FAMILY VARIATION IN AGE TRENDS OF WOOD DENSITY TRAITS IN YOUNG COASTAL DOUGLAS-FIR[1]

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ABSTRACT

Changes in ring density and its components with increasing distance from the pith (i.e., age trends) were examined in 15-year-old trees from 60 open-pollinated families of coastal Douglas-fir [*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco]. Earlywood, latewood, and overall densities of each annual ring, obtained by X-ray densitometry of increment cores, were weighted by the area of the ring occupied by each trait, relative to the total stem cross-sectional area at breast height for the trait. Age trends in weighted values differed among traits but, with the exception of earlywood density, family variation was not detected. Weighted earlywood density (WED) steadily increased from pith to bark in some trees, while in other trees a plateau occurred at age 11 or later. Significant family differences were found in the proportion of trees reaching a plateau in WED by age 12. This proportion was under moderate genetic control (family $h^2 = 0.30$) and was not genetically correlated with overall core density or stem growth at age 15. Although there are reasons to hypothesize that the plateau in WED is an indication of transition from juvenile to mature wood formation, this hypothesis needs to be verified in older trees.

Keywords: Genetic variation, X-ray densitometry, ring density components, age affects, juvenile wood.

Wood density normally follows a predictable pattern of ring-to-ring variation in the radial direction across the stem (i.e., a predictable "age trend"). Some coniferous species show a tendency towards increasing ring density outward from the pith, at least for the first 10 to 20 years, before levelling off (Harris and Birt 1972; Cown and Parker 1978). Ring density in young coastal Douglas-fir [*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco], on the other hand, decreases for the first 3 to 5 annual rings from the pith, followed by a gradual increase as the distance from the pith increases (Cown and Parker 1979; Megraw 1985; Jozsa and Brix 1989).

Overall ring density is determined by three interacting components: earlywood density,

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latewood density, and the proportion of latewood in the ring (Nicholls et al. 1980). Each of these components follows different age trends in Douglas-fir (Megraw 1985; Abdel-Gadir and Krahmer 1933a), and thus the influence of individual components on overall ring density changes with increasing distance from the pith.

Substantial genetic variation in the slope of the age trend (i.e., the rate of change per year) for overall ring density has been observed in loblolly pine (*Pinus taeda* L.) (Loo et al. 1985). Similarly, genetic variation might also be present for the slope of age trends of overall ring density and its components in Douglas-fir (Abdel-Gadir and Krahmer 1993a, b). Steeper slopes of age trends imply larger ring-to-ring density variation. Thus, if genetic differences in the slope of age trends are large enough, it may be possible to increase the uniformity of wood density across the stem by selecting for trees or families with smaller slopes.

Probably more important, however, is the possibility of using genetic differences in age trends of overall ring density and its components to breed for earlier transition from juvenile to mature wood formation (Loo et al. 1985; Hodge and Purnell 1993; Abdel-Gadir and Krahmer 1993b). Juvenile wood, formed during the early years of growth, normally has relatively low density and several other undesirable characteristics, some of which are associated with low density (Paul 1957; Yang et al. 1986). Thus, reducing the proportion of low density juvenile wood by selecting for a shorter juvenile wood formation phase is an attractive option for improving wood quality.

An approach proposed for estimating the age of transition to mature wood formation in loblolly pine employs the age trend of overall ring density values (Loo et al. 1985). The age of transition is considered to be the age at which the slope of the trend reaches a plateau (Loo et al. 1985; Bendtsen and Senft 1986). A similar approach has been suggested for Douglas-fir when wood cores containing at least 45 rings from the pith are available (Abdel-Gadir and Krahmer 1993a, b). This method, however, is not useful in younger trees because overall ring density normally continues to increase gradually up to at least age 40 in Douglas-fir (Megraw 1985; Abdel-Gadir and Krahmer 1993a), while the juvenile period may end as early as 15 rings from the pith (Erickson and Harrison 1974; Cown 1976; Hoag 1988; Abdel-Gadir and Krahmer 1993a, b). An alternative approach would be to use the age trends of overall ring density and its components obtained after first weighting each trait by the area of the annual ring occupied by the trait, relative to the total stem cross-sectioned area for the trait at the point of sampling. Since the contribution of each ring to overall wood density depends on ring area, and density and area of individual rings are commonly interrelated (McKimmy and Campbell 1982), this alternative approach helps to identify age trends in density by first adjusting for the effects of differential ring area across the stem (Kanowski 1985). The age trend of weighted overall ring density in Douglas-fir has been observed to increase steadily for around 15 rings from the pith and then level off, suggesting that this trend might be a useful indicator of the age of transition to mature wood in this species (M. Hoag, National Particle Board Association, Gaithersburg, Maryland, personal communication).

In this study, age trends in weighted values of overall ring density and its components are analyzed in 15-year-old trees of 60 open-pollinated families of Douglas-fir. Although trees at this early age would normally be expected to produce only juvenile wood, the age trends may reveal that some trees approach the transition from juvenile to mature wood sooner (at younger ages) than others. In addition, because changes in the age trend of weighted overall ring density must be associated with changes in one or more of the individual components, the age trends of the components may be more sensitive to changes occurring early in the transition phase. The objectives of the study were: (1) to determine the extent of genetic variation in age trends of weighted ring density traits and their relationships with overall density of increment cores and stem growth, and (2) to explore the possibility of selection for a shorter juvenile wood formation phase in coastal Douglas-fir.

MATERIALS AND METHODS

Measurements

Total height and diameter at breast height (DBH) were measured in 1987 on 15-year-old trees in the Coyote Creek progeny test plantation, located near Eugene, Oregon. In the following summer, a single pith to bark (5-mm diameter) increment core sample was collected at breast height (1.37 m) from each of the same trees.

The open-pollinated families included in this study correspond to sets 2 and 4 (30 families each) of the Noti Breeding Unit, in the Umpqua Tree Improvement Cooperative (Silen and Wheat 1979). Parent trees are located in natural stands in the central Coast Range of Oregon, between 150 and 450 m elevation. Each set of families was planted as a separate randomized complete block design experiment with four replications. Families in each block were represented at planting by a four-tree, noncontiguous plot, with trees assigned to planting spots at random. At the time increment core samples were taken, survival in these two sets was about 85%.

Information on wood density and its components for each core sample was obtained by using a direct scanning X-ray densitometry system (Hoag and McKimmy 1988; Vargas-Hernandez and Adams 1991). After discarding the first and last annual rings from all samples (because they were usually incomplete), widths and average density values for earlywood, latewood, and the overall ring were determined for each of the remaining rings. The transition from earlywood to latewood was defined as the point where density was midway between the minimum and maximum densities of the ring (Green and Worrall 1964). The number of growth rings measured in each core sample varied because trees reached the breast-height sampling position at different ages. Annual rings were numbered in descending order from furthest (age 15) to closest to the pith, so they represented the age of the tree at the time each ring was formed. Only core samples having the first annual ring at age 7 or age 8 (n = 737, 91% of total trees sampled) were included in the analyses.

For each ring in an increment core sample, weighted density (WD) values for overall, earlywood, and latewood densities were calculated using the following equation:

$$WD = D \cdot (A/\Sigma A), \qquad (1)$$

where

D = Average density of the trait of interest in the particular ring (i.e., overall, earlywood, or latewood density),

A = Cross-sectional area of the trait of interest in the particular ring (at breast height and assuming circular rings), and

ΣA = Total stem cross-sectional area of the trait of interest at breast height.

Latewood proportion (LP) is defined as the proportion of the cross-sectional area of the ring occupied by latewood. Since LP is already expressed as a proportion, no adjustment for ring area was needed.

Statistical analysis

Inspection of age-trend plots showed that age trends differed among traits (Fig. 1). Weighted overall ring density (WORD) and weighted latewood density (WLD) appeared to increase steadily across the whole core. Latewood proportion showed a decreasing but irregular trend in early years, then steadily increased after age 11. The general form of the age trends for these traits was consistent over all trees. The age trend in weighted earlywood density (WED), on the other hand, differed among trees. In some trees, WED appeared to steadily increase over all rings, whereas in others, a plateau was observed at age 11 or later.

For each core sample, a linear regression model was fitted to the portion of each age trend that steadily increased with increasing age (i.e., all rings for WORD and WLD, the first 5 rings for WED, and the last 5 rings for

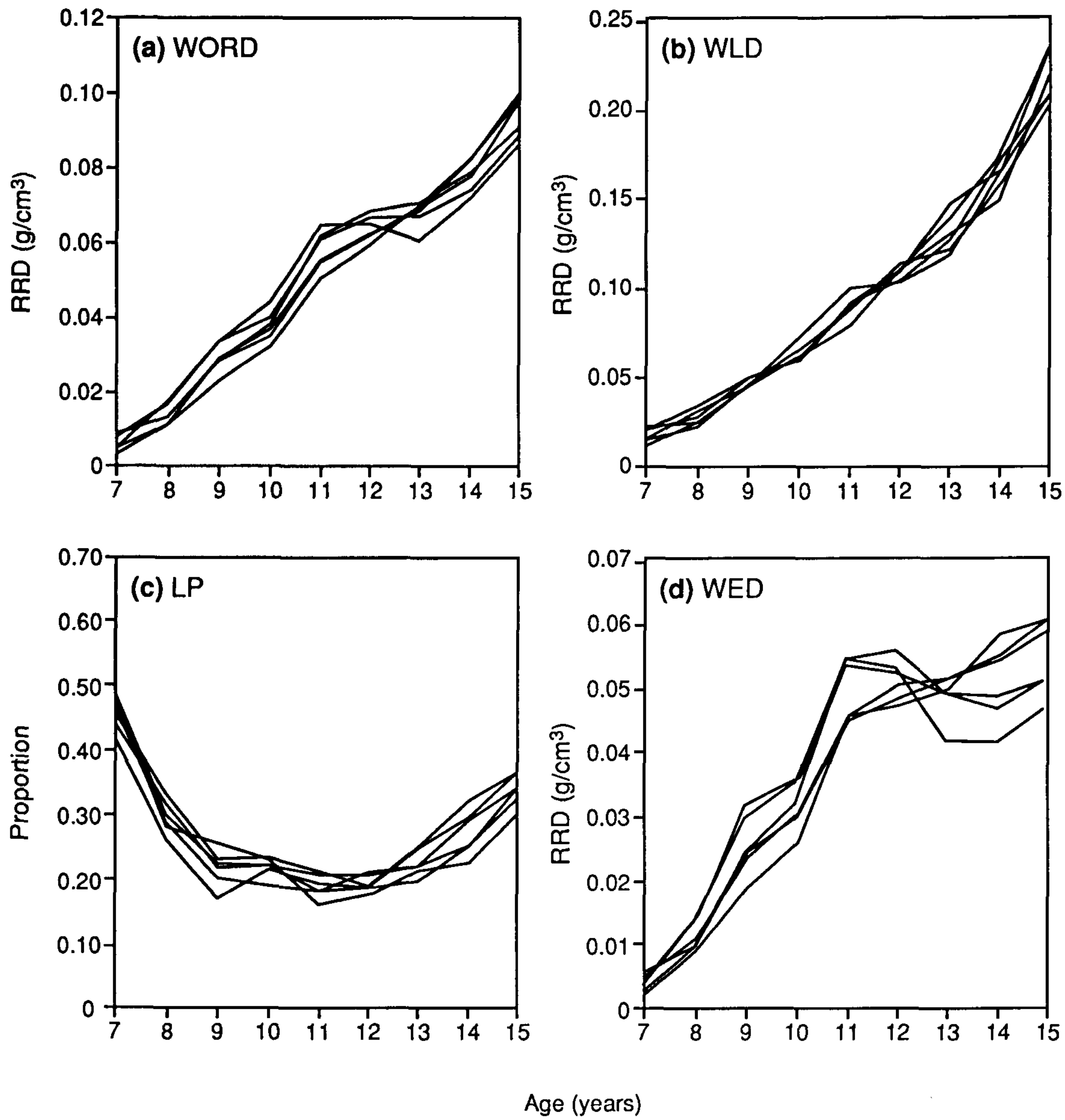

FIG. 1. Age trends of weighted density traits and latewood proportion (LP) in a representative sample of six open-pollinated families of coastal Douglas-fir. Each point represents the average family value for the ring produced at that age (WORD = weighted overall ring density; WLD = weighted latewood density; WED = weighted earlywood density).

LP). Coefficients of determination (R^2) for the linear regressions were normally high for all traits (in most cases $R^2 > 0.90$). To examine family differences in the slopes of these age trends, analyses of variance of the slopes for all traits were performed according to a random-effects model (Table 1), using the SAS GLM procedure (SAS Institute 1987). Type III sums of squares, which are least-squares estimates that take into account the imbalance in number of observations per plot, were used to estimate the mean squares for each source of

TABLE 1. *Form of variance and covariance analyses for age trends of weighted wood density traits.*

Source of variation	Degrees of freedom	Expected mean squares[1]
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/set	$(b - 1)s$	$\sigma_w^2 + k_4\sigma_e^2 + k_5\sigma_{b(s)}^2$
Families/set	$(f - 1)s$	$\sigma_w^2 + k_2\sigma_e^2 + k_3\sigma_{f(s)}^2$
Blocks•Fam./set	$(f - 1)(b - 1)s$	$\sigma_w^2 + k_1\sigma_e^2$
Within-plot	$\sum_{i=1}^{t} (n_i - 1)$	σ_w^2

s = number of sets; b = number of blocks/set; f = number of families/set; k_j = coefficient associated with the j[th] variance component; n_i = number of trees in plot i; t = total number of plots in the experiment; 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.

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

variation. *F*-tests were used to determine significance of family differences in the slope of the age trends.

Because the plateau observed in the age trend for WED might be related to an earlier transition from juvenile to mature wood formation, it was of interest to determine whether families differed in the age at which this plateau is reached. The age at which WED reached the plateau was identified by fitting a two-segment regression line, using piecewise regression techniques (Neter et al. 1983). With this method, two regression lines were fitted simultaneously, one to the rapid increase in WED that occurred in early rings, and the second to the relatively stable values for this trait that occurred later. Regression models in which the age of intersection of the two segments was varied from age 9 to age 15, were fitted to each sample. The point (age) of intersection of the two regression segments in the best fitting model (i.e., the model with the lowest error sum of squares) estimated the age at which the plateau was reached. Families were then compared on the basis of the proportion of trees per plot that reached the plateau in WED by age 12. Age 12 was chosen because after this point, the age of slope change was estimated poorly, if at all, and because most trees having a plateau (as estimated by the two-segment regression), did so by age 12. To test for family differences in the proportion of trees reaching the WED plateau by age 12, plot values were subjected to an analysis of variance using the same random-effects model as used for the other traits (Table 1), but without the within-plot source of variation (since average plot values are used instead of individual tree values). Nonuniform error variance among families was eliminated by a logit transformation of plot proportions (Weisberg 1985), but since the results of analysis of the transformed and nontransformed variables were nearly identical, the results for the plot proportions (untransformed) are presented.

To determine the degree of genetic control of age trends, family heritability estimates were calculated for those traits that showed significant family differences ($P \leq 0.05$), following the procedures described in Vargas-Hernandez and Adams (1991). Genetic relationships of age trends with overall density of the core sample, and with stem growth traits (i.e., height, DBH, volume) at age 15 (Vargas-Hernandez 1990), were investigated by estimating genetic correlations and standard errors of these estimates (Becker 1984). Genetic correlations were calculated only when both traits in a pair showed significant family differences.

RESULTS AND DISCUSSION

Genetic variation in age trends of ring density and its components

Weighted overall ring density increased, on average, 0.011 g/cm^3 per year across increment

TABLE 2. *Estimates of genetic correlations between the proportion of trees with a plateau in WED (weighted earlywood density) by age 12 and overall core density and stem growth traits at age 15.*[1]

Trait	Overall core density	Stem growth traits		
		DBH	Height	Volume[2]
Proportion of trees with a plateau in WED by age 12	0.09 (0.24)	−0.04 (0.32)	−0.12 (0.30)	−0.11 (0.30)

[1] Standard errors of genetic correlation estimates are given in parentheses.
[2] Estimated from height and DBH using the equation for young Douglas-fir given in Adams and Joyce (1990).

core samples (Fig. 1). Weighted latewood density increased over twice as fast (0.026 g/cm^3 per year) over the same period of time. Latewood proportion, though irregular during the early growth rings, increased on average 3.5% per year in the later growth rings (portion of the core that showed a steady increase). Weighted earlywood density increased at about the same rate in the first five years (0.013 g/cm^3) as overall density did over the entire period. Analyses of variance, however, showed no significant family differences ($P \leq 0.05$) in the slopes of the age trends for any density trait, indicating little or no genetic variation. Thus, there appears to be little opportunity for increasing uniformity of wood density in the juvenile section of Douglas-fir trees by selecting for flatter slopes in age trends.

On average, the proportion of trees per plot with a plateau in WED by age 12 was 0.82, but this proportion varied significantly ($P <$ 0.01) among families, with a range of 0.30 to 1.00. Even though the plateau in the WED trend appeared to occur as early as ring 6 from the pith, there are reasons to believe that the plateau may be related to the transition from juvenile to mature wood. As indicated earlier, in a previous study of Douglas-fir (M. Hoag personal communication) WORD was found to reach a plateau at around 15 rings from the pith, which coincides with the age normally assumed as the transition from juvenile to mature wood in this species (Erickson and Harrison 1974; Cown 1976; Senft et al. 1985; Hoag 1988). In the present study, trees did not exhibit a plateau in WORD, presumably because they were too young (i.e., the number of rings from the pith were <10), but a plateau in WED was observed in many trees. Perhaps earlywood is more sensitive to changes in cell morphology accompanying the transition from juvenile to mature wood formation, and the plateau in WORD is not observed until later because WLD and latewood proportion are still increasing at these early ages, more than compensating for the plateau in WED.

If these assumptions are correct, then the differences among families in the proportion of trees reaching a plateau in WED by age 12, might be used as an early indicator of genetic differences in age of transition to mature wood formation, which is important for reducing the age at which trees can be selected for this trait. Furthermore, with an estimated family heritability of 0.30 (SE = 0.10), WED should respond fairly well to selection. This estimate of family heritability is similar to that obtained for the age of transition to mature wood formation in *Pinus taeda* (Loo et al. 1985). Estimated narrow sense heritability for ring density transition age in *Pinus elliottii* Engelm. was reported to be 0.17 (Hodge and Purnell 1993).

Genetic relationships between age trends and overall core density and stem growth

Because family differences in the slopes of the age trends were not significant, genetic correlations involving these traits were not estimated. The proportion of trees with a plateau in WED by age 12 was not genetically correlated with overall core density, nor with stem growth traits (Table 2). These results can be contrasted to those of Loo et al. (1985) for *P. taeda,* where the age of transition to mature wood (as estimated from age trends in average ring density) was negatively correlated with both diameter growth ($r_A = -0.61$) and overall core density ($r_A = -0.68$), i.e., an earlier age of transition was associated with both faster growth and higher wood density. In another *P. taeda* study, however, Bendtsen and Senft (1986) suggested that the age of transition from juvenile to mature wood was not related to growth rate or overall density, but correlation estimates were not given. In *P. elliottii,* ring density transition age was negatively correlated with juvenile wood density ($r_A = -0.53$), but uncorrelated with diameter growth ($r_A = -0.08$) (Hodge and Purnell 1993).

The lack of genetic relationships between the proportion of trees with a plateau in WED at age 12 and overall core density and stem growth suggests that selecting for families with higher proportions of individuals with a plateau in WED would result in a shorter juvenile wood formation phase without negatively influencing wood density or growth rate. Before proceeding, though, it will be necessary to confirm that a plateau in the WED trend is, indeed, strongly related to the age of transition from juvenile to mature wood formation. This could be done by examining age trends of weighted ring density traits in trees that are already producing mature wood, and determining the genetic relationship between the plateau in WED and the plateau in WORD. Obviously, this assumes that the plateau in WORD is an acceptable indicator of the age of transition to mature wood formation in this species. This assumption can be tested by comparing the age trend in WORD to changes in other characteristics (e.g., latewood proportion, tracheid length, fibril angle, or mechanical properties) normally associated with transition to mature wood.

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