Stiffness of Douglas-fir lumber: effects of wood properties and genetics

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Abstract: Because stiffness (modulus of elasticity (MOE)) is important for structural wood products, breeders and silviculturists seek to efficiently measure and improve this trait. We studied MOE in a 25-year-old progeny test of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) using field-based tools (ST300 and HM200) to measure stress wave MOE of standing trees and logs. We measured density, static bending MOE, and transverse vibration MOE on 2 × 4s, and density, SilviScan MOE, and SilviScan microfibril angle on small clearwood samples. Bending MOE had moderate to strong phenotypic and genetic correlations with stress wave MOE of trees and logs, transverse vibration MOE of 2 × 4s, and the densities of 2 × 4s and basal wood discs but was weakly correlated with the numbers and sizes of knots. The best lumber grade had the highest bending stiffness and smallest edge knots. Bending stiffness had a strong positive correlation with the density of small clearwood samples and a moderate negative correlation with microfibril angle. Compared with microfibril angle and edge knots, path analyses indicated that density had the strongest direct effect on bending MOE. We recommend that breeders measure and select for stress wave velocity to improve bending stiffness in Douglas-fir. Genetic gains can be increased by including wood density, but genetic selection for fewer or smaller knots will be ineffective.

Résumé : En raison de son importance pour les produits structuraux, les généticiens et les sylviculteurs cherchent à améliorer la rigidité du bois (module d'élasticité (MOE)) et à la mesurer de façon efficace. À l'aide de mesures (ST300 et HM200) du MOE par onde de contrainte prises sur le terrain, nous avons étudié le MOE d'arbres sur pied et de billes provenant d'un test de descendance de douglas de Menzies (*Pseudotsuga menziesii* (Mirb.) Franco) âgé de 25 ans. Nous avons mesuré la densité, le MOE en flexion statique et le MOE en vibration transverse sur des 2 × 4 ainsi que la densité, le MOE SilviScan et l'angle des microfibrilles SilviScan sur de petites éprouvettes de bois sans défauts. Le MOE en flexion avait des corrélations phénotypiques et génétiques allant de modérées à fortes avec le MOE mesuré par onde de contrainte des arbres et des billes, le MOE en vibration transverse des 2 × 4 et la densité des 2 × 4 et des rondelles de bois à la base mais il était faiblement corrélé avec le nombre et la taille des nœuds. La meilleure qualité de bois scié avait la plus grande rigidité en flexion et les plus petits nœuds de rive. La rigidité en flexion avait une forte corrélation positive avec la densité des petites éprouvettes de bois sans défauts et une corrélation négative modérée avec l'angle des microfibrilles. Comparativement à l'angle des microfibrilles et aux nœuds de rive, les analyses des pistes causales ont indiqué que la densité avait le plus grand effet direct sur le MOE en flexion. Nous recommandons que les généticiens mesurent la vitesse de propagation d'une onde de contrainte et sélectionnent sur cette base afin d'améliorer le MOE en flexion du douglas de Menzies. Les gains génétiques peuvent être améliorés en incluant la densité du bois, mais une sélection génétique pour un moins grand nombre ou de plus petits nœuds sera inefficace.

[Traduit par la Rédaction]

Introduction

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is the principal lumber species in the Pacific Northwest because it is widely distributed, grows quickly, and has excellent wood quality. Douglas-fir is widely used to make structural lumber, plywood, laminated veneer lumber, poles, and pilings because its wood is strong, stiff, highly workable, and dimensionally stable (Bormann 1984). Nonetheless, the quality of Douglas-fir wood products may decline because rotations are becoming shorter (<50 years), resulting in younger and smaller logs that have larger proportions of juvenile corewood.

Received 3 June 2010. Accepted 7 December 2010. Published at www.nrcresearchpress.com/cjfr on xx May 2011.

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Corewood, which is the wood produced near the pith of the tree (often called juvenile wood), is distinguished from outerwood by differences in wood properties. In softwoods, corewood generally has lower stiffness, lower density, lower cell wall thickness, lower latewood percentage, higher microfibril angles (MFA), and greater longitudinal shrinkage compared with outerwood (Burdon et al. 2004). For many fast-growing species such as loblolly pine, corewood is typically confined to the first 10 rings. In Douglas-fir, however, there is a gradual transition in wood properties that plateaus between the ages of 15 and 40, depending on the trait (Abdel-Gadir and Krahmer 1993; Peterson et al. 2007). Wood stiffness is an important target of genetic and silvicultural improvement because it is one of the most important properties of structural wood products. Furthermore, because many wood properties have high heritabilities and sufficient genetic variation, there is a strong interest in including wood stiffness in breeding programs of Douglas-fir (Howe et al. 2006) and other tree species (Baltunis et al. 2007; Roth et al. 2007).

Wood stiffness, or modulus of elasticity (MOE), is the ratio of applied load (stress) to deformation (strain) of a rigid body of wood and can be estimated from the slope of the line that describes the relationship between load and deflection (Wang et al. 2001). Direct estimates of MOE can be obtained using static bending tests in which a known load is applied at mid-span to a piece of lumber supported at its ends and the resulting deformation is measured (ASTM International 2005). Although bending tests provide direct, reliable estimates of stiffness, they are expensive and time consuming. Therefore, it is impractical to measure bending stiffness on the thousands of trees typically found in genetic test plantations. Fortunately, several inexpensive techniques are now available to rapidly estimate wood stiffness on many trees.

Transverse vibrations and stress waves can be used to estimate bending stiffness. Transverse vibration MOE is measured by striking a beam that is supported at its ends and measuring the frequency of oscillation and rate of decay of the resulting transverse vibrations (Wang et al. 2001). Stress wave MOE is based on the one-dimensional wave theory and is calculated from wood density (DEN) and the velocity of stress wave propagation (VEL), i.e., stress wave MOE = DEN × VEL^2 (Wang et al. 2001). Stress wave velocity is also referred to as acoustic velocity. The transverse vibration and stress wave techniques have been widely adopted by the forest product industry, and tools that measure stress wave velocity have been developed that allow foresters to estimate the MOE of logs and standing trees in the field. The Director HM200 (Fibre-gen, Christchurch, New Zealand; www.fibre-gen.com) can be used to estimate the stiffness of logs, whereas the Director ST300 (Fibre-gen) can be used to estimate the stiffness of standing trees (Carter et al. 2005). Because stress wave velocity and stress wave MOE are highly correlated with bending stiffness, the HM200, ST300, and related tools provide new opportunities to improve bending stiffness via stand management, log sorting, and tree breeding (Cherry et al. 2008; Kumar et al. 2006; Roth et al. 2007).

In addition to the methods described above, MOE can be estimated at a finer scale using the SilviScan system (Evans and Ilic 2001). Studies on lumber and small clearwood samples (e.g., small samples with no knots or defects) suggest that MOE estimated using SilviScan can explain much of the variation in bending MOE (Lachenbruch et al. 2010; Raymond et al. 2007). In addition to MOE, SilviScan can be used to estimate microfibril angle and wood density.

Stress wave MOE and wood density were found to be moderately to highly heritable in a study of 39 wind-pollinated families of Douglas-fir grown at four locations in the Pacific Northwest (Johnson and Gartner 2006), suggesting that breeders can select for stress wave MOE or velocity to improve wood stiffness. However, bending MOE was not measured, so it was impossible to directly estimate genetic gains in bending MOE, which is the target trait. Cherry et al. (2008) subsequently studied stress wave MOE and bending MOE in Douglas-fir to determine whether the HM200 and ST300 could be used to genetically improve bending stiffness. Bending MOE was moderately heritable and had a strong genetic correlation with stress wave MOE measured with the HM200. Cherry et al. (2008) concluded that the HM200 could be used to genetically improve bending stiffness, but gains would be lower using the ST300 on standing trees. In this paper, we describe additional properties of the 2 × 4s studied by Cherry et al. (2008). Because wood density, MFA, and knots have important effects on wood stiffness (Cown et al. 1999; Evans and Ilic 2001; Ifju and Kennedy 1962; Yang and Evans 2003), we studied these traits, as well as lumber grade. Our specific objectives were to (*i*) compare genetic parameters of direct (static bending) and indirect (transverse vibration) estimates of wood stiffness, (*ii*) evaluate the genetic and (or) phenotypic relationships among wood stiffness traits, wood density, MFA, and knots, and (*iii*) determine whether visual grades of Douglas-fir lumber differ in wood properties.

Materials and methods

Plant materials

We studied the properties of logs and lumber harvested from a 25-year-old (from seed) wind-pollinated progeny test in northwestern Washington State (for details, see Cherry et al. 2008). Parent trees were organized into four sets (groups) based on their geographic origin, and their progeny were planted in 1982 and 1983 at a spacing of 3.05 × 3.05 m at three locations. At each planting location, each set of 30–40 families (total of 130 families) was planted as a separate adjacent experiment with eight replications of four trees per family in noncontiguous plots. This paper focuses on the trees harvested from the Shine test plantation (47°52′N, 122°41.7′W, 122 m above sea level). After traits were measured in the field, the plantation was thinned in September 2005, and eight trees from each of 50 families (four sets × 12–13 families per set) were selected for milling into lumber, excluding trees with questionable identity or poor stem form. Of the original 400 trees selected, 383 were milled into lumber and analyzed.

Measurements

Measured traits are summarized in Table 1. We measured stem diameter at breast height (DBH) in 2005 before thinning. On the trees chosen for milling (mill trees), we measured stress wave velocity near breast height using the ST300 (VEL_{ST}). Three velocity measurements were recorded on opposite sides of each tree (i.e., six measurements per tree), and

Table 1. Wood properties of Douglas-fir logs, 2 × 4s, and small clearwood samples harvested from a 25-year-old wind-pollinated progeny test of Douglas-fir.

	Mean value or percentage in class			
Abbreviation	Logs	2 × 4s	SilviScan 2 × 4 subset	Description
Stiffness (modulus of elasticity (MOE)) (GPa)				
MOE_B	10.9	10.8	11.2	Static bending MOE measured on 2 × 4s
$AMOE_B$	11.0	10.9	11.2	MOE_B adjusted for ring age and ring orientation
MOE_{TV}	9.7	9.8	10.1	Transverse vibration MOE measured on 2 × 4s
MOE_{HM}	9.5	—	—	HM200 MOE of green logs
MOE_{ST}	12.5	—	—	ST300 MOE of standing trees
MOE_{SC}	—	—	12.5	MOE of small clearwood samples estimated using SilviScan
Density (kg·m^{-3})				
DEN_{GD}	822.9	—	—	Green wood density of wood discs
DEN_{BD}	477.1	—	—	Basic wood density of wood discs
DEN_L	477.4	476.4	484.1	Air-dried density of lumber
$ADEN_L$	478.3	476.3	483.5	Air-dried density of lumber adjusted for ring age
DEN_{SC}	—	—	503.4	Air-dried density of small clearwood samples
Stress wave (acoustic) velocity (m·s^{-1})				
VEL_{HM}	3392	—	—	HM200 velocity measured on green logs
VEL_{ST}	3872	—	—	ST300 velocity measured on standing trees
Knots (mm or number)				
KNT_{EDG} (mm)	15.9	15.9	14.0	Diameter of the largest edge knot on a 2 × 4 (average of two faces)
KNT_{CNT} (mm)	17.4	17.8	19.3	Diameter of the largest center knot on a 2 × 4 (average of two faces)
KNT_{TOT} (no.)	6.7	6.8	6.8	Number of knots on a 2 × 4 greater than 12.7 mm (average of two faces)
Diameter growth (cm)				
DBH	22.1	—	—	Stem diameter at breast height
Other lumber properties				
MC (%)	73.6	—	—	Moisture content of basal wood discs
Ring age (years)	8.8	9.1	9.3	Average ring age of the 2 × 4
Ring orientation (class)	—	R = 18.0% T = 79.2 D = 2.8	R = 0% T = 100 D = 0	Ring orientation (R, radial; T, tangential; D, diagonal) of the 2 × 4 in relation to the bending load (Fig. 1)
Microfibril angle (degrees)				
MFA_{SC}	—	—	14.1	Microfibril angle of small clearwood samples estimated using SilviScan

Note: Log values (n = 282–373) were derived from the corresponding values measured on 2 × 4s (n = 1281–1383). Small clearwood samples were collected from a subset of the 2 × 4s (SilviScan subset = 3 samples from each of 56–58 2 × 4s).

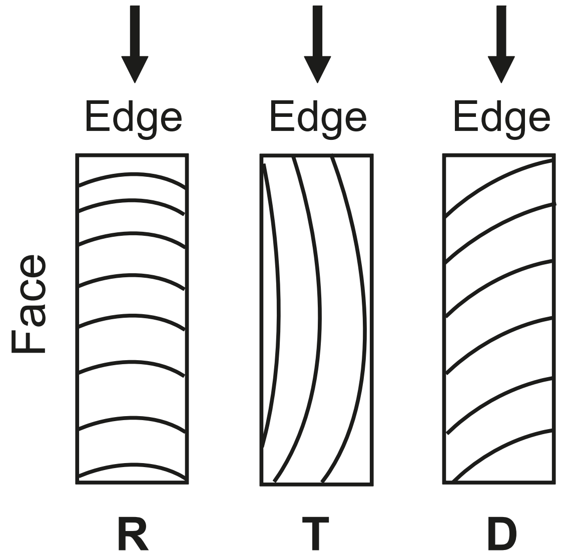
these were later averaged to get a single estimate per tree. After the trees were felled, the mill trees were delimbed, a wood disc about 5 cm thick was cut from the base of each tree, the basal log was bucked to a length of ~2.7 m, and stress wave velocity was measured using the HM200 (VEL_{HM}). We used debarked wood discs to measure green wood density (DEN_{GD} = green mass/green volume). The wood discs were kiln-dried to <7% moisture content (MC), and basic wood density was estimated for each disc (DEN_{BD} = dry mass/green volume). Stress wave MOE (GPa) was calculated according to eq. 1, using either VEL_{ST} (for MOE_{ST}) or VEL_{HM} (for MOE_{HM}):

$$[1] \qquad MOE = VEL^2 \times DEN_{GD} \times 10^{-9}$$

The logs were milled into 2 × 4s (~3.8 × 8.9 × 274 cm; ~1.5 × 3.5 × 108 in.) using a portable sawmill (model LT40, Wood-Mizer Products Inc., Indianapolis, Indiana). The 2 × 4s (1 to 10 per tree) were left unplaned, kiln-dried to <7% MC, cut to a length of 213 cm, and then arranged to reconstruct the log. The average ring age of each 2 × 4 was estimated as the mean of the youngest and oldest rings. We also categorized each 2 × 4 into one of three ring orientation classes based on the orientation of the annual rings in relation to the applied load used to measure stiffness (Fig. 1). Because the load was applied to the (3.8 cm) edge of the 2 × 4, the radial (R) and tangential (T) classes consisted of 2 × 4s with rings that were roughly parallel (radial) or perpendicular (tangential) to the edge of the 2 × 4 (Fig. 1). The 2 × 4s that did not fall into one of these two classes were classified as diagonal (D). This resulted in 242 radial, 1067 tangential, and 38 diagonal 2 × 4s for testing.

We measured the edge and face dimensions of each 2 × 4 at both ends and at mid-span, and then calculated the air-

Fig. 1. Ring orientation classes of the 2 × 4s relative to the applied load used to measure bending MOE. Orientation: R, radial; T, tangential; D, diagonal.



dried density (DEN_L) as mass/volume. We counted all knots greater than 1.3 cm in diameter (KNT_{TOT}) and measured the sizes of the largest edge (KNT_{EDG}) and center (KNT_{CNT}) knots on the faces of each 2 × 4. Edge knots are knots that intersect any edge of the 2 × 4, whereas center knots are all other knots. The data for each knot trait were then averaged across both faces.

We measured MOE_B (GPa) on all 2 × 4s according to ASTM D198-05 (ASTM International 2005). A 40 kip MTS Universal Testing Machine (model 332.21, MTS Systems Corporation, Minneapolis, Minnesota) was used for the four-point bending test (third-point loading) at the wood engineering laboratory of Oregon State University as described by Cherry et al. (2008). When relevant, the 2 × 4s were oriented with the pith toward the bottom of the 2 × 4 (i.e., opposite the load).

The transverse vibration technique was used to estimate MOE_{TV} using a Metriguard E-computer (model 340, Metriguard Inc., Pullman, Washington). The 2 × 4 was supported by two tripods and then set into vibration by tapping the 2 × 4 once with a hammer at mid-span. MOE^*_{TV} was calculated (in psi) according to the following equation using the manufacturer's (Metriguard Inc.) software:

[2] $$MOE^*_{TV} = \frac{wL^3f^2}{Kbh^3}$$

where w is the weight of the 2 × 4 (lb), L is the span length (in.), f is the undamped vibration frequency (Hz), b is the standard 2 × 4 face dimension (3.5 in.), h is the standard 2 × 4 edge dimension (1.5 in.), and K is the internal calibration constant. MOE_{TV} was calculated by including the actual 2 × 4 dimensions and then converting to GPa by multiplying by 6.895×10^{-6}:

[3] $$MOE_{TV} = \frac{11.813 \times MOE^*_{TV}}{bh^3} \times 6.895 \times 10^{-6}$$

where b and h are the actual 2 × 4 face and edge dimensions (in inches).

We measured microfibril angle (MFA), density, and MOE of small clearwood samples taken from a subset of families and 2 × 4s. We selected 60 2 × 4s with MOE_B values ranging from 7.5 to 15.0 GPa with the following constraints. Because MOE_B and DEN_{BD} were significantly correlated with ring age and ring orientation, we first selected all 2 × 4s with a mean ring age between 9.0 and 9.5 years and a tangential ring orientation. We then selected 30 families from which we could select at least two 2 × 4s that had been milled from separate logs (60 logs = 60 2 × 4s). Therefore, our final set of 2 × 4s consisted of two 2 × 4s from each of 30 families. Three small clearwood samples (15.0 × 15.0 × 38.1 mm) were cut from the top end of each 2 × 4 using a band saw, resulting in 180 samples that were used to measure MFA via X-ray diffractometry (MFA_{SC}) (SilviScan-3, CSIRO, Clayton, Australia). Wood density (DEN_{SC}) was measured gravimetrically from mass and volume, and average stiffness (MOE_{SC}) was predicted as $MOE_{SC} = A(I_{CV}DEN_{SC})^B$, where I_{CV} is the coefficient of variation of the azimuthal intensity profile (~0 to ~1) obtained from X-ray diffraction, and A and B are constants that depend on the SilviScan experimental conditions (Evans 2006). To reduce measurement error, we averaged the values for the three samples to get a single estimate of MFA_{SC}, DEN_{SC}, and MOE_{SC} for each 2 × 4. All 2 × 4s were visually graded into select structural (STR), No. 1 (S1), No. 2 (S2), No. 3 (S3), and economy (E) by a professional lumber inspector using the National Grading Rule for coastal Douglas-fir dimensional lumber (West Coast Lumber Inspection Bureau 1995). The single 2 × 4s in the S3 and E grades were excluded from further analyses.

Statistical analyses

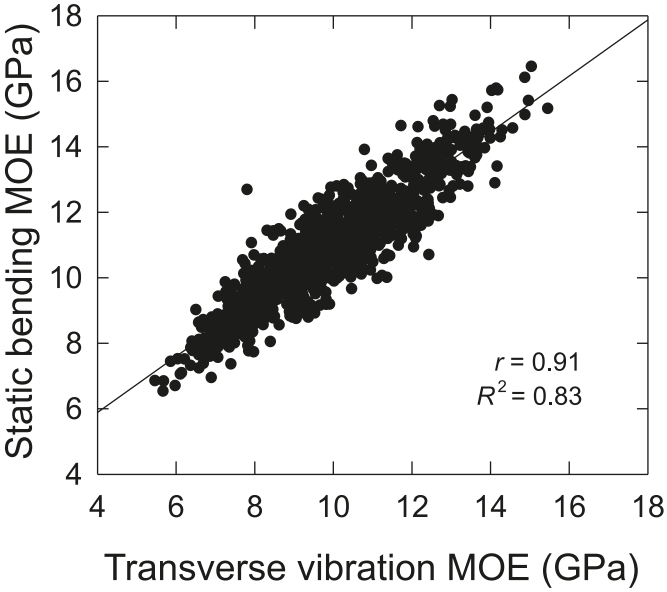
During the analyses, we removed outliers and checked for normality and homoskedasticity of residuals as described by Cherry et al. (2008). We then conducted genetic analyses at the log level (i.e., using 2 × 4 means) using the SAS Mixed Procedure and the following linear model:

[4] $$Y_{srfl} = \mu + S_s + R(S)_{sr} + F(S)_{sf} + R \times F(S)_{srf} + \varepsilon_{srfl}$$

where Y_{srfl} is the observation for log l of family f in replication r in set s; μ is the overall mean; S_s is the random effect of set s with variance σ^2_S; $R(S)_{sr}$ is the random effect of replication r in set s with variance $\sigma^2_{R(S)}$; $F(S)_{sf}$ is the random effect of family f in set s with variance $\sigma^2_{F(S)}$; $R \times F(S)_{srf}$ is the random interaction effect between family f and replication r in set s with variance $\sigma^2_{R \times F(S)}$; and ε_{srfl} is the residual error. We also analyzed MOE_B and DEN_L of individual 2 × 4s with and without ring age and ring orientation as covariates. MOE_B was significantly associated with ring age and ring orientation, whereas lumber density was significantly associated with ring age. Using the results from the analyses of covariance, MOE_B and DEN_L were adjusted to a mean ring age of 9.1 years and a tangential ring orientation (eqs. 5 and 6):

[5] $$AMOE_B = MOE_B + (0.272 \times D) + (0.367 \times R) + 0.229 \times (9.112 - \text{ring age})$$

Fig. 2. Relationship between static bending MOE (MOE_B) and transverse vibration MOE (MOE_{TV}) measured on 2 × 4s harvested from a 25-year-old Douglas-fir progeny test.



$$\text{[6]} \quad \mathrm{ADEN}_L = \mathrm{DEN}_L + 3.467 \times (9.112 - \text{ring age})$$

where $D = 1$ if ring orientation is diagonal and 0 otherwise; $R = 1$ if ring orientation is radial and 0 otherwise; and ring age is the mean ring age of the 2 × 4. Individual-tree narrow-sense heritabilities were estimated as

$$h_i^2 = \frac{3\sigma^2_{F(S)}}{\sigma^2_{F(S)} + \sigma^2_{R\times F(S)} + \sigma^2_{\varepsilon}}$$

where $\sigma^2_{F(S)}$, $\sigma^2_{R\times F(S)}$, and σ^2_{ε} are variance components estimated using model 7, and additive genetic correlations (r_A) were estimated as described by Cherry et al. (2008).

We used the SAS Corr Procedure to study the linear relationships between pairs of traits, regression analysis and the BIC to select models for predicting MOE_B, and path analysis to decompose the correlation coefficients into their direct and indirect components (Li 1975). We used analyses of variance and Tukey's studentized range test (HSD) to determine whether MOE_B, DEN_L, and KNT_{EDG} differed among lumber grades.

Results and discussion

Phenotypic correlations among wood stiffness traits

Transverse vibration, stress wave velocity, and static bending often produce different estimates of MOE, and this has been attributed to differences in sensitivity to moisture content, shear, growth ring orientation, and the presence of knots (Gerhards 1975; Halabe et al. 1997; Lindström et al. 2002; Raymond et al. 2007; Ross et al. 1999). Nonetheless, MOE_{TV} was highly correlated with MOE_B, indicating that transverse vibration MOE is a good indirect measure of Douglas-fir bending stiffness. The phenotypic correlation between these traits was 0.91 (R^2 = 83%) on both a lumber and log basis (Fig. 2; Table 2). This relationship was stronger (R^2 = 85% to 98%) in some other softwoods (Ross and Pellerin 1994; Wang et al. 2001) and weaker in southern pine species (r_p = ~0.84; R^2 = 70%) (Halabe et al. 1997). These differences may have a biological basis or may result from differences in the range of variation in the measured traits.

Because MOE_B and MOE_{TV} are too costly to measure in large breeding programs, other methods for estimating bending MOE (e.g., stress wave velocity and wood density) have been studied and appear to be valuable for genetically improving wood stiffness in Douglas-fir (Cherry et al. 2008; Johnson and Gartner 2006). Among the field traits, MOE_{HM} had the highest correlation with MOE_B (r_p = 0.65; R^2 = 42%), followed by VEL_{HM}, DEN_{BD}, MOE_{ST}, DEN_{GD}, and VEL_{ST} (Table 3). These correlations were only slightly weaker using MOE_{TV}.

Briggs et al. (2008) studied the relationships between the MOE of Douglas-fir lumber (transverse vibration) and stress wave velocity of logs (HM200) and trees (TreeSonic). In their study, the R^2 value for the relationship between log velocity (HM200) and lumber MOE (59%) was much stronger than the analogous relationship that we observed (R^2 = 29% between VEL_{HM} and MOE_{TV}). Briggs et al. (2008) also observed a higher R^2 value (42%) for the relationship between tree velocity (TreeSonic) and lumber MOE than the analogous relationship that we observed between VEL_{ST} and MOE_{TV} (R^2 = 11%). Their trees had more variation in MOE, which may account for their larger R^2 values. Therefore, results from the current and previous studies suggest that stress wave velocity and wood density explain only modest amounts of variation in bending stiffness at the individual tree level. However, because genetic correlations are generally higher than phenotypic correlations (see below), measurements of stress wave velocity and wood density should be useful for genetically improving wood stiffness.

Other studies also suggest that the HM200 is better than standing-tree tools for estimating wood stiffness. The HM200 performed better than the TreeSonic and much better than the ST300 for estimating the stiffness of Douglas-fir lumber and veneer (Amishev and Murphy 2008*a*, 2008*b*; Briggs et al. 2008). Log assessment tools are believed to be inherently more precise because they sample more wood (i.e., whole log versus the outerwood), sample both heartwood and sapwood, estimate stress wave velocity from resonant frequencies rather than time-of-flight (TOF), may be less affected by knots, can more easily sample above the highly variable zone of low-stiffness wood near the base of the tree, and are easier to use (Amishev and Murphy 2008*b*; Carter et al. 2005). However, the precision of standing-tree tools may be increased by increasing the distance between the probes, taking many measurements per tree, and adjusting for the TOF wave form and tree DBH (Mora et al. 2009; Wagner et al. 2003). In contrast to the modest (TreeSonic) or weak (ST300) relationships discussed above, correlations between standing-tree measurements and bending stiffness were sometimes stronger in other species (Mora et al. 2009).

Wood stiffness is phenotypically correlated with wood density, MFA, and knots

Wood density, MFA, and knots affect wood stiffness (Cown et al. 1999; Evans and Ilic 2001; Ifju and Kennedy 1962; Yang and Evans 2003). Therefore, we used 2 × 4s to study the relationships between wood stiffness, density, and

Table 2. Phenotypic correlations between wood properties of Douglas-fir 2 × 4s (above the diagonal) and logs (below the diagonal) using the full 2 × 4 data set (1281–1383 2 × 4s from 282–373 logs).

Trait	MOE_B	$AMOE_B$	MOE_{TV}	DEN_L	$ADEN_L$	KNT_{EDG}	KNT_{CNT}	KNT_{TOT}	Ring age
MOE_B	—	0.89	0.91	0.67	0.57	–0.21	0.11	0.02ns	0.42
$AMOE_B$	0.96	—	0.74	0.63	0.66	–0.15	–0.05ns	–0.06	–0.04ns
MOE_{TV}	0.91	0.86	—	0.69	0.56	–0.14	0.19	0.07	0.51
DEN_L	0.67	0.66	0.71	—	0.96	0.02ns	0.12	0.09	0.23
$ADEN_L$	0.65	0.68	0.69	1.00	—	0.07	0.02ns	0.05ns	–0.06
KNT_{EDG}	–0.12	–0.09ns	–0.06ns	0.05ns	0.07ns	—	0.16	0.27	–0.14
KNT_{CNT}	–0.10ns	–0.12	–0.02ns	–0.01ns	–0.01ns	0.43	—	0.47	0.33
KNT_{TOT}	–0.07ns	–0.08ns	–0.02ns	0.01ns	0.01ns	0.34	0.55	—	0.14
Ring age	0.12	–0.13	0.18	0.04ns	–0.09ns	–0.09ns	0.09ns	0.03ns	—

Note: All traits were measured on 2 × 4s, and log means were then calculated from the corresponding 2 × 4 values. All correlations are significant at $p < 0.05$ except where indicated by ns. Traits are described in Table 1.

Table 3. Phenotypic correlations between wood properties of Douglas-fir logs measured in the laboratory or in the field.

	Traits measured in the field							
Trait	MOE_{HM}	MOE_{ST}	VEL_{HM}	VEL_{ST}	DEN_{GD}	DEN_{BD}	MC	DBH
Laboratory traits (2 × 4s)								
MOE_B	0.65	0.45	0.57	0.35	0.42	0.50	–0.24	–0.13
$AMOE_B$	0.66	0.46	0.58	0.38	0.40	0.51	–0.27	–0.24
MOE_{TV}	0.59	0.41	0.54	0.33	0.37	0.46	–0.23	0.02ns
DEN_L	0.46	0.38	0.38	0.28	0.38	0.60	–0.41	–0.05ns
$ADEN_L$	0.46	0.38	0.39	0.29	0.37	0.60	–0.43	–0.10ns
KNT_{EDG}	–0.07ns	–0.05ns	0.02ns	0.00ns	–0.12	–0.02ns	–0.10ns	0.08ns
KNT_{CNT}	–0.09ns	–0.09ns	–0.05ns	–0.08ns	–0.09ns	–0.05ns	–0.03ns	0.34
KNT_{TOT}	–0.09ns	0.01ns	0.00ns	0.06ns	–0.10ns	–0.01ns	–0.08ns	0.08ns
Ring age	–0.01ns	–0.04ns	–0.08ns	–0.10ns	0.11ns	–0.01ns	0.11ns	0.37
Field traits								
MOE_{HM}	—	0.59	0.89	0.40	0.58	0.57	–0.17	–0.30
MOE_{ST}	0.59	—	0.39	0.90	0.55	0.52	–0.15	–0.31
VEL_{HM}	0.89	0.40	—	0.41	0.15	0.33	–0.28	–0.21
VEL_{ST}	0.40	0.90	0.41	—	0.14	0.29	–0.25	–0.26
DEN_{GD}	0.58	0.55	0.15	0.14	—	0.65	0.16	–0.30
DEN_{BD}	0.57	0.52	0.33	0.29	0.65	—	–0.65	–0.23
MC	–0.17	–0.15	–0.28	–0.25	0.16	–0.65	—	0.00ns
DBH	–0.30	–0.31	–0.21ns	–0.26	–0.30ns	–0.23	0.00ns	—

Note: Laboratory traits are the log means for traits measured on the full 2 × 4 data set (1281–1383 2 × 4s from 282–373 logs). Field traits were measured on standing trees, logs, or wood discs collected in the field. All correlations are significant at $p < 0.05$ except where indicated by ns. Traits are described in Table 1.

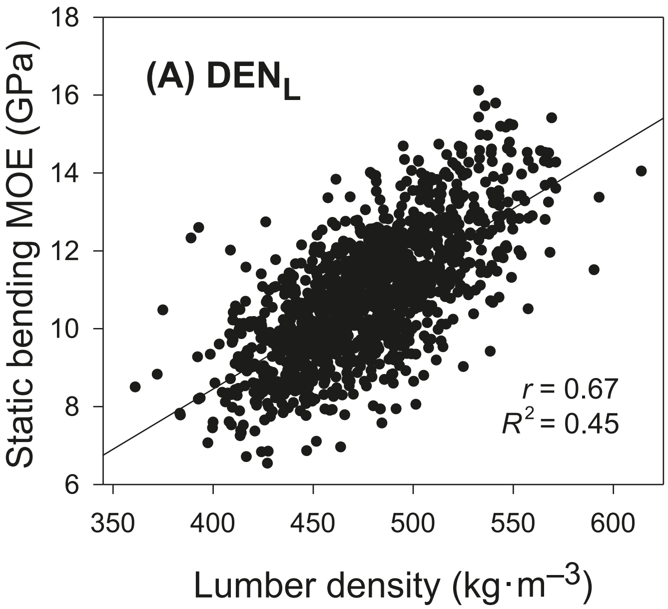
knots and small clearwood specimens to study the associations between stiffness, density, and MFA.

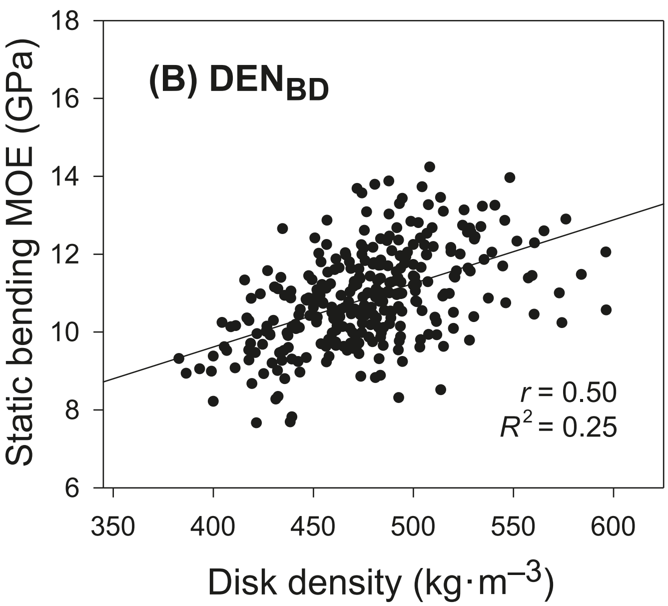
Wood density was positively correlated with bending stiffness

Using the full data set (i.e., all 2 × 4s), the phenotypic correlation between lumber density (DEN_L) and MOE_B was 0.67 on both a log and lumber basis (Table 2; Fig. 3). In the 2 × 4 subset, this correlation was 0.70 (not shown) and nearly the same as the correlation between DEN_{SC} and MOE_B (r_p = 0.73) (Table 4). These correlations are roughly comparable with the correlations between bending MOE and density in another study of small clearwood samples collected from 183 Douglas-fir trees (Lachenbruch et al. 2010). In that study, the correlation between MOE and density ranged from 0.59 on an individual-specimen basis to 0.76 on a tree basis. The correlation between bending MOE (small clears) and density (r_p = 0.44) was smaller for 60 Douglas-fir trees growing in New Zealand, but this is not surprising because density was measured on 5 mm outerwood cores (Knowles et al. 2004). In contrast, the correlations were larger (0.75–0.94) when lumber or small clears were used to estimate the bending MOE and wood density of 18 Douglas-fir trees (Knowles et al. 2003). Although MOE_B was moderately correlated with lumber density (DEN_L; r_p = 0.67), Cherry et al. (2008) previously noted that the phenotypic correlation between MOE_B and basal disc density (DEN_{BD}) was only 0.50 (Table 3; Fig. 3), perhaps because the wood discs were collected from an atypical part of the tree (Amishev and Murphy 2008*b*) and included outerwood that was not sampled by the rectangular 2 × 4s. The correlation between MOE_B and DEN_L was probably higher because both traits were measured on the same 2 × 4.

Cherry et al. (2008) questioned whether breeders should measure and select for wood density because (*i*) predicted gains in bending stiffness increased only a modest amount

Fig. 3. Relationships between static bending MOE (MOE_B) and densities measured on 2 × 4s and discs harvested from a 25-year-old Douglas-fir progeny test: (A) air-dried lumber density (DEN_L); (B) basic density of wood discs (DEN_{BD}).





when selection was based on MOE_{HM} (DEN_{GD} × VEL_{HM}^2) rather than VEL_{HM}, (*ii*) wood density has a negative genetic correlation with growth, and (*iii*) wood density is expensive to measure on increment cores, which is the method of choice for measuring wood density in Douglas-fir breeding programs. Nonetheless, the correlation between density and stiffness may be stronger using breast-height discs or increment cores rather than the basal wood discs that we used. In any case, the density of lumber, basal discs, or small clears explained less than 52% of the phenotypic variation in MOE_B at the individual-tree level.

MFA was negatively correlated with bending stiffness

On a lumber basis, MFA_{SC} had a moderate negative phenotypic correlation with MOE_B (r_p = –0.42), which is slightly weaker than the correlations observed in other studies of Douglas-fir (r_p = –0.50 to –0.58; Knowles et al. 2003; Lachenbruch et al. 2010). The correlation between MFA and bending stiffness in Douglas-fir was generally weaker than in radiata pine (–0.45 to –0.82; Downes et al. 2002; Raymond et al. 2007), loblolly pine (–0.71; Bendtsen and Senft 1986), red pine (–0.68; Deresse et al. 2003), eastern cottonwood (–0.62; Bendtsen and Senft 1986), and *Eucalyptus* spp. (–0.93; Yang and Evans 2003). These negative correlations are expected from the negative mechanistic association that exists between MFA and axial stiffness of the cell wall (Cave 1968).

MOE increased five- to six-fold in radiata pine and loblolly pine when MFA decreased from about 40° to 10°, and this decrease was associated with increasing ring age (Bendtsen and Senft 1986; Cave 1968). Our variation in MFA_{SC} (9.2° to 21.6°) was modest because we selected small clearwood samples from 2 × 4s that had an average ring age of only 9.0 to 9.5 years. In studies of mostly older Douglas-fir (17 to 49 years old), the variation in MFA (9.4° to 24.2°; Lachenbruch et al. 2010) and the correlation between MFA and the stiffness of small clears (–0.50 to –0.58) were also modest (Knowles et al. 2003; Lachenbruch et al. 2010).

Earlier studies on radial variation of Douglas-fir MFA using polarized light microscopy and the pit aperture method yielded more variation in MFA than we observed (~10° to ~30°; Erickson and Arima 1974; Ifju and Kennedy 1962), but correlations between stiffness and MFA were not reported. Based on our analysis, MFA_{SC} explained only 17% of the phenotypic variation in 2 × 4 MOE_B compared with 49%–52% for DEN_L and DEN_{SC} (from correlations in Table 4). Density was also much better than MFA for predicting bending stiffness in other studies of Douglas-fir. In Oregon, the R^2 was 34% to 45% for wood density compared with 25% for MFA (Lachenbruch et al. 2010). In New Zealand, the R^2 was 79% to 88% for wood density compared with 31% to 34% for MFA (Knowles et al. 2003). Although MFA was not strongly associated with bending stiffness in our samples (which were chosen to minimize variation in vertical tree position and ring age), the correlation between MFA and bending stiffness may be stronger in a more diverse set of samples (e.g., samples with younger and older ring ages) with greater variation in MFA.

Although the correlation between MFA_{SC} and MOE_B was only moderate (r_p = –0.42), the correlation between MFA_{SC} and MOE_{SC} was strong (r_p = –0.87; Table 4). Strong correlations between SilviScan MFA and SilviScan MOE have been reported (Baltunis et al. 2007; Knowles et al. 2003) but overestimate the true correlation between MFA and bending stiffness because of autocorrelation (i.e., both traits are predicted using X-ray diffraction data). The correlations between MFA and density traits were weakly to moderately negative in our study (Table 4) and in two other studies of Douglas-fir (Knowles et al. 2003; Lachenbruch et al. 2010).

Knots were weakly correlated with bending stiffness

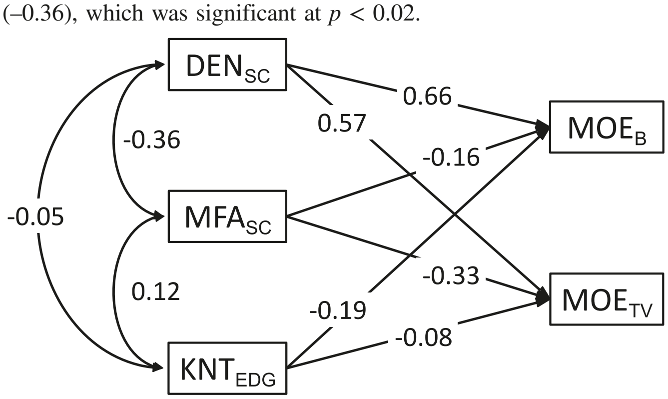
On a lumber and log basis, MOE_B had a weak negative correlation with KNT_{EDG} (r_p = –0.21 and –0.12), weak positive or nonsignificant correlation with KNT_{CNT} ($|r_p| \leq 0.11$), and no significant phenotypic correlation with KNT_{TOT} (Ta-

Table 4. Phenotypic correlations between wood properties for the subset of 2 × 4s (n = 56–58) used to measure microfibril angle (MFA).

	Small clears			2 × 4s				Trees, logs, or wood discs				
Trait	MOE_{SC}	MFA_{SC}	DEN_{SC}	MOE_B	MOE_{TV}	DEN_L	KNT_{EDG}	MOE_{HM}	VEL_{HM}	DEN_{GD}	DEN_{BD}	MC
Correlations among logs (one 2 × 4 per log)												
MOE_{SC}	—	–0.87	0.73	0.67	0.74	0.63	–0.15ns	0.42	0.45	0.22ns	0.17ns	0.01ns
MFA_{SC}	–0.87	—	–0.36	–0.42	–0.55	–0.30	0.12ns	–0.34	–0.24ns	–0.18ns	0.06ns	–0.24ns
DEN_{SC}	0.73	–0.36	—	0.72	0.70	0.86	–0.05ns	0.29ns	0.48	0.15ns	0.44	–0.37
Correlations among family means (two logs per family, one 2 × 4 per log)												
MOE_{SC}	—	–0.92	0.81	0.77	0.84	0.64	0.03ns	0.55	0.59	0.26ns	0.29ns	–0.10ns
MFA_{SC}	–0.92	—	–0.58	–0.62	–0.73	–0.42	0.02ns	–0.52	–0.46	–0.30ns	–0.18ns	–0.08ns
DEN_{SC}	0.81	–0.58	—	0.81	0.78	0.83	0.05ns	0.27	0.50	0.08ns	0.25ns	–0.25ns

Note: "Small clear" variables are the mean values from three small clearwood samples from each 2 × 4; "2 × 4" variables are measurements made on one 2 × 4 per log; and the remaining variables were measured on standing trees, logs, or basal wood discs. Family mean correlations were estimated using two logs per family, and one 2 × 4 per log. All correlations are significant at p < 0.05 except where indicated by ns. Traits are described in Table 1.

Fig. 4. Path diagram showing the relationships between selected wood properties (DEN_{SC}, MFA_{SC}, and KNT_{EDG}) and direct and indirect measures of stiffness of 2 × 4s harvested from a 25-year-old Douglas-fir progeny test. All path coefficients (i.e., straight-line relationships between traits) were significant at p < 0.0001. All correlation coefficients (i.e., curved-line relationships) were nonsignificant, except the correlation between DEN_{SC} and MFA_{SC} (–0.36), which was significant at p < 0.02.



ble 2). Knots lower lumber stiffness because they cause deviations from optimal grain orientation, concentrate stress, and often increase checking during drying (Megraw 1986). Negative associations between knot traits and stiffness have also been found in spruce and pine (Beaulieu et al. 2006; Samson and Blanchet 1992; Xu 2002).

Although one of the knot traits (KNT_{EDG}) was consistently correlated with stiffness, the correlation was weak, presumably because the knots were small and few. The largest knot was only 47 mm in diameter, and the average sizes of KNT_{EDG} and KNT_{CNT} were below 18 mm. Furthermore, there were only about seven knots per 2 × 4. In white spruce lumber, the correlation between knot size (mean = 17 mm) and bending MOE was moderately negative (r_p = –0.40; Beaulieu et al. 2006), and the correlation between the number of knots and bending MOE was significant but low (r_p = –0.21). The effects of knots may have been greater in white spruce because the spruce lumber seemed to have many more knots (38 knots per board >10 mm) than we found in our 2 × 4s (seven knots > 12.7 mm). In contrast to progeny tests that are planted on a uniformly spaced grid, variation in spacing is expected to be much larger in operational plantations and naturally regenerated stands. Because variation in spacing should lead to greater variation in knot size, the correlations between knot traits and stiffness may be stronger in these stands.

Combined effects of wood properties on bending stiffness

We used path analysis to partition the correlations between MOE_B and wood density, MFA, knots, and tree diameter into their direct and indirect components. Path analysis is an extension of multiple linear regression that accounts for the covariance between independent variables before the strength of relationships with the dependent variable (MOE_B) are estimated via path coefficients. Our main objective was to provide information for deciding which traits to include in breeding programs for wood stiffness. A secondary objective was to develop operationally useful equations for predicting bending stiffness from other wood properties using multiple regression. These analyses were conducted at both the 2 × 4 and log levels.

Examples of two path diagrams are shown in Fig. 4. This figure shows the direct and indirect relationships between stiffness (MOE_B or MOE_{TV}) and DEN_{SC}, MFA_{SC}, and KNT_{EDG}. Focusing on DEN_{SC}, these analyses indicate that density had the greatest direct effect on both MOE_B (0.66) and MOE_{TV} (0.57) (Fig. 4; Table 5). For MOE_B, KNT_{EDG} had the second greatest effect (–0.19), and the effect of MFA_{SC} was nonsignificant (–0.16). In contrast, these effects were reversed for MOE_{TV}: MFA_{SC} had the second greatest effect (–0.33), and the effect of KNT_{EDG} was nonsignificant (–0.08). Therefore, transverse vibration tests apparently underestimate the negative effects of knots and inflate the relative importance of MFA on bending stiffness. The results were essentially the same when we analyzed DEN_L (2 × 4 density) instead of DEN_{SC}, and taken together, the adjusted R^2 of these models ranged from 56% to 62%. Overall, these results indicate that density had a moderate direct effect on bending stiffness, whereas the effects of MFA and knots were smaller or nonsignificant.

At the log level, path analyses indicated that DBH had a small or nonsignificant direct effect on MOE_B (first set of models in Table 6). As expected, the model that included lumber density (DEN_L) was better than the model that included disc density (DEN_{BD}) (R^2 = 59% versus 46%) because lumber density and MOE_B were measured on the same 2 × 4s. In models that excluded DEN_{GD} and DBH, both wood density (DEN_{BD} or DEN_L) and VEL_{HM} had significant

Table 5. The 2 × 4-level path coefficients (paths) and regression coefficients (regressions) for predicting bending stiffness (MOE_B) from Douglas-fir wood density (DEN_L or DEN_{SC}), microfibril angle (MFA_{SC}), and edge knots (KNT_{EDG}).

Trait	Intercept (GPa)	DEN_{SC}/DEN_L (10^{-2} kg·m^{-3})	MFA_{SC} (10^{-2} degrees)	KNT_{EDG} (10^{-2} mm)	Adj. R^2 (%)
MOE_{bl} versus density, MFA, and knots					
Univariate correlation		0.723/0.699	–0.416	–0.243	
DEN_{SC} paths		0.657	–0.157ns	–0.191	
DEN_{SC} regressions	1.110	2.382	–8.263ns	–5.164	56
DEN_L paths		0.671	–0.180ns	–0.286	
DEN_L regressions	–0.424	2.903	–9.450ns	–7.745	59
MOE_{tv} versus density, MFA, and knots					
Univariate correlation		0.699/0.696	–0.550	–0.150	
DEN_{SC} paths		0.574	–0.334	–0.081ns	
DEN_{SC} regressions	1.605	2.305	–19.421	–2.429ns	58
DEN_L paths		0.607	–0.348	–0.167ns	
DEN_L regressions	–0.367	2.902	–20.213	–5.002ns	62

Note: All independent variables were measured on 2 × 4s, except for DEN_{SC} and MFA_{SC}, which are the means of three small clearwood samples per 2 × 4. Units for the regression coefficients are displayed below the variable names. All correlations and coefficients are significant at $p < 0.05$ except where indicated by ns. Adj. R^2, adjusted R^2. Traits are described in Table 1.

Table 6. Log-level path coefficients (paths) and regression coefficients (regressions) for predicting bending stiffness (MOE_B) from Douglas-fir wood density (DEN_{BD} or DEN_L, and DEN_{GD}), stress wave velocity (VEL_{HM}), and tree diameter (DBH).

	Intercept (GPa)	DEN_{BD}/DEN_L (10^{-2} kg·m^{-3})	DEN_{GD} (10^{-2} kg·m^{-3})	VEL_{HM} (10^{-2} m·s^{-1})	DBH (10^{-2} cm)	Adj. R^2 (%)
Univariate correlation		0.498/0.671	0.418	0.565	–0.125	
All log-level traits included						
DEN_{BD} paths		0.207	0.240	0.482	0.099	
DEN_{BD} regressions	–9.053	0.699	0.617	0.315	3.658	46
DEN_L paths		0.457	0.198	0.370	0.036ns	
DEN_L regressions	–10.317	1.779	0.508	0.242	1.318ns	59
Dry wood density and stress wave velocity included						
DEN_{BD} paths		0.350	—	0.450	—	
DEN_{BD} regressions	–4.770	1.181	—	0.295	—	43
DEN_L paths		0.533	—	0.364	—	
DEN_L regressions	–7.118	2.076	—	0.238	—	56

Note: All independent variables were measured on standing trees, logs, or basal wood discs, except for DEN_L, which are log means of values obtained from individual 2 × 4s. Units for the regression coefficients are displayed below the variable names. All correlations and coefficients are significant at $p < 0.05$ except where indicated by ns. Adj. R^2, adjusted R^2. Traits are described in Table 1.

direct effects on MOE_B, and the model that included only DEN_L and VEL_{HM} explained nearly as much variation as the model that included all log-level traits (R^2 = 56% versus 59%). Path analyses that used MOE_{TV} instead of MOE_B yielded the same general results.

Effects of ring age and ring orientation on wood stiffness and density

Both MOE_B and lumber density (DEN_L) were positively correlated with ring age (r_p = 0.42 and 0.23, respectively; Fig. 5). Wood stiffness also increased from pith to cambium in other studies of Douglas-fir, and this trend is consistent with a general decrease in MFA and increase in wood density (Erickson and Arima 1974; Ifju and Kennedy 1962; Knowles et al. 2003; Megraw 1986). We were unable to study the relationship between MFA and ring age, however, because the 2 × 4s that we used to analyze MFA were chosen to have a ring age of only 9.0 to 9.5 years.

MOE_B was also associated with the orientation of the growth rings in relation to the applied load (Fig. 1). MOE_B obtained by radial loading was significantly less than that obtained when the load was applied either tangentially or diagonally to the growth rings (Fig. 6). However, the 2 × 4s with tangentially or diagonally applied loads also had higher average ring ages (i.e., ring age = 9.6 and 11.7 years) than did the 2 × 4s that received the radially applied load (i.e., 6.4 years). Therefore, we also analyzed MOE_B using ring age as a covariate (Fig. 6). Although differences were smaller, this adjusted MOE_B was still significantly greater in the 2 × 4s with tangential orientation than in those with radial orientation (Fig. 6). In contrast to our findings, bending stiffness of small clearwood samples was not significantly different among ring orientation classes in a previous study of Douglas-fir (Grotta et al. 2005).

The correlation between lumber density (DEN_L) and ring age (r_p = 0.23) was weaker than the correlation between

Fig. 5. Relationships between (A) static bending MOE (MOE_B) and (B) air-dried lumber density (DEN_L) and ring age of 2 × 4s harvested from a 25-year-old Douglas-fir progeny test.

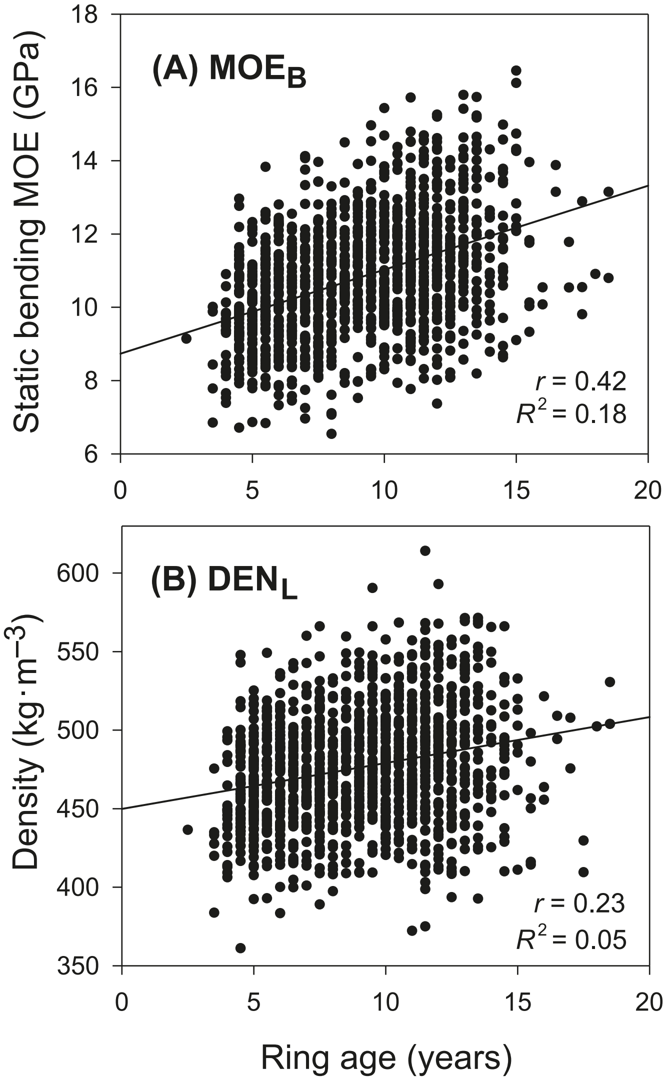
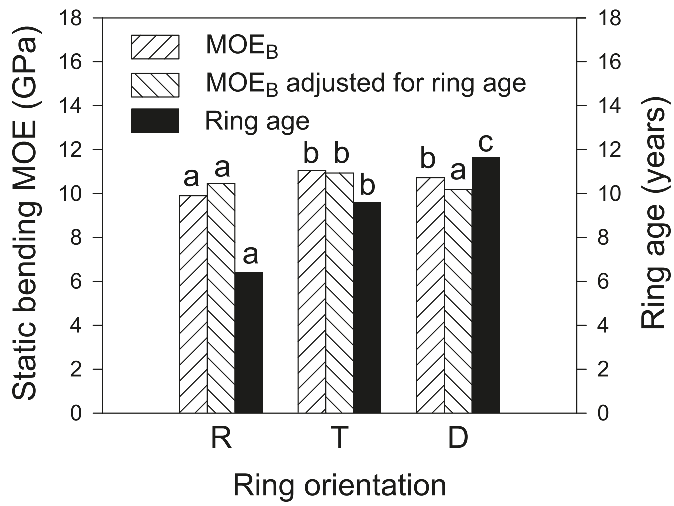


Fig. 6. Relationships between ring orientation (R, radial; T, tangential; D, diagonal) and static bending MOE (MOE_B), ring age, and MOE_B adjusted for ring age of 2 × 4s harvested from a 25-year-old Douglas-fir progeny test. Within each trait, ring orientation classes identified with the same letter are not significantly different at p = 0.05 using the Tukey–Kramer multiple comparison test.



MOE_B and ring age (r_p = 0.42), and DEN_L did not differ among ring orientation classes. Furthermore, the radial increase in wood density appeared to be less than the radial increase in stiffness in this study (Fig. 5) and in another study of Douglas-fir (Knowles et al. 2003). To account for the effects of ring age and ring orientation on stiffness and density, we adjusted MOE_B using ring age and ring orientation as covariates (= $AMOE_B$), and adjusted DEN_L using ring age as a covariate (= $ADEN_L$) (Table 7). Nonetheless, results from analyses of $AMOE_B$ and $ADEN_L$ were nearly identical to the results from analyses of MOE_B and DEN_L (Tables 2, 3, and 8).

Bending MOE and knots, but not density, were associated with lumber grade

Visual grading of structural lumber is designed to classify lumber based on the defects that affect the quality and value of lumber for structural purposes. These defects include knots, checks, shakes, splits, and warp. The STR grade is the best grade in terms of strength and appearance, followed by the S1 and S2 grades. Both MOE_B and MOE_{TV} differed among lumber grades, indicating that visual grading can be used to sort Douglas-fir lumber into classes that have small but significant (p < 0.0001) differences in wood stiffness. For example, the STR grade had a higher mean MOE_B (11.5 GPa) than either the S1 or S2 grades (10.5 and 9.6 GPa, respectively; Fig. 7). Because lumber graded as STR is often used when high stiffness is desired, our differences in MOE can be used to judge the design and monetary value of different lumber grades of Douglas-fir. Because we did not analyze 2 × 4s with splits, checks, or warps, the difference in average MOE among lumber grades probably reflects differences in knots and traits associated with ring width. The STR grade had a lower mean KNT_{EDG} (14.1 mm) than either the S1 or S2 grades (16.7 and 17.9 mm, respectively; Fig. 7). Unlike stiffness and knots, DEN_L did not differ among grades (p = 0.54).

Genetics of Douglas-fir wood quality

Previous studies of Douglas-fir indicated that bending MOE, stress wave traits, and wood density had moderate to high heritabilities and genetic correlations, suggesting that breeders can select for stress wave MOE, stress wave velocity, or wood density to achieve various levels of genetic improvement in wood stiffness (Cherry et al. 2008; Johnson and Gartner 2006). In particular, Cherry et al. (2008) reported that MOE_B and MOE_{HM} had individual-tree heritabilities of 0.31 and a high genetic correlation (0.92). Furthermore, relative efficiencies, the relative gains in MOE_B expected from selection for correlated traits, were 78%–93% for the HM200 traits, 57%–58% for the ST300 traits, 38% for the density of basal discs (DEN_{BD}), and 98% for the density of lumber (DEN_L) (Cherry et al. 2008).

The bending MOE data reported in Cherry et al. (2008) came from the experiments reported in this paper. From the

Table 7. Covariance parameter estimates for ring age and ring orientation in relation to bending load (R, radial; T, tangential; D, diagonal) in the analyses of MOE_B and DEN_L of lumber harvested from a 25-year-old wind-pollinated progeny test of Douglas-fir (standard errors are given in parentheses).

			Ring orientation*		
Trait	Intercept	Ring age	R	T	D
MOE_B	8.513 (0.14)	0.229 (0.01)	0.0 (nd)	0.367 (0.08)	0.095 (0.19)
DEN_L	446.20 (4.65)	3.467 (0.17)	ns	ns	ns

Note: Traits are described in Table 1.

*All fixed effects are significant at $p < 0.0001$ except where indicated by ns; nd indicates that the standard error was not determined.

Table 8. Genetic correlations between wood properties of 50 Douglas-fir families using the full 2 × 4 data set (1281–1383 2 × 4s from 282–373 logs).

Trait (h^2)	MOE_B	$AMOE_B$	MOE_{TV}	DEN_L
MOE_B (0.31)	—	—	—	—
$AMOE_B$ (0.35)	0.99	—	—	—
MOE_{TV} (0.33)	1.03	1.04	—	—
DEN_L (0.41)	0.91	0.93	0.91	—
$ADEN_L$ (0.42)	0.88	0.92	0.90	1.00
KNT_{EDG} (0.03ns)	nd	nd	nd	nd
KNT_{CNT} (0.00ns)	nd	nd	nd	nd
KNT_{TOT} (0.14ns)	nd	nd	nd	nd

Note: Traits are described in Table 1. All traits were measured on 2 × 4s, and log means were then calculated from the corresponding 2 × 4 values. h^2 values are individual-tree heritabilities. nd, not determined because of nonsignificant genetic variation for the knot traits.

current study, we conclude that MOE_{TV} has a slightly higher heritability (0.33) than alternative measures of wood stiffness, and a nearly perfect genetic correlation with MOE_B ($r_A = 1.03$) (Table 8). Furthermore, we show that the heritability of MOE_B can be increased by adjusting MOE_B for the confounding influences of ring age and ring orientation (i.e., $AMOE_B$; Table 8). The heritability of $AMOE_B$ was 0.35 compared with the heritability of 0.31 for MOE_B. In contrast, there was little difference in heritability between the unadjusted and adjusted values of wood density (i.e., DEN_L versus $ADEN_L$; Table 8). Knowledge of genetic parameters for MOE_{TV} and $AMOE_B$ could influence detailed studies of wood properties but will not affect operational breeding programs because it is too costly to mill the number of trees needed to obtain these measurements. Therefore, to improve Douglas-fir wood stiffness, we continue to recommend that breeders measure wood stiffness using the HM200 whenever possible. If logs cannot be measured, standing-tree tools such as the ST300 or TreeSonic can be used to obtain modest improvements in wood stiffness.

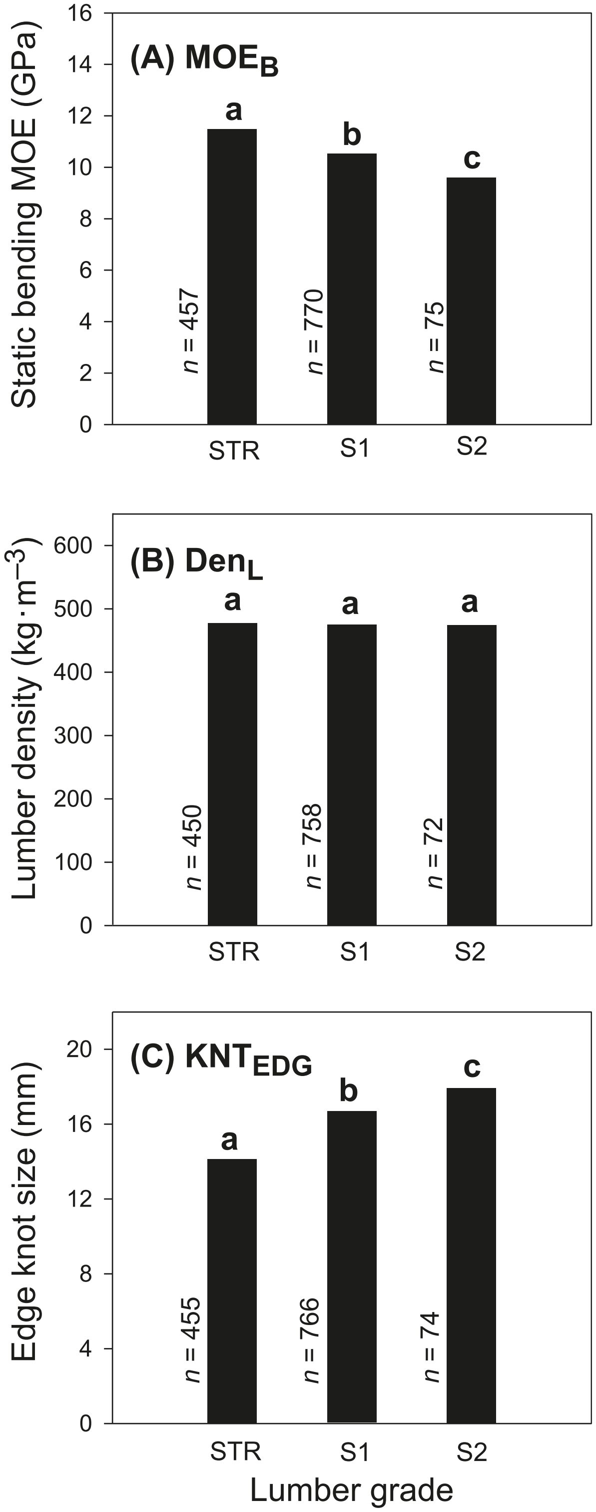
Because we used a coefficient of relationship (CR) of 0.33 to account for relatedness among wind-pollinated siblings (i. e., σ^2_A was estimated as $3\sigma^2_{F(S)}$), the heritabilities reported above would have been one-third higher (i.e., 0.41 to 0.47) if we had used a coefficient of relationship of 0.25 (i.e., assumed that the progeny were true half-sibs). In another study of Douglas-fir, Johnson and Gartner (2006) reported an across-site heritability of 0.55 for stress wave MOE, also based on a CR of 0.33 ($h^2 = 0.73$ if CR was assumed to be 0.25). In radiata pine, the heritabilities of stress wave MOE ranged from 0.18 to 0.53 using a CR of 0.25 for open-pollinated families (Kumar 2004; Kumar et al. 2002). Because our heritabilities were based on observations from a single site, they may overestimate multisite heritabilities that include genotype–environment interaction (G × E). G × E was very small, however, in our multisite analysis of stress wave velocity (Cherry et al. 2008).

We did not report genetic correlations with knot traits because there was no significant genetic variation for these traits (Table 8). Ramicorn branches can be a serious defect in Douglas-fir (Howe et al. 2006), but trees with ramicorns were excluded from our study. In contrast, we conclude that selection for nonramicorn branch traits would be ineffective for improving wood stiffness in Douglas-fir because the genetic correlation between these traits is probably low (i.e., based on our phenotypic correlations) and little genetic improvement in branch traits is possible. We found no genetic variance in our knot traits, and genetic variation in relative branch diameter was low in two previous studies of 12- to 18-year-old Douglas-fir (coefficient of additive genetic variation = 5%–6%; King et al. 1992; St. Clair 1994). By using single trait selection, for example, it might be possible to reduce relative branch diameter by about 9% to14%, which is only about 2–3 mm for trees that had a mean branch diameter of ~2 cm (King et al. 1992; St. Clair 1994) (see Cherry et al. 2008 for selection assumptions). Furthermore, gains in branch traits would be considerably less if even one additional trait, e.g., volume growth, were considered (Wright 1976, p.164). Genetic improvement in branch or knot traits may be more effective in other species.

Conclusions and implications for tree improvement

Breeders are interested in genetically improving Douglas-fir wood stiffness. Therefore, we studied the relationships between MOE_B (the target trait) and traits that could be used as indirect selection criteria (i.e., stress wave MOE, stress wave velocity, transverse vibration MOE, density, and MFA) and other traits that affect MOE_B (i.e., knots, ring age, and ring orientation). Results from our static bending tests were previously combined with measurements from progeny tests to conclude that MOE_{HM} is very effective, VEL_{HM} is moderately effective, and wood density may be effective for improving MOE_B (i.e., depending on how density is measured; Cherry et al. 2008). Compared with DEN_L, DEN_{BD} was not very effective for improving wood stiffness, presumably because it is derived from a much smaller sample of atypical wood near the stump. However, because it is too costly to measure log density (DEN_L), breeders will need to rely on

Fig. 7. Relationships between lumber grade (STR, select structural; S1, select 1; S2, select 2) and wood properties of 2 × 4s harvested from a 25-year-old Douglas-fir progeny test: (A) static bending MOE (MOE_B); (B) air-died lumber density (DEN_L); and (C) diameter of the largest edge knot (KNT_{EDG}). Lumber grades marked with same letter are not statistically different from one another at p = 0.05 using the Tukey–Kramer multiple comparison test.



less costly and more practical methods for measuring wood density (e.g., increment cores, Pilodyn, Resistograph). Additional work would be needed to estimate the relationships between these alternative measures of wood density and bending stiffness. Furthermore, we previously cautioned breeders against selecting for wood density alone because of its consistent negative genetic correlation with growth in this and other studies of Douglas-fir (Cherry et al. 2008).

In this study, we (*i*) expanded our measured traits to include MFA and knots, (*ii*) evaluated the need to control for ring age and ring orientation, and (*iii*) studied whether stiffness differs among lumber grades. Although our regression models indicated that 56% to 59% of the variation in 2 × 4 stiffness can be explained by density, MFA, and knots (Table 5), we found little evidence that breeders should measure and select for MFA and knots. First, density had a greater direct effect on MOE_B than did MFA, which is consistent with other results (Lachenbruch et al. 2010). Furthermore, because density was even more important in mature wood than in juvenile wood of radiata pine (Cown et al. 1999), the relative importance of wood density versus MFA may become even stronger over time. In our study, wood density alone explained 49% to 52% of the variation in 2 × 4 MOE_B. Given the high cost of measuring MFA, the excellent ability to predict MOE_B from stress wave velocity and wood density (discussed above), and corroborating evidence from another study (Lachenbruch et al. 2010), we recommend that Douglas-fir breeders refrain from measuring and selecting for MFA to improve wood stiffness. Nonetheless, measurements of MFA will be valuable for research aimed at understanding the biological and physical basis of wood stiffness, within-tree variation in wood stiffness and age–age correlations, and the molecular basis of genetic variation in stiffness (Baltunis et al. 2007; Kumar et al. 2006). Second, because MOE_B was weakly correlated with knots and there was no significant genetic variation for knot traits, it will be difficult or impossible to markedly improve wood stiffness by selecting for smaller branches or knots in Douglas-fir breeding programs. Overall, operational breeding programs should concentrate on measuring and selecting for stress wave velocity and (perhaps) wood density to improve wood stiffness.

Although we developed equations to predict MOE_B from wood properties measured in the laboratory and field (Tables 5 and 6), absolute estimates of MOE are not necessary for making genetic selections and obtaining genetic gain. We also demonstrated that MOE_{TV} is an excellent indirect measure of MOE_B. Therefore, future studies of lumber stiffness could use transverse vibration tests instead of the static bending tests, which are more time consuming, more expensive, and require large specialized equipment. We also demonstrated that information on ring age and ring orientation can be used to improve estimates of bending stiffness and increase heritabilities.

Acknowledgements

We thank the Pacific Northwest Tree Improvement Research Cooperative for funding, Glenn Holloway and Donald DeVisser for lumber grading, Milo Clauson for advice on measuring wood properties, and Scott Kolpak and Annie Simmonds for editorial help.

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