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Genetic variation in basic density and modulus of elasticity of coastal Douglas-fir

G. R. Johnson · Barbara L. Gartner

Abstract Douglas-fir trees from 39 open-pollinated families at four test locations were assessed to estimate heritability of modulus of elasticity (MOE) and basic density. After trees were felled, sound velocity was measured on 4-m logs with the Director HM200. Disks were taken to estimate dry and green wood density; dynamic MOE was estimated as green density × (sound velocity)^2. Heritability estimates of MOE (across-site h^2=0.55) were larger than those for total height (0.15) and diameter at breast height (DBH; 0.29), and similar to those for density (0.59). Negative genetic correlations were found for MOE with height (r_A=−0.30) and DBH (r_A=−0.51), and were similar to those found for density with height (r_A=−0.52) and DBH (r_A=−0.57). The partial correlations of height with MOE and density, while holding DBH constant, were positive, implying that the observed negative correlations between height and the wood properties were a function of the high positive correlation between height and DBH and the strong negative correlations between DBH and the wood properties. Taper [DBH/(height−1.4)] was found to be negatively associated with MOE. Selection for MOE may produce greater gains than selection for density because MOE had a larger coefficient of additive variation

(9.6%) than density (5.1%). Conversely, selection for growth may have a more negative impact on MOE than density because of the greater genetic variation associated with MOE. Family mean correlations of the wood quality traits with stem form and crown health were mostly nonsignificant.

Keywords MOE · Density · Heritability · Genetic correlation

Introduction

Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] is of economic importance for forest product industries in western North America, New Zealand, parts of Europe, and other places where acceptable growth rates can be achieved. In the Pacific Northwest, its primary uses are for building and construction purposes such as dimension lumber, piles, and plywood (Alden 1997; Forest Products Laboratory 1999), but it is found in many other solid and composite products as well. Modulus of elasticity (stiffness, MOE) is an important trait associated with structural quality, but very little information is available in the literature on the genetic variation of MOE in Douglas-fir. To obtain direct measures of static MOE, boards must be cut from a tree and subjected to bending tests, a process requiring considerable expense. MOE of clear straight-grained wood is impacted strongly by wood density and microfibril angle (Megraw 1986; Cave and Walker 1994; Andrews 2002; Knowles et al. 2003). Information for genetic variation is available in the literature for wood density because of its ease to measure from wood cores, but is lacking for microfibril angle because of its high costs to measure and, potentially, the large amount of variation found within individual trees.

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Genetic studies in the literature suggest that most of the variation found among trees in even-aged stands for wood density is controlled genetically; that is, narrow-sense heritability estimates range from 0.5 to greater than 0.9 (Table 1). The reported genetic correlations between wood density and growth are strongly negative, ranging from −0.5 to −1.0 (Bastien et al. 1985; King et al. 1988; Vargas-Hernandez and Adams 1991; St. Clair 1994).

This adverse genetic correlation is of concern to tree breeders. The primary trait of selection in most Douglas-fir tree-breeding programs is growth (Woods 1993), and if one selects only upon growth, wood density will decrease in the resulting population. Because of this correlation, wood density is often a secondary trait of selection (Woods 1993). By including density in the selection criteria, one cannot achieve the full potential of growth gains because of the adverse correlation. Wood density is not the primary wood trait desired, but is a surrogate for MOE. If genetic correlations were not as strong for growth and MOE as for growth and density (MOE is also affected by microfibril angle), then more gain can potentially be achieved in growth traits if MOE was included in the selection criteria instead of density.

Tools have become available recently to obtain rapid indirect estimates of dynamic MOE by measuring the velocity of sound through logs. Theoretically, MOE = green density × velocity^2 (Pellerin and Ross 2002). This study used the Director HM200 acoustic tool (Fibre-gen, Auckland, New Zealand, http://www.fibre-gen.com) to examine the genetic patterns of variation of MOE and its correlations with other traits in 20-year-old trees. The wood at this age becomes the juvenile core of a mature tree and is of poorer quality in terms of wood density and MOE than wood that will be formed in the mature, outer wood (Megraw 1986; Jozsa and Middleton 1994). Therefore, genetic changes in this portion of a tree will have the greatest financial impact.

Methods and materials

Four 20-year-old progeny test sites were chosen from ten potential sites in the first-generation Nehalem breeding program

(part of the Northwest Tree Improvement Cooperative). This series of trials is located in the Coast Range of northern Oregon. The average height of the four sites at age 20 ranged from 15.4 to 16.5 m, and average DBH ranged from 19.1 to 19.4 cm (Table 2). These trials were a reps-in-sets design that tested ten sets, each containing 40 different families (a total of 400 families). Three replications were established for each set, with four noncontiguous trees per replication (for a total of 12 trees per family per site). Replications for each set were planted adjacent to one another at each site. We chose set 10 from this study because it had higher-than-average age-11 DBH heritability (0.24 vs 0.18 for all sets) to gain more precise estimates of genetic correlations. The trials were designed so that diagonals can be removed, and equal family representation would remain. We measured all trees in set 10 for DBH at age 20 and selected the diagonals with the higher heritability to fell, thereby improving correlation estimates. One of the 40 families was a full-sib family and was dropped from the analyses, leaving 39 wind-pollinated families. Data were available for a total of 749 trees after culling extreme outliers (20 trees, mostly disks with moisture contents less than 45%) and removing trees missing disks or where there were doubts about disk identity.

Trees were felled in the spring (March/April) of 2005. Immediately after felling, height was measured, branches were removed, a 4-m log was cut from the base of the tree, and sound velocity was obtained with the HM200. A disk 25 to 50 mm thick was cut at about 1.5 m and was weighed shortly after the trees were felled to obtain green (fresh) weights. Bark was not removed from the disks because it was tightly attached since diameter growth had not begun. The disks were stored in a refrigerator until volumes can be obtained through the water displacement method. Unfortunately, one of the balances used to obtain the green volumes was later found to be defective, and the data were discarded for all disks because we could not determine which balance was used for most disks. Green volumes were later estimated from dry volumes (see succeeding section).

The disks were kiln-dried for 2 days and stored for a week until they were measured for dry weight. Weights and volumes were later measured on the disks a month after the

Table 1 Narrow-sense heritability estimates for wood density in Douglas-fir from the literature

Heritability	Sites (n)	Families (n)	Author
>0.8	1	>160 open-pollinated	Bastien et al. 1985
0.90	1	88 full sibs	King et al. 1988
0.54–0.71	2	22 half-sibs	Loo-Dinkins and Gonzalez 1991
0.59	1	60 open-pollinated	Vargas-Hernandez and Adams 1991
0.54	1	20 open-pollinated	St. Clair 1994
0.72	21[a]	658 open-pollinated	Johnson and Jayawickrama 2002

[a] This study examined different families at different sites; heritabilities are averaged across sites and therefore do not account for genotype × environment interaction.

Table 2 Locations, site means, and individual tree standard deviations (in parenthesis) of the four sites assessed for MOE

	Coal Creek	Sarajarvie	Slick Rock	Vesper
Latitude	45° 46′N	45° 59′N	45° 16′N	46° 00′N
Longitude	123° 52′W	123° 30′W	123° 37′W	123° 22′W
Height, age 11 (m)	8.0 (1.0)	7.8 (1.1)	7.3 (0.9)	7.6 (0.9)
Height, age 20 (m)	15.4 (2.0)	16.6 (2.1)	16.1 (2.0)	16.5 (1.7)
DBH, age 11 (cm)	12.2 (2.3)	10.8 (2.0)	10.4 (1.6)	10.4 (1.5)
DBH, age 20 (cm)	19.4 (4.2)	19.6 (4.1)	19.3 (3.5)	19.6 (3.5)
MOE, age 20 (GPa)	8.96 (1.30)	8.40 (1.16)	8.56 (1.14)	8.31 (1.09)
Density age, 20 (kg/m^3)	446 (34)	406 (26)	414 (27)	404 (26)

disks were removed from the oven (after the error was found with the balance); these weights were used as the final weights. Moisture content (water weight/dry weight, expressed as percentage) of the disks at that time averaged 5.6%. Dry weights were estimated as 0.947 × the final weight. Green volume was estimated as 1.13 × the dry volume. This value of 13% was based on data from disks with accurate estimates of initial green volume and is close to the standard value of 12.4% reported for Douglas-fir (Forest Products Laboratory 1999).

Green density was calculated as green weight divided by estimated green volume. Basic density, hereafter referred to as density, was estimated as the dry weight divided by estimated green volume. MOE was estimated as green density (kilograms per cubic meter) × [sound velocity (kilometers per second)]^2 / 100,000. Taper (millimeter per meter) was calculated as DBH/(height − 1.4 m); thus, it represents the rate of taper in a stem.

Unbiased heritability estimates for age-19 traits were calculated with the formula:

$$Heritability\left(h^2\right) = \sigma^2_{additive} \Big/ \sigma^2_{phenotypic}$$
$$= \left(3 \times \sigma^2_{family}\right) \Big/ \left(\sigma^2_{family} + \sigma^2_{family\text{-}site} + \sigma^2_{family\text{-}rep(site)} + \sigma^2_{error}\right)$$

The additive genetic variation ($\sigma^2_{additive}$) was estimated at three times the family variance (σ^2_{family}) instead of four because open-pollinated Douglas-fir progenies are expected to be more closely related than true half-sibs (Squillace 1974; Campbell 1979). The coefficient of additive variation (CAV) was calculated as the square root of the additive genetic variance divided by the overall mean of the trait × 100 to put into units of percentage. Variance components were obtained with the MIXED procedure of SAS (Littell et al. 1996), where all sources of variation were modeled as random variables. The model contained the following variables: site, replication within site, family, site by family, family by rep within site, and the within-plot error. The standard errors for heritability estimates were calculated

using the equations given in Becker (1984) for sire groups. F tests for family effect were estimated with the same model, but family was designated as a fixed effect.

Type B genetic correlations examining the correlation of the same traits measured for a pair of sites (r_B) assumed that the genetic variation, but not the environmental variation, was the same at each site, and used the Yamada (1962) formula cited in Burdon (1977):

$$r_b = \sigma^2_{family} \Big/ \left(\sigma^2_{family} + \sigma^2_{family\text{-}site}\right).$$

Genetic correlations among traits (r_A) were calculated using standardized data (mean, 0; standard deviation, 1) with the following equation:

$$r_A = \sigma_{family\ cross\text{-}product\ AB} \Big/ \left(\sigma^2_{family\ trait\ A} \times \sigma^2_{family\ trait\ B}\right)^{1/2},$$

where

- $\sigma_{family\ cross\text{-}product\ AB}$ is the family covariance component for traits A and B;
- $\sigma^2_{family\ trait\ A}$ is the family variance component for trait A; and
- $\sigma^2_{family\ trait\ B}$ is the family variance component for trait B.

Across-site family means were calculated for the age-20 variables using the felled trees (four sites). Across-site family means were determined for age-11 foliage traits

measured on five Swiss needle cast (SNC)-impacted sites, two of which were common to the age-20 sites. Foliage traits were needle retention of the second-year foliage on the secondary lateral branches (scored as 0 to 9, where 0=0 to 10% retention, and 9=91 to 100% retention), crown density (scored as 1=sparse crown to 6=dense crown), and color (assessed as 1=yellow, 2=green, and 3=dark green). Details on these traits and analysis are presented in Johnson (2002). Family means were also calculated from all ten sites for the age-11 form traits. Sinuosity was measured as the deviation of the curved stem portion from a straight line; units were based on tree diameter at the curve (1=1/4 diameter, 2=1/2 diameter, etc.), for example, if deviation was one full-stem diameter, the score was a 4. Ramicorn was number of whorls having at least one ramicorn branch, and forking was the number of whorls having at least one fork. Best linear unbiased prediction (BLUP) estimates were available for height and diameter at age 11 (ten sites) and DBH at age 17 (five SNC sites). "Family mean" correlations were calculated among trait means and BLUP estimates.

The standard errors of the family mean correlations were estimated by bootstrapping. Fifty separate random samples of 30 families were selected, and the correlations among the traits were calculated. The standard deviation of these 50 estimates was used as an estimate of the standard error.

Environmental correlations (r_E) were estimated from the genetic correlations (r_A), the average of the within-site individual tree correlations (r_P), and the across-site estimate of heritability (h^2). Given that

$$r_P = r_A h_a h_b + r_E \left(1 - h_a^2\right)^{1/2} \left(1 - h_b^2\right)^{1/2} \text{ (Searle 1961),}$$

where the subscripts for h refer to traits a and b, r_E can be estimated as:

$$r_E = \left(r_P - r_A h_a h_b\right) \Big/ \left[\left(1 - h_a^2\right)^{1/2} \left(1 - h_b^2\right)^{1/2}\right].$$

Partial correlation coefficients for family means and individual trees were obtained for DBH and height with MOE and density to examine path analyses. From the path diagram (Fig. 1), one can examine the direct path of height (or DBH) on a wood property (β_1) and the indirect path that occurs from the correlation of height with DBH ($r \times \beta_2$). The simple correlation between height and a wood property is the sum of the direct and indirect paths. A more thorough explanation of path analysis can be found in Sokal and Rohlf (1995). Partial correlation coefficients were determined by standardizing all the traits (mean, 0; standard deviation, 1) and running a regression with the wood property as the dependent variable and height and DBH as the independent variables; the regression coefficients represent the partial correlations. For individual phenotypic
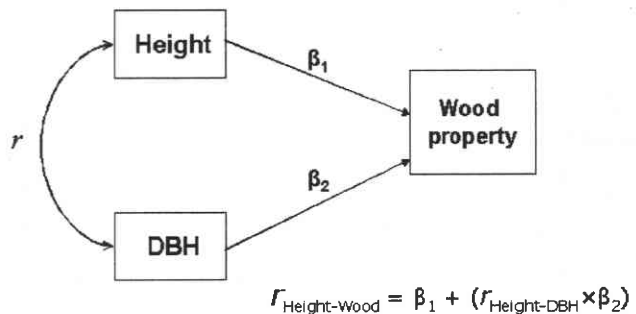

$$r_{\text{Height-Wood}} = \beta_1 + \left(r_{\text{Height-DBH}} \times \beta_2\right)$$

Fig. 1 Path diagram of the effect of height and DBH on wood properties

values, the regression coefficients were averaged over the four sites.

Potential gains from breeding were examined by examining selection differentials (the difference between the mean of the selected families minus the overall mean) and by examining the standard gain equation:

$$Response = ih^2 \sigma_{phenotypic} = i\,h\,\sigma_{additive},$$

where i is the selection intensity.

Response from indirect selection was examined with selection differentials and the equation for indirect selection:

Response in trait 2 when selecting on trait 1 = $i\,r_A\,h_{\text{trait }1}\,h_{\text{trait }2}\,\sigma_{\text{Phenotype-trait }2}$.

Percentage gains were estimated as the response divided by the trait mean times 100.

Results and discussion

Heritability and variation

Family differences were found for all traits examined (Table 3). At the individual sites, family differences were statistically significant for all traits ($p=0.05$) except for height at Slick Rock ($p=0.054$) and Sarajarvie ($p=0.210$), and taper at Coal Creek ($p=0.489$) and Slick Rock ($p=0.073$). Among-site differences were found for all age-20 variables except DBH ($p=0.937$) and taper ($p=0.064$). At age 11, the one site most impacted by SNC (Coal Creek) had significantly larger DBHs than the other three sites, but this difference had disappeared by age 20. SNC had probably reduced the diameter growth rate at this site and Slick Rock (the other SNC-impacted site) relative to the two other sites where SNC was not as severe.

Heritability estimates are shown in Table 4. Heritability estimates for MOE were moderate to high at all four sites (0.32–1.00), and the unbiased heritability estimate calculated over all four sites was 0.55. In general, MOE had larger heritabilities than the growth traits and similar heritabilities

Table 3 Trait means, coefficient of variation for family means (%), coefficient of additive variation (%), range of family means, family F value (probability in parenthesis), and number of test sites providing data

Trait	Mean	CV (%)	CAV* (%)	Min	Max	Family F value[a]	Test sites
Height, age 5 (m)	1.8	7.2		1.5	2.0		10
Height, age 11 (m)	7.6	4.4		7.0	8.3		10
Height, age 20 (m)	16.1	4.0	3.9	14.7	17.4	2.10 (0.0016)	4
DBH, age 11 (mm)	109	6.5		86	109		10
DBH, age 17 (mm)	176	7.2		152	207		5
DBH, age 20 (mm)	194	7.4	10.3	166	221	2.94 (0.0001)	4
MOE, age 20 (GPa)	8.55	6.4	9.6	7.31	9.87	4.21 (0.0001)	4
Sound velocity, age 20 (km/s)	3.15	2.7	3.9	2.90	3.32	4.06 (0.0001)	4
Density, age 20 (kg/m^3)	415	3.3	5.1	384	461	5.50 (0.0001)	4
Green density, age 20 (kg/m^3)	861	2.8	4.2	803	923	4.29 (0.0001)	4
Moisture content, age 20 (%)	108	4.9	7.0	95	123	2.58 (0.0001)	4
Taper, age 20 (mm/m)	13.2	14.5	5.7	11.8	14.7	2.13 (0.0013)	4
Needle retention, age 11	4.89	17.1		2.69	6.57		5
Crown density, age 11	3.88	4.4		3.57	4.26		5
Color, age 11	1.89	3.3		1.73	1.98		5
Sinuosity, age 11	1.98	22.3		1.32	3.11		10
Forking, age 11	0.14	38.5		0.05	0.23		10
Ramicorns, age 11	0.66	20.2		0.36	0.94		10

[a] These values only provided for age-20 data.

to those found for density (Table 4). Similar heritability estimates for MOE have been obtained for *Pinus radiata* (Kumar 2004; Kumar et al. 2002). Moisture content was moderately heritable, and heritabilities were usually larger than those found for the growth traits.

Because we selected sets and diagonals to maximize the age-20 DBH heritabilities, the estimated heritabilities for the other traits may be biased. However, one would expect that the relative heritabilities are unaffected. In the literature, wood density has larger heritabilities than growth, which was the case found in this study. Therefore,

one can reasonably conclude from our data that MOE is moderately to highly heritable, much like density.

The family by site variation for MOE was relatively small; it was only 22% of the family variation, and the average genetic correlation across sites (r_B) was 0.79 (Table 4). The r_B value for MOE was larger than the values for the growth traits measured on the same trees but smaller than that for density (r_B=0.86). The family rankings for the wood quality traits were extremely stable over sites in this study, as evidenced by the very small genotype × environmental interaction values. The growth traits and

Table 4 Heritability estimates and standard errors (in parenthesis) of age-20 variables for the felled Douglas-fir trees at four sites, the average type-B genetic correlation (r_B) among sites (range in parenthesis), and the ratio of the family × site variance component to the family variance component

	Height	DBH	DBH[a]	MOE	Velocity	Density	Green density	Moisture content	Taper
Coal Creek	0.23 (0.27)	0.34 (0.29)	0.28 (0.16)	0.69 (0.32)	0.62 (0.32)	0.55 (0.31)	0.59 (0.32)	0.50 (0.31)	0.04 (0.24)
Sarajarvie	0.13 (0.23)	0.39 (0.27)	0.39 (0.18)	1.00 (0.32)	0.80 (0.31)	0.80 (0.31)	0.88 (0.31)	0.48 (0.28)	0.36 (0.26)
Slick Rock	0.29 (0.25)	0.30 (0.25)	0.28 (0.16)	0.32 (0.25)	0.32 (0.25)	0.56 (0.28)	0.46 (0.27)	0.65 (0.29)	0.20 (0.23)
Vesper	0.57 (0.29)	0.65 (0.30)	0.40 (0.18)	0.58 (0. 29)	0.49 (0.28)	0.64 (0.30)	0.57 (0.29)	0.46 (0.28)	0.34 (0.26)
Across sites	0.15 (0.09)	0.29 (0.12)	0.25 (0.09)	0.55 (0.17)	0.48 (0.16)	0.59 (0.18)	0.55 (0.17)	0.36 (0.14)	0.17 (0.10)
r_B	0.56 (0.11–1.00)	0.71 (0.23–1.00)	0.86 (0.57–1.00)	0.79 (0.62–1.00)	0.85 (0.75–1.00)	0.86 (0.76–1.00)	0.84 (0.70–1.00)	0.62 (0.45–0.74)	0.71 (0.05–1.0)
$\sigma^2_{fam \times site}/\sigma^2_{fam}$	1.00	0.37	0.36	0.22	0.18	0.08	0.11	0.48	0.31

[a] This includes data from all trees, including the unfilled diagonals.

Table 5 Genetic correlations, within-site individual phenotypic correlations averaged over four sites, and estimated environmental correlations among age-20 traits

Trait 1	Trait 2	Genetic	Correlations Phenotypic	Environmental
MOE	Density	0.76	0.60	0.39
MOE	Velocity	0.90	0.89	0.89
MOE	Height	−0.30	−0.05	0.05
MOE	DBH	−0.51	−0.28	−0.14
MOE	Moisture content	−0.33	−0.17	−0.04
MOE	Taper	−0.70	−0.34	−0.21
Density	Velocity	0.54	0.42	0.28
Density	Height	−0.52	−0.17	−0.02
Density	DBH	−0.57	−0.40	−0.30
Density	Moisture content	−0.56	−0.58	−0.62
Density	Taper	−0.63	−0.39	−0.32
Velocity	Height	−0.09	−0.08	−0.09
Velocity	DBH	−0.27	−0.25	−0.25
Velocity	Moisture content	−0.50	−0.39	−0.31
Velocity	Taper	−0.44	−0.26	−0.20
Height	DBH	0.97	0.69	0.63
Height	Moisture content	0.16	0.22	0.24
DBH	Moisture content	0.02	0.29	0.42

moisture content had proportionally more genotype × environmental interaction variation than the wood quality traits, but the r_B values for growth are well within the range of reported type-B genetic correlations found in the literature (e.g., Stonecypher et al. 1996; Johnson 1997).

Correlations and gains

As expected, MOE was strongly correlated with density and sound velocity (Table 5). The genetic correlation appeared stronger than the environmental correlation for MOE and density, but all correlations were similar for MOE and velocity (Table 5). The similarity of the MOE–velocity correlations is reasonable because MOE was calculated as a function of velocity.

Negative genetic and family mean correlations were found consistently between the wood traits (MOE, density, and velocity) and the growth traits of height and DBH (Tables 5 and 6). These correlations were stronger between DBH and the wood traits than between height and the wood traits. This general pattern was also found by Vargas-Hernandez and Adams (1991).

Table 6 Family mean correlations and their estimated standard error (in parentheses) among age-20 wood traits and other traits measured at ages 11, 17, or 20

	MOE	Density	Velocity	Moisture content
MOE (20)[a]	–	0.72 (0.05)	0.91 (0.02)	−0.28 (0.09)
Density (20)		–	0.53 (0.06)	−0.58 (0.07)
Velocity (20)			–	−0.46 (0.06)
Height (11)	−0.16 (0.06)	−0.18 (0.06)	−0.11 (0.07)	0.04 (0.08)
Height (20)	−0.19 (0.08)	−0.32 (0.06)	−0.09 (0.09)	0.11 (0.08)
DBH (11)	−0.49 (0.07)	−0.52 (0.06)	−0.30 (0.10)	0.04 (0.09)
DBH (17)	−0.47 (0.07)	−0.53 (0.08)	−0.34 (0.08)	0.20 (0.09)
DBH (20)	−0.43 (0.07)	−0.48 (0.08)	−0.28 (0.08)	0.12 (0.10)
Taper (20)	−0.53 (0.08)	−0.51 (0.10)	−0.37 (0.09)	0.08 (0.13)
Sinuosity (11)	−0.03 (0.10)	−0.05 (0.12)	0.01 (0.10)	0.03 (0.10)
Forking (11)	−0.06 (0.10)	−0.20 (0.09)	−0.08 (0.10)	0.28 (0.09)
Ramicorn (11)	0.02 (0.11)	−0.06 (0.06)	0.12 (0.11)	−0.10 (0.07)
Needle retention (11)	−0.10 (0.09)	−0.09 (0.11)	−0.22 (0.08)	0.32 (0.06)
Crown density (11)	−0.28 (0.09)	−0.15 (0.14)	−0.19 (0.09)	−0.12 (0.13)
Crown color (11)	−0.21 (0.11)	−0.18 (0.15)	−0.18 (0.11)	0.07 (0.15)

Standard error obtained by bootstrapping (see text for details). Levels of statistical significance for n=39 (probability/correlation): 0.01:0.41, 0.05:0.32, 0.10:0.27, 0.15:0.24.
[a] Assessment age.

Table 7 Individual phenotypic correlations (*r*) and partial correlations (*β*) for height and DBH with MOE and density

	Phenotypic correlations (*r*)			Partial correlations (*β*)	
	$r_{\text{ht-dbh}}$	$r_{\text{ht-wood}}$	$r_{\text{dbh-wood}}$	$\beta_{\text{ht-wood}}$	$\beta_{\text{dbh-wood}}$
Individual tree phenotypic					
MOE	0.69	−0.05	−0.28	0.27	−0.47
Density	0.69	−0.17	−0.40	0.19	−0.52
Family mean					
MOE	0.84	−0.19	−0.43	0.58	−0.91
Density	0.84	−0.32	−0.48	0.31	−0.74

Further examination of the partial correlation coefficients in the path analysis showed that the direct paths (β_1 in Fig. 1) of height with MOE and density were positive (Table 7). In general, the regression coefficients for the individual tree regressions of wood properties as a function of height and DBH were all statistically significant (8/8 DBH regression coefficients and 6/8 height coefficients). When the family means were used in the regressions, only the height coefficient for density was not statistically significant ($b=0.31$, $f_{1/36}=1.16$, $p=0.253$). Burdon and Low (1992) found this same trend of negative correlations between height and density but positive partial correlations in *P. radiata*. This positive direct impact of height on the wood properties is also seen in the negative genetic and family mean correlations of taper with the wood properties (Tables 5 and 6). Families that are more cylindrical than conical appear to be more dense and stiff. This finding is consistent with modeling efforts that show that to avoid buckling, trees that are more conical will need stiffer wood (Mike Watt and John Moore, personal communication).

Of the wood traits, density had the strongest negative correlations with growth, and velocity had the weakest (Table 5). It can be that microfibril angle, another factor affecting MOE, has a very weak association with growth rate and reduces the impact of growth rate on MOE. There were also negative environmental correlations between DBH and the wood traits, but the environmental correlations were smaller than the genetic correlations for DBH with MOE and density. The environmental correlations between height and the wood properties were essentially zero ($|0.1|$ or less, Table 5).

Family mean correlations among the wood traits and the younger growth traits showed the same trends as the age-20 traits (Table 6). The age-20 wood traits were not associated with any of the form traits. There was some indication of a small negative correlation between wood quality and foliage health, but only the correlations of MOE with crown density ($r=−0.30$) and moisture content with needle retention ($r=0.32$) showed any statistical significance ($p=0.10$). The latter correlation can be real because higher needle retention has been shown to be associated with higher moisture contents among stands in this SNC hazard zone (Johnson et al. 2003).

Although stronger adverse correlations were found between density and growth than for MOE and growth, selection on growth alone can reduce MOE more than density. Table 8 shows selection differentials and percent differences when selecting the top four families for different traits. More reduction was found for MOE than density when examining the selection differentials of the four tallest or largest DBH families (Table 8). The estimated decrease per unit of selection intensity (i) when selecting for DBH resulted in a decrease of 1.6% for density and 2.7% for MOE. Reduction from selecting upon height was 1.0% for density and 1.1% for MOE.

Modulus of elasticity had more genetic variation than density; that is, MOE had almost twice the coefficient of variation for family means and CAV compared with density (Table 3). This increased genetic variation can be real, or it may be a function of MOE being derived from two variables (green density and velocity), thereby having artificially increased the variation in MOE. Unfortunately, we could not get direct measurements of MOE. However, the overall family means were averages of approximately 20 trees, so the variation seen in the family means should be a good approximation of direct measurements, and the coefficient of variation (CVs) for family means were greater for MOE than that for density (Table 3). Other evidence supports the finding that MOE would have a higher CV than density. The average phenotypic CV for trees within stands from a data set examining 10 to 12 trees within each of 22 stands (data

Table 8 Overall means and selection differentials (% in parentheses) for selecting the best four families for DBH, height, MOE, and density

	Trait means and selection differentials (%)			
	DBH (mm)	Height (cm)	MOE (Gpa)	Density (kg/m³)
Overall mean	194	161	8.55	415
Top four families for DBH	217 (12.0)	169 (4.7)	8.12 (−5.1)	405 (−2.4)
Top four families for height	211 (8.6)	171 (8.1)	8.40 (−1.8)	412 (−0.8)
Top four families for MOE	182 (−6.5)	157 (−2.7)	9.49 (11.0)	436 (5.2)
Top four families for density	170 (−12.5)	153 (−4.8)	9.42 (10.1)	439 (5.9)
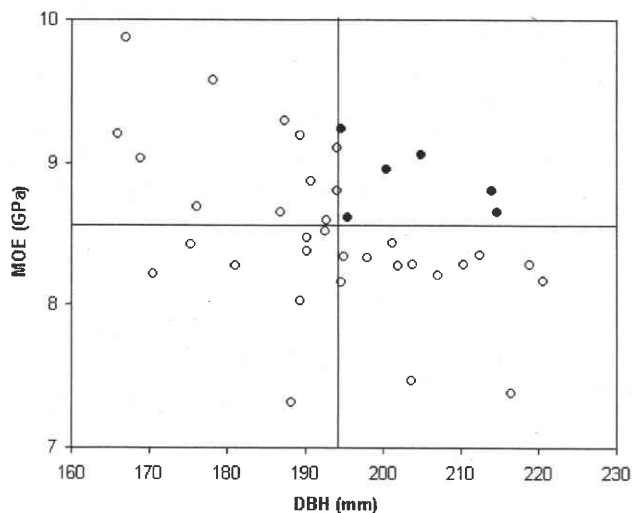
Fig. 2 Plot of the family means of DBH and MOE. *Filled circles* indicate families with above-average DBH and MOE

from Johnson et al. 2005) was 13.2% for MOE and 8.8% for density. Kumar et al. (2002) also found higher CVs for family means of MOE than for density in *P. radiata* families.

This adverse correlation between growth and wood quality does not prohibit the improvement of both MOE (or density) and growth. Examination of the family means (Fig. 2) demonstrates that 6 of the 39 families had improved DBH and MOE. These six families averaged a 5% increase in both DBH and MOE. There is also sufficient genetic variation available to make significant improvements in growth while keeping density or MOE at the population mean. For example, when the DBH variance components were estimated with density or MOE as a covariate (fixed effect in model), there was only a minor decrease in the heritability (h^2=0.24 with MOE, h^2=0.23 with density) and additive coefficient of variation (9.0% with MOE and 8.4% with density) compared with the initial estimate of heritability (0.29) and additive coefficient of variation (10.3%).

There also appears to be more potential for increasing MOE than density because of MOE's relatively high CAV. The selection differentials indicate that more gain can be achieved through direct selection for MOE than for direct selection for density (Table 8), and the estimated percent gains yielded similar results. Estimated gain per unit i was 10.7% for MOE and 6.2% for density. As technology becomes available for quick and easy assessments of MOE on standing trees, MOE can more easily be included in the selection criteria of Douglas-fir breeding programs. MOE will probably become an important trait in future selection strategies as rotation ages shorten and MOE decreases as a function of more juvenile wood in logs coming from the forest.

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