

Genetic variation in direct and indirect measures of wood stiffness in coastal Douglas-fir

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Abstract: We studied wood stiffness (estimated by modulus of elasticity, MOE), wood density, wood moisture content, and growth in a progeny test (50–130 families per trait; 1–3 sites) of coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco). We measured MOE directly using lumber bending tests (MOE_{bl}) and indirectly using tools (HM200 and ST300) that can be used to measure acoustic velocity in logs (Vel_{HM}) or standing trees (Vel_{ST}). Acoustic MOEs in logs and standing trees (MOE_{HM} and MOE_{ST}) were obtained from the velocities and green wood density. For backward selection, we estimated genetic gains in MOE_{bl} of 8.6%–12.3%. Relative efficiencies (REs), the relative gains in MOE_{bl} expected from indirect selection for correlated traits, were 78%–93% for the HM200 traits, 57%–58% for the ST300 traits, 38% for the basic wood density of basal discs (Den_{bd}), and 98% for the oven-dry density of logs estimated from the lumber (Den_{ol}). The HM200 is an efficient tool for improving MOE_{bl}, but gains will be lower using the ST300 on standing trees. Indirect selection on Den_{bd} should be used with caution because the RE was low and Den_{bd} was negatively correlated with growth (–0.49 to –0.73).

Résumé : Les auteurs ont examiné la rigidité du bois (MOE), sa densité, sa teneur en humidité ainsi que la croissance des arbres dans un test de descendance (50–130 familles par propriété et 1–3 sites) de douglas de Menzies typique (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco). Le MOE a été mesuré de manière directe au moyen d'essais de flexion statique (MOE_{bl}) avec des pièces de bois et de manière indirecte au moyen d'appareils (HM200 et ST300) capables de mesurer la vitesse sonique dans des billes (Vel_{HM}) ou dans des arbres sur pied (Vel_{ST}). Les MOE acoustiques (MOE_{HM} et MOE_{ST}) ont été obtenus à partir de ces vitesses et de la densité du bois à l'état vert. Dans le cas de la sélection en retour, les auteurs ont estimé que le gain génétique pour le MOE_{bl} variait de 8,6–12,3 %. L'efficacité relative (ER), soit le gain relatif en MOE_{bl} espéré à la suite d'une sélection indirecte pour les propriétés corrélées, atteignait : 78–93 % pour les propriétés mesurées au moyen du HM200; 57–58 % pour les propriétés mesurées au moyen du ST300; 38 % pour la densité basale des disques de souche (Den_{bd}) et 98 % pour la densité anhydre des billes estimée à partir de pièces de bois (Den_{ol}). Le HM200 s'avère un outil efficace pour l'amélioration du MOE_{bl} alors que les gains reliés à l'utilisation du ST300 avec les arbres sur pied sont plus faibles. La sélection indirecte à partir de la Den_{bd} devrait être pratiquée avec prudence puisque l'ER était faible et que la Den_{bd} était négativement corrélée avec la croissance (–0,49 à –0,73).

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Introduction

Wood stiffness is one of the most important properties of structural wood products and is particularly important for Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco), which is known for its strong, stiff, and dense wood (Forest Products Laboratory 1999). Because corewood (wood from the inner core of a tree) is less stiff than outerwood, the quality of Douglas-fir wood products may decline as rotation lengths decrease and proportionally more of the wood is derived from the inner core (Megraw 1985; Kretschmann et al. 1993). Furthermore, because wood properties are genetically variable and often highly heritable, it may be valuable to incorporate wood stiffness into Douglas-fir breeding programs (Howe et al. 2006).

Breeding for wood properties is facilitated by measure-

ment techniques that are inexpensive, non-destructive, rapid, and applicable to small trees. Direct estimates of wood stiffness (modulus of elasticity, MOE) can be obtained by applying a load to a wood sample and measuring the wood's resistance to deflection (Carter et al. 2005), but these bending tests are time consuming, costly, and difficult to perform on standing trees (but see Launay et al. 2002). Alternatively, an indirect estimate of bending stiffness can be obtained by measuring green wood density and the velocity of acoustic waves traveling through the wood and then calculating acoustic MOE using one-dimensional wave theory (acoustic MOE = green wood density × velocity²; Pellerin and Ross 2002). Because green wood density is costly to measure, it is important to understand whether stiffness can be adequately predicted from acoustic velocity alone.

New tools for estimating acoustic velocity have been de-

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veloped (Lindström et al. 2002; Toulmin and Raymond 2007), providing new opportunities to enhance wood stiffness through tree breeding and stand management (Kumar et al. 2002, 2006; Briggs et al. 2005). The Fibre-gen Director HM200 (HM200) can be used to measure acoustic velocity and estimate the stiffness of logs, whereas the Fibre-gen Director ST300 (ST300) can be used to measure acoustic velocity in standing trees. Acoustic velocity or acoustic MOE can be used as a surrogate for bending stiffness because both are highly correlated with direct estimates of MOE obtained from bending tests (Andrews 2002; Carter et al. 2005).

The HM200 and ST300 differ in a few important aspects. The ST300 estimates the time-of-flight (TOF) for a single acoustic wave passing through the outerwood of a standing tree between a transmitter probe and a receiver probe (Carter et al. 2005), whereas the HM200 estimates the acoustic velocity from the resonant frequencies created by repeated acoustic echoing between the log ends. Because the ST300 only measures acoustic velocity of the outer, generally stiffer wood of the tree, the stiffness of the entire log tends to be overestimated, and it may be sensitive to large knots and branches, especially in small-diameter trees (Briggs et al. 2007). In contrast, the HM200 measures acoustic velocity of the entire log, thereby capturing information on both the stiffer outerwood and less stiff corewood. In logs, HM200 velocities seem to be reduced by the presence of bark, but bark has little effect on ST300 velocities (Grabianowski et al. 2006; Lasserre et al. 2007). Because TOF is measured over a short distance (typically 1 m), manufacturers recommend taking at least three consecutive readings every time the ST300 probes are inserted. Furthermore, because of within-tree variation in wood properties, readings should be taken on multiple sides of the tree (Wagner et al. 2003; Lasserre et al. 2007; Toulmin and Raymond 2007).

There is limited information on the genetics of wood stiffness in coastal Douglas-fir. Previous studies of Douglas-fir wood properties focused mainly on wood density, which is under moderate to high genetic control (McKimmy 1966; King et al. 1988; Vargas-Hernandez and Adams 1991, 1992; Koshy 1993; Johnson and Gartner 2006). Because wood density has a moderate negative genetic correlation with tree growth, breeders have been concerned that selection for increased growth will lead to a decline in wood quality (King et al. 1988; Vargas-Hernandez and Adams 1991; Koshy 1993; Johnson and Gartner 2006). More recently, genetic studies of other Douglas-fir wood properties have been reported. Using the HM200, moderate heritabilities were found for acoustic MOE in a test of 39 wind-pollinated families at four test locations (Johnson and Gartner 2006) and Ukrainetz et al. (2007) detected quantitative trait loci for Douglas-fir wood density and microfibril angle traits.

Genetic control of wood stiffness and its component traits has been extensively studied in radiata pine (*Pinus radiata* D. Don). Moderate to high heritabilities have been observed for wood density, microfibril angle, bending MOE, and acoustic MOE (Cown et al. 1992; Kumar et al. 2002; Kumar 2004; Lindström et al. 2004; Dungey et al. 2006; Baltunis et al. 2007; Wu et al. 2008). Bending MOE and acoustic MOE

are strongly genetically (Kumar et al. 2002) and phenotypically (Lindström et al. 2004) correlated in radiata pine, and acoustic tools have been used to indirectly select for genotypes with increased wood stiffness in New Zealand (Kumar et al. 2002; Kumar 2004). Differences in bending MOE in this species have been largely attributed to differences in microfibril angle (Lindström et al. 2004, 2005; Baltunis et al. 2007). Bending stiffness has a near-zero (Kumar 2004) to moderately negative (Kumar et al. 2002) genetic correlation with growth in radiata pine.

Wood stiffness is also under moderate additive genetic control in hybrid larch (*Larix gmelinii* (Rupr.) Rupr. var. *japonica* (Maxim. ex Regel) Pilg. × *Larix kaempferi* (Lam.) Carrière) (Fujimoto et al. 2006). For this hybrid, indirect selections for acoustic MOE and wood density seem to be highly efficient for improving bending MOE. Acoustic velocity in standing trees measured with the ST300 was moderately heritable across sites in 8-year-old slash pine (*Pinus elliottii* Engelm.) (Li et al. 2007).

Interest in breeding for Douglas-fir wood quality is increasing. Therefore, it is important to understand whether acoustic tools or wood density can be used to indirectly improve bending stiffness, and if so, whether tree growth will be adversely impacted. Conversely, it is also important to understand whether bending stiffness will be adversely affected in breeding programs that focus on improving volume growth. Therefore, our objectives were to (i) estimate genetic gains for Douglas-fir bending stiffness, (ii) determine whether the HM200 and ST300 can be used to improve bending stiffness in operational breeding programs, and (iii) examine genetic and phenotypic relationships among wood stiffness, wood density, and growth traits. We studied wood stiffness and other traits in three wind-pollinated first-generation progeny test plantations. We used the HM200 and ST300 to measure acoustic MOE, and bending tests to measure bending MOE on lumber milled from a subset of trees harvested at one of the progeny test locations.

Materials and methods

Plant materials

We used materials from the Port Gamble progeny test series owned and managed by Olympic Resource Management. Parent trees were randomly selected from the Kitsap and Olympic peninsulas of northwestern Washington, allocated into four sets by geographic region of origin, and then used to establish a wind-pollinated first-generation progeny test at three locations.

Wind-pollinated seeds from the parent trees were sown in 1981 in Stryo-8 plug containers. In 1982, seedlings were planted at two progeny test locations (Watershed, 47°49'N, 122°36.6'W, 137 m a.s.l. and Opsata, 47°47'N, 122°34.4'W, 91 m a.s.l.) on the Kitsap Peninsula. The following year, Plug + 1 transplant seedlings were planted at the Shine progeny test location (47°52'N, 122°41.7'W, 122 m a.s.l.) on the Olympic Peninsula. The three test plantations were established using a reps-in-sets design. Eight blocks (reps) were nested within each of 4 sets consisting of 30–40 families apiece (130 families in total) and 4 trees per family were planted randomly within each block at a spacing of 3.05 m × 3.05 m (10 ft × 10 ft). The progeny tests were

thinned in autumn 2005 (Shine, Opsata) or spring 2006 (Watershed) after 25 growing seasons. About 50% of the trees were systematically thinned by removing every other column or every other diagonal in the plantation.

Measurements

Diameter at breast height (DBH, centimetres) was measured on all trees at ages 13 (DBH₁₃) and 25 (DBH₂₅) prior to thinning. Tree height (metres) was measured at age 13 (Ht₁₃). Tree stem taper at age 13 (Taper₁₃, centimetres per metre) was estimated as DBH₁₃ / (Ht₁₃ - 1.4 m) and volume at the same age (Vol₁₃, cubic metres) was estimated as $(\pi/40\,000)DBH_{13}^2 Ht_{13}$.

Wood discs were cut from the base (~0.3 m from the ground) of every butt log at Shine and then used to measure green wood density (Den_{gd}, kilograms per cubic metre), basic wood density (Den_{bd}, kilograms per cubic metre), and moisture content (MC, percentage). These discs, which included the pith, were either whole (round) or half (semi-circular) and about 5 cm thick. For each disc, we measured the green disc mass and green volume, using water displacement for the latter. The discs were transported to Oregon State University (OSU), kiln-dried at 60 °C to <7% MC and weighed again. Den_{gd} and Den_{bd} were estimated for each tree as disc mass (kilograms) / disc green volume (cubic metres). MC was estimated as $(Den_{gd} - Den_{bd}) / 100Den_{bd}$.

Prior to harvesting, the ST300 was used to measure acoustic velocity (Vel_{ST}) on a subset of trees that were to be thinned at Shine and Opsata. Eight trees in each of 12–13 families were measured per set at each location. Vel_{ST} was measured near breast height on two opposite sides of the stem using probes spaced about 1 m apart, with 3 measures taken per side; these values were later averaged to obtain one Vel_{ST} value per tree. After harvesting, we calculated acoustic MOE (MOE_{ST}) for the trees at Shine. We used the HM200 to measure acoustic velocity (Vel_{HM}) on the basal log of each thinned tree at Shine and Watershed and acoustic MOE (MOE_{HM}) at Shine. One acoustic measurement was recorded on each delimited log according to the manufacturer's instructions, and the lengths of each log, which varied from 2.0 to 12.2 m, were measured. We used Den_{gd} plus either Vel_{HM} or Vel_{ST} to estimate MOE_{HM} or MOE_{ST} from the one-dimensional wave equation:

$$[1] \quad MOE \text{ (GPa)} = Den_{gd} \text{ (kg} \cdot \text{m}^{-3}) [Vel \text{ (m} \cdot \text{s}^{-1})]^2 \times 10^{-9}$$

(Carter et al. 2005).

The trees measured with the ST300 at Shine were also used for milling the basal logs into 2 × 4 (3.8 cm × 8.9 cm × 2.13 m; ~1.5 in. × 3.5 in. × 7 ft) dimensional lumber. The basal logs were shipped to OSU and then milled into 2 × 4s using a WoodMizer portable sawmill. Each log yielded from one to ten 2 × 4s. The lumber was kiln-dried at 60 °C to <7% moisture content, and the dimensions (thickness, width, and length) of each 2 × 4 were then measured. Lumber oven-dry density (kg·m⁻³) was estimated as 2 × 4 oven-dry mass / volume, and the mean lumber density of each tree (Den_{ol}, kg·m⁻³) was then obtained by averaging the densities of all 2 × 4s per tree.

Bending MOE (MOE_{bl}) was measured using a four-point

bending test (third-point loading) at the OSU Wood Engineering Laboratory with a 40 kip MTS Model 332.21 Universal Testing Machine (MTS Systems Corp.) and LabView software. Each 2 × 4 was loaded on edge with a span-to-depth ratio of 17:1. A 226.8 kg (500 lb) maximum load was applied at a deflection rate of 5.1 cm (2 in.)·min⁻¹, and loading was halted prior to failure. The slope of the deflection curve (P/Δ) below the proportional limit was used to calculate MOE for each 2 × 4, where P is the applied load between 45 and 204 kg (100–450 lbs) and Δ is the deflection resulting from P . MOE_{bl} was then estimated as

$$[2] \quad MOE_{bl} \text{ (GPa)} = \left(\frac{P}{\Delta}\right) \left(\frac{23L^3}{108bh^3}\right) (6.894 \times 10^{-6})$$

(ASTM 2005).

L is the span length between the beam supports, 1.52 m (60 in.); b is the measured 2 × 4 thickness (inches); h is the measured 2 × 4 width (inches); and 6.894×10^{-6} is the factor used to convert pounds per square inch to gigapascals. The MOE_{bl} for each log was then obtained by averaging the values for all corresponding 2 × 4s.

Statistical analyses

For each trait, we removed a few (≤ 2) obvious outliers based on bivariate plots and then removed a few (≤ 4) additional outliers if the internally-studentized residuals (eqs. 3 and 4) exceeded 4 SDs from the mean (Neter et al. 1996). Residuals were also checked for normality (via various normality tests), homoskedasticity (via residual plots), and goodness-of-fit (via Akaike's and Sawa's information criteria). These analyses indicated that no data transformations were needed. Components of variance and covariance were estimated using a mixed-model analysis and restricted maximum likelihood (SAS Proc Mixed version 9.1.3). The linear model for traits across multiple locations was

$$[3] \quad Y_{lsrfn} = \mu + L_l + S_s + LS_{ls} + R(LS)_{r(ls)} + F(S)_{f(s)} + LF(S)_{lf(s)} + RF(LS)_{rf(ls)} + \varepsilon_{(lsrf)n}$$

where Y_{lsrfn} is the n th tree of the f th family in the r th replication of the s th set in the l th location; μ is the overall mean; L_l is the random effect of the l th location; S_s is the random effect of the s th set; LS_{ls} is the interaction between the l th location and s th set; $R(LS)_{r(ls)}$ is the random effect of the r th replication in the s th set and l th location; $F(S)_{f(s)}$ is the random effect of the f th family in the s th set; $LF(S)_{lf(s)}$ is the interaction between the l th location and f th family in the s th set; $RF(LS)_{rf(ls)}$ is the interaction between the r th replication and f th family in the s th set and l th location; and $\varepsilon_{(lsrf)n}$ is the residual error.

The linear model for traits at a single location was

$$[4] \quad Y_{srfn} = \mu + S_s + R(S)_{r(s)} + F(S)_{f(s)} + RF(S)_{rf(s)} + \varepsilon_{(srf)n}$$

where terms were as described above, with the location effect eliminated.

Narrow-sense heritabilities across locations were estimated as

$$[5] \quad h_i^2 = \frac{3\sigma_{F(S)}^2}{[\sigma_E^2 + \sigma_{RF(LS)}^2 + \sigma_{LF(S)}^2 + \sigma_{F(S)}^2]}$$

for individual trees and

$$[6] \quad h_{F(S)}^2 = \frac{\sigma_{F(S)}^2}{\left[\frac{\sigma_E^2}{k_1} + \frac{\sigma_{RE(LS)}^2}{k_2} + \frac{\sigma_{LE(S)}^2}{k_3} + \sigma_{F(S)}^2\right]}$$

for family means, where σ_E^2 , $\sigma_{RF(LS)}^2$, $\sigma_{LF(S)}^2$, and $\sigma_{F(S)}^2$ are variance components estimated using eq. 3 and SAS Proc Mixed and k_1 , k_2 , and k_3 are ratios of the variance component coefficients from the family (set) expected mean square (EMS). The latter coefficients were generated using the random statement in a SAS Proc GLM analysis of Vel_{HM}. For the $h_{F(S)}^2$ values, a single set of EMS coefficients was used for all traits, to facilitate comparisons among traits that had different numbers of measured trees per family. This approach assumes that the family means for all traits are based on a mean of 22.5 trees per family for the multiple-site heritabilities and 12.3 trees per family for the single-site heritabilities (as described below). The additive genetic variation was estimated as $3\sigma_{F(S)}^2$, to account for possible relationships among wind-pollinated progeny (Squillace 1974). Heritabilities of traits measured at a single location were estimated in an analogous manner (excluding variance components involving location), and SEs of the heritabilities were estimated using the Delta method (Lynch and Walsh 1998).

Type A genetic (r_A), environmental (r_E), and phenotypic (r_P) correlations were estimated as

$$r_{X,Y} = \frac{\text{Cov}_{X,Y}}{\sqrt{\sigma_X^2 \sigma_Y^2}}$$

Additive genetic correlations (r_A) were calculated using family (set) variance-covariance components, r_E was calculated using the family (set) \times replication variance-covariance components, and r_P was calculated using their sums. For r_E estimation, we assumed that measurement and other nonenvironmental sources of error were low. The covariance components were estimated using SAS Proc Mixed (Saxton 2004), and the SEs of the correlations were estimated using the Delta method (Lynch and Walsh 1998).

Potential genetic gains were estimated using two backward selection scenarios, assuming that the parents would be selected among all available sets and that the selected genotypes would be placed in a grafted wind-pollinated seed orchard with random mating and no pollen contamination. Gains from parental selection were estimated based on choosing (i) the best 25 of 200 parents (12.5% selection intensity; $i_F = 1.636$ for $n = 200$) or (ii) the best 25 of 1000 parents (2.5% selection intensity; $i_F = 2.338$ for $n = 1000$) (Falconer and Mackay 1996). The second scenario assumes that the parents from five first-generation programs are combined, which is realistic given the recent expansion of the second-generation breeding zones for the Northwest Tree Improvement Cooperative breeding programs (Howe et al. 2006).

Backward genetic gains (ΔG) were then estimated using single-site statistics as described in eq. 7:

$$[7] \quad \Delta G (\%) = (2) \left\{ \frac{i_F \sigma_{pF(S)} h_{F(S)}^2}{\bar{X}} \right\} (100)$$

where $\sigma_{pF(S)}$ is the phenotypic SD of family means and \bar{X} is the family mean. To facilitate comparisons among traits, the family heritabilities used in these equations were the single-site heritabilities that were calculated assuming that the same number of trees per family was measured for each trait (see above).

The correlated response to indirect selection (ΔCR) is the gain that will be achieved in MOE_{bl} when selection is based on a second correlated trait that is used as an indirect selection criterion. ΔCR was estimated for backward selection as described in eq. 8:

$$[8] \quad \Delta CR (\%) = (2) \left\{ \frac{r_A [i_F h_{F(S)\text{indirect}} h_{F(S)\text{MOEbl}} \sigma_{pF(S)\text{MOEbl}}]}{\bar{X}_{\text{MOEbl}}} \right\} (100)$$

We also estimated relative gain efficiencies (RE) for improving bending stiffness via backward selection. RE indicates the percent gain that can be achieved in MOE_{bl} by indirectly selecting on a correlated trait, such as acoustic velocity, relative to the gain that can be obtained by directly selecting for MOE_{bl}. RE (%) values were estimated as $(\Delta CR / \Delta G_{\text{MOEbl}})100$.

Results

Sample descriptors and genetic variation

All traits were measured at a single test location (Shine), except for Vel_{HM} and Vel_{ST} (two locations) and DBH₂₅ (three locations; Table 1). The numbers of trees measured per family per location ranged from 6.8 to 24.2. Family variation was significant for all traits, but differences among sets were not significant for any trait. We also analyzed the HM200 traits using log length as a covariate, but this approach did not affect the results in any meaningful way (data not shown). No significant genotype by environment (G \times E) interactions were observed for Vel_{HM} or Vel_{ST}, but there was a significant location by family (set) interaction for DBH₂₅.

Compared with the mean MOE_{bl}, the mean MOE_{HM} underestimated bending stiffness by approximately 10%, but the mean MOE_{ST} overestimated bending stiffness by approximately 15%. Similar differences between the acoustic MOE estimated from the HM200 and the ST300 have been observed in other species (Chauhan and Walker 2006; Grabianowski et al. 2006; Lasserre et al. 2007; Wang et al. 2007).

Heritabilities

The single-site individual-tree heritabilities were moderate for all wood properties ($h_i^2 = 0.23$ – 0.43) and low for DBH₂₅ ($h_i^2 = 0.18$) (Table 1). The corresponding family heritabilities ($h_{F(S)}^2$) were moderate for all wood property traits and DBH₂₅ ($h_{F(S)}^2 = 0.40$ – 0.63). Multiple-site heritabilities are also presented in Table 1.

Genetic correlations

We estimated genetic, environmental, and phenotypic cor-

Table 1. Sample sizes, descriptive statistics, and heritabilities (\pm SE) of traits measured at the Port Gamble progeny test locations.

	MOE _{bl} (GPa)	MOE _{HM} (GPa)	MOE _{ST} (GPa)	Vel _{HM} (m·s ⁻¹)	Vel _{ST} (m·s ⁻¹)	Den _{gd} (kg·m ⁻³)	Den _{bd} (kg·m ⁻³)	Den _{ol} (kg·m ⁻³)	MC (%)	DBH ₂₅ (cm)
Sample size										
No. of locations	1	1	1	2	2	1	1	1	1	3
No. of families	50	127	50	129	50	127	127	50	127	130
No. of trees	371	1422	339	2906	800	1571	1409	372	1408	9421
Trees per family	7.4	11.2	6.8	22.5	16.0	12.4	11.1	7.4	11.1	72.5
Trees per family per location	7.4	11.2	6.8	11.2	8.0	12.4	11.1	7.4	11.1	24.2
Family mean and variation (single-site)										
Mean	10.8	9.7	12.4	3433	3865	817.7	473.3	477.0	73.6	21.4
Min.	9.8	8.4	10.9	3260	3586	771.2	431.0	445.1	63.6	18.2
Max.	12.9	11.1	14.6	3751	4081	871.6	525.7	529.8	84.3	24.5
CPV (%)*	5.4	5.6	7.0	2.4	3.1	2.4	3.3	3.6	6.0	6.0
CGV (%)*	3.6	3.9	4.1	1.8	2.1	1.7	2.4	2.5	4.0	4.6
Heritabilities (single-site)										
h_i^2	0.31 (0.14)	0.31 (0.07)	0.30 (0.14)	0.33 (0.07)	0.43 (0.14)	0.26 (0.06)	0.34 (0.07)	0.41 (0.15)	0.23 (0.06)	0.18 (0.03)
$h_{F(S)}^2$	0.53 (0.13)	0.54 (0.06)	0.54 (0.13)	0.56 (0.05)	0.63 (0.09)	0.49 (0.06)	0.57 (0.06)	0.61 (0.10)	0.45 (0.07)	0.40 (0.05)
Heritabilities (multiple-site)										
h_i^2	—	—	—	0.30 (0.05)	0.29 (0.09)	—	—	—	—	0.11 (0.02)
$h_{F(S)}^2$	—	—	—	0.65 (0.06)	0.66 (0.07)	—	—	—	—	0.39 (0.05)

Note: MOE_{bl}, lumber static bending modulus of elasticity; MOE_{HM}, modulus of elasticity estimated using Vel_{HM} and Den_{gd}; MOE_{ST}, modulus of elasticity estimated using Vel_{ST} and Den_{gd}; Vel_{HM}, acoustic velocity measured by HM200; Vel_{ST}, acoustic velocity measured by ST300; Den_{gd}, green wood density of basal discs; Den_{bd}, basic wood density of basal discs; Den_{ol}, oven-dry density of 2 × 4s; MC, green wood moisture content of basal discs; DBH₂₅, diameter at breast height at age 25.

*CPV, coefficient of phenotypic variation; CGV, coefficient of genetic variation.

Table 2. Narrow-sense genetic (r_A), environmental (r_E), and phenotypic (r_P) correlations (\pm SE) between wood property traits at the Shine progeny test location.

Trait 1	Trait 2	Families	Trees	r_A	r_E	r_P
Direct (MOE_{bl}) versus indirect estimates of wood stiffness						
MOE _{bl}	MOE _{HM}	50	282	0.92 (0.16)	0.62 (0.04)	0.65 (0.01)
MOE _{bl}	MOE _{ST}	50	304	0.57 (0.27)	0.44 (0.05)	0.45 (0.02)
MOE _{bl}	Vel _{HM}	50	338	0.75 (0.18)	0.54 (0.04)	0.56 (0.02)
MOE _{bl}	Vel _{ST}	50	364	0.53 (0.23)	0.33 (0.05)	0.35 (0.02)
MOE _{bl}	Den _{bd}	50	307	0.37 (0.37)	0.51 (0.05)	0.50 (0.02)
MOE _{bl}	Den _{ol}	50	370	0.91 (0.10)	0.64 (0.03)	0.67 (0.01)
HM200 versus ST300						
MOE _{HM}	MOE _{ST}	50	308	0.93 (0.15)	0.57 (0.04)	0.61 (0.01)
Vel _{HM}	Vel _{ST}	50	367	0.94 (0.12)	0.36 (0.05)	0.44 (0.02)
Acoustic measures of wood stiffness estimated with versus without Den_{gd}						
MOE _{HM}	Vel _{HM}	127	1422	0.92 (0.03)	0.87 (0.01)	0.87 (0.00)
MOE _{ST}	Vel _{ST}	50	339	0.92 (0.05)	0.91 (0.01)	0.90 (0.01)
Acoustic measures of wood stiffness versus density						
MOE _{HM}	Den _{bd}	127	1274	0.66 (0.10)	0.52 (0.02)	0.53 (0.01)
MOE _{HM}	Den _{ol}	50	281	0.68 (0.24)	0.44 (0.05)	0.46 (0.02)
Vel _{HM}	Den _{bd}	127	1275	0.41 (0.14)	0.25 (0.03)	0.27 (0.01)
Vel _{HM}	Den _{ol}	50	338	0.66 (0.20)	0.34 (0.05)	0.38 (0.03)

Note: MOE_{bl}, lumber static bending modulus of elasticity; MOE_{HM}, modulus of elasticity estimated using Vel_{HM} and Den_{gd} (green wood density of basal discs); MOE_{ST}, modulus of elasticity estimated using Vel_{ST} and Den_{gd}; Vel_{HM}, acoustic velocity measured by HM200; Vel_{ST}, acoustic velocity measured by ST300; Den_{bd}, basic wood density of basal discs; Den_{ol}, oven-dry density of 2 × 4s.

relations for selected pairs of traits, to specifically assess the relationships between (i) direct and indirect measures of wood stiffness, (ii) acoustic measures of wood stiffness measured with the HM200 and the ST300, (iii) acoustic measures of wood stiffness estimated with and without Den_{gd}, (iv) stiffness and wood density, and (v) wood properties and wood growth (Tables 2 and 3).

The genetic correlation between MOE_{bl} and MOE_{HM} was extremely high ($r_A = 0.92$; Table 2) and higher than the genetic correlation between MOE_{bl} and Vel_{HM} ($r_A = 0.75$). The genetic correlations between MOE_{bl} and the ST300 traits (MOE_{ST}, Vel_{ST}) were moderate ($r_A = 0.53$ – 0.57). The SEs of these estimates were moderately high because of the relatively small number of trees that were milled to measure MOE_{bl}.

The genetic correlations between the two acoustic tools (MOE_{HM} versus MOE_{ST} and Vel_{HM} versus Vel_{ST}) were extremely high ($r_A = 0.93$ – 0.94 ; Table 2). The acoustic velocities (Vel_{HM} and Vel_{ST}) were highly correlated with the acoustic MOEs (MOE_{HM} and MOE_{ST}) that were estimated using both velocity and Den_{gd}. The r_A values between acoustic velocity and acoustic MOE were 0.92 for both the HM200 and ST300 (Table 2).

The genetic correlation between Den_{ol} and MOE_{bl} was very high ($r_A = 0.91$) and much larger than the correlation between Den_{bd} and MOE_{bl} ($r_A = 0.37$; Table 2). The genetic correlations between Den_{bd} and the various measures of wood stiffness ranked as follows: Den_{bd} versus MOE_{HM} > Den_{bd} versus Vel_{HM} > Den_{bd} versus MOE_{bl}. These r_A values were 0.66, 0.41, and 0.37 (Table 2) and consistent with the trend observed in a previous study of Douglas-fir (Den_{bd} versus MOE_{HM} > Den_{bd} versus Vel_{HM}; Johnson and Gartner 2006). Presumably, the correlation between Den_{bd} and

MOE_{HM} is the largest because of autocorrelation, which exists because Den_{bd} and Den_{gd} were measured on the same wood discs and Den_{gd} is used in calculating MOE_{HM}.

The genetic correlations between MOE_{bl} and the growth traits (DBH₂₅, DBH₁₃, Ht₁₃, and Vol₁₃) were weakly to moderately positive ($r_A = 0.10$ – 0.46 ; Table 3). In contrast, the genetic correlations between Vel_{HM} and the growth traits were near-zero or weakly negative. Of these, the correlation between Vel_{HM} and DBH₂₅ was the strongest ($r_A = -0.20$). The genetic correlations between MOE_{HM} and the growth traits ($r_A = -0.55$ to -0.87) were stronger, consistently negative, and not substantially different from the correlations between Den_{bd} and the growth traits ($r_A = -0.49$ to -0.73). However, the genetic correlations between Den_{ol} and the growth traits were near zero or weakly negative ($r_A = -0.01$ to -0.19). Stem taper had weak negative correlations with all wood properties ($r_A = 0.00$ to -0.23).

Genetic gains in wood stiffness and density

Gains from parental (backward) selection were 14% for MOE_{HM} and 9% for Den_{bd} (2.5% selection intensity; Table 4). Gains from parental selection were 12% for MOE_{bl} (2.5% selection intensity), only slightly lower than the estimated gains in MOE_{HM} and MOE_{ST}. Gains from progeny (forward) selection based on combined family and within-family performance (i.e., choosing the best individual of 100 progeny from each of the selected families) were approximately equal to those from backward selection (data not shown).

Relative efficiencies and correlated responses to selection

We also estimated the indirect genetic gains for MOE_{bl}

Table 3. Narrow-sense genetic (r_A) correlations (\pm SE) for wood properties versus growth traits measured at the Port Gamble progeny test locations.

	DBH ₂₅	DBH ₁₃	Ht ₁₃	Vol ₁₃	Taper ₁₃
MOE _{bl}	0.10 (0.40)	0.18 (0.48)	0.46 (0.52)	0.20 (0.46)	-0.23 (0.36)
MOE _{HM}	-0.55 (0.16)	-0.75 (0.26)	-0.65 (0.20)	-0.87 (0.32)	0.00 (0.17)
Vel _{HM}	-0.20 (0.15)	0.02 (0.15)	0.08 (0.16)	0.06 (0.16)	-0.15 (0.13)
Den _{bd}	-0.49 (0.17)	-0.59 (0.24)	-0.52 (0.21)	-0.73 (0.31)	-0.07 (0.16)
Den _{ol}	-0.01 (0.34)	-0.19 (0.36)	-0.05 (0.40)	-0.18 (0.35)	-0.22 (0.31)

Note: MOE_{bl}, lumber static bending modulus of elasticity; MOE_{HM}, modulus of elasticity estimated using Vel_{HM} and Den_{gd} (green wood density of basal discs); Vel_{HM}, acoustic velocity measured by HM200; Den_{bd}, basic wood density of basal discs; Den_{ol}, oven-dry density of 2 × 4s; DBH₂₅, diameter at breast height at age 25; DBH₁₃, diameter at breast height at age 13; Ht₁₃, height at age 13; Vol₁₃, stem volume at age 13; Taper₁₃, stem taper at age 13.

Table 4. Genetic gains, correlated responses to selection, and relative efficiencies for backward selection of parents based on progeny performance in the Port Gamble progeny test.

Parental selection intensity (%)	MOE _{bl} (GPa)	MOE _{HM} (GPa)	MOE _{ST} (GPa)	Vel _{HM} (m·s ⁻¹)	Vel _{ST} (m·s ⁻¹)	Den _{gd} (kg·m ⁻³)	Den _{bd} (kg·m ⁻³)	Den _{ol} (kg·m ⁻³)	MC (%)	DBH ₂₅ (cm)
Gain from direct backward selection (ΔG, %)										
12.5	8.6	9.5	9.7	4.4	5.5	3.9	6.0	6.4	-8.9	9.5
2.5	12.3	13.6	13.9	6.3	7.8	5.6	8.6	9.1	-12.7	13.6
Correlated response in MOE_{bl} from indirect backward selection (ΔCR, %)*										
12.5	8.6	8.0	4.9	6.7	4.9	0.7	3.3	8.4	-1.6	0.7
2.5	12.3	11.4	7.0	9.6	7.1	1.0	4.7	12.0	-2.2	1.1
Relative efficiency of indirect backward selection (RE = $\Delta CR / \Delta G_{MOE_{bl}}$, %)[†]										
12.5	100.0	93.3	57.4	77.9	57.6	8.5	38.1	97.8	-18.3	8.7
2.5	100.0	93.3	57.4	77.9	57.6	8.5	38.1	97.8	-18.3	8.7

Note: MOE_{bl}, lumber static bending modulus of elasticity; MOE_{HM}, modulus of elasticity estimated using Vel_{HM} and Den_{gd}; MOE_{ST}, modulus of elasticity estimated using Vel_{ST} and Den_{gd}; Vel_{HM}, acoustic velocity measured by HM200; Vel_{ST}, acoustic velocity measured by ST300; Den_{gd}, green wood density of basal discs; Den_{bd}, basic wood density of basal discs; Den_{ol}, oven-dry density of 2 × 4s; MC, green wood moisture content; DBH₂₅, diameter at breast height at age 25.

* ΔCR is the correlated response (indirect gain) in MOE_{bl} when selection is based on the listed trait.

[†]RE is the gain in MOE_{bl} obtained by basing selection on a second correlated trait relative to the gain that could be obtained by selecting for MOE_{bl} directly.

when selection is based on other traits. If selections were based on acoustic MOE, the indirect gains in MOE_{bl} would be about 93% (MOE_{HM}) or 57% (MOE_{ST}) of the gains resulting from direct selection on MOE_{bl} itself (Table 4). If selections were based on acoustic velocity, the RE in MOE_{bl} would be approximately 78% for Vel_{HM} and 58% for Vel_{ST}. When selecting on density, the RE in MOE_{bl} would be approximately 38% for Den_{bd} and 98% for Den_{ol}.

If selections were based on DBH₂₅, indirect gains in MOE_{bl} would be positive but low (RE = 9%). Under a reverse scenario, with selection based on MOE_{bl}, indirect gains in DBH₂₅ would also be positive and low (RE = 12%; data not shown). However, if selections were based on Den_{bd}, the indirect response in DBH₂₅ would be moderately negative (RE = -64%; data not shown).

Discussion

Genetic gains in wood stiffness

We assessed genetic gains in wood stiffness based on analyses of MOE_{bl} and MOE_{HM}. MOE_{bl}, our direct measure of wood stiffness, was measured on a modest number of trees, whereas MOE_{HM}, an indirect measure of wood stiffness, was measured on a much larger sample. Taken together, these two traits provide information on the genetics of wood stiffness and the potential for improvement through

selective breeding. Both traits were measured at a single site, but there seems to be relatively little G × E interaction for wood stiffness based on previous analyses of acoustic MOE (Johnson and Gartner 2006) and our multisite analyses of Vel_{HM} and Vel_{ST}. Results indicate that substantial genetic gains can be made in wood stiffness and gains in wood stiffness are expected to be larger than gains in wood density, which is consistent with previous results for Douglas-fir (Johnson and Gartner 2006) and other species (Kumar 2004; Fujimoto et al. 2006).

Acoustic tools can be used to improve wood stiffness

Although gains in acoustic MOE have been reported for Douglas-fir (Johnson and Gartner 2006), previous studies did not address how gains in acoustic MOE would translate into gains in bending MOE, the main trait of interest. Our results indicate that acoustic measures of wood stiffness (MOE_{HM}, Vel_{HM}, MOE_{ST}, and Vel_{ST}) are useful for genetically improving MOE_{bl}. In particular, the HM200 can be used in progeny tests to obtain 78%–93% of the gains in MOE_{bl} that would be achieved by directly selecting for MOE_{bl}. Similar analyses in radiata pine yielded relative efficiencies of 80%–91% when HM200 velocity was used to indirectly select for bending stiffness of small clearwood samples (small clears) (Kumar et al. 2002; Kumar 2004).

Gains in MOE_{bl} can also be achieved using the ST300,

but the RE was only about 57%. The better performance of the HM200 was mainly because of the higher genetic correlation between the HM200 traits and MOE_{bl} than between the ST300 traits and MOE_{bl} . These results were expected because the HM200 provides an integrated measurement of acoustic velocity throughout the entire log, whereas the ST300 only measures TOF in the outerwood of the tree (Carter et al. 2005). In radiata pine, higher REs for bending stiffness of small clears were observed for two tools that are designed to be used on standing trees. The RE for acoustic velocity measured with the FAKOPP was 66% (Kumar et al. 2002), whereas the RE for acoustic velocity measured with the IML Hammer (IMLH) was 118% (owing to a near-perfect genetic correlation between IMLH velocity and MOE and a higher heritability for IMLH velocity than for MOE; Kumar 2004).

In our study, the REs for the ST300 traits were constrained by the modest genetic correlation with MOE_{bl} , but these correlations had high SEs. In addition, the high genetic correlation between MOE_{ST} and MOE_{HM} ($r_A = 0.93$), coupled with the high genetic correlation between MOE_{HM} and MOE_{bl} ($r_A = 0.92$), suggests that our r_A values may have underestimated the true relationship between MOE_{ST} and MOE_{bl} . Therefore, although our results indicate that the REs for the ST300 will be lower than those for the HM200, uncertainty remains about their exact values.

When the HM200 is used to predict wood stiffness, it is possible to measure green wood density on wood discs taken from the logs and then use the acoustic velocities and green wood densities to estimate MOE. Because it is costly and time-consuming to measure disc density, we estimated the gains in bending stiffness that would be sacrificed by selecting for velocity alone. These analyses show that gains in MOE_{bl} would only decrease slightly if selection were based on Vel_{HM} rather than on MOE_{HM} ; previous analyses of Douglas-fir progeny tests support this conclusion (Johnson and Gartner 2006).

Because the ST300 and related tools are used on standing trees, densities are not normally measured. However, outerwood density could be measured using increment cores, but this would be costly. Based on our results, selecting on Vel_{ST} appears to be justified because nothing seems to be gained by measuring Den_{gd} . Gains in MOE_{bl} are approximately equal when selections are based on MOE_{ST} (estimated using Den_{gd} and Vel_{ST}), compared with using Vel_{ST} alone. Since we measured Den_{gd} on wood discs that included both corewood and outerwood, we might have obtained slightly different results if we had measured the green density of the outerwood that was sampled by the ST300.

Gains in wood stiffness may be low when selections are based on wood density

A primary reason for improving wood density in Douglas-fir is to increase the stiffness of structural lumber and veneer. Our results, however, suggest that gains in bending stiffness may be low if selection is based on the density of basal wood discs (RE = 38%) because Den_{bd} had a low genetic correlation with MOE_{bl} ($r_A = 0.37 \pm 0.37$). However, because this correlation had a high SE, there is a good chance that this correlation was underestimated. The modest

correlation between Den_{bd} and MOE_{bl} may also result from high within-tree variation in wood properties (McKimmy 1959; Megraw 1985; Knowles et al. 2003), and the sampling error inherent in estimating log density from a single basal wood disc. This hypothesis is supported by the observation that Den_{ol} was highly correlated with bending stiffness ($r_A = 0.91$), but Den_{bd} and Den_{ol} were only moderately correlated with each other ($r_A = 0.67$). Therefore, we conclude that density is a good surrogate for bending stiffness if one can obtain a good estimate of whole-tree wood density. The genetic correlation between Den_{bd} and Den_{ol} may be modest because Den_{bd} sampled only a small vertical portion of the tree, whereas some of the outerwood was lost when the trees were milled into lumber and was not included our estimate of Den_{ol} . Furthermore, compared with the 2×4 s used to estimate Den_{ol} , our basal wood discs had fewer knots (which are denser than normal wood).

Other phenotypic correlations suggest that the relationship between density and wood stiffness is strong when these traits are measured on the same samples of wood, that is, when sampling variation is not an issue. When wood density and bending stiffness were measured on small clears, Lachenbruch and others found an individual-tree phenotypic correlation of 0.76 (B. Lachenbruch, personal communication, 9 November 2007), and Knowles et al. (2003) found a phenotypic correlation of 0.92. These correlations are larger than the individual-tree phenotypic correlation we found between Den_{bd} and MOE_{bl} ($r_p = 0.50$), and between Den_{ol} and MOE_{bl} ($r_p = 0.67$). In radiata pine and hybrid larch, strong genetic correlations ($r_A > 0.7$) were found between wood density and bending stiffness measured on small clears, suggesting that wood density would be a good surrogate for bending stiffness (RE = 78%–86%; Kumar et al. 2002; Fujimoto et al. 2006), but other researchers reported weak or moderate genetic and phenotypic correlations between these traits (Downes et al. 2002; Lindström et al. 2004; Kumar 2004).

Compared with basal wood discs, densities estimated at breast height might be better surrogates for bending stiffness. For example, Knowles et al. (2003) reported an individual-tree phenotypic correlation of 0.75 when density was measured on the outer rings of breast height increment cores, and wood stiffness was measured on timber sawn from 18 Douglas-fir trees growing in New Zealand.

When information on bending stiffness is lacking, it is tempting to judge the relationship between density and wood stiffness by evaluating correlations between Den_{bd} and MOE_{HM} , but these traits are autocorrelated because Den_{bd} and Den_{gd} (which is used for calculating MOE_{HM}) are measured on the same wood disc. Therefore, it may be better to judge the true relationship between density and wood stiffness by examining the genetic correlation between Den_{bd} and Vel_{HM} , which was substantially lower than the correlation between Den_{bd} and MOE_{HM} ($r_A = 0.41$ versus $r_A = 0.66$). A similar relationship was found in a previous study of Douglas-fir. The density of breast height wood discs had a genetic correlation of 0.54 with acoustic velocity and 0.76 with acoustic MOE when both traits were measured with the HM200 (Johnson and Gartner 2006). These results support our conclusion that the density of wood discs is only moderately genetically correlated with wood stiffness.

Furthermore, their results indicate that correlations between wood density and log acoustic stiffness may be slightly stronger if discs at breast height are used instead of basal discs. In radiata pine, the genetic correlation between wood density and log acoustic velocity ranged from 0.44 to 0.84 when density was measured at breast height (Kumar et al. 2002; Kumar 2004).

Overall, our results suggest that breeders should be cautious about using wood density to improve bending stiffness in operational breeding programs of Douglas-fir (i.e., when selection is based on measuring the density of small wood samples from each tree). In addition, selection for increased wood density may be disadvantageous because it is negatively correlated with growth (discussed in the next section). Jointly, wood density and microfibril angle may be better predictors of bending stiffness (Cave and Walker 1994), but microfibril angle explained little of the phenotypic variation in bending stiffness in previous studies of Douglas-fir (Knowles et al. 2003; B. Lachenbruch et al., personal communication, 9 November 2007). Furthermore, because microfibril angle is costly to measure, it is unlikely that this trait will be widely used in operational breeding programs.

Relationships between wood properties and growth

Although volume growth is the primary breeding objective for Douglas-fir, breeders have been concerned that selection for increased growth may adversely affect wood quality (Howe et al. 2006). Our results, however, suggest that improvement in growth could have a small positive impact on bending stiffness and vice versa. In contrast, growth was negatively correlated with Den_{bd} ($r_A = -0.49$ to -0.73), which is consistent with previous studies (Bastien et al. 1985; King et al. 1988; Vargas-Hernandez and Adams 1991; St. Clair 1994; Johnson and Gartner 2006). Surprisingly, however, the correlations between Den_{ol} and these same growth traits were much lower ($r_A = -0.01$ to -0.19). The reasons why these correlations were much stronger when density was measured on wood discs rather than lumber are unclear, but as discussed above, Den_{bd} and Den_{ol} sampled different portions of the stem and the wood discs had fewer knots compared with the lumber. In summary, the relationship between growth and density differed when density was measured on wood discs (moderate negative correlation) compared with lumber (weak negative correlation).

The genetic correlations between growth and MOE_{HM} were also negative ($r_A = -0.55$ to -0.87), but these should be judged with caution because they could be driven by the adverse correlation between Den_{bd} and growth, rather than by wood stiffness per se. This caution is supported by the observation that growth was only weakly correlated with Vel_{HM} ($|r_A| \leq 0.20$). Johnson and Gartner (2006) found similar results: they found moderate negative genetic correlations between density and DBH ($r_A = -0.57$) and between acoustic MOE and DBH ($r_A = -0.51$), but a much weaker correlation between velocity and DBH ($r_A = -0.27$).

$Taper_{13}$ was weakly correlated with wood properties at age 25 (Table 3), which contrasts with the results of Johnson and Gartner (2006). These authors found moderately negative genetic correlations between Douglas-fir taper and acoustic MOE, velocity, and density ($r_A = -0.44$ to -0.70).

These observations lead to three main conclusions. First, there is no strong evidence that selection for growth will have a large adverse impact on bending stiffness. Second, our data indicate that selection for growth may adversely affect the density of wood discs, but may have little effect on the average density of the lumber cut from the tree (although the reasons for this are unclear). Third, breeders seeking to improve wood stiffness and growth should consider selecting on acoustic velocity rather than on acoustic MOE. Using density to calculate acoustic MOE may contribute little to gains in bending stiffness and may lead to adverse effects on growth. Alternatively, acoustic velocity, density, and growth traits might be used in a selection index to achieve optimal changes in growth and wood stiffness.

Implications for genetic improvement

Information on the genetics of wood stiffness is valuable for designing strategies for improving wood stiffness, maintaining wood stiffness when selection is practiced on other traits, or simply understanding how wood stiffness will change in programs that seek to improve growth. In an aggressive program aimed at improving wood stiffness, every effort should be made to measure acoustic velocity on logs using a tool such as the HM200. Log acoustic velocity is particularly valuable because it samples the entire log, thereby avoiding sampling problems caused by large within-tree variation in wood stiffness and its component traits.

Optimal approaches for improving wood stiffness must consider the advantages and disadvantages of the HM200 (high quality data versus the need to harvest trees) with those of the standing tree tools (unnecessary to harvest trees versus lower quality data). The best approaches for improving wood stiffness may involve a strategy that capitalizes on the strengths of both tools. Some of the options for forward selection are discussed below.

To make forward selections from progeny tests, a breeder could estimate family breeding values by measuring Vel_{HM} on a subset of the progeny in the progeny test. Because Vel_{HM} heritabilities are favorable, $G \times E$ interaction is low, and family performance is very important for making forward selections, this approach should be effective if Vel_{HM} is measured on a modest number of trees from each family, either at a single progeny test site or in a single replication from each of a few sites. It does not seem necessary or desirable to measure Den_{gd} because it is relatively costly to measure, adds little to the gains in bending stiffness, and may limit genetic improvement in volume growth (e.g., MOE_{HM} is negatively correlated with growth). The Vel_{HM} data could be augmented by nondestructively measuring Vel_{ST} on the remaining progeny, and these data could then be used to choose the best remaining trees (Vel_{ST}) in the best families (Vel_{HM} and Vel_{ST}). The drawbacks to this approach are the costs of harvesting the trees to measure Vel_{HM} and the loss of some potential forward selections, unless the harvested trees are grafted into a clonal archive.

Alternatively, multistage selection could be used. For example, all trees could be measured with the ST300 and families with low acoustic velocities could be removed from further consideration. The HM200 could then be used on a subset of the trees in the remaining families, and final parental or family selections could be based on Vel_{HM} . For-

ward selections could be made among the nonharvested trees based on family means for Vel_{HM} plus individual-tree values for Vel_{ST} . If a modest number of forward selections are made, it might even be possible to graft provisional selections into a clonal archive and then measure Vel_{HM} on the provisional selections themselves. Finally, in any program where wood stiffness is the primary breeding objective, it seems wise to measure Vel_{HM} whenever progeny tests are thinned or harvested.

In programs that seek to improve growth and either maintain or monitor wood stiffness, data from standing tree tools should be sufficient because they are moderately correlated with bending stiffness and selection for growth should not have a major adverse impact on bending stiffness. Unfortunately, we do not know how the standing tree tools will perform on younger and smaller trees where branches could be a problem. Although we used the ST300 on 25-year-old trees, forward selections are typically made on Douglas-fir trees that are ≤ 15 years old. Therefore, it would be desirable to test how the standing tree tools perform on much younger trees.

Wood density is now measured in some Douglas-fir breeding programs, presumably because it is positively correlated with wood stiffness and strength. Our data, however, suggest that breeders should be cautious about selecting for increased wood density because Den_{bd} was moderately correlated with bending stiffness and had a moderate negative correlation with growth. The modest correlation between Den_{bd} and bending stiffness may result from high within-tree variation in wood properties because Den_{ol} had a high genetic correlation with bending stiffness. Within-tree variation in wood properties contributes to high within-tree sampling variation that presumably affects the usefulness of data from increment cores as well. Although increment cores are typically used to obtain estimates of wood density in breeding programs, we do not know whether breast height increment cores are better than basal wood discs at predicting whole-log wood density or bending stiffness. However, we recommend that breeders focus on standing-tree acoustic velocity rather than wood density to make selections designed to increase bending stiffness.

Our study suggests that future research on wood stiffness should focus on (i) quantitatively evaluating alternative selection scenarios such as those described above, (ii) testing standing tree tools on younger trees, and (iii) obtaining additional information on the genetic and phenotypic correlations between indirect and direct measures of bending stiffness. We are carrying out further research to estimate the minimum and optimal sample sizes for obtaining robust estimates of heritability and genetic gain for direct and indirect estimates of MOE.

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