Genetic variation of wood density components in young coastal Douglas-fir: implications for tree breeding[1]

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The genetic control of wood density components (earlywood density, latewood density, and latewood proportion) and their relationships with overall density in coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) were examined to assess the usefulness of this information in breeding for wood density. The genetic relationships of wood density with intraring density variation and bole volume growth were also investigated. Increment cores were taken at breast height from 15-year-old trees of 60 open-pollinated families. Averages across each core for overall wood density, its components, and intraring density variation were determined by using X-ray densitometry. Bole volume at age 15 for the same trees was derived from tree height and diameter at breast height measurements. Although wood density components varied significantly among families and were under moderate genetic control (individual-tree heritability (h_i^2) > 0.24), none had a higher heritability than overall density ($h_i^2 = 0.59$). Density components had strong genetic correlations with overall density ($r \geq 0.74$) but were also strongly related among themselves ($0.57 \leq r \leq 0.92$). Thus, density components have limited value in improving the efficiency of selection for overall density. Overall density was positively correlated with intraring density variation ($r = 0.72$) and negatively correlated with bole volume ($r = -0.52$). Comparison of several selection indices incorporating wood density and one or more growth traits, however, showed that it is possible to obtain substantial gains in bole volume without loss in (or even with a modest increase in) wood density. By restricting the response in wood density, the change in intraring density variation can also be limited.

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Le contrôle génétique des composantes de la densité du bois (densité du bois de printemps, densité du bois d'été et proportion et bois d'été) et leurs relations avec la densité globale ont été étudiés chez le sapin de Douglas de la côte (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*), afin de vérifier l'utilité de ce type d'information pour l'amélioration quant à la densité du bois. Les relations génétiques de la densité du bois avec la variation de densité au sein d'un même cerne annuel et la croissance en volume de la tige ont aussi été étudiées. Des carottes ont été prélevées à hauteur de poitrine chez des arbres âgés de 15 ans représentatifs de 60 familles issues de pollinisation libre. Pour chaque carotte, des moyennes de densité générale, des composantes de cette densité et des variations de densité intracerne ont été obtenues par densitométrie aux rayons X. Pour les mêmes arbres, le volume de la tige à 15 ans fut calculé à partir des mesures de leur hauteur et de leur diamètre à hauteur de poitrine. Quoique les composantes de la densité du bois montraient une variation significative parmi les familles et se retrouvaient sous contrôle génétique modéré (héritabilité individuelle au niveau de l'arbre (h_i^2) > 0,24), aucune de ces dernières n'affichait d'héritabilité supérieure à celle de la densité globale ($h_i^2 = 0{,}59$). Les composantes de la densité montraient de fortes corrélations génétiques avec la densité globale ($r \geq 0{,}74$) et étaient aussi fortement corrélées entre elles ($0{,}57 \leq r \leq 0{,}92$). Les composantes de la densité ont donc une valeur limitée quant à améliorer l'efficacité de la sélection pour la densité globale. La densité globale était positivement corrélée avec la variation de densité intracerne ($r = 0{,}72$) et négativement corrélée avec le volume de la tige ($r = -0{,}52$). Toutefois, la comparaison de quelques indices de sélection incorporant la densité du bois et un ou plusieurs caractères de croissance a montré qu'il était possible d'obtenir des gains intéressants en volume de la tige sans perte (ou même avec une augmentation modérée) en densité du bois. En restreignant la réponse en densité du bois, le changement en variation de densité intracerne peut aussi être limité.

[Traduit par la rédaction]

Introduction

With the move in forest management to shorter rotations, wood quality has become a major concern, mainly because of the higher proportion of low-density juvenile wood found at harvest age in younger and faster grown trees (Bendtsen 1978). Wood density is probably the most important indicator of wood quality because of its important role in determining wood strength, pulp yield, and several other wood properties (Panshin and DeZeeuw 1980). One alternative for offsetting some of the negative effects of short-rotation trees on wood quality would be to breed for increased juvenile-wood density. Increasing density of the juvenile core would improve the quality of this section of the tree and might help to increase uniformity of wood density across the stem (Nicholls et al. 1980). In addition, earlier studies have shown a strong correlation between juvenile and mature wood (Cown 1976; McKimmy and Campbell 1982); thus, improvement in mature-wood density should result as well.

Efficient application of breeding methods to increase juvenile-wood density in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), however, is hampered by lack of precise information on the genetic control of this trait. Reported heritability estimates for Douglas-fir wood density have varied widely (Cown 1976; Bastien et al. 1985; King et al. 1988).

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Understanding the genetics of wood density is complicated by the composite nature of this trait. In temperate softwoods, ring density is the product of the proportion of each ring that is earlywood or latewood and the relative densities of each (Nicholls et al. 1980); that is,

$$[1] \quad \mathrm{RD} = \mathrm{ED} + \mathrm{LP}(\mathrm{LD} - \mathrm{ED})$$

where ED is earlywood density, LD is latewood density, and LP is latewood proportion (i.e., proportion of annual ring that is latewood).

A particular value of wood density can result from various combinations of its components. Therefore, knowledge of the genetic control of these components and their interrelationships would help in understanding the genetics of overall wood density. Moreover, information about the relative influence of individual components on overall wood density might prove useful for increasing the efficiency of selection for this trait, either by selecting directly for one or more components, as suggested by Nicholls et al. (1980), or by incorporating them as secondary traits in selection indices (Sales and Hill 1976). Selection indices employing secondary traits can improve the response in the trait of interest if one or more of the secondary traits has higher heritability than the trait of interest and has a high genetic correlation with that trait (Baker 1986). In addition, if two or more secondary traits that are strongly correlated with the primary trait are included in the index, the index will be more efficient if the secondary traits are weakly interrelated among themselves (White and Hodge 1991).

In previous studies, undesirable genetic relationships between wood density and other economic traits in Douglas-fir have been observed. Particularly important are the negative genetic correlation between wood density and bole volume (Bastien et al. 1985; King et al. 1988) and the strong positive correlation between wood density and intraring density variation (IRV) (Bastien et al. 1985). High IRV causes increased variation of veneer thickness and more veneer fissures (Birot et al. 1983). Because gains from selection on wood density alone might be offset by a significant reduction in growth rate, or by a concomitant increase in IRV, it is important to verify these relationships in other populations of Douglas-fir.

Knowledge of the genetic relationships among individual wood density components, bole volume, and IRV might help minimize undesirably correlated responses when selecting for increased wood density. By selecting for components that show the least negative genetic correlations with growth, wood density could be improved yet have the least negative impact on growth rate. In a similar fashion, when wood density is the target of selection, individual density components might minimize the impact on IRV (Nicholls et al. 1980).

The objectives of this study were (*i*) to determine the genetics of wood density components in Douglas-fir and the interrelationships of these components with overall wood density, IRV, and bole volume and (*ii*) to evaluate the implications of these relationships for tree breeding.

Materials and methods

Plant material

Sixty open-pollinated families of coastal Douglas-fir (*P. menziesii* var. *menziesii*) growing in the Coyote Creek progeny test plantation near Eugene, Oregon, were used in this study. These families correspond to sets 2 and 4 (30 families each) of the Noti Breeding Unit in the Umpqua Tree Improvement Cooperative (Silen and Wheat 1979). The parent trees were phenotypically selected in natural stands between elevations of 150 and 450 m in the central Coast Ranges of Oregon. Each set of families was planted in 1974 (1-0 plug seedlings) in a separate randomized complete block design with four replications. Families in each block were represented by a four-tree noncontiguous plot, with trees assigned to planting spots at random. When the measurements for this study were made, survival for these two sets was about 85%. Mortality during the first 2 years after planting was replaced with trees from the original families; however, replacements were not included in the analyses.

Measurements

At the end of the 1987 growing season, when all trees were 15 years old from seed, they were measured for total height (H, dm) and diameter at breast height (dbh, cm). Individual-tree bole volume (VOL, dm^3) was estimated using the equation for young Douglas-fir given in Adams and Joyce (1990):

$$[2] \quad \mathrm{VOL} = 14.7196 - (0.4396H) - (2.2659\ \mathrm{dbh}) + (0.0901H\ \mathrm{dbh})$$

Wood density traits were determined by taking an increment core at breast height (1.37 m) from the south side of each tree during the summer of 1988; all cores extended from bark to pith. The cores were dried to an equilibrium moisture content of about 9%, sawn to a uniform thickness of 1.5 mm in cross section, and chemically extracted with a solution of toluene–ethanol (2:1 v/v) for 24 h. After extraction, the cores were dried again to the initial equilibrium moisture content (9%) and kept in this condition throughout the remaining analyses.

Intraring density information for each core sample was obtained with a direct-scanning X-ray densitometry system (Hoag and McKimmy 1988). The first and last annual rings from the samples were discarded because they were usually incomplete. For each of the remaining rings, minimum, maximum, and average density values and total ring width were obtained. Widths and average densities for earlywood and latewood, as well as latewood proportion, were also determined by using the average of the minimum and maximum ring densities to define the point of transition from earlywood to latewood.

Many criteria have been used to evaluate IRV. The criterion most recently used, however, is the standard deviation of density values (all X-ray data points) across the annual ring (Walker and Dodd 1988). In this study, IRV for an individual ring was estimated by the following equation:

$$[3] \quad \mathrm{IRV} = [(\mathrm{RD} - \mathrm{ED})^2 (1 - \mathrm{LP}) + (\mathrm{RD} - \mathrm{LD})^2\ \mathrm{LP}]^{0.5}$$

This equation assumes that within-ring variation is primarily due to average differences in earlywood and latewood densities. Values obtained with this equation were closely correlated ($r = 0.96$) with the standard deviation of density values in a sample of 111 annual rings.

Weighted averages across the total core were calculated for individual ring variables, including overall density, earlywood density, latewood density, and IRV, by weighting each individual ring value by its respective width. Latewood proportion of the overall core was obtained as the sum of latewood width of individual rings divided by the length of the core sample.

TABLE 1. Form of the variance and covariance analyses for wood density and growth traits at age 15

Source variation	df	Expected mean squares*
Sets	$s - 1$	$\sigma_w^2/k + \sigma_e^2 + b\sigma_{f(s)}^2 + f\sigma_{b(s)}^2 + bf\sigma_s^2$
Blocks/set	$(b - 1)s$	$\sigma_w^2/k + \sigma_e^2 + f\sigma_{b(s)}^2$
Families/set	$(f - 1)s$	$\sigma_w^2/k + \sigma_e^2 + b\sigma_{f(s)}^2$
(Block × families)/set (plot error)	$(f - 1)(b - 1)s$	$\sigma_w^2/k + \sigma_e^2$
Within-plot	$\sum_{i=1}^{t} (n_i - 1)$	σ_w^2

NOTE: s, number of sets; b, number of blocks per set; f, number of families per set; k, harmonic mean of trees per plot for all sets; 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.

*For covariance analyses, cross products are used instead of mean squares.

Estimating genetic parameters

Variance and covariance analyses for all wood traits averaged across the core and for growth traits at age 15 (diameter, height, and bole volume) were performed by using plot means. Missing values for two plots (from a total of 240) were estimated according to the method of Steel and Torrie (1980). Within-plot variances and covariances, as well as the harmonic mean of trees per plot, were estimated separately by pooling individual-plot values. Components of variance and covariance were estimated from the appropriate mean squares and cross products according to a random-effects model (Table 1). Standard errors of variance components were estimated by the procedures of Namkoong (1979).

The genetic control of wood density traits was determined by estimating individual-tree heritabilities (Falconer 1981) and family heritabilities appropriate to the selection system (Namkoong et al. 1966). Because open-pollinated families in the progeny test came from parent trees in wild stands, the additive genetic variance (σ_A^2) was estimated as 3 times the family component of variance ($\sigma_{f(s)}^2$), which assumes individuals in these families are related to a greater extent than are half-sibs (Campbell 1979). The family heritability of interest is that appropriate to estimating gain from the progeny of a clonal seed orchard after roguing clones on the basis of their open-pollinated families in a progeny test. This family heritability is not as defined in the traditional sense (Falconer 1981), but is calculated as

$$[4] \quad h_f^2 = \frac{\mathrm{COV_A}(x, y)}{\sigma_{P_x}^2}$$

where $\mathrm{COV_A}(x, y)$ is the additive genetic covariance between the mean of an ortet's progeny and the mean of the offspring from its seed orchard clone (y), and $\sigma_{P_x}^2$ is the phenotypic variance of family means in the progeny test (Namkoong et al. 1966). Since the open-pollinated offspring of a seed orchard clone and its ortet have only their female parentage in common, the additive covariance between x and y is that expected for half-sibs, such that the $\mathrm{COV_A}(x, y) = (1/4)\sigma_A^2$. Standard errors of heritability estimates were calculated according to the procedures of Osborne and Paterson (1952). The relationships among traits were examined by estimating genetic correlations between pairs of traits as well as the standard errors of these correlations, as in Becker (1984). It should be noted that estimates of additive variances and covariances may be biased in this study because all estimates are from a single test site. In particular, heritability estimates will be biased upwards if family × site interactions exist.

Evaluating breeding implications

Implications of the genetic relationships between wood density and its components and between wood density, IRV, and bole growth were evaluated by determining the expected genetic gains (response) for these traits in the offspring of a clonal seed orchard, where clones are selected on the basis of the performance of the open-pollinated progenies of their ortets (parent trees). Gains in a trait of interest (e.g., wood density) from direct selection, or from indirect selection based on another (individual) trait, were estimated by using equations for direct and indirect response (Namkoong et al. 1966; Falconer 1981). When one or more density components were used as secondary traits to select for wood density, or multiple trait selection was of interest (e.g., selection for wood density and bole volume), index methods were employed (Lin 1978). For example, the effectiveness of wood density components as secondary traits in selecting parent trees for increased overall core density, while reducing the correlated response in IRV, was explored by constructing several unrestricted selection indices (Lin 1978). The breeding value of trees in this case was considered to be a function of overall core density alone. Expected gains in wood density and bole volume when both traits are selected simultaneously were assessed by constructing restricted and unrestricted indices. Selection indices with the Kempthorne-type restriction (Lin 1978) were used to optimize the response in bole volume while limiting the change in overall core density to zero. Unrestricted selection indices were employed when the method of desired gains was used to determine economic weights of the two traits (Cotterill and Jackson 1985). The RESI program described by Cotterill and Jackson (1981) was used to calculate the index coefficients and to compute expected genetic gains from applying the selection indices.

Results and discussion

Genetic control of wood density components and IRV

Analyses of variance showed significant differences ($p < 0.01$) among families in average core values for all wood

TABLE 2. Estimates of population means ($\bar{X}$), additive (σ_A^2) and phenotypic (σ_P^2) variances, and individual-tree (h_i^2) and family (h_f^2) heritabilities for various wood density traits at age 15

Trait	$\bar{X}$*	σ_A^2	σ_P^2	h_i^2	h_f^2
Earlywood density (g/cm^3)	0.346 (0.324-0.375)	0.000 30	0.000 64	0.47 ± 0.11	0.51 ± 0.04
Latewood density (g/cm^3)	0.824 (0.763-0.875)	0.000 74	0.002 08	0.36 ± 0.10	0.46 ± 0.05
Latewood proportion	0.227 (0.202-0.260)	0.000 31	0.001 28	0.24 ± 0.08	0.39 ± 0.06
Overall density (g/cm^3)	0.455 (0.419-0.499)	0.000 65	0.001 10	0.59 ± 0.12	0.55 ± 0.03
Intraring density variation (g/cm^3)	0.198 (0.175-0.217)	0.000 09	0.000 36	0.25 ± 0.09	0.39 ± 0.06

NOTE: SE is presented with individual-tree and family heritabilities.

*Range over 60 family means is shown in parentheses. Differences among families for all traits were significant ($p < 0.01$). Density values are based on a moisture content of 9% in the samples. Approximate values of basic density (based on ovendry weight) can be calculated by dividing $\bar{X}$ by 1.095.

TABLE 3. Estimates of genetic correlations between wood density components and intraring density variation at age 15

Trait	Latewood density	Latewood proportion	Overall density	Intraring density variation
Earlywood density	0.61 (0.14)	0.92 (0.12)	0.97 (0.02)	0.56 (0.19)
Latewood density		0.57 (0.20)	0.74 (0.10)	0.99 (0.05)
Latewood proportion			0.95 (0.06)	0.58 (0.18)
Overall density				0.72 (0.12)

NOTE: Standard errors of estimates are given in parentheses.

density traits considered (Table 2). The mean for overall core density is slightly larger than values reported elsewhere for juvenile wood in Douglas-fir (Cown 1976; McKimmy and Campbell 1982; King et al. 1988). It is difficult to determine, however, whether the greater overall density in these 60 families represents a real difference among populations, because estimates of juvenile-wood density are greatly influenced by the methods employed, particularly the moisture content used as a reference (9% moisture content was used in this study), as well as by the number of rings included and their distance from the pith (Cown 1976).

As reported previously in Douglas-fir (Bastien et al. 1985; King et al. 1988), wood density traits have low coefficients of variation, but they are moderately to strongly inherited (Table 2). Estimates of heritability in this study, as in the earlier reports for Douglas-fir, may be somewhat upwardly biased because measurements were restricted to a single test site and family × site interactions were not accounted for. Nevertheless, it is clear that wood density traits are under sufficiently strong genetic control that they should respond well to selection in tree improvement programs, even though phenotypic variation may be low. None of the individual wood density components had estimates of heritability greater than that found for overall density. The same results were found in a provenance-progeny study of Douglas-fir in France (Bastien et al. 1985). Wood density components, however, appear to be under stronger genetic control than overall wood density in juvenile *Pinus radiata* D. Don (Nicholls et al. 1980).

Genetic relationships among wood density traits: implications for breeding

All of the wood density components were strongly correlated genetically with overall density, and they were also strongly interrelated among themselves (Table 3). Thus, these traits are probably controlled to a large extent by the same set of genes. Similar conclusions were reached in an earlier study with Douglas-fir (Birot et al. 1983), although the genetic relationships between traits were not as strong as reported here. IRV was strongly and positively correlated with overall density, an unfavorable association that has also been observed in other populations of Douglas-fir (Bastien et al. 1985).

Even though the components were strongly correlated with overall density, the lower heritabilities of the components and their strong interrelationships meant that expected response in overall density from direct selection for this trait (Table 4, selection criterion 1) was always greater than that from indirect selection based on one or more components (Table 4, selection criteria 2, 3, 4, and 5). For similar reasons, adding the components as secondary traits in a selection index (Table 4, selection criteria 6 and 7) did not increase the expected response to selection for overall density. Inclusion of secondary traits in an index designed to select for a desired trait is more efficient than selection based on the desired trait alone only when the heritability of the desired trait is lower than the secondary traits or when the secondary traits have low genetic but high phenotypic correlations with the desired trait (Sales and Hill 1976). Further, IRV = intra-ring density variation

TABLE 4. Expected response in overall core density and correlated response in intraring density variation at age 15 when different wood density components are used as selection criteria

	Response (%)[†]	
Selection criterion*	Overall core density	Intraring density variation
1. Overall CD	5.66	3.47
2. ED	5.29	2.60
3. LP	4.53	2.35
4. LD	3.83	4.36
5. ED and LP	5.48	2.74
6. CD and ED	5.66	3.46
7. CD, ED, and LP	5.66	3.55

*CD, core density; ED, earlywood density; LP, latewood proportion; LD, latewood density.

[†] Response expected in seed orchard offspring when the top 20% of parental clones (selection intensity (i) = 1.354) are selected.

TABLE 5. Estimates of genetic correlations between core density components and growth traits at age 15

Trait	dbh	Height	Volume
Earlywood density	−0.66	−0.24	−0.55
	(0.18)	(0.21)	(0.18)
Latewood density	−0.44	−0.08	−0.30
	(0.24)	(0.24)	(0.23)
Latewood proportion	−0.54	−0.10	−0.46
	(0.25)	(0.26)	(0.18)
Overall density	−0.63	−0.19	−0.52
	(0.18)	(0.21)	(0.18)
Intraring density variation	−0.51	−0.07	−0.38
	(0.27)	(0.26)	(0.26)
dbh	—	0.77	0.96
		(0.13)	(0.02)
Height		—	0.90
			(0.06)

NOTE: Standard errors of estimates are given in parentheses.

adding several secondary traits to an index is not appreciably better than direct selection if the secondary traits are strongly correlated with each other (Baker 1986; White and Hodge 1991).

Although direct selection for overall core density might be the most efficient selection criterion for improving wood density, selection for that trait will lead to an estimated 3.47% increase in IRV as a correlated response (Table 4, selection criterion 1). Basing selection for wood density on earlywood density and latewood proportion (Table 4, selection criterion 5), however, appears to produce nearly the same response in overall density while reducing the response in IRV to 2.74%.

Genetic relationships between wood density and growth traits: implications for breeding

Moderately strong negative correlations were found between bole volume and all density components (Table 5). These unfavorable correlations appear to be due primarily to strong negative relationships between wood density traits and diameter growth (dbh). Strong negative correlations between wood density and diameter growth in Douglas-fir have also been found in earlier studies (McKimmy and Campbell 1982; Bastien et al. 1985; King et al. 1988).

The emphasis in most tree improvement programs for coastal Douglas-fir is on improving bole volume growth (Silen and Wheat 1979). The observed negative correlation between bole volume and IRV (Table 5) is presumably helpful because it indicates that selecting for increased growth rate would reduce IRV. The negative correlation between bole volume and overall wood density, however, is a potential problem, since selection for bole volume alone will lead to trees with lower juvenile wood densities. Moreover, the use of individual wood density components either as indirect or auxiliary traits for selection of wood density would not alleviate this problem, since they have similarly strong negative correlations with volume growth.

How the genetic relationships between wood density and growth traits affect breeding for both volume growth and overall core density was explored by using various selection criteria (Table 6). Selection for volume alone without regard for wood density (selection criterion 1) will produce the maximum estimated increase in volume growth (13.37%), and the largest reduction in IRV, but it will reduce overall core density (−2.41%), which in turn will decrease wood strength. Although at first sight a reduction of 2.41% in average wood density might appear unimportant, especially when compared with the gains obtained in bole volume, the impact of this reduction is substantial in terms of dry weight of fiber per hectare. For example, if a managed stand of coastal Douglas-fir produces 1000 m^3/ha in a 60-year rotation (which seems reasonable for a class II site according to Curtis et al. (1982)) and if average wood density is 0.455 g/cm^3, then a decrease of 2.41% in wood density would represent a reduction of about 11 000 kg of dry fiber per hectare.

Selection for core density alone (criterion 2), on the other hand, is expected to increase wood density by 5.66%, but such selection will lead to an increase in IRV, a substantial reduction in volume growth (−8.47%), and in consequence, bole weight will be reduced by 3.29% with respect to the original population. Because of the large economic value placed on bole volume, this option is unlikely to ever receive serious consideration. Nevertheless, along with option 1 (criterion 1) it is a useful point of reference for showing the results of assigning different economic weights to these traits.

From the results of these two extreme situations, it is obvious that multitrait selection will be necessary to prevent undue loss in either wood density or bole volume. Restricted selection indices offer one of the best approaches for limiting the change in one trait while improving the other (Cotterill and Jackson 1981). A selection index imposing the restriction of no change in overall core density (criterion 3) would produce 20% less volume than expected if selection were on volume alone, but total bole weight would remain about the same, with the additional advantage of no reduction in wood strength. Selection based on height growth alone (criterion 4) also seems to be a good option, giving slightly less volume gain and only about one-third the loss in wood density expected if selection were on volume alone. Total bole weight, however, was higher with this selection criterion than with any other explored. Fries (1986) obtained similar results when comparing selection methods to improve dry stem biomass in *Pinus contorta* Dougl. The better overall response from selection for height than for volume alone

TABLE 6. Expected response in intraring density variation, overall core density, bole volume, and bole weight at age 15 when different selection criteria are used

	Response (%)[†]			
Selection criterion*	Intraring density variation	Overall core density	Volume	Bole weight[‡]
1. VOL	−1.50	−2.41	13.37	10.64
2. Overall CD core density	3.47	5.66	−8.47	−3.29
3. VOL and CD (0% change)[§]	0.00	0.00	10.53	10.53
4. HT	−0.28	−0.89	12.19	11.19
5. HT and CD (0% change)[§]	0.27	0.00	10.97	10.97
6. VOL, HT, and CD (0% change)[§]	0.14	0.00	11.11	11.11
7. VOL, HT, and CD (+1.2% change)[§]	0.55	1.13	8.95	10.18

*VOL, volume; CD, core density; HT, height.

[†] Response expected in seed orchard offspring when the top 20% of parental clones (selection intensity (i) = 1.354) are selected on the basis of the various selection criteria given in the left-hand column.

[‡] Bole weight = (average bole volume) × (average core density).

[§] Selection index in which the response in overall core density was restricted to the percentage indicated.

is due to the strong positive correlation between height and volume and to the previously mentioned weak negative correlation between wood density and height (Table 5).

Because of the weak negative correlation observed between height and overall core density, a selection index based on these two traits was constructed with the goal of optimizing gains in bole volume (Binet 1965), while limiting the response in overall core density (selection criterion 5, Table 6). This selection index is expected to produce nearly as much response in bole weight as does selection for height alone, without decreasing overall core density and with only a small reduction in volume growth (compared with criterion 1). The overall response in bole volume is not modified substantially when volume is added to this index (criterion 6). The last alternative (criterion 7) illustrates that if less gain in bole volume is acceptable, it is possible to obtain a slight increase in overall density (1.2%) with only a small reduction in bole weight (less than 10% with respect to its maximum response). More emphasis on increasing wood density, however, may not be desirable because it causes gain in volume to drop rapidly. Increasing the response in overall density would also have a negative effect on IRV.

Choosing the last option may have additional important implications. First, even a slight increase in juvenile-wood density is helpful in offsetting reductions in overall wood density expected from shorter rotations. Kellogg (1982) estimated that the move to shorter rotations in coastal Douglas-fir would result in a decrease of 2–5% in average wood density because of the larger proportion of juvenile wood in younger trees. Thus, an increase of 1.2% in overall density of juvenile wood would be important in reducing that deficit. In addition, King et al. (1988) argued that selecting for a positive response in two negatively correlated traits may help to break the negative correlation caused by pleiotropic gene action.

Final decisions regarding the weighting given to wood density and volume growth in selection indices will require more information about their relative contributions to product value in this species (i.e., their contribution to the value of lumber, plywood, pulp, etc.). It should be remembered, however, that increasing emphasis on selection for one of these traits will always be accompanied by a smaller response in the other. Maximum gains cannot be obtained on both traits at the same time.

If simultaneous improvement in both traits is desired, it might be worthwhile considering other breeding strategies. Dean et al. (1983) suggested that one possible solution for improving two negatively correlated traits is to select for them in separate "lines" or populations in accordance with the multiple-population concept of Burdon and Namkoong (1983). The hybrid progeny of such lines might have better growth and wood density than can be achieved through the simultaneous selection in one line.

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