree heritabilities (h_i^2) were estimated as in Falconer (1981). Because open-pollinated families in the progeny test came from parent trees in wild stands, additive genetic variance (σ_A^2) was estimated as three times the family component of variance ($\sigma_{f(s)}^2$), assuming individuals in these families are related to a greater extent than are half-sibs (Campbell 1979). Family heritabilities of interest were those appropriate to calculating expected gain from parent tree (ortet) selection, where ortets are selected on the basis of their open-pollinated offspring in a progeny test, and clones of the selected ortets are put into a seed orchard to produce improved offspring. These heritabilities were estimated according to Namkoong et al. (1966):

$$h_f^2 = COV_A(X, Y)/\sigma_{Px}^2 \tag{2}$$

where $COV_A(X, Y) = \frac{1}{4}\sigma_A^2$, is the additive genetic covariance between the mean of an ortet's progeny (X) and the mean of the offspring from its seed orchard clone (Y), and σ_{Px}^2 is the phenotypic variance of family means in the progeny test (Vargas-Hernandez and Adams 1991). Standard errors of heritability estimates were calculated following the procedures of Osborne and Paterson (1952). Because the data in this study are from a single test site, estimates of additive variances and covariances may be biased. Heritability estimates, particularly, will be biased upwards if family × site interactions exist.

To describe age-age correlations for wood density and its components, genetic and phenotypic correlations for all pairwise combinations of core ages, 7 through 15, were calculated for each wood density trait. Genetic correlations were esti-

mated using the appropriate variance and covariance components according to Becker (1984), while phenotypic correlations were estimated as simple correlation coefficients (Falconer 1981). Standard errors of genetic correlations were calculated as outlined by Becker (1984). Because the annual rings in a younger core make up part of the same core at an older age (i.e., they have rings in common), age-age correlations for average core values can exist even when the wood properties of different aged rings are uncorrelated (Lambeth et al. 1983). To determine the degree to which individual rings of increasingly different ages are correlated for each wood trait, genetic and phenotypic correlations were calculated between individual ring values for all pairwise combinations of ring ages.

The relative efficiency of parent tree (ortet) selection for CD-15 based on earlier measurements of overall core density was estimated using equation (1) and family heritabilities. The effectiveness of wood density components as additional traits in early selection for CD-15 was assessed by using index selection methods (Lin 1978). Information on one or more wood density components as well as overall core density at an early age were incorporated into selection indices by imposing a Binet-type restriction (Cotterill and Jackson 1981, Burdon 1989). The Binet restriction is intended to maximize indirect genetic response in traits which are of economic value but for some reason are not actually measured (Cotterill and Dean 1988), as in this case overall density at age 15, which might not be measured in the interest of reducing the length of the selection cycle. Expected gains in CD-15 from index selection were estimated using the RESI computer program (Cotterill and Jackson 1981). The RE of index selection was then calculated by dividing the gain from index selection by the gain expected from direct selection for CD-15.

RESULTS AND DISCUSSION

AGE TRENDS IN POPULATION MEANS, VARIANCE COMPONENTS, AND HERITABILITY

As described in the Methods section, values for overall core density and its components in breast height increment cores were estimated retrospectively for trees ages 7 to 15 yr (i.e., for 9 different core ages). Population means for earlywood density and overall core density both decreased slowly with increasing core age, but leveled off in the last 2 yr (Figure 1). Latewood proportion decreased sharply during the first 4 yr, from 0.384 at age 7 to 0.214 at age 11, and then also leveled off. Latewood density, unlike the other wood density traits, increased steadily from 0.659 g/cm^3 at age 7 up to 0.824 g/cm^3 at age 15. These age trends resemble those reported previously for average ring density and its components in young Douglas-fir (Cown and Parker 1979, Megraw 1985). The age trend for overall density appears flatter than in previous reports because cumulative core densities are used in Figure 1 rather than individual ring densities, and the scale on the Y axis is broader than normal.

Analyses of variance showed significant differences ($P \le 0.05$) among families for all wood density traits, at all core ages. A strong decrease in the magnitude of the coefficient of environmental variance, and consequently in the coefficient of phenotypic variance, was observed for all traits between the seventh and twelfth years (Figure 2). The reduction in environmental variance with increasing core
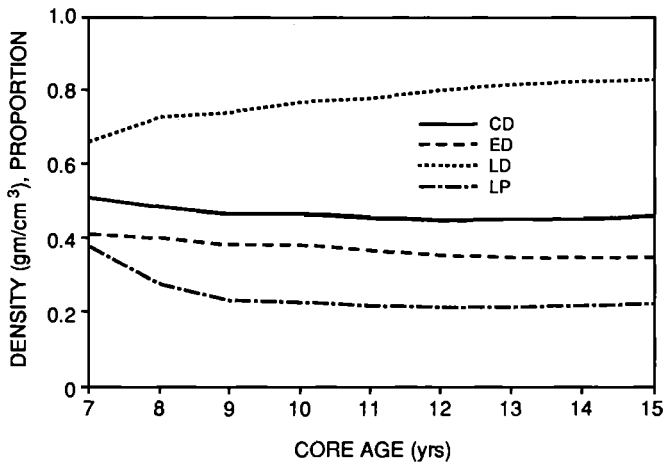
FIGURE 1. Age-associated changes in population means for overall core density (*CD*) and its components. *ED* = earlywood density; *LD* = latewood density; and, *LP* = latewood proportion.

age can be attributed to the higher precision in estimating the average values of wood density traits as the number of growth rings included in the sample increased. The coefficient of additive genetic variance followed different age trends among traits, slightly increasing for earlywood density and overall core density, but decreasing for the other two traits (Figure 2). The absolute changes in additive variance, however, were small compared to the overall reduction observed in environmental and phenotypic variances for all traits.

The age trends in variance components for latewood density and latewood proportion resemble those normally observed for growth traits in young conifer plantations (Lambeth et al. 1983, Foster 1986, Gill 1987, Cotterill and Dean 1988), in which all the coefficients of variation decrease with age, and there is a larger decline in the coefficient of environmental variance, than in the coefficient of additive variance.

The strong decrease observed for all traits in the coefficient of environmental variance, resulted in steady increases in heritability estimates, especially between the seventh and twelfth years (Figure 2). At all ages, overall core density showed the strongest genetic control. Standard errors of heritability estimates for all traits were very similar, normally lower than 0.10 [the largest error (0.13) was obtained at age 15 for overall core density]. Earlywood density and latewood proportion always gave the highest and lowest heritability estimates, respectively, among the components, except at age 7, when all the components had similar values. This suggests that latewood proportion is more strongly affected by environmental variation than any other wood density component. Based on average values of individual rings at different ages, Nicholls (1967), and Nicholls and Brown (1971) also found much lower heritabilities for latewood proportion than for average ring density in *Pinus radiata*.

Previous studies in Douglas-fir found similar increases in the heritability of wood density (McKimmy 1966) and its components (Cown 1976) with increasing age, at least for the first 10–15 growth rings from the pith. A strict comparison between different studies, however, is difficult because in some cases heritability estimates are based on individual growth rings (Cown 1976) or core sections
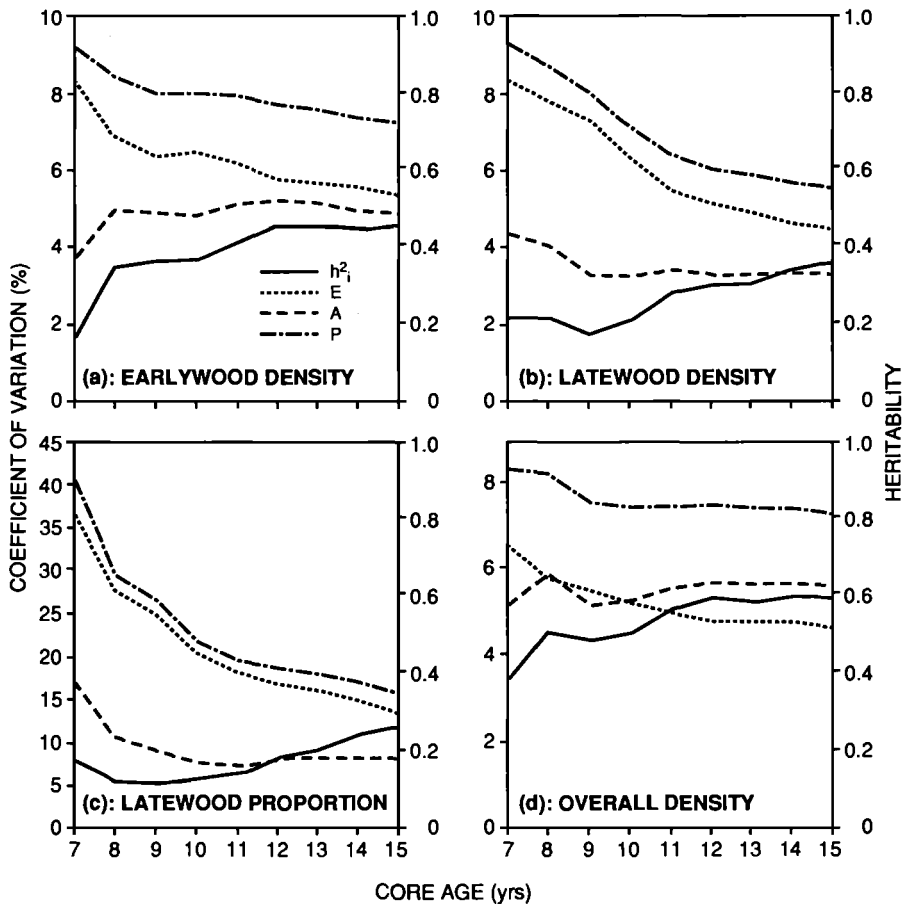
FIGURE 2. Age trends in phenotypic (*P*), environmental (*E*), and additive (*A*) variance components (expressed as coefficients of variation), and individual-tree heritability (h_i^2), for overall core density and its components.

(McKimmy 1966), rather than on the whole core, as in this study. Nevertheless, it seems that the degree of genetic control for wood density traits in Douglas-fir changes with age.

Knowledge of age trends in heritability is important for early selection. Most studies on the efficiency of early selection have assumed that heritability remains constant with age (Squillace and Gansel 1974, Lambeth 1980, Gonzalez and Richards 1988). If heritability really increases with age, as in this case for juvenile wood density in Douglas-fir, assuming the same heritability at younger ages as that for age 15 would overestimate the relative efficiency of early selection.

AGE-AGE CORRELATIONS

With the exception of latewood proportion, genetic correlations for overall core density and its components at younger ages, with their respective values at age 15, were stronger and more stable than the corresponding phenotypic correlations (Figure 3). This indicates that as the age interval increases, genetic corre-
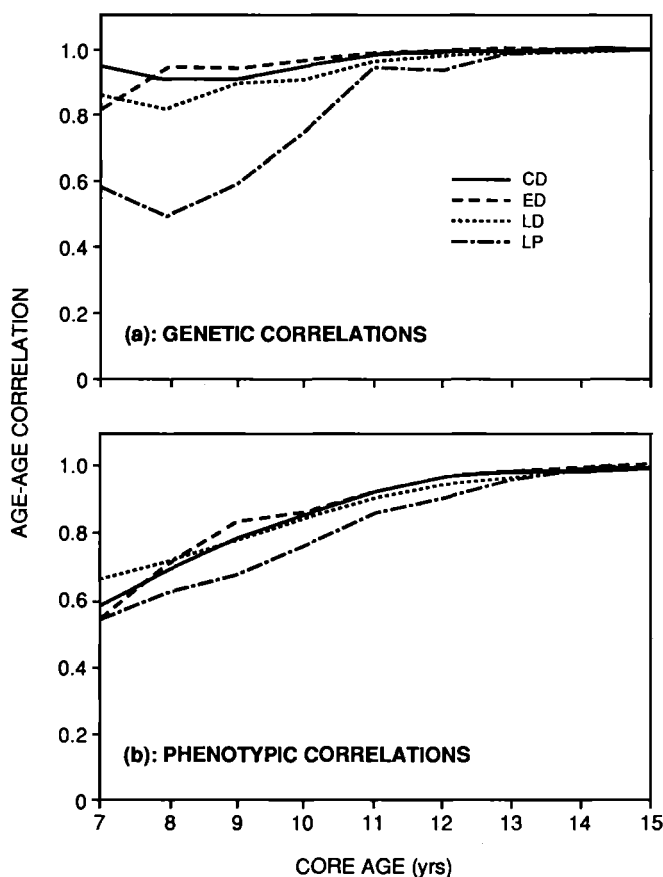
FIGURE 3. Genetic (a) and phenotypic (b) correlations for overall core density (*CD*) and its components at different ages, with their respective values at age 15. *ED* = earlywood density; *LD* = latewood density; and, *LP* = latewood proportion.

lations decline more slowly than phenotypic correlations. Similar results have been observed for growth traits (Lambeth et al. 1983, Cotterill and Dean 1988, Riemenschneider 1988). Therefore, using age-age phenotypic correlations rather than genetic correlations to evaluate efficiency of early selection as was done by Lambeth (1980) and Gonzalez and Richards (1988), will underestimate potential gains from early selection, especially if selection is applied at very young ages. Standard errors of genetic correlations were normally lower than 0.05 when the difference in core age was 6 yr or less, but increased to about 0.15 when the difference in age was 8 yr. Thus, a larger error might be expected in estimates of potential gains from early selection at younger ages.

There seems to be no clear explanation for the different results found for latewood proportion, in which age-age genetic correlations at early core ages were weaker than the respective phenotypic correlations. One possibility could be a larger influence of environmental effects on the phenotypic correlations for this trait. Lambeth et al. (1983) argued that the magnitude of age-age genetic correlations for a particular trait normally corresponds to its degree of genetic control, since genetic correlations are estimated on the basis of genetic effects. In addi-

tion, trends of decreasing age-age genetic correlations with decreasing genetic control of traits were reported by Squillace and Gansel (1974). Apparently, when the genetic control of a trait is weak, as is the case of latewood proportion, environmental correlations might cause phenotypic correlations to be stronger than genetic correlations.

Genetic correlations estimated between individual growth rings at different ages were almost as strong as the age-age genetic correlations for corresponding overall core density traits. Rings separated in age by as much as 5–7 yr had mean estimates of genetic correlations between 0.7 and 0.8 for most traits. Standard errors of genetic correlations between individual rings, however, were larger (between 0.10 and 0.30 in most cases) than those for overall core density values. Thus, averaging wood density traits over several rings resulted in more precise estimates of genetic correlations. These results indicate that the strong age-age genetic correlations observed in overall core density traits were not merely due to autocorrelation. Phenotypic correlations between individual ring values at different ages, however, were considerably lower than those observed for age-age correlations of overall core density and its components involving similar age differences. Therefore, it seems that autocorrelation has a greater influence on phenotypic correlations, probably because of a stronger effect of shared environment on phenotypic than on genetic correlations.

Efficiency of Early Selection for Overall Core Density

The relative efficiencies of different selection criteria for early selection of CD-15 are presented in Table 2. As expected from the strong age-age genetic correlations for overall core density, early selection for CD-15 was quite efficient, even at age 7 when selection was based on information from one growth ring only. Early selection at age 7, based on overall density alone, is expected to produce about 79% of the gain in CD-15 that would be obtained if selection were delayed until age 15. The efficiency of early selection based on overall density alone steadily improves with increasing core age, and by age 11 early selection is nearly as effective as direct selection at age 15.

Using information on density components, as well as overall density in selection indices, seems to improve the relative efficiency of early selection, but only at the earliest ages (Table 2). Relative efficiencies, however, were improved by only 4 to 8%, even when all three density components were included along with overall core density in the selection index. The limited usefulness of wood density components for increasing the efficiency of early selection for overall core density can be partially attributed to the strong genetic correlations found between overall core density at younger ages and CD-15, which were always greater than 0.9. White and Hodge (1991) showed that if the genetic correlation between a single selected trait and a target trait is high, very little additional improvement in the target trait can be expected when additional traits are incorporated into the selection index.

The ability to utilize density components in indices for early selection requires *a priori* information on the genetic and phenotypic covariances between the core density components at the age of selection and overall wood density at the target age. These data would not be available unless they were generated in a previous generation of the same breeding population or in another breeding population. The

TABLE 2.

Relative efficiencies (%) of early selection for overall core density at age 15 (CD-15) when different selection criteria are used.[a]

Age of selection	$h_f^2 \pm$ s.e.[c]	Overall core density	(CD and ED)	(CD and LD)	(CD and LP)	(CD, ED, LD, and LP)
		Selection criteria[b]				
15	0.56 ± 0.04	100.0	100.0	100.0	100.0	—
7	0.39 ± 0.08	79.5	82.8	82.2	82.3	86.2
8	0.53 ± 0.05	87.6	89.7	88.5	90.0	90.3
9	0.53 ± 0.05	89.0	91.0	89.3	91.0	91.5
10	0.54 ± 0.05	92.0	93.1	93.0	93.4	93.4
11	0.55 ± 0.04	97.7	97.8	97.9	97.8	98.5
12	0.56 ± 0.04	99.0	99.1	99.3	99.1	99.3
13	0.56 ± 0.04	99.4	99.4	99.5	99.5	99.6
14	0.56 ± 0.04	99.9	99.9	99.9	99.9	100.0

[a] Relative efficiency is genetic gain in CD-15 from early selection, relative to gain expected when selection is applied directly to CD-15.

[b] CD, ED, LD, and LP represent, respectively, overall core density, earlywood density, latewood density, and latewood proportion at age of selection.

[c] Estimated family heritability of overall core density at each age of selection.

accuracy of such estimates for the population of concern may, therefore, be questioned. Although this problem is common to any criterion used for early selection, it becomes more serious as the number of traits included in the selection index increases, because the weights assigned to the traits in the index are sensitive to changes in the correlations between traits (Burdon, 1989). In addition, the extra cost associated with obtaining information on the individual density components must be compared against the additional gains expected from the increase in selection efficiency.

This study investigated age-age genetic correlations in juvenile wood density only. Although selection at age 15 may be appropriate for improving density of juvenile wood, the degree to which selection at this age would be adequate for improving density of mature wood is uncertain. Previous studies in Douglas-fir, however, suggest that wood density at age 15 is correlated strongly enough with mature wood density (McKimmy and Campbell 1982, Gonzalez and Richards 1988), that selection at age 15 should be effective in improving mature wood density as well. Since heritability for wood density remains relatively stable between ages 10 to 15, and genetic correlations between these ages are high, indirect response in mature wood density should be nearly as great if selection is applied at age 10, as at age 15.

LITERATURE CITED

BECKER, W.A. 1984. Manual of quantitative genetics. Ed. 4. Academic Enterprises, Pullman, WA. 186 p.

BURDON, R.D. 1989. Early selection in tree breeding: Principles for applying index selection and inferring input parameters. Can. J. For. Res. 19:499–504.

CAMPBELL, R.K. 1979. Genecology of Douglas-fir in a watershed in the Oregon cascades. Ecology 60:1036–1050.

COTTERILL, P.P., and C.A. DEAN. 1988. Changes in the genetic control of radiata pine to 16 years and efficiencies of early selection. Silvae Genet. 37:138–146.

COTTERILL, P.P., and N. JACKSON. 1981. Short note: Index selection with restrictions in tree breeding. Silvae Genet. 30:106–108.

COWN, D.J. 1976. Densitometric studies on the wood of young coastal Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco). Ph.D. thesis, University of British Columbia. Vancouver, B.C. 241 p.

COWN, D.J., and M.L. PARKER. 1979. Densitometric analysis of wood from five Douglas-fir provenances. Silvae Genet. 28:48–53.

FALCONER, D.S. 1981. Introduction to quantitative genetics. Ed. 2. Longham Inc., New York. 340 p.

FOSTER, G.S. 1986. Trends in genetic parameters with stand development and their influence on early selection for volume growth in loblolly pine. For. Sci. 32:944–959.

GILL, J.G.S. 1987. Juvenile-mature correlations and trends in genetic variances in Sitka spruce in Britain. Silvae Genet. 36:189–194.

GONZALEZ, J.S., and J. RICHARDS. 1988. Early selection for wood density in young coastal Douglas-fir trees. Can. J. For. Res. 18:1182–1185.

GREEN, H.V., and J. WORRALL. 1964. Wood quality studies I. A scanning microphotometer for automatically measuring and recording certain wood characteristics. Tappi 47:419–427.

HOAG, M., and M.D. McKIMMY. 1988. Direct scanning X-ray densitometry of thin wood sections. For. Prod. Jour. 38:23–26.

LAMBETH, C.C. 1980. Juvenile-mature correlations in *Pinaceae* and implications for early selection. For. Sci. 26:571–580.

LAMBETH, C.C., J.P. VAN BUIJTENEN, and S.D. DUKE. 1983. Early selection is effective in 20-year-old genetic tests of loblolly pine. Silvae Genet. 32:210–215.

LIN, C.Y. 1978. Index selection for genetic improvement of quantitative characters. Theor. Appl. Genet. 52:49–56.

LOO, J.A., C.G. TAUER, and J.P. VAN BUIJTENEN. 1984. Juvenile-mature relationships and heritability estimates of several traits in loblolly pine (*Pinus taeda*). Can. J. For. Res. 14:822–825.

MAGNUSSEN, S. 1988. Minimum age-to-age correlations in early selections. For. Sci. 34:928–938.

McKEAND, S.E. 1988. Optimum age for family selection for growth in genetic tests of loblolly pine. For. Sci. 34:400–411.

McKIMMY, M.D. 1966. A variation and heritability study of wood specific gravity in 46-year-old Douglas-fir from known seed sources. Tappi 49:542–549.

McKIMMY, M.D., and R.K. CAMPBELL. 1982. Genetic variation in the wood density and ring width trends in coastal Douglas-fir. Silvae Genet. 31:43–55.

MEGRAW, R.A. 1985. Douglas-fir wood properties. P. 81–96 *in* Proc. symp. Douglas-fir: Stand management for the future, Oliver, C.D., D.P. Hanley, and J.A. Johnson (eds.). University of Washington, Seattle, WA.

NAMKOONG, G., E.B. SNYDER, and R.W. STONECYPHER. 1966. Heritability and gain concepts for evaluating breeding systems such as seedling orchards. Silvae Genet. 15:76–84.

NANSON, A. 1969. Juvenile and correlated trait selection and its effect on selection programs. P. 17–26 *in* Proc. IUFRO second meeting of the working group on quantitative genetics.

NEBGEN, R.J., and W.J. LOWE. 1985. The efficiency of early and indirect selection in three sycamore genetic tests. Silvae Genet. 34:72–75.

NICHOLLS, J.W.P. 1967. Preliminary observations on the change with age of the heritability of certain wood characteristics in *Pinus radiata* clones. Silvae Genet. 16:18–20.

NICHOLLS, J.W.P., and A.G. BROWN. 1971. The ortet-ramet relationship in wood characteristics of *Pinus radiata*. Appita 25:200–209.

OSBORNE, R., and W.S.B. PATERSON. 1952. On the sampling variance of heritability estimates derived from variance analyses. Proc. Roy. Soc. Edinburgh. B. 64:456–461.

RIEMENSCHNEIDER, D.E. 1988. Heritability, age-age correlations, and inferences regarding juvenile selection in jack pine. For. Sci. 34:1076–1082.

SAS Institute. 1987. SAS/STAT Guide for personal computers. Version 6 Ed. SAS Institute Inc.,
Cary, NC. 1028 p.

Silen, R.R., and J.G. Wheat. 1979. Progressive tree improvement program in coastal Douglas-fir. J.
For. 77:78–83.

Squillace, A.E., and C.R. Gansel. 1974. Juvenile:mature correlations in slash pine. For. Sci.
20:225–229.

Stonecypher, R.W., and B.J. Zobel. 1966. Inheritance of specific gravity in five-year-old seedlings of
loblolly pine. Tappi 49:303–305.

Vargas-Hernandez, J., and W.T. Adams. 1991. Genetic variation of wood density components in
young coastal Douglas-fir: Implications for tree breeding. Can. J. For. Res. 21:1801–1807.

White, T.L., and G.R. Hodge. 1991. Indirect prediction of genetic values. Silvae Genet. 40:20–28.

AUTHORS AND ACKNOWLEDGMENTS

J. Vargas-Hernandez is currently with Programa Forestal, Colegio de Postgraduados, Chapingo, Edo.
de Mexico 56230, Mexico. W.T. Adams is with the Dept. of Forest Science, College of Forestry,
Oregon State University, Corvallis, OR 97331. This is paper No. 2744 of the Forest Research
Laboratory, Oregon State University. Financial support was provided by the Pacific Northwest Tree
Improvement Research Cooperative and the Department of Forest Products, Oregon State University. Thanks are due to Dr. Robert Krahmer and Eini Lowell for their help in the use of the x-ray
densitometer.