

AN ABSTRACT OF THE THESIS OF

Oguz S. Urhan for the degree of Master of Science in Forest Science presented on June 13, 2013.

Title: Early Genetic Selection for Wood Stiffness in Juvenile Douglas-fir and Western Hemlock.

Abstract approved:

Glenn T. Howe

Wood modulus of elasticity (MOE), also known as wood stiffness, is one of the most important wood properties. Wood stiffness is a measure of the resistance to deflection, and is important because some products such as laminated veneer lumber, plywood, and dimension lumber require stiff and strong wood. Incorporating wood stiffness into breeding programs could help maintain acceptable wood quality and increase economic profits for wood producers. There is limited information on the genetics of wood stiffness in young Douglas-fir plantations, and the genetics of wood stiffness has not been studied in western hemlock. Therefore, my objectives were to use young (8- to 12-year-old) genetic test plantations of Douglas-fir and western hemlock to (1) determine the best approach for measuring acoustic velocity, and then use the best approach to (2) estimate additive and non-additive genetic variation, heritabilities, and potential genetic gains, (3) estimate genetic and phenotypic correlations between acoustic velocity and growth traits, and (4) discuss implications of these results for operational tree improvement. I studied acoustic velocity at two genetic test plantations of Douglas-fir (Fir Grove and Roaring River) and one test

plantation of western hemlock (Toledo) using the TreeSonic and Microsecond Timer standing-tree tools, and two vertical placements of the sensors. These tools can be used to measure acoustic velocity in standing-trees, an indirect measure of wood stiffness. My results show that (1) the effects of standing-tree tool, vertical placement, and DBH-adjustment methods were non-significant, (2) acoustic velocity had significant genetic variation in Douglas-fir and western hemlock, (3) heritability of acoustic velocity was higher than the heritabilities of growth and form traits, and (4) substantial genetic gains in acoustic velocity are possible. My results also indicate that the mean acoustic velocity and modulus of elasticity were higher in Douglas-fir than in western hemlock. Although mean stiffness was higher for Douglas-fir, the distributions of acoustic velocity and modulus of elasticity overlapped between the species.

These results indicate that comparable genetic gains are possible using both the TreeSonic and Microsecond Timer tools. Because of practical considerations, and higher measurement rates, I recommend that breeders use the TreeSonic and the same-face approach. I found positive genetic correlations between growth and acoustic velocity in western hemlock. This provides an opportunity to focus on improving wood stiffness in western hemlock so that it can better compete with Douglas-fir for products in which stiffness is important. Near optimal genetic gains are possible using 10 trees per family for wood stiffness. Because dominance variation was non-significant for Douglas-fir and western hemlock, near optimal gains in wood stiffness and growth traits can be obtained by collecting open pollinated seed from

orchards (i.e., without control crossing) as long as pollen contamination is not a problem.

©Copyright by Oguz S. Urhan
June 13, 2013
All Rights Reserved

Early Genetic Selection for Wood Stiffness in Juvenile Douglas-fir and Western
Hemlock

by
Oguz S. Urhan

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented June 13, 2013
Commencement June 2014

Master of Science thesis of Oguz S. Urhan presented on June 13, 2013.

APPROVED:

Major Professor, representing Forest Science

Head of the Department of Forest Ecosystem and Society

Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to reader upon request.

Oguz S. Urhan, Author

ACKNOWLEDGEMENTS

First, I would like to express my gratitude to my supervisor, Prof. Glenn T. Howe for his countless help, guidance, and encouragement throughout my study. I am sincerely grateful for the research discussions and ideas, as well as his continuous support during my research and the writing of this thesis. I would never accomplish the whole body of research without his help. I am honored to have the opportunity to learn under his guidance, and truly grateful for what he has done.

I am very grateful to my committee members, Prof. Barbara Lachenbruch and Prof. Glen Murphy for valuable feedbacks, suggestions, and kind guidance during my study. I would also like to thank Prof. Kevin Boston, my Graduate Council Representative, for volunteering his time to serve on my committee. I would also like to thank Scott Kolpak for all his support, help and guidance throughout my thesis.

This work could not have been completed without cooperation and support of the Northwest Tree Cooperative. I am very grateful to Keith Jayawickrama, Denise Cooper and Lauren Magalska.

I would like to acknowledge the student workers that helped with field work over the past three years. Annie Simmonds, Kyle Pritchard and Sean Smith were all very helpful.

This project was supported by the Center for Advanced Forestry Systems, the Pacific Northwest Tree Improvement Research Cooperative. I would like to express my gratitude to Turkish Government Scholarship for their financial support.

On a personal level, I would like to thank my parents for their love, prayers, encouragement and support all these years. I would also like to thank my friends for their prayers.

TABLE OF CONTENTS

	<u>Page</u>
1 Introduction.....	1
1.1 Importance of Douglas-fir and western hemlock.....	1
1.2 Approaches for measuring wood stiffness.....	4
1.3 Thesis Project.....	6
1.3.1 Tools.....	7
1.3.2 Vertical placement of sensors.....	9
2 Materials and methods.....	13
2.1 Plant materials.....	13
2.1.1 Fir Grove plantation.....	16
2.1.2 Roaring River plantation.....	16
2.1.3 Toledo plantation.....	17
2.2 Measured variables.....	18
2.2.1 Height and DBH.....	18
2.2.2 Sensor distance.....	18
2.2.3 Time of flight (TOF).....	19
2.2.4 Stem form.....	19
2.2.5 Measurement rate.....	20
2.3 Derived variables.....	20
2.3.1 Flight paths.....	20
2.3.2 Acoustic velocity and density.....	23
2.3.3 Volume and Taper.....	24

TABLE OF CONTENTS (Continued)

	<u>Page</u>
2.4 Statistical analysis	24
2.4.1 Data cleaning and outlier detection	24
2.4.2 Removal of non-significant interaction terms	26
2.5 Variances and heritabilities	27
2.5.1 Variances	27
2.5.2 Heritabilities	28
2.6 Differences among tools and sensor placements	30
2.7 Correlations and genetic gain.....	31
2.7.1 Correlations	31
2.7.2 Genetic gain.....	33
2.8 Expected family heritabilities and genetic gains when the number of replications is varied	34
3 Results.....	35
3.1 Statistical models	35
3.2 The effects of standing-tree tool, vertical placement, and DBH-adjustment were non-significant.....	36
3.3 Hit-to-hit variation for TOF was less using the opposite-face approach compared to the same-face approach	38
3.4 Measurement rates were highest when I used the TreeSonic and same-face approach	38
3.5 Comparison of Douglas-fir and western hemlock wood stiffness traits	40
3.6 AV^2 had significant genetic variation in Douglas-fir and western hemlock..	43
3.7 The heritability of AV^2 was higher than for the growth and form traits.....	43

TABLE OF CONTENTS (Continued)

	<u>Page</u>
3.8 Substantial genetic gains in AV^2 are possible.....	51
3.9 Growth traits were weakly to moderately correlated with AV^2	51
3.10 There was no substantial increase in family heritabilities or genetic gains for wood stiffness when the number of trees per family was increased beyond 10 trees	52
4 Discussion	54
4.1 The effect of standing-tree tool was non-significant.....	54
4.2 The effect of vertical placement was non-significant	56
4.3 Measurement rates were highest when I used the TreeSonic and same-face approach	60
4.4 AV^2 had significant genetic variation in Douglas-fir and western hemlock..	61
4.5 The heritability for AV^2 was higher than for the growth and form traits	64
4.6 Substantial genetic gains in AV^2 are possible.....	66
4.7 Growth traits were weakly to moderately correlated with AV^2	66
4.8 There was no substantial increase in family heritabilities or genetic gains for wood stiffness when the number of trees per family was increased beyond 10 trees.	69
4.9 Implications.....	70
4.10 Future research.....	71
References	73
Appendix	79

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
2.1: Two nested mating designs used to study the genetics of wood stiffness	15
2.2: Hypothesized acoustic wave flight paths were used to calculate associated distances and acoustic velocities	22
3.1: Comparison of Douglas-fir and western hemlock wood stiffness traits measured at five operational plantations and three genetic test plantations.....	42
3.2: Full-sib family heritabilities and genetic gains in relation to the number of trees measured per family at two genetic test plantations of Douglas-fir (Fir Grove and Roaring River) and one plantation of western hemlock (Toledo).....	53

LIST OF TABLES

<u>Table</u>	<u>Page</u>
3.1: Estimates of individual-tree genotypic and family heritabilities at the Toledo, Roaring River, and Fir Grove plantations using two standing tree acoustic tools (TreeSonic and Microsecond Timer)	37
3.2: Measurement rates at the Roaring River and Toledo plantations using two acoustic tools and two vertical placements	39
3.3: Variance components and heritabilities for squared acoustic velocity variables measured on 8-year-old Douglas-fir trees at the Fir Grove plantation using the TreeSonic acoustic tool and two vertical placements (same-face and opposite-face) of the sensors.	45
3.4: Variance components and heritabilities for squared acoustic velocity variables measured on 12-year-old Douglas-fir trees at the Roaring River plantation using two standing-tree tools (TreeSonic and Microsecond Timer) and two vertical placements (same-face and opposite-face) of the sensors.....	46
3.5: Variance components and heritabilities for squared acoustic velocity variables measured on 12-year-old western hemlock trees at the Toledo plantation using two standing-tree tools (TreeSonic and Microsecond Timer) and two vertical placements (same-face and opposite-face) of the sensors.....	48
3.6: Genotypic, environmental and phenotypic correlations between squared acoustic velocity versus growth and form traits, and genotypic heritabilities for growth traits at the Toledo, Roaring River, and Fir Grove genetic test plantations.....	50

LIST OF APPENDIX TABLES

<u>Table</u>	<u>Page</u>
A1: Variance components for squared acoustic velocity measured on 8-year-old Douglas-fir trees at the Fir Grove plantation using the TreeSonic standing-tree tool and two sensor placements (same-face and opposite-face).....	80
A2: Variance components for squared acoustic velocity measured on 12-year-old Douglas-fir trees at the Roaring River plantation using two standing-tree tools (TreeSonic and Microsecond Timer) and two sensor placements (opposite-face and same-face)	81
A3: Variance components for squared acoustic velocity measured on 12-year-old western hemlock trees at the Toledo plantation using two standing-tree tools (TreeSonic and Microsecond Timer) and two sensor placements (opposite-face and same-face)	83
A4: Reduced model variance components for squared acoustic velocity measured on 8-year-old Douglas-fir trees at the Fir Grove plantation using the TreeSonic standing-tree tool and two sensor placements (same-face and opposite-face).	85
A5: Reduced model variance components for squared acoustic velocity measured on 12-year-old Douglas-fir trees at the Roaring River plantation using two standing-tree tools (TreeSonic and Microsecond Timer) and two sensor placements (opposite-face and same-face).	86
A6: Reduced model variance components for squared acoustic velocity measured on 12-year-old western hemlock trees at the Toledo plantation using two standing-tree tools (TreeSonic and Microsecond Timer) and two sensor placements (opposite-face and same-face)	88
A7: A comparison of $\sigma_{P_1}^2$ and $\sigma_{P_2(P_1)}^2$ variance components for squared acoustic velocity measured on 8-year-old Douglas-fir trees at the Fir Grove plantation using the TreeSonic standing-tree tool and two sensor placements (same-face and opposite-face)	90
A8: A comparison of $\sigma_{P_1}^2$ and $\sigma_{P_2(P_1)}^2$ variance components for squared acoustic velocity measured on 12-year-old Douglas-fir trees at the Roaring River plantation using two standing-tree tools (TreeSonic and Microsecond Timer) and two sensor placements (opposite-face and same-face).....	91

LIST OF APPENDIX TABLES (Continued)

<u>Table</u>	<u>Page</u>
A9: A comparison of σ_{P1}^2 and $\sigma_{P2(P1)}^2$ variance components for squared acoustic velocity measured on 12-year-old western hemlock trees at the Toledo plantation using two standing-tree tools (TreeSonic and Microsecond Timer) and two sensor placements (opposite-face and same-face).....	92

1 INTRODUCTION

1.1 Importance of Douglas-fir and western hemlock

Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirb.) Franco) is one of the most important lumber species in western North America (Silen, 1978). Douglas-fir wood is widely used for building and construction purposes such as structural lumber, plywood, and laminated veneer lumber (Bormann, 1984; Alden, 1997). Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) is also an important commercial species in the Pacific Northwest, having a large distribution along the coast of western North America (Packee, 1990; Jayawickrama, 2003). Its wood is highly valued because of its strength, desirable pulping characteristics, and homogeneous density. Western hemlock wood is widely used for pulping, wood paneling, cabinets, framing, and dimension lumber (Jayawickrama, 2003).

Wood properties vary within the tree in two ways: from the base to the top of the tree, and from pith to bark (Megraw, 1986; Burdon et al., 2004; Wang, 2011). This results from variation in juvenile versus mature wood in the radial and vertical directions, and variation between corewood and outerwood in the radial direction (Burdon et al., 2004). Broadly speaking, this results in four types of wood. Mature wood is produced higher in the tree, mature corewood near the pith and mature outerwood towards the outside of the tree (Burdon et al., 2004). Juvenile wood is produced near the base of the tree, juvenile corewood near the pith, and juvenile outerwood towards the outside of the tree (Burdon et al., 2004). Compared to other types of wood, juvenile corewood generally has different wood properties such as

lower wood stiffness, lower density, and larger microfibril angle (Senft et al., 1985; Maguire et al., 1991; Jozsa and Middleton, 1994; Zobel and Sprague, 1998; Evans and Ilic, 2001; Burdon et al., 2004).

Wood quality is defined as a suite of characteristics that makes logs and lumber economically valuable for their end uses (Jozsa and Middleton, 1994). Because of intensive silvicultural practices, trees reach harvestable sizes at shorter rotations than they have in the past (Allen et al., 2005). The transition from longer to shorter rotations will result in changes in the proportion of juvenile corewood in the tree, which is inferior for most uses.

Wood modulus of elasticity (MOE), also known as wood stiffness, is one of the most important wood quality traits. Wood stiffness is a measure of the resistance to deflection, and is important because some products such as laminated veneer lumber, plywood, and dimension lumber require stiff and strong wood. Incorporating wood stiffness into breeding programs could help maintain acceptable wood quality, and may increase economic profits for wood producers. It should be possible to improve wood stiffness via breeding because stiffness is highly heritable and has sufficient genetic variation in Douglas-fir and other tree species (Kumar et al., 2002; Lindström et al., 2004; Dungey et al., 2006; Howe et al., 2006; Baltunis et al., 2007; Matheson et al., 2008; Mora et al., 2009). Furthermore, wood stiffness is an ideal wood property to improve because the methods and tools available to measure wood stiffness are inexpensive, fast, and non-destructive.

Wood stiffness can be estimated directly or indirectly. Direct estimates of MOE can be obtained by applying a load to a wood sample and measuring the wood's resistance to deflection (Carter et al., 2005; Kumar et al., 2006). The resulting measure of stiffness is called bending MOE, or static MOE (MOE_s). This procedure requires destructive sampling, expensive equipment, and sample preparation (Carter et al., 2005). Consequently, methods and tools have been developed to measure wood stiffness indirectly (Lindström et al., 2002; Toulmin and Raymond, 2007). For example, wood stiffness can be estimated from the velocity of acoustic waves (acoustic velocity, AV) that pass through wood according to the following formula: $MOE_d = \text{wood density} \times \text{acoustic velocity}^2$, where density is typically expressed in $\text{kg}\cdot\text{m}^{-3}$, and velocity is typically expressed in $\text{m}\cdot\text{s}^{-1}$ (Pellerin and Ross, 2002; Chauhan et al., 2005; Lasserre et al., 2007). When MOE is estimated using this formula, it is called dynamic modulus of elasticity (MOE_d). If stiffness is measured on live or recently cut trees, green wood density is used. Because it is costly to measure density, it is desirable to estimate wood stiffness using acoustic velocity alone, if possible (Cherry et al., 2008).

There have been four published studies on the inheritance of AV in older Douglas-fir trees (> 20 years old) (Johnson and Gartner, 2006; Cherry et al., 2008; Jayawickrama et al., 2011; Vikram et al., 2011). However, the genetic improvement of wood stiffness in western hemlock and young Douglas-fir (< 12 years old) has not been studied. Several factors might have important effects on the use of AV as an indirect measure of MOE on young trees. These include branching habit (knots) and

wood properties. For example, the branching habit of young Douglas-fir and western hemlock trees might affect the measurement of AV, and hence, the estimation of wood stiffness. This is because knots are rich in compression wood, and compression wood causes changes in the speed of acoustic waves (Jung, 1979; Wang et al., 2001a). In addition, the branching habit of young Douglas-fir and western hemlock is different. For example, young Douglas-fir trees have large branches around the main whorl, but young western hemlock trees have many secondary branches located between the main whorls. The larger whorl branches in Douglas-fir, and the secondary branches in western hemlock may differentially affect the measurement of acoustic velocity. Therefore, it is important to understand the differences in the genetics of wood stiffness and measurement approaches between Douglas-fir and western hemlock, and between younger and older trees.

1.2 Approaches for measuring wood stiffness

The most common approaches for indirectly measuring AV are the “resonance” methods for felled trees and “time-of-flight (TOF)” methods for standing-trees (Lindström et al., 2002). For felled trees, AV can be estimated based on the first resonance frequency and the length of the log or piece of lumber. The resonance method has been shown to be more accurate than the TOF method. This is mostly because the acoustic waves sample more wood (Lasserre et al., 2007). Furthermore, the acoustic waves travel back and forth many times through the log, providing an average acoustic velocity value. Compared to TOF, the resonance technique was

found to be more reliable for evaluating the veneer quality of seven Douglas-fir stands (Amishev and Murphy, 2008).

Several other studies have shown that MOE_s measured using bending tests is highly correlated with MOE_d (Kumar et al., 2002; Wang et al., 2002; Kumar, 2004). In a previous study of Douglas-fir using the Director Hitman200 (HM200; Fibre-Gen, New Zealand), the genetic correlation was 0.92 between MOE_s and MOE_d , and 0.75 between MOE_s and AV (Cherry et al., 2008). A number of log-based acoustic tools are available to measure wood stiffness, including the HM200, the Fiber-Gen Hitman LG-640, and the Fakopp Resonance Log Grader (RLG; Fakopp Enterprise, Hungary).

Compared to the log-based tools, standing-tree acoustic tools can be used to estimate AV more rapidly and non-destructively. The main advantage of using standing-tree acoustic tools, rather than log-based tools, is that AV can be measured without harvesting the trees. In most cases, it is not acceptable to harvest trees in genetic tests. Therefore, there is increasing interest in using standing-tree acoustic tools in genetic test plantations. The disadvantage of the standing-tree acoustic tools is that they measure only a small proportion of the tree—generally 1.0 to 1.5 m near DBH, and measure only outerwood, which is stiffer than corewood. Therefore, the correlation between AV and whole-tree wood stiffness is lower than for log-based tools.

The standing-tree tools have two sensors (start and stop), and were originally developed to detect decay in trees. The Fibre-Gen ST300, TreeTap (developed by the University of Canterbury), Fakopp TreeSonic, Fakopp Microsecond Timer, and

Fakopp Ultrasonic Timer are some of the standing-tree acoustic tools that have been used to measure AV indirectly. The start and stop sensors are hammered 20 to 40 mm into the stem at a 45° angle (described below), and then acoustic waves are induced by striking the start sensor with a hammer. TOF, which is the time taken for the acoustic wave to travel from the start sensor to the stop sensor, is displayed on the screen. Acoustic velocity can be calculated based on the distance (d) between the sensors and TOF ($AV = d/TOF$). In Douglas-fir, the genetic correlation between MOE_s and AV measured using the ST300 was 0.53 (Cherry et al., 2008). In the same study, they reported a genetic correlation of 0.93 between MOE_d estimated using the HM200 and the ST300. More recently, Kolpak et al. (unpublished) measured young Douglas-fir and western hemlock trees, and found modest to high phenotypic correlations (0.39 to 0.88) between AV^2 measurements measured using four standing-tree tools versus MOE_d measured using the HM200.

In Douglas-fir, moderate to high heritabilities have been reported for wood stiffness measured with acoustic tools (Johnson and Gartner, 2006; Cherry et al., 2008; Jayawickrama et al., 2011). Moderate to high heritabilities were also reported for wood stiffness on other coniferous species (Kumar et al., 2002; Kumar, 2004; Lindström et al., 2004; Dungey et al., 2006; Kumar et al., 2006; Li et al., 2007; Roth et al., 2007; Wielinga et al., 2009).

1.3 Thesis Project

This project was supported by the Center for Advanced Forestry Systems (CAFS), a cooperative project that links forestry research universities and industry

members to enhance forest management. The CAFS wood stiffness project had two phases: a Phase 1 phenotypic study, and a Phase 2 genetic study. The objectives of Phase 1 were to evaluate alternative approaches for measuring wood stiffness on young trees of Douglas-fir and western hemlock in operational plantations, and to evaluate the effect of branches on acoustic velocity measurements. In Phase 1, Kolpak et al. (unpublished) used (1) two vertical placements of the sensors (same-face and opposite-face), (2) four standing-tree acoustic tools (TreeSonic with standard sensors, TreeSonic with SDO2 sensors, Microsecond Timer, and Ultrasonic Timer), and (3) the HM200 log-based tool across five operational plantations. Measurements were taken by placing the sensors within interwhorls versus across whorls to evaluate the effect of whorl branches. In Phase 2, I studied wood stiffness of Douglas-fir and western hemlock at three genetic test plantations. Based on results from Phase 1, I removed the Ultrasonic Timer and TreeSonic with standard sensors. Because it was not possible to harvest the trees in the genetic test plantations, I did not use the HM200 in Phase 2. Furthermore, the correlations between MOE_d measured with the HM200 and AV^2 measured with the standing-tree tools were higher when measurements were taken across whorls (Kolpak et al. 2009), probably because of the longer sensor distances. Therefore, TOF was measured across whorls to sample more wood in Phase 2.

1.3.1 Tools

There are several types of acoustic tools to measure TOF. The TreeSonic is manufactured by Fakopp Enterprise to measure TOF. The TreeSonic can be used with two different types of sensor: the standard sensor and the smaller SDO2 sensor.

Because we were interested in studying small trees, Kolpak et al. (unpublished) included the SDO2 sensor in Phase 1. Another important characteristic is that the TreeSonic does not have buttons to turn the tool on and off, and the last measurement is cleared automatically from the screen when the start sensor is tapped for the next measurement. The Microsecond Timer is also manufactured by Fakopp, but works only with the SDO2 sensors, and is mostly used to detect decay or holes in trees. The Microsecond Timer has buttons on the tool to turn it on and off, and to clear the last measurement from the screen. The Fakopp Ultrasonic Timer also works with SDO2 sensors. The main difference between the Ultrasonic Timer versus the TreeSonic and Microsecond Timer is that the Ultrasonic Timer measures ultrasonic waves instead of acoustic waves. Because of this difference, the Ultrasonic Timer can only be used across short distances (15 to 25 cm). Rather than a hammer, the ultrasonic wave is generated by electronic excitation of the sensor. The Ultrasonic Timer is mostly used to test seedlings because of the limited distances that can be spanned.

The HM200 was designed by Fibre-Gen to measure acoustic velocity on felled trees or logs. Because the length of the log is input into the tool, the HM200 automatically estimates acoustic velocity. The main difference between the HM200 versus the other tools described above is that the HM200 uses the resonance method, and cannot be used on standing trees.

Based on the preliminary research in Phase 1, I decided to use the TreeSonic (SDO2 sensor) and the Microsecond Timer for the second phase of this project in the genetic test plantations. To determine the optimal tool to measure stiffness in genetic

test plantations, Kolpak et al. (unpublished) compared AV^2 taken using standing-tree tools versus MOE_d measured using the HM200. The HM200 was regarded as the benchmark because it measures whole-tree acoustic velocity on harvested logs, and has been shown to be a good surrogate for MOE_s (Kumar et al., 2002; Wang et al., 2002; Kumar, 2004; Cherry et al., 2008). Kolpak et al. (unpublished) reported moderate to high correlations (0.39 to 0.88) between acoustic velocity measured using the standing-tree tools versus MOE_d measured using the HM200. The correlations were highest for the TreeSonic (both standard and SDO2 sensors) and the Microsecond Timer. The correlation between AV^2 measured using the Ultrasonic Timer versus MOE_d measured using the HM200 was weak (Kolpak et al. unpublished), possibly due to the short distances between the sensors. Therefore, I did not use the Ultrasonic Timer in the genetic test plantations. Although the TreeSonic plus standard sensors had the highest correlation (0.88) with MOE_d (Kolpak et al. unpublished), I used the TreeSonic plus the SDO2 sensors because the correlation was also high (0.84; Kolpak et al. unpublished). In addition, the SDO2 sensors were more practical to use on small trees.

1.3.2 Vertical placement of sensors

There are two vertical placements that can be used to measure acoustic velocity on standing-trees. In the same-face approach, the start and stop sensors are placed on the same-face of the tree with a known distance between the two sensors, usually about one meter (Wang et al., 2001b; Grabianowski et al., 2006; Cherry et al., 2008; Mahon et al., 2009; Jayawickrama et al., 2011). In the opposite-face approach,

the start and stop sensors are placed on opposite-faces of the tree (Kolpak et al. unpublished; Matheson et al., 2002; Wagner et al., 2003; Joe et al., 2004; Mahon et al., 2009). For the same-face approach, the vertical distance between the two sensors is used to calculate acoustic velocity because the flight path of the acoustic waves is assumed to be known. While this is a good approach for the same-face approach, it is unclear what the actual flight path is for the opposite-face approach because wood properties vary within the tree. Therefore, Mahon et al. (2009) described five DBH-adjustment methods associated with five potential flight paths (described in Materials and Methods).

Differences in flight path adjustments may affect the accuracy and precision of AV measurements. There have been two studies to compare vertical sensor placements. In the first study, Mahon et al. (2009) compared the same-face versus five DBH-adjusted opposite-face methods on 100 loblolly pine trees. The opposite-face approach was recommended to measure wood stiffness (Mahon et al., 2009). In the second study, Wagner et al. (2003) compared the same-face and opposite-face approaches using the Fluke 99B Scopemeter on 24 Douglas-fir trees. They did not use an adjustment method because their opposite-face approach involved placing the sensors on opposite faces of the tree at the same height. Therefore, the radial distance between the sensors was used as the TOF distance. They reported a higher correlation between MOE_d and AV using the opposite-face approach.

In the first phase of this project, Kolpak et al. (unpublished) compared the same-face versus the opposite-face approaches in the operational plantations. They

reported that the correlations between the tools were generally higher using the same-face approach, but the sample size was too small to draw definitive conclusions. Therefore, in the second phase of this project, I decided to use both the same-face and opposite-face approaches in genetic test plantations of Douglas-fir and western hemlock. In addition, Kolpak et al. (unpublished) reported that measuring acoustic velocity across the whorl did not adversely affect the AV, and allowed longer TOF distances to be used.

There is limited information on the genetics of wood stiffness in young Douglas-fir plantations, and the genetics of wood stiffness has not been studied in western hemlock. Furthermore, an opposite-face approach has been recommended in loblolly pine and older Douglas-fir trees (Wagner et al., 2003; Mahon et al., 2009). In the most recent study of Douglas-fir, the same-face approach was used to measure wood stiffness (Jayawickrama et al., 2011). There is also no information about additive and non-additive genetic variation for wood stiffness in Douglas-fir or western hemlock. Therefore, my objectives were to use young (8-12 year-old) genetic test plantations of Douglas-fir and western hemlock to (1) determine the best approach for measuring acoustic velocity, and then use the best approach to (2) estimate additive and non-additive genetic variation, heritabilities, and potential genetic gains, (3) estimate genetic and phenotypic correlations between acoustic velocity and growth traits, and (4) discuss implications of these results for operational tree improvement. I studied acoustic velocity at two genetic test plantations of Douglas-fir (Fir Grove and

Roaring River) and one test of western hemlock (Toledo) using the TreeSonic and
Microsecond Timer, and two vertical placements of the sensors.

2 MATERIALS AND METHODS

2.1 Plant materials

I chose three genetic test plantations from twenty candidate plantations of Douglas-fir and western hemlock. These plantations are part of two second-cycle breeding programs managed by the Northwest Tree Improvement Cooperative (NWTIC) and Hemlock Tree Improvement Cooperative (HEMTIC). The selected Douglas-fir plantations were Fir Grove and Roaring River, and the hemlock plantation was Toledo. The selected plantations were chosen based on having high heritabilities for growth traits, high survival, and locations close to Corvallis. For both species, the parents for the second cycle of breeding were chosen using backward or forward selection. Backward selection is selection of parent trees based on the performance of their progeny. Forward selection is selection of the best individuals from progeny test plantations (i.e., progeny of potential backward selections). In both cases, trees were selected based on their breeding values.

From the available families at each test plantation, I constructed two nested mating designs. In a nested design, each maternal or paternal parent is mated with several maternal or paternal parents, and each mating produces several progeny. This type of mating design is useful for estimating additive and non-additive genetic variation. In my experiment, I constructed two nested mating designs that were distinguished by cross-type (CT, Figure 2.1). In the first cross-type (males nested in females, M(F)), each female parent was mated with two male parents. In the second cross-type (females nested in males, F(M)), each male parent was mated with two

female parents (Figure 2.1). In these mating designs, the first parent was designated as Parent #1 (P1), and the second parent was designated as Parent #2 (P2 (P1)). Each parent was used in only one cross-type.

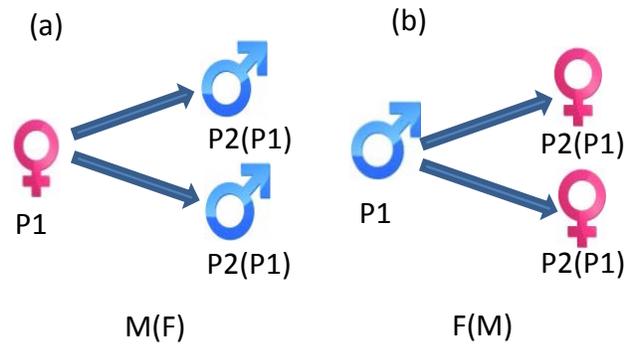


Figure 2.1: Two nested mating designs used to study the genetics of wood stiffness: (a) males nested in females (M(F)) and (b) females nested in males (F(M)). P1 is Parent #1 and P2(P1) is Parent #2 nested within Parent #1. ♂ and ♀ represent the male and female parents.

2.1.1 Fir Grove plantation

Douglas-fir second-cycle parent trees were chosen using backward selection from four first-generation programs: BLM Yamhill, GP Toledo Plus, GP Toledo Roadside Low and Burnt Woods Phase-II. Other parents were chosen using forward selection from five other first-generation programs: Dallas High, Dallas Valley Side, Burnt Woods Phase-I, Dallas Valley-Addition, and Vernonia Sunday Creek. Second-cycle parents were mated using a double-pair mating design to produce two crosses per parent. From the available 154 families, I chose 28 full-sib families for the M(F) cross-type (i.e., 14 female P1 parents), and 26 full-sib families for the F(M) cross-type (i.e., 13 male P1 parents).

The Fir Grove plantation is located near Pedee, Oregon (44° , 48', 23.0" N, 123° , 26', 48.2" W, and 268 m elevation). The plantation was established in 2005 with 1-year old seedlings using an alpha experimental design consisting of 154 families, 11 blocks, 20 replications, and 1 to 2 trees per family per replication. Survival at the Fir Grove plantation was 89.3% at age 7. Out of 781 available trees in my chosen full-sib families, I measured 708. I did not measure trees that were dead, apparently mislabeled, or too small to measure acoustic velocity.

2.1.2 Roaring River plantation

Douglas-fir parent trees were chosen using backward selection from six first-generation programs: BLM McKenzie, BLM Molalla Bu-30, BLM Snow Peak Bu-33, Oakridge Rigdon Lowell Low, Oakridge Rigdon Lowell Mid Series-2, and Molalla. Other parents were chosen using forward selection from three programs:

Molalla, Snow Peak Low, and Snow Peak High. Parent trees were mated using a double-pair mating design. From the available 216 families, I chose 40 full-sib families for the M(F) cross-type (i.e., 20 female P1 parents), and 38 full-sib families for the F(M) cross-type (i.e., 19 male P1 parents).

The Roaring River plantation is located near Scio, Oregon (44°, 38', 24.4" N, 122°, 41', 52.6" W, and 433 m elevation). The plantation was established in 2001 with 1-year old seedlings using an alpha experimental design consisting of 216 families, 4 blocks, 20 replications, and 1 to 2 trees per family per replication. Survival at the Roaring River plantation was 96.4% at age 10. Out of 1369 available trees in my chosen full-sib families, I measured 1300. I did not measure trees that were dead, apparently mislabeled, or too small to measure acoustic velocity.

2.1.3 Toledo plantation

Western hemlock parent trees were chosen using backward selection from five first-generation programs in British Columbia (BC), Washington, and Oregon: one BC Ministry of Forests program (Coastal), and four NWTIC programs (Forks, Grays Harbor, Cavenham Phase-I, and Tillamook). Thirty unique parents from each of five first-generation programs (150 unrelated parents overall) were used as second-cycle parents. Each first-generation program was divided into five 6-parent half diallels (15-full-sib families/diallel if completely balanced). There would be 375 families (15 families/diallel x 5 diallels/program x 5 programs) if the mating plan was completely balanced. From the available 375 families, I chose 40 full-sib families for the M(F)

cross-type (i.e., 20 female P1 parents), and 40 full-sib families for the F(M) cross-type (i.e., 20 male P1 parents).

The Toledo plantation is located near Toledo, Oregon (44°, 40', 17.26" N, 123°, 57', 57.39" W and 118 m elevation). The plantation was established in 2001 with 1-year old seedlings using a randomized complete block design (RCBD) with 20 replications, and 1 to 2 trees per family per replication. Survival at the Toledo plantation was 95.2% at age 10. Out of 1085 available trees in my chosen full-sib families, I measured 1052. I did not measure trees that were dead, apparently mislabeled, or too small to measure acoustic velocity.

2.2 Measured variables

2.2.1 Height and DBH

Measurements of total height (HT, cm) and stem diameter at breast height (DBH, cm) were obtained for all plantations. At the Fir Grove plantation, the NWTIC provided DBH and HT data that were recorded when the trees 7 years old, which is a year younger than the age at which I measured acoustic velocity. At the Roaring River plantation, the NWTIC provided DBH and HT data that were recorded when the trees 12 years old, which is the same age that I measured acoustic velocity. At the Toledo plantation, I measured DBH when the trees were 12 years old. The NWTIC provided HT data that were recorded a year earlier at age 11.

2.2.2 Sensor distance

On each tree, I placed the acoustic tool start sensor about 0.5 m above breast height, and the stop sensor about 0.5 m below breast height. Sensors were placed at

45° angles to the stem, and about 25 mm into the tree. Sensors were always positioned on the same aspect of each tree to minimize environmental variation. I measured the vertical distance (S) between the start and stop sensors to the nearest millimeter, avoiding stem deflection or branches. The actual measured distances ranged from 75.0 to 125.0 cm.

2.2.3 Time of flight (TOF)

At the Fir Grove plantation, I measured time-of-flight (TOF) using the Fakopp TreeSonic tool (TS, Fakopp Enterprise, Hungary). At the Roaring River and Toledo plantations, I measured TOF using the Fakopp TreeSonic and Fakopp Microsecond Timer (MS, Fakopp). Both tools were used with the SDO2 sensor. I used same-face (SF) and opposite-face (OF) vertical sensor placements to take TOF measurements. For the same-face method, the start and stop sensors were positioned on the same side of the stem. After recording two consecutive same-face measurements, the stop (bottom) sensor was moved to the opposite side of the stem, and I recorded two consecutive opposite-face measurements. Except for analyses of hit-to-hit variation, these values were averaged before data analysis. Only one operator was used to record the TOF measurements across all sites. If the tree was forked, TOF was measured on the largest fork.

2.2.4 Stem form

I recorded ramicorn branching, crookedness, and forking if these defects occurred between the sensors. Ramicorn branches are large, steeply-angled branches (Helms, 1998). Ramicorn branches were recorded as present or absent. Crookedness is

defined as stem displacement from the vertical that occurs within an interwhorl (Campbell, 1965). Crookedness was recorded as present or absent. I also recorded the number of forks (i.e., number of stems minus one).

2.2.5 Measurement rate

I recorded TOF at the Roaring River plantation after the trees were pruned. In contrast, I measured unpruned trees at the Toledo plantation. All trees in these plantations were measured using the TreeSonic and Microsecond Timer acoustic tools, and a two-person crew. Measurement rates were calculated as the ratio of the number of the trees measured to the elapsed time (trees/hour). I recorded the time needed to complete the combined same-face and opposite-face measurements to compare measurement efficiency of the TreeSonic and Microsecond Timer.

2.3 Derived variables

2.3.1 Flight paths

Using S as the sensor distance, C as the stem circumference ($DBH \cdot \pi$), and E as the circumference of an ellipse calculated using Ramanujan's second approximation, I calculated six potential flight paths (P) as described by Mahon et al. (2009) (Figure 2.2). To account for sensor insertion, I calculated the path lengths using adjusted sensor distances ($S' = S - 0.035$ m) and adjusted stem diameters ($D' = DBH - 0.035$ m). The stem between the sensors was assumed to be a cylinder with diameter equal to DBH .

- i. For the opposite-face unadjusted-method (OU), the flight path was assumed unknown, so I used S' as the flight path ($P_{OU} = S'$).

- ii. For the opposite-face across-adjusted method (OA), I assumed the acoustic waves travelled radially through the center of the tree (pith) to the opposite-face, and then longitudinally down to the stop sensor ($P_{OA} = S' + D'$).
- iii. For the opposite-face diagonally-adjusted method (OD), I assumed the acoustic waves travelled directly to the stop sensor, passing through the center of the tree ($P_{OD} = \sqrt{(S')^2 + (D')^2}$).
- iv. For the opposite-face circumference-adjusted method (OC), I assumed the acoustic waves travelled circumferentially to the opposite-face of the tree in the outerwood, and then travelled longitudinally down to the stop sensor ($P_{OC} = (S' + C/2)$).
- v. For the opposite-face ellipse-adjusted method (OE), I assumed the acoustic waves travelled the shortest elliptical distance between the sensors through the outerwood ($P_{OE} = E/2$).
- vi. For the same-face method (SF), I assumed the acoustic waves travelled longitudinally down to the stop sensor on the same face of the tree ($P_{SF} = S'$).

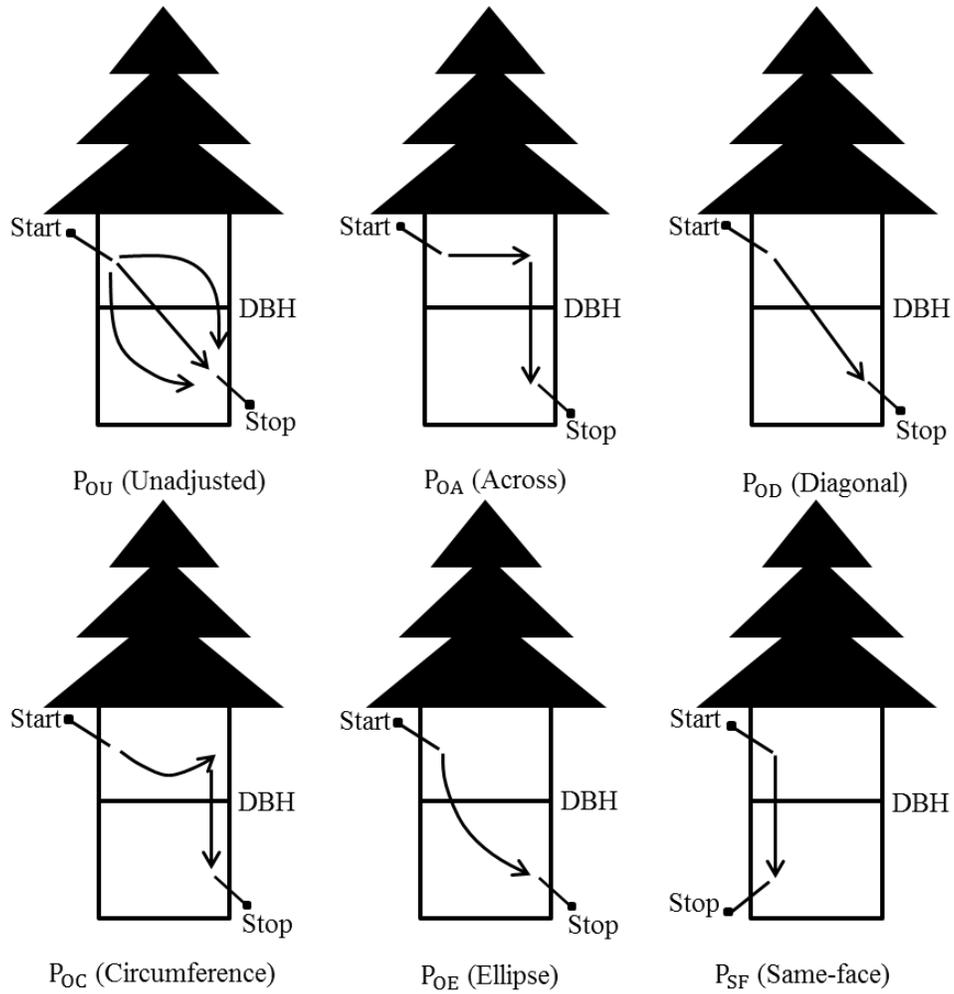


Figure 2.2: Hypothesized acoustic wave flight paths (P) were used to calculate associated distances and acoustic velocities (modified from Mahon et al. 2009).

2.3.2 Acoustic velocity and density

2.3.2.1 Acoustic velocity

I analyzed squared acoustic velocity (AV^2) because dynamic modulus of elasticity (MOE_d) is linearly related to AV^2 . That is, $MOE_d = DEN \cdot AV^2$ where DEN is the green wood density.

AV^2 was calculated for each flight path according to Equation 1.

$$[1] \quad AV^2 = (P/TOF)^2$$

Where:

AV^2 is the squared acoustic velocity

P is the flight path for the specified adjustment method (OU, OA, OD, OC, OE, and SF).

TOF is the time of flight taken directly from the TreeSonic or Microsecond Timer.

This resulted in six AV^2 variables (AV_{OU}^2 , AV_{OA}^2 , AV_{OD}^2 , AV_{OC}^2 , AV_{OE}^2 , and AV_{SF}^2).

2.3.2.2 Density

Green wood densities (DEN) were taken from Kolpak et al. (unpublished). They studied five operational plantations of Douglas-fir and western hemlock operational plantations when the trees were 7 to 15 years old. They sampled stem wood disks at breast height, wrapped them in plastic, and kept them frozen until they measured green wood density in the laboratory. For each disk, they measured green disk mass and green volume using the water displacement method, and then calculated green wood density as green disk mass/green volume. Mean green wood density was $970 \text{ kg} \cdot \text{m}^{-3}$ based on 61 Douglas-fir trees, and $1000 \text{ kg} \cdot \text{m}^{-3}$ based on 60 western

hemlock trees. I then estimated MOE_d for Douglas-fir and western hemlock ($MOE_d = DEN \cdot AV^2$).

2.3.3 Volume and Taper

Stem volume index (VOL, cm^3) was calculated as $HT \cdot DBH^2$, and then converted to dm^3 before being used in subsequent calculations. Taper (TAP) was calculated as the ratio of DBH to HT.

2.4 Statistical analysis

I identified data outliers, removed non-significant interaction terms from the statistical models, pooled the variances when appropriate, and then estimated genetic variances, heritabilities, and potential genetic gains for the Fir Grove, Roaring River, and Toledo test sites. The genetic test plantations were mostly established using one tree per family per replication. However, for some families two trees were planted. The residual terms in the following models represent this within-replication variation.

2.4.1 Data cleaning and outlier detection

In Step 1, I removed observations that had obvious data entry errors, and then removed observations corresponding to trees that were dead, severely damaged, or planted as a replacement tree. For the remaining trees, I used the restricted maximum likelihood (REML) method to estimate variance components using SAS PROC MIXED and the following linear models. For the final analysis, I excluded outliers that had studentized residuals that exceeded three standard deviations from the mean for AV_{SF}^2 , AV_{OC}^2 , HT, or DBH.

I used Model [2] for analyzing the Fir Grove and Roaring River data.

$$[2] \quad Y_{ijklmn} = \mu + R_i + CT_j + P1(CT)_{jk} + P2(CT, P1)_{jkl} + R * CT_{ij} + \\ R * P1(CT)_{ijk} + R * P2(CT, P1)_{ijkl} + B(R)_{im} + B(R) * CT_{ijm} + \\ B(R) * P1(CT)_{ijkm} + B(R) * P2(CT, P1)_{ijklm} + e_{ijklmn}$$

where:

Y_{ijklmn}	is the n^{th} observation in the m^{th} block from the l^{th} Parent #2 in the k^{th} Parent #1 in the j^{th} cross-type in the i^{th} replicate
μ	is the population mean
R_i	is the random effect of the i^{th} replicate
CT_j	is the fixed effect of the j^{th} cross-type
$P1(CT)_{jk}$	is the random effect of the k^{th} Parent #1 in the j^{th} cross-type
$P2(CT, P1)_{jkl}$	is the random effect of the l^{th} Parent #2 in the k^{th} Parent #1 in the j^{th} cross-type
$R * CT_{ij}$	is the random interaction of the i^{th} replicate and j^{th} cross-type
$R * P1(CT)_{ijk}$	is the random interaction of the i^{th} replicate and k^{th} Parent #1 in the j^{th} cross-type
$R * P2(CT, P1)_{ijkl}$	is the random interaction of the i^{th} replicate and l^{th} Parent #2 in the k^{th} Parent #1 and j^{th} cross-type
$B(R)_{im}$	is the random effect of the m^{th} block in the i^{th} replicate
$B(R) * CT_{ijm}$	is the random interaction between the m^{th} block in the i^{th} replicate and j^{th} cross-type
$B(R) * P1(CT)_{ijkm}$	is the random interaction between the m^{th} block in the i^{th} replicate and k^{th} Parent #1 in the j^{th} cross-type
$B(R) * P2(CT, P1)_{ijklm}$	is the random interaction between the m^{th} block in the i^{th} replicate and the l^{th} Parent #2 in the k^{th} Parent #1 and j^{th} cross-type
e_{ijklmn}	is the residual error

I used Model [3] for analyzing the Toledo data.

$$[3] \quad Y_{ijklm} = \mu + R_i + CT_j + P1(CT)_{jk} + P2(CT, P1)_{jkl} + R * CT_{ij} + R * P1(CT)_{ijk} + R * P2(CT, P1)_{ijkl} + e_{ijklm}$$

where μ , R_i , CT_j , $P1(CT)_{jk}$, $P2(CT, P1)_{jkl}$, $R * CT_{ij}$, $R * P1(CT)_{ijk}$, and $R * P2(CT, P1)_{ijkl}$ are as described above.

2.4.2 Removal of non-significant interaction terms

In Step 2, I removed interaction terms if the corresponding variance components were not significantly different from zero ($P > 0.05$) for all six AV^2 variables and growth traits (HT and DBH). This resulted in the following reduced models.

$$[4] \quad \begin{array}{l} \text{Fir} \\ \text{Grove} \end{array} \quad Y_{ijklm} = \mu + R_i + CT_j + P1(CT)_{jk} + P2(CT, P1)_{jkl} + R * P2(CT, P1)_{ijkl} + e_{ijklm}$$

$$[5] \quad \begin{array}{l} \text{Roaring} \\ \text{River} \end{array} \quad Y_{ijklmn} = \mu + R_i + CT_j + P1(CT)_{jk} + P2(CT, P1)_{jkl} + B(R)_{im} + e_{ijklmn}$$

$$[6] \quad \text{Toledo} \quad Y_{ijklm} = \mu + R_i + CT_j + P1(CT)_{jk} + P2(CT, P1)_{jkl} + R * P1(CT)_{ijk} + R * P2(CT, P1)_{ijkl} + e_{ijklm}$$

In step 3, I used the COVTEST statement and general contrast option to calculate P-values in SAS PROC GLIMMIX for the following tests. First, I tested whether the variance component for P1 (σ_{P1}^2) differed between the M(F) and F(M) cross-types. Second, I tested whether the variance component for P2(P1) ($\sigma_{P2(P1)}^2$) differed between the M(F) and F(M) cross-types.

Because σ_{P1}^2 and $\sigma_{P2(P1)}^2$ did not differ between the cross-types for any of the analyses, and because the fixed effect of CT was non-significant for all analyses, I

reduced the models by removing the CT term. This resulted in the following reduced models.

$$[7] \quad \begin{array}{l} \text{Fir} \\ \text{Grove} \end{array} \quad Y_{ijkl} = \mu + R_i + P1_j + P2(P1)_{jk} + R * P2(P1)_{ijk} + e_{ijkl}$$

$$[8] \quad \begin{array}{l} \text{Roaring} \\ \text{River} \end{array} \quad Y_{ijklm} = \mu + R_i + P1_j + P2(P1)_{jk} + B(R)_{il} + e_{ijklm}$$

$$[9] \quad \text{Toledo} \quad Y_{ijkl} = \mu + R_i + P1_j + P2(P1)_{jk} + R * P1_{ij} + R * P2(P1)_{ijk} + e_{ijkl}$$

Finally, in Step 4, I tested whether the variance component $\sigma_{P_1}^2$ differed from the variance component $\sigma_{P_2(P_1)}^2$ by using the COVTEST statement and general contrast option in SAS PROC GLIMMIX ($P < 0.05$). For each plantation, $\sigma_{P_1}^2$ was not significantly different from $\sigma_{P_2(P_1)}^2$. Therefore, I pooled these terms, resulting in the following final models for Fir Grove, Roaring River, and Toledo.

$$[10] \quad \begin{array}{l} \text{Fir Grove} \\ \text{and Toledo} \end{array} \quad Y_{ijk} = \mu + R_i + F_j + F * R_{ij} + e_{ijk}$$

$$[11] \quad \begin{array}{l} \text{Roaring} \\ \text{River} \end{array} \quad Y_{ijkl} = \mu + R_i + F_j + B(R)_{ik} + e_{ijkl}$$

where: μ , R_i and $B(R)_{ik}$ are as described above and

F_j is the random effect of the j^{th} full-sib family

$F * R_{ij}$ is the random interaction of the j^{th} family and i^{th} replicate

2.5 Variances and heritabilities

2.5.1 Variances

Variance components were estimated using the SAS PROC MIXED procedure and Models 7 through 11. $\sigma_{P_1}^2$ is the variance component for Parent #1, $\sigma_{P_2(P_1)}^2$ is the

variance component for Parent #2 nested in Parent #1, σ_{P1r}^2 is the variance component for the interaction between Parent #1 and replication, $\sigma_{P2(P1)r}^2$ is the variance component for the interaction between Parent #2 and replication, σ_f^2 is the variance component for full-sib family, σ_{fr}^2 is the variance component for the interaction between full-sib family and replication, and σ_e^2 is the residual variance. $\sigma_{P1+P2(P1)}^2$ was estimated as the sum of the σ_{P1}^2 and $\sigma_{P2(P1)}^2$ variance components (Becker, 1984). σ_{P1}^2 was assumed to represent one quarter of the additive genetic variance (σ_A^2), whereas $\sigma_{P2(P1)}^2$ was initially assumed to represent one quarter of the additive genetic variance plus one quarter of the dominance variance (σ_D^2) (Becker, 1984). This assumes that there are no maternal effects and no epistasis. σ_f^2 approximates $\sigma_{P1}^2 + \sigma_{P2(P1)}^2$.

The additive genetic coefficient of variation (AGCV, %) was calculated as the square root of the additive genetic variance divided by the trait mean multiplied by 100.

2.5.2 Heritabilities

2.5.2.1 Individual-tree heritability

I estimated individual-tree heritabilities using three different approaches (Becker, 1984). First, I estimated individual-tree narrow-sense heritabilities (h_a^2) using Equation 12,

$$[12] \quad h_a^2 = \frac{\sigma_A^2}{\sigma_P^2} = \frac{4\sigma_{P1}^2}{\sigma_P^2}$$

where σ_p^2 was estimated as $\sigma_{P_1}^2 + \sigma_{P_2(P_1)}^2 + \sigma_{P_2(P_1)r}^2 + \sigma_e^2$ for Fir Grove (Model 7), $\sigma_{P_1}^2 + \sigma_{P_2(P_1)}^2 + \sigma_e^2$ for Roaring River (Model 8), and $\sigma_{P_1}^2 + \sigma_{P_2(P_1)}^2 + \sigma_{(P_1)r}^2 + \sigma_{P_2(P_1)r}^2 + \sigma_e^2$ for Toledo (Model 9).

Second, I estimated genotypic heritabilities h_{g1}^2 using Equation 13,

$$[13] \quad h_{g1}^2 = \frac{\sigma_A^2 + 1/2\sigma_D^2}{\sigma_p^2} = \frac{2(\sigma_{P_1}^2 + \sigma_{P_2(P_1)}^2)}{\sigma_p^2}$$

where σ_p^2 is as described above for Fir Grove, Roaring River and Toledo.

Third, I estimated the genotypic heritability h_{g2}^2 using Equation 14,

$$[14] \quad h_{g2}^2 = \frac{2\sigma_f^2}{\sigma_p^2}$$

where σ_p^2 was estimated as $\sigma_f^2 + \sigma_{fr}^2 + \sigma_e^2$ for Fir Grove and Toledo (Model 10), and $\sigma_f^2 + \sigma_e^2$ for Roaring River (Model 11). h_{g1}^2 estimates the individual-tree narrow-sense heritability if the dominance variance is assumed to equal zero. h_{g2}^2 is an approximation of h_{g1}^2 .

2.5.2.2 Family heritability

I estimated family heritabilities (h_{g1}^2) using Equation 15,

$$[15] \quad h_{g1}^2 = \frac{\sigma_{P_1}^2 + \sigma_{P_2(P_1)}^2}{\sigma_p^2}$$

where $\sigma_p^2 = \sigma_{P_1}^2 + \sigma_{P_2(P_1)}^2 + \sigma_{P_2(P_1)r}^2/k + \sigma_e^2/k$ for Fir Grove, $\sigma_{P_1}^2 + \sigma_{P_2(P_1)}^2 + \sigma_e^2/k$ for Roaring River, and $\sigma_{P_1}^2 + \sigma_{P_2(P_1)}^2 + (\sigma_{(P_1)r}^2 + \sigma_{P_2(P_1)r}^2)/k + \sigma_e^2/k$ for Toledo. k is the number of trees per replication (and the number of trees per family) if

I assume that there is one tree per family per replication. I also varied k from 2 to 20 to

estimate potential genetic gains and family heritabilities for wood stiffness in relation to the number of trees per family. The variance components were estimated using Model 7 for Fir Grove, Model 8 for Roaring River, and Model 9 for Toledo plantations.

2.6 Differences among tools and sensor placements

I used Model 16 and the SAS PROC MIXED procedure to test whether h_{g1}^2 differed among acoustic tools (TS and MS), sites (FG, RR and T), species (WH and DF), vertical placements (SF and OF), and adjustment methods (OU, OA, OD, OC, OE and SF). I pooled non-significant 3-way and higher interaction terms. Because I measured AV at two different ages for Douglas-fir (8 and 12 years old), and at one age for western hemlock (12 years old), I omitted the species term from the model. Therefore, the results pertain to Douglas-fir and western hemlock overall.

$$[16] \quad Y_{ijklm} = \mu + S_i + H_j + A(H)_{jk} + T_l + S * T_{il} + H * T_{jl} + S * H_{ij} + S * A(H)_{ijk} + T * A(H)_{jkl} + S * H * T_{ijl} + e_{ijklm}$$

where:

Y_{ijklm}	is the m^{th} observation from the l^{th} tool using the k^{th} adjustment method within the j^{th} vertical placement at the i^{th} site
μ	is the population mean
S_i	is the random effect of the i^{th} site
H_j	is the fixed effect of the j^{th} vertical placement
$A(H)_{jk}$	is the fixed effect of the k^{th} adjustment method in the j^{th} vertical placement
T_l	is the fixed effect of the l^{th} tool

$S * T_{il}$	is the random interaction between the i^{th} site and l^{th} vertical placement
$H * T_{jl}$	is the fixed interaction between the j^{th} vertical placement and l^{th} tool
$S * H_{ij}$	is the random interaction between the i^{th} site and j^{th} vertical placement
$S * A(H)_{ijk}$	is the random interaction between the i^{th} site and k^{th} adjustment method in the j^{th} vertical placement
$T * A(H)_{jkl}$	is the fixed interaction between the l^{th} tool and k^{th} adjustment method in the j^{th} vertical placement
$S * H * T_{ijl}$	is the random interaction between the l^{th} tool and j^{th} vertical placement and i^{th} site
e_{ijklm}	is the residual error

2.7 Correlations and genetic gain

Because there were no differences between tools, vertical placements, or adjustment methods, I focused on using the TreeSonic and the same-face approach for the remaining analyses.

2.7.1 Correlations

Genotypic (r_{g1}), environmental (r_E), and phenotypic (r_P) correlations were estimated using Equation 17,

$$[17] \quad r_{X,Y} = \frac{\text{Cov}_{X,Y}}{(\sigma_X^2 * \sigma_Y^2)^{1/2}}$$

where $r_{X,Y}$ is the correlation between traits x and y, $\text{Cov}_{X,Y}$ is the genotypic (g1), phenotypic (P), or environmental (E) covariance component between traits x and y, and σ_X^2 and σ_Y^2 are the corresponding variance components for traits x and y.

2.7.1.1 Genotypic correlation

The genotypic covariances between traits x and y were estimated using the Models 7 – 9 for the corresponding genetic test plantations and Equation 18, where $(\sigma_{g1(x)}^2)$ is the estimated genotypic variance for trait x, $(\sigma_{g1(y)}^2)$ is the estimated genotypic variance for trait y, and $\sigma_{g1(x+y)}^2$ is the estimated genotypic variance for a new trait equal to x + y. (Hannrup et al., 2000). The genotypic variances for traits x, y, and (x + y) were estimated as $2(\sigma_{P1}^2 + \sigma_{P2(P1)}^2)$.

$$[18] \quad \text{Cov}_{X,Y} = \frac{1}{2}(\sigma_{g1(x+y)}^2 - \sigma_{g1(x)}^2 - \sigma_{g1(y)}^2)$$

It is important to note that the genotypic correlations must be interpreted with caution. When the absolute mean value and standard deviations of traits x and y differed substantially, genotypic correlations estimated using the PROC Mixed were sometimes out of the bounds (i.e., greater than 1 or less than -1). Therefore, traits with low absolute mean values were re-scaled before calculating variance components for each trait.

2.7.1.2 Phenotypic correlations

The phenotypic covariances between traits x and y were estimated using the Models 7 – 9 for the corresponding genetic test plantations and Equation 19, where $(\sigma_{P(x)}^2)$ is the estimated phenotypic variance for trait x, $(\sigma_{P(y)}^2)$ is the estimated phenotypic variance for trait y, and $\sigma_{P(x+y)}^2$ is the estimated phenotypic variance of a new trait equal to x + y. The phenotypic variance components were estimated as $\sigma_{P1}^2 + \sigma_{P2(P1)}^2 + \sigma_{P2(P1)r}^2 + \sigma_e^2$ for Fir Grove (Model 7), $\sigma_{P1}^2 + \sigma_{P2(P1)}^2 + \sigma_e^2$ for

Roaring River (Model 8), and $\sigma_{P1}^2 + \sigma_{P2(P1)}^2 + \sigma_{(P1)r}^2 + \sigma_{P2(P1)r}^2 + \sigma_e^2$ for Toledo (Model 9).

$$[19] \quad \text{Cov}_{X,Y} = \frac{1}{2}(\sigma_{P(x+y)}^2 - \sigma_{P(x)}^2 - \sigma_{P(y)}^2)$$

2.7.1.3 Environmental correlation

The environmental covariances between traits x and y were estimated using the Models 7 – 9 for the corresponding genetic test plantations and Equation 20, where $\sigma_{E(x)}^2$ is the environmental variance component for trait x ($= \sigma_{P(x)}^2 - \sigma_{g1(x)}^2$), $\sigma_{E(y)}^2$ is the environmental variance component for trait y ($= \sigma_{P(y)}^2 - \sigma_{g1(y)}^2$), and $\sigma_{E(x+y)}^2$ is the environmental covariance component for a new trait equal to x + y ($= \sigma_{P(x+y)}^2 - \sigma_{g1(x+y)}^2$). I assumed that measurement and other non-environmental sources of error were low.

$$[20] \quad \text{Cov}_{X,Y} = \frac{1}{2}(\sigma_{E(x+y)}^2 - \sigma_{E(x)}^2 - \sigma_{E(y)}^2)$$

2.7.2 Genetic gain

Potential genetic gains from full-sib family selection were estimated assuming that full-sib families would be selected and planted in a seed orchard with control crossing and no pollen contamination. Gains from full-sib family selection were estimated based on choosing the best 20 of 200 unrelated full-sib families based on the results from the progeny test plantations. This is equal to a 10% selection intensity ($i = 1.742$ for $n = 200$; Falconer and Mackay, 1996). Percent gain was estimated using Equation 21.

$$[21] \quad \Delta G(\%) = \left\{ \frac{i \sigma_{\bar{p}} h_{g1}^2}{\bar{x}} \right\} (100)$$

Where $\sigma_{\bar{p}}$ is the standard deviation of family means estimated from variance components, \bar{x} is the trait mean, and i and h_{g1}^2 are as described above.

2.8 Expected family heritabilities and genetic gains when the number of replications is varied

As described above, I used SAS Proc Mixed to estimate variance components for each genetic test plantation. I used the Models 7 – 9, the same-face vertical placement, and the TreeSonic acoustic tool. Family heritabilities were estimated assuming that 10 trees were measured per family (i.e., one tree per family per replication). Family heritabilities and genetic gains were estimated using Equation 15 and Equation 21 based on a constant set of variance components, but a variable number of trees per family (e.g., from 2 to 20 trees).

3 RESULTS

I measured acoustic velocity on 8- to 12-year-old trees at two genetic test plantations of Douglas-fir (Fir Grove and Roaring River) and one plantation of western hemlock (Toledo). These plantations were measured using two standing-tree acoustic tools and two vertical placements of the sensors. The mean DBH of the trees was 5.8 cm at age 7, 11.4 cm at age 12, and 10.4 cm at age 12, and the mean height was 4.6 m at age 7, 8.6 m at age 12 and 7.2 m at age 11 at the Fir Grove, Roaring River, and Toledo plantations. One of my objectives was to develop optimal measurement approaches and selection scenarios for improving juvenile wood stiffness. Therefore, I first determined the best measurement approach, and then used the best approach to estimate (1) genetic variation, heritabilities, and potential genetic gains, and (2) genotypic correlations between acoustic velocity and growth traits.

3.1 Statistical models

As described in the Materials and Methods, I removed all non-significant ($P > 0.05$) block and interaction terms from the full model for each plantation. For Fir Grove, I removed the terms $R*CT$, $R*P1(CT)$, $B(R)$, $B(R)*(CT)$, $B(R)*P1(CT)$, and $B(R)*P2(CT,P1)$ (Table A1), resulting in reduced Model 4. For Roaring River, I removed the terms $R*CT$, $R*P1(CT)$, $R*P2(CT,P1)$, $B(R)*(CT)$, $B(R)*P1(CT)$, and $B(R)*P2(CT,P1)$ (Table A2), resulting in reduced Model 5. For Toledo, I removed the interaction term $R*CT$ (Table A3), resulting in reduced Model 6.

For each plantation, the P1 variance component (σ_{P1}^2) was not significantly different between the M(F) and F(M) cross-types ($P > 0.152$; Tables A4-A6). In

addition, the P2 variance component ($\sigma_{P2(P1)}^2$) was not significantly different between the cross-types ($P > 0.524$; Tables A4-A6). The fixed effect of cross-type was not significant for any of the three plantations ($P > 0.513$). Therefore, I removed the CT term, resulting in reduced Models 7-9 for the Fir Grove, Roaring River and Toledo plantations. Finally, because σ_{P1}^2 and $\sigma_{P2(P1)}^2$ were not significantly different from each other ($P > 0.091$), I pooled the P1 and P2(P1) terms, resulting in Model 10 for the Fir Grove and Roaring River plantations (Tables A7 and A8), and Model 11 for the Toledo plantation (Table A9).

3.2 The effects of standing-tree tool, vertical placement, and DBH-adjustment were non-significant

I used the genotypic heritability (h_{g1}^2) to test for overall differences between two acoustic tools, two vertical placements, and six flight path adjustments. These heritabilities ranged from 0.492 to 0.905 for the various measurement approaches at the three plantations (Table 3.1). There were no differences between the (1) TreeSonic and Microsecond Timer ($P > 0.883$), (2) same-face and opposite-face approach ($P > 0.622$), or (3) six DBH adjustments ($P > 0.744$).

Table 3.1: Estimates of individual-tree genotypic (h_{g1}^2) and family ($h_{\bar{g}1}^2$) heritabilities at the Toledo, Roaring River, and Fir Grove plantations using two standing tree acoustic tools (TreeSonic and Microsecond Timer). Heritabilities are presented for 6 acoustic velocity variables ($AV_{OU}^2, AV_{OA}^2, AV_{OD}^2, AV_{OC}^2, AV_{OE}^2$, and AV_{SF}^2 ; $\text{km}^2 \cdot \text{s}^{-2}$)

	Opposite-face ^a					Same-face ^a	
	h_{g1}^2					$h_{\bar{g}1}^2$	
	OU	OA	OD	OC	OE	SF ^b	SF
TreeSonic							
Fir Grove (DF) ^c	0.905	0.853	0.904	0.818	0.900	0.898	0.891^d
Roaring River (DF)	0.527	0.528	0.531	0.501	0.539	0.561	0.796
Toledo (WH)	0.492	0.566	0.504	0.554	0.535	0.513	0.775
Microsecond Timer							
Roaring River (DF)	0.533	0.537	0.537	0.513	0.544	0.588	0.806
Toledo (WH)	0.495	0.558	0.507	0.539	0.534	0.495	0.767

^a I used five opposite-face adjustment approaches (OU = unadjusted, OA = across adjusted, OD = diagonally adjusted, OC = circumference adjusted, and OE = ellipse adjusted) and one same-face adjustment approach (SF = same-face) (Mahon et al 2009).

^b Bold numbers highlight the heritabilities for the recommended vertical placement.

^c DF = Douglas-fir and WH = western hemlock.

^d These family heritabilities ($h_{\bar{g}1}^2$) are based on 10 trees (replications) per family.

3.3 Hit-to-hit variation for TOF was less using the opposite-face approach compared to the same-face approach

I took two consecutive TOF measurements for each vertical sensor placement. The hit-to-hit variation between the two consecutive TOF measurements was slightly less when I used the opposite-face approach. For example, the hit-to-hit coefficient of variation (standard deviation divided by the trait mean) was 4.8% for the same-face approach, and 4.6% for the opposite-face approach at the Fir Grove plantation. Therefore, the hit-to-hit variation for the opposite-face approach was 3.9% less than the variation for the same-face approach at Fir Grove. Similarly, the hit-to-hit variation was 11.2% and 6.6% less using the opposite-face approach at the Roaring River and Toledo plantations.

3.4 Measurement rates were highest when I used the TreeSonic and same-face approach

The measurement rate was higher when I used the TreeSonic compared to the Microsecond Timer (Table 3.2). For example, measurement rate was 32 trees/hour for the TreeSonic and 27 trees/hour for the Microsecond Timer at Roaring River. Based on the analysis of h_{g1}^2 , measurement rates, and practical considerations, I decided to focus the rest of my analyses on AV^2 measured using the TreeSonic and same-face approach. Using this approach, the mean AV^2 was 7.9, 9.2 and 8.6 $\text{km}^2 \cdot \text{s}^{-2}$ at the Fir Grove, Roaring River, and Toledo plantations.

Table 3.2: Measurement rates at the Roaring River and Toledo plantations using two acoustic tools and two vertical placements.

	Same-face plus Opposite face ^a	
	Roaring River (Pruned) ^b Trees/hour	Toledo (Not pruned) ^c Trees/hour
TreeSonic	32	19
Microsecond Timer	27	15

^aTime recorded to complete the combined same-face and opposite-face measurements.

^bTOF measurements were taken after the trees were pruned at the Roaring River.

^cTOF measurements were taken from the unpruned trees at the Toledo plantation.

3.5 Comparison of Douglas-fir and western hemlock wood stiffness traits

I compared mean AV^2 and MOE_d between Douglas-fir and western hemlock in operational plantations and genetic tests. I measured AV^2 using the TreeSonic, and I estimated MOE_d using AV^2 and the mean green wood density (DEN) for each species. Mean DEN was estimated as $970 \text{ kg}\cdot\text{m}^{-3}$ for Douglas-fir and $1000 \text{ kg}\cdot\text{m}^{-3}$ for western hemlock based on wood discs taken from DBH on 61 Douglas-fir and 60 western hemlock trees measured in the operational plantations (Kolpak et al., unpublished).

The mean AV^2 and MOE_d were higher for Douglas-fir compared to western hemlock. For example, the mean AV^2 was $8.5 \text{ km}^2\cdot\text{s}^{-2}$ for Douglas-fir and $6.6 \text{ km}^2\cdot\text{s}^{-2}$ for hemlock across the five operational plantations (Figure 3.1a). Similarly, the mean AV^2 was $9.2 \text{ km}^2\cdot\text{s}^{-2}$ for 12-year-old Douglas-fir and $8.6 \text{ km}^2\cdot\text{s}^{-2}$ for 12-year-old western hemlock (Figure 3.1b). I also saw the same pattern for MOE_d . The mean MOE_d was 8.2 GPa for Douglas-fir and 6.6 GPa for hemlock across the five operational plantations (Figure 3.1c). The mean MOE_d was 8.9 GPa for 12-year-old Douglas-fir and 8.6 GPa for 12-year-old western hemlock in the genetic test plantations (Figure 3.1d).

The difference in AV^2 between Douglas-fir and western hemlock was greater for the five operational plantations than for the genetic test plantations (i.e., 12-year-old Douglas-fir and western hemlock genetic tests). This was also true for MOE_d . The Douglas-fir and western hemlock trees were planted on the same site across the five operational plantations, but planted at different locations for the genetic

test plantations. Therefore, the between-species difference in AV^2 that was estimated from the operational plantations is probably more generally applicable.

Although mean stiffness was higher for Douglas-fir, the distributions of AV^2 and MOE_d overlapped between the species. Considering only the 12-year-old plantations, for example, 25% of the western hemlock families (20 out of 80) had higher MOE_d than the mean for Douglas-fir (8.9 GPa). Furthermore, 10% of the western hemlock families (8 out of 80) had higher AV^2 than the mean for Douglas-fir.

AV^2 and MOE_d were higher for older trees. Mean AV^2 was $7.9 \text{ km}^2 \cdot \text{s}^{-2}$ for 8-year-old Douglas-fir at Fir Grove and $9.2 \text{ km}^2 \cdot \text{s}^{-2}$ for 12-year-old Douglas-fir at Roaring River. Similarly, MOE_d was 7.7 GPa at Fir Grove and 8.9 GPa at Roaring River.

As shown in Figure 3.1, the variation in AV^2 and MOE_d was higher in the operational plantations than in the genetic tests. The main reason for this is that individual tree values are reported for the operational plantations, whereas family means are reported for the genetic tests. In addition, AV^2 and MOE_d were measured across multiple age classes (7 to 15 years old) across the five operational plantations, but each of the genetic tests was a single age (8 or 12 years old).

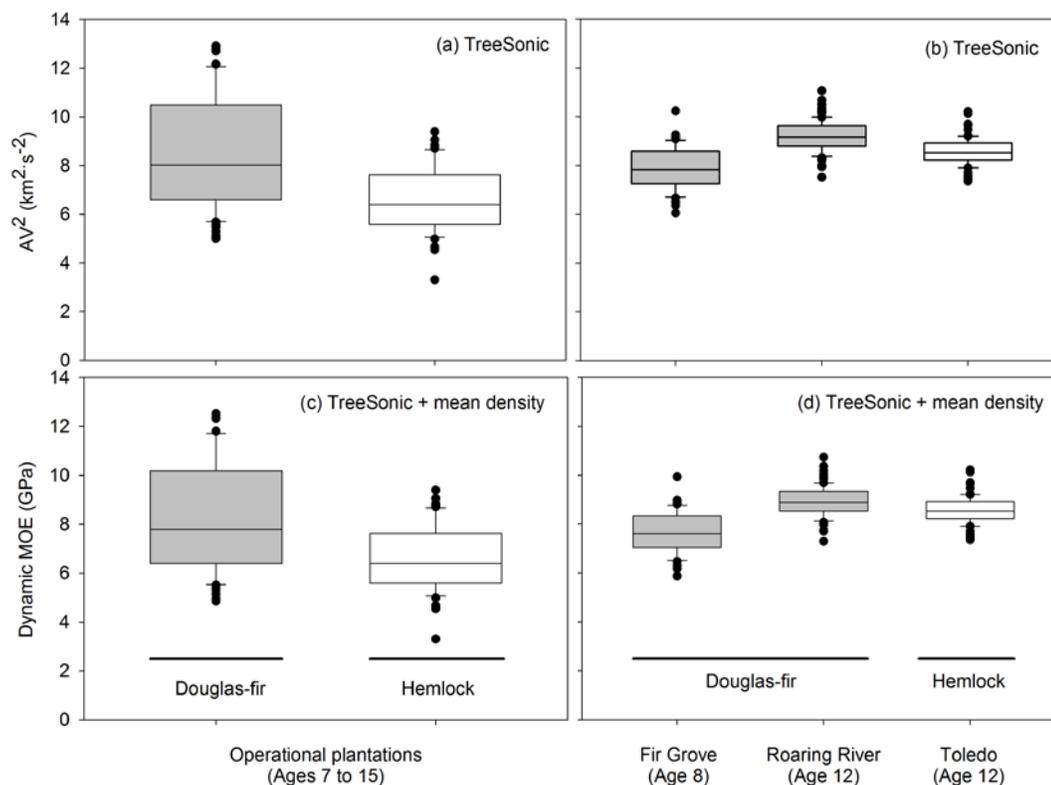


Figure 3.1: Comparison of Douglas-fir and western hemlock wood stiffness traits measured at five operational plantations and three genetic test plantations. Squared acoustic velocity (AV^2) was measured using the TreeSonic standing-tree tool and dynamic MOE (MOE_d) was estimated using AV^2 and the mean green wood density (DEN) for each species ($MOE_d = DEN \cdot AV^2$). Mean DEN was $970 \text{ kg} \cdot \text{m}^{-3}$ for Douglas-fir and $1000 \text{ kg} \cdot \text{m}^{-3}$ for western hemlock (Kolpak et al. unpublished). Values are shown for individual trees at the operational plantations and family means at the genetic test plantations.

3.6 AV^2 had significant genetic variation in Douglas-fir and western hemlock

Generally, AV^2 had more genetic variation than did the growth traits (HT, DBH, and VOL). Based on the additive genetic coefficient of variation (AGCV), AV^2 tended to have more genetic variation (AGCV = 8.4 to 14.8%) than did HT (AGCV = 6.4 to 7.8%) or DBH (AGCV = 7.9 to 11.5%). Because the σ_{P1}^2 variance component for AV^2 was not significantly different from $\sigma_{P2(P1)}^2$, there seemed to be no substantial dominance variation for either Douglas-fir or western hemlock ($P > 0.375$; Tables A7-A9). In addition, the σ_{P1}^2 and $\sigma_{P2(P1)}^2$ variance components were not significantly different between the M(F) and F(M) cross-types ($P > 0.391$; Tables A4-A6). This indicates that maternal effects were not large in either Douglas-fir or western hemlock.

3.7 The heritability of AV^2 was higher than for the growth and form traits

For each same-face variable (AV_{SF}^2) and five opposite-face variables (AV_{OU}^2 , AV_{OA}^2 , AV_{OD}^2 , AV_{OC}^2 and AV_{OE}^2), I estimated (1) family heritabilities (h_{g1}^2) and (2) individual-tree heritabilities using three approaches (Tables 3.3-3.5). As explained in the Method and Materials, σ_{P1}^2 was initially assumed to represent the additive genetic variance ($1/4\sigma_A^2$), whereas $\sigma_{P2(P1)}^2$ was assumed to represent additive genetic variance plus dominance variance ($1/4\sigma_A^2 + 1/4\sigma_D^2$) (Becker, 1984). Because dominance variation seemed to be low for Douglas-fir and western hemlock, I concluded that both σ_{P1}^2 and $\sigma_{P2(P1)}^2$ estimate one quarter of the additive genetic variance. Furthermore, if dominance is assumed to be zero, the genotypic heritabilities (h_{g1}^2 and h_{g2}^2) estimate individual-tree narrow-sense heritabilities. Therefore, I used two times the summed

value of $\sigma_{P_1}^2$ and $\sigma_{P_2(P_1)}^2$ as my best estimate of the additive genetic variance, and $h_{g_1}^2$ as my best estimate of narrow-sense heritability.

The individual-tree heritabilities ($h_{g_1}^2$) for HT, DBH, VOL (0.17-0.36), and TAP (0.12-0.33) were 2 to 4 times lower (Table 3.6) than the heritabilities for AV^2 , which ranged from 0.51 to 0.90 (Table 3.1). Interestingly, $h_{g_1}^2$ for AV^2 at Fir Grove (0.90) was considerably higher than at Roaring River (0.56) or Toledo (0.51) (Tables 3.3-3.5). Another interesting observation was that the $h_{g_1}^2$ for TAP was much higher in Douglas-fir (0.23-0.33) than in hemlock (0.12) (Table 3.6). Family heritabilities ranged from 0.78 to 0.89 when I assumed that 10 trees would be measured per family (Tables 3.3-3.5).

Table 3.3: Variance components (Var) and heritabilities (h^2) for squared acoustic velocity variables (AV^2 ; $\text{km}^2 \cdot \text{s}^{-2}$) measured on 8-year-old Douglas-fir trees at the Fir Grove plantation using the TreeSonic acoustic tool and two vertical placements (same-face and opposite-face) of the sensors.

Effects ^b	Opposite-face ^a						Same-face ^a					
	OU		OA		OD		OC		OE		SF ^c	
	Var #1	Var #2	Var #1	Var #2	Var #1	Var #2	Var #1	Var #2	Var #1	Var #2	Var #1	Var #2
TreeSonic												
R	0.034	0.034	0.039	0.038	0.034	0.034	0.046	0.045	0.034	0.034	0.043	0.042
P1	0.288	-	0.325	-	0.288	-	0.350	-	0.290	-	0.308	-
P2(P1)	0.394	-	0.436	-	0.395	-	0.465	-	0.397	-	0.373	-
Pooled(F)	-	0.681	-	0.761	-	0.681	-	0.815	-	0.686	-	0.681
R*P2(P1)	0.761	-	0.865	-	0.762	-	0.942	-	0.766	-	0.610	-
Pooled	-	0.759	-	0.865	-	0.762	-	0.943	-	0.767	-	0.608
Residual	0.064	0.064	0.159	0.159	0.066	0.066	0.237	0.237	0.073	0.073	0.226	0.226
h_a^2	0.764	-	0.729	-	0.763	-	0.703	-	0.760	-	0.813	-
h_{g1}^2 and h_{g2}^2	0.905	0.906	0.853	0.852	0.904	0.903	0.818	0.817	0.900	0.899	0.898	0.899
h_{g1}^2	0.892	-	0.881	-	0.892	-	0.874	-	0.891	-	0.891	-

^a I used five opposite-face adjustment approaches (OU = unadjusted, OA = across adjusted, OD = diagonally adjusted, OC = circumference adjusted, and OE = ellipse adjusted) and one same-face adjustment approach (SF = same-face) (Mahon et al 2009).

^b Variance components were estimated as described in the Materials and Methods using two alternative models: Var #1 = Model [7] and Var #2 = Model [10]. R = replication, P1 = Parent #1, P2 = Parent #2, and F = full-sib family. h_a^2 is the individual-tree narrow sense heritability and h_{g1}^2 is the individual-tree genotypic heritability estimated using Model [7] (Becker 1984). h_{g2}^2 is the individual-tree genotypic heritability estimated using Model [10]. h_{g1}^2 is the full-sib family heritability estimated using Model [7], and assuming 10 measured trees per family.

^c Bold numbers highlight the variance components and heritabilities of the recommended approach.

Table 3.4: Variance components (Var) and heritabilities (h^2) for squared acoustic velocity variables (AV^2 ; $\text{km}^2 \cdot \text{s}^{-2}$) measured on 12-year-old Douglas-fir trees at the Roaring River plantation using two standing-tree tools (TreeSonic and Microsecond Timer) and two vertical placements (same-face and opposite-face) of the sensors.

Effects ^b	Opposite-face ^a						Same-face ^a					
	OU		OA		OD		OC		OE		SF ^c	
	Var#1	Var #2	Var #1	Var #2	Var #1	Var #2	Var #1	Var #2	Var #1	Var #2	Var #1	Var #2
TreeSonic												
R	0.114	0.113	0.117	0.116	0.112	0.112	0.121	0.120	0.109	0.109	0.150	0.149
B(R)	0.051	0.051	0.093	0.093	0.053	0.053	0.125	0.126	0.060	0.060	0.061	0.061
P1	0.064	-	0.096	-	0.065	-	0.125	-	0.069	-	0.122	-
P2(P1)	0.221	-	0.281	-	0.222	-	0.327	-	0.228	-	0.228	-
Pooled(F)	-	0.285	-	0.377	-	0.287	-	0.452	-	0.296	-	0.349
Residual	0.797	0.797	1.052	1.052	0.795	0.795	1.351	1.351	0.806	0.806	0.897	0.897
h_a^2	0.237	-	0.269	-	0.241	-	0.277	-	0.251	-	0.391	-
h_{g1}^2 and h_{g2}^2	0.527	0.526	0.528	0.528	0.531	0.530	0.501	0.501	0.539	0.538	0.561	0.560
h_{g1}^2	0.782	-	0.782	-	0.783	-	0.770	-	0.787	-	0.796	-

Table 3.4 (Continued)

Effects ^b	Opposite-face ^a						Same-face ^a					
	OU		OA		OD		OC		OE		SF	
	Var#1	Var #2	Var #1	Var #2	Var #1	Var #2	Var #1	Var #2	Var #1	Var #2	Var #1	Var #2
Microsecond Timer												
R	0.049	0.049	0.065	0.065	0.049	0.049	0.079	0.079	0.051	0.050	0.053	0.053
B(R)	0.039	0.040	0.077	0.077	0.041	0.042	0.106	0.107	0.047	0.048	0.050	0.050
P1	0.047	-	0.073	-	0.047	-	0.098	-	0.050	-	0.059	-
P2(P1)	0.180	-	0.217	-	0.180	-	0.245	-	0.183	-	0.210	-
Pooled(F)	-	0.226	-	0.290	-	0.227	-	0.342	-	0.232	-	0.268
Residual	0.622	0.622	0.791	0.790	0.620	0.620	0.993	0.993	0.623	0.623	0.645	0.645
h_a^2	0.220	-	0.270	-	0.223	-	0.294	-	0.235	-	0.258	-
h_{g1}^2 and h_{g2}^2	0.533	0.533	0.537	0.536	0.537	0.536	0.513	0.513	0.544	0.543	0.588	0.587
h_{g1}^2	0.784	-	0.786	-	0.786	-	0.775	-	0.789	-	0.806	-

^a I used five opposite-face adjustment approaches (OU = unadjusted, OA = across adjusted, OD = diagonally adjusted, OC = circumference adjusted, and OE = ellipse adjusted) and one same-face adjustment approach (SF = same-face) (Mahon et al 2009).

^b Variance components were estimated as described in the Materials and Methods using two alternative models: Var #1 = Model [8] and Var #2 = Model [11]. R = replication, B = block, P1 = Parent #1, P2 = Parent #2, and F = full-sib family. h_a^2 is the individual-tree narrow sense heritability and h_{g1}^2 is the individual-tree genotypic heritability estimated using Model [8] (Becker 1984). h_{g2}^2 is the individual-tree genotypic heritability estimated using Model [11]. h_{g1}^2 is the full-sib family heritability estimated using Model [8], and assuming 10 measured trees per family.

^c Bold numbers highlight the variance components and heritabilities of the recommended approach.

Table 3.5: Variance components (Var) and heritabilities (h^2) for squared acoustic velocity variables (AV^2 ; $\text{km}^2 \cdot \text{s}^{-2}$) measured on 12-year-old western hemlock trees at the Toledo plantation using two standing-tree tools (TreeSonic and Microsecond Timer) and two vertical placements (same-face and opposite-face) of the sensors.

Effects ^b	Opposite-face ^a						Same-face ^a					
	OU		OA		OD		OC		OE		SF ^c	
	Var #1	Var #2	Var #1	Var #2	Var #1	Var #2	Var #1	Var #2	Var #1	Var #2	Var #1	Var #2
TreeSonic												
R	0.077	0.076	0.111	0.111	0.077	0.077	0.146	0.146	0.081	0.080	0.076	0.075
P1	0.132	-	0.225	-	0.135	-	0.310	-	0.148	-	0.143	-
P2(P1)	0.116	-	0.200	-	0.120	-	0.268	-	0.133	-	0.116	-
Pooled (F)	-	0.246	-	0.421	-	0.254	-	0.573	-	0.280	-	0.258
R*P1	0.086	-	0.140	-	0.087	-	0.198	-	0.092	-	0.065	-
R*P2(P1)	0.094	-	0.231	-	0.101	-	0.459	-	0.122	-	0.158	-
Pooled (F*R)	-	0.191	-	0.404	-	0.199	-	0.705	-	0.227	-	0.223
Residual	0.578	0.566	0.702	0.668	0.569	0.557	0.851	0.801	0.557	0.543	0.530	0.529
h_a^2	0.524	-	0.600	-	0.535	-	0.594	-	0.562	-	0.566	-
h_{g1}^2 and h_{g2}^2	0.492	0.491	0.566	0.564	0.504	0.503	0.554	0.551	0.535	0.533	0.513	0.511
h_{g1}^2	0.765	-	0.798	-	0.771	-	0.793	-	0.785	-	0.775	-

Table 3.5 (Continued)

Effects ^b	Opposite-face ^a						Same-face ^a					
	OU		OA		OD		OC		OE		SF ^c	
	Var #1	Var #2	Var #1	Var #2	Var #1	Var #2	Var #1	Var #2	Var #1	Var #2	Var #1	Var #2
Microsecond Timer												
R	0.075	0.074	0.076	0.076	0.074	0.073	0.082	0.082	0.072	0.071	0.081	0.080
P1	0.134	-	0.209	-	0.135	-	0.280	-	0.145	-	0.139	-
P2(P1)	0.077	-	0.137	-	0.081	-	0.186	-	0.091	-	0.078	-
Pooled (F)	-	0.209	-	0.343	-	0.215	-	0.460	-	0.234	-	0.215
R*P1	0.069	-	0.121	-	0.073	-	0.176	-	0.079	-	0.067	-
R*P2(P1)	0.196	-	0.351	-	0.198	-	0.606	-	0.214	-	0.102	-
Pooled (F*R)	-	0.269	-	0.489	-	0.275	-	0.807	-	0.298	-	0.177
Residual	0.376	0.371	0.425	0.406	0.367	0.363	0.480	0.455	0.356	0.350	0.489	0.481
h_a^2	0.628	-	0.675	-	0.633	-	0.647	-	0.658	-	0.634	-
h_{g1}^2 and h_{g2}^2	0.495	0.492	0.558	0.554	0.507	0.504	0.539	0.534	0.534	0.531	0.495	0.493
h_{g1}^2	0.767	-	0.794	-	0.773	-	0.787	-	0.785	-	0.767	-

^aI used five opposite-face adjustment approaches (OU = unadjusted, OA = across adjusted, OD = diagonally adjusted, OC = circumference adjusted, and OE = ellipse adjusted) and one same-face adjustment approach (SF = same-face; Mahon et al. 2009).

^bVariance components were estimated as described in the Materials and Methods using two alternative models: Var #1 = Model [9] and Var #2 = Model [10]. R = replication, P1 = Parent #1, P2 = Parent #2, and F = full-sib family. h_a^2 is the individual-tree narrow sense heritability and h_{g1}^2 is the individual-tree genotypic heritability estimated using Model [9] (Becker 1984). h_{g2}^2 is the individual-tree genotypic heritability estimated using Model [10]. h_{g1}^2 is the full-sib family heritability estimated using Model [9], and assuming 10 measured trees per family.

^cBold numbers highlight the variance components and heritabilities of the recommended approach.

Table 3.6: Genotypic (r_{g1}), environmental (r_E) and phenotypic (r_P) correlations between squared acoustic velocity (AV^2) versus growth and form traits, and genotypic heritabilities (h_{g1}^2) for growth traits at the Toledo, Roaring River, and Fir Grove genetic test plantations.

Traits ^a	Genotypic correlation			Environmental correlation			Phenotypic correlation			Genotypic heritability		
	Fir Grove (DF) ^b	Roaring River (DF)	Toledo (WH) ^b	Fir Grove (DF)	Roaring River (DF)	Toledo (WH)	Fir Grove (DF)	Roaring River (DF)	Toledo (WH)	Fir Grove (DF)	Roaring River (DF)	Toledo (WH)
HT	0.333	0.019	0.539	0.559	0.103	0.078	0.319	0.063	0.211	0.258	0.363	0.171
DBH	0.050	-0.212	0.356	0.554	-0.088	-0.272	0.178	-0.131	-0.046	0.269	0.256	0.211
VOL	0.121	-0.149	0.460	0.488	-0.095	-0.240	0.197	-0.114	0.012	0.293	0.305	0.230
TAP	-0.248	-0.326	-0.106	0.304	-0.196	-0.305	-0.052	-0.231	-0.226	0.326	0.230	0.123

^a HT = Height, DBH = Diameter at breast height, VOL = Volume index (height*DBH²), and TAP = the ratio of DBH to height.

^b DF = Douglas-fir and WH = western hemlock.

3.8 Substantial genetic gains in AV^2 are possible

For each plantation, potential genetic gains from full-sib family selection were estimated based on choosing the best 20 of 200 unrelated full-sib families. These potential genetic gains were 17.20% for Fir Grove, 9.98% for Roaring River, and 9.12% for Toledo.

3.9 Growth traits were weakly to moderately correlated with AV^2

AV^2 had a weak genotypic correlation with growth traits (HT, DBH, and VOL) in Douglas-fir (-0.21 to 0.33; Table 3.6), but a moderately positive genotypic correlation in western hemlock (0.36 to 0.54; Table 3.6). In addition, AV^2 had a weak to moderate negative genotypic correlation with TAP in both species (-0.11 to -0.33; Table 3.6).

Environmental and phenotypic correlations between AV^2 versus growth and form traits varied among species and plantations (Table 3.6). For example, AV^2 had weak environmental and phenotypic correlations with growth traits at Roaring River and Toledo (0.21 to -0.27), but weak to moderate positive correlations at Fir Grove (0.18 to 0.56). The environmental and phenotypic correlations were weakly negative (-0.20 to -0.30) between AV^2 and TAP for 12-year-old Douglas-fir and western hemlock, but weakly positive or near zero (0.30 and -0.05) for 8-year-old Douglas-fir.

3.10 There was no substantial increase in family heritabilities or genetic gains for wood stiffness when the number of trees per family was increased beyond 10 trees

I studied whether using more trees per family would substantially increase family heritabilities and gain estimates. Figure 3.2 shows the expected increase in family heritabilities and genetic gains when the number of trees per family is increased or decreased from the actual mean sample sizes of 11.4 trees at Fir Grove, 16.5 trees at Roaring River, and 12.9 trees at Toledo. Using more than 10 trees per family did not substantially improve heritabilities or gains. For example, if I measured 16 trees in each family at Roaring River, the resulting family heritability would be 0.86 and the genetic gain would be 10.4%. In contrast, the family heritability is estimated to be 0.80, and the genetic gain is expected to be 10.0%, when 10 trees per family are measured. With more intensive sampling (e.g., 20 trees per family), the estimated family heritability is estimated to be 0.89, and the genetic gain is expected to be 10.5%.

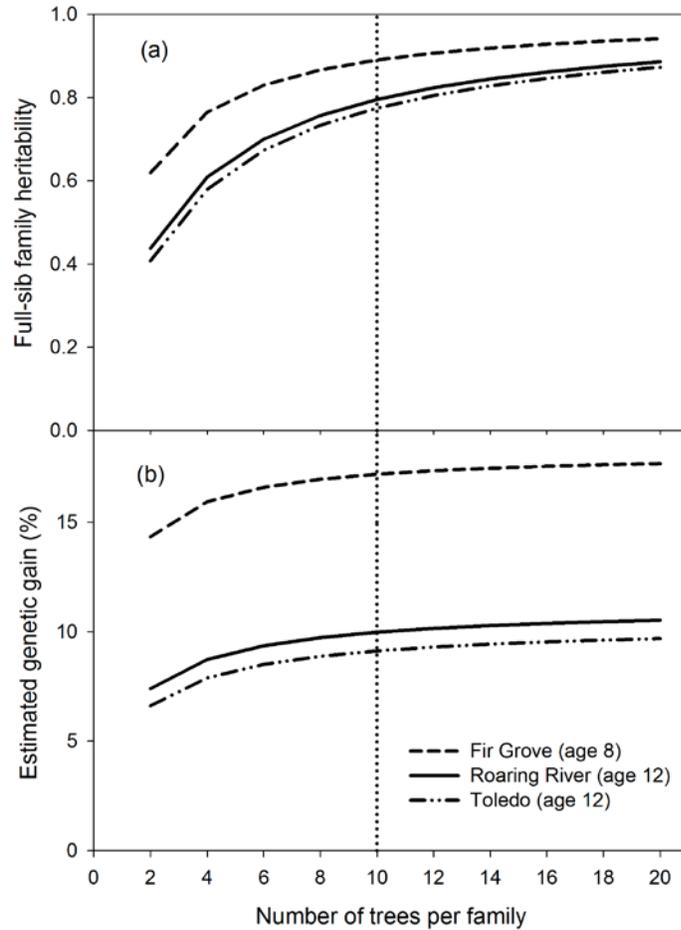


Figure 3.2: Full-sib family heritabilities (a) and genetic gains (b) in relation to the number of trees measured per family at two genetic test plantations of Douglas-fir (Fir Grove and Roaring River) and one plantation of western hemlock (Toledo). Potential genetic gains from full-sib family selection were estimated assuming that the best 20 of 200 unrelated full-sib families are selected.

4 DISCUSSION

Methods and tools have been developed for measuring TOF, which can be used to indirectly estimate wood stiffness (Wang et al., 2004; Carter et al., 2005). Because standing-tree acoustic tools are nondestructive, fast, and easier to use than log-based tools, they are being used to improve wood stiffness in tree breeding programs. Differences among tools, sensors, sensor placements, and flight path adjustments may affect the accuracy and precision of TOF measurements, and thus, AV^2 . I compared measurement approaches, and then used the best approach to estimate genetic parameters for AV^2 .

Kolpak et al. (unpublished) reported that AV^2 measurements taken using the TreeSonic and Microsecond Timer (with SDO2 sensors) are moderately to highly correlated with MOE measured using the HM200 log-based tool, and are easier to use on small trees compared to the TreeSonic with standard sensors. I used genotypic heritabilities (h_{g1}^2) to compare tools (TreeSonic versus Microsecond Timer), vertical placements (same-face versus opposite-face), and flight path adjustments (paths = P_{OU} , P_{OA} , P_{OD} , P_{OC} , P_{OE} and P_{SF}). Because I measured the same trait (AV^2) on the same trees and families, differences in heritability reflect differences in environmental variability and measurement error.

4.1 The effect of standing-tree tool was non-significant

Based on heritabilities, I found no significant difference between the TreeSonic and Microsecond Timer. The mean heritability using the Microsecond Timer

($h_{g1}^2 = 0.653$) was nearly the same as the heritability using the TreeSonic ($h_{g1}^2 = 0.651$). Matheson et al. (2008) compared MOE measurements taken using acoustic tools, including a Fakopp acoustic wave timer and the IML Electronic Hammer on 38 *Pinus radiata* (radiata pine) trees. They used the Director HM200 to estimate benchmark values for wood stiffness. The Pearson correlation coefficient was 0.94 between the IML and HM200, 0.85 between the Fakopp and HM200, and 0.89 between the Fakopp and IML (Matheson et al., 2008). In a more recent study, Kolpak et al. (unpublished) also compared AV measurements taken using the HM200, Microsecond Timer, Ultrasonic Timer, and the TreeSonic with standard and SDO2 sensors. They measured 62 Douglas-fir and 60 hemlock trees in operational forest plantations. The HM200 was also used as a benchmark in this study. In Douglas-fir, the correlation between the HM200 and the standing tree tools ranged from 0.74 to 0.88 for AV^2 and MOE_d using the same-face approach, whereas in hemlock, the correlation ranged from 0.39 to 0.56 (Kolpak et al. unpublished). Using an opposite-face approach, there was a moderate correlation (0.66) between measurements taken with the Microsecond Timer and the HM200 in radiata pine (Joe et al., 2004).

These results suggest that standing-tree acoustic tools give similar results to each other (Kolpak et al. unpublished; Matheson et al., 2008). In addition, because the TreeSonic and Microsecond Timer yielded comparable heritabilities in this study, decisions about which tool to use can be based on operational considerations. For example, measurement rates were slightly higher when I used the TreeSonic

(discussed below), suggesting that the TreeSonic is a slightly more efficient tool for standing-tree TOF measurements (Table 3.2).

4.2 The effect of vertical placement was non-significant

Two approaches have been described for measuring acoustic velocity on standing-trees. In the same face approach, the start and stop sensors are placed on the same-face of the tree, usually about 1 meter apart (Wang et al., 2001b; Grabianowski et al., 2006; Cherry et al., 2008; Mahon et al., 2009; Jayawickrama et al., 2011). In the opposite-face approach, the start and stop sensors are placed on opposite-faces of the tree, usually about 1 meter apart (Kolpak et al. unpublished; Matheson et al., 2002; Wagner et al., 2003; Joe et al., 2004; Mahon et al., 2009). Using the opposite-face approach, the distance between the sensors is a function of tree diameter and the vertical distance between the sensors. Because the sensors of standing-tree tools are placed about 25 mm into the stem, acoustic velocity is measured only in the outerwood, at least for the same-face approach (Andrews, 2000; Wang et al., 2002). However, using the opposite-face approach, the acoustic waves may pass through the center of the tree to reach the stop sensor. Therefore, these approaches may differ in the amount and type of wood that is sampled. Mahon et al. (2009) used five DBH-adjusted flight paths to calculate acoustic velocity for the opposite-face approach. In this study, I compared the heritabilities of one same-face variable (AV_{SF}^2) and five opposite-face variables (AV_{OU}^2 , AV_{OA}^2 , AV_{OD}^2 , AV_{OC}^2 and AV_{OE}^2).

Three studies focused on comparing the same-face versus opposite-face approach, and three criteria were used to compare these approaches. The first criterion was the correlation between AV and MOE_d. For example, Wagner et al. (2003) compared the same-face and opposite-face approaches for 24 Douglas-fir trees using the coefficient of determination between dynamic MOE_d and acoustic velocity. They reported that the coefficient of determination was slightly greater using the opposite-face approach ($r^2 = 0.495$) compared to same-face approach ($r^2 = 0.466$). In addition, Kolpak et al. (unpublished) compared the same-face and opposite-face approaches in operational forest plantations of Douglas-fir and western hemlock using the correlation between AV² and MOE_d. They reported that the correlation between measurements taken using the TreeSonic and Microsecond Timer versus the HM200 were modest to high (0.40 to 0.84). Although the correlations were generally higher using the same-face approach, they were not able to draw definitive conclusions because of the small sample size.

The second criterion was whether the resulting estimates of AV were associated with tree diameter. The path between the start and stop sensors is generally assumed to be a direct line between the sensors using the same-face approach. However, the acoustic waves may not travel along the direct line between the sensors using the opposite-face approach because of intra-tree variation in wood properties (e.g., corewood versus outerwood). This might lead to an underestimation of the acoustic velocity, especially for larger trees (Mahon et al., 2009). Previous studies on

acoustic velocity reported that there was no relationship or a weak relationship between acoustic velocity and DBH using the same-face method (Chauhan et al., 2005; Toulmin and Raymond, 2007). Therefore, it is important to understand the relationship between AV and DBH using the opposite-face approach. Mahon et al. (2009) examined this using slope coefficients, which describe the strength of the relationship between AV and DBH. If the correct flight path is assumed, and the correct DBH-adjustment is used, then we expect no significant relationship between AV and DBH (i.e., the slope coefficient will not be significantly different from zero). Mahon et al. (2009) compared slope coefficients for five DBH-adjustments using 100 loblolly pine trees from a research plot. Trees were sampled based on desirable sawing properties, such as straightness and small branching. The slope coefficients were significantly different from zero for AV_{OU}^2 , AV_{OA}^2 , AV_{OD}^2 , and AV_{OE}^2 , but not for AV_{OC}^2 and AV_{SF}^2 (Mahon et al., 2009). This indicates that the estimated acoustic velocity was unrelated to DBH when these latter two variables (and associated adjustment methods) were used.

The third criterion was the repeatability of successive measurements. For example, Mahon et al. (2009) compared the same-face versus opposite-face approaches based on the hit-to-hit variation in AV. The hit-to-hit variation (residual error variance) for the opposite-face approach was about 62% less than the residual error variance for same-face approach. Because the variation was 62% less using the opposite-face approach, the opposite-face approach was recommended (Mahon et al.,

2009). Furthermore, because AV was unrelated to DBH using the circumferential adjustment method (AV_{OC}^2), this method was recommended for measuring wood stiffness.

In my study, I tested the repeatability by comparing the heritabilities of AV^2 for each vertical placement and DBH-adjustment method. Although, the mean genotypic heritability using the same-face approach ($h_{g1}^2 = 0.659$) was slightly higher than the heritability using the opposite-face approach ($h_{g1}^2 = 0.645$), this difference was non-significant ($P = 0.622$). In addition, the heritabilities were not significantly different among the six DBH-adjusted acoustic velocities, although h_{g1}^2 was highest using the ellipse adjustment (AV_{OE}^2 , $h_{g1}^2 = 0.659$). I tested the hit-to-hit variation in TOF using the coefficient of variation. The hit-to-hit variation for the opposite-face approach was slightly lower than the hit-to-hit variation for the same-face approach.

The criteria used by Mahon et al. (2009) and Wagner et al. (2003) to compare measurement approaches differed from my study. I used heritabilities, whereas Wagner et al. (2003) used the coefficient of determination for the regression of dynamic MOE (Metrigard) on acoustic velocity. In addition, their opposite-face approach involved placing the sensors on opposite faces of the tree at the same height. This method is typically used to detect decay in tree stems. Mahon et al. (2009) tested whether slope coefficients were significantly different from zero, and whether hit-to-hit variation differed between the same-face and opposite face approaches. The different approaches used to compare vertical placements, and the different

measurement techniques used by Wagner et al (2003) may explain why my results differed from Mahon et al. (2009) and Wagner et al. (2003).

The trees I used were younger (8 to 12 years old), and smaller than those in the Mahon et al. (2009) and Wagner et al. (2003) studies. In my study, mean DBH at the three plantations ranged from 5.7 cm to 11.3 cm. In contrast, DBH ranged from 30.2 cm to 37.3 cm in the previous study of Douglas-fir (Wagner et al., 2003), and 25.4 cm in loblolly pine (Mahon et al., 2009). The trees I measured may have had higher proportions of juvenile corewood than the trees in these other studies. In general, juvenile corewood has different wood properties than outerwood and mature wood, including lower wood stiffness, lower density, lower strength, lower specific gravity, thinner cell walls, greater fibril angle, and higher lignin content (Senft et al., 1985; Maguire et al., 1991; Jozsa and Middleton, 1994; Haygreen and Bowyer, 1996; Evans and Ilic, 2001; Burdon et al., 2004). Furthermore, the numbers of trees used in these analyses differed. Mahon et al. (2009) used 100 loblolly pine trees and Wagner et al. (2003) used 24 Douglas-fir trees to test repeatability. Overall, I measured 2938 trees using the same-face and opposite-face approaches, and there was no significant difference in heritability. However, the same-face approach was easier and faster to use in the field.

4.3 Measurement rates were highest when I used the TreeSonic and same-face approach

Differences in the design of acoustic tools affect measurement rates (Table 3.2), and measurement speed is particularly important when measuring wood

stiffness on the large numbers of trees that are typically found in genetic test plantations. The Microsecond Timer has buttons to turn the tool on and off, and to clear the last measurement from the screen. Because of accumulated sap, these buttons become difficult to use, thereby affecting measurement productivity. In addition, if the previous measurement is not cleared before the next measurement, the same TOF will be recorded for different measurements, and this will cause error. The TreeSonic does not have a reset button or on/off button. Instead, the last measurement is automatically reset when the start sensor is tapped. In addition, the TreeSonic is water-resistant, which is more suitable for all-weather conditions. Overall, the TreeSonic and same-face approach is faster, easier to use, and better for all-weather conditions.

4.4 AV² had significant genetic variation in Douglas-fir and western hemlock

Genetic variance can be partitioned into additive and non-additive genetic components. Additive genetic variance is generally more important in breeding programs because it is the main reason that offspring resemble their parents (Falconer and Mackay, 1996). Non-additive genetic variation includes other sources of genetic variation that cause progeny to perform differently from their expected breeding values (Zobel and Talbert, 1984). Unlike open-pollinated mating designs, nested designs can be used to estimate non-additive genetic variation and maternal effects (i.e., in addition to additive genetic variation).

Genetic variation was higher for AV² than for DBH and HT. The additive genetic coefficient of variation (AGCV) can be used to compare the relative amounts

of genetic variation among traits. Cornelius (1994) compiled the AGCV for seven traits of forest trees from 67 published papers. The median AGCV was 5.1% for specific gravity, 11.65% for straightness, 8.6% for DBH, and 8.5% for HT (Cornelius, 1994). These results are consistent with my study. In Douglas-fir and hemlock, AV^2 tended to have higher AGCVs (8.4 to 14.8%) compared to HT and DBH (6.4 to 11.5%).

In my study, I assumed $\sigma_{P_1}^2$ represents one quarter of the additive genetic variance and $\sigma_{P_2(P_1)}^2$ represents one quarter of the additive genetic variance plus one quarter of the dominance variance (Becker, 1984). That is, I assumed other sources of non-additive genetic variation were zero. Because $\sigma_{P_1}^2$ was not significantly different from the $\sigma_{P_2(P_1)}^2$, I found no evidence for substantial dominance variation in Douglas-fir and western hemlock for AV^2 . Dominance genetic variance was also non-significant for wood density of 12-year-old Douglas-fir (King et al., 1988b). In another study of Douglas-fir, dominance variance was non-significant for growth traits (height, DBH, and volume) (King et al., 1988a). These results suggest that additive genetic variance is the most important source of genetic variance for these traits. Although $\sigma_{P_1}^2$ was not significantly different from $\sigma_{P_2(P_1)}^2$ at any of my plantations, $\sigma_{P_1}^2$ was 2 to 4 times lower than $\sigma_{P_2(P_1)}^2$ at Roaring River (Table A5). This suggests that non-additive variation could be present in Douglas-fir, but $\sigma_{P_1}^2$ and $\sigma_{P_2(P_1)}^2$ were not significantly different because of the high standard errors associated with estimates of variance components (Matheson et al., 2008).

The phenotype of an individual can be affected by its genotype, its environment, or its maternal parent. For example, maternal parent has an important effect on seed weight in Douglas-fir (Sorensen and Campbell, 1985). Therefore, I tested maternal effects on wood stiffness. My estimate of $\sigma_{P_1}^2$ was not significantly different between the two cross-types. That is, I concluded that $\sigma_{P_1}^2$ was the same for the males-within-female cross-type (M(F)) and the females-within-male cross-type (F(M)) ($P > 0.391$; Tables A7-A9). Likewise, $\sigma_{P_2(P_1)}^2$ was not significantly different between the two cross-types ($P > 0.634$; Tables A7-A9). This suggests that maternal effects are not important for wood stiffness of Douglas-fir or western hemlock.

There is sufficient genetic variation in AV^2 to incorporate wood stiffness into tree improvement programs (Howe et al., 2006). However, non-additive genetic variance in Douglas-fir and western hemlock has not been investigated for wood stiffness. There are two types of combining abilities. General combining ability (GCA) is the average performance of an individual's offspring across multiple crosses (Falconer and Mackay, 1996). Specific combining ability (SCA) is the deviation of a specific cross from the expected or average GCA of its parents (Falconer and Mackay, 1996). Although GCA is a reflection of the parent's additive genetic value, SCA is a reflection of the parent's non-additive genetic value (mostly dominance variation) (Zobel and Talbert, 1984). Because dominance variation was non-significant for Douglas-fir and western hemlock, recurrent selection for additive genetic value will be an effective approach for genetically improving traits such as stiffness and growth.

This suggests that near optimal gains in wood stiffness and growth traits can be obtained by collecting open pollinated seed from orchards (i.e., without control crossing) as long as pollen contamination is not a problem.

4.5 The heritability for AV^2 was higher than for the growth and form traits

Successful breeding programs depend on having sufficient heritabilities to achieve genetic gains. Heritabilities for AV^2 were 2 to 4 times higher than heritabilities for HT, DBH, VOL, and TAP. For example, heritabilities for growth and form traits were low to moderate, ranging from 0.12 to 0.36. In contrast, heritabilities for AV^2 were high, ranging from 0.51 to 0.90. Because measurement error is expected to be much lower than environmental variability, it appears that AV^2 had less environmental variation than did the growth traits. Therefore, to achieve comparable heritabilities, fewer trees would need to be measured for wood stiffness than for growth traits. Previous studies reported low to moderate heritabilities for growth traits, and moderate to high heritabilities for AV, AV^2 and MOE (Johnson and Gartner, 2006; Cherry et al., 2008; Wielinga et al., 2009; Jayawickrama et al., 2011), which are consistent with my results.

In Douglas-fir, heritabilities for AV^2 seemed to be higher in the first eight rings from the pith. For example, the heritability at Fir Grove (0.90) was much higher than at Roaring River (0.56), and the trees were four years younger (ages 8 versus 12). These results are consistent with other studies. For example, Dungey et al. (2006) compared the heritabilities of corewood and outerwood stiffness in two radiata pine

plantations. The heritability for wood stiffness (0.77) was highly significant in corewood (ring 10) in one plantation (Dungey et al., 2006). In the same study, they reported heritabilities ranging from 0.35 to 0.89 for rings ages 4 to 14 (highest for ring 4) in another plantation. In other studies, heritabilities were high in the corewood and moderate in the outerwood (Kumar et al., 2006; Li et al., 2007).

Wood stiffness and other wood properties vary from pith to bark (Burdon et al., 2004). For example, specific gravity in Douglas-fir decreases until rings 8 to 10, and then gradually increases with increasing ring number from the pith until ring age 50 or more (Megraw, 1986). If the objective of a tree breeding program is to maximize the gain in the corewood stiffness, selection for wood stiffness should be most effective at early ages (e.g., ages 6-10). However, because I did not replicate age classes in my study, I do not know whether the particularly high heritability at Fir Grove is related to the young age of the trees, or some other factors.

The genetic parameters for TAP might be important. For example, Johnson and Gartner, (2006) reported that denser and stiffer families had a more cylindrical than conical form. In addition, a relationship between MOE and TAP was found in radiata pine and *Picea sitchensis* (Sitka spruce) (Watt et al., 2006; Lasserre et al., 2009; Moore et al., 2009). For example, taper was used as a measure of stem form, and a positive relationship ($r^2 = 0.61$) was found between taper and wood stiffness in radiata pine (Watt et al., 2006). TAP was as heritable as HT, DBH, and VOL, and was much more heritable in Douglas-fir than in hemlock. For example, heritability for TAP

ranged from 0.12 to 0.32 in Douglas-fir and western hemlock. In previous studies of older Douglas-fir, the heritability of TAP ranged from 0.14 to 0.17 (Jayawickrama et al., 2011) and 0.04 to 0.36 (Johnson and Gartner, 2006), which is consistent with my results.

4.6 Substantial genetic gains in AV^2 are possible

Potential genetic gains in AV^2 from full-sib family selection were 17.2% for Fir Grove, 10.0% for Roaring River, and 9.1% for Toledo. Predicted gains of 7.1% to 24% have been reported for parental selection of older Douglas-fir (Johnson and Gartner, 2006; Cherry et al., 2008; Jayawickrama et al., 2009; Jayawickrama et al., 2011) and for other species (Kumar, 2004; Li et al., 2007; Matheson et al., 2008).

Wood properties, including wood stiffness, vary within the tree (Burdon et al., 2004). Because I measured acoustic velocity at breast height, the gain I reported might not reflect gain at the whole-tree level. Because the sensors of the standing-tree tools were placed about 25 mm into the stem, AV^2 reflects the stiffness of the outerwood, which is generally stiffer than corewood (Andrews, 2000; Wang et al., 2002).

Therefore, the stiffness and hence the estimated gain of the entire tree might be biased.

4.7 Growth traits were weakly to moderately correlated with AV^2

Tree value is mostly determined by stem volume, and the main objective of most tree breeding programs is to improve growth traits (Campbell, 1964; Silen and Wheat, 1979). Because volume growth is the main objective, it is important to understand the correlations between growth and quality traits. If the correlations

between these traits are positive, selection for one trait will cause an increase in the other. If the desired traits have negative correlations (e.g., wood density is generally negatively correlated with growth traits), tree breeders must balance the gain between the two traits of interest.

In my study, I estimated genetic correlations using genotypic variances $2(\sigma_{P_1}^2 + \sigma_{P_2(P_1)}^2)$, which have expectations of $1/4 \sigma_A^2 + 1/4 \sigma_D^2$ when maternal effects and epistasis are ignored. The resulting genetic and environmental correlations between AV^2 and growth traits were highly variable (Table 3.6). The genetic correlations between AV^2 and growth traits were weakly negative for Douglas-fir at Roaring River and weakly positive or near zero at Fir Grove. In a study of 23-year-old Douglas-fir trees, a low positive genetic correlation (0.17) was found between AV^2 and HT, whereas genetic correlations between AV^2 and other growth traits were weakly to moderately negative (Jayawickrama et al., 2011). In a study of 8-year-old slash pine trees, a low positive genetic correlation (0.19) was found between AV^2 and HT, whereas genetic correlations between AV^2 and other growth traits were weakly negative (Li et al., 2007). In addition, Roth et al. (2007) reported that families with the fastest growth also had the highest AV^2 in loblolly pine. These low genetic correlations indicate that it will be possible to select Douglas-fir genotypes with fast growth and high juvenile corewood stiffness. This was also found in slash pine and loblolly pine (Li et al., 2007; Roth et al., 2007).

Genetic correlations between growth traits and AV^2 were moderately positive for western hemlock, ranging from 0.36 to 0.54. The exact reason why hemlock had moderate positive genetic correlations with growth traits is unknown. These positive genetic correlations indicate that it will be possible to select western hemlock genotypes with fast growth and high juvenile corewood stiffness. Stiffness of western hemlock has been reported to be slightly lower than that of Douglas-fir. For example, wood stiffness of Douglas-fir was 10.8 GPa measured using a static bending test (Green et al., 1999; Cherry et al., 2008), whereas western hemlock wood stiffness was reported to be 9.0 GPa (Green et al., 1999) and 7.4 GPa (Wang et al., 2001a). Wood stiffness values for western hemlock are mostly from old growth forests or second-growth forests managed without using intensive silvicultural practices (Jayawickrama, 2003). Therefore, they do not reflect wood stiffness of genetically improved trees. Because I found positive genetic correlations between acoustic velocity and growth traits in hemlock, breeders should be able to improve both growth and acoustic velocity. This provides an opportunity to focus on improving wood stiffness in western hemlock so that it can better compete with Douglas-fir for wood products in which stiffness is important. In addition, I found that 25% of the western hemlock families had higher MOE_d than the mean for Douglas-fir (8.9 GPa).

Genetic correlations between TAP and AV^2 were weakly to moderately negative across the sites, ranging from -0.11 to -0.33. Negative genetic correlations

between TAP and AV or AV^2 were previously reported in Douglas-fir (Johnson and Gartner, 2006; Cherry et al., 2008; Jayawickrama et al., 2011).

Genetic correlations are associated with large standard errors, particularly when relatively few trees are measured per family. For example, 10 to 12 trees per family was reported as a low sample size for estimating genetic correlations in radiata pine (Matheson et al., 2008). I measured 11.4 trees per family at Fir Grove, 16.5 trees at Roaring River and 12.9 at Toledo. The site with the highest numbers of trees per family sampled (e.g., Roaring River) also tended to produce genetic correlations between AV^2 and growth traits (HT, DBH and VOL) that were the most consistent with other studies. Therefore, using different numbers of trees per family (i.e., fewer trees per family at Fir Grove and Toledo) may have contributed to the variation in genetic correlations among the genetic test plantations.

4.8 There was no substantial increase in family heritabilities or genetic gains for wood stiffness when the number of trees per family was increased beyond 10 trees.

As discussed above, AV^2 has more genetic variation and greater individual-tree heritabilities than growth traits such as HT, DBH and VOL. Jayawickrama et al. (2011) suggested measuring 20 to 25 trees per family across three to four genetic tests (i.e., 20-25 trees total) to obtain family heritabilities for acoustic velocity that are comparable to those typically achieved for growth traits. Decisions about how many trees per family and how many genetic tests to measure also depend on costs. For example, genetic gain was 10% when I measured 10 trees per family at Roaring River.

With more intensive sampling, such as 20 trees per family, genetic gains are expected to increase by only 0.5%. I recommend that breeders measure 10 trees per family for improving wood stiffness in young Douglas-fir and western hemlock.

Unlike AV^2 , there is considerable genetic x environmental interaction (GxE) for growth traits among plantations. Therefore, the current approach is to establish ≈ 20 trees per family in each plantation is better approach. After mortality, there should be a sufficient number of live trees to measure across all plantations to obtain good heritabilities for growth traits. In this study, I estimated genetic gains and heritabilities for AV^2 based on the data from single plantations. However, it will be more important to measure multiple plantations for growth traits because GxE interactions are more common.

4.9 Implications

These results indicate that comparable genetic gains are possible using either the TreeSonic with SDO2 sensor or Microsecond Timer, and either the same-face or the opposite-face approach. Because of practical considerations, and higher measurement rates, I recommend that breeders use the TreeSonic and same-face approach. I found positive genetic correlations between growth and acoustic velocity in western hemlock. This provides an opportunity to focus on improving wood stiffness in western hemlock so that it can better compete with Douglas-fir for products in which stiffness is important. Near optimal genetic gains are possible using 10 trees per family for wood stiffness. Because dominance variation was

non-significant for Douglas-fir and western hemlock, near optimal gains in wood stiffness and growth traits can be obtained by collecting open pollinated seed from orchards (i.e., without control crossing) as long as pollen contamination is not a problem.

4.10 Future research

My results indicate that acoustic tools can be used to measure acoustic velocity in young (8- to 12-year-old) Douglas-fir and western hemlock trees. This is the first study that addressed the genetics of wood stiffness in young Douglas-fir and western hemlock plantations. Although we now have estimates of genetic parameters for younger and older trees, we do not know the magnitude of juvenile-mature wood correlations. Therefore, this is an important area of future research. Second, my estimates of heritabilities and genetic gains are based on single plantations. Therefore, I do not know if the age related differences in heritabilities and potential genetic gains that were found between younger (8-year-old) and older (12-year-old) Douglas-fir plantations were related to tree age or other factors. More research is needed to investigate age related differences in genetic parameters for acoustic velocity in Douglas-fir and western hemlock. Third, my results indicated that genetic correlations between AV^2 and growth traits were positive for western hemlock. This may give breeders a good opportunity to improve both growth and wood stiffness simultaneously. However, my results were based on single plantations, so I don't know if the genetic correlations I found are broadly applicable to western hemlock. In

addition, genetic correlations are associated with high standard errors. Therefore, more studies are needed to test this relationship in western hemlock using multiple test plantations and more trees per family. Finally, previous studies of Douglas-fir wood stiffness were mostly done using open-pollinated families, which do not provide information about non-additive genetic effect (e.g., dominance variation). Although, I found no evidence for substantial dominance variation in Douglas-fir or western hemlock, the variance of Parent 1 was 2 to 4 times lower than the variance of Parent 2 in one of the Douglas-fir plantations (Roaring River). This suggests that non-additive genetic variation for wood stiffness could be present in Douglas-fir. Therefore, more genetic studies are needed using mating designs that allow additive and non-additive sources of genetic variation to be estimated.

REFERENCES

- Alden, H.A., 1997. Softwoods of North America. USDA Forest Service, Forest Products Laboratory. General Technical Report, FPL-GTR-102. Madison, WI.
- Allen, H.L., Fox, T.R., Campbell, R.G., 2005. What is ahead for intensive pine plantation silviculture in the South? *South. J. Appl. For.* 29, 62-69.
- Amishev, D., Murphy, G.E., 2008. Implementing resonance-based acoustic technology on mechanical harvesters/processors for real-time wood stiffness assessment: Opportunities and considerations. *I. J. For. Eng.* 19, 48-56.
- Andrews, M., 2000. Where are we with sonics? In, *Capturing the Benefits of Forestry Research: Putting Ideas to Work* Wood Technology Research Centre, University of Canterbury, New Zealand, pp. 57-61.
- Baltunis, B.S., Wu, H.X., Powell, M.B., 2007. Inheritance of density, microfibril angle, and modulus of elasticity in juvenile wood of *Pinus radiata* at two locations in Australia. *Can. J. For. Res.* 37, 2164-2174.
- Becker, W.A., 1984. *A Manual of Quantitative Genetics*. Academic Enterprises, Pullman, WA.
- Bormann, B.T., 1984. Douglas-fir an American wood. USDA Forest Service. FS-235. Washington, DC.
- Burdon, R.D., Kibblewhite, R.P., Walker, J.C., Megraw, R.A., Evans, R., Cown, D.J., 2004. Juvenile versus mature wood: A new concept, orthogonal to corewood versus outerwood, with special reference to *Pinus radiata* and *P. taeda*. *For. Sci.* 50, 399-415.
- Campbell, R.K., 1964. Recommended traits to be improved in a breeding program for Douglas-fir. Weyerhaeuser Company, Forestry Research Center, Timberland Division Weyerhaeuser Res. Note. No. 57. Centralia, WA.
- Campbell, R.K., 1965. Phenotypic variation and repeatability of stem sinuosity in Douglas-fir. *Northwest Sci.* 39, 47-59.
- Carter, P., Briggs, D., Ross, R.J., Wang, X., 2005. Acoustic testing to enhance western forest values and meet customer wood quality needs. USDA Forest Service, Pacific Northwest Research station. General Technical Report, PNW-GTR-642. Portland, OR. 121-129 pp.

- Chauhan, S.S., Entwistle, K.M., Walker, J.C.F., 2005. Differences in acoustic velocity by resonance and transit-time methods in an anisotropic laminated wood medium. *Holzforschung* 59, 428-434.
- Cherry, M.L., Vikram, V., Briggs, D., Cress, D.W., Howe, G.T., 2008. Genetic variation in direct and indirect measures of wood stiffness in coastal Douglas-fir. *Can. J. For. Res.* 38, 2476-2486.
- Cornelius, J., 1994. Heritabilities and additive genetic coefficients of variation in forest trees. *Can. J. For. Res.* 24, 372-379.
- Dungey, H.S., Matheson, A.C., Kain, D., Evans, R., 2006. Genetics of wood stiffness and its component traits in *Pinus radiata*. *Can. J. For. Res.* 36, 1165-1178.
- Evans, R., Ilic, J., 2001. Rapid prediction of wood stiffness from microfibril angle and density. *Forest. Prod. J.* 51, 53-57.
- Falconer, D.S., Mackay, F.C., 1996. *Introduction to Quantitative Genetics*. 4th edition. Longman, New York.
- Grabianowski, M., Manley, B., Walker, J., 2006. Acoustic measurements on standing trees, logs and green lumber. *Wood Sci. Technol.* 40, 205-216.
- Green, D.W., Winandy, J.E., Kretschmann, D.E., 1999. Mechanical properties of wood. USDA Forest Service, Forest Products Laboratory. General Technical Report, FPL-GTR-113. Madison, WI. 4.1-4.45 pp.
- Hannrup, B., Ekberg, I., Persson, A., 2000. Genetic correlations among wood, growth capacity and stem traits in *Pinus sylvestris*. *Scand. J. For. Res.* 15, 161-170.
- Haygreen, J.G., Bowyer, J., 1996. *Forest Products and Wood Science: an introduction*. 3th edition. Iowa State University Press, Ames, Iowa.
- Helms, J.A., editor, 1998. *The Dictionary of Forestry*. Society of American Foresters, Bethesda, MD.
- Howe, G.T., Jayawickrama, K.J., Cherry, M.L., Johnson, G.R., Wheeler, N.C., 2006. Breeding Douglas-fir. *Plant Breed. Review.* 27, 245-353.
- Jayawickrama, K., 2003. Genetic improvement and deployment of western hemlock in Oregon and Washington: review and future prospects. *Silvae Genet.* 52, 26-35.
- Jayawickrama, K.J.S., Ye, T.Z., Gupta, R., Cherry, M.L., 2009. Including wood stiffness in tree improvement of coastal Douglas-fir in the US Pacific Northwest: A

literature review and synthesis. Oregon State University, Forest Research Laboratory. Research Contribution 50. Corvallis, OR. 99 pp.

Jayawickrama, K.J.S., Ye, T.Z., Howe, G.T., 2011. Heritabilities, intertrait genetic correlations, G x E interaction and predicted genetic gains for acoustic velocity in mid-rotation coastal Douglas fir. *Silvae Genet.* 60, 8-18.

Joe, B., Dickson, R., Raymond, C., Ilic, J., Matheson, C., 2004. Prediction of *Eucalyptus Dunnii* and *Pinus Radiata* timber stiffness using acoustics. RIRDC Publ. No. 04/013. 118 pp.

Johnson, G.R., Gartner, B.L., 2006. Genetic variation in basic density and modulus of elasticity of coastal Douglas-fir. *Tree Genet. Genom.* 3, 25-33.

Jozsa, L.A., Middleton, G.R., 1994. A discussion of wood quality attributes and their practical implications. Forintek Canada Corp., Western Laboratory. Publ. SP-34. Vancouver, B.C

Jung, J., 1979. Stress-wave grading techniques on veneer sheets. USDA Forest Service, Forest Products Laboratory. General Technical Report, FPL-GTR-27. Madison, WI. 10 pp.

King, J.N., Yeh, F.C., Heaman, C.H., 1988a. Selection of growth and yield traits in controlled crosses of coastal Douglas-fir. *Silvae Genet.* 37, 158-164.

King, J.N., Yeh, F.C., Heaman, J.C., Dancik, B.P., 1988b. Selection of wood density and diameter in controlled crosses. *Silvae Genet.* 37, 152-157.

Kumar, S., 2004. Genetic parameter estimates for wood stiffness, strength, internal checking, and resin bleeding for radiata pine. *Can. J. For. Res.* 34, 2601-2610.

Kumar, S., Dungey, H.S., Matheson, A.C., 2006. Genetic parameters and strategies for genetic improvement of stiffness in radiata pine. *Silvae Genet.* 55, 77-84.

Kumar, S., Jayawickrama, K.J.S., Lee, J., Lausberg, M., 2002. Direct and indirect measures of stiffness and strength show high heritability in a wind-pollinated radiata pine progeny test in New Zealand. *Silvae Genet.* 51, 256-261.

Lasserre, J.-P., Mason, E.G., Watt, M.S., 2007. Assessing corewood acoustic velocity and modulus of elasticity with two impact based instruments in 11-year-old trees from a clonal-spacing experiment of *Pinus radiata* D. Don. *For. Ecol. Manage.* 239, 217-221.

Lasserre, J.-P., Mason, E.G., Watt, M.S., Moore, J.R., 2009. Influence of initial planting spacing and genotype on microfibril angle, wood density, fibre properties and modulus of elasticity in *Pinus radiata* D. Don corewood. *For. Ecol. Manage.* 258, 1924-1931.

Li, X., Huber, D.A., Powell, G.L., White, T.L., Peter, G.F., 2007. Breeding for improved growth and juvenile corewood stiffness in slash pine. *Can. J. For. Res.* 37, 1886-1893.

Lindström, H., Harris, P., Nakada, R., 2002. Methods for measuring stiffness of young trees. *Holz als Roh-und Werkstoff* 60, 165-174.

Lindström, H., Harris, P., Sorensson, C.T., Evans, R., 2004. Stiffness and wood variation of 3-year old *Pinus radiata* clones. *Wood Sci. Technol.* 38, 579-597.

Maguire, D.A., Kershaw, J.A., Hann, D.W., 1991. Predicting the effects of silvicultural regime on branch size and crown wood core in Douglas-fir. *For. Sci.* 37, 1409-1428.

Mahon, J.M., Lewis, J., Schimleck, L.R., Clark, A., Daniels, R.F., 2009. A comparison of sampling methods for a standing tree acoustic device. *South. J. Appl. For.* 33, 62-68.

Matheson, A.C., Dickson, R.L., Spencer, D.J., Joe, B., Ilic, J., 2002. Acoustic segregation of *Pinus radiata* logs according to stiffness. *Ann. Forest Sci.* 59, 471-477.

Matheson, A.C., Gapare, W.J., Ilic, J., Wu, H.X., 2008. Inheritance and genetic gain in wood stiffness in radiata pine assessed acoustically in young standing trees. *Silvae Genet.* 57, 56-64.

Megraw, R.A., 1986. Douglas-fir wood properties. In: Oliver, C.D.O., Hanley, D.P., Johnson, J.A. (Eds.), *Douglas-fir: Stand management for the future*. Institute of Forest Resources, University of Washington, Seattle, WA, pp. 81-96.

Moore, J., Achim, A., Lyon, A., Mochan, S., Gardiner, B., 2009. Effects of early re-spacing on the physical and mechanical properties of Sitka spruce structural timber. *For. Ecol. Manage.* 258, 1174-1180.

Mora, C.R., Schimleck, L.R., Isik, F., Mahon, J.M., Clark, A., Daniels, R.F., 2009. Relationships between acoustic variables and different measures of stiffness in standing *Pinus taeda* trees. *Can. J. For. Res.* 39, 1421-1429.

- Packee, E.C., 1990. Western hemlock. In: *Burns, R.M., Honkala, B.H.* (Eds.), *Silvics of North America: 1. Conifers*, Agriculture Handbook 654. USDA Forest Service, Washington, DC, pp. 613-622.
- Pellerin, R.F., Ross, R.J., 2002. *Nondestructive evaluation of wood*. Forest Products Society, Madison, WI.
- Roth, B.E., Li, X., Huber, D.A., Peter, G.F., 2007. Effects of management intensity, genetics and planting density on wood stiffness in a plantation of juvenile loblolly pine in the southeastern USA. *For. Ecol. Manage.* 246, 155-162.
- Senft, J.F., Bendtsen, B.A., Galligan, W.L., 1985. Weak wood: Fast-grown trees make problem lumber. *J. For.* 83, 476-485.
- Silen, R.R., 1978. *Genetics of Douglas-fir*. U.S. Forest Service Washington office. Research paper WO-35.
- Silen, R.R., Wheat, J.G., 1979. Progressive tree improvement program in coastal Douglas-fir. *J. For.* 77, 78-85.
- Sorensen, F.C., Campbell, R.K., 1985. Effect of seed weight on height growth of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) seedlings in a nursery. *Can. J. For. Res.* 15, 1109-1115.
- Toulmin, M.J., Raymond, C.A., 2007. Developing a sampling strategy for measuring acoustic velocity in standing *Pinus radiata* using the TreeTap time of flight tool. *N. Z. J. For. Sci.* 37, 96-111.
- Vikram, V., Cherry, M.L., Briggs, D., Cress, D.W., Evans, R., Howe, G.T., 2011. Stiffness of Douglas-fir lumber: effects of wood properties and genetics. *Can. J. For. Res.* 41, 1160-1173.
- Wagner, F.G., Gorman, T.M., Wu, S.-Y., 2003. Assessment of intensive stress-wave scanning of Douglas-fir trees for predicting lumber MOE. *Forest. Prod. J.* 53, 36-39.
- Wang, J., Biernacki, J.M., Lam, F., 2001a. Nondestructive evaluation of veneer quality using acoustic wave measurements. *Wood Sci. Technol.* 34, 505-516.
- Wang, X., 2011. Fundamentals of acoustic measurements on trees and logs and their implication to field application. In: *Divos, F.* (Ed.), *Proc 17th International Nondestructive Testing and Evaluation of Wood Symposium*, University of West Hungary, Sopron, Hungary, Sept 14-16, 2011, pp. 25-33.

- Wang, X., Ross, R.J., Green, D.W., Brashaw, B.K., Englund, K., Wolcott, M., 2004. Stress wave sorting of red maple logs for structural quality. *Wood Sci. Technol.* 37, 531-537.
- Wang, X., Ross, R.J., McClellan, M., Barbour, R.J., Erickson, J.R., Forsman, J.W., McGinnis, G.D., 2001b. Nondestructive evaluation of standing trees with a stress wave method. *Wood Fiber Sci.* 33, 522-533.
- Wang, X.P., Ross, R.J., Mattson, J.A., Erickson, J.R., Forsman, J.W., Geske, E.A., Wehr, M.A., 2002. Nondestructive evaluation techniques for assessing modulus of elasticity and stiffness of small-diameter logs. *Forest. Prod. J.* 52, 79-85.
- Watt, M.S., Moore, J.R., Façon, J.-P., Downes, G.M., Clinton, P.W., Coker, G., Davis, M.R., Simcock, R., Parfitt, R.L., Dando, J., Mason, E.G., Bown, H.E., 2006. Modelling the influence of stand structural, edaphic and climatic influences on juvenile *Pinus radiata* dynamic modulus of elasticity. *For. Ecol. Manage.* 229, 136-144.
- Wielinga, B., Raymond, C.A., James, R., Matheson, A.C., 2009. Genetic parameters and genotype by environment interactions for green and basic density and stiffness of *Pinus radiata* D. Don estimated using acoustics. *Silvae Genet.* 58, 112-122.
- Zobel, B.J., Sprague, J.R., 1998. *Juvenile wood in forest trees.* Springer-Verlag, Berlin Germany. 300 pp.
- Zobel, B.J., Talbert, J.T., 1984. *Applied forest tree improvement.* John Wiley & Sons. 505 pp.

APPENDIX

Table A1: Variance components (Var) for squared acoustic velocity (AV^2 ; $\text{km}^2 \cdot \text{s}^{-2}$) measured on 8-year-old Douglas-fir trees at the Fir Grove plantation using the TreeSonic standing-tree tool and two sensor placements (same-face and opposite-face). The fixed effect of cross-type is not shown because the estimated G matrix was not positive definite. A large P-value ($\text{Pr} > 0.05$) indicates that the corresponding variance component was not significantly different from zero.

Effects ^b	Opposite-face ^a						Same-face ^a					
	OU		OA		OD		OC		OE		SF ^c	
	Var	Pr > Z	Var	Pr > Z	Var	Pr > Z	Var	Pr > Z	Var	Pr > Z	Var	Pr > Z
TreeSonic												
R	0.034	0.055	0.039	0.060	0.034	0.055	0.046	0.058	0.034	0.056	0.043	0.043
P1(CT)	0.308	0.032	0.348	0.032	0.309	0.032	0.374	0.032	0.311	0.032	0.329	0.025
P2(CT,P1)	0.394	0.001	0.436	0.001	0.395	0.001	0.465	0.002	0.397	0.001	0.373	0.001
R*CT	0.000	ND	0.000	ND	0.000	ND	0.000	ND	0.000	ND	0.000	ND
R*P1(CT)	0.000	ND	0.000	ND	0.000	ND	0.000	ND	0.000	ND	0.000	ND
R*P2(CT,P1)	0.761	0.001	0.865	0.001	0.762	0.001	0.942	0.003	0.766	0.001	0.610	0.021
B(R)	0.000	ND	0.000	ND	0.000	ND	0.000	ND	0.000	ND	0.000	ND
B(R)*(CT)	0.000	ND	0.000	ND	0.000	ND	0.000	ND	0.000	ND	0.000	ND
B(R)*P1(CT)	0.000	ND	0.000	ND	0.000	ND	0.000	ND	0.000	ND	0.000	ND
B(R)*P2(CT,P1)	0.000	ND	0.000	ND	0.000	ND	0.000	ND	0.000	ND	0.000	ND
Residual	0.064	0.239	0.159	0.238	0.066	0.239	0.237	0.238	0.073	0.238	0.226	0.223

^aI used five opposite-face adjustment approaches (OU = unadjusted, OA = across adjusted, OD = diagonally adjusted, OC = circumference adjusted, and OE = ellipse adjusted) and one same-face adjustment approach (SF = same-face) (Mahon et al 2009).

^bVariance components were estimated as described in the Materials and Methods using Model [2]: $Y_{ijklmn} = \mu + R_i + CT_j + P1(CT)_{jk} + P2(CT, P1)_{jkl} + R * CT_{ij} + R * P1(CT)_{ijk} + R * P2(CT, P1)_{ijkl} + B(R)_{im} + B(R) * CT_{ijm} + B(R) * P1(CT)_{ijkm} + B(R) * P2(CT, P1)_{ijklm} + e_{ijklmn}$ where R = replication, CT = cross-type, P1 = Parent #1, P2 = Parent #2, B = block, parentheses indicate that the effect is nested, and ND indicates that P-values could not be determined.

^cBold numbers highlight the variance components and P-values of the recommended approach.

Table A2: Variance components (Var) for squared acoustic velocity (AV^2 ; $\text{km}^2 \cdot \text{s}^{-2}$) measured on 12-year-old Douglas-fir trees at the Roaring River plantation using two standing-tree tools (TreeSonic and Microsecond Timer) and two sensor placements (opposite-face and same-face). The fixed effect of cross-type is not shown because the estimated G matrix was not positive definite. A large P-value ($\text{Pr} > 0.05$) indicates that the corresponding variance component was not significantly different from zero.

Effects ^b	Opposite-face ^a						Same-face ^a					
	OU		OA		OD		OC		OE		SF ^c	
	Var	Pr > Z	Var	Pr > Z	Var	Pr > Z	Var	Pr > Z	Var	Pr > Z	Var	Pr > Z
TreeSonic												
R	0.114	0.007	0.118	0.012	0.113	0.007	0.122	0.018	0.109	0.008	0.151	0.006
P1(CT)	0.069	0.110	0.100	0.093	0.070	0.109	0.127	0.082	0.074	0.105	0.127	0.036
P2(CT,P1)	0.221	0.000	0.285	0.000	0.223	0.000	0.332	0.000	0.229	0.000	0.230	0.000
R*CT	0.000	ND	0.000	ND	0.000	ND	0.000	ND	0.000	ND	0.000	ND
R*P1(CT)	0.000	ND	0.000	ND	0.000	ND	0.000	ND	0.000	ND	0.000	ND
R*P2(CT,P1)	0.000	ND	0.000	ND	0.000	ND	0.000	ND	0.000	ND	0.000	ND
B(R)	0.051	0.005	0.084	0.006	0.052	0.008	0.110	0.006	0.057	0.007	0.053	0.017
B(R)*(CT)	0.000	ND	0.019	0.225	0.001	0.468	0.032	0.174	0.006	0.370	0.015	0.235
B(R)*P1(CT)	0.011	0.435	0.000	ND	0.009	0.446	0.000	ND	0.003	0.481	0.000	ND
B(R)*P2(CT,P1)	0.000	ND	0.000	ND	0.000	ND	0.000	ND	0.000	ND	0.000	ND
Residual	0.786	<.0001	1.042	<.0001	0.785	<.0001	1.335	<.0001	0.799	<.0001	0.889	<.0001

Table A2 (Continued)

Effects ^b	Opposite-face ^a						Same-face ^a					
	OU		OA		OD		OC		OE		SF	
	Var	Pr > Z	Var	Pr > Z	Var	Pr > Z	Var	Pr > Z	Var	Pr > Z	Var	Pr > Z
Microsecond Timer												
R	0.049	0.016	0.065	0.021	0.049	0.016	0.080	0.025	0.050	0.017	0.053	0.018
P1(CT)	0.051	0.128	0.078	0.087	0.051	0.126	0.105	0.066	0.054	0.118	0.064	0.110
P2(CT,P1)	0.180	0.000	0.217	0.000	0.180	0.000	0.245	0.000	0.183	0.000	0.210	0.000
R*CT	0.000	ND	0.000	ND	0.000	ND	0.000	ND	0.000	ND	0.000	ND
R*P1(CT)	0.000	ND	0.000	ND	0.000	ND	0.000	ND	0.000	ND	0.000	ND
R*P2(CT,P1)	0.000	ND	0.000	ND	0.000	ND	0.000	ND	0.000	ND	0.000	ND
B(R)	0.039	0.005	0.077	0.001	0.041	0.004	0.106	0.001	0.047	0.002	0.050	0.002
B(R)*(CT)	0.000	ND	0.000	ND	0.000	ND	0.001	0.482	0.000	ND	0.000	ND
B(R)*P1(CT)	0.000	ND	0.004	0.477	0.000	ND	0.008	0.462	0.000	ND	0.002	0.484
B(R)*P2(CT,P1)	0.000	ND	0.000	ND	0.000	ND	0.000	ND	0.000	ND	0.000	ND
Residual	0.622	<.0001	0.787	<.0001	0.620	<.0001	0.985	<.0001	0.623	<.0001	0.643	<.0001

^a I used five opposite-face adjustment approaches (OU = unadjusted, OA = across adjusted, OD = diagonally adjusted, OC = circumference adjusted, and OE = ellipse adjusted) and one same-face adjustment approach (SF = same-face) (Mahon et al 2009).

^b Variance components were estimated as described in the Materials and Methods using Model [2]: $Y_{ijklmn} = \mu + R_i + CT_j + P1(CT)_{jk} + P2(CT, P1)_{jkl} + R * CT_{ij} + R * P1(CT)_{ijk} + R * P2(CT, P1)_{ijkl} + B(R)_{im} + B(R) * CT_{ijm} + B(R) * P1(CT)_{ijkm} + B(R) * P2(CT, P1)_{ijklm} + e_{ijklmn}$ where R = replication, CT = cross-type, P1 = Parent #1, P2 = Parent #2, B = block, parentheses indicate that the effect is nested, and ND indicates that P-values could not be determined.

^c Bold numbers highlight the variance components and P-values of the recommended approach.

Table A3: Variance components (Var) for squared acoustic velocity (AV^2 ; $\text{km}^2 \cdot \text{s}^{-2}$) measured on 12-year-old western hemlock trees at the Toledo plantation using two standing-tree tools (TreeSonic and Microsecond Timer) and two sensor placements (opposite-face and same-face). The fixed effect of cross-type is not shown because the estimated G matrix was not positive definite. A large P-value ($\text{Pr} > 0.05$) indicates that the corresponding variance component was not significantly different from zero.

Effects ^b	Opposite-face ^a						Same-face ^a					
	OU		OA		OD		OC		OE		SF ^c	
	Var	Pr > Z	Var	Pr > Z	Var	Pr > Z	Var	Pr > Z	Var	Pr > Z	Var	Pr > Z
TreeSonic												
R	0.077	0.014	0.111	0.014	0.077	0.014	0.146	0.014	0.081	0.013	0.076	0.014
P1(CT)	0.136	0.007	0.233	0.006	0.139	0.007	0.323	0.005	0.153	0.007	0.148	0.005
P2(CT,P1)	0.116	0.001	0.200	0.001	0.120	0.001	0.268	0.001	0.133	0.001	0.116	0.001
R*CT	0.000	ND	0.000	ND	0.000	ND	0.000	ND	0.000	ND	0.000	ND
R*P1(CT)	0.086	0.010	0.140	0.003	0.087	0.009	0.198	0.003	0.092	0.007	0.065	0.039
R*P2(CT,P1)	0.096	0.341	0.232	0.244	0.102	0.329	0.460	0.166	0.123	0.298	0.159	0.242
Residual	0.577	0.007	0.702	0.017	0.568	0.007	0.850	0.035	0.556	0.008	0.529	0.010

Table A3 (Continued)

Effects ^b	Opposite-face ^a						Same-face ^a					
	OU		OA		OD		OC		OE		SF	
	Var	Pr > Z	Var	Pr > Z	Var	Pr > Z	Var	Pr > Z	Var	Pr > Z	Var	Pr > Z
Microsecond Timer												
R	0.075	0.012	0.076	0.016	0.074	0.012	0.082	0.020	0.072	0.013	0.081	0.012
P1(CT)	0.135	0.002	0.215	0.003	0.137	0.003	0.288	0.003	0.148	0.003	0.142	0.002
P2(CT,P1)	0.077	0.002	0.137	0.001	0.081	0.002	0.186	0.001	0.091	0.001	0.078	0.003
R*CT	0.000	ND	0.000	ND	0.000	ND	0.000	ND	0.000	ND	0.000	ND
R*P1(CT)	0.069	0.013	0.121	0.002	0.073	0.009	0.176	0.002	0.078	0.006	0.067	0.018
R*P2(CT,P1)	0.197	0.169	0.352	0.092	0.200	0.160	0.607	0.036	0.215	0.138	0.104	0.320
Residual	0.375	0.034	0.423	0.052	0.366	0.033	0.479	0.074	0.354	0.035	0.488	0.014

^a I used five opposite-face adjustment approaches (OU = unadjusted, OA = across adjusted, OD = diagonally adjusted, OC = circumference adjusted, and OE = ellipse adjusted) and one same-face adjustment approach (SF = same-face) (Mahon et al 2009).

^b Variance components were estimated as described in the Materials and Methods using Model [3] $Y_{ijklm} = \mu + R_i + CT_j + P1(CT)_{jk} + P2(CT, P1)_{jkl} + R * CT_{ij} + R * P1(CT)_{ijk} + R * P2(CT, P1)_{ijkl} + e_{ijklm}$, where R = replication, CT = cross-type, P1 = Parent #1, P2 = Parent #2, parentheses indicate that the effect is nested, and ND indicates that P-values could not be determined.

^c Bold numbers highlight the variance components and P-values of the recommended approach.

Table A4: Reduced model variance components (Var) for squared acoustic velocity (AV^2 ; $\text{km}^2 \cdot \text{s}^{-2}$) measured on 8-year-old Douglas-fir trees at the Fir Grove plantation using the TreeSonic standing-tree tool and two sensor placements (same-face and opposite-face). P-values were calculated based on the probabilities of general chi-square mixture distribution. A large P-value ($\text{Pr} > 0.05$) indicates that the corresponding variance component was not significantly different between the M(F) and F(M) cross-types. In addition, P-values from the F-test indicated that the fixed effect of cross-type was non-significant.

Effects ^b		Opposite-face ^a						Same-face ^a					
		OU		OA		OD		OC		OE		SF ^c	
		Var	Pr > ChiSq	Var	Pr > ChiSq	Var	Pr > ChiSq	Var	Pr > ChiSq	Var	Pr > ChiSq	Var	Pr > ChiSq
TreeSonic													
CT (F-test)		-	0.945	-	0.879	-	0.944	-	0.843	-	0.936	-	0.926
P1	F(M)	0.215	0.574	0.224	0.509	0.216	0.572	0.228	0.471	0.215	0.564	0.251	0.637
	M(F)	0.402	-	0.471	-	0.403	-	0.515	-	0.407	-	0.409	-
P2(P1)	F(M)	0.405	0.915	0.427	0.963	0.404	0.915	0.441	0.897	0.406	0.923	0.375	0.958
	M(F)	0.375	-	0.440	-	0.377	-	0.482	-	0.380	-	0.362	-

^a I used five opposite-face adjustment approaches (OU = unadjusted, OA = across adjusted, OD = diagonally adjusted, OC = circumference adjusted, and OE = ellipse adjusted) and one same-face adjustment approach (SF = same-face) (Mahon et al 2009).

^b Variance components were estimated as described in the Materials and Methods using Model [4]: $Y_{ijklm} = \mu + R_i + CT_j + P1(CT)_{jk} + P2(CT, P1)_{jkl} + R * P2(CT, P1)_{ijkl} + e_{ijklm}$, where R = replication, CT = cross-type, P1 = Parent #1, P2 = Parent #2, and parentheses indicate that the effect is nested.

^c Bold numbers highlight the variance components and P-values of the recommended approach.

Table A5: Reduced model variance components (Var) for squared acoustic velocity (AV^2 ; $\text{km}^2 \cdot \text{s}^{-2}$) measured on 12-year-old Douglas-fir trees at the Roaring River plantation using two standing-tree tools (TreeSonic and Microsecond Timer) and two sensor placements (opposite-face and same-face). P-values were calculated based on the probabilities of the general chi-square mixture distribution. A large P-value ($\text{Pr} > 0.05$) indicates that the corresponding variance component was not significantly different between the M(F) and F(M) cross-types. In addition, P-values from the F-test indicated that the fixed effect of cross-type was non-significant.

		Opposite-face ^a						Same-face ^a					
		OU		OA		OD		OC		OE		SF ^c	
Effects ^b		Var	Pr > ChiSq	Var	Pr > ChiSq	Var	Pr > ChiSq	Var	Pr > ChiSq	Var	Pr > ChiSq	Var	Pr > ChiSq
		TreeSonic											
CT (F-test)		-	0.902	-	0.706	-	0.884	-	0.616	-	0.835	-	0.968
P1	F(M)	0.112	0.404	0.188	0.206	0.116	0.381	0.250	0.152	0.127	0.320	0.182	0.391
	M(F)	0.018	-	0.000	-	0.016	-	0.000	-	0.011	-	0.062	-
P2(P1)	F(M)	0.233	0.934	0.278	0.862	0.233	0.953	0.314	0.804	0.235	0.992	0.250	0.832
	M(F)	0.222	-	0.306	-	0.225	-	0.357	-	0.236	-	0.222	-

Table A5 (Continued)

Effects ^b		Opposite-face ^a						Same-face ^a					
		OU		OA		OD		OC		OE		SF	
		Var	Pr > ChiSq	Var	Pr > ChiSq	Var	Pr > ChiSq	Var	Pr > ChiSq	Var	Pr > ChiSq	Var	Pr > ChiSq
Microsecond Timer													
CT (F-test)		-	0.835	-	1.000	-	0.847	-	0.914	-	0.884	-	0.955
P1	F(M)	0.082	0.485	0.138	0.285	0.084	0.462	0.187	0.219	0.092	0.404	0.127	0.242
	M(F)	0.019	-	0.015	-	0.018	-	0.019	-	0.015	-	0.004	-
P2(P1)	F(M)	0.195	0.776	0.222	0.962	0.194	0.791	0.241	0.945	0.194	0.837	0.222	0.839
	M(F)	0.166	-	0.216	-	0.168	-	0.251	-	0.173	-	0.199	-

^a I used five opposite-face adjustment approaches (OU = unadjusted, OA = across adjusted, OD = diagonally adjusted, OC = circumference adjusted, and OE = ellipse adjusted) and one same-face adjustment approach (SF = same-face) (Mahon et al 2009).

^b Variance components were estimated as described in the Materials and Methods using Model [5]: $Y_{ijklmn} = \mu + R_i + CT_j + P1(CT)_{jk} + P2(CT, P1)_{jkl} + B(R)_{im} + e_{ijklmn}$, where R = replication, CT = cross-type, P1 = Parent #1, P2 = Parent #2, B = block, and parentheses indicate that the effect is nested.

^c Bold numbers highlight the variance components and P-values of the recommended approach.

Table A6: Reduced model variance components (Var) for squared acoustic velocity (AV^2 ; $\text{km}^2 \cdot \text{s}^{-2}$) measured on 12-year-old western hemlock trees at the Toledo plantation using two standing-tree tools (TreeSonic and Microsecond Timer) and two sensor placements (opposite-face and same-face). P-values were calculated based on the probabilities of the general chi-square mixture distribution. A large P-value ($\text{Pr} > 0.05$) indicates that corresponding variance components were not significantly different between the M(F) and F(M) cross-types. In addition, P-values from the F-test indicated that the fixed effect of cross-type was non-significant.

	Opposite-face ^a						Same-face ^a						
	OU		OA		OD		OC		OE		SF ^c		
Effects ^b	Var	Pr > ChiSq	Var	Pr > ChiSq	Var	Pr > ChiSq	Var	Pr > ChiSq	Var	Pr > ChiSq	Var	Pr > ChiSq	
TreeSonic													
CT (F-test)	-	0.621	-	0.793	-	0.637	-	0.881	-	0.684	-	0.649	
P1	F(M)	0.172	0.600	0.191	0.563	0.172	0.664	0.202	0.282	0.171	0.865	0.159	0.919
	M(F)	0.114	-	0.296	-	0.122	-	0.468	-	0.150	-	0.147	-
P2(P1)	F(M)	0.086	0.546	0.150	0.531	0.089	0.538	0.210	0.601	0.099	0.524	0.092	0.634
	M(F)	0.130	-	0.226	-	0.135	-	0.296	-	0.151	-	0.128	-

Table A6 (Continued)

Effects ^b		Opposite-face ^a						Same-face ^a					
		OU		OA		OD		OC		OE		SF	
		Var	Pr > ChiSq	Var	Pr > ChiSq	Var	Pr > ChiSq	Var	Pr > ChiSq	Var	Pr > ChiSq	Var	Pr > ChiSq
Microsecond Timer													
CT (F-test)		-	0.513	-	0.629	-	0.529	-	0.699	-	0.556	-	0.602
P1	F(M)	0.169	0.564	0.180	0.573	0.168	0.615	0.186	0.270	0.166	0.821	0.166	0.707
	M(F)	0.114	-	0.266	-	0.119	-	0.412	-	0.143	-	0.129	-
P2(P1)	F(M)	0.064	0.826	0.114	0.773	0.067	0.787	0.160	0.838	0.074	0.765	0.058	0.591
	M(F)	0.076	-	0.139	-	0.082	-	0.184	-	0.092	-	0.087	-

^a I used five opposite-face adjustment approaches (OU = unadjusted, OA = across adjusted, OD = diagonally adjusted, OC = circumference adjusted, and OE = ellipse adjusted) and one same-face adjustment approach (SF = same-face) (Mahon et al 2009).

^b Variance components were estimated as described in the Materials and Methods using Model [6]: $Y_{ijklm} = \mu + R_i + CT_j + P1(CT)_{jk} + P2(CT, P1)_{jkl} + R * P1(CT)_{ijk} + R * P2(CT, P1)_{ijkl} + e_{ijklm}$, where R = replication, CT = cross-type, P1 = Parent #1, P2 = Parent #2, and parentheses indicate that the effect is nested.

^c Bold numbers highlight the variance components and P-values of the recommended approach.

Table A7: A comparison of σ_{P1}^2 and $\sigma_{P2(P1)}^2$ variance components (Var) for squared acoustic velocity (AV^2 ; $\text{km}^2 \cdot \text{s}^{-2}$) measured on 8-year-old Douglas-fir trees at the Fir Grove plantation using the TreeSonic standing-tree tool and two sensor placements (same-face and opposite-face). P-values were calculated based on the probabilities of the general chi-square mixture distribution. A large P-value ($\text{Pr} > 0.05$) indicates that the σ_{P1}^2 variance component was not significantly different from the $\sigma_{P2(P1)}^2$ variance component.

Effects ^b	Opposite-face ^a						Same-face ^a					
	OU		OA		OD		OC		OE		SF ^c	
	Var	Pr > ChiSq	Var	Pr > ChiSq	Var	Pr > ChiSq	Var	Pr > ChiSq	Var	Pr > ChiSq	Var	Pr > ChiSq
TreeSonic												
P1	0.288	0.654	0.326	0.679	0.288	0.654	0.350	0.691	0.290	0.654	0.308	0.782
P2(P1)	0.393	-	0.436	-	0.395	-	0.465	-	0.397	-	0.373	-

^a I used five opposite-face adjustment approaches (OU = unadjusted, OA = across adjusted, OD = diagonally adjusted, OC = circumference adjusted, and OE = ellipse adjusted) and one same-face adjustment approach (SF = same-face) (Mahon et al 2009).

^b Variance components were estimated as described in the Materials and Methods using Model [7]: $Y_{ijklm} = \mu + R_i + P1_j + P2(P1)_{jk} + R * P2(P1)_{ijk} + e_{ijkl}$, where R = replication, P1 = Parent #1, P2 = Parent #2, and parentheses indicate that the effect is nested.

^c Bold numbers highlight the variance components and P-values of the recommended approach.

Table A8: A comparison of σ_{P1}^2 and $\sigma_{P2(P1)}^2$ variance components (Var) for squared acoustic velocity (AV^2 ; $\text{km}^2 \cdot \text{s}^{-2}$) measured on 12-year-old Douglas-fir trees at the Roaring River plantation using two standing-tree tools (TreeSonic and Microsecond Timer) and two sensor placements (opposite-face and same-face). P-values were calculated based on the probabilities of the general chi-square mixture distribution. A large P-value ($\text{Pr} > 0.05$) indicates that the σ_{P1}^2 variance component was not significantly different from the $\sigma_{P2(P1)}^2$ variance component.

Effects ^b	Opposite-face ^a						Same-face ^a					
	OU		OA		OD		OC		OE		SF ^c	
	Var	Pr > ChiSq	Var	Pr > ChiSq	Var	Pr > ChiSq	Var	Pr > ChiSq	Var	Pr > ChiSq	Var	Pr > ChiSq
TreeSonic												
P1	0.069	0.113	0.102	0.152	0.070	0.115	0.130	0.190	0.074	0.120	0.129	0.375
P2(P1)	0.221	-	0.281	-	0.222	-	0.327	-	0.228	-	0.228	-
Microsecond Timer												
P1	0.051	0.091	0.078	0.151	0.051	0.092	0.105	0.220	0.054	0.100	0.064	0.100
P2(P1)	0.180	-	0.217	-	0.180	-	0.245	-	0.183	-	0.210	-

^a I used five opposite-face adjustment approaches (OU = unadjusted, OA = across adjusted, OD = diagonally adjusted, OC = circumference adjusted, and OE = ellipse adjusted) and one same-face adjustment approach (SF = same-face) (Mahon et al 2009).

^b Variance components were estimated as described in the Materials and Methods Model [8]: $Y_{ijklm} = \mu + R_i + P1_j + P2(P1)_{jk} + B(R)_{il} + e_{ijklm}$, where R = replication, P1 = Parent #1, P2 = Parent #2, B = block, and parentheses indicate that the effect is nested.

^c Bold numbers highlight the variance components and P-values of the recommended approach.

Table A9: A comparison of σ_{P1}^2 and $\sigma_{P2(P1)}^2$ variance components (Var) for squared acoustic velocity (AV^2 ; $\text{km}^2 \cdot \text{s}^{-2}$) measured on 12-year-old western hemlock trees at the Toledo plantation using two standing-tree tools (TreeSonic and Microsecond Timer) and two sensor placements (opposite-face and same-face). P-values were calculated based on the probabilities of general chi-square mixture distribution. A large P-value ($\text{Pr} > 0.05$) indicates that the σ_{P1}^2 variance component was not significantly different from the $\sigma_{P2(P1)}^2$ variance component.

Effects ^b	Opposite-face ^a						Same-face ^a					
	OU		OA		OD		OC		OE		SF ^c	
	Var	Pr> ChiSq	Var	Pr> ChiSq	Var	Pr> ChiSq	Var	Pr> ChiSq	Var	Pr> ChiSq	Var	Pr> ChiSq
TreeSonic												
P1	0.139	0.672	0.236	0.700	0.143	0.684	0.324	0.677	0.156	0.710	0.149	0.616
P2(P1)	0.107	-	0.188	-	0.111	-	0.253	-	0.125	-	0.110	-
Microsecond Timer												
P1	0.140	0.256	0.219	0.345	0.142	0.279	0.292	0.370	0.152	0.304	0.144	0.252
P2(P1)	0.070	-	0.126	-	0.074	-	0.172	-	0.083	-	0.072	-

^a I used five opposite-face adjustment approaches (OU = unadjusted, OA = across adjusted, OD = diagonally adjusted, OC = circumference adjusted, and OE = ellipse adjusted) and one same-face adjustment approach (SF = same-face) (Mahon et al 2009).

^b Variance components were estimated as described in the Materials and Methods using Model [9]: $Y_{ijkl} = \mu + R_i + P1_j + P2(P1)_{jk} + R * P1_{ij} + R * P2(P1)_{ijk} + e_{ijkl}$, where R = replication, P1 = Parent #1, P2 = Parent #2, and parentheses indicate that the effect is nested.

^c Bold numbers highlight the variance components and P-values of the recommended approach.