AN ABSTRACT OF THE THESIS OF

<u>Vikas Vikram</u> for the degree of <u>Master of Science</u> in <u>Forest Science</u> presented on <u>December 5, 2008.</u>

Title: Stiffness of Douglas-fir Lumber: Effects of Wood Properties and Genetics.

Abstract approved:

Glenn T. Howe

Wood stiffness is one of the most important properties of lumber and veneer. We studied wood stiffness (modulus of elasticity, MOE), wood density, microfibril angle, and knots in a 25 year-old wind-pollinated progeny test (50 families, ~ 373 trees) of coastal Douglas-fir to understand the potential for genetically improving wood stiffness. We measured the stress wave MOE of standing trees (MOE_{ST}) and logs (MOE_{HM}) using field-based tools (ST300 and HM200) that measure stress wave velocity. We then milled the logs into 2x4s to obtain direct estimates of MOE using bending tests (MOE_{bl}) and indirect estimates using transverse vibration (MOE_{tv}) and stress wave (MOE_{sw}) techniques. On basal wood disks, we measured green (DEN_{gd}) and dry (DEN_{dd}) wood density; on 2x4s, we measured lumber density (DEN_{dl}), sizes of the largest edge (KNT_{edg}) and center knots (KNT_{ent}), number of knots (KNT_{tot}), and lumber grade; and on small clearwood samples, we measured dry density (DEN_{sc}), as well as MOE (MOE_{sc}) and microfibril angle (MFA_{sc}) using the SilviScan system. MOE_{bl} had moderate to strong phenotypic (r_p) and additive genetic (r_a) correlations with MOE_{HM}, MOE_{ST}, MOE_{tv}, and MOE_{sw} ($r_p = 0.45$ to 0.91; $r_a = 0.57$ to 1.03) suggesting that the HM200 and ST300 tools

can be used to genetically improve bending stiffness. MOE_{bl} had moderate to strong genetic correlations with DEN_{dl} and DEN_{dd} (r_a = 0.37 to 0.91), and weak correlations with KNT_{edg} and KNT_{tot} (r_a = -0.24 and 0.22). MOE_{bl} had a strong phenotypic correlation with DEN_{sc} (r_p = 0.72) and moderate negative correlation with MFA_{sc} (r_p = -0.42). Together, DEN_{dl} , MFA_{sc} , and KNT_{edg} explained 49% to 62% of the variance in 2x4 MOE_{bl} , MOE_{tv} , and MOE_{sw} . Compared to MFA_{sc} and KNT_{edg} , path analysis suggested that density had the strongest direct effect on MOE_{bl} . Nonetheless, because density is negatively correlated with growth, and because field-based stress wave tools are now available, there is no great need to measure wood density or MFA to improve wood stiffness. Because the phenotypic and genetic correlations between knot traits and bending MOE are either weak or nonsignificant, knot traits do not seem to be important to include in breeding programs for structural lumber. The STR lumber grade had a higher MOE_{bl} and lower KNT_{edg} than either the S1 or S2 grades.

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Stiffness of Douglas-fir Lumber: Effects of Wood Properties and Genetics

by Vikas Vikram

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

1. Introduction

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is one of the principal lumber species in the Pacific Northwest because it is widely distributed, grows fast, and has excellent wood quality. Douglas-fir is widely used to make structural lumber, plywood, laminated veneer lumber (LVL), 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; Senft et al. 1985; Maguire et al. 1991; Busing and Garman 2002).

Although shorter rotations may increase economic returns from wood production, they will result in younger and smaller logs that have larger proportions of juvenile corewood. Juvenile wood, which is the wood produced by the cambium of a young tree, is distinguished from mature wood by differences in wood properties such as wood density. In Douglas-fir, the gradual transition from juvenile wood to mature wood is generally thought to occur when the tree is 10 to 26 years old (Peterson et al. 2007). The wood produced during the juvenile phase of growth has lower stiffness, lower density, lower cell wall thickness, lower late wood percentage, higher microfibril angles (MFA), and greater longitudinal shrinkage compared to wood produced during the mature phase of growth (Kretschmann and Bendsten 1992; Zobel and Sprague 1998; Burdon et al. 2004; Li et al. 2007; Roth et al. 2007). In general, the same trends in wood properties are seen between the wood produced near the pith (corewood) compared to wood produced towards the outside of the tree (outerwood) (Burdon et al. 2004). The distinction between

corewood and outerwood is based on "ring age" or the number of rings from the pith, with first 10 rings typically designated as corewood. In this paper, we adopt the concepts and terminology of Burdon et al. (2004), who described juvenile versus mature variation in wood properties in both the radial and vertical directions, and corewood versus outerwood variation in the radial direction.

Zobel (1972) suggested that genetic improvement can help foresters achieve acceptable wood quality even though rotations are getting shorter, and Senft et al. (1985) predicted that genetics and silviculture can be combined to improve the wood properties of trees in fast-growing plantations. Wood stiffness is an important target of genetic and silvicultural improvement because it is one of the most important properties of structural wood products (Roth et al. 2007). 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 (Cown et al. 1992; Kumar et al. 2002; Lindström et al. 2004; Fugimoto et al. 2006; Baltunis 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 curve that describes the relationship between stress and strain (Carter et al. 2005). 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 resultant deformation is measured (ASTM 2005). Although bending tests provide direct, reliable

estimates of stiffness, they are expensive and time consuming (Kumar et al. 2006). Therefore, it is not feasible to measure bending stiffness on the large numbers of trees that are typically found in genetic test plantations. Fortunately, several inexpensive indirect techniques are now available to rapidly estimate wood stiffness on many trees.

Transverse vibrations and stress waves can be used to reliably predict bending stiffness based on Jayne's hypothesis (Jayne 1959). According to Jayne's hypothesis, the energy storage and dissipation properties of wood are controlled by the same mechanisms that determine the bending stiffness of wood. Transverse vibration MOE is calculated from the frequency of oscillation and rate of decay of transverse vibrations of a wooden beam supported at its ends (Pellerin 1965; Ross et al. 1991; Ross and Pellerin 1994). Stress wave MOE is calculated based on the one-dimensional wave theory (i.e., stress wave $MOE = DEN \times VEL^2$, where DEN is wood density and VEL is the velocity of stress wave propagation) (Pellerin and Ross 2002). Stress wave velocity is also referred as acoustic velocity or acoustic stress wave velocity (Chauhan and Walker 2006). Stress waves are typically generated by an impact, and the velocity of the resulting stress wave is estimated from the transmission time between two given points. The transverse vibration and stress wave techniques have been widely adopted by the forest product industry to grade lumber and to assess or predict the engineering properties of woodbased materials. In addition to these mill- or laboratory-based applications, 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 Fiber-gen Director HM200 can be used to estimate the stiffness of logs, whereas the Fiber-gen Director ST300 can be used to estimate the stiffness of standing trees (Rippy et al. 2000; Andrews 2002; Carter 2005; Wang et al. 2007, Cherry et al. 2008). Because stress wave velocity and stress wave MOE are highly correlated with bending stiffness, the HM200, ST300, and related tools can provide new opportunities to improve bending stiffness via tree breeding, stand management, or log sorting (Wang et al. 2007). Studies on Douglas-fir and radiata pine, for example, have shown that the HM200 and ST300 can be used to improve wood stiffness in tree breeding programs (Lindström et al. 2002; Kumar et al. 2002, 2004; Briggs et al. 2005; Johnson and Gartner 2006).

In addition to the methods described above, MOE can be predicted at a finer scale using the SilviScan system, which uses X-ray diffractometry and X-ray densitometry to predict MOE (Evans 2006). Studies on lumber and small clearwood samples (e.g., $10 \times 10 \times 150 \text{ mm}$ samples with no knots or defects) suggest that MOE estimated using Silviscan can explain 60 to 90% of the variation in bending MOE (Ross and Pellerin 1994; Halabe et al. 1995; Ilic 2001; Wang et al. 2001, 2002; Wang et al. 2007; Raymond et al. 2007). In addition to MOE, Silviscan can be used to predict other wood properties such as microfibril angle, wood density, cell wall thickness, and tracheid diameter (Evans 1994, 1999; Evans et al. 1996, 1999, 2001).

Indirect selection is an approach used to achieve genetic gain in a desired target trait by measuring and selecting individuals based on a second correlated trait. Compared to the target trait, indirect selection may be valuable when the measured trait is (1) more rapid

or less expensive to measure, (2) more highly heritable, or (3) can be measured at an earlier age (e.g., using stem diameter of 10 year-old-trees to select for stem volume at rotation age). Because bending MOE is difficult and expensive to measure, and requires destructive sampling, indirect methods for predicting bending stiffness would be particularly valuable for tree breeding programs. The percentage gain that can be achieved in a target trait by indirectly selecting for a correlated trait is called the relative gain efficiency, or simply relative efficiency (RE). These relative efficiencies depend on the intensities of selection, genetic correlation between the target and measured traits, and their heritabilities (White et al. 2007). Therefore, we studied whether stress wave MOE and wood density can be used as indirect selection criteria for genetically improving bending MOE.

Stress wave MOE and wood density were moderately to highly heritable in a recent study of 39 wind-pollinated families of Douglas-fir grown at four locations in the Pacific Northwest (Johnson and Gartner 2006). Furthermore, both stress wave velocity and wood density were strongly correlated with stress wave MOE, in part because MOE is a function of these two traits. Although MOE, velocity, and density were negatively correlated with height and diameter growth, the correlations between growth and density were stronger than the correlations between growth and either MOE or velocity. Johnson and Gartner (2006) recommended that breeders select for stress wave MOE or velocity to improve Douglas-fir wood stiffness. Despite these encouraging results, Johnson and Gartner (2006) did not directly measure bending MOE. Therefore, it was still unclear what gains to expect when these tools are used to indirectly improve bending MOE.

Cherry et al. (2008) subsequently studied stress wave MOE and bending MOE in Douglas-fir to determine whether the HM200 and ST300 can be used to genetically improve bending stiffness. Based on data from 25-year-old trees from 130 wind-pollinated families growing in 3 progeny test plantations, they concluded that stress wave MOE is heritable and substantial gains can be made in stress wave MOE by using the HM200 or ST300. Bending MOE, which was measured on 2x4s milled from one progeny test plantation, was moderately heritable and had a strong genetic correlation with stress wave MOE measured with the HM200. Compared to the ST300, predicted gains in bending MOE were higher when selections were based on the HM200 traits (i.e., stress wave MOE or stress wave velocity). Results also suggested that selection for bending stiffness or stress wave velocity would have no large adverse effects on growth, although selection for increased wood density would adversely affect growth. Therefore, breeders should be cautious about using wood density alone to improve wood stiffness. Furthermore, because wood density is relatively costly to measure and adds little to the gains in bending stiffness when it is used to predict stress wave MOE (i.e., DEN x VEL²), there is no real need to measure wood density. In this paper, we report on additional properties of the 2x4s studied by Cherry et al. (2008), including additional laboratory-based measures of wood stiffness, knot traits, MFA (microfibril angle), and lumber grade.

Because wood stiffness is a composite trait, it may be valuable to understand how the underlying component wood properties affect stiffness. Density, MFA, and knots are

believed to be the most important wood properties affecting the stiffness of wood (Tsoumis 1991; Evans and Ilic 2001; Yang and Evans 2003). MFA is the mean helical angle of microfibrils in the S2 layer of the cell wall measured from vertical. MFA and density accounted for 94% of the variation in stress wave MOE in radiata pine (Evans and Ilic 2001) and 93% of the variation in MOE in loblolly pine (Megraw et al. 1999). Knots cause defects in wood that can reduce the stiffness of wood (Macdonald and Hubert 2002; Wang et al. 2003). For example, studies on Sitka spruce and Norway spruce suggest that lumber stiffness decreases with increasing average knot size (Brazier 1993; Kliger et al. 1995). Therefore, we investigated the effects of density, MFA, and knots on Douglas-fir stiffness to provide breeders and forest managers with information needed to develop efficient breeding strategies. Our specific objectives were to (1) estimate the genetic variances and heritabilities of direct and indirect estimates of Douglas-fir wood stiffness, (2) estimate the genetic correlations between wood stiffness traits, (3) determine whether transverse vibration and stress wave MOE can be used to indirectly select for improved bending stiffness, (4) evaluate the genetic and/or phenotypic relationships between bending stiffness, wood density, MFA, and knots, and (5) determine whether visual grades of Douglas-fir lumber differ in wood properties.

2. Materials and Methods

2.1. Plant materials

We studied the wood properties of lumber harvested from a 25 year-old (from seed) wind-pollinated progeny test on the Olympic peninsula in northwestern Washington (47°52.9' N; 122°41.7' W; 122 m elevation) (Table 1). Parent trees were randomly selected from native stands on the Kitsap and Olympic Peninsulas in Washington, and then organized into 4 sets (groups) based on their geographic origin. Wind-pollinated seeds were collected from each parent in 1979 or 1980, and sown into styro-8 blocks in 1981. The progeny test was established in 1983 by Olympic Resource Management, Port Gamble, Washington at a spacing of 3.05 x 3.05 m (10 x 10 ft) at three locations (Watershed and Opsata on the Kitsap peninsula, and Shine on the Olympic peninsula). At each location, 130 families were planted in a reps-in-sets design. Each set of 30 to 40 families was planted as a separate adjacent experiment with 8 replications of 4 trees per family in non-contiguous plots. After traits were measured in the field (described below), the Shine progeny test plantation was thinned in September 2005, and 8 trees from each of 50 families (4 sets x 12-13 families per set) were selected for milling into lumber, excluding trees that had questionable identity or poor stem form. The harvested trees were transported to Thompson Timber Company, Philomath, Oregon for milling. Of the original 400 trees selected, 383 were milled into lumber and analyzed as part of this study. Other data from all three progeny test plantations were previously reported by Cherry et al. (2008).

Table 1. Wood properties of trees from a 25-year-old wind-pollinated progeny test of Douglas fir.

Abbreviation	Description
Stiffness (MOE is	modulus of elasticity) (GPa)
MOE_{bl}	Static bending MOE
$AMOE_{bl}$	MOE _{bl} adjusted for ring age (RA) and ring orientation (RO)
MOE_{tv}	Transverse vibration MOE
MOE_{sw}	Stress wave MOE
MOE_{pca}	Principal component MOE from analyses of MOE _{bl} , MOE _{tv} , and MOE _{sw}
$AMOE_{pca}$	MOE _{pca} adjusted for ring age (RA) and ring orientation (RO)
MOE_{HM}	HM200 MOE of green logs
MOE_{ST}	ST300 MOE of standing trees
MOE_{sc}	MOE of small clearwood samples estimated using SilviScan
Density (kg m ⁻³)	
$\mathrm{DEN}_{\mathrm{gd}}$	Green wood density of wood disks
$\mathrm{DEN}_{\mathrm{dd}}$	Dry (basic) wood density of wood disks
$\mathrm{DEN}_{\mathrm{dl}}$	Dry density of lumber
$ADEN_{dl}$	Dry density of lumber adjusted for ring age (RA)
$\mathrm{DEN}_{\mathrm{sc}}$	Dry density of small clearwood samples
Acoustic velocity	$(m s^{-1})$
$\mathrm{VEL}_{\mathrm{HM}}$	HM200 velocity measured on green logs
VEL_{ST}	ST300 velocity measured on standing trees
Knots (mm, numb	per, or score)
$KNT_{edg}(mm)$	Diameter of the largest edge knot on a 2x4 (average of two faces)
KNT_{cnt} (mm)	Diameter of the largest center knot on a 2x4 (average of two faces)
KNT_{tot} (no.)	Number of knots on a 2x4 greater than 12.7 mm (average of two faces)
$KNT_{pca}(score)$	Principal component of knots derived from KNT_{edg} , KNT_{cnt} , and KNT_{tot}
Diameter growth	(cm)

Diameter growth (cm)

DBH₂₅ Stem diameter at breast height

Other lumber properties

RA (years) Average ring age of the 2x4

RO (class) Ring orientation of the 2x4 in relation to the bending load (radial,

tangential, or diagonal)

Microfibril angle (degrees)

MFA_{sc} Microfibril angle of small clearwood samples estimated using SilviScan

2.2. Field measurements

We measured stem diameter at breast height (DBH₂₅), the number of ramicorn branches (i.e., large, steeply-angled branches), and stem crookedness in the summer of 2005 (i.e., before the test was thinned). The number of ramicorn branches present between the root collar and 3 m, 3 to 6 m, and above 6 m was recorded. We also visually estimated the crookedness of each tree using a scale of 1-10. A score of 1 indicated that the tree was nearly straight, whereas a score of 10 indicated that the tree was very crooked.

On the subset of trees chosen for milling (mill logs), we measured stress wave velocity (VEL $_{ST}$) near breast height using the ST300. Three velocity measurements were recorded on opposite sides of each tree (i.e., 6 measurements per tree), and these were later averaged to get a single estimate per tree. After the trees were felled, the mill logs were de-limbed, the basal logs were bucked to lengths of about \sim 3 m (\sim 9 ft), the log lengths were measured using a logger's tape, and stress wave velocities (VEL $_{HM}$) were measured using the HM200. We repeated the HM200 measurement whenever the confidence reading was below 85%. This reading indicates the quality of each velocity measurement on a scale of 0-99%, with 99% being the highest quality (Anon. 2003). The bark thickness of basal wood disks from the butt end of the mill trees were recorded and then debarked. The distance from the pith to the tenth and twentieth annual rings, heartwood diameter, total number rings, green weight, and green volume of the disk using the water displacement method was then measured.

2.3. Wood properties of trees

The mill logs and disks were transported to Oregon State University, and the disks were then kiln dried for 48 hours to a moisture content (MC) of < 7% at a wet bulb temperature of 65°C and dry bulb temperature of 82°C. The disks were then kept at ambient temperature and MC until the following measurements were made. Green wood density (DEN_{gd}) of the disks was estimated as:

$$[1] DEN_{gd} = \frac{M_{gd}}{VOL_{gd}}$$

where DEN_{gd} (kg m⁻³) is the green density, M_{gd} is the green mass, and VOL_{gd} is the volume of the green wood disk.

The dry wood density of the disks (DEN_{dd}) was estimated as:

$$[2] DEN_{dd} = \frac{M_{dd}}{VOL_{od}}$$

where DEN_{dd} (kg m⁻³) is the dry (basic) wood density, M_{dd} is the mass of the dry wood disk, and VOL_{gd} is the volume of the green wood disk.

Stress wave MOE (GPa) was calculated according to the following equation using either VEL_{ST} (for MOE_{ST}) or VEL_{HM} (for MOE_{HM}).

[3]
$$MOE = VEL^2 \times DEN_{gd} \times 10^{-9}$$

where VEL (m $\mbox{s}^{\mbox{-}1})$ is the stress wave velocity and DEN $_{gd}$ is as described above.

2.4. Log milling

The logs were milled into 2x4s ($\sim 3.8 \times 8.9 \times 300$ cm; $\sim 1.5 \times 3.5 \times 108$ in) using a portable sawmill (Wood-Mizer model LT40, Indianapolis, IN). The number of 2x4s varied from 1 to 10 per tree depending on the log diameter, straightness, and taper. The 2x4s were left unplaned, kiln dried to < 7% MC, and then measured as described below.

2.5. Wood properties of lumber and logs

The 2x4s were cut to a uniform length of 213 cm (84 in), and then arranged to reconstruct the log from which they were cut. The ring age (RA) and ring orientation (RO) were then recorded for each 2x4. The average RA of each 2x4 was later estimated as the mean of the youngest and oldest rings. We categorized each 2x4 into one of three RO classes (radial, tangential, or diagonal) based on the orientation of the annual rings in relation to the applied load used for measuring stiffness (Fig. 1). Because the load was applied to the short (3.8 cm) edge of the 2x4, the radial and tangential classes consisted of 2x4s with rings that were either parallel (radial) or perpendicular (tangential) to the short edge of the 2x4. The 2x4s that did not fall into one of these two classes were classified as diagonal. This resulted in 242 radial, 1067 tangential, and 38 diagonal 2x4s for testing.

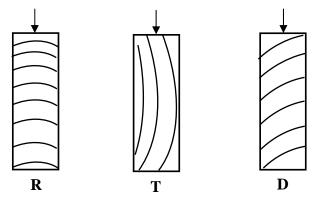


Fig. 1. Ring orientation classes of the 2x4s relative to the applied load used to measure bending MOE. R is Radial, T is Tangential, and D is Diagonal orientation.

We measured the widths and thicknesses of the 2x4s at both ends and at mid-span in inches. We calculated the density of each 2x4 in g in⁻³ according to the following equation, and then converted the density to kg m⁻³ by multiplying by 1.6387 x 10².

[4]
$$DEN_{dl} = \frac{w}{lbh} \times 1.6387 \times 10^2$$

where DEN_{dl} (kg m⁻³) is the dry lumber density, w is the weight (g), l is the length (in), b is the average measured width (in) (\sim 8.9 cm; \sim 3.5 in), and h is the average measured thickness (in) (\sim 3.8 cm; \sim 1.5 in) of the 2x4.

We counted the total number of knots (KNT_{tot}) greater than 1.3 cm (0.5 in) in diameter, the size of the largest edge knot (KNT_{edg}), and the size of the largest center knot (KNT_{ent}) on the two largest faces of each 2x4. Edge knots are knots that intersect any edge of the 2x4, whereas center knots are knots that are not edge knots. The knot data were later averaged across both faces to obtain a single value for each 2x4.

We measured static bending MOE (MOE_{bl}), transverse vibration MOE (MOE_{tv}), and stress wave MOE (MOE_{sw}) on all 2x4s. We measured MOE_{bl} in accordance with ASTM D198-05 (ASTM 2005). A 40 kip MTS Model 332.21 Universal Testing Machine (MTS Systems Corporation, Minneapolis, MN) was used for the four-point bending test (third-point loading), at the wood engineering laboratory of Oregon State University. LabView software was used to record the data. The 2x4s were loaded on edge using a span length (L) of 152.4 cm (60 in) and a span-to-depth ratio (L/b) of 17:1, where b is the 2x4 width. The 2x4s were oriented with the pith toward the bottom of the 2x4 (i.e., opposite the load). The maximum applied load was 227 kg (about 500 lbs) at a deflection rate of 5.1 cm min⁻¹ (2 in min⁻¹), and loading was stopped before ultimate failure. The MOE_{bl} was calculated in psi (pounds per square inch) according to the following equation and then converted to GPa by multiplying by 6.895 x 10⁻⁶.

[5]
$$MOE_{bl} = \frac{23L^3}{108hb^3} \times \frac{P}{\Lambda} \times 6.895 \times 10^{-6}$$
 (ASTM 2005)

where L is the span length between the beam supports (in), h is the average measured thickness of the 2x4 (in), b is the average measured width of the 2x4 (in), P is the applied load below the proportional limit (lb), and Δ is the deflection resulting from the load P (in). The slope of the deflection curve (P/ Δ) between 100 and 450 lb (45 to 204 kg) was used to calculate MOE_{bl}.

The transverse vibration technique was used to estimate MOE_{tv} using a Metriguard Model 340 E-computer (Metriguard Inc., Pullman, WA). The E-computer consists of two tripod assemblies (one with a load cell and other with a knife-edge), an electronic

interface unit, and a personal computer with display options. The 2x4 was supported by the tripods, and then set into vibration by gently tapping the 2x4 with a hammer at mid-span. MOE^*_{tv} was calculated in psi according to the following equation (Metriguard 1990) using the software supported by the manufacturer.

[6]
$$MOE_{tv}^* = \frac{wL^3f^2}{Kbh^3}$$

where w is the weight of the 2x4 (lb), L is the span length (in), f is the vibration frequency (Hz), b is the standard 2x4 width (3.5 in), h is the standard 2x4 thickness (1.5 in), and K is the internal calibration constant to accommodate the units used and the support conditions. MOE_{tv} was then calculated by accounting for the actual width and thickness of each 2x4, and then converting the units to GPa by multiplying by 6.895×10^{-6} (See Appendix 1 for details).

[7]
$$MOE_{tv} = \frac{11.8125 \times MOE_{tv}^*}{bh^3} \times 6.895 \times 10^{-6}$$

where MOE^*_{tv} is as described above, b is the actual 2x4 width (in), and h is the actual 2x4 thickness (in).

MOE_{sw} was measured using a Metriguard 239A Stress Wave Timer (Metriguard Inc., Pullman, WA), which consists of a pendulum impactor, two accelerometers that detect the propagation times of the stress waves, and a display unit. MOE was determined from the velocity of propagation (V), density of the 2x4 (D), and acceleration due to gravity (g) (Metriguard 1991). In our study, MOE_{sw} was calculated in psi according to the

following equation, and then converted to GPa by multiplying by 6.895×10^{-6} (See Appendix 2 for details).

[8]
$$MOE_{sw} = \left[\frac{V^2 D \times 2.20462 \times 10^9}{g} \right] 6.895 \times 10^{-6}$$

where V is the stress wave velocity (in s⁻¹) calculated from the stress wave propagation time and distance between the transducers (i.e., length of the 2x4), D is the density of the 2x4 (lb in⁻³), and g is the acceleration due to gravity (386 in s⁻²).

2.6. Wood properties of small clearwood samples

We measured MFA, density, and MOE of small clearwood samples collected from a subset of the families and 2x4s. We selected 60 2x4s that spanned a wide range of values for MOE_{bl} (7.5 to 15.0 GPa), with the following constraints. Because MOE_{bl} and DEN_{dd} were significantly correlated with RA and RO, we first selected all 2x4s with a mean RA between 9.0 and 9.5 years, and a tangential RO (Fig. 1). We then selected 30 families from which we could select at least two 2x4s that had been milled from separate logs (60 logs = 60 2x4s). Therefore, our final set of 2x4s consisted of 2 2x4s from each of 30 families. Preliminary analyses suggested that the data from the selected 60 2x4s followed a normal distribution for MOE_{bl} and DEN_{dl}. Three small clearwood samples (15.0 x 15.0 x 38.1 mm) were cut from the top end of each 2x4 using a band saw, resulting in 180 samples that were shipped to CSIRO, Australia for SilviScan analysis. The SilviScan system (SilviScan-3, CSIRO, Clayton, Australia) was used to measure MFA (MFA_{sc}, degrees) using X-ray diffractometry. Wood density (DEN_{sc}, kg m⁻³) was measured

gravimetrically from mass and volume. The average stiffness (MOE_{sc}, GPa) of each sample was predicted using the following equation:

[9]
$$MOE_{sc} = A(I_{CV}DEN_{sc})^{B}$$
 (Evans 2006)

Where I_{CV} is the coefficient of variation of the azimuthal intensity profile (~0 to ~1) obtained from the X-ray diffraction patterns, DEN_{sc} is the wood density of the small clearwood samples measured gravimetrically (kg m⁻³), and A and B are constants that depend on the SilviScan experimental conditions (Evans 2006).

2.7. Lumber grading

All 2x4s were visually graded into select structural (STR), No.1 (S1), No.2 (S2), No.3 (S3), and economy (E) by a district supervisor from the West Coast Lumber Inspection Bureau, Portland, OR using the National Grading Rule for coastal Douglas-fir dimensional lumber (West Coast Lumber Inspection Bureau 1995). Grades were assigned based on the presence or absence of various defects such as size and type of knots, and the presence of checks, grain, shake, splits, and warp.

2.8. Statistical analyses

Analyses were conducted at both the lumber and log levels. We first removed obvious outliers (e.g., data entry errors) based on bivariate plots between all pairs of variables using SAS Proc Insight (SAS®, version 9.3.1). We then removed observations with internally-studentized residuals (Equation 10, below) that exceeded 4 standard deviations from the mean (Neter et al. 1996). The normality of the residuals was evaluated using

Darling test using Proc Univariate. Homoskedasticity of the residuals was checked using residual plots. Proc Means was used to calculate log means of wood properties of 2x4s processed from each log. Paired t-tests were used to determine whether the different measures of MOE were significantly different from each other in our populations of 2x4s (i.e., MOE_{bl}, MOE_{tv}, and MOE_{sw},) and logs (i.e., MOE_{HM} and MOE_{ST}).

2.8.1. Phenotypic relationships among wood properties

The SAS Corr Procedure was used to calculate phenotypic correlations between pairs of traits at both the lumber and log levels (i.e., after calculating log means). The Princomp Procedure was used to estimate the principal components of 2x4 MOE (MOE_{pca}) using MOE_{bl}, MOE_{tv}, and MOE_{sw}; and knots (KNT_{pca}) using KNT_{edg}, KNT_{cnt}, and KNT_{tot} at the lumber level. Principal components analysis (PCA) is a commonly used statistical technique to reduce multidimensional data sets to lower dimensions. MOE_{pca} and KNT_{pca} represent the first principal components from each of these analyses, explaining 88.4% and 54.0% of the variance in these two multivariate traits.

2.8.2. Genetics of wood properties

Genetic analyses at the lumber level were conducted using the SAS Mixed Procedure and the following linear model:

[10]
$$Y_{srfl} = \mu + S_s + R(S)_{sr} + F(S)_{sf} + R*F(S)_{srf} + \varepsilon_{srfl}$$

where: Y_{srfl} is the observation for the l^{th} log of the f^{th} family in the r^{th} replication in the s^{th} set; μ is the overall mean; S_s is the random effect of the s^{th} set with variance σ^2_{S} ; $R(S)_{sr}$ is the random effect of r^{th} replication in the s^{th} set with variance $\sigma^2_{R(S)}$; $R(S)_{sf}$ is the random effect of f^{th} family in the s^{th} set with variance $\sigma^2_{R(S)}$; $R*F(S)_{srf}$ is the random interaction effect between the f^{th} family and the r^{th} replication in the s^{th} set with variance $\sigma^2_{R*F(S)}$; and \mathcal{E}_{srfl} is the residual error.

We analyzed MOE_{bl} , MOE_{pca} , and DEN_{dl} with and without RA and RO as covariates using the model described in equation 10. MOE_{bl} and MOE_{pca} were significantly associated with RA and RO, whereas lumber density was significantly associated with RA. Using the coefficients derived from the analyses of covariance, the value of each 2x4 was adjusted to a mean RA of 9.1 years and a tangential RO (equations 11, 12, and 13).

[11]
$$AMOE_{bl} = MOE_{bl} + (0.2721*D) + (0.3673*R) + 0.2295*(9.11184-RA)$$

[12]
$$AMOE_{pca} = MOE_{pca} + (0.3211*D) + (0.4416*R) + 0.3066*(9.11184-RA)$$

[13]
$$ADEN_{dl} = DEN_{dl} + 3.4672*(9.11184-RA)$$

where, D is equal to 1 if RO is diagonal, and 0 otherwise; R is equal to 1 if RO is radial, and 0 otherwise; and RA is the mean ring age of the 2x4.

Individual-tree narrow-sense heritabilities were estimated as:

[14]
$$h_i^2 = 3 \times \sigma_{F(S)}^2 / [\sigma_{F(S)}^2 + \sigma_{R*F(S)}^2 + \sigma_{\varepsilon}^2]$$

where $\sigma^2_{F(S)}$, $\sigma^2_{R^*F(S)}$, and σ^2_{ε} are variance components estimated using model 10 and SAS Proc Mixed. The additive genetic variation was estimated as 3 $\sigma^2_{F(S)}$ based on the assumption that wind-pollinated progenies of Douglas-fir are more closely related than are true half-sibs (Squillace 1974). Narrow-sense genetic (r_A), error (r_E), and phenotypic (r_B) correlations were estimated as:

[15]
$$r_{X,Y} = \frac{Cov_{X,Y}}{\sqrt{\sigma_X^2 \times \sigma_Y^2}}$$

where $Cov_{x,y}$ is either the genetic covariance component (r_A) , error covariance component (r_E) , or phenotypic covariance component (r_P) for traits X and Y, and σ_X^2 and σ_Y^2 are the corresponding variance components. Additive genetic correlations (r_A) were calculated using family(set) variance-covariance components, r_E was calculated using family(set) x replication variance-covariance components, and r_P was calculated using their sums. The covariance components were estimated using SAS Proc Mixed, and the standard errors of the correlations were estimated using the Delta method (Lynch and Walsh 1998).

2.8.3. Phenotypic relationships between wood properties of small clearwood samples We analyzed the small clearwood data using correlation analysis, linear regression, and path coefficient analysis. Prior to statistical analyses, small clearwood samples from two of the 2x4s were removed because of questionable identity. Values obtained from each

of the three samples were averaged to get a single estimate of MFA_{sc}, DEN_{sc}, and MOE_{sc} for each 2x4. We used the SAS Corr Procedure to study the linear relationships between pairs of traits (i.e., MOE_{bl}, MOE_{tv}, MOE_{sw}, MOE_{sc}, MFA_{sc}, DEN_{sc}, DEN_{dl}, and KNT_{edg}). We used regression analysis and the BIC (Bayesian Information Criterion) to select models for predicting MOE_{bl}, and path analysis to decompose the correlation coefficients into their direct and indirect components (Li 1975). For each variable and model, the residuals were checked for normality and homogeneity of variance using the procedures described for the other wood properties.

2.8.4. Differences between lumber grades

We used analyses of variance to determine whether MOE_{bl}, DEN_{dl}, and KNT_{edg} differed among lumber grades. Tukey's Studentized range test (Honestly Significant Difference, HSD) was used to test for significant differences between lumber grades.

3. Results

The 25 year-old trees we studied had a DBH₂₅ that ranged from 11.1 to 36.7 cm, with a mean of 22.1 cm. The means, ranges, and coefficients of variation of the wood properties of the lumber and logs from these trees are shown in Tables 2 and 3. The average MC of the 2x4s at the time of MOE estimation was about 7%.

3.1. Direct and indirect tests yielded different estimates of wood stiffness

The mean MOE_{bl}, MOE_{tv}, and MOE_{sw} of 2x4s ranged from 7.0 to 10.8 GPa (Table 2). MOE_{tv} and MOE_{sw} underestimated MOE_{bl} by 10 to 35% (p < 0.0001), and the coefficient of variation in unadjusted stiffness ranged from 14.9% for MOE_{bl} to 17.8% for MOE_{sw}. MOE_{pca} of individual 2x4s ranged from 7.3 to 18.3, with a coefficient of variation of 16.0%. The mean stiffness of logs (Table 3) was similar to the mean stiffness of 2x4s. The ST300 overestimated MOE_{bl} by 14.7% (12.5 vs 10.9 GPa; p < 0.0001), whereas the HM200 underestimated MOE_{bl} by 12.8% (9.5 vs 10.9 GPa; p < 0.0001; Table 3). On average, the VEL_{ST} of logs was 14.2% higher than VEL_{HM} (3872 vs 3392 m s⁻¹; p < 0.0001), and the mean MOE_{ST} of logs was 31.6% higher than the MOE_{HM} (12.5 vs 9.5 GPa; p < 0.0001; Table 3).

Table 2. Wood properties of Douglas-fir 2x4s harvested from a 25-year-old wind-pollinated progeny test of Douglas-fir.

Trait ^a	N	Mean	STD	MIN	MAX	CV%				
Stiffness (GPa)										
MOE_{bl}	1347	10.8	1.6	6.5	16.5	14.9				
$AMOE_{bl}$	1335	10.9	1.5	6.7	15.3	13.4				
MOE_{tv}	1362	9.8	1.7	5.5	15.5	17.6				
MOE_{sw}	1338	7.0	1.2	3.9	13.0	17.8				
MOE_{pca}	1292	12.2	1.9	7.3	18.3	16.0				
$AMOE_{pca}$	1281	12.3	1.7	7.6	17.0	13.8				
Density (kg m ⁻³)										
DEN_{dl}	1341	476.4	36.2	345.9	614.1	7.6				
$ADEN_{dl}$	1329	476.3	35.3	330.7	605.8	7.4				
Knots (mm, num	iber, or	score)								
$KNT_{edg}\left(mm\right)$	1379	15.9	6.3	0.0	47.0	39.6				
KNT_{cnt} (mm)	1381	17.8	4.8	0.0	38.0	26.9				
KNT_{tot} (no.)	1383	6.8	3.2	0.0	21.0	46.6				
KNT _{pca} (score)	1370	22.3	5.6	0.0	44.5	25.1				
Ring age (years)										
RA	1377	9.1	3.0	2.5	18.5	32.6				
Ring orientation (percentage of 2x4s in each class) ^b										
RO (class)	1347	R = 18.0,	T = 79.2, a	and $D = 2.8^\circ$	% of 2x4s					

^aTraits are described in Table 1. N is the number of 2x4s, Mean is the arithmetic mean, STD is the standard deviation, MIN is the minimum value, MAX is the maximum value, and CV% is the coefficient of variation (STD/Mean x 100).

^bR is radial, T is tangential, and D is diagonal orientation.

Table 3. Wood properties of Douglas-fir butt logs (2.7 m long) harvested from a 25-year-old wind-pollinated progeny test of Douglas-fir. Log values were derived from the corresponding values measured on 2x4s.

Trait ^a	Measured ^b	N	Mean	STD	MIN	MAX	CV%		
Stiffness (GPa)									
MOE_{bl}	L	371	10.9	1.3	7.7	14.2	11.7		
$AMOE_{bl}$	L	369	11.0	1.3	7.8	14.7	11.5		
MOE_{tv}	L	370	9.7	1.3	6.5	14.1	13.0		
MOE_{sw}	L	372	7.0	0.9	3.9	9.4	12.4		
MOE_{pca}	L	367	12.2	1.5	8.5	16.1	12.3		
$AMOE_{pca}$	L	365	12.4	1.5	7.6	16.7	12.2		
MOE_{HM}	F	282	9.5	1.3	5.2	15.3	13.4		
MOE_{ST}	F	305	12.5	1.7	7.6	18.2	13.8		
Density (kg m ⁻³)									
$\mathrm{DEN}_{\mathrm{gd}}$	F	310	822.9	49.7	675.7	984.9	6.0		
DEN_{dd}	F	308	477.1	37.9	382.9	596.4	7.9		
DEN_{dl}	L	372	477.4	32.8	372.1	577.8	8.0		
$\mathrm{ADEN}_{\mathrm{dl}}$	L	370	478.3	32.9	365.6	577.9	8.0		
Acoustic velocity	y (m s ⁻¹)								
VEL_{HM}	F	339	3392	195	2550	4170	5.7		
VEL_{ST}	F	366	3872	224	3202	4548	5.8		
Knots (mm, number, or score)									
$KNT_{edg}(mm)$	L	373	15.9	4.6	1.8	39.0	28.8		
$KNT_{cnt}(mm)$	L	373	17.4	3.7	0.0	32.5	21.5		
$KNT_{tot}(no.)$	L	373	6.7	2.9	0.3	18.5	43.1		
KNT_{pca} (score)	L	373	22.0	4.9	0.0	39.8	22.3		

Table 3 continued on next page

Table 3. cont. Wood properties of Douglas-fir butt logs (2.7 m long) harvested from a 25-year-old wind-pollinated progeny test of Douglas-fir. Log values were derived from the corresponding values measured on 2x4s.

Trait ^a	Measured ^b	N	Mean	STD	MIN	MAX	CV%
Diameter growt DBH ₂₅	h (cm) F	372	22.1	3.4	11.1	36.7	15.6
Ring age (years)) L	371	8.8	1.4	4.5	12.0	15.6

^aTraits are described in Table 1. N is the number of logs, Mean is the arithmetic mean, STD is the standard deviation, MIN is the minimum value, MAX is the maximum value, and CV% is the coefficient of variation (STD/Mean x 100).

^b 'Measured' indicates that the trait was measured on individual 2x4s in the laboratory (L) or on logs or standing trees in the field (F).

3.2. Phenotypic correlations between bending stiffness and indirect estimates of wood stiffness

The correlations between MOE_{bl} and MOE_{tv} ($r_p = 0.91$) were stronger than the correlations between MOE_{bl} and MOE_{sw} ($r_p = 0.77$ to 0.80; Table 4) at both the log and lumber levels. At the lumber level, the linear regression models used to predict MOE_{bl} from MOE_{tv} and MOE_{sw} are given in Equations 16 and 17 (Figs. 2A and 2B).

[16]
$$MOE_{bl} = 2.47655 + 0.85523*MOE_{tv}$$
; $R^2 = 0.83$; $p < 0.0001$

[17]
$$MOE_{bl} = 3.78289 + 1.00292*MOE_{sw}$$
; $R^2 = 0.59$; $p < 0.0001$

A plot of MOE_{bl} versus MOE_{sw} appeared to have two populations of values (Fig. 2B), but we were unable to explain this effect. As expected, MOE_{pca} was strongly correlated with each of its component traits MOE_{bl} , MOE_{tv} , and MOE_{sw} ($r_p = 0.80$ to 0.98). At the log level, the linear regression models used to predict MOE_{bl} from MOE_{tv} and MOE_{sw} are given in Equations 18 and 19.

[18]
$$MOE_{bl} = 1.95715 + 0.91428*MOE_{tv}$$
; $R^2 = 0.83$; $p < 0.0001$

[19]
$$MOE_{bl} = 2.60955 + 1.18415*MOE_{sw}$$
; $R^2 = 0.64$; $p < 0.0001$

 MOE_{HM} and MOE_{ST} had moderate phenotypic correlations with MOE_{bl} ($r_p = 0.65$ and 0.45; Table 5). The linear regression models used to predict MOE_{bl} from MOE_{HM} and MOE_{ST} are given in Equations 20 and 21.

[20]
$$MOE_{bl} = 5.01170 + 0.61636*MOE_{HM}$$
; $R^2 = 0.42$; $p < 0.0001$

[21]
$$MOE_{bl} = 6.88308 + 0.32165*MOE_{ST}$$
; $R^2 = 0.20$; $p < 0.0001$

 MOE_{sc} was moderately correlated with the other direct and indirect estimates of stiffness (MOE_{bl} , MOE_{tv} , and MOE_{sw}) (r_p = 0.63 to 0.74). The linear regression model used to predict MOE_{bl} from MOE_{sc} is given in Equation 22.

[22]
$$MOE_{bl} = 5.83509 + 0.43178*MOE_{sc}$$
; $R^2 = 0.45$; $p < 0.0001$

Table 4. Phenotypic correlations between laboratory measures of wood properties of 2x4s (above the diagonal) and butt logs (below the diagonal) harvested from a 25-year-old wind-pollinated progeny test of Douglas-fir. All traits were measured on individual 2x4s, and log values were derived from the corresponding values measured on 2x4s.^a

Trait ^b	MOE_{bl}	$AMOE_{bl}$	MOE_{tv}	MOE_{sw}	MOE_{pca}	$AMOE_{pca}$	$\mathrm{DEN}_{\mathrm{dl}}$	ADEN _{dl}	KNT_{edg}	KNT _{cnt}	KNT _{tot}	KNT _{pca}	RA
MOE_{bl}	_	0.89	0.91	0.77	0.98	0.86	0.67	0.57	-0.21	0.11	0.02 ^{ns}	-0.04 ^{ns}	0.42
$AMOE_{bl}$	0.96	_	0.74	0.61	0.83	0.97	0.63	0.66	-0.15	-0.05 ^{ns}	-0.06	-0.13	-0.04 ^{ns}
$MOE_{tv} \\$	0.91	0.86	_	0.79	0.98	0.81	0.68	0.56	-0.14	0.19	0.07	0.06	0.51
MOE_{sw}	0.80	0.75	0.83	_	0.80	0.64	0.63	0.51	-0.13	0.18	0.04^{ns}	0.05^{ns}	0.46
MOE_{pca}	0.97	0.93	0.97	0.84	_	0.86	0.70	0.58	-0.18	0.15	0.03^{ns}	0.00^{ns}	0.47
$AMOE_{pca}$	0.94	0.97	0.92	0.79	0.95	_	0.66	0.69	-0.11	-0.02 ^{ns}	-0.05 ^{ns}	-0.09	-0.04 ^{ns}
DEN_{dl}	0.67	0.66	0.71	0.70	0.71	0.70	_	0.96	0.02^{ns}	0.12	0.09	0.11	0.23
ADEN_{dl}	0.65	0.68	0.69	0.67	0.69	0.72	1.00		0.07	0.02^{ns}	0.05^{ns}	0.06	-0.06
KNT_{edg}	-0.12	-0.09^{ns}	-0.06^{ns}	-0.10 ^{ns}	-0.10 ^{ns}	-0.05 ^{ns}	0.05^{ns}	0.07^{ns}		0.16	0.27	0.66	-0.14
KNT_{cnt}	-0.10 ^{ns}	-0.12	-0.02 ^{ns}	0.00^{ns}	-0.07^{ns}	-0.08 ^{ns}	-0.01 ^{ns}	-0.01 ^{ns}	0.43	_	0.47	0.77	0.33
KNT_{tot}	-0.07^{ns}	-0.08 ^{ns}	-0.02^{ns}	-0.04 ^{ns}	-0.06 ^{ns}	-0.05 ^{ns}	0.01^{ns}	0.01^{ns}	0.34	0.55	_	0.75	0.14
KNT_{pca}	-0.12	-0.12	-0.04 ^{ns}	-0.06^{ns}	-0.10 ^{ns}	-0.08 ^{ns}	0.02^{ns}	0.03^{ns}	0.73	0.85	0.78		0.16
RA	0.12	-0.13	0.18	0.16	0.15	-0.13	0.04^{ns}	-0.09 ^{ns}	-0.09 ^{ns}	0.09^{ns}	0.03^{ns}	0.01^{ns}	

 $[^]a All$ correlations are significant at p $\!<\!0.05$ except where indicated by ns. $^b Traits$ are described in Table 1.

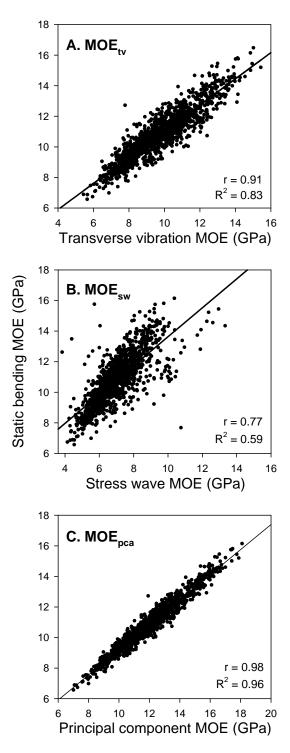


Fig. 2. Relationships between static bending MOE (MOE_{bl}) and other measures of wood stiffness measured on 2x4s harvested from a 25-year-old Douglas-fir progeny test. **A.** MOE_{tv} is transverse vibration MOE. **B.** MOE_{sw} is stress wave MOE. **C.** MOE_{pca} is principal component MOE score.

Table 5. Phenotypic correlations between wood properties of butt logs harvested from a 25-year-old wind-pollinated progeny test of Douglas-fir.^a

				Traits me	easured in th	ne field		
Trait ^b	Mea- sured ^c	MOE_{HM}	MOE_{ST}	VEL_{HM}	VEL _{ST}	$\mathrm{DEN}_{\mathrm{gd}}$	$\mathrm{DEN}_{\mathrm{dd}}$	DBH ₂₅
Stiffness								
$MOE_{bl} \\$	L	0.65	0.45	0.57	0.35	0.42	0.50	-0.13
$AMOE_{bl} \\$	L	0.66	0.46	0.58	0.38	0.40	0.51	-0.24
$MOE_{tv} \\$	L	0.59	0.41	0.54	0.33	0.37	0.46	0.02^{ns}
$MOE_{sw} \\$	L	0.52	0.35	0.47	0.25	0.34	0.41	0.06^{ns}
MOE_{pca}	L	0.63	0.44	0.56	0.35	0.40	0.49	-0.07^{ns}
$AMOE_{pca}$	L	0.63	0.44	0.58	0.38	0.36	0.49	-0.18
MOE_{HM}	F	1.00	0.59	0.89	0.40	0.58	0.57	-0.30
MOE_{ST}	F	0.59	1.00	0.39	0.90	0.55	0.52	-0.31
Density								
$DEN_{gd} \\$	F	0.58	0.55	0.15	0.14	1.00	0.65	-0.30
$DEN_{dd} \\$	F	0.57	0.52	0.33	0.29	0.65	1.00	-0.23
$DEN_{dl} \\$	L	0.46	0.38	0.38	0.28	0.38	0.60	-0.05 ^{ns}
$ADEN_{dl} \\$	L	0.46	0.38	0.39	0.29	0.37	0.60	0.10
Acoustic vel	locity							
VEL_{HM}	F	0.90	0.40	1.00	0.41	0.15	0.33	-0.21
VEL_{ST}	F	0.39	0.89	0.41	1.00	0.14	0.29	-0.26
Knots								
KNT_{edg}	L	-0.07^{ns}	-0.05^{ns}	0.02^{ns}	0.00^{ns}	-0.12	-0.02^{ns}	0.08^{ns}
KNT_{cnt}	L	-0.09^{ns}	-0.09^{ns}	-0.05^{ns}	-0.08^{ns}	-0.09^{ns}	-0.05^{ns}	0.34
KNT_{tot}	L	-0.09^{ns}	0.01^{ns}	0.00^{ns}	0.06^{ns}	-0.10 ^{ns}	-0.01 ^{ns}	0.08^{ns}
KNT_{pca}	L	-0.10^{ns}	-0.06^{ns}	-0.01_{ns}	-0.01 ^{ns}	-0.14	-0.03 ^{ns}	0.22
Age and dia	meter g	rowth						
ŘÀ	L	-0.01 ^{ns}	-0.04^{ns}	-0.08^{ns}	-0.10 ^{ns}	0.11^{ns}	-0.01 ^{ns}	0.37
DBH ₂₅	F	-0.30	-0.31	-0.21	-0.26	-0.30	-0.23	1.00

 $[^]a All$ correlations are significant at p $\!<\!0.05$ except where indicated by ns. $^b Traits$ are described in Table 1.

c'Measured' indicates that the trait was measured on individual 2x4s in the laboratory (L) or on logs or standing trees in the field (F).

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

We used 2x4s to study the relationships between knots, wood density, and stiffness.

We also used small clearwood samples from a subset of the 2x4s to study the relationships between MFA, wood density, and stiffness. The means, ranges, and coefficients for variation for wood properties measured on the full set of 2x4s was presented in Table 2, whereas data for the 2x4 subset are shown in Table 6.

 MOE_{bl} was moderately to strongly correlated with lumber density (DEN_{dl} and ADEN_{dl}), but only moderately correlated with disk density (DEN_{gd} or DEN_{dd}) (Tables 4-5; Fig. 3). For example, the correlations between MOE_{bl} and lumber density ranged from 0.57 to 0.67 at the lumber level (Table 4, above the diagonal) and from 0.65 to 0.67 at the log level (Table 4, below the diagonal). The phenotypic correlations between MOE_{bl} versus DEN_{gd} and DEN_{dd} ranged from 0.42 to 0.50 (Table 5). MOE_{pca} had moderate to high correlations with lumber, log, and disk densities (r_p = 0.40 to 0.71; Tables 4 and 5).

Table 6. Wood properties of a subset of 2x4s and small clearwood samples harvested from a 25-year-old wind-pollinated progeny test of Douglas-fir.

Trait ^a	N	Mean	STD	MIN	MAX	CV%
Stiffness (GPa))					
$\mathrm{MOE}_{\mathrm{bl}}$	58	11.2	1.6	7.5	15.0	14.4
$\mathrm{MOE}_{\mathrm{tv}}$	58	10.1	1.8	7.9	13.0	17.4
$\mathrm{MOE}_{\mathrm{sw}}$	58	7.2	1.1	4.8	9.4	15.4
MOE_{sc}	58	12.5	2.5	7.4	19.8	19.9
MFA (degrees	3)					
MFA_{sc}	58	14.1	3.1	9.2	21.6	22.0
Density (kg m	3)					
$\mathrm{DEN}_{\mathrm{dl}}$	56	484.1	37.1	409.1	566.0	7.7
DEN_{sc}	58	503.4	44.3	411.3	618.3	8.8
Knots (mm or	numbe	er)				
KNT_{edg}	58	14.0	5.9	2.0	27.0	42.4
KNT_{cnt}	58	19.3	4.0	12.0	29.0	20.7
KNT_{tot}	58	6.8	2.8	1.0	14.0	41.2
Ring age (year	rs)					
RA	58	9.3	0.3	9.0	9.5	3.2
Ring orientati	on (per	centage of 2x	4s in each c	lass) ^b		
RO (class)	58	R = 0, T = 1	00, and D =	0% of 2x4s		

^aTraits are described in Table 1. N is the number of 2x4s, Mean is the arithmetic mean, STD is the standard deviation, MIN is the minimum value, MAX is the maximum value, and CV% is the coefficient of variation (STD/Mean x 100). The small clearwood samples were collected from the base of each corresponding 2x4. ^bR is radial, T is tangential, and D is diagonal orientation.

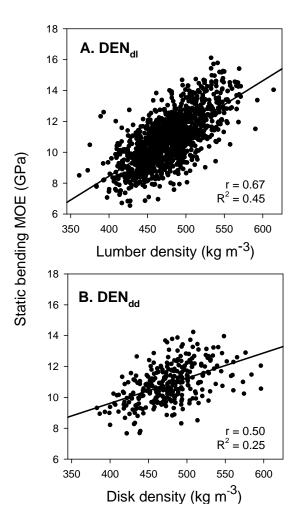


Fig. 3. Relationships between static bending MOE (MOE_{bl}) and densities measured on 2x4s and disks harvested from a 25-year-old Douglas-fir progeny test. **A.** DEN_{dl} is the dry lumber density. **B.** DEN_{dd} is the dry disk density.

The linear regression model used to predict lumber MOE_{bl} from lumber DEN_{dl} is given in equation 22, whereas the model used to predict log MOE_{bl} from log DEN_{dl} is given in equation 23.

[22]
$$MOE_{bl} = -3.49926 + 0.03006*DEN_{dl}$$
; $R^2 = 0.45$; $p < 0.0001$

[23]
$$MOE_{bl} = -1.57479 + 0.02605*DEN_{dl}$$
; $R^2 = 0.45$; $p < 0.0001$

The linear regression models used to predict log MOE_{bl} from DEN_{dd} and DEN_{gd} are given in equations 24 and 25.

[24]
$$MOE_{bl} = 3.08410 + 0.01633*DEN_{dd}$$
; $R^2 = 0.25$; $p < 0.0001$

[25]
$$MOE_{bl} = 2.30556 + 0.01042*DEN_{gd}$$
; $R^2 = 0.17$; $p < 0.0001$

 DEN_{sc} was moderately correlated with MOE_{bl} , MOE_{tv} , and MOE_{sw} (r_p = 0.69 to 0.72) and highly correlated with DEN_{dl} (r_p = 0.86; Table 7). As a result, the correlations between DEN_{dl} and stiffness (MOE_{bl} , MOE_{tv} , and MOE_{sw}) were nearly identical to the correlations involving DEN_{sc} .

Table 7. Phenotypic correlations between wood properties of 2x4s and small clearwood samples harvested from a 25 year-old wind-pollinated progeny test of Douglas-fir (n = 56-58).^a

Trait ^b	MOE_{bl}	MOE_{tv}	MOE_{sw}	MOE_{sc}	MFA_{sc}	DEN_{sc}	DEN _{dl}			
Stiffness of	Stiffness of lumber									
MOE_{bl}	_	_	_	_	_	_	_			
MOE_{tv}	0.93	_	_	_		_	_			
MOE_{sw}	0.79	0.74	_	_		_	_			
Wood prop	Wood properties of small clearwood samples									
MOE_{sc}	0.67	0.74	0.63	_	_	_	_			
MFA_{sc}	-0.42	-0.55	-0.46	-0.87	_	_	_			
DEN_{sc}	0.72	0.70	0.69	0.73	-0.36	_	_			
Density										
$\mathrm{DEN}_{\mathrm{dl}}$	0.70	0.70	0.66	0.63	-0.30	0.86	_			
Knots										
KNT_{edg}	-0.24 ^{ns}	-0.15^{ns}	-0.09^{ns}	-0.15^{ns}	0.12^{ns}	-0.05^{ns}	0.09^{ns}			
KNT_{cnt}	0.03^{ns}	0.18^{ns}	0.23^{ns}	0.33	-0.38	0.20^{ns}	0.21^{ns}			
KNT _{tot}	0.10^{ns}	0.08^{ns}	0.22^{ns}	0.14^{ns}	-0.01 ^{ns}	0.29	0.36			

 $^{^{}a}$ All correlations are significant at p < 0.05 except where indicated by ns.

The correlations between MFA_{sc} versus MOE_{bl}, MOE_{tv}, and MOE_{sw} (r_p = -0.42 to -0.55) were negative and considerably weaker than the correlation between MFA_{sc} and MOE_{sc} (r_p = -0.87; Table 7). MFA_{sc} was also weakly and negatively correlated with DEN_{dl} (r_p = -0.30) and DEN_{sc} (r_p = -0.36).

On a lumber basis, MOE_{bl} was weakly correlated with KNT_{edg} and KNT_{cnt} (r_p = -0.21 and 0.11), and uncorrelated with KNT_{tot} and KNT_{pca} (p > 0.05; Table 4, Fig. 4). MOE_{tv} , MOE_{sw} , and MOE_{pca} were also weakly correlated with the presence of knots at both the

^bTraits are described in Table 1.

log and lumber levels (Table 4). The correlations between stiffness and knot traits at the log level were similar to those at lumber level (Table 4, below the diagonal).

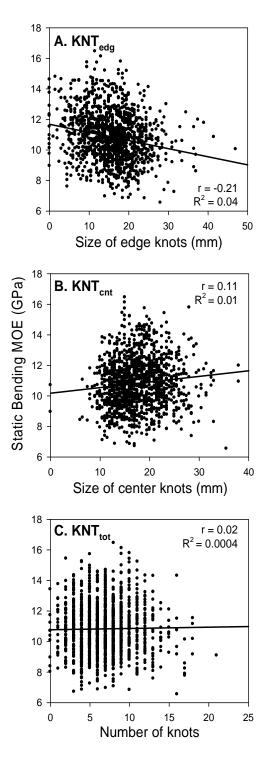


Fig. 4. Relationships between static bending MOE (MOE_{bl}) and knot traits measured on 2x4s harvested from a 25-year-old Douglas-fir progeny test. **A.** KNT_{edg} is the diameter of the largest edge knot. **B.** KNT_{cnt} is the diameter of the largest center knot. **C.** KNT_{tot} is the total number of knots greater than 12.7 mm.

3.4. Combined effects of density, MFA, and knots

Together, density (DEN_{dl} or DEN_{sc}), MFA_{sc}, and KNT_{edg} explained 49% to 62% of the variance in 2x4 MOE_{bl}, MOE_{tv}, and MOE_{sw} (Fig. 5). The path coefficients suggest that density (DEN_{dl} or DEN_{sc}) had a much greater direct effect on MOE than did MFA_{sc} or KNT_{edg} (Fig. 5). The path coefficients between MFA_{sc} and MOE_{bl} (-0.16 to -0.19) were considerably weaker than the path coefficients between MFA_{sc} and either MOE_{tv} or MOE_{sw} (-0.24 to -0.35). In the lumber subset (i.e., 2x4s from which small clearwood samples were collected), KNT_{edg} had no significant correlation with MOE_{bl}, MOE_{tv}, or MOE_{sw} (p > 0.05; Table 7), but it did have weak negative correlations with these stiffness traits in the full lumber dataset (r_p = -0.13 to -0.21, p < 0.0001; Table 4).

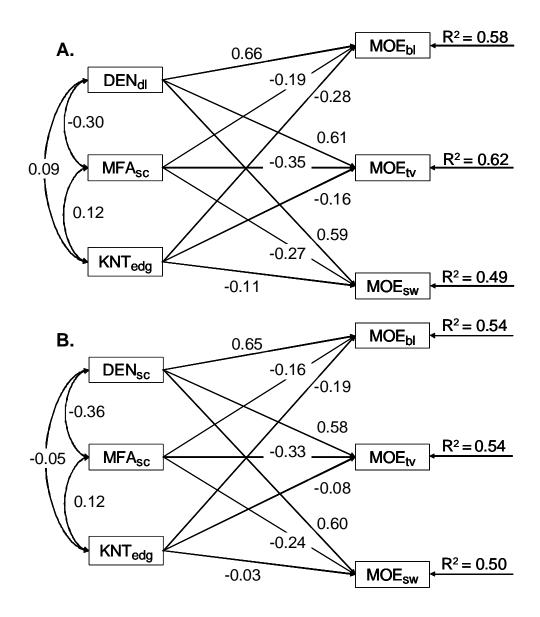


Fig. 5. Path diagram showing the relationships between selected wood properties (DEN_{dl}, DEN_{sc}, MFA_{sc}, and KNT_{edg}) versus direct and indirect measures of stiffness of 2x4s harvested from a 25-year-old Douglas-fir progeny test. All path coefficients (i.e., straight-line relationships between traits) were significant at p < 0.0001. The correlation coefficients (i.e., curved-line relationships) between density (DEN_{dl} and DEN_{sc}) versus MFA_{sc} (-0.30 and -0.36) were significant at p < 0.02, whereas all other correlations were nonsignificant.

3.5. Effects of ring age and ring orientation on bending stiffness, density, and knots On a lumber basis, MOE_{bl} and DEN_{dl} were positively correlated with RA ($r_p = 0.42$ and 0.23; Fig. 6). MOE_{bl} was also higher when the load was applied tangentially to the growth rings as compared to radially or diagonally (Fig. 7). The 2x4s with tangentially or diagonally applied loads also had higher average ring ages (i.e., 9.6 and 11.7 years) compared to the 2x4s with radially applied loads (6.4 years). As expected, DEN_{dl} was unaffected by ring orientation (data not shown). Based on these results, we adjusted MOE_{bl} and MOE_{pca} using RA and RO as covariates (= $AMOE_{bl}$ and $AMOE_{pca}$), and adjusted DEN_{dl} using RA as covariate (= $ADEN_{dl}$). These were the only statistically significant covariates in the analyses of MOE_{bl} , MOE_{pca} , and DEN_{dl} (Table 8).

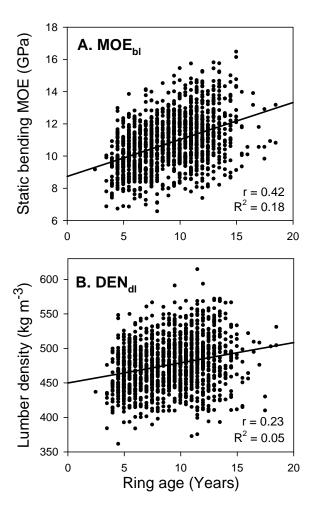


Fig. 6. Relationships between static bending MOE (MOE_{bl}) and lumber density (DEN_{dl}) versus ring age (RA) of 2x4s harvested from a 25-year-old Douglas-fir progeny test. **A.** MOE_{bl} is static bending MOE of lumber. **B.** DEN_{dl} is dry lumber density.

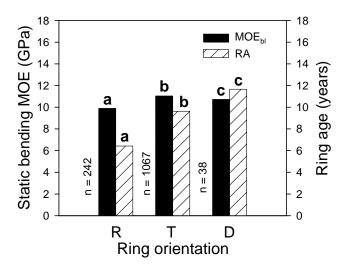


Fig. 7. Relationships between ring orientation versus static bending MOE (MOE_{bl}) and ring age (RA) of 2x4s harvested from a 25-year-old Douglas-fir progeny test. **R** is radial, **T** is tangential, and **D** is diagonal ring orientation. All differences among ring orientation classes are significant at p = 0.05 using Tukey's HSD.

Table 8. Covariance parameter estimates for ring age (RA) and ring orientation (RO) in the analyses of MOE_{bl} , MOE_{pca} , and DEN_{dl} of lumber harvested from a 25-year-old wind pollinated progeny test of Douglas-fir (standard errors are given in parentheses).^a

			Ring orientation (RO) ^b		
Trait	Intercept	Ring age (RA) ^b	R ^c	T ^c	D ^c
MOE _{bl}	8.5134 (0.14)	0.2295 (0.01)	0.0 (nd)	0.3673 (0.08)	0.0953 (0.19)
MOE_{pca}	9.1275 (0.16)	0.3066 (0.01)	0.0 (nd)	0.4416 (0.10)	0.1205 (0.22)
DEN_{dl}	446.20 (4.65)	3.4672 (0.17)	ns	ns	ns

^aTraits are described in Table 1.

^bAll fixed effects are significant at p < 0.0001 except where indicated by ns. nd indicates that the standard error was not determined.

^cRing orientation of 2x4s in relation to bending load.

3.6. Bending MOE and knots, but not density were associated with lumber grade The lumber grades of the 2x4s differed significantly in MOE_{bl} and KNT_{edg}, but not in DEN_{dl} (Fig. 8). MOE_{bl}, MOE_{tv}, and MOE_{sw} were higher for the STR grade followed by the S1 and S2 grades (p < 0.0001). Because we had only one 2x4 in each of the S3 and E grades, we did not include those 2x4s in these analyses. In contrast to stiffness, the largest edge knots were observed for the S2 grade, followed by the S1 and STR grades. DEN_{dl} ranged from 474.7 to 478.0 kg m⁻³ among the three visual grades.

3.7. Stiffness and density are heritable

 MOE_{bl} had a moderate narrow-sense individual-tree heritability ($h_i^2 = 0.31$) (Table 9). Heritabilities of MOE_{tv} , MOE_{sw} , and MOE_{pca} were similar to that of MOE_{bl} ($h_i^2 = 0.22$ to 0.38; Table 9). The heritabilities of lumber stiffness adjusted to a ring age of 9.1 years and a radial ring orientation ($AMOE_{bl}$ $h_i^2 = 0.35$ and $AMOE_{pca}$ $h_i^2 = 0.40$) were higher than the heritabilities of the unadjusted traits. DEN_{dl} and $ADEN_{dl}$ had moderately high heritabilities ($h_i^2 = 0.41$ to 0.42), the heritabilities of Den_{gd} and Den_{dd} were low to moderate ($h_i^2 = 0.14$ to 0.29), and the heritabilities of other wood properties are presented in Table 9.

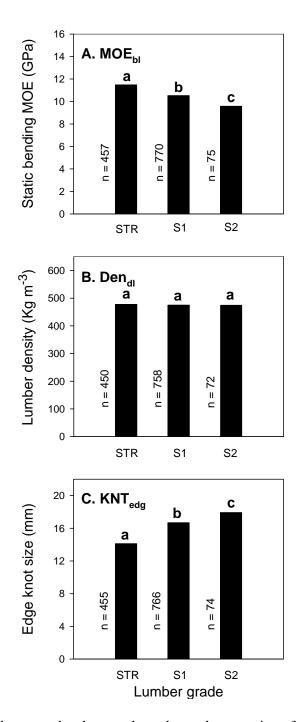


Fig. 8. Relationships between lumber grade and wood properties of 2x4s harvested from a 25-year-old Douglas-fir progeny test. **A.** MOE_{bl} is static bending MOE. **B.** DEN_{dl} is dry lumber density. **C.** KNT_{edg} is the diameter of the largest edge knot. Lumber grade STR is select structural, S1 is select 1, and S2 is select 2. Lumber grades marked with same letter are not statistically different from one-another at p = 0.05 using Tukey's HSD.

Table 9. Variance components, individual-tree narrow-sense heritabilities (h_i²), and standard errors of heritabilities (SE) for Douglas-fir wood properties and growth in a 25-year-old wind-pollinated progeny test of Douglas-fir.

Variance components ^b									
Trait ^a	σ^2_S	$\sigma^2_{F(S)}$	$\sigma^2_{R(S)}$	$\sigma^2_{R^*F(S)}$	$\sigma^2_{\ arepsilon}$	${h_i}^2$			
Stiffness (GP	a)								
MOE_{bl}	0.00	0.15	0.19	0.18	1.13	0.31			
$AMOE_{bl}$	0.00	0.18	0.14	0.05	1.27	0.35			
$\mathrm{MOE}_{\mathrm{tv}}$	0.02	0.16	0.15	0.26	1.03	0.33			
MOE_{sw}	0.00	0.05	0.06	0.19	0.45	0.22			
MOE_{pca}	0.00	0.25	0.25	0.21	1.47	0.38			
$AMOE_{pca}$	0.00	0.27	0.18	0.00	1.74	0.40			
MOE_{HM}	0.00	0.16	0.18	0.00	1.32	0.33			
MOE_{ST}	0.13	0.18	0.45	0.00	2.30	0.22			
Density (kg n	n ⁻³)								
$\mathrm{DEN}_{\mathrm{gd}}$	39.43	205.43	400.98	0.00	1894.94	0.29			
$\mathrm{DEN}_{\mathrm{dd}}$	22.87	59.81	160.77	0.00	1215.14	0.14			
$\mathrm{DEN}_{\mathrm{dl}}$	47.59	140.14	26.41	51.92	825.60	0.41			
$ADEN_{dl} \\$	53.27	144.43	22.44	22.05	860.17	0.42			

Table 9 continued on the next page.

Table 9 cont. Variance components, individual-tree narrow-sense heritabilities (h_i²), and standard errors of heritabilities (SE) for Douglas-fir wood properties and growth in a 25year-old wind-pollinated progeny test of Douglas-fir.

Variance components ^b									
Trait ^a	σ^2_S	$\sigma^2_{F(S)}$	$\sigma^2_{R(S)}$	$\sigma^2_{R^*F(S)}$	$\sigma^2_{\ arepsilon}$	h _i ²			
Acoustic V	elocity (m s ⁻¹)							
VEL_{HM}	0	4600	2215	0	31533	0.38			
VEL_{ST}	3485	4392	4091	0	39649	0.30			
Knots (mm	, number, or	score)							
KNT_{edg}	0.00	0.20	0.57	3.95	16.18	0.03			
KNT_{cnt}	0.00	0.00	0.00	0.44	13.42	0.00			
KNT_{tot}	0.00	0.38	0.00	0.05	7.87	0.14			
KNT_{pca}	0.00	0.31	0.00	2.60	21.17	0.04			
Diameter g	rowth (cm)								
DBH ₂₅	0.20	0.50	0.00	1.50	9.66	0.13			

^aTraits are described in Table 1. $^{b}\sigma_{S}^{2}$, $\sigma_{F(S)}^{2}$, $\sigma_{R^{*}F(S)}^{2}$, and σ_{ε}^{2} are variance components associated with S_{s} , $F(S)_{sf}$, $R^{*}F(S)_{srf}$, and ε_{srfl} in model 10.

3.8. Genetic correlations between stiffness traits and density

The genetic correlations between MOE_{bl} versus MOE_{tv} and MOE_{sw} were higher than their respective phenotypic correlations ($r_a = 1.03$ and 0.98; Table 10). MOE_{bl} , MOE_{tv} , and MOE_{sw} were also highly correlated with $AMOE_{bl}$, MOE_{pca} , and $AMOE_{pca}$. The genetic correlations between the laboratory measures of stiffness (MOE_{bl} , MOE_{tv} , and MOE_{sw}) versus the field measures (MOE_{HM} and MOE_{ST}) were moderate to strong ($r_a = 0.54$ to 0.93; Table 10). The genetic correlation between DEN_{dl} versus MOE_{bl} , MOE_{tv} , and MOE_{sw} ranged from 0.81 to 0.91. The genetic correlation between DEN_{dd} versus MOE_{bl} , MOE_{tv} , and MOE_{sw} ranged from 0.37 to 0.48 (Table 11).

3.9. Genetic control of knots

 KNT_{tot} was weakly heritable ($h_i^2 = 0.14$), whereas KNT_{ent} and KNT_{edg} had no significant genetic variation (Table 12). KNT_{tot} had a favorable but weak genetic correlation with bending stiffness (Table 12).

Table 10. Narrow-sense genetic (r_A) , error (r_E) , and phenotypic (r_P) correlations between stiffness and velocity traits of butt logs harvested from a 25-year-old wind-pollinated progeny test of Douglas-fir (standard errors are given in parentheses).

Trait 1 ^a	Trait 2	Families	Trees	r_{A}	$r_{ m E}$	r_{P}
Direct and	indirect e	estimates of	wood s	tiffness		
MOE_{bl}	$MOE_{tv} \\$	50	368	1.03 (0.03)	0.89 (0.01)	0.91 (0.00)
MOE_{bl}	MOE_{sw}	50	370	0.98 (0.07)	0.78 (0.02)	0.80 (0.01)
MOE_{bl}	MOE_{pca}	50	367	1.01 (0.01)	0.97 (0.00)	0.97 (0.00)
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)
$MOE_{tv} \\$	MOE_{sw}	50	369	0.99 (0.05)	0.81 (0.02)	0.83 (0.01)
$MOE_{tv} \\$	MOE_{pca}	50	367	1.00 (0.01)	0.96 (0.00)	0.97 (0.00)
$MOE_{tv} \\$	MOE_{HM}	50	279	0.93 (0.16)	0.56 (0.05)	0.59 (0.02)
$MOE_{tv} \\$	MOE_{ST}	50	302	0.65 (0.24)	0.39 (0.05)	0.42 (0.02)
MOE_{sw}	MOE_{pca}	50	367	0.98 (0.05)	0.83 (0.02)	0.84 (0.01)
MOE_{sw}	MOE_{HM}	50	281	0.89 (0.22)	0.49 (0.05)	0.52 (0.02)
MOE_{sw}	MOE_{ST}	50	304	0.54 (0.28)	0.33 (0.06)	0.35 (0.02)
MOE_{pca}	MOE_{HM}	50	278	0.91 (0.16)	0.60 (0.04)	0.63 (0.02)
MOE_{pca}	MOE_{ST}	50	300	0.62 (0.24)	0.42 (0.05)	0.44 (0.02)
MOE_{HM}	MOE_{ST}	50	279	0.96 (0.20)	0.55 (0.05)	0.59 (0.01)
Stiffness v	s stress wa	ve velocity				
MOE_{bl}	VEL_{HM}	50	338	0.75 (0.18)	0.55 (0.04)	0.57 (0.02)
MOE_{bl}	VEL_{ST}	50	364	0.49 (0.17)	0.33 (0.04)	0.35 (0.02)
$MOE_{tv} \\$	VEL_{HM}	50	336	0.80 (0.17)	0.51 (0.02)	0.54 (0.01)
MOE_{tv}	VEL_{ST}	50	363	0.60 (0.14)	0.29 (0.01)	0.34 (0.01)
MOE_{sw}	VEL_{HM}	50	338	0.67 (0.25)	0.45 (0.05)	0.47 (0.02)
MOE_{sw}	VEL_{ST}	50	365	0.51 (0.26)	0.22 (0.05)	0.25 (0.03)
MOE_{pca}	VEL_{HM}	50	334	0.78 (0.16)	0.53 (0.04)	0.56 (0.02)
MOE_{pca}	VEL _{ST}	50	360	0.57 (0.15)	0.32 (0.04)	0.35 (0.02)
VEL_{HM}	VEL_{ST}	50	335	0.96 (0.16)	0.33 (0.05)	0.41 (0.02)

^aTraits are described in Table 1.

Table 11. Narrow-sense genetic (r_A) , error (r_E) , and phenotypic (r_P) correlations between stiffness, density, and growth traits of butt logs harvested from a 25-year-old wind-pollinated progeny test of Douglas-fir (standard errors are given in parentheses).

Trait 1 ^a	Trait 2	Families	Trees	r_{A}	$r_{\rm E}$	$r_{\rm P}$
Stiffness v	s density	of wood				
$MOE_{bl} \\$	$\mathrm{DEN}_{\mathrm{dd}}$	50	307	0.37 (0.37)	0.51 (0.05)	0.50 (0.02)
$MOE_{tv} \\$	$DEN_{dd} \\$	50	305	0.48 (0.29)	0.46 (0.05)	0.46 (0.02)
$MOE_{sw} \\$	$DEN_{dd} \\$	50	307	0.40 (0.37)	0.41 (0.05)	0.41 (0.02)
MOE_{pca}	$DEN_{dd} \\$	50	303	0.46 (0.29)	0.49 (0.05)	0.49 (0.02)
MOE_{HM}	DEN_{dd}	50	280	0.47 (0.43)	0.58 (0.04)	0.57 (0.02)
MOE_{ST}	DEN_{dd}	50	303	0.50 (0.36)	0.53 (0.04)	0.52 (0.02)
MOE_{bl}	DEN_{dl}	50	370	0.91 (0.01)	0.64 (0.03)	0.67 (0.01)
$MOE_{tv} \\$	DEN_{dl}	50	369	0.91 (0.08)	0.68 (0.03)	0.71 (0.01)
MOE_{sw}	DEN_{dl}	50	372	0.81 (0.13)	0.70 (0.03)	0.70 (0.01)
MOE_{pea}	DEN_{dl}	50	367	0.88 (0.09)	0.69 (0.03)	0.71 (0.01)
MOE_{HM}	DEN_{dl}	50	281	0.68 (0.24)	0.44 (0.05)	0.46 (0.02)
MOE_{ST}	DEN_{dl}	50	304	0.56 (0.24)	0.35 (0.05)	0.38 (0.03)
Stiffness v	s orowth					
MOE _{bl}	DBH ₂₅	50	370	0.10 (0.40)	-0.14 (0.05)	-0.12 (0.02)
MOE_{tv}	DBH ₂₅	50	369	0.20 (0.04)	0.00 (0.06)	0.02 (0.02)
MOE_{sw}	DBH ₂₅	50	371	0.57 (0.39)	0.02 (0.06)	0.06 (0.02)
MOE_{pca}	DBH ₂₅	50	366	0.15 (0.45)	-0.09 (0.06)	-0.07 (0.02)
MOE_{HM}	DBH ₂₅	50	282	0.61 (0.53)	-0.38 (0.06)	-0.30 (0.03)
MOE_{ST}	DBH ₂₅	50		-0.24 (0.36)	-0.32 (0.06)	-0.31 (0.03)

^aTraits are described in Table 1.

Table 12. Narrow-sense genetic (r_A) , error (r_E) , and phenotypic (r_P) correlations between stiffness and knot traits of butt logs harvested from a 25-year-old wind-pollinated progeny test of Douglas-fir (standard errors are given in parentheses).

Trait 1 ^a	Trait 2	Families	Trees	r_A	$r_{\rm E}$	r_{P}
Stiffness v	vs knots					
MOE_{bl}	KNT_{edg}	50	371	$0.24 (1.14)^{b}$	-0.13 (0.06)	-0.12 (0.02)
MOE_{bl}	$KNT_{ent} \\$	50	371	$0.00 (0.00)^{b}$	-0.10 (0.05)	-0.09 (0.02)
MOE_{bl}	$KNT_{tot} \\$	50	371	0.22 (0.43)	-0.09 (0.06)	-0.07 (0.02)

^aTraits are described in Table 1.

^bGenetic variation was not significant for trait 2.

4. Discussion

4.1. Direct and indirect tests yielded different estimates of wood stiffness

We used three techniques (static bending, transverse vibration, and stress waves) to estimate the stiffness of Douglas-fir lumber. Although the resulting estimates are highly correlated with each other, these techniques use different principles to estimate MOE. Growth ring orientation, moisture content, knots, and shear effects may differentially influence estimates of MOE obtained from these techniques (Gerhards 1975; Mack 1979, cited in Hansen et al. 2004; Gerhards 1982; Ilic 2001; Beall 2002; Wang et al. 2003; Greens and Rosales 2006). Therefore, we used PCA to combine the advantages of alternative measurement techniques and to lessen the impacts of measurement errors (i.e., by combining independent estimates of MOE). Although the resulting MOE PCA scores (MOE_{pca}) may be superior to any of the single estimates of MOE, comparable results were obtained from analyses of MOE_{bl} and MOE_{pca}. Therefore, we focus our discussion on MOE_{bl}.

On average MOE_{tv} and MOE_{sw} underestimated MOE_{bl} by 10 to 35%. In other studies, differences among estimation methods were attributed to shear effects (Lindström et al. 2002; Raymond et al. 2007) and moisture content (Gerhards 1975; Wu 1999). Shear is the slippage of wood layers along the grain that occurs when wood is subjected to slowly increasing loads, such as the loads we used in our bending tests (Mack 1979, cited in Hansen et al. 2004). When this occurs, the apparent bending MOE of 2x4s is expected to be lower than the MOE of individual rings. Because shear effects do not influence

 MOE_{tv} and MOE_{sw} , these estimates were expected to be higher than MOE_{bl} , but this was not the case.

Estimates of MOE may also be affected by moisture content when moisture content is below the fiber saturation point. Although bending stiffness increases by 2% for each 1% reduction in bound water (Gerhards 1975), stress wave velocity increases by only 1% (Wu 1999). Therefore, MOE_{bl} may be larger than MOE_{sw} because our 2x4s were below the fiber saturation point (< 7% MC). Stress wave MOE also underestimated bending MOE in sweet gum, southern pine, and 4-year-old radiata pine (Gerhards 1975; Halabe et al. 1997; Lindström et al. 2004), but overestimated bending MOE in western hemlock, Sitka spruce, lodgepole pine, and 3-year-old radiata pine (Wang et al. 2001; Lindström et al. 2002). Therefore, it seems that a consistent relationship may not be found among these alternative measures of MOE. Although the different measurement techniques ranked our 2x4s consistently (discussed below), they yielded different absolute estimates of MOE, and it is unclear whether these absolute differences will be repeated in other situations.

Of the two field-based stress wave tools, the ST300 overestimated MOE_{bl} by 15%, whereas the HM200 underestimated MOE_{bl} by 13%. Although both tools are based on the same principle (stress waves), the ST300 measures stress wave velocity in the outerwood of the tree, whereas the HM200 provides an integrated estimate of stress wave velocity across the whole log. Because the outerwood is denser and stiffer than the juvenile core (Megraw et al. 1986), the higher values for VEL_{ST} and MOE_{ST} (i.e., as compared to VEL_{HM} and MOE_{HM}) were expected. Although we developed equations to

predict MOE_{bl} from the lab and field-based tools (discussed below), absolute estimates of MOE are not necessary for making genetic selections and obtaining genetic gain.

4.2. Phenotypic correlations between bending stiffness and indirect estimates of wood stiffness

Our study suggests that the MOE_{bl} of 2x4s and logs can be predicted from MOE_{tv} ($R^2 = 0.83$) and MOE_{sw} ($R^2 \ge 0.59$) (Fig. 2). Our correlations between bending stiffness and transverse vibration MOE were comparable to those observed in red pine ($r_p = 0.97$), jack pine ($r_p = 0.92$), and southern pine ($r_p = 0.83$) (Ross et al. 1994; Halabe et al. 1997). In contrast, our correlations between bending stiffness and stress wave MOE were lower than those observed in radiata pine and Eucalyptus ($r_p = 0.89$ to 0.95) (Ilic 2001; Wang et al. 2001, 2002; Lindstöm et al. 2002, 2004; Raymond et al. 2007; Wang et al. 2007). In the plot of MOE_{bl} versus MOE_{sw} (Fig. 2B), two populations of values appeared to be present, but we are unable to explain this effect. Therefore, we may have underestimated the true correlation between MOE_{bl} and MOE_{sw} in Douglas-fir.

Because MOE_{bl} is costly and time-consuming to measure, it is not feasible to use MOE_{bl} for making genetic selections in large-scale breeding programs. However, the correlation between MOE_{bl} and MOE_{sw} indicates that field tools based on stress waves (e.g., HM200 and ST300) will be useful for predicting bending stiffness in Douglas-fir breeding programs, and quantitative genetic analysis support these conclusions (Cherry et al. 2008).

On a log and tree basis, bending stiffness was more highly correlated with MOE_{HM} $(R^2 = 0.42)$ than with MOE_{ST} $(R^2 = 0.20)$. In radiata pine, bending stiffness was also more strongly correlated with HM200 MOE than with ST300 MOE (Wang et al. 2003). A number of reasons have been cited for the better performance of the HM200 compared to the ST300 (Andrews 2000; Carter et al. 2005; Cherry et al. 2008). First, because the HM200 samples a greater amount of wood than does the ST300 (i.e., whole log versus only the outerwood between the ST300 probes), it is less affected by within-tree variation in MOE. Second, the HM200 estimates stress wave velocity from the resonant frequencies of waves that repeatedly reverberate between the ends of the logs. In contrast, the ST300 estimates velocity from a single pass of the stress wave (time-offlight). Compared to resonance-based methods on logs, large knots and branches greatly affect the precision of time-of-flight measurements made on standing trees (Briggs et al. 2005). The HM200 is also less complicated and demanding to operate than the ST300 because the ST300 measurements are influenced by the insertion angle of the probes and hammer impact angle (Andrews 2000). Nonetheless, simply increasing the distance between the probes and taking many measurements per tree can improve the prediction potential of standing tree tools such as the ST300 (Wanger et al. 2003).

4.3. Wood stiffness is phenotypically correlated with wood density, MFA, and knots Wood density, MFA, and knots are believed to be the most important traits affecting the stiffness of wood (Ifju and Kennedy 1962; Tsoumis 1991; Beaulieu et al. 2006). Furthermore, reports from studies that focused on clearwood MOE suggested that density and MFA are the most important traits in knot free wood (Evans and Ilic 2001; Yang and

Evans 2003; Xu et al. 2004). Therefore, we used 2x4s to study the relationships between wood stiffness, density, and knots; and small clearwood specimens to study the associations between stiffness, density, and MFA.

4.3.1. Correlations between bending stiffness and wood density

On a tree basis, the phenotypic correlation between MOE_{bl} and DEN_{dl} ($r_p = 0.67$) was stronger than the correlation between MOE_{bl} and DEN_{dd} ($r_p = 0.50$), and roughly comparable to the correlation between MOE and density in small clearwood samples of Douglas-fir ($r_p = 0.76$; B. Lachenbruch, pers. comm., 8 August 2008). One reason for the higher correlation between MOE_{bl} and DEN_{dl} is that these traits were measured on the same 2x4s, whereas DEN_{dd} was measured on basal wood disks. The basal wood disks sampled a different vertical portion of a tree (immediately below the 2x4s) and sampled outerwood that was not sampled by the rectangular 2x4s. In radiata pine, the radial variation in density is greater than the vertical variation (Xu et al. 2004). Therefore, it appears that within-tree variation in wood properties resulted in only a moderate correlation between DEN_{dl} and DEN_{dd} ($r_p = 0.60$), and between MOE_{bl} and DEN_{dd}. In contrast to our results, bending stiffness was more strongly correlated with the density of wood disks collected at breast height ($r_p = \sim 0.75$; Knowles et al. 2003, cited in Johnson and Gartner 2006; Johnson and Gartner 2006). Therefore, densities obtained from breastheight increment cores may be more strongly correlated with bending stiffness than are densities obtained from basal wood disks. Although increment core densities are often used to select superior trees for seed orchards and tree breeding, the density of increment cores was not evaluated in this study.

The phenotypic correlation between DEN_{dl} and DEN_{sc} ($r_p = 0.80$; 2x4 basis) was stronger than the correlation between DEN_{dl} and DEN_{dd} ($r_p = 0.60$; log basis), perhaps because the 2x4s and small clearwood samples shared the same growth rings. In contrast, the wood disks sampled a larger proportion of outerwood and greater number of growth rings than did the 2x4s. Because variation in wood density (i.e., measured on lumber, disks, or small clearwood samples) explained less than 45% of the phenotypic variation in MOE_{bl} , we studied whether better predictive equations could be developed by incorporating additional traits (discussed below).

4.3.2. MFA was negatively correlated with stiffness

On a lumber basis, MOE_{bl} had a moderate negative phenotypic correlation with MFA_{sc} ($r_p = -0.42$). Comparable negative correlations between stiffness and MFA have been reported in Douglas-fir and several other species, including radiata pine, loblolly pine, red pine, western pine, and Eucalyptus spp. (Downes et al. 2002; Knowles et al. 2003, cited in Johnson and Gartner 2006; Yang and Evans 2003; Baltunis et al. 2007; Raymond et al. 2007; B. Lachenbruch, pers. comm., 8 August 2008). Studies on the elastic properties of cell wall layers using fiber composite models suggest that small MFAs increase wood stiffness because cell layers with vertically oriented microfibrils (i.e., small MFAs) are stiffer than cell layers with more horizontally oriented microfibrils (i.e., large MFAs; Cave 1968; Megraw 1985; Cave and Walker 1994).

Compared to our results, the phenotypic correlation between bending stiffness and MFA was generally stronger in radiata pine (-0.45 to -0.82; Bendsten and Senft 1986; Downes

et al. 2002; Raymond et al. 2007), red pine (-0.68; Deresse et al. 2003), cottonwood (-0.62; Bendsten and Senft 1986), and Eucalyptus *spp*. (-0.93; Yang and Evans 2003). MOE increased 5- to 6-fold in radiata pine, loblolly pine, and Sitka spruce when MFA decreased from 40° to 10°, and this decrease was associated with increasing ring age (Cave 1968; Bendsten and Senft 1986). Our variation in MFA_{sc} (9.2° to 21.6°) may be modest because we selected small clearwood samples from 2x4s that had a ring age of only 9.0 to 9.5 years. Similarly, the variation in MFA (9.4° to 23.2°), and the correlation between MFA and stiffness (-0.34 to -0.45) were modest in studies involving older Douglas-fir (17 to 49-years old; B. Lachenbruch, pers. comm., 8 August 2008). However, the correlation between MFA and bending stiffness was slightly stronger (-0.56 to -0.58) in a study of increment cores collected from 41-year-old Douglas-fir trees growing in New Zealand (Knowles et al. 2003, cited in Johnson and Gartner 2006).

Earlier studies on the 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°; Ifju and Kennedy 1962; Erickson and Arima 1974) but correlations between stiffness and MFA were not reported. Based on our analysis, MFA_{sc} explained only 18% of the phenotypic variation in MOE_{bl} compared to 52% for Den_{sc}. 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 is expected to 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 MOE_{bl} and MFA_{sc} was only moderate (r_p = -0.42), the correlation between MOE_{sc} and MFA_{sc} was strong (r_p = -0.87). Strong correlations between SilviScan MOE and SilviScan MFA have been widely reported (Knowles et al. 2003, cited in Johnson and Gartner 2006; Baltunis et al. 2007). These correlations, however, are expected to overestimate the true correlation between bending stiffness and MFA because SilviScan MOE and SilviScan MFA are predicted from the same data; i.e., azimuthal intensity profile calculated from X-ray diffraction data.

4.3.3. Knots were weakly correlated with stiffness

On a lumber basis, MOE_{bl} had a weak negative phenotypic correlation with KNT_{edg} (r_p = -0.21), weak positive correlation with KNT_{cnt} (r_p = 0.11), and no significant phenotypic correlation with KNT_{tot} . Knots lower lumber stiffness because they cause deviations from optimal grain orientation and concentrate stress (i.e., at the knot) (Megraw 1986; Kabir et al. 2003). Negative associations between knot traits and stiffness have been reported in white spruce, Scots pine, Japanese larch and other species (Samson 1993; Forest Products Laboratory 1999; Takeda and Hashizume 1999; As et al. 2006; Beaulieu et al. 2006).

Although two of the knot traits had significant correlations with 2x4 stiffness, these correlations were weak, presumably because the knots were small and few. The largest knot was only 47 mm (1.85 in) in diameter, and the average sizes of KNT_{edg} and KNT_{cnt} were below 18 mm (0.70 in). Furthermore, there were only about 7 knots per 2x4. In white spruce lumber, the correlation between knot size (mean = 17 mm) and bending MOE was also low and negative ($r_p = -0.20$; Beaulieu et al. 2006), but the correlation

between the number of knots and bending MOE was moderate (r_p = -0.40), perhaps because the lumber had many more knots (38 per board) than we found in our 2x4s. In contrast to progeny tests that are planted on a uniformly spaced grid, variation in spacing should be larger in operational plantations and naturally regenerated stands. Because variation in spacing should lead to greater variation in knot traits (Roth et al. 2007), the correlations between knot traits and stiffness may be stronger in these stands. In white spruce, knot traits also had moderately negative correlations with MOR on a family mean basis (Beaulieu et al. 2006), but we did not measure MOR in this study.

4.4. Combined effects of density, MFA, and knots

We used path analysis to partition the correlations between stiffness versus density, MFA, and knots 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 are estimated via path coefficients (i.e., straight-line relationships in Fig. 5). The correlations between the variables are indicated by the curved-line relationships in Fig. 5. Compared to MFA_{sc} and KNT_{edg}, the larger path coefficients for DEN_{dl} and DEN_{sc} suggest that wood density has the greatest direct effect on 2x4 stiffness (Fig. 5). Both the path coefficients and correlation coefficients indicate that edge knots had a weak negative effect on bending stiffness.

4.5. Use of SilviScan for Douglas-fir tree improvement

Results from the 2x4 subset indicate that information on wood density, MFA, and edge knots can be combined to predict wood stiffness of Douglas-fir lumber ($R^2 = 54$ to 58%), but density alone was almost as good ($R^2 = 49$ to 52%). Although SilviScan variables can be used to predict bending stiffness, MOE_{sc} explained only 45% of the variation in MOE_{bl}. Nonetheless, SilviScan has been valuable for studying radial and vertical variation in MOE, MFA, and density at a fine scale (Baltunis et al. 2007). For example, SilviScan analyses have shown that density is relatively uniform from the base to the top of radiata pine trees (within the corewood), whereas stiffness increases from the pith to the outside of the bole (Cown et al. 1992; Xu et al. 2004). Our results suggest that similar fine scale analyses of Douglas-fir wood properties would be possible using SilviScan. However, because MFA added little to the prediction of wood stiffness in our study and is difficult to measure on thousands of trees in progeny tests, we do not recommend incorporating MFA or SilviScan MOE into Douglas-fir breeding programs if standing-tree or whole log stress wave measurements can be obtained (e.g., Cherry et al. 2008).

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

We observed a radial increase in MOE_{bl} with increasing RA (r_p = 0.42), presumably because the older outerwood had a higher wood density (discussed below) and lower MFA than the younger juvenile core (Cave and Walker 1994). Wood stiffness also increased from the pith to cambium in Douglas-fir and radiata pine (Cown et al. 1992; Knowles et al. 2003, cited in Johnson and Gartner 2006; Xu et al. 2004). We were

unable to study the relationship between MFA and RA because the 2x4s we used to analyze MFA were chosen to have a RA of 9.0 to 9.5 years. MFA was associated with ring age, however, in other studies of Douglas-fir (Ifju and Kennedy 1962; Erickson and Arima 1974; Knowles et al. 2003, cited in Johnson and Gartner 2006).

MOE_{bl} was also associated with the orientation of the growth rings in relation to the applied load (Fig. 1). Compared to the radially applied load, MOE_{bl} was greater when the load was applied either tangentially or diagonally to the growth rings. However, the 2x4s with tangentially or diagonally applied loads also had higher average ring ages (i.e., 9.6 and 11.7 years) than did the 2x4s that received the radially applied load (i.e., 6.4 years).

Because ring orientation and ring age are related (Fig. 7), the differences in MOE_{bl} among ring orientation classes may result from differences in ring age plus differences in RO *per se*. In contrast to our findings, bending stiffness of small clearwood samples did not differ significantly among ring orientation classes in a previous study of Douglas-fir, but ring age was not held constant (Grotta et al. 2005).

The correlation between DEN_{dl} and RA (r_p = 0.25) was weaker than the correlation between MOE_{bl} and RA (r_p = 0.42), and DEN_{dl} did not differ among RO classes. In radiata pine, the radial increase in wood density was also weaker than the radial increase in stiffness (Cown et al. 1992; Xu et al. 2004), which is consistent with our results. To account for the influence of RA and RO on stiffness and density, we adjusted MOE_{bl} using RA and RO as covariates (= AMOE_{bl}), and adjusted DEN_{dl} using RA as a

covariate (= $ADEN_{dl}$). Nonetheless, because the results from analyses of $AMOE_{bl}$ and $ADEN_{dl}$ were nearly identical to the results from analyses of MOE_{bl} and DEN_{dl} , we focused our discussion on these latter two traits.

4.7. Bending MOE and knots, but not density, were associated with lumber grade Visual grades of Douglas-fir lumber differed in MOE_{bl}, MOE_{tv}, and MOE_{sw}, 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_{bl} (11.5 GPa) than either S1 or S2 grades (10.5 and 9.6 GPa; Fig. 8). Visual grading of structural lumber is based on specific grading rules that are 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 warps. However, because we did not analyze 2x4s with splits, checks, or warps, the differences in average MOE among lumber grades probably reflects the presence of knots. 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; Fig. 8). The STR grade, the best grade in terms of strength and appearance, is used for making high quality posts, beams, and interior paneling. In descending order of quality, the STR grade is followed by S1, S2, S3, and E grades. Because we had only one 2x4 in each of the S3 and E grades, we did not include those 2x4s in these analyses. In contrast to the stiffness and knot traits, DEN_{dl} did not differ among lumber grades (p = 0.54).

4.8. Genetics of Douglas-fir wood quality

Previous studies of Douglas-fir indicated that stress wave MOE, bending MOE, and wood density had moderate to high heritabilities (Johnson and Gartner 2006; Cherry et al. 2008). Johnson and Gartner (2006) suggested that breeders can select for stress wave MOE or velocity to improve stiffness. In a subsequent study, Cherry et al. (2008) suggested that breeders should select for HM200 or ST300 traits to achieve gains in bending stiffness. The bending MOE data reported in Cherry et al. (2008) came from the experiments reported in this paper.

Our laboratory analyses of transverse vibration MOE and stress wave MOE suggest that wood stiffness is under modest genetic control ($h_i^2 = 0.22$ to 0.33). These estimates are comparable to the heritabilities of MOE_{bl}, MOE_{HM}, and MOE_{ST} reported by Cherry et al. (2008) ($h_i^2 = \sim 0.30$). Because we used a coefficient of relationship of 0.33 to account for relatedness among wind-pollinated siblings (i.e., σ^2_A was estimated as $3\sigma^2_{F(S)}$), these heritabilities would have been a third higher (i.e., 0.29 to 0.44) had we used a coefficient of relationship of 0.25 (i.e., assumed the progeny were true half-sibs). Although previous estimates of the heritabilities of stress wave MOE in Douglas-fir (0.30 to 0.55) were also based on a coefficient of relationship of 0.33 (Johnson and Gartner 2006; Cherry et al. 2008), the heritabilities of stress wave MOE in radiata pine and hybrid larch ranged from 0.47 to 0.70 using a coefficient of relationship of 0.25 (Kumar 2002, 2004; Fugimoto et al. 2006). Because our heritabilities were based on observations from a single site, they may overestimate multi-site heritabilities that include among-site genotype by environment interaction (G x E). G x E was nonsignificant, however, in our multi-site

analysis of stress wave velocity (Cherry et al. 2008) and in a previous study of Douglasfir stress wave MOE (Johnson and Gartner 2006).

In addition to the strong phenotypic correlations, MOE_{tv} and MOE_{sw} had strong genetic correlations with MOE_{bl} (r_a = 1.03 to 0.98) and moderate to strong genetic correlations with MOE_{HM} and MOE_{ST} (r_a = 0.54 to 0.93). The strong genetic correlation between MOE_{bl} and MOE_{sw} (r_a = 0.98) is consistent with our earlier findings that field-based stress wave tools can be used to achieve genetic gains in bending stiffness (Cherry et al. 2008).

 MOE_{bl} had a weak positive genetic correlation with KNT_{tot} (r_a = 0.22), but this correlation also had a high standard error (SE = 0.43), and the phenotypic correlations between these traits were non-significant on a lumber and log basis. Furthermore, the genetic correlations between MOE_{bl} versus KNT_{edg} and KNT_{cnt} are unreliable because there was no significant genetic variation for these knot traits. As discussed above, the family mean correlations between knot traits and lumber bending MOE were moderately negative in white spruce, but genetic correlations were not reported (Beaulieu et al. 2006).

Previous studies of Douglas-fir suggested that simultaneous improvement in stem volume and wood quality would be challenging because fast growing families produce a greater number of larger branches (King et al. 1992; St.Clair 1994). Our study suggests that selection for smaller or fewer knots will not have any large positive impact on bending

stiffness of Douglas-fir because the phenotypic and genetic correlations between knot traits and bending MOE are either weak or nonsignificant, and knot traits are weakly heritable ($h^2 \le 0.14$).

4.9. Conclusions

We demonstrated that stress wave tools such as the HM200 and ST300 can be used to genetically improve bending stiffness of Douglas-fir. Because breeders can avoid costly and labor-intensive bending tests, stress wave MOE or velocity are good indirect traits to use to genetically improve bending MOE of Douglas-fir. Our findings support the recommendations of Cherry et al. (2008) that breeders should consider the advantages and disadvantages of the HM200 and ST300 before using them in breeding programs. Compared to the ST300 traits, the HM200 traits are more strongly genetically correlated with bending MOE, but require tree harvesting. Therefore, if harvesting is possible, we recommend that breeders use the HM200 to get higher gains in bending stiffness. Estimates of MOE from the ST300 may be less reliable than estimates from the HM200, but the ST300 is still useful for improving stiffness, particularly when the trees cannot be destructively sampled, and when family means are used to identify desirable genotypes.

Estimates of wood stiffness from stress wave tools are clearly superior to estimates from either MFA or wood density alone. Although previous studies in pine suggested that density and MFA are good surrogate traits for stiffness, our results suggest that stress wave measurements are more reliable. Furthermore, because wood density is negatively correlated with diameter growth, it is not wise to select for higher density alone. In

Douglas-fir, MFA had only a moderate to weak phenotypic correlation with bending MOE. In summary, no real advantage is apparent for including density or MFA as selection criteria in Douglas-fir breeding programs. Instead, we recommend that breeders focus on stress wave velocity as a more reliable method for making selections to increase bending stiffness without adversely affecting growth.

Although, large branches or knots are generally regarded as detrimental to wood quality, our results suggest little need to focus on knots in breeding programs for structural lumber.

The HM200 or ST300 can also be used by silviculturists and forest managers to predict the bending stiffness of logs or standing trees. These tools should help silviculturists define the relationships between MOE versus site characteristics and silvicultural regimes, thereby enhancing the ability of growth models to predict the financial outcomes of management alternatives. Standing-tree tools can be used to monitor the effects of silvicultural practices such as thinning and fertilization, evaluate the value of plantations, plan harvest operations, and improve the marketing or processing options of logs.

Lastly, our results suggest that wood engineers and wood scientists can use transverse vibration or stress wave MOE to predict bending MOE of Douglas-fir 2x4s. Because Douglas-fir is widely used as structural lumber, the ability to predict bending MOE will help engineers to determine the safety margins of Douglas-fir wood structures without conducting bending tests.

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Appendix

A1: Estimation of MOEtv

E-computer estimates the transverse vibration MOE in psi based on the equation given below (Metriguard 1991).

$$MOE^{1}_{tv} = \frac{wL^3f^2}{Kbh^3}$$

where w is the weight of the 2x4 (lb), L is the span length (in), f is the vibration frequency, b is the 2x4 width (in), h is the 2x4 thickness (in), and K is the calibration constant to accommodate the units used and the support conditions of the instrument. Because we had to test \sim 1500 2x4s in this study, we used a default width of 3.5 in and thickness of 1.5 in rather than adjusting the E-computer for the excat dimensions of each 2x4. Later, we recalculated the MOE_{tv} (psi) of individual 2x4s based on the actual width and thickness using the following simplified equation:

$$MOE_{tv} = \frac{11.8125 \times MOE_{tv}^{1}}{bh^{3}}$$

MOE_{tv} was then converted to GPa by multiplying by 6.895 x 10⁻⁹.

The SAS code used to arrive this equation is given below:

```
Extraction of transverse vibration moe ;
ecmoe= (11.8125*moeec)/(w*t**3);
/*
HOW "(11.8125*moeec)/(w*t**3)" ??

MOE of E-computer= [(weight)* (length^3)* (f^2)] / K *w* (t^3) [Unit-10^6psi]
weight= weight of test specimen
```

```
K= adjustment constant used to accomodate units used and the support
conditions;
f = undamped natural frequency;
w= width of 2x4 (in)-the default is set as 3.5in
t=the thickness of 2x4 (in), default is set as 1.5 in
length=span between the blades of e-computer (a constant)=82''in
To get the board specific MOE for given width and thickness (the two
variables which will change in a 2x4 because e-computer was setup with
a default width and thickness setting):
After accounting for constants Ecomputer MOE depends on,
                   E= constant/ w thickness^3
where width is 3.5 inch and thickness is 1.5 inch
MOE of a particular board of given dimensions is
                  E'= constant/(width') (thickness'^3)
where width' is the width of a particular board and thickness' is
thickness of a particular board
So solve for E'/E:
MOE specific for a particular board, E'= [width* thickness^3 *
E]/width' * thickness'^3
=[11.8125*E]/width'* thickness'^3
                                     where b' and h' are board
specific.
* /
**conversion to SI units(GPa);
ecmoesi= ecmoe*6.894757
A2: Estimation of MOE<sub>sw</sub>
The SAS code used to arrive this equation is given below: (MOE_{sw} = v^2d/g)
Extraction of stresswave moe from weight and time;
moestress=(length)**2/(time*10**-6)**2
                                           /*v^2*/
      * (weight*.00220462)/(length*w*t) /*d*/
      /(386.08858);
                                                       /*g*/
moestress= [(v^2) d]/q
v= velocity of propagation=distance between transducers(in)/propagation
```

time(sec)