RELATIONSHIPS BETWEEN INTRA-RING VARIABLES IN MATURE DOUGLAS-FIR TREES FROM PROVENANCE PLANTATIONS[1]

A. Yassin Abdel-Gadir[2]
Research Associate

R. L. Krahmer
Professor Emeritus

and

M. D. McKimmy
Professor Emeritus

Department of Forest Products, College of Forestry
Oregon State University
Corvallis, OR 97331

(Received April 1992)

ABSTRACT

Relationships among a variety of densitometric characteristics of juvenile and mature wood from 360 trees growing in two plantations of a 1912 Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] Heredity Study were examined. Variables included earlywood density (EWD) and width (EWW); latewood density (LWD), width (LWW), and proportion (LWP); average ring density (RD); and total ring width (RW). The RD components (EWD and LWD) had strong phenotypic and genetic correlations with their respective RW components (EWW and LWW). However, no phenotypic correlation existed between average RD and total RW, and genotypic correlation was weak. The relationship between wood density and radial growth varied by plantation and genotype. The potential exists for improving wood density in juvenile and mature wood by selection, with only a minor impact on radial growth. Selection during the juvenile period to improve mature wood quality is feasible for RD, EWD, LWW, and LWP. Further, selection to improve juvenile RW does not result in reduced wood density during maturity.

Keywords: Douglas-fir, juvenile wood, mature wood, ring density correlations.

INTRODUCTION

A phenotypic correlation coefficient is a measure of the closeness of the relationship between two observed (phenotypic) characteristics. Such a relationship might be inherent, a response to the environmental conditions, or both. Genetic correlation between two traits is an expression of whether or not the traits are inherited as a unit. The main basis for this correlation is the control of two or more traits by a single gene or, more often, by a group of genes (Falconer 1989). Thus, genetic correlations can be used in breeding programs to indicate the relative size and direction of change brought about in a trait of interest through selection for a trait that is more easily observed, measured, or inherited.

This paper describes relationships between seven densitometric variables determined by Abdel-Gadir et al. (1993) for wood in two Douglas-fir [*Pseudotsuga menziesii* (Mirb.)

[1] This is Paper 2813 of the Forest Research Laboratory, Oregon State University, Corvallis.

[2] A. Y. Abdel-Gadir completed this study while a Graduate Research Assistant in the Department of Forest Products, College of Forestry, Oregon State University, Corvallis.

Franco] genetic plantations. The objectives of the study were: (1) to examine the extent of phenotypic and genetic correlations among some intra-ring characteristics within and between juvenile and mature wood zones, and (2) to analyze the influence of planting site, provenance, and family on the relationship between ring density and ring width. Only a relatively small number of families were available for the study and these families were from different populations. Therefore, no attempt was made to calculate correlated responses or to suggest selection strategies.

MATERIALS AND METHODS

The study material was obtained from two plantations of the 1912 Douglas-fir Heredity Study, described in detail by Munger and Morris (1936). The sample, collected by McKimmy and Campbell (1982), contained 360 mature trees from 30 half-sib families (parent trees) representing 10 provenances (geographic seed sources). The provenance locations ranged from northern Oregon to northern Washington, and altitudes, from about 30 m to 1,170 m. The planting locations were Wind River in southwestern Washington (335 m elevation) and Mount Hood in northwestern Oregon (850 m elevation).

Abdel-Gadir et al. (1993) made measurements by X-ray densitometry on two 12-mm cores from each tree in two replications in each of the two plantations. Detailed description of the equipment and scanning procedure is given by Hoag and McKimmy (1988). In each sample core, juvenile wood was represented by rings 6–15 from the pith because ring 6 was the closest ring to the pith available in every core. Mature wood was represented by rings 15–25 from the bark because rings near the bark were narrow and intra-ring density profiles could not be resolved accurately with the X-ray densitometer. Nonweighted averages for seven intra-ring characteristics of juvenile wood samples and mature wood samples were determined: earlywood density (EWD), latewood density (LWD), average ring density (RD), earlywood width (EWW), latewood width (LWW), total ring width (RW), and latewood proportion (LWP). Densities were determined in g/cm^3 and widths in mm; all measurements were made at 9% moisture content. Intra-ring variables were based on an earlywood-latewood boundary established by a density of 0.5 g/cm^3 in the transition zone.

Phenotypic correlation coefficients among all characteristics were calculated based on tree averages (360 observations). Moreover, the relationship between wood density and ring width was determined in each of the provenances and families, as well as with family and provenance averages over and within plantations.

Using the family components of variance ($\sigma_{f(x)}{}^2$ and $\sigma_{f(y)}{}^2$) and covariance ($COV_{f(x,y)}$), additive genetic correlations (Eq. 1) between two characteristics (x, y) were computed as the family intra-class correlation coefficients (Falconer 1989).

$$r_a = \frac{COV_{f(x,y)}}{[\sigma_{f(x)}{}^2 \cdot \sigma_{f(y)}{}^2]^{1/2}} \quad (1)$$

Estimates of family variance and covariance were obtained from analyses of variance using the model described by Eq. 2.

$$Y_{ijkl} = \mu + f_i + p_j + (fp)_{ij} + b_k + + (fb)_{ik} + e_{ijkl} \quad (2)$$

where Y_{ijkl} is the observation of tree l of family i in block k within plantation j; μ is the overall mean; f_i is the effect of family i; p_j is the effect of plantation j; $(fp)_{ij}$ is the interaction of family i and plantation j; b_k is the effect of block k within plantation j; $(fb)_{ik}$ is the interaction of family i and block k; and e_{ijkl} is the normally and independently distributed random deviation of tree l of family i in block k within plantation j. All analyses were carried out using the Statistical Analysis System computing package (SAS Institute 1988).

RESULTS AND DISCUSSION

Correlations among traits

Table 1 lists the phenotypic correlation coefficients between all pairs of the seven densitometric characteristics in juvenile (upper

TABLE 1. *Correlation coefficients[a] between all possible pairs of intra-ring characteristics in juvenile and mature wood.[b]*

	EWD	LWD	RD	EWW	LWW	RW	LWP
EWD		−0.29 (0.0001)	0.56 (0.0001)	−0.67 (0.0001)	−0.22 (0.0001)	−0.56 (0.0001)	0.38 (0.0001)
LWD	−0.14 (0.007)		0.56 (0.0001)	−0.23 (0.0001)	0.72 (0.0001)	0.56 (0.0001)	0.55 (0.0001)
RD	0.54 (0.0001)	0.72 (0.0001)		−0.61 (0.0001)	0.60 (0.0001)	0.04 (0.45)	0.93 (0.0001)
EWW	−0.54 (0.0001)	0.40 (0.0001)	−0.23 (0.0001)		0.64 (0.0001)	0.96 (0.0001)	−0.14 (0.009)
LWW	0.24 (0.0001)	0.45 (0.0001)	0.54 (0.0001)	0.16 (0.003)		0.84 (0.0001)	0.65 (0.0001)
RW	−0.23 (0.0001)	0.11 (0.04)	−0.06 (0.23)	0.80 (0.0001)	0.72 (0.0001)		0.15 (0.004)
LWP	0.63 (0.0001)	0.53 (0.0001)	0.94 (0.0001)	−0.67 (0.0001)	0.59 (0.0001)	−0.11 (0.04)	

[a] Juvenile wood above and mature wood below diagonal. Coefficients are significantly different from zero at the probability levels given between parentheses.
[b] EWD = earlywood density, LWD = latewood density, RD = average ring density, EWW = earlywood width, LWW = latewood width, RW = total ring width, and LWP = latewood proportion.

right) and mature (lower left) wood. All of these relationships were linear. During the juvenile period, RD was positively, moderately, and equally correlated with EWD and LWD. Each of these components explained about 30% of the variation in RD among trees. There was a slight trend indicating that the higher EWD trees had slightly lower LWD. Ring density had a very strong correlation with LWP; about 87% of the phenotypic variation in RD among trees could be explained by variation in LWP. This result and the results of Smith (1955) and Kennedy (1961) suggest that variation in RD and LWP depends on almost the same set of factors. Most of these relationships were similar during maturity.

Being negatively correlated with EWW and positively with LWW, RD appeared to have a weak, nonsignificant correlation with RW in both zones (Table 1). In contrast, the RD components had strong, significant correlations with their respective RW components, but the signs were different. Growth rate and density were negatively correlated in earlywood (EWD and EWW), but positively correlated in latewood (LWD with LWW). These results demonstrate the tendency for fast growth to be associated with thin-walled tracheids in earlywood, but with thick-walled tracheids in latewood. Such trends were probably a direct response of the differentiating cells in the cambial zone to the relative availability of photosynthates and growth regulators at different times during the growing season.

The relatively high, positive correlation (r = 0.64) between EWW and LWW during juvenility suggests that trees with early fast growth had a tendency to maintain that growth rate throughout the season. However, the EWW-LWW correlation dropped dramatically (r = 0.16) when the trees approached maturity; this decrease was accompanied by a comparable increase in the size of the negative correlation between LWP and EWW (Table 1).

Phenotypic correlation coefficients between some traits are low; therefore, trees that are highly valued for one trait may or may not be highly valued for another—for example, trees that have high EWD may or may not have high LWD. Fast-growing trees may be high- or low-gravity trees, and they may have low or high proportions of thick-walled tracheids. These observations, coupled with the high positive RW-LWW relationship, do not support the general understanding that a fast growth rate results in low-gravity trees due to the lack of latewood. The relationship between RW and LWP, albeit not strong, was positive in juvenile wood, and negative in mature wood.

Results of the additive genetic correlations (r_a) are presented in Fig. 1. Because genetic correlation coefficients usually have high standard errors, Goggans (1964) has suggested that only the sign and the relative size of the genetic correlation be considered. In this study, estimates were obtained for the pairs where family components of variance were significantly ($P \leq 0.05$) different from zero. This was the case for most of the properties studied in juvenile wood, as well as for EWD, LWW, LWP, and RD in mature wood. Family variation was biased upwards because the families were from different populations. Therefore, this discussion is limited to trends rather than magnitudes of individual correlations.

Results indicate that the inverse phenotypic relationship between EWD and EWW and the positive one between LWD and LWW (Table 1) had substantial genetic bases in juvenile wood (Fig. 1). In contrast to these relationships, a weak, negative genetic correlation existed between average RD and RW. The lack of sizable correlation between RD and RW suggests that selection for juvenile wood density may be carried out with little or no prejudice against growth rate. Because of this independent inheritance, fast growth rates also can be combined with either dense or light wood in a breeding program. Contrary to these results, King et al. (1988) and Bastien et al. (1985) reported significant correlations between wood density and diameter and volume growth in unrelated populations of Douglas-fir.

The moderately strong genetic correlation between juvenile EWD and LWD ($r_a = 0.56$) indicates that these traits were not inherited independently. These two density components had a strong, positive genetic correlation with average RD (Fig. 1). A selection program aiming only at high EWD to indirectly increase RD or to reduce density variation within growth rings may bring about a decrease in radial growth because of the close, negative

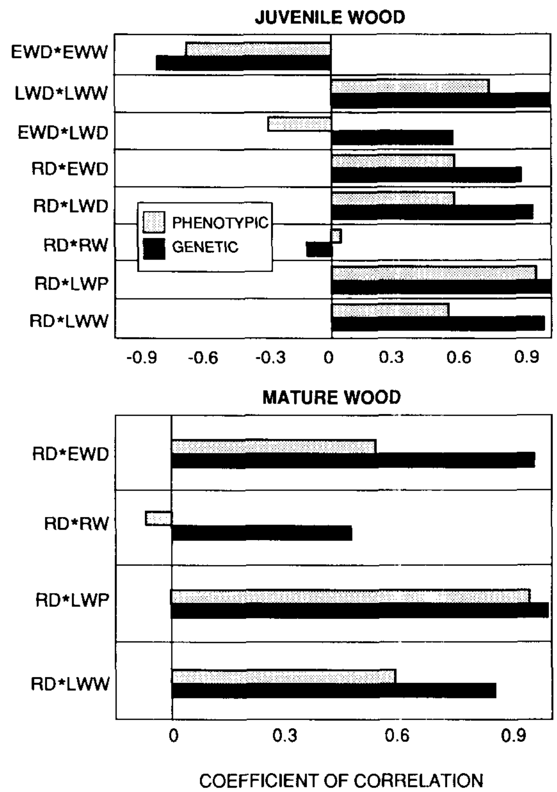

FIG. 1. Comparison of genetic and phenotypic correlations for intra-ring characteristics in juvenile and mature wood. (EWD = earlywood density, EWW = earlywood width, LWD = latewood density, LWW = latewood width, RD = average ring density, RW = total ring width, and LWP = latewood proportion.)

EWD-EWW genetic relationship. Further, selection for LWW and LWP may inherently result in increased wood density. Because LWW and LWP are easily measured, this association, if coupled with moderate to strong heritabilities, could potentially alleviate at least some of the laboratory expense associated with determining wood density.

Family differences were significant for only four traits in mature wood; therefore, few genetic correlations were calculated in mature wood. Genetic relationships of mature wood RD with EWD, LWW, and LWP remained as high as they were in the juvenile wood zone. This dependent inheritance suggests that these intra-ring characteristics are controlled to a

TABLE 2. *Correlation coefficients[a] among all possible pairs of intra-ring characteristics between juvenile (J) and mature (M) wood.[b]*

	MEWD	MLWD	MRD	MEWW	MLWW	MRW	MLWP
JEWD	0.48 (0.0001)	−0.31 (0.0001)	−0.03 (0.61)	−0.12 (0.02)	−0.14 (0.006)	−0.17 (0.001)	−0.02 (0.66)
JLWD	0.02 (0.75)	0.84 (0.0001)	0.72 (0.0001)	−0.32 (0.0001)	0.43 (0.0001)	0.04 (0.42)	0.60 (0.0001)
JRD	0.45 (0.0001)	0.42 (0.0001)	0.63 (0.0001)	−0.39 (0.0001)	0.34 (0.0001)	−0.07 (0.20)	0.57 (0.0001)
JEWW	−0.05 (0.31)	0.33 (0.0001)	0.29 (0.0001)	0.16 (0.002)	0.51 (0.0001)	0.43 (0.0001)	0.26 (0.0001)
JLWW	0.24 (0.0001)	0.57 (0.0001)	0.70 (0.0001)	−0.14 (0.006)	0.74 (0.0001)	0.34 (0.0001)	0.66 (0.0001)
JRW	0.05 (0.30)	0.45 (0.0001)	0.47 (0.0001)	0.06 (0.25)	0.65 (0.0001)	0.44 (0.0001)	0.44 (0.0001)
JLWP	0.40 (0.0001)	0.42 (0.0001)	0.64 (0.0001)	−0.39 (0.0001)	0.43 (0.0001)	−0.01 (0.82)	0.63 (0.0001)

[a] Coefficients are significantly different from zero at the probability levels given in parentheses.
[b] EWD = earlywood density, LWD = latewood density, RD = average ring density, EWW = earlywood width, LWW = latewood width, RW = total ring width, and LWP = latewood proportion.

large extent by the same set of genes. Although differences among families for RW were not significant in mature wood, the genetic correlation of this trait with mature RD was estimated (Fig. 1) to suggest the direction of this relationship, which is lacking in the literature. Although phenotypic correlation was negligible, the genetic association between RW and RD appears to be favorable in mature wood.

Juvenile-mature wood correlations

Table 2 lists the correlation coefficients for all possible combinations of characteristics between juvenile and mature wood. Correlations for EWD, LWD, RD, EWW, LWW, RW, and LWP between juvenile and mature wood were highly significant ($P \leq 0.001$).

Juvenile-mature phenotypic correlations were highest for LWD ($r = 0.84$) and LWW ($r = 0.74$). Thus, the values of juvenile wood for these traits were consistently indicative of those of the mature wood. Juvenile-mature wood correlations for EWD and RW were moderate; variation in each of these traits during the juvenile period explained around 20% of the variation in the respective trait during maturity. The weakest phenotypic juvenile-mature wood relationship was that for EWW. The correlations for RD or LWP between juvenile and mature wood suggest that a tree that produces high-gravity wood or LWP during the early years of growth (rings 6–15) would continue to do so during the mature period; for each of these traits the juvenile wood values explained about 40% of the mature wood values. These results concur with those of McKimmy (1966) and Keller and Thoby (1977) to indicate that correlations of wood density near the pith with that of mature wood are poor; however, these correlations improve progressively as comparisons are made between measurements on wood samples that are relatively close in age.

Genetic correlations (r_a) were obtained for the traits that exhibited significant differences among families during both juvenile and mature periods (Fig. 2). The positive phenotypic relationships for these traits apparently had strong genetic bases. In all cases, the genotypic correlation was generally greater than the phenotypic one. Nepveu (1976) noted that, if environmental effects at the juvenile and mature stages are assumed to be independent, then the phenotypic covariance becomes a genetic covariance. He further suggested that the phenotypic correlation becomes a lower limit for the corresponding genetic correlation because the denominator in the former ratio is greater than that of the latter. In this study, at least for RD, LWW, and LWP, phenotypic juvenile-mature correlation coefficients can help explain the corresponding genetic correlations. The magnitudes of the genetic correlations indicate that trees with high-gravity wood during the early years of growth would inherently produce high-gravity wood when they reach maturity. Consequently, juvenile selection for RD appears to be feasible. Similarly, selection for EWD, LWW, or LWP of the mature wood can be achieved to a great extent by selecting for these traits in young trees.

In addition to these single-trait correlations, relationships between density in mature wood and intra-ring variables in juvenile wood were explored. Mature wood RD was most highly correlated with juvenile latewood traits (LWD, LWW, and LWP), and least correlated with juvenile earlywood traits (EWD and EWW; Table 2). The moderately positive, phenotypic correlation between mature RD and juvenile RW indicates that trees that grew fast during the juvenile period tended to produce denser wood during the mature period (Table 2). The juvenile-mature genetic correlation between these two traits was $r_a = 0.16$ (± 0.09), indicating that juvenile selection to improve radial growth does not affect wood density during maturity. Such selection may, in fact, bring about a slight increase in mature wood density. However, mature RW had a nonsignificant phenotypic relationship with juvenile RD.

A separate set of analyses based on family (plot) means was conducted to see how well average mature wood density of families can be predicted through their average juvenile wood properties. The single juvenile trait that best predicted family performance during maturity was juvenile latewood width (JLWW; $P = 0.0001$), which explained about 73% of the variation in mature wood density (MRD). The standard deviation from the regression was 0.0236 and the fitted equation was:

$$\text{MRD} = 0.439 + 0.110\text{JLWW} \quad (3)$$

To increase the precision and predictive power of Eq. 3, all juvenile wood variables were allowed in the model by stepwise regression (PROC REG; SAS 1988); the significance level for entry and staying in the model was specified as $\alpha = 0.05$. Juvenile ring density (JRD; $P = 0.0001$), latewood density (JLWD; $P = 0.019$), and ring width (JRW; $P = 0.0001$) were significant in predicting mature wood density. Standard errors of these three regression coefficients were, respectively, 0.102, 0.087, and 0.003. The fitted response function was:

$$\text{MRD} = -0.063 + 0.79\text{JRD} + 0.21\text{JLWD} + 0.025\text{JRW} \quad (4)$$

Latewood width was excluded from the model because it was highly correlated with the entering variables. Although the multiple regression (Eq. 4) resulted in some increase in the amount of explained variation (adjusted R^2 = 80%) and a decrease in the mean error square, its major improvement over the simple regression (Eq. 3) was in Mallow's C_p statistic (a measure of total squared error for a model related to the number of parameters; Neter et al. 1989). For Eq. 3, when JLWW was the only independent variable in the regression model, the C_p value was 39.5, whereas for Eq. 4 the

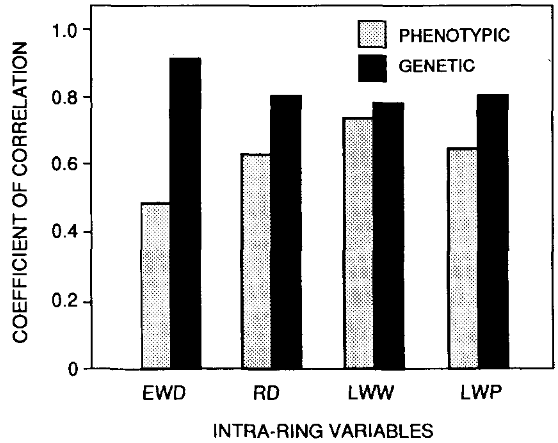

FIG. 2. Comparison of genetic and phenotypic correlations between juvenile and mature wood for intra-ring characteristics with significant family effects. (EWD = earlywood density, RD = average ring density, LWW = latewood width, and LWP = latewood proportion.)

TABLE 3. *Correlation coefficients[a] between ring density and ring width based on groupings of interest.*

	Juvenile wood			Mature wood		
	Mount Hood	Wind River	Pooled data	Mount Hood	Wind River	Pooled data
All rings			−0.09 (0.0001)			−0.13 (0.0001)
Tree averages	−0.25 (0.0007)	0.16 (0.03)	0.04 (0.43)	−0.30 (0.0001)	−0.15 (0.05)	−0.06 (0.23)
Family averages	−0.25 (0.05)	−0.12 (0.33)	0.20 (0.02)	−0.23 (0.08)	−0.01 (0.95)	0.12 (0.17)
Provenance averages	−0.25 (0.29)	0.02 (0.94)	0.35 (0.03)	−0.28 (0.23)	−0.04 (0.87)	0.24 (0.14)

[a] Coefficients are significantly different from zero at the probability levels given in parentheses.

C_p value was 4.0 (=number of parameters in the model). This suggests that the multiple regression had a small total mean squared error with no indication of bias in the model. Nonetheless, Eq. 3 might be appealing because LWW is easier to measure than wood density and/or any of its primary components.

Relationship between wood density and growth rate within groups

The relationship between wood density and growth rate is of special interest because both traits are economically important. The terms "rate of growth" and "growth rate parameters" or "growth rate components" are used occasionally when referring to RW and/or its components. These radial characteristics are not ideal measures of the rate of growth, which should be assessed as a three-dimensional property. However, they are part of volume growth, have high correlation with height growth, and are included in most lumber grading systems because of their indirect relationship with several wood quality parameters. In timber grading, minimum standards of structural-grade timber quality have been established on the basis of number of rings per unit length.

Many foresters believe that faster growing trees have lower wood density. Although this appears to be the case for some tree species such as spruce (Keith 1961; Olesen 1976), most hard pines show a lack of correlation between growth rate and wood density (Goggans 1962; Goddard and Cole 1966; Matziris and Zobel 1973; Megraw 1985). Early studies on Douglas-fir have shown that ring width is one of the factors that explain variation in wood density (Janka 1921; Drow 1957; Mozina 1960). Knigge (1962) observed that wood near the pith is lighter than outer wood of similar growth rate. He suggested that the influence of growth rate on wood density is more obvious during early years of growth. McKimmy (1959) noted that "a constant rate of growth with differing percentage of summer wood caused more variation in specific gravity than did a constant percentage of summer wood under differing rate of growth." In a later study, he confirmed that growth rate did not significantly affect wood density (McKimmy 1966).

In this study, average ring widths varied between 2.3 and 7.7 mm in juvenile wood and between 0.9 and 3.0 mm in mature wood. As indicated previously, however, with correlations based on tree averages, no relationship exists between wood density and rate of radial growth in either juvenile or mature wood. This finding is in agreement with that of Smith and Kennedy (1983), who, working with 10,000 trees, concluded that the impact of fast growth on wood density was only slight. The data at hand allow further investigation of this relationship because data can be sorted into groups of interest and means of different combinations can be examined. These results are given in Tables 3, 4, and 5.

Correlation analysis of all ring data (10 rings

TABLE 4. *Correlation coefficients[a] between average ring density and total ring width based on tree averages in each of 10 provenances.*

Provenance	Juvenile wood	Mature wood
Carson	0.14 (0.22)	−0.01 (0.91)
Race Track	−0.08 (0.50)	−0.07 (0.57)
Wind River	0.11 (0.37)	0.19 (0.11)
Darrington	0.32 (0.006)	0.05 (0.65)
Lakeview	0.04 (0.73)	0.15 (0.20)
Granite Falls	−0.04 (0.71)	−0.09 (0.47)
Hazel	−0.27 (0.02)	−0.33 (0.005)
Fortson	0.02 (0.89)	−0.08 (0.50)
Gates	0.09 (0.45)	−0.08 (0.62)
Palmer	0.04 (0.71)	−0.22 (0.06)

[a] Coefficients are significantly different from zero at the probability levels given in parentheses.

per zone in each tree) indicated significant negative correlations (Table 3), but nonetheless was of no practical importance. Ring width explained less than 1% of the variation in RD in juvenile wood and less than 2% in mature wood.

When tree averages in juvenile wood were sorted by plantation, the relationship was negative in the slow-growing trees at Mount Hood but positive in the fast-growing trees at Wind River. During the mature period, RD and RW were inversely correlated in both plantations; however, the correlation seems to be stronger in the plantation with low-gravity trees (Mount Hood). These results support the significant plantation effect that was established for these traits in a previous study (Abdel-Gadir et al., 1993).

The results of family mean correlations between RD and RW over plantations suggest that, in juvenile wood, fast-growing families tend to produce high-density wood; this relationship was insignificant in mature wood. Correlation of family means by plantation indicates that the RD-RW relationship was nonsignificant at the plantation that produced faster growth (Wind River); the less favorable growth conditions at Mount Hood allowed expression of a negative correlation between the two traits. Similar results were obtained in a study involving 34 open-pollinated families of 7-year-old Douglas-fir (Megraw 1985). Considering provenance means for RD and RW, the only significant correlation was the positive correlation, based on averages over plantations, in juvenile wood.

The relationship between RD and RW when the genetic constitution is kept constant was examined also. The results (Table 4) indicate that the association between the two traits is population-specific. During the juvenile period, the relationship was nonsignificant in 8 of the 10 provenances. In the other two provenances, a distinct negative correlation was evident in the Hazel provenance and a positive correlation in the Darrington provenance. Both provenances were from the Stillaquamish River Valley in northwest Washington and, relative to the others, they ranked, respectively, fourth and ninth for RD. Also, during the mature period RD related significantly to RW in only two provenances, Hazel and Palmer (Table 4), which ranked fourth and sixth for RD, respectively. The relationship was negative in

TABLE 5. *Average ring density (RD, g/cm³), total ring width (RW, mm), and correlation coefficient (r) between average ring density (RD) and total ring width (RW) in each of seven latewood proportion (LWP) classes.*

LWP classes	Juvenile wood			Mature wood		
	RD	RW	*r*	RD	RW	*r*
0.200–0.249	0.446	4.10	−0.175**[a]	0.440	2.04	−0.398**
0.250–0.299	0.472	4.16	−0.159**	0.467	1.95	−0.310**
0.300–0.349	0.500	4.16	−0.110**	0.495	1.88	−0.172**
0.350–0.399	0.529	4.18	−0.105*	0.520	1.81	−0.031[ns]
0.400–0.449	0.556	3.84	0.062[ns]	0.549	1.79	0.045[ns]
0.450–0.499	0.580	3.93	0.107*	0.577	1.79	0.100*
0.500–0.549	0.606	3.68	0.165*	0.603	1.70	0.210**

[a] ** = Significant at the 0.0001 level; * = significant at the 0.002 level; and ns = not significant at the 0.05 level.

both cases. Similarly, results of analyses in the various families (not shown here) revealed that, even in families from the same provenance, the RD-RW correlation can be positive, negative, or nonexistent. In juvenile wood, the correlation was positive in four families (r = from 0.44 to 0.51); only one of these families continued to have a positive, significant relationship during maturity. A negative association between RD and RW was found in two families (r = from −0.49 to −0.40) during the juvenile period and in four families (r = from −0.53 to −0.41) during maturity. These results have implications for the tree breeder interested in manipulating wood density. Besides the relative ranks of genotypes for wood density, the kind and extent of the RD-RW relationship in genotypic groups can be an important consideration in selection efforts.

Another set of analyses was conducted to eliminate any effect that LWP might have on the RW-RD relationship. Data were grouped in seven LWP classes that were represented in both juvenile and mature wood (Table 5). At the same LWP, wood density of the juvenile wood was equal to, or slightly higher than, that of the mature wood despite the large difference in RW. Within these LWP classes, RD-RW correlations, although weak, were interesting. There was a trend towards negative correlation in the rings with low LWP and positive correlation in the rings with high LWP (Table 5). Further, the correlation coefficient between RD and RW had its highest negative value in the lowest LWP class; as LWP increased, the negative correlation decreased to a minimum and then started to increase.

CONCLUSIONS

Being negatively correlated with EWW and positively with LWW, tree average RD appears to have a weak, nonsignificant phenotypic correlation with RW, but a very strong correlation with LWP in both juvenile and mature wood. When data are sorted by plantation, tree RD relates negatively to RW at the less favorable site, but the relationship is weak in the fast-growing trees at the more favorable site.

Based on provenance or family averages over plantations, the relationship between wood density and ring width is either positive or nonexistent. When correlations are performed under uniform environments, trees that are genetically faster growing tend to produce wood of lower density in the less favorable plantation.

Although there is a slight trend suggesting that higher EWD trees have low LWD, the two traits exhibit a genetically positive correlation. Fast growth is genetically associated with low density in earlywood but with high density in latewood. The resulting weak (negative) genetic correlation between RD and RW indicates that it is feasible to develop a strain of Douglas-fir with high juvenile wood density with low impact on radial growth. In the various provenances and families, the relationship between RD and RW can be positive, negative, or nonexistent.

For each of the traits, the observed mature wood values relate significantly and positively to the juvenile wood values; phenotypic correlations are highest for RD, LWD, LWW, and LWP and lowest for EWW. Juvenile-mature genetic correlations indicate that selection to improve juvenile wood density will bring about favorable changes in mature wood density. Juvenile selection to improve traits at rotation age is also feasible for EWD, LWW, and LWP. Trees with wide rings during the early years of growth tend to produce high-gravity wood when they reach maturity; however, the genetic correlation (positive) is weak.

REFERENCES

Abdel-Gadir, A. Y., R. L. Krahmer, and M. D. McKimmy. 1993. Intra-ring variations in mature Douglas-fir trees from provenance plantations. Wood Fiber Sci. 25(2):170–181.

Bastien, J. C., B. Roman-Amat, and G. Vonnet. 1985. Natural variability of some wood quality traits of coastal Douglas-fir in a French progeny test: Implications on breeding strategy. Pages 169–186 *in* W. Ruetz and J. Nather, eds. Proceedings of the technical workshop: Breeding strategies for Douglas-fir as an introduced species. Schriftenreihe der Forstlichen Bundesversuchsanstalt No. 21. International Union of Forestry Research Organizations, Vienna, Austria.

DROW, J. T. 1957. Relationship of locality and rate of growth to density and strength of Douglas-fir. USDA For. Serv. FPL Rep. 2078. Forest Products Lab., Madison, WI. 56 pp.

FALCONER, D. S. 1989. Introduction to quantitative genetics, 3rd ed. Longman Inc., New York, NY.

GODDARD, R. E., AND D. E. COLE. 1966. Variation in wood production of six-year-old progenies of selected slash pines. Tappi 49(8):359–362.

GOGGANS, J. F. 1962. The correlation, variation and inheritance of wood properties in loblolly pine. Tech. Rep. 14. North Carolina State University, School of Forestry, Raleigh, NC. 155 pp.

———. 1964. Correlation and heritability of certain wood properties in loblolly pine (*Pinus taeda* L.). Tappi 47(6): 318–322.

HOAG, M. L., AND M. D. MCKIMMY. 1988. Direct scanning X-ray densitometry of thin wood sections. Forest Prod. J. 38(1):23–26.

JANKA, G. 1921. Über die technische Qualität des Douglastannenholzes. Centralbl. Gesamte Forstwesen 47:185–189.

KEITH, C. T. 1961. Characteristics of annual rings in relation to wood quality for white spruce. Forest Prod. J. 11(3):122–126.

KELLER, R., AND M. THOBY. 1977. Liaisons entre l'état juvénile et l'état adulte pour quelques caractéres technologiques et auxométriques chez le Douglas (*Pseudotsuga menziesii*). Ann. Sci. For. 34:175–203.

KENNEDY, R. W. 1961. Variation and periodicity of summerwood in some second-growth Douglas-fir. Tappi 44(3):161–166.

KING, J. N., F. C. YEH, J. C. HEAMAN, AND B. P. DANCIK. 1988. Selection of wood density and diameter in controlled crosses of coastal Douglas-fir. Silvae Genetetica 37(3/4):152–157.

KNIGGE, W. 1962. Untersuchungen über die Abhängigkeit der mittleren Rohdichte nordamerikanischer Douglasienstämme von unterschiedlichen Wuchsbedingungen. Holz Roh- Werkst. 20(9):352–360.

MATZIRIS, M. I., AND B. J. ZOBEL. 1973. Inheritance and correlation of juvenile characteristics in loblolly pine (*Pinus taeda* L.). Silvae Genetetica 22(1/2):38–45.

MCKIMMY, M. D. 1959. Factors related to variation of specific gravity in young-growth Douglas-fir. Bull. 8. Forest Products Research Center, Corvallis, OR. 52 pp.

———. 1966. A variation and heritability study of wood specific-gravity in 46-year-old Douglas-fir from known seed sources. Tappi 49(12):542–549.

———, AND R. K. CAMPBELL. 1982. Genetic variation in the wood density and ring width trends in coastal Douglas-fir. Silvae Genetetica 31(2/3):43–55.

MEGRAW, R. A. 1985. Wood quality factors in loblolly pine. Tappi Press, Technology Park, Atlanta, GA. 123 pp.

MOZINA, I. 1960. Ueber den Zusammenhang zwischen Jahrringbreite und Raumdichte bei Douglasienholz. Holz Roh- Werkst. 18(11):409–413.

MUNGER, T. T., AND W. G. MORRIS. 1936. Growth of Douglas-fir trees of known seed source. Tech. Bull. 537. USDA, Washington, DC. 40 pp.

NEPVEU, G. 1976. Wood quality juvenile-mature correlations. Doc. 1976/3. Inst. Natl. Rech. Agron. Cent. Natl. Rech. For., Nancy, France.

NETER, J., W. WASSERMAN, AND M. H. KUTNER. 1989. Applied linear regression models. R. D. Irwin Inc., Homewood, IL. 667 pp.

OLESEN, P. O. 1976. The interrelation between basic density and ring width of Norway spruce. Forst Forsøgsvaes., Dan. 34(4):341–359.

SAS INSTITUTE. 1988. SAS/STAT user's guide. Version 6.03 ed. SAS Institute Inc., Cary, NC. 1,028 pp.

SMITH, D. M. 1955. Relationship between specific gravity and percentage of summerwood in wide-ringed, second-growth Douglas-fir. USDA For. Serv. FPL. Rep. 2045. Forest Products Lab., Madison, WI. 19 pp.

SMITH, J. H., AND R. W. KENNEDY. 1983. Effect of stand management on tree, log, and wood quality of Douglas-fir. IAWA Bull. n.s. 4(1):12.