# Consideration of wood quality in variable retention systems: British Columbia as an

example

by

Adam Polinko

B.S., Northern Arizona University, 2011

M.S., Northern Arizona University, 2014

# A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

### THE REQUIREMENTS FOR THE DEGREE OF

### DOCTOR OF PHILOSOPHY

in

# THE FACULTY OF GRADUATE AND POSTDOCTORAL STUDIES

(Forestry)

### THE UNIVERSITY OF BRITISH COLUMBIA

(Vancouver)

October 2019

© Adam Polinko, 2019

The following individuals certify that they have read, and recommend to the Faculty of Graduate and Postdoctoral Studies for acceptance, the dissertation entitled:

# Consideration of wood quality in variable retention systems: British Columbia as an example

submitted by	Adam Polinko	in partial fulfillment of the requirements for	
the degree of	Doctor of Philosophy		
in	Forestry		
Examining Co Bruce Larson,	<b>mmittee:</b> Forest Resources Management		
Supervisor			
Ian Cameron,	President of Azura Formetrics Ltd.		
Supervisory C	ommittee Member		
Julie Cool, Wood Science			
Supervisory C	ommittee Member		
Richard Barichello, Land and Food Systems			
University Exa	aminer		
Peter Marshall, Forest Resources Management			
University Exa	aminer		

#### Abstract

Demands for high quality wood are expected to increase as wood products begin to replace concrete and steel, particularly in tall buildings. Even as markets change, forest managers will be required to balance conflicting management objectives. Managing for wood quality may be a significant part of the solution to continue meeting social, ecological and economic criteria. Variable retention systems are used to meet ecological objectives, such as wildlife habitat and biodiversity as well as visual quality objectives around the world. Despite their widespread use, most wood quality research has focused on even-aged systems that lack vertical and horizontal complexity, one of the primary objectives of retention systems. To better understand wood quality in retention systems, a framework was created for simulating lumber recovery in coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) that is spatially explicit from end to end. A literature review of the interaction between the live crown and silviculture on wood density was also undertaken. I advocate that wood density is not influenced by competition from neighboring overstory trees or from trees of the same cohort. Simulations of retention systems demonstrate that retention of overstory trees to improve social or ecological management objectives occurs at a cost associated with the reduction in volume from overstory competition. The increase in wood quality (branch size, frequency, and distribution) associated with increasing overstory retention is negligible when compared to the loss in volume. This work provides an accurate estimate of the costs and implications for wood products associated with alternative silviculture systems and sustainable forest management.

# Lay Summary

In the future, more buildings will be built out of wood because of its positive impact on the global carbon cycle. Forest managers must consider this increase in demand for wood while also improving services like scenic beauty and wildlife habitat. To increase these services foresters can leave trees behind after harvest. There are many factors that influence the strength of wood. This work attempts to understand the factors that change the strength of wood when managers leave trees behind. I found that the density of wood will not appreciably change when younger trees are competing with older trees left behind. Using computer simulations, I learned that despite changes in wood quality, the growth of trees is significantly reduced when younger trees compete with older trees that are left behind. This work provides an accurate estimate of the costs associated with providing services like visual quality and wildlife habitat.

### Preface

The research questions and objectives presented in this dissertation were developed during conversations with myself, my supervisor and supervisory committee. The following people provided data for exploration, calibration and validation in this dissertation: Cosmin Fillipescu of the Canadian Wood Fibre Centre, Jason Cross of the Stand Management Cooperative, Catherine Bealle-Statland, and Jim Goudie (retired) of the British Columbia Ministry of Forests, Lands, Natural Resource Operations and Rural Development, and Phil Evans of The University of British Columbia.

Catalin Ristea, Giuseppe Costanzo, Peter Kort (formerly) and Steve Vallerand of FPInnovations provided Optitek support and insight throughout my dissertation. Ken Polsson of the British Columbia Ministry of Forests, Lands, Natural Resource Operations and Rural Development provided TASS simulations for Chapters one and four. Grace Carsky, Stephanie Lau, Judah Melton and Sushil Nepal assisted with field data collection. I performed the field work and data collection, data analysis, interpreted results and wrote the text.

# **Table of Contents**

Abstractiii
Lay Summaryiv
Prefacev
Table of Contents vi
List of Tablesx
List of Figures xii
List of Abbreviationsxv
Acknowledgements xvi
Dedication xvii
Chapter 1: Introduction1
1.1 Primary goal
1.2 Dissertation Overview
Chapter 2: Modeling Douglas-fir branch distribution and size for use in a three-
dimensional sawmill simulator6
2.1 Introduction
2.2 Methods
2.2.1 Calibration data

2.2.2	Validation data	8
2.2.3	Statistical methods	12
2.2.4	Model validation	15
2.3 H	Results	17
2.3.1	Number of branches in the internode	17
2.3.2	Vertical distribution of branches within an internode	21
2.3.3	Branch azimuth	25
2.3.4	Diameter of branches	25
2.3.5	Length of branches	28
2.3.6	Branch Mortality	30
2.3.7	Overall approach	31
2.4 I	Discussion	36
2.4.1	Conclusions	42
Chapter 3: Financial perspectives of simulated product recovery in variable retention		
systems		43
3.1 I	Introduction	43

3.2	Methods	3
3.2.2	1 TASS simulations	3
3.2.2	2 Optitek simulations	2
3.2.3	3 Statistical analysis	4
3.3	Results	5
3.3.	1 Tree and stand-level response	5
3.3.2	2 Financial analysis	5
3.4	Discussion	1
3.4.2	1 Conclusion	3
Chapter	4: The influence of silviculture and the live crown on wood density in Douglas-fir:	
A synthe	sis80	0
4.1	Introduction	)
4.2	Intra-ring variation of wood density	1
4.3	Radial variation of wood density	4
4.4	Wood density response to thinning and fertilization	9
4.5	The effect of growth rate on wood density	2
	vii	i

4.6	Models of wood density	. 93
4.7	The effect of retention systems on wood density in Douglas-fir	95
4.8	Conclusions	96
Chapter	· 5: Conclusions	97
5.1	Additional future directions	100
5.2	Operational considerations	101
5.3	Closing statement	103
Referen	ces	.104

# List of Tables

Table 2.1 Tree level metrics (mean and standard error) for three datasets
Table 2.2 Candidate predictors 15
Table 2.3 Parameter estimates for number of branches in an internode. 21
Table 2.4 Parameters and statistics of the two-component mixture Weibull model
Table 2.5 Parameter estimates for the diameter of branches in an internode. 26
Table 2.6 Parameter estimates for the length of branches in an internode. 29
Table 2.7 Summary statistics (mean and standard error) of predicted vs empirical branch
characteristics
Table 4.1 NLGA grade rules for structural joists and planks and structural light framing (NLGA
2014)
Table 4.2 Target and empirical retention densities (mean and standard error) for five levels of
aggregate and dispersed retention. Aggregate retention is further divided in to 1, 4 and 16
separate groups
Table 4.3 Branch diameter summary for five levels of aggregate and dispersed retention.
Aggregate retention is further divided in to 1, 4 and 16 separate groups
Table 4.4 Linear mixed-effects model output

Table 4.5 Linear mixed-effects model	output	66
--------------------------------------	--------	----

# List of Figures

Figure 2.1 Locations of stand management cooperative installations
Figure 2.2 Overview of model outline
Figure 2.3 Distribution of branches along internodes by internode age class for calibration data.
Figure 2.4 Observed vs predicted number of branches in an internode. Observed data are from
the SMC dataset
Figure 2.5 Two component finite-mixture distribution to estimate the vertical distribution of
branches within an internode. 0 represents the bottom of the internode and 1 represents the top of
the internode. Histograms represent the empirical data, dashed lines re
Figure 2.6 Empirical and predicted distributions of the relative position of branches within an
internode. 0 represents the bottom of the internode and 1 represents the top of the internode 24
Figure 2.7 Empirical and predicted branch diameter by the relative position of branches within
an internode. 0 represents the bottom of the internode and 1 represents the top of the internode.27
Figure 2.8 Distributions of diameter relative to the largest diameter in an internode for the SMC
validation data and predicted data. See section 2.2.2 for description of SMC data
Figure 2.9 Branch length by branch diameter for predicted and empirical (SMC validation data).
See manuscript for description of SMC data
xii

Figure 2.10 Predicted and empirical branch azimuth (degrees) and diameter (cm) for four trees
sampled from a rectangular espacement trial. See section 2.2.2 for data description
Figure 2.11 Simulated and empirical height vs age (left), simulated height to live crown vs age
(center) and distribution of branch diameters (right) for four trees from a rectangular espacemet
trial
Figure 3.1 Radial variation of wood density at breast height for 54 Douglas-fir sampled near
Cowichan Lake Research Station, British Columbia (Goudie unpublished)
Figure 4.1 10% retention in three aggregate grouping patterns: One, four and sixteen groups 50
Figure 4.2 TASS visualizations of retention simulations
Figure 4.3 Percent mortality by retained basal area for aggregate (left) and dispersed (right)
retention
Figure 4.4 Mean tree volume by level of retention in aggregate (a.) or dispersed (b.) spatial
patterns
Figure 4.5 Mean tree volume (a.) and mean maximum branch diameter (b.) for edge trees vs
matrix trees. Edge trees are trees that were nearest to retained cohorts. Matrix trees are the same
trees simulated without competition from retained cohorts and only competition from
neighboring trees of the same age

Figure 4.6 Mean tree volume (m <sup>3</sup> ha <sup>-1</sup> ) for edge trees vs matrix trees. Edge trees are trees that
were nearest to retained cohorts. Matrix trees are the same trees simulated without competition
from retained cohorts and only competition from neighboring trees of the same age
Figure 4.7 Total volume (m <sup>3</sup> ha <sup>-1</sup> ) by level of retention in aggregate (a.) or dispersed (b.) spatial
patterns
Figure 4.8 Gross present value for aggregate (a.) and dispersed (b.) retention
Figure 4.9 Gross present value by merchantable volume

# List of Abbreviations

- AIC Akaike's Information Criterion
- BC British Columbia
- DBH Diameter at Breast Height
- RMSE Root Mean Squared Error
- TASS Tree and Stand Simulator

### Acknowledgements

First, I would like to thank my Supervisor Dr. Bruce Larson for being an exceptional mentor and friend. His curiosity and enthusiasm across all topics, but most notably forestry, is contagious. I thank Ian Cameron for his support, mentorship and friendship. I sincerely appreciate the advice and feedback of Dr. Julie Cool and Dr. Paul McFarlane throughout my time at UBC.

The fellow graduate students, staff and faculty that have supported me through friendship and collegiality at UBC are too long to list in accordance with the UBC formatting requirements. Thank you to Juliana Magalhaes for the many adventures, patience, friendship and encouragement. I would also like to thank Dr. Jordan Burke, Judah Melton and Emily Murphy for their friendship and shared enthusiasm across many different interests.

There are many friends, family and colleagues that have influenced my life and who I would like to thank. My dog Sitka provided enthusiastic support through three degrees. I thank my fiancé Stephanie, for her support, encouragement and patience. Finally, I thank my grandparents, parents and my sister who have provided advice and shaped my life in many ways.

# Dedication

To my family, friends and colleagues.

#### **Chapter 1: Introduction**

Wood has been used as to meet basic human needs, such as an energy source for heating and cooking and for shelter for millennia. In addition, wood has been made into products such as paper, weapons, and modes of transportation which have shaped civilization. The industrial revolution and changes in technology have given rise to building materials and energy sources that replaced wood as a primary source. We now understand the implications of these materials and energy sources on the global carbon cycle (Gustavsson and Sathre 2006). The world population is expected to reach between 9.6 and 12.3 billion in the next century (Gerland et al. 2014). Demands for uniform, high quality wood are expected to increase as wood products begin to replace traditional building materials, such as concrete and steel and are increasingly used in pharmaceutical, biochemical and biofuel applications (Wegner et al. 2010; Skog et al. 2014).

Sustainable forest management includes balancing social, environmental and economic objectives in space and time (Toman and Ashton 1996). These multi-faceted objectives often conflict, as meeting social and environmental goals requires a reduction in harvest volume and loss in revenue (Zielke et al. 2008). Silviculture in the Pacific Northwest has shifted from large scale clearcuts to alternative systems that include varied retention and age distributions. This shift is largely a result of changes in forest policy and societal values in the early 1990's (DeBell and Curtis 1993). It has been hypothesized that managing for wood quality may allow managers to simultaneously meet social, environmental and economic goals (Briggs 2010). Wood quality is defined as a "suitability of use" in an end product (Briggs 2010). Therefore, properties that are suitable for use in one product may exclude other products and applications of wood (Pretzsch

and Rais 2016). This dissertation constrains wood quality to focus on construction and structural applications.

The two of the most influential properties that relate to wood strength are knots and wood density. Knots arise from branches and create spiral grain which is prone to failure under load. The size and distribution of knots on a piece of dimensional lumber can affect the overall strength and value of lumber (Lowell et al. 2014a). The larger the size of knots and the larger the number of knots, the lower the strength and value of a piece of lumber. Knots can be classified as live or dead where live knots occur from branches that were still hydraulically attached to the main stem. Dead knots can create problems when sawing, as the lack of hydraulic connection causes knots to be loosely connected or often fall out of sawn lumber (Shmulsky and Jones 2011). Wood density is directly related to strength in dimensional products. Wood density is linearly related to modulus of elasticity in dimensional products (Shmulsky and Jones 2011).

Douglas-fir (*Pseudotsuga menziessii* (Mirb.) Franco) in the Pacific Northwest is known for its strength and visually appealing growth characteristics. Douglas-fir was historically used for ship masts, telephone poles, building construction and window and door applications (Barbour et al. 2003). The Douglas-fir region of the Pacific Northwest ranges from Oregon to southeast Alaska. It is characterized by warm, wet winters and cool, dry summers (Waring and Franklin 1979). Elevation and precipitation influence vegetation communities which have been extensively classified (Waring and Franklin 1979; Pojar et al. 1987). Prior to the 1960's, forest management in the Pacific Northwest was largely industrialized, commodity based and production focused

(Curtis et al. 2007). Since this time, the environmental movement and changes in North American forest policy have shifted the paradigm from production to consideration of social and ecological objectives (Thomas 1997; Curtis et al. 2007). As public perceptions changed, the role of multiple objectives in forest management became more important. At the same time, silviculture in the US Pacific Northwest shifted from large scale clearcuts to selection and retention systems. Similar changes occurred in British Columbia, where concerns of harvest practices on visual quality and the environment lead to changes in silvicultural practices in the early 1990's (Sheppard et al. 2004). Since this time, there have been numerous studies on the effects of retention systems and ecological wellbeing.

There are many empirical examples of the effects of silviculture and wood quality of Douglas-fir (e.g. Erickson and Harrison 1974, Briggs et al. 2007). Additionally, many researchers have developed models of branches (e.g. Maguire et al. 1991, 1994, Nemec et al. 2012) and wood density (e.g. Kantavichai et al. 2010, Filipescu et al. 2014). Despite this, many wood quality models lack the ability to adapt in time and space (Briggs 2010). In addition, studies on the financial implications of retention systems are rare and effects on wood quality remain undocumented.

The Tree and Stand Simulator (TASS) is a distance dependent, individual tree growth and yield model developed by Ken Mitchell for Douglas-fir in 1975 (Mitchell 1975a). Height and crown expansion are the primary drivers in TASS. Detailed crown information is recorded for each tree, which drives inter-tree competition in the model. The spatially explicit detailed crown

information and individual tree records make TASS well suited for investigating wood quality in complex structures.

#### 1.1 Primary goal

The goal of this dissertation is to evaluate the hypothesis that improving wood quality may offset the reduction in volume associated with meeting social and ecological objectives. I set out to understand the changes in wood quality in response to silvicultural systems that incorporate complex stand structures. To examine this hypothesis, I create models of knot size and distribution to construct a virtual lumber recovery system that is spatially explicit from end to end. This system combines TASS derived growth and yield data, models of knot size and distribution and a spatially explicit sawmill optimization model to examine questions regarding wood quality and lumber recovery in structurally complex silviculture systems. Specifically, my objectives are to: 1) create models of knot size and distribution for asymmetric crowns, 2) compare and evaluate the revenue peformance of retention systems through changes in wood quality, and 3) synthesize the literature regarding silviculture, tree growth and wood density in relation to retention systems.

#### **1.2 Dissertation Overview**

**Chapter 2** describes a modeling approach for predicting branch development through time in asymmetric crowns intended to be integrated into the Tree and Stand Simulator (Mitchell 1975a). The approach uses predictive variables from the branch, internode and tree level. An internode is defined as one annual year of height growth. Branches are assigned to an internode following the

first year of growth using a series of 5 predictive equations. First, the number of branches in an internode is predicted followed by the location of branches in an internode, branch azimuth, branch diameter and finally branch length. In subsequent years, the number of branches in an internode as well as branch diameter and length are predicted to account for branch mortality and growth, respectively. Branch mortality occurs systematically from the lowest branch in an internode and progresses upwards. Following mortality, dead branches are stored for later representation as tight knots in the sawmill simulator.

**Chapter 3** implements the entire modeling framework to investigate the financial tradeoffs of meeting social and ecological objectives using retention systems. The simulation approach combines TASS derived growth and yield data with the modeling approach described in Chapter 2. Virtual logs were harvested and sent to Optitek, a spatially explicit sawmill optimization model developed by FPInnovations. The simulation approach is the first virtual lumber recovery approach that is spatially explicit from end to end. Five retention densities from 10% to 50% in steps of 10% were simulated for both aggregate and dispersed retention. The spatial distribution of aggregate retention was further examined by distributing aggregate groups into groups of one, four or sixteen separate groups. Retention simulations were compared to a clearcut alternative of the same age.

**Chapter 4** synthesizes, in detail, the large amount of literature regarding wood density in Douglas-fir. Specific attention is given to the role of the live crown and silvicultural intervention in understanding Douglas-fir wood density.

Chapter 2: Modeling Douglas-fir branch distribution and size for use in a three-dimensional sawmill simulator.

#### 2.1 Introduction

Knots are the most influential wood property affecting strength and the most targeted in silvicultural treatments (Shmulsky and Jones 2011). Both branch size and number of branches are important in traditional dimensional products and engineered wood products. Tracheids surrounding branches often exhibit angles perpendicular to the longitudinal tracheids of the main stem, which can cause a distortion of grain surrounding the branch, resulting in reduced strength, stiffness and visual quality (Barbour et al. 2003; Lowell et al. 2014b). Branch location and size can be manipulated with silvicultural planning and treatments. Initial planting density is related to branch size, where higher densities produce the lowest branch diameters (Briggs et al. 2007; Hein et al. 2008a; Newton et al. 2012) where competition drives the base of the crown upwards.

There has been extensive work to model the number, distribution and size of branches in coastal Douglas-fir (Maguire et al. 1991, 1994; Hein et al. 2008b; Nemec et al. 2012 as examples); usually with the objective of integration to a forest growth and yield model or to make inferences regarding crown morphology. However, many models of branch size and distribution have been developed for trees growing in uniform stand conditions that result in symmetric crowns. Crown asymmetry, and more broadly crown plasticity, has been found to be associated with the direction of prevailing solar radiation and the spatial distribution, size and density of neighboring trees in Scots pine (*Pinus sylvestris* L.; Rouvinen and Kuuluvainen 1997). Umeki (1997) found,

through simulation, that crown asymmetry can increase survival and mean tree size. Models of branch distribution and architecture in symmetric crowns may be inaccurate when estimating branch architecture and distribution in asymmetric crowns found in more complex forest structures. Growth and yield models must also be well suited to model complex forest structure.

The Tree and Stand Simulator (TASS), is a distance-dependent, individual-tree growth and yield model. TASS was developed by initially for white spruce (Mitchell 1969) and later Douglas-fir (Mitchell 1975a). TASS has since been adapted to incorporate eight species in coastal and interior British Columbia (Di Lucca 1998). Individual tree crowns are modeled in TASS and are the primary driver of tree growth, producing annual estimates of crown expansion and volume increment (Mitchell 1975a). By design, TASS can produce trees with asymmetric crowns and provide outputs of the height to the base of live crown, crown width and foliar volume in eight crown octants, making TASS well suited to simulate the asymmetric crowns that may be common in complex forest structures.

Many forest growth and yield models include the capability to estimate lumber recovery through sawmill simulators. These sawmill simulators are typically based on inputs of knot indices (Di Lucca 1998 as an example). Newer computing abilities and improved wood quality models allow three-dimensional log outputs that can be analyzed by modern sawmill optimization software. Optitek is a sawmill optimization software developed by FPInnovations (Goulet 2006) that allows the user to saw a three-dimensional log in a variety of sawmill configurations. The ability to predict wood quality variables annually in TASS provides a unique opportunity to integrate a powerful forest growth and yield model and modern sawmill optimization software.

The objective of this study is to develop branch distribution and architecture equations that can model branch ontogeny in asymmetric, TASS derived Douglas-fir crowns. The outputs of this study will be used in Optitek in later Chapters.

2.2 Methods

#### 2.2.1 Calibration data

Calibration data included 54 destructively sampled Douglas-fir originating from the Cowichan Lake Research Station in southwest Vancouver Island (Nemec et al. 2012). Candidate trees were selected for symmetric crowns and minimal damage (no forks or ramicorn branches). Tree ages ranged from 15 – 74 years (mean 28.1 years, median 15 years). Of the 54 sampled, 30 trees were 15 years old. A summary of tree metrics can be seen in Table 2.1. Trees were felled and the distance from the ground to each internode was recorded. Six to ten internodes in the live crown were randomly selected for sampling per tree. All branches in each selected internode were measured for horizontal and vertical diameter, length and assessed for damage. Damaged branches were not included in further analyses. The final dataset was comprised of 336 internodes and 6306 branches aged 1 to 57 years (median 5 years).

#### 2.2.2 Validation data

Validation data came from two different sources. The first validation dataset consisted of Douglas-fir measurements collected by the Stand Management Cooperative (Figure 2.1; hereafter SMC data). The dataset included 211 Douglas-fir, 2024 internodes and 43620 branches with a median tree age of 13 years (ranging from 9 - 31 years; Table 2.1). The trees originated from a larger effort to study crown structure of Douglas-fir (Maguire et al. 1994).

Data type	Number of trees	DBH (cm)	Height (m)	crown base (m)
Calibration data				
	54	25.94 (2.46)	16.9 (1.21)	5.11 (0.9)
SMC Data				
	203	10.12 (0.38)	6.65 (0.21)	0.59 (0.02)
	415	9.78 (0.20)	8.36 (0.16)	0.55 (0.03)
	160	15.57 (0.26)	10.89 (0.13)	1.6 (0.05)
	325	8.51 (0.18)	6.21 (0.10)	0.19 (0.03)
	181	9.19 (0.32)	7.04 (0.17)	0.91 (0.05)
	323	12.46 (0.23)	8.54 (0.10)	0.61 (0.02)
	356	14.55 (0.30)	8.66 (0.13)	0.51 (0.03)
	210	7.98 (0.07)	5.87 (0.04)	0.55 (0.02)
	31	18.20 (1.23)	14.94 (0.45)	6.03 (0.09)
	42	27.70 (1.42)	21.59 (0.37)	10.49 (0.19)
	34	13.05 (0.2)	10.39 (0.21)	3.78 (0.07)

Height to live

Rectangularity data



Figure 2.1 Locations of stand management cooperative installations.

The second validation dataset consisted of four 52-year-old trees that were felled from a rectangularity trial at the Malcolm Knapp Research Forest near Maple Ridge, British Columbia. The trial was established in 1967 using 2+0 stock. The trial was established to study the feasibility of rectangular spacing on alternating rows of Douglas-fir and western hemlock (*Tsuga heterophila* (Raf.) Sarg.) and also Douglas-fir only plots for use in mechanized forestry. Trees

that were felled originated from a Douglas-fir only plot planted at 2.7 x 5.5 m spacing. The 2.7 x 5.5 m plot, located on the edge of the trial, experienced significant wind disturbance between the 1997 and 2007 measurements and as a result 33% of the plot was blown down.

A total of four trees were selected near the edge of the gap to assist in unobstructed felling and also to sample trees with a greater amount of crown asymmetry compared to trees growing alongside neighbors. I attempted to select trees with minimal defects (lean, sweep, crooks or forks etc.); however several ramicorn branches were observed after trees were on the ground. To measure the azimuth of branches, a north line was painted on each tree prior to felling. This line was continued up the stem after the tree was on the ground. A full census of branch diameters and branch angles was completed for all branches in the live crown. I measured two diameters for each branch using digital calipers, one perpendicular and one parallel to the stem. Branch angle was measured at by standing the internode vertically and measuring the insertion point using a clinometer. Branches were visually assessed as node or internode branches, where nodal branches were typically larger, occurring at the top of an internode. Branch length was systematically sampled for every 10th branch in both the node and internode designations. For each selected branch, branch length and radius was measured. Branch length was the absolute length along the first order branch beginning from the insertion point. Branch location or the azimuth was measured by taking the circumference of the stem above or below and then recording the distance from north to determine the azimuth.

#### 2.2.3 Statistical methods

The vertical distribution and architecture of branches is generally found to be related to the position and size of annual internodes within the live crown. Trees tend to be made up of hierarchical sets of units, where internodes are nested within trees and branches are nested within internodes. Several existing models of branch distribution and size have used the hierarchical nature of conifer architecture to model branch distribution and size (Maguire et al. 1994 and Nemec et al. 2012 as examples). I chose a hierarchical, five component model design (Figure 2.2). The model uses internodes as a unit within the stem, similar to Maguire et al. (1994) in coastal Douglas-fir. My framework uses an approach similar to a framework developed for loblolly pine (*Pinus taeda* L.; Trincado and Burkhart 2009). The framework integrates TASS derived crown and height data which allows for the input of asymmetric crown variables. Repeated branch measurements were unavailable in the calibration dataset. Branch growth and mortality were predicted using annual estimates of branch diameter and number of branches in an internode as a proxy. A summary of the modeling approach can be seen in Figure 2.2.



#### Figure 2.2 Overview of model outline

For each component, a variety of modeling approaches were evaluated, including generalized additive models, nonlinear equations and random forest regression. A suite of branch level, internode level and tree level predictors were used during model development (Table 2.2). I explored generalized additive models (GAMs) to predict branch location within the internode using shoot and tree level variables as well as traditional distributions, such as the Weibull and

beta distributions. I chose to evaluate a multi-component mixture distribution using the *mixdist* package in R (Macdonald and Du 2018). As opposed to parametric distributions, finite mixture distributions allow the additive mixture of two different distributions. I explored both gamma and Weibull distributions as two-component finite mixture distributions. Two component mixture distributions were evaluated for fit using a chi-squared test.

Branch azimuth has been found to be uniformly distributed in whorled species (Trincado and Burkhart 2009) and other species. I tested the assumption of uniformity for internodes less than 5 years of age in the calibration data using both the Kuiper and Rao spacing tests. I performed both tests to branches on each sample internode independently. Tests were completed using the R package *circular* (Agostinelli and Lund 2017).

Model selection was conducted by evaluating the root mean squared error between modeling approaches. Additional consideration was given to the ability to link predictive models to TASS and the ability to interpret and program models using relatively simple code with minimal use of external packages following the development philosophy of TASS. In short, models were selected that produced the lowest root mean squared error, the lowest Akaike Information Criterion (AIC; Akaike 1974), and maintained mathematical simplicity. Once a modeling approach was selected, final variable selection was conducted by evaluating likelihood ratio tests between nested models as well as evaluating AIC and RMSE. All analysis was completed in the R statistical language (R Core Team 2013).

#### **Table 2.2 Candidate predictors**

#### Description

#### **Branch level**

Relative position of branch in the internode Distance of branch from the apex of the tree Relative position of branch in the crown

#### Internode level

Internode age Number of branches in an internode Internode length

#### **Tree level**

Tree height DBH Crown ratio Height to DBH ratio

#### 2.2.4 Model validation

Candidate models were validated in two ways 1) Individual components were validated against the SMC data and 2) the modeling approach including all model components was validated

against the rectangularity data. Individual components were visually evaluated against data and the root mean squared error was evaluated for each component. The modeling approach as a whole was validated by simulating the rectangularity trials in TASS. This process required a TASS simulation that was as close as possible to the empirical plot measurements in the rectangularity trial. A TASS simulation was constructed using a plot-specific height-age curve, custom tree vigor coefficients derived from the height age curve and controlled mortality derived from plot measurements. One of the pitfalls of the rectangularity trial at MKRF is the lack of early plot measurement related to a change in administration of several espacement trials on the research forest starting in the early 1980's. Thus, repeated and reliable plot measurements do not begin until 1982 for this particular trial. Plot measurements beginning at age 17 were conducted in 1982, 1985, 1989, 1994, 1998, 2007, 2012 and 2017. To produce the plot specific height growth curve, I first compared the permanent plot data to Bruce (1981), the default site curve that drives height growth in TASS. Top height is defined as the largest k trees in a plot. I used Garcia and Batho's (2005) equation to estimate k. A custom height age curve was developed using a Chapman-Richards growth function (Pienaar and Turnbull 1973). Custom vigor coefficients calculated based on the height curve where:

#### **Equation 2.1**

$$vigor = \frac{2017 \ tree \ height}{2017 \ top \ height}$$

Mortality was estimated from plot measurements. Mortality pre-1982 was evenly distributed between 1967 and 1982. While evaluating appropriate TASS runs, I noticed that the base of the

live crown in each octant would decrease after many years of increasing or remaining stable. This issue was attributed to the sudden increase in available neighboring growing space from mortality of an adjacent tree. To correct for this, I built a function to ensure that the base of the live crown never decreased. This correction was applied after TASS runs were completed. Simulated and empirical distributions of branch diameters were compared after calibration was completed.

#### 2.3 Results

#### 2.3.1 Number of branches in the internode

I evaluated several shoot and tree level candidate variables to predict the number of branches in an internode (Table 2.2). In addition to various exploratory nonlinear equation forms, several existing nonlinear equations were available to predict the number of branches in an internode (Maguire et al. 1994; Weiskittel et al. 2007; Nemec et al. 2012).

I observed that most branches occurred near the top of the internode throughout all internode ages with a second peak near the center in younger internodes (Figure 2.3). These results are similar to Maguire et al. (1994). In some cases, the relative position of a branch within the internode exceeded 1.0 (100%). I attributed this to error in measurement of the location of branches near the top of the internode. In Douglas-fir, younger internodes are easily defined by bud-scale scars from the terminal bud; however, older internodes must be defined by larger nodal branches. This effect is evident in Figure 2.3, where older branches (> 15 years) are primarily located above the internode.



Figure 2.3 Distribution of branches along internodes by internode age class for calibration data.

Neither crown ratio nor height to diameter ratio were important predictors of the number of branches. The final equation form was modified from Maguire et al. (1994):

Equation 2.2

$$NBR = b_0 \cdot SHLEN^{b_1} \cdot \exp(b_2 \cdot BRAGE)$$

where *SHLEN* is the length of the internode, *BRAGE* is the age of the internode and b0 - b2 are model coefficients (Table 2.3). The root mean squared error (*RMSE*) for this equation was 4.385. However, the RMSE increased to 11.877 when compared to the SMC dataset (Figure 2.4).).


Figure 2.4 Observed vs predicted number of branches in an internode. Observed data are from the SMC

dataset.

Parameter	Estimate	SE	<i>t</i> -Value	p > t
$b_0$	27.296127	0.579524	47.10	< 0.0001
$b_1$	1.047147	0.074250	14.10	< 0.0001
$b_2$	- 0.055183	0.004071	- 13.55	< 0.0001

Table 2.3 Parameter estimates for number of branches in an internode.

#### **2.3.2** Vertical distribution of branches within an internode

A two-component Weibull finite mixture distribution was selected to estimate the vertical distribution of branches within an internode ( $\chi^2(19) = 392.12, p \le 0.001$ ). The vertical distribution was approximated by the relative position of a branch within an internode, where 0.0 represents the base of the internode and 1.0 represents the top of the internode. The probability distributions were left untruncated to allow for branches that originate in the internode were measured above bud scale scars. The first component estimates the distribution of intermodal (non-whorl) branches. The second component estimates the distribution of nodal (whorl-like) branches near the top of the internode (Figure 2.5; Table 2.4).



Relative positioin in the internode

Figure 2.5 Two component finite-mixture distribution to estimate the vertical distribution of branches within an internode. 0 represents the bottom of the internode and 1 represents the top of the internode. Histograms represent the empirical data, dashed lines represent individual Weibull distributions, and solid lines represent the sum of the two distributions. Arrows estimate the mean of each distribution.

Component	Weight	Shape	Scale	Mean	SD	$\chi^2$ test p
1	0.8226	1.865016	0.4904635	0.4355	0.24245	< 0.0001
2	0.1774	29.11747	0.9506705	0.9329	0.04012	

Visual comparison against the SMC data suggested that the two-component Weibull approach generally approximated the vertical distribution of branches (Figure 2.6). However, the associated chi-squared test highlights the differences between the two distributions  $(\chi^2(82994000) = 82997000, p = 0.3831;$  Figure 2.6).



Figure 2.6 Empirical and predicted distributions of the relative position of branches within an internode. 0 represents the bottom of the internode and 1 represents the top of the internode.

### 2.3.3 Branch azimuth

Branch azimuth was uniformly distributed around the internode in the calibration data. To ensure a uniform distribution of branch azimuth amongst (or within) octants, I developed an algorithm to distribute branches uniformly between octants. Octants are numbered 1 through 8, beginning at 0 degrees and proceeding clockwise. The algorithm first generates a random location bounded within the location of the four odd numbered octants, followed by random locations within the even numbered octants. Location assignment begins at the topmost branch (relative position  $\geq 1.0$ ) and proceeds down the internode to the lowest branch in an internode.

# 2.3.4 Diameter of branches

Tree-level, shoot-level and branch-level predictors were evaluated for branch diameter. I evaluated multiple non-linear branch diameter equations as well as generalized additive models and random forest approaches. The final equation form was similar to Nemec et al. (2012):

#### **Equation 2.3**

$$brD = \exp(\beta_0 + \beta_1 \log(dfa) + \beta_2(relDIC) + \beta_3 \log(relDIST) + \beta_4 \log(brage))$$

where *brD* is branch diameter, *dfa* is the distance from the branch to the tree apex, *relDIC* is the relative position in the crown, *relDIST* is the relative position within the internode and *brage* is the age of the branch. Model parameters can be seen in Table 2.5. The RMSE for this equation is 0.62 cm.

Parameter	Estimate	SE	<i>t</i> -Value	p > t
$b_0$	-0.76636	0.03240	-23.65	< 0.0001
$b_1$	0.49368	0.02562	19.27	< 0.0001
$b_2$	0.77451	0.02933	26.41	< 0.0001
$b_3$	1.11106	0.02034	54.62	< 0.0001
$b_4$	0.23972	0.01748	13.71	< 0.05

Table 2.5 Parameter estimates for the diameter of branches in an internode.

Validation against the SMC data increased the RMSE slightly to 0.665 cm (Figure 2.7). I evaluated the relationship between maximum branch diameter in an internode and relative branch diameter between the predicted and SMC data. I used a bootstrapped Kolmogrov-Smirnov test with 100,000 permutations from the R package *Matching* (Sekhon 2011) to adjust for asymmetry in the relative diameter distribution. Visual comparison and a chi-squared test  $(\chi^2(11125000) = 11575000, p \le 0.001)$  suggested that the distributions were similar. The Kolmogrov-Smirnov test, however, indicated that the cumulative frequencies were different  $(D(0.16046), p \le 0.001;$  Figure 2.8).



Figure 2.7 Empirical and predicted branch diameter by the relative position of branches within an internode. 0 represents the bottom of the internode and 1 represents the top of the internode.



Figure 2.8 Distributions of diameter relative to the largest diameter in an internode for the SMC validation data and predicted data. See section 2.2.2 for description of SMC data.

# 2.3.5 Length of branches

I chose to predict branch length from branch diameter to maintain allometric relationships between the two variables. Tree-level, shoot-level and branch-level predictors were evaluated for branch diameter. Along with other equation forms, I evaluated a nonlinear equation developed to predict branch diameter as a function of branch length and other predictors. The equation was then solved for branch length and fit accordingly. The final equation form is:

#### **Equation 2.4**

$$brL = \beta_0 * (dfa^{\beta_1}) * brD^{\beta_4} * relDIST^{-\beta_3}$$

where *brL* is branch length, *df a* is the distance from the branch to the tree apex, *brD* is branch diameter, *relDIST* is the relative position within the internode and  $\beta_1 - \beta_4$  are model coefficients (Table 2.6; Figure 2.9). The RMSE for this equation is 0.26 m.

Table 2.6 Parameter estimates for the length of branches in an internode.

Parameter	Estimate	SE	<i>t</i> -Value	p > t
$b_0$	0.7585	0.006452	117.6	< 0.0001
$b_1$	0.4202	0.01071	39.24	< 0.0001
$b_2$	-0.1292	0.01486	-8.696	< 0.0001
$b_3$	0.6552	0.005794	113.1	< 0.0001

Visual comparison with the SMC data suggested that the model adequately predicted length (Figure 2.9). The RMSE for against the validation data was 0.861 m.



Figure 2.9 Branch length by branch diameter for predicted and empirical (SMC validation data). See manuscript for description of SMC data.

# 2.3.6 Branch Mortality

I do not directly predict branch mortality in this model. Instead, I chose to predict the number of living branches and interpret a reduction in the number of branches in an internode as branch

mortality. To determine which branches died, branches are killed beginning at the bottom of the internode and moving upwards. Additional mortality occurs when the base of the live crown in TASS rises. Because TASS can provide crown metrics in 8 different crown octants, mortality will follow crown asymmetry. When a branch is killed, the branch no longer grows in diameter or length, and a record of the branch is kept and is later passed to the sawmill simulator.

# 2.3.7 Overall approach

The overall approach predicted a similar number of live branches for the rectangularity data, except for Tree 111. Both branch diameter and branch length were larger in the predicted data compared to the empirical data (Table 2.7). The Kuiper and Rao spacing tests of the rectangularity data suggested that the number of branches were not uniformly distributed in Tree 106 ( $p \le 0.01$ ). Only the Kuiper test suggested asymmetry of branches in tree 111 ( $p \le 0.05$ ). I compared the asymmetry of the rectangularity data using an estimate of the R<sup>2</sup> value between the linear circular relationship of the 95<sup>th</sup> quantile branch diameters and azimuth (Pewsey et al. 2013). Tree 106 was the only tree that showed a significant asymmetric relationship ( $R^2 =$ 0.33,  $p \le 0.01$ ; Figure 2.10). Comparison of empirical and predicted data indicated agreement between predicted and empirical data. Most notable is the larger asymmetry in predicted branch diameters compared to empirical data (Figure 2.10).

	Number of	Mean branch	Median branch	Mean branch
	branches	diameter (cm)	diameter (cm)	length (m)
Tree 90				
Empirical	233	1.85 (0.09)	1.38 (0.09)	1.91 (10.99)
Simulated	199	2.09 (0.08)	2.18 (0.08)	2.03 (0.080)
<b>Tree 106</b>				
Empirical	269	1.11 (0.07)	0.64 (0.07)	1.06 (7.58)
Simulated	102	1.24 (0.06)	1.11 (0.06)	1.2 (0.060)
Tree 111				
Empirical	421	1.22 (0.06)	0.54 (0.06)	1.05 (6.10)
Simulated	129	1.41 (0.07)	1.28 (0.07)	1.37 (0.06)
Tree 117				
Empirical	273	2.70 (0.12)	2.17 (0.12)	2.35 (14.60)
Simulated	181	1.82 (0.07)	1.70 (0.070)	1.77 (0.07)

Table 2.7 Summary statistics (mean and standard error) of predicted vs empirical branch characteristics.



Figure 2.10 Predicted and empirical branch azimuth (degrees) and diameter (cm) for four trees sampled from a rectangular espacement trial. See section 2.2.2 for data description. Red dots represent empirical data and blue dots represent simulated data.

Bootstrapped Kolmogrov-Smirnov tests with 100000 permutations suggested that the distribution of branch diameters in an internode were of different distributions (D(0.240 - 0.545),  $p \le 0.001$ ). Agreement between distributions appeared to be related to the consistency of the empirical vs predicted height to base of live crown vs age curve (Figure 2.11).



Figure 2.11 Simulated and empirical height vs age (left), simulated height to live crown vs age (center) and distribution of branch diameters (right) for four trees from a rectangular espacemet trial. Red dots represent empirical data and blue dots represent simulated data.

Trees with asymmetric crowns had smaller branches in the higher side of live crown compared to trees with a symmetric crown (Figure 2.12). The relative pattern of branch diameter in crown asymmetry is apparent, despite predictive errors for the height and the base of the live crown.



Figure 2.12 Empirical and simulated branch diameter and vertical distribution for a Douglas-fir sampled from a rectangularity trial. Red dots represent octants in 0 - 180 degrees of the crown. Blue dots represent octants in 180 - 360 degrees of the crown.

### 2.4 Discussion

Crown ratio or slenderness ratio were not important predictors for the number of branches in an internode, which was surprising. Maguire et al. (1994) included the diameter at breast height (DBH) relative to the largest DBH in the plot and Weiskittel et al. (2007b) used crown ratio to estimate the canopy position of a tree. Maguire et al. (1994) hypothesized that trees with a more dominant canopy position contained a larger number of branches per unit of internode because of increased light due to a favorable canopy position. The calibration data included trees across all canopy positions. Maguire et al. (1994) used data from younger, even-aged stands, making the slenderness ratio more representative of social position compared to a dataset that included trees of varying stand conditions and social positions, similar to the calibration data. The variable internode length may adequately describe social position in the model as height increment varies with social position.

The relationship between the number of branches in an internode and social position have been described using Milton's law of resource availability and allocation (Sprugel 2002). Milton's law can be summarized by the generalization that trees of a lower canopy position (and thus less resources) will retain branches longer than trees of a more dominant canopy position. The concept reversed Sprugel's earlier work which stated that branches were largely autonomous (Sprugel et al. 1991). Duchateau et al. (2015) provided further support for this hypothesis for black spruce (*Picea mariana* (Mill.) B.S.P.), where increased height to diameter ratio was associated with smaller knots of longer duration. Duchateau et al. (2015) further hypothesized that the relationship between dominant canopy position and increased number of branches

resulted from the focus on pseudo-whorled branches. Despite collecting a census of branches within a sampled internode, I did not find a relationship between canopy position and the number of branches.

The relationship between shoot length and number of branches is well established in models of Douglas-fir branches (Maguire et al. 1994; Weiskittel et al. 2007; Hein et al. 2008b) including the one presented in this chapter. Shoot length is representative of the height increment of a given year. Height increment between individual trees prior to crown closure should be relatively consistent or at least less variable compared to after crown closure, which is largely a result of differentiation. Differentiation in an even-age, single species stand is a result of genetic variation, differences in the microsite, variation in age of establishment (if naturally regenerated) and the physical position of the tree relative to neighboring trees. Following crown closure, height increment may be reduced in trees experiencing heavy competition. Maguire et al. (1994) used young Douglas-fir that had not yet reached crown closure and Hein et al. (2008b) used 20-30 year old, widely spaced Douglas-fir. Both of these stands likely had reduced competition and thus, less variation in height increment compared to a stand with a large amount of differentiation. Using the height increment relative to the top height increment may be useful in further examining the relationship between the number of branches, height increment and canopy position. Although the calibration data included samples of trees of lower canopy position, more effort in sampling a diversity of canopy positions may be needed to elucidate this relationship. In addition, Duchateau et al. (2015) collected knot information using X-ray computed tomography

(CT scanning) imaging which likely has a lower measurement error compared to the field methods used to collect the calibration data.

The finite mixture distribution approach provides a simple model compared to the empirical distributions (Maguire et al. 1994) or unsuccessful attempts (Trincado and Burkhart 2009) in previous models and other species. Nemec et al. (2012) used a nonhomogenous poisson process (NHPP) to estimate the location of branch clusters (branches located on the same 1cm position in an internode) for the same calibration dataset. Leemis (1991) provides a nonparametric method of generating an empirical cumulative distribution function (ECDF) for a NHPP, however, I was unable to simulate a vertical distribution that matched the ECDF shown in Nemec et al. (2012). This may be a result of a cluster being defined as branches that occupy the same 1 cm increment along an internode. This may have resulted in an equal probability of branches being distributed across the internode and the apparent lack of a function for  $\lambda$ , which estimates the number of branches in a cluster at any given cluster location.

One of the limitations of the finite-mixture distribution approach is the inability to account for internode age. During simulation, it is equally probable for younger internodes to contain branches that have a relative position greater than 1.0 compared to older internodes (Figure 2.3). The SMC dataset contains a larger proportion of younger trees compared to the calibration data, which may explain the differences between calibration and validation data. Despite these limitations, the success in prediction of branch diameter suggests that this method is generally appropriate, as branch diameter is largely associated with the relative position within the internode.

I found that branch location was uniformly distributed within an internode in the first 5 years of growth, which has been found in internodes of all ages in loblolly pine (Doruska and Burkhart 1994) and sitka spruce (Cochrane and Ford 1978). Weiskittel et al. (2007b) found that the density of branches per unit length was lower on north aspects and hypothesized that this was due to reduced light availability on northern aspects. Briggs et al. (2007) found a greater number of branches in rectangular spacing compared to square spacing. This was also thought to be a function of increased light which caused more branches to be included in their samples because of a minimum branch diameter cutoff. I also found minimal asymmetry in branch diameter or branch number in our rectangularity trials, which was surprising. The only tree that was significantly asymmetric was tree 106. This tree had the most surrounding competition relative to the other trees sampled. Douglas-fir will produce epicormic branches in response to gap openings (Punches and Puettmann 2018) which was observed on some of the sampled trees and may explain additional uniformity in our sampled trees.

My model provided a relatively accurate prediction of branch diameter but underpredicted in some cases. Branch diameter in Douglas-fir is commonly predicted using tree level variables, primarily the position in the crown and stem size (Maguire et al. 1994, 1999; Weiskittel et al. 2007). These tree metrics are thought to reflect stand conditions, particularly stand density. The branch diameter equation presented above uses similar predictors, where branch diameter is a function of the position within the internode, the position within the crown and the age of the branch. Branch diameter growth is generally shaped as a negative exponential function that begins rapidly at early ages and then tapers off as branches grow older and are subjected to

increased shade (Garber and Maguire 2005). Though my equation above does not estimate branch growth, static estimates of branch diameter show an increasing trend with branch age. Other authors (Maguire et al. 1994; Weiskittel et al. 2007b; Hein et al. 2008b as examples) have predicted maximum branch diameter in an internode followed by the distribution of relative diameter to maximum branch diameter. Although distributions of predicted and empirical relative diameter were statistically different, the primary difference appears to be related to smaller branches at the base of the internode.

Surprisingly, stem diameter was a significant predictor but had little effect on branch diameter. Branch diameter is thought to be a function of age, available light and leaf area. Both thinning and fertilization can increase branch diameter, though the mechanisms are different. Thinning increases available light and belowground resources resulting in a stagnation of lifting crowns and increased branch diameter (Weiskittel et al. 2007; Lowell et al. 2014b). The effect of thinning on branch diameter can be thought of as similar to the effect of stand density, where branch diameters are smaller in denser stands and subsequent reduction of stand density can increase branch diameter (Lowell et al. 2014b; Ashton and Kelty 2018). Fertilization generally increases foliar efficiency through increased needle mass and water use efficiency (Brix 1981; Brix and Mitchell 1986). The results of fertilization suggest that sites of higher quality would likely produce changes in branch architecture. Other models of branch diameter have included tree diameter to account for changes in site quality (Maguire et al. 1994; Weiskittel et al. 2007). The limited importance of tree diameter in the calibration dataset may highlight the limited variation in site quality within the dataset. Branch length was found to be a function of branch diameter, the distance from the top of the tree and the relative position in the internode. Young Douglas-fir has been shown to increase lateral branch growth over terminal leader growth when grown in low light understory conditions (Williams et al. 1999). Many studies that investigate the effect of silviculture and physiology of branches investigate branch length as a metric of response to stand and environmental conditions (Brix 1981; Chen and Sumida 2018 as examples).

The distribution of predicted and empirical branch diameter appeared to be related, despite the lack of statistical significance by means of a Kolmogrov-Smirnov test. The lack of statistical significance was likely a result of the empirical distribution containing more smaller branches compared to those of the predicted trees. In TASS, a tree's foliage cannot live underneath the foliage of another neighboring tree (Mitchell 1975a). Thus, one of the major limitations in simulating the rectangularity study is the lack of plot measurements prior to 1982. Asymmetry may be exaggerated because of my decisions in surrounding tree mortality. Larger branch diameters in the predicted distribution may be a result of greater asymmetry due to incorrect estimates of neighboring tree mortality. In addition, the lack of an empirical stem map limited the ability to compare the direction of crown asymmetry due to the reconstructed nature of the implied stem map.

The likelihood of a branch surviving in an asymmetric crown is dependent on the initial octant at which it is assigned in year 1 of the simulation. The similarity in branch number at the end of the simulation suggests that the assumption of a uniform distribution in branch location is appropriate. I chose not to include branch shedding in the overall model, as Douglas-fir can

maintain branches for periods upwards of 80 years, longer than a typical rotation of second growth Douglas-fir (Fahey et al. 1991). Despite the lack of a mortality function, static estimates of the number of branches in an internode as well as crown lift in TASS appear to sufficiently capture branch mortality.

# 2.4.1 Conclusions

Crown structure and subsequent branch architecture is influenced by the availability of light (Williams et al. 1999), genetic variation (St. Clair 1994) and stand conditions through time (Mitchell 1975a; Weiskittel et al. 2007). The primary purpose of many models of branch geometry is to supplement a forest growth and yield model. This model is no exception. Several authors state that model outputs will inform associated models about changes in crown morphology (Weiskittel et al. 2007; Hein et al. 2008b). The model presented above is unique, in that branches are post-processed using data that is generated from a model that is driven, in-part, by the dynamics of crown interaction. This approach provides estimates of branch geometry, vertical distribution and orientation along the stem in asymmetric crowns. This approach, along with TASS, can be used to examine branch response to complex forest structures. Future versions of this model might explore the relationship between the TASS foliage shell, foliar volume and vigor coefficients. Exploration into these variables will be limited by the availability of TASS-centric metrics across a diversity of sites and canopy positions. A pruning module could also be added but would necessitate the prediction of branch occlusion following pruning.

Chapter 3: An analysis of simulated product recovery in variable retention systems.

#### 3.1 Introduction

Retention systems are the most common alternative to clearcutting in the Pacific Northwest. The primary goal of retention systems is to retain components of stand structure to maintain forest functions post-harvest (Franklin et al. 1997; Lindenmayer et al. 2012). These structures include live and dead trees, coarse woody debris, and multi-layered stand structure, typical in old forests. The focus on retention of structural attributes makes retention systems well suited to many forests around the world (Gustafsson et al. 2012; Lindenmayer et al. 2012). The structure and age distribution of retention systems depends on the amount of aggregation and spatial distribution of retention.

Structural heterogeneity is often driven by disturbance in unmanaged forests (Oliver and Larson 1996). Disturbances often vary in intensity, severity and frequency, resulting in a mosaic of biological legacies at the levels of the stand and the landscape. Retention systems strive to recreate horizontal and vertical structure found in unmanaged forests. The effects of stand structure can be subdivided into horizontal and vertical components (Maguire et al. 2007). Much of the retention system literature focuses on horizontal distribution of retention, where both the amount and distribution of retention can be important (Aubry et al. 2009). The residual structure of retention systems incorporates a wide range of gaps and edges across a spectrum of residual tree densities (horizontal stand structure). In dispersed retention, the density and spatial pattern

of residual trees can be limited to only several trees per hectare at the low end or may be similar to a heavy thinning or single tree selection. The same is true for aggregate retention, where the same residual density can be distributed into many aggregate groups or aggregated into one single group. Vertical structure is created in natural stands from repeated disturbances of varying severity through time, through extended periods of competition related mortality or through distinct layers of species and age-classes. Regeneration methods such as single-tree and groupselection can create vertical heterogeneity. In practice, less attention is paid to vertical stand structure in retention systems.

The new paradigm of retention systems in the Pacific Northwest has resulted in a large body of literature regarding the effect of forest management on biodiversity (Aubry et al. 2009; Baker et al. 2015) and visual quality (Sheppard et al. 2004; Aubry et al. 2009). A disproportionate number of studies investigated the financial implications of retention systems in terms of volume (Hansen et al. 1995; Nyvold et al. 2005; Pastur et al. 2009). A central component to retention systems is lifeboating, where retained structure provides habitat, energy and a climate favorable to forest organisms (Franklin et al. 1997). Species diversity is often positively correlated with complex and variable forest structures (Brokaw and Lent 1999; Tews et al. 2004).Retention of aggregate groups has been shown to generally support forest associated plants, beetles and spiders compared to adjacent harvests in coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco; Baker et al. 2015). However, the influence of retention is largely dependent on taxa and many organisms are susceptible to edge effects in aggregate refugia (Aubry et al. 2009; Baker et al. 2015).

Trees of the Pacific Northwest forests were historically known for tight rings and knot free wood, characteristics that take hundreds of years to develop (Barbour et al. 2003). Concerns of wood quality grew in the 1970's as second growth forests began to replace the high quality old growth forests (Barbour et al. 2003). Since this time, there have been hundreds of lumber recovery studies in the Pacific Northwest (e.g. Kellog 1989; Fahey et al. 1991; Stevens and Barbour 2000). The conclusions of Kellog (1989) and Fahey et al. (1991) indicated that rapid initial growth of intensively managed second-growth Douglas-fir would result in a larger proportion of juvenile wood and a subsequent decrease in wood quality and value. Juvenile wood is defined by a period of rapid initial growth that coincides with low wood density (Shmulsky and Jones 2011). Branch size is also an important predictor of lumber value (Aubry et al. 1998).

Empirical wood quality data in retention systems are limited, but much can be inferred from traditional lumber recovery studies (sensu Maguire and Halpern 2006). Several studies have investigated economic returns of retention systems in terms of volume. Hansen et al. (1995) found that an increase in retention level and rotation age reduced economic return. Pastur et al. (2009) found that losses in volume from retention were economically similar to shelterwood systems in southern Patagonia. In Tasmania, clearcut systems economically outperformed selection and retention systems in eucalyptus forests (Nyvold et al. 2005).

Several studies investigated the role of knots in sawmill simulations. Belley (2014) found an increase in value between 9.5% and 15.1% and 15.2% and 23.0% for white spruce (*Picea glauca* (Moench)) and jack pine (*Pinus banksiana* Lamb.) respectively. Todoroki et al. (2005) found that internal knot characteristics, such as knot location, were important predictors of

lumber recovery using real and simulated data using AUTOSAW (Todoroki 1990). Inline computer tomography (CT) scanners may be a solution for improving product recovery by measuring and optimizing cutting patterns based on knots and other internal defects. Inline CT scanners are not widely adopted in sawmills (Schajer 2016), however, several prototypes are available (e.g. Giudiceandrea et al. 2011; An and Schajer 2014). As these new technologies become available, inline computational techniques must be developed to optimize processing time (Fredrikssona et al. 2014) and understand the potentials and limitations of this new sawing technology.

Optitek is a three-dimensional sawmill simulator that optimizes lumber recovery based on lumber grades and prices (Goulet 2006). Mill configurations can be specified for most Canadian mills. Optitek was originally designed for use with laser scanned logs. Virtual logs can also be simulated and passed through the Optitek system (Belley 2014). Optitek uses brute force optimization to optimize cutting pattern based on user specified products, grades and prices. There are a number of studies that use Optitek to simulate lumber recovery in native species of New Brunswick and Quebec (e.g. Duchesne et al. 2013; Pitt et al. 2013; Auty and Achim 2014) but no studies that use Optitek for West Coast species.

TASS (Tree And Stand Simulator) is an individual-tree, distance-dependent, growth and yield model originally developed for Douglas-fir (Mitchell 1975a, 1975b). TASS is driven by height growth and crown expansion, making it well suited to examine silvicultural questions that involve complex forest structure. Height growth in TASS is dependent on a predefined site-index curve where each tree's height growth is scaled based on a normally distributed vigor coefficient and the ratio of foliar volume and maximum foliar volume. Maximum foliar volume is a speciesspecific coefficient representing the maximum volume of foliage on an open grown tree on any given site. TASS has been developed with several stochastic elements. The abovementioned vigor coefficients, mortality as well as variation in planting arrangement among other variables contain levels of variability driven by pseudo-random number generators which can be seeded to produce a fully deterministic model. In a TASS simulation, the crown profile is monitored in three dimensions and no part of the live crown can live underneath another live crown in TASS II. Crowns compete in two dimensions (from overhead) and the rate of crown rise is governed by an equation that approximates a crown interaction zone. This interaction zone is a zone where crowns overlap and is generally a function of crown abrasion and foliar retention. In Mitchell (1975a), the interaction zone was defined as 5 years of foliage shell (approximately the time of foliage retention in Douglas-fir). In each year of TASS simulation, height growth is initiated followed by predicted crown expansion and diameter increment. Diameter increment in TASS is based on Pressler's hypothesis, where diameter increment is proportionate to the area of foliage directly above. Each year, diameter increment is increased in a tapered manner, allowing for stem taper without using a true taper function. The result is that stem diameter can be calculated at any point along the stem, making TASS trees easy to convert into three dimensions.

Managers in the Pacific Northwest must constantly balance social, ecological and economic management objectives. As management paradigms, goals and objectives change through time, it is important to understand the economic implications of these management decisions. Lumber recovery studies are inherently expensive and time consuming. Despite this, managing for wood

quality may be a solution to balance economic objectives with other conflicting objectives (Briggs 2010). To understand the effect of retention systems on the growth and lumber recovery of a regenerated stand, this chapter will use TASS and Optitek to investigate balancing economic, social and ecological management objectives. Specifically, the objectives are to: 1) Examine the effect of retention on tree volume, 2) Quantify the lumber recovery from retention systems and 3) Estimate the price structure necessary for retention systems to outperform a clearcut.

### 3.2 Methods

# 3.2.1 TASS simulations

To understand the effect of retention on wood production and quality, TASS simulations were created to simulate a wide range of retention densities and spatial arrangements. Simulations were conducted on a 1-hectare simulation space. An initial cohort of 1000 stems ha<sup>-1</sup> coastal Douglas-fir were established at regular spacing to represent the retention cohort. Trees were grown to 55 years when the first harvest was implemented. A second cohort of 1000 stems per hectare coastal Douglas-fir was established at year 56 and grown for 60 years for a total of 116 years of simulation. (I.e. at the end of the simulation the retention trees were 116 years old and the "regeneration" cohort was 60 years old). To represent a base case scenario (no overstory competition), three clearcut simulations were conducted. Clearcut simulations included 1000 stems per hectare of coastal Douglas-fir at regular spacing grown for 60 years.

Simulations consisted of a range of 10% – 50% retention densities in steps of 10% (Figure 3.1). Aggregate groups were assigned by area to accurately prescribe retention in TASS. For example, 10% aggregate retention involved retaining trees on 10% of the simulation area. Different spatial arrangements of aggregate retention were configured by dividing the total area to be retained into either one, four or sixteen groups of squares uniformly distributed within the simulation space (Figures 3.1 & 3.2). Different levels of dispersed retention were achieved by the thinning to the specified density in TASS. Codominant and dominant trees were selected as retention trees to emulate a silvicultural prescription that maximizes the wind-firmness of residual trees. Leaving codominant and dominant trees using the thinning subroutine in TASS results in a uniform distribution of trees that will have maximum effect on regeneration (Figure 3.2). Three replicates of each simulation were created by changing the seeds that initialize the streams of pseudo-random deviates that are used in the subroutines that influence mortality, variability in planting spacing and assignment of vigor coefficients.



Figure 3.1 10% retention in three aggregate grouping patterns: One, four and sixteen groups.



Figure 3.2 TASS visualizations of retention simulations.

Following TASS simulation, branches and knots were assigned to tree stems as post processing in the R statistical computing environment (R Core Team 2013). Inputs to the branch routine described in Chapter 2 included the height, age and octant-level crown information. The second cohort of TASS-grown trees were harvested and then sent to Optitek. Only trees in the "regeneration" cohort were run through Optitek and considered in the volume and value calculations with the assumption that the "retention" cohort would continue to be maintained for forest structure.

# 3.2.2 Optitek simulations

Trees simulated in TASS were converted to Optitek logs using software developed in conjunction with FPInnovations. TASS trees were converted to a three-dimensional log assuming that the stem is circular using TASS-derived annual height, diameter, knot size, and knot location as inputs. The end result is a three-dimensional log that reflects the dimensions of the tree boles as simulated in TASS but does not include sweep, checks, cracks or other defects. Knots were assigned in three dimensional space using a knot model similar to that of Samson (1993).

I used a sawmill layout similar to that of a typical coastal British Columbia mill. The mill produces a variety of products that range from 2x4's to 3x10's. In addition to the original mill configuration, I added a slasher that optimized bucking to maximize value. Grades were assigned using the NLGA grade rules for Structural Joists and Planks and Structural Light Framing (NLGA 2014). Only wane and knot rules were considered during simulation (Table 3.1). Both live and dead knots were considered to be tight knots.

Table 3.1 NLGA grade rules for structural joists and planks and structural light framing (NLGA 2014).

Grade	Knot summary	Wane summary	
Select Structural	Sound, firm, encased and pith knots	<sup>1</sup> / <sub>4</sub> the thickness and <sup>1</sup> / <sub>4</sub> the width	
	should not exceed <sup>3</sup> / <sub>4</sub> " at edge wide	full length or equivalent on each	
	face and <sup>7</sup> / <sub>8</sub> " at the centerline wide	face so long as that wane does not	
	face. One unsound or equivalent	exceed $\frac{1}{2}$ the thickness or $\frac{1}{3}$ the	
	smaller knot of ¾" is allowed per 4	width for up to $\frac{1}{4}$ the length.	
	linear feet.		
NO. 1	Sound, firm, encased and pith knots	<sup>1</sup> / <sub>4</sub> the thickness and <sup>1</sup> / <sub>4</sub> the width	
	should not exceed 1" at edge wide	full length or equivalent on each	
	face and $1 \frac{1}{2}$ " at the centerline wide	face so long as that wane does not	
	face. One unsound or equivalent	exceed $\frac{1}{2}$ the thickness or $\frac{1}{3}$ the	
	smaller knot of 1" is allowed per 3	width for up to $\frac{1}{4}$ the length.	
	linear feet.		
NO. 2	Sound, firm, encased and pith knots	$\frac{1}{3}$ the thickness and $\frac{1}{3}$ the width	
	should not exceed 1 <sup>1</sup> / <sub>4</sub> " at edge	full length or equivalent on each	
	wide face and 2" at the centerline	face so long as that wane does not	
	wide face. One unsound or	exceed $\frac{2}{3}$ the thickness or $\frac{1}{2}$ the	
	equivalent smaller knot of 1 1/4" is	width for up to $\frac{1}{4}$ the length.	
	allowed per 2 linear feet.		
NO. 3	Sound, firm, encased and pith knots	$\frac{1}{2}$ the thickness and $\frac{1}{2}$ the width	
	should not exceed 1 <sup>3</sup> / <sub>4</sub> " at edge	full length or equivalent on each	
	wide face and 2 $\frac{1}{2}$ " at the centerline	face so long as that wane does not	
	wide face. One unsound or	exceed <sup>7</sup> / <sub>8</sub> the thickness or <sup>3</sup> / <sub>4</sub> the	
	equivalent smaller knot of 1 1/4" is	width for up to ¼ the length.	
	allowed per 1 linear feet.		

Prices for the different product were specified based on historic data. Select, NO. 1 and NO. 2 grades were the same price and NO. 3 grade was a mean of 37% lower than other grades (min 20%, max 42.9%).

#### 3.2.3 Statistical analysis

I summarized retention simulations using the relative density of retention (percent of trees per hectare), the relative basal (percent of basal area retained) and canopy cover (the proportion of crown-projection area). All analyses were completed in the R statistical computing environment, version 3.5.2 (R Core Team 2013). To compare the effects of the number of groups and retained basal area, linear mixed models were evaluated using the lme4 package (Bates et al. 2015).

The effect of retention on neighboring trees was evaluated by comparing a subset of trees that were affected by neighboring retention trees. First, a pairwise comparison of each retention tree and each tree in the simulation was conducted to find the trees closest to each retention tree. Second, I selected all trees that had crown interaction by manipulating equation 8 in Mitchell (1975) to find the maximum crown radius for each crown octant. Crown interaction was defined as a distance between two trees that is less than the average maximum crown radius of the two octants facing the neighboring trees. Following edge tree selection, I compared edge trees with non-edge trees planted in the same location. Mortality, tree vigor and planting variation in TASS are all controlled by initial seeds given to the CPU during random number generation. Thus, it is possible to compare the effect of edge without confounding variables.

Optitek's decision hierarchy will always choose the highest grade when prices per product are the same between grades. To find the price differential where increasing wood quality from edge tree competition would outperform a clearcut, I incrementally adjusted the price differential between structural select and NO. 1 grade by 1% until the gross income of a retention system was greater than that of a clearcut. If no solution was reached after 1000 iterations, the process was terminated. I compared the shift in lumber grade between retention densities and patterns using a ratio of the volume of pieces weighted by grade over the unweighted total volume of pieces (Todoroki et al. 2005). A weight of 4 was assigned to Structural Select, a weight of 3 was assigned to NO. 1, a weight of 2 was assigned to NO. 2 and a weight of 1 was assigned to NO. 3. This metric provides a relative number of grade, where a value of 4 would indicate 100% of all pieces were of select structural grade.

## 3.3 Results

# **3.3.1** Tree and stand-level response

Retained trees per hectare, basal area and canopy cover generally followed target densities of aggregate retention in all groups. Retained basal area and canopy cover were higher in dispersed retention compared to target densities due to the criteria to retain dominant or codominant trees (Table 3.2).
Table 3.2 Target and empirical retention densities (mean and standard error) for five levels of aggregate and

 dispersed retention. Aggregate retention is further divided in to 1, 4 and 16 separate groups.

Dotontion dongity	n	<b>Retained trees per</b>	Retained basal area	<b>Canopy cover</b>
Retention density	groups	hectare (%)	(%)	(%)
Aggregate retention				
(% retention by area)				
10	1	10.15 (0.15)	9.91 (0.21)	9.67 (0.33)
10	4	10.54 (0.31)	10.4 (0.25)	10.33 (0.33)
10	16	8.69 (0.11)	8.5 (0.17)	8.67 (0.33)
20	1	19.79 (0.17)	19.43 (0.12)	19.33 (0.33)
20	4	20.38 (0.4)	20.31 (0.17)	20.33 (0.33)
20	16	21.8 (0.3)	22.41 (0.59)	23 (1.15)
30	1	30.92 (0.75)	30.66 (0.35)	30.67 (0.33)
30	4	28.47 (0.44)	28.27 (0.07)	28.33 (0.33)
30	16	27.72 (0.7)	27.49 (0.89)	27.67 (1.2)
40	1	40.01 (0.45)	39.7 (0.07)	39.67 (0.33)
40	4	39.97 (0.12)	40.09 (0.48)	40 (0.58)
40	16	40.13 (0.41)	39.65 (0.11)	39 (0)
50	1	49.01 (0.24)	49.37 (0.31)	49.33 (0.67)
50	4	49.84 (0.49)	50.24 (0.22)	50.33 (0.33)
50	16	54.34 (0.23)	53.91 (0.38)	53 (0.58)

#### **Dispersed retention**

#### (% retention by tree density)

10	9.99 (0.03)	24.07 (0.1)	34.67 (0.33)
20	20.02 (0.01)	42.19 (0.36)	61.67 (0.33)
30	30.02 (0.02)	56.15 (0.3)	79.67 (0.33)
40	40.01 (0.02)	67.14 (0.24)	91.67 (0.33)
50	50.04 (0.02)	75.98 (0.14)	97.67 (0.33)

-

#### Clearcut

0

Mortality of the regenerated cohort ranged from 30.9% to 100.0% and increased with increasing density of retention (Figure 3.3). There was 100% mortality in the regenerated cohort in 50% dispersed retention. Mortality in dispersed and aggregate retention generally followed a similar trend through time (not shown).

-

-



Figure 3.3 Percent mortality by retained basal area for aggregate (left) and dispersed (right) retention.

Mean tree volume decreased through all levels of aggregate and dispersed retention (Figure 3.4). Mean height and diameter followed similar trends for both aggregate and dispersed retention (not shown).



Figure 3.4 Mean tree volume by level of retention in aggregate (a.) or dispersed (b.) spatial patterns.

Increasing the number of groups from 1 to 4 and from 4 to 16 resulted in a decreased mean tree volume for all treatments except for 10 % retention from 1 to 4 squares. Mean tree volume slightly increased between retention densities of 10 to 50 percent where the number of groups were equal to 1 (Figure 3.4).

Maximum branch diameter was similar between most levels of aggregate retention. Maximum branch diameter decreased as the level of retention increased for all levels of dispersed retention (Table 3.3).

 Table 3.3 Branch diameter summary for five levels of aggregate and dispersed retention. Aggregate retention

 is further divided in to 1, 4 and 16 separate groups.

Retention density	<i>n</i> groups	Branch diameter (cm)			
·		Mean	Minimum	Max	
Aggregate ret	ention				
(% retention l	by area)				
10	1	1.70 (0.00)	0.01 (0)	7.18 (0.02)	
10	16	1.67 (0.00)	0.01 (0)	7.00 (0.02)	
10	4	1.69 (0.00)	0.01 (0)	7.14 (0.02)	
20	1	1.70 (0.00)	0.01 (0)	7.16 (0.02)	
20	16	1.65 (0.00)	0.01 (0)	6.86 (0.02)	
20	4	1.68 (0.00)	0.01 (0)	7.03 (0.03)	
30	1	1.69 (0.00)	0.01 (0)	7.15 (0.01)	
30	16	1.63 (0.00)	0.01 (0)	6.79 (0.01)	
30	4	1.67 (0.01)	0.01 (0)	7.00 (0.03)	
40	1	1.68 (0.01)	0.01 (0)	7.07 (0.03)	
40	16	1.60 (0.00)	0.01 (0)	6.60 (0.04)	
40	4	1.66 (0.01)	0.01 (0)	6.94 (0.04)	
50	1	1.68 (0.01)	0.01 (0)	7.00 (0.03)	
50	16	1.53 (0.01)	0.01 (0)	6.08 (0.05)	
50	4	1.64 (0.01)	0.01 (0)	6.80 (0.05)	
Dispersed rete	ention				
(% retention l	by tree density)				
10		1.58 (0.00)	0.01 (0.00)	6.42 (0.02)	
20		1.39 (0.01)	0.02 (0.00)	5.40 (0.05)	
30		1.17 (0.01)	0.02 (0.00)	4.26 (0.09)	
40		0.94 (0.02)	0.02 (0.00)	3.14 (0.10)	
50		0.76 (0.04)	0.02 (0.00)	2.28 (0.17)	
Clearcut					
0		1.65 (0.00)	0.01 (0.00)	6.97 (0.02)	

Trees that grew closest to retention (edge trees) were 51.7% smaller in volume than the same trees that did not grow near retention trees (matrix trees; Figure 3.5a). Edge trees had lower maximum branch diameters compared to matrix trees (Figure 3.5b). Mean volume was similar when considering only trees that had crown contact with retention trees (Figure 3.6). In some cases, neighboring trees overtopped trees that experienced heavy competition from adjacent retention (Figure 3.6). The proximity to the retained cohort combined with mortality in the retention cohort also resulted in additional growing spaces and larger trees.



Figure 3.5 Tree volume (a.) and maximum branch diameter (b.) for edge trees vs matrix trees. Edge trees are trees that were nearest to retained cohorts. Matrix trees are trees of the same spatial location simulated without competition from retained cohorts.



Figure 3.6 Mean tree volume (m<sup>3</sup>ha<sup>-1</sup>) for edge trees vs matrix trees. Edge trees are trees that had crown contact with retention trees. Matrix trees are the same trees simulated without competition from retained cohorts and only competition from neighboring trees of the same age.

Total volume (m<sup>3</sup>ha<sup>-1</sup>) was greatest in clearcut simulations and decreased with increasing retention in both aggregate and dispersed retention. In aggregate retention the volume decreased

linearly; with increased retention and in dispersed retention it decreased exponentially (Figure 3.8).



Figure 3.7 Total volume (m<sup>3</sup>ha<sup>-1</sup>) by level of retention in aggregate (a.) or dispersed (b.) spatial patterns.

For aggregate retention, a linear mixed model of the percent retained basal area as a fixed effect and the number of aggregate groups as a random effect showed that a 1% increase in retained basal area decreased total volume by 1.4% (Table 3.4). A linear mixed effect model of the number of aggregate groups as a fixed effect and the percent retained basal area as a random effect showed that increasing the number of groups from 1 to 4 groups decreased total volume by 5.7% and 20.3% from 4 to 16 groups (Table 3.5).

#### Table 3.4 Linear mixed-effects model output

Fixed effects						
	Estimate	Std. Error	df	t	р	
Intercept	858.1386	36.3068	2.092	23.64	< 0.01	
Basal area	-14.1816	0.2642	41.0001	-53.68	< 0.001	
Random effects						

	Variance	Std. Dev
n groups	3846	62.02
Residual	309.5	17.59

#### Table 3.5 Linear mixed-effects model output

Fixed effects					
	Estimate	Std. Error	df	t	р
Intercept	621.412	69.978	4.056	8.88	< 0.001
4 groups	-35.393	10.073	38	-3.514	< 0.01
16 groups	-126.407	10.073	38	-12.549	< 0.001
Random effects					
	Variance	Std. Dev			
Target density	24231	155.66	-		
Residual	761	27.59			

# 3.3.2 Revenue analysis

Clearcuts revenue outperformed all levels of retention (Figure 3.8). Revenue was linearly related to merchantable volume (Figure 3.9). Increased retention from both aggregate and dispersed retention reduced the merchantable volume in the regenerated cohort. Recovery (\$/nominal mBF) increased in trees that grew adjacent to retention (Figure 3.10a.), however, the mean value per tree decreased by 47% (Figure 3.10b.).



Figure 3.8 Revenue for aggregate (a.) and dispersed (b.) retention.



Figure 3.9 Revenue by merchantable volume.



Figure 3.10 Dollars per nominal thousand board feet (\$/mBF; a.) and dollars per tree (b.) for edge and matrix trees. Edge trees are trees that were nearest to retained cohorts. Matrix trees are the same trees simulated without competition from retained cohorts.

There was no shift in the per hectare weighted grade average in both dispersed and aggregate retention (not shown). Edge trees showed less than 1% of a grade shift compared to matrix trees (Figure 3.11).



Figure 3.11 Grade-weighted average between edge and matrix trees. Edge trees are trees that were nearest to retained cohorts. Matrix trees are the same trees simulated without competition from retained cohorts. A weighted average of 4 is equal to 100% Select Structural grade and a weighted average of 1 is equal to 100% NO.4 grade. See text for NLGA grade rules.

The price differential between select and NO. 1 grades required for retention systems to financially outperform clearcuts was greater than 999.99% for all levels and spatial arrangements of retention. There was not enough grade shift in edge trees to offset the reduction in merchantable volume associated from retention.

## 3.4 Discussion

Retention systems are often used to meet social and ecological objectives but usually disregard economic objectives. Here, I quantitatively demonstrate that meeting ecological and social objectives occurs at a cost. There were small increases in wood quality (knot size and distribution) in neighboring trees but they were insufficient to financially offset the loss in tree volume from competition by neighboring retention trees and total volume by the area occupied by retained trees.

The reduction in tree and total volume by retained trees is a function of two mechanisms. The first is direct competition from neighboring retention trees. Trees growing adjacent to retention trees were smaller in volume compared to a tree with the same vigor and planting location that was not growing adjacent to a retention tree. As TASS is driven by height growth and crown expansion, the older and more dominant retention trees reduced the crown area of the regenerated cohort and subsequently reduced tree volume. The diameter increment model in TASS is based on Pressler's hypothesis that states that the area of increment is proportional to the amount of crown above (Larson 1963). In some cases, regenerated trees that were planted close to the retained trees died early, allowing more growing space for a neighboring tree than what otherwise would have been available. Variability in the retention group also increased available growing space to neighboring trees where small gaps from mortality increased the crown area of adjacent trees resulting in increased tree volume as well as increased knot size and frequency. The second mechanism of volume reduction occurs from the physical space, and

subsequent growing space, occupied by the retained cohort. In my simulations, retaining trees by density is also equivalent to retaining trees by area and volume. For example, 10% retention by tree density also represents 10% retention by volume. Even if we expect no reduction in volume from competition with retention trees, there will still be a volume reduction due to the lack of per hectare growing space. This effect is analogous to the effects of thinning on total stand yield. Thinning is an intermediate treatment that improves the growing conditions of residual trees by removing a proportion of the stand. If properly implemented, thinning can result in an increase in mean tree volume. However, increasing tree volume occurs at a tradeoff to total stand volume, which will always be lower when compared to an unthinned control (Assmann 1970; Ashton and Kelty 2018). In the retention simulations presented here, the number of trees per hectare is lower by at least the density of retained trees and total stand volume is reduced. Total stand volume is further reduced from competition with the newly established cohort and retention trees. These two mechanisms make retention systems financially uncompetitive compared to traditional clearcut systems.

Mean tree volume increased when aggregate retention was limited to one group, which was surprising. The range of retention simulations represent a gradient of edge. As retention density increases the linear length of edge also increases. Increasing the number of aggregate groups to the level of dispersed retention additionally increases the linear length of edge. Simulations of aggregate groups of 1 had the lowest length of linear edge in each of the simulations. As mentioned above, crown area in some trees increased when adjacent to the edge or adjacent to trees that experienced early mortality. This edge effect is apparent when the number of groups is

limited to 1 throughout all levels of aggregate retention and groups of 4 in 10% retention. After which, the amount of competition from edge increases to a threshold that pushes the mean tree volume further down and the rate of volume reduction increases beyond the average volume reduction occurring in the stand. This is evident when comparing dispersed and aggregate retention. Despite similar retention densities, basal area and canopy cover were more similar to 30% aggregate retention, due to the selection of dominant and codominant trees. The concept that edge increases by increasing the number of groups highlights the limitations of using the linear length of edge as a metric when designing retention systems, which is that edge is fractal. The length of edge in my simulations was defined by the dimensions of the squares that I used to identify the aggregations of trees to be retained. Defining "length of edge" in operational situations from tree locations at the edge of such aggregations is problematic because the edges involves fractal geometry, which means that the length of edge depends on the scale of measurement. Canopy cover (crown projection area) was useful in understanding gross income in simulations of aggregate retention, simply because of its relationship with retained basal area. In dispersed retention, canopy cover may be a better proxy for linear edge, as all of the surrounding crown area acts as an edge to the regenerated cohort. For aggregate retention, however, canopy cover is of less value in determining the effect of competition on the regenerating cohort.

Several studies have simulated or measured the effect of retention on volume that are similar to the results shown here (e.g. Zenner et al. 1998; Maguire and Halpern 2006; Lam and Maguire 2011). Acker et al. (1998) found a decrease in mean annual increment (MAI) of the younger

cohort with increasing retained basal area in a mixed-species, dispersed retention stand dominated by Douglas-fir and western hemlock (Tsuga heterophylla (Raf.) Sarg.). Acker et al. (1998) and Zenner et al. (1998) suggest that thinning a dense younger cohort may be a solution to mitigate losses in volume from competition from residual trees, however, my results suggest that dispersed retention has a larger impact compared to similar aggregate retention densities and thinning would likely not mitigate the edge effects of dispersed retention. In addition, Acker et al. (1998) measured a mixed-species stand that includes shade-tolerant species and reduction in MAI is likely less than in a single-species stand composed of shade-intolerant species. Acker et al. (1998) reported that their regression model predicted an increase in the MAI of the younger cohort at lower retention densities but did not speculate as to why this may be occurring. This is consistent with my results that show that at low amounts of edge, tree volumes can increase due to mortality of the new cohort and proximity to retained trees opening additional growing space. Birch and Johnson (1992) found a 4% to 16% reduction in volume in dispersed retention in a simulation study of Douglas-fir in using the ORGANON (Hann 2011) growth and yield model. Retention densities for dispersed retention ranged from 5.4 to 49.4 stems per hectare, half of the retention density investigated in my study. Volume reduction in aggregate retention was proportionate to the area of retention (Birch and Johnson 1992), similar to the results shown here.

Wood quality did not increase as much as expected. Merchantable volume was the primary driver of revenue and attempts to modify the price structure for wood quality to offset the volume lost from retention were unsuccessful. In today's lumber prices, 1000% price differential

would be \$3800 / Mbf for a No.1 2x4 and \$380 for a NO. 2 2x4. Previous simulation and empirical studies of lumber recovery show that increased retention generally results in lower return on investment. Birch and Johnson (1992) found that net present value of all regenerated stands was directly related to the density of retention. Hansen et al. (1995) found a reduction in volume and value in the younger cohort in simulations of Douglas-fir growing under 5 - 150retained trees per hectare. The value of retained trees offset the loss in value of younger trees in lower densities. While Hansen et al. (1995) incorporated planting costs to their economic model,

I did not consider costs associated with operations, planting and vegetative control when implementing retention systems. Relative to a clearcut, implementation of retention systems necessitates operating around residual trees which slows productivity and further increases the cost of implementation. The decrease in productivity associated with retention is thought to be greater in dispersed retention, where spatial heterogeneity is greatest. Thus, the increased operational costs would likely further bring down the net present value of the future cohort. Operational costs are often presented as per hectare estimates the addition of operational costs at the inter-hectare level would necessitate time in motion data relative to density and spatial pattern of retention. Data of this resolution were unavailable. Costs associated with vegetative control and planting likely have an inverse relationship to operational costs, where the plantable area and subsequent costs are reduced with increased retention.

The effect of retention and gross income is best understood at the individual-tree level. If we assume that one retained tree is equivalent to at least one new cohort tree at the end of the second rotation then an increase in wood quality equal to or greater in price to that of one tree is

necessary for wood quality to accommodate for the loss in volume associated with retention. Increases in wood quality by reducing maximum branch size were apparent but did not result in a shift in grade. More than an additional 50% reduction in maximum branch diameter would be necessary to force a mean edge tree to comply with a NO. 1 grade. The lack of grade shift is likely a result of the smaller volume in trees competing with overstory retained trees. In general, reducing knot size must come at a cost of reduced tree volume, which is apparent in my simulations. The grade-weighted average in trees that were closest to retention had wider variation compared to trees uninfluenced by the retention. This is likely a result of decreased branch size in trees that had a large amount of grade shift but smaller tree size may have adversely affected the wane rules as well as the maximum size product that can be sawn from any given tree. Strategic retention of extremely low densities (2 to 4 trees per hectare) may offset the reduction in volume. However, the magnitude of volume reduction and corresponding wood quality increase is dependent on the proximity of adjacent trees to the retention cohort and such low densities would be unlikely to meet visual or ecological objectives.

My simulations were planted at a relatively low density (1000 stems per hectare). Branch size, and subsequently knot size are reduced by increasing tree density (Lowell et al. 2014a). The maximum branch diameters throughout most of the retention simulations were larger than the criteria for Structural Select or NO. 1 grades. These knots likely occurred in the lowest log and are a result of the wide spacing. It is likely that an optimum planting density exists that would cause a greater shift between the select structural and NO. 1 grades, however, this was not explored in this chapter. Rais et al. (2014) noted that properties associated with strength

(knottiness, density, modulus of elasticity) were best at 4,000 stems ha<sup>-1</sup> (the highest density studied). Such high densities, however, would require thinning to improve and maintain volume increment to be comparable to lower densities.

In these simulations, I assumed that the Optitek simulated value (the combined value of all products produced from a tree) was the real value of any given tree. Optitek optimizes cutting pattern to maximize profit based on a set of prices, grades and products. To approach these prices in real life, an inline CT scanner would be necessary. Inline CT scanners can improve a sawmills rate of return Pernkopf et al. (2019) but have not been adopted widely, due to their high price of implementation. The simulation presented in this study assumes that trees are free of sweep, checks, cracks and forks which would further devalue the trees entering the mill. In a study of second-growth Douglas-fir, Kellog (1989) found that sweeps and forks or crooks were found in 14 and 8 percent of log sorts, respectively. Knots are generally classified as live or dead and have implications for strength and grade (Lowell et al. 2014a). Both the frequency and size of knots can affect the tensile strength of dimensional products in Douglas-fir (Johnson and Kunesh 1975) I considered all knots to be tight (live), which may have artificially increased the value of some trees. The revenues presented here represent a best-case scenario and are unlikely comparable to current sawmill capabilities and log sorts.

In addition to problems of evaluating optimization, several other issues exist in using a simulation to evaluate lumber recovery. As with all models, TASS uses a hierarchy of assumptions to approximate reality. The growing conditions in TASS do not directly consider aspect, slope and latitude. The integration of all variation in site is dictated in TASS by the

height growth curve that drives crown expansion. Maguire and Halpern (2006) suggest that aspect and species composition may be important in determining future growing conditions in retention systems. In TASS II, the version used in this study, there is no consideration of sun angle or aspect on tree growth. This may be of less consequence for shade-intolerant coastal Douglas-fir, but it is still worth examining. Models of sunlight have been developed (Brunner 1998) and implemented in TASS III, a version which is still under development. It is logical to assume that dispersed retention would have a larger effect on percent available canopy light (PACL) than aggregate retention, particularly in northern latitudes. Aggregate retention may reduce light nearest to the edge but will allow for direct sunlight given that the tree height surrounding the edge does not exceed the highest sun angle at any given latitude. Thus, the influence of dispersed retention on volume growth and value recovery may be larger than simulated in this study.

# 3.4.1 Conclusion

Managers must constantly balance multiple competing management objectives. This study demonstrates that increases in wood quality did not sufficiently offset the reduction in volume from competition by retained trees. The results presented here provide an accurate estimate of the loss in gross income associated with meeting social or ecological objectives. Although I quantified the changes in value of wood products in response to varying densities of retention, quantifying the additional value of social and ecological services may be a solution to balance economic objectives. For example, improving visual quality and scenic beauty through retention systems may increase tourism and recreation value to some areas. Incorporating carbon storage

or willingness to pay through certification may be the only solutions for incentivizing retention systems to meet sustainable forest management objectives (Diaz et al. 2018). Widespread adoption of retention systems may be necessary for managers to meet multiple objectives and to meet global targets of sustainable forest management (Lindenmayer et al. 2012). Aubry et al. (2009) recommends retaining at least 15% of stands to improve public perception, provide suitable microsites and improve habitat for plants and animals at risk. However, increasing social and ecological services ultimately comes at the cost of volume and revenue in the regenerated cohort, despite marginal increases in wood quality. Chapter 4: The influence of silviculture and the live crown on wood density in Douglas-fir: A synthesis.

#### 4.1 Introduction

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) is one of the most economically important species in the Pacific Northwest. Douglas-fir is known for its high wood density which results in higher strength (Lachenbruch et al. 2010) and pulp yields. Wood density is also an important functional trait that is important in the hydraulic function of the xylem (e.g. Dalla-Salda et al. 2011). Wood density is defined as the mass per unit volume of wood and is relative to moisture content. Specific gravity, the ratio of the density of wood to the density of water, and wood density are often used synonymously but have different definitions (Shmulsky and Jones 2011).

Patterns of wood density can be examined from pith to bark and as well as vertically. In general, variation in wood density is hierarchically arranged where inter-cellular properties integrate to the cellular level, the cellular level is integrated to the inter-annual ring level and annual rings are integrated to the tree level. At each scale, the proximity to important developmental organs, (i.e., terminal and lateral buds) may change. Wood density not only varies in space but in time, where wood properties are a function of daily, monthly and annual variation in the interaction between the gene and the environment. Larson (1963, 1969) hypothesized that the proximity of the cambium to the live crown was responsible for the vertical and horizontal patterns in wood density and has been widely cited despite limited empirical evidence. Multiple competing hypotheses exist to explain the radial and vertical variation of wood density within the stem. This

synthesis will review the literature regarding wood development, explore the evidence surrounding Larson's (1963, 1969) hypothesis and examine the interaction between silviculture and wood. Specific attention will be given to retention systems.

# 4.2 Intra-ring variation of wood density

Diameter growth occurs in the vascular cambium where perclinial cell division occurs to produce radial rows of xylem and phloem. Following detachment, secondary wall formation and lignification occurs among other processes. These sequences give rise to earlywood and latewood and are influenced by the seasonality at which xylem and phloem cells are detached from cambial mother cells (Pallardy 2010). Earlywood cells are characterized by a thinner cell wall and larger radial diameter compared to latewood. Earlywood density is related to cell size and latewood density is related to cell wall thickness in most Northern Hemisphere conifers (Björklund et al. 2017). The transition between earlywood and latewood is gradual in some species; however, the transition is abrupt in Douglas-fir (Pallardy 2010).

The transition from earlywood to latewood characteristic cells is thought to be hormonal (Larson 1960). All primary hormones (auxins, gibberellins, cytokinins, abscisic acid, and ethylene) are present in the cambium, however, the role of these hormones on cambial development remains uncertain. Applications of auxin caused larger radial diameter "earlywood" characteristics in red pine (*Pinus resinosa* Aiton; Larson 1960) and promoted cambial growth in sitka spruce (*Picea sitchensis* (Bong.) Carrière; Little and Wareing 1981). Changes in growth habits and foliage are thought to bring on hormonal changes. As an example, earlywood is formed during the active terminal growth. Larson (1969) hypothesized that earlywood and latewood formation were

related to the initiation cambial activity (and earlywood formation) and coincides with active terminal growth. Similarly, latewood production begins at approximately the same time as budset. However, these processes may be only correlated and under the same hormonal control Renninger et al. (2006).

The functional mechanisms of wood density are only just beginning to be understood. Wood density is thought to be an adaptive mechanism of drought avoidance in conifers (Hacke et al. 2001). Increases in wood density are a result of decreased soil moisture and are related to the increase in proportion of latewood in an annual ring (Zobel and van Buijtenen 2012). In loblolly pine (*Pinus taeda* L.), latewood formation coincided with increased drought stress and subsequent decreases in available auxin (Gilmore et al. 1966). A sudden increase in available moisture through irrigation or precipitation will continue to produce latewood cells throughout the remainder of the growing season (Zobel and van Buijtenen 2012).

Wood density and specific gravity of annual rings is higher during dry summers compared to wet summers in Douglas-fir (Lassen and Okkonen 1969). Douglas-fir growing in France that survived a major drought showed higher ring density and latewood density compared to trees that did not survive (Martinez-Meier et al. 2008). Much of the water transport in trees occurs through earlywood, which is primarily driven by the large tracheid size compared to latewood (Tyree and Zimmermann 2002). The production of latewood decreases the specific conductivity in an annual ring but increases the available water stored (Domec and Gartner 2002) and is thought to be an adaptive mechanism to avoid implosion and cavitation in the hydraulic transport system (Hacke et al. 2001). Douglas-fir in a lower social position and thus trees with lower

resource availability display denser wood than those of a higher social position (Wellwood 1952). Both temperature and soil moisture play a role in wood density. Earlywood density is more dependent on summer temperatures of the previous year and thus stored photosynthates and latewood density is dependent on early spring temperatures of the current year (Björklund et al. 2017). Stoehr et al. (2009) found that temperature difference between the coldest and warmest month, July precipitation, and mean annual precipitation accounted for 47% of the site to site variation in wood density of 10 full-sib families of young Douglas-fir.

Both intra-ring variation and radial variation of wood density are inherited traits in Douglas-fir (Vargas-Hernandez and Adams 1991; Abdel-Gadir 1993). Abdel-Gadir et al. (2007) found a strong provenance effect for ring density, latewood width, latewood density, and latewood proportion. Heritability of wood density in open-pollinated Douglas-fir families in northern Oregon was found to be relatively high (0.59; Johnson and Gartner 2006). Similar results were shown for Douglas-fir in southern British Columbia (0.47; Ukrainetz et al. 2008). Many of the studies related to genetic variation of wood density are related to selection for wood quality in breeding programs (e.g. Gonzalez and Richards 1988; Vargas-Hernandez and Adams 1991). Montwé et al. (2015) hypothesized that less productive provenances originating from dryer and cooler sites may invest in latewood to improve hydraulic safety, allowing for higher resilience to drought compared to more productive provenances originating from wetter sites. Selectively breeding trees that originate from dryer areas may be an opportunity to improve wood quality and drought resistance at the same time (Dalla-Salda et al. 2011; Montwé et al. 2015).

# 4.3 Radial variation of wood density

The mechanism behind radial variation from pith to bark in conifers has been widely studied and debated. The area near the pith is commonly referred to as juvenile wood but has been referred to as crown-formed wood (Larson 1969) and corewood. Wood outside of this zone is referred to as mature wood or outerwood. Larson (1969) proposed crown-formed to account for wood formed near the crown in mature trees that had juvenile characteristics. Burdon et al. (2004) expanded this definition to include mature and juvenile corewood and outerwood. These terms are intended to be concatenated to describe, for example, wood formed in the crown of a mature tree as mature corewood. Hereafter, I will refer to juvenile wood as corewood and mature wood as outerwood. Juvenile and mature will only be used to describe the relative age of entire trees.

In conifers, corewood contains short tracheid lengths, thinner cell walls, lower latewood proportion, higher  $S_2$  microfibril angle and lower density. Many of the physiological differences between corewood and outerwood can be summarized as changes in wood density. Most conifers display a similar pattern in radial variation of wood density from pith to bark. This has been referred to as the typical radial pattern by Lachenbruch et al. (2011). In general, there is a decrease in wood density during the first several years of growth followed by a gradual increase until an asymptote is reached and density stabilizes (Figure 1).



Figure 4.1 Radial variation of wood density at breast height for 54 Douglas-fir sampled near Cowichan Lake Research Station, British Columbia (Goudie unpublished).

The transition from corewood to outerwood happens gradually, is under genetic control (Abdel-Gadir 1993), can vary between trees, sites, and species and is dependent on how the transition is defined and modelled (Fabris 2000; Abdel-Gadir and Krahmer 2007). In Douglas-fir, Di Lucca (1989) found that the juvenile-mature transition occurred at year 20 on an average site on Vancouver Island. Fabris (2000) found a mean of 21 years on a wet site in southern British Columbia. Abdel-Gadir and Krahmer (2007) found a transition of between 16 and 30 years with a mean of 26 depending on the property used to define the transition in Douglas-fir from Wyoming and Oregon.

There are multiple competing hypotheses regarding the formation of corewood and outerwood. Lachenbruch et al. (2011) present two hypotheses as to the mechanisms that drive radial variation from pith to bark in trees. The cambial age hypothesis suggests that younger cambial derivatives early in life or cambium formed higher in the live crown of mature trees have more corewood characteristics. The stem diameter hypothesis relies on stem diameter reflecting the total number of cell divisions in the cambium. Lachenbruch continues to evaluate hydraulic and mechanical adaptive functions of the general corewood and outerwood trend. Hydaulic efficiency may be one adaptive mechanism of corewood formation, where corewood can resist high negative pressures in the xylem as opposed to outerwood, which has higher specific conductivity compared to corewood. A mechanical function hypothesis allows for younger trees to withstand bending from wind, snow and other abiotic disturbances. The existence of these hypotheses does not necessarily preclude the live crown as a mechanism of the transition between corewood and outerwood.

In angiosperms, a study of three heavily buttressed tropical species suggested that the transition from corewood to outerwood was due to mechanical loading and had little to do with cambial age or the proximity to live crown (Christensen-Dalsgaard et al. 2008). Although a mechanical loading hypothesis has not been examined in conifers, Fabris (2000) found that trees with a slenderness ratio greater than 1.0 had a more abrupt transition between corewood and outerwood compared to trees with a slenderness ratio of less than 0.8, suggesting the loading hypothesis may have some merit. Kucera (1994) hypothesized that the transition from juvenile to mature wood was related to the culmination of height increment in Norway Spruce. The culmination of

height increment may also be related to the amount of mechanical loading. This has not been examined further in Douglas-fir.

Gartner (2007) hypothesized that the photosynthetically active bark that occurs in younger parts of the stem may provide a mechanism for controlling the transition from corewood to outerwood. Photosynthetically active bark persists in Douglas-fir from 12 to 43 years and correlates with the location of corewood along the vertical distribution of the stem. Photosynthetic bark may provide a signal to produce outerwood when light conditions fall below a threshold. This hypothesis has not been further tested. Painting photosynthetically active bark and measuring corewood after several years may provide more evidence to this hypothesis.

Larson (1963, 1969) suggested the proximity to live foliage as a mechanism of corewood formation in trees, where the vascular cambium is exposed to increased levels of growth hormones compared to areas outside of the live crown. Evidence to date for this hypothesis is variable, however, the hypothesis is widely cited as a mechanism controlling the development of corewood and outerwood. The most notable attempt to study this hypothesis is that of Gartner et al. (2002) where wood density in the previous three years was unrelated to the position in or out of the live crown. Spacing trials have also been measured to evaluate the effect of the live crown on wood density. Trees planted at narrower spacings have lower live crown ratios compared to trees at wider spacings. Both Fabris (2000) and Robbins (2000) found no relationship between wood density at breast height and tree spacing.

Pruning has been suggested as a method to test the live crown proximity hypothesis where pruning live branches should produce a transition to outerwood. The results of pruning in

Douglas-fir have been mixed. There are several studies that provide evidence supporting the crown proximity hypothesis in Douglas-fir, however most are of low quality. Jozsa (1995) found that wood density increased following pruning but only provided one tree as a control. DiLucca (1989) found an increase in wood density following pruning in two Douglas-fir trees. Studies with a better sampling design are more inconclusive. Gartner et al. (2007) found that only those of the youngest age class and tallest lift produced an increase in wood density following pruning. This response was thought to be a function of removing more vigorous branches. Briggs (1995) stated evidence of the influence of pruning on corewood and outerwood transitions should include changes among all properties associated with corewood and that the current evidence was likely due to spurious results caused by poor design, sample size or an increase in density related to decreased resource availability.

Larson (1969) indicated that the transition from corewood to outerwood does not occur directly at the base of the live crown but rather at an indeterminate point in the lower crown where the influence of lateral buds is strong enough to influence the cambium. This vertical pattern was proposed by Gartner et al. (2002) and confirmed by Gartner et al. (2007) who measured a slight increase in wood density in response to the pruning of vigorous branches. The contribution of branches to net photosynthate is dependent on the vigor and social class of a tree. Trees of dominant or codominant social classes will shed branches more readily than trees of intermediate or suppressed classes (Sprugel 2002). The trend in social class and branch retention also suggests that the influence of the live crown on the juvenile core should also vary based on the social position of a given tree. Fabris (2000) found that the transition point from corewood to

outerwood was below the live crown in faster growing trees (slenderness ratio  $\leq$  .8) with longer live crown ratios compared to slower growing trees with smaller live crown ratios (slenderness ratio  $\geq$  1.0) where the transition occurred above the base of the live crown. Slower growing trees showed rapid transitions between corewood and outerwood compared to faster growing trees. Auxin gradients are thought to be higher in more vigorous trees. To my knowledge, there have been no measurements made of the vertical trend in auxin between dominant and suppressed trees, however, this may explain some of the variability in studies of transition from corewood to outerwood.

## 4.4 Wood density response to thinning and fertilization

Thinning increases the available growing space to residual trees. If implemented with the correct timing and intensity, diameter growth is increased in residual trees. Response of wood density to thinning in Douglas-fir is mixed. Several studies have shown a decrease in wood density and specific gravity, likely due to an increase in earlywood (Erickson and Harrison 1974; Filipescu et al. 2014). Conversely, Jozsa and Brix (1989) and Kantavichai et al. (2010) reported higher specific gravity post-thinning. Because of the relationship between moisture and wood density in Douglas-fir, thinning response is likely dependent on the site and timing of thinning. From the perspective of single species, even-aged stands, thinning of younger stands would result in an increase in corewood and thus lower density wood. Response of wood density in older stands is more likely dependent on the site and the intensity of thinning.

Thinning reduces competition and increases growing space. Growing space incorporates all of the necessary elements of tree growth (e.g. physical space, sunlight, nutrients and CO2; Oliver

and Larson 1996). Along with increasing available light, thinning also increases available soil moisture (Brix and Mitchell 1986; Aussenac and Granier 1988).

There are several effects of thinning on wood density that are plausible and equally likely. The first is that the proportion of latewood is reduced by improving moisture conditions. This effect would be more likely in a thinning that removed a sufficient amount of trees to cause a positive change in moisture deficit and retained trees that could capitalize on the increased resource. Latewood proportion can also be reduced by the early cessation of growth in response to moisture deficit (Kantavichai et al. 2010). This scenario would be more likely if an insufficient amount of trees were removed to cause a change in soil moisture, the site was exceptionally poor, or the trees that were retained were of lower crown classes and were unable to cope with the sudden increase in respiratory demands. Drew and Downes (2009) measured thinning response in radiata pine (Pinus radiata D. Don.) and found that the rate of diameter growth was similar to an unthinned control and that diameter response was a function of a longer duration growing season. This work has not been replicated in Douglas-fir, but if similar patterns of thinning response exist, it is easy to conceive that thinning would increase latewood production as diameter growth continued later in the growing season on sites with sufficient moisture to continue diameter growth throughout the growing season.

Thinning may have the potential to reduce the size of the juvenile core. Fabris (2000) found that denser initial spacing reduced the size and accelerated the transition between corewood and outerwood. This treatment effect means that the crown proximity hypothesis proposed by Larson (1963, 1969) may be at least somewhat relevant. Conceivably, thinning can be timed with the

formation of mature wood to promote the radial growth of mature wood and thus produce the juvenile core of a tree grown at high densities. Fabris (2000) hypothesized that the rapid growth of trees at wide spacings may eventually develop a proportion of corewood equal to that of trees grown at higher densities over longer rotations. However, the amount of corewood is likely more important when producing dimensional lumber. As with most silvicultural interventions, additional entries to the stand occur at a cost. Thinning can likely produce an improvement in the proportion of corewood in Douglas-fir, however, the financial incentives to produce this type of wood must be present.

Fertilization has been shown to decrease wood density and specific gravity (Erickson and Harrison 1974; Jozsa and Brix 1989). Jozsa and Brix (1989) found a decrease in ring wood density for three to four years post-treatment, during the period of increasing foliar biomass. Brix (1983) found that increased foliar nitrogen caused an increase in foliar biomass which subsequently resulted in increased tree diameter in later years. Wood density responded in the first year following treatment and diameter growth responded in the second year following treatment. Jozsa and Brix (1989) hypothesized that the decrease in wood density immediately following fertilization was related to increasing available carbohydrates that increased cell wall formation. On the same site, Brix and Mitchell (1986) demonstrated that fertilization improves water use efficiency in Douglas-fir. Decreased wood density in response to fertilization can be explained in the context of the relationship between moisture limitation and site. Decreases in wood density following fertilization is likely a reflection of improved water use efficiency as a result of fertilization (Brix and Mitchell 1986).
The mechanism that drives the increase in water use efficiency in response to fertilization is unknown. Brix and Mitchell (1986) hypothesized that the increase in water use efficiency was due to an increased stomatal control of water loss. An alternative hypothesis is that the increased production of earlywood cells increases the specific conductivity within the xylem (in sensu Domec and Gartner 2002). This would suggest that increased carbohydrates contributed to cell formation in addition to cell wall formation as hypothesized by Jozsa and Brix (1989). Models of wood development lend further support to this hypothesis, where earlywood and latewood transitions are modeled as a function of carbohydrate availability (Cartenì et al. 2018).

#### 4.5 The effect of growth rate on wood density

Much of the confusion in general trends of wood density seems to be driven by differences between corewood and outerwood, which are functionally different (Lachenbruch et al. 2011; Zobel and van Buijtenen 2012). Initial diameter growth in Douglas-fir is rapid while the live crown is expanding and is unobstructed by neighboring trees. This results in rapid diameter growth and coincides with the occurrence of corewood. Rapid initial growth only seems to be correlated with corewood but does not cause decreases in wood density. This is apparent in espacement trials where tree density did not influence the radial variation of wood density from pith to bark Fabris (2000). In general, there appears to be no relationship between growth rate and wood density in Douglas-fir and hard pines. In a study of 10,000 trees, Smith and Kennedy (1983) found no relationship between growth rate and wood density (as cited in Abdel-Gadir et al. 2007). Abdel-Gadir et al. (2007) found that ring width accounted for 1% of the variation in corewood and 2% of the variation in mature wood. Devine and Harrington (2009) report

changes in wood density associated with vegetation control, thinning and fertilization as evidence supporting the effect of growth rate on wood density. It is clear from the discussion above that changes in wood density in response to silvicultural treatments are a function of the interaction between wood development and available moisture.

Rings per inch is a common metric used for wood quality in British Columbia (Ministry of Forests, Lands, Natural Resource Operations and Rural Development, 2011). However, the metric does not correlate directly with wood density. As an example, Jozsa and Middleton (1994) prescribe 4 rings per inch as a measure of "Medium Grain with the caveat "...fewer than four rings per inch are acceptable if the rings contain >33% latewood". The authors emphasize that the rings per inch metric only ensures that the amount of juvenile core is reduced as the juvenile core has higher growth rates compared to mature wood. The effect of the corewood is larger than those of variation in wood density in studies of lumber recovery on Vancouver Island (Kellog 1989). Rings per inch, however, is generalized to plantation grown trees and may not apply to naturally regenerated stands, due to the potential for slower initial growth in young trees. In general, rings per inch is an appropriate metric for grading lumber based on visual grain or grades that are dependent on grain for other products, such as the application of paint. Rings per inch does not directly reflect wood density but only describes the changes in wood density associated with limiting the amount of corewood in a given piece of lumber.

#### 4.6 Models of wood density

Many models of wood density have been developed for other species (Sattler et al. 2014, Auty et al. 2014, Kimberley et al. 2015 as examples), most of which use site level (e.g. temperature,

precipitation, site quality) and tree level variables (e.g. cambial age). Models of wood density have been developed for Douglas-fir (e.g. Kantavichai et al. 2010; Filipescu et al. 2014)) but accurate models of wood density are still elusive. Kantavichai et al. (2010) found that ring age, ring area, March to May mean temperature, July soil moisture deficit, and whether or not biosolids had been applied were important predictors in their mixed-effects logistic model. Filipescu et al. (2014) also used a mixed-effects logistic model to predict annual ring density using cambial age, stand density (as stand density index), and total climatic moisture deficit of June and July. One of the best model fits comes from Kimberley et al. (2017) where a regression model of radial variation in wood density accounted for 81% of the variability where 19% of the variability was attributed to the radial profile of wood density and 62% was attributed to stand level variation.

Most models of wood density use cambial age as a predictor of radial variation from pith to bark. To my knowledge, stem diameter has not been used in models of radial variation. Kimberley et al. (2017) found a slight negative trend with outerwood wood density and diameter. Models of wood density overwhelmingly support the cambial age hypothesis examined by Lachenbruch et al. (2011). The relationship between stem diameter and wood density may be an effect of the uniform plantations that exist in New Zealand, where diameter is a better proxy for age than in more complicated stand structures. Kimberley et al. (2017) developed a model of the wood density of a disk at a given height on a given tree. The model accounted for 79% of the vertical variation in wood density using only the relative height of a disk as a predictor. This model does not preclude the crown proximity hypothesis when considering that variation in wood density

between trees and between sites controls the bulk of wood density and the crown proximity hypothesis may only influence the transition between corewood and outerwood.

### 4.7 The effect of retention systems on wood density in Douglas-fir

As demonstrated in Chapter 3, retention systems cause a reduction in volume to the regenerated cohort. Diameter increment in the new cohort is reduced by the reduction in crown area from competition with neighboring retention trees. The lack of relationship between diameter increment and wood density suggests that the wood density of a new cohort that is competing with retention trees would be relatively unaffected. Temperature, available moisture, and genetic variation would likely drive wood density in retention systems. On particularly dry sites, increased moisture competition from overstory trees may increase wood density in the regenerated cohort, however, empirical evidence of this effect is limited.

Evidence from espacement trials suggests that trees growing under heavier competition may transition from juvenile to mature wood at an earlier time and more abruptly than trees grown at wider spacing (Fabris 2000). Changes in live crown ratio as a result of espacement may be responsible for this transition. Trees growing adjacent to retention may experience similar levels of competition, causing a reduction in the mean area of corewood compared to trees that were unaffected by overstory retention. In Chapter 3, dispersed retention caused more volume reduction compared to aggregate retention, likely because of the increased amount of edge. The effect of retention on the area of corewood would likely be more dramatic in dispersed retention compared to aggregate retention, considering the increased competition. The reduction in corewood coincides with a reduction in diameter increment which is likely to continue under

competition from retained overstory trees. Although the area of corewood is reduced in trees experiencing competition, the continued reduction in diameter increment will likely result in a similar proportion of corewood and outerwood at shorter rotations compared to trees grown without overstory competition, which will sustain a higher diameter increment following transition from corewood to outerwood.

### 4.8 Conclusions

There is little evidence that wood density is influenced by the proximity of the cambium to the live crown. The role that the live crown plays in the transition from corewood to outerwood remains uncertain. Wood density is, in part, a functional mechanism of drought avoidance and varies between individual trees, sites and provenances. Considering the functional role of wood density, there is opportunity to simultaneously improve wood quality and drought tolerance in planted stock (Montwé et al. 2015).

Intermediate silvicultural treatments are often concerned with improving the growth of residual trees. It is easy to interpret the effects of silviculture on wood density as a result of increased growth from treatment. However, most evidence on the effect of thinning and fertilization on wood density regards a change in the relationship between the site and the tree and changes in tree growth as a result of thinning or fertilization have little effect on wood density. The lack of relationship between growth and wood density can be extended to retention systems, where a reduction in growth from increased competition with retained overstory trees would have no effect on wood density, however, site specific cases that change the relationship between the tree and the available growing space may exist.

# **Chapter 5: Conclusions**

This dissertation investigated the hypothesis that improving wood quality could be a solution to meeting both ecological and social management objectives while improving financial management objectives. The first objective of this dissertation was to address gaps in wood quality modeling by creating models that were adaptable to complex stand structures. A second objective was to evaluate the potential for increases in wood quality to account for managing stands for social and ecological objectives through the use of retention systems. A third objective was to review the literature regarding changes in wood density associated with changes in the live crown and stand structure.

In Chapter 2, model testing and evaluation suggested that the modeling approach predicted frequency, size, and distribution of branches with accuracy and that the precision of model prediction was dependent on the similarity between the empirical height age curve and the TASS derived height age curve. The hierarchy of models is similar to a framework proposed by Trincado and Burkhart (2009) for *Pinus taeda* L. However, this modeling approach is the first to predict branch number, size and distribution in an asymmetric crown. Previous models of branch development do not consider the location within the crown or prescribe a uniform distribution around the stem (Maguire 1994; Trincado and Burkhart 2009). Even if the location of a branch is considered, prior models of branch development do not consider the relative position in the crown in the development of branches into the future.

There are several opportunities to expand on the research highlighted in Chapter 2. The first is to improve the accuracy of data collection and increase the sample size by using computerized tomography scanning (CT) to directly measure internal knot structure. The methods used in this dissertation involved direct measurements of live branches as proxies for knot position and size. High resolution CT scanning would allow for the reconstruction of the internal knot structure through time. This technology has been used in *Picea mariana* (Mill.) Britton, Sterns & Poggenb. (Duchateau et al. 2015). The increase in accuracy of data collection will allow future models to answer questions regarding branch autonomy (Sprugel et al. 1991; Sprugel 2002), the effect of social position on branch development and crown asymmetry. In its current form, this model will allow further exploration into the role of multiple age classes and branch development.

Chapter 3 revealed that the removal of available growing area had the largest effect on volume and financial recovery. There was a slight increase in wood quality in trees that competed with neighboring retention trees, however, the reduction in volume associated with retention was much larger. This simulation represents the best estimate to date of the true financial cost of meeting social and ecological objectives.

Although the chapter only investigates a single species stand, the results of this research have implications for retention systems and other similar structured silviculture systems used around the world. This simulation approach can be used to answer questions regarding lumber recovery and wood quality through a wide variety of species, ages and management intensities. Incorporating additional species, particularly shade tolerant species, may improve the financial

returns of retention systems by diversifying the product portfolio and potentially reducing the edge effect. Simple additions, such as differentiating live and dead knots in the grade profile of Optitek could improve estimates of lumber recovery. Incorporation of wood density, modulus of elasticity or machine stress rating may allow further refinement in the recovery estimates. Quantifying the value added through meeting social and ecological objectives may make investment in retention systems favorable, despite the loss in volume associated with increased competition. Future research could quantify the impact of tourism, visual quality, wildlife habitat or human health on the financial performance of retention systems.

The conclusions of Chapter 4 suggest that wood density is largely a response to both temperature and moisture conditions on the site. Models of wood density investigating the radial profile of wood density from pith to bark most frequently support the cambial age hypothesis where the development of corewood and then outerwood (juvenile and mature wood) is a developmental adaptation with several mechanistic advantages (Lachenbruch et al. 2011). Based on the results of Chapter 3, the reduction in growth rate by competition from overstory trees is likely to have little effect on wood density. The increase in the height of the base of the live crown as a result of increased competition in retention systems may, however, play a role in the transition between corewood and outerwood (juvenile and mature wood). Hypotheses regarding the formation of corewood and outerwood remain to be tested.

The effect of growth rate, the most targeted variable by silvicultural intervention, is largely irrelevant to the density of wood. Because of the limited relationship between growth rate and thinning, metrics like rings per inch are only useful in controlling the grain or the amount of

corewood in a stem. The review provides hypotheses regarding a hydraulic mechanism to explain the response of wood density to thinning and fertilization. The role of pruning in wood density remains unclear. There are two methods in which silviculture can play a role in management for wood density. The first is the opportunity to simultaneously increase wood quality and improve drought resistance by selecting provenances that are functionally adapted to dryer ecosystems. The second is the potential to control the size of the juvenile core through planting at high density and thinning following the transition to outerwood.

Future research regarding wood density must harness the power of large datasets spread across the entire range of a species. Quantitative techniques such as structural equation modeling and artificial neural networks may further elucidate the role of site conditions and the live crown in both radial and vertical trends of wood density. In addition, physiological research is needed to provide empirical evidence of the mechanisms behind wood development and wood density.

# 5.1 Additional future directions

Forest inventory has been rapidly changing in recent years. Technology such as LiDAR and digital aerial photogrammetry (DAP) allow remote inventories of high-resolution data. Future research might investigate the role of incorporating LiDAR and DAP directly into the simulation approach developed and used in this dissertation. TASS records crowns in three-dimensional space and crown profiles derived from DAP or LiDAR are fairly similar to the data recorded in TASS. Knot size and distribution may be directly derived from a point cloud crown profile or integrated into TASS for further growth analyses.

When evaluating the growth and development of trees and stands it is clear that inference and empirical evidence must be collected across a wide range of sites. The effect of site is particularly relevant in the study of wood density. Large- or small-scale research installations must be replicated across multiple sites to truly understand stand development and tree growth. For example, spacing trials are useful for understanding wood development and the influence of the live crown. Fabris (2000) studied wood properties and corewood and outerwood transitions in a spacing trial located at Malcolm Knapp Research Forest. Despite the compelling conclusions, Malcolm Knapp Research Forest is a particularly wet site averaging 2200mm of rain a year (Malcolm Knapp Research Forest 2019). It is questionable whether similar trends would be found in spacing trials of Douglas-fir growing on dryer sites. Techniques, such as meta-analysis, may provide additional answers regarding the role of site on wood density and branch patterns.

# 5.2 Operational considerations

This dissertation was, in part, motivated by the increased regulation of retention systems throughout the range of coastal Douglas-fir. Retention systems can have positive influences on biodiversity and visual quality. Despite this, the economic benefits of these services remain unquantified. Ultimately, managers should partition retention across the landscape in areas that are visually or biologically sensitive. Increasing visual stewardship and subsequent social capital may be more valuable for managers in close proximity to communities or recreation areas relative to the reduction in volume on a site. On sites with low social pressure, retention systems

may still provide biodiversity benefits that may be valued higher than the revenue generation from fibre.

The objective of retention systems is to maintain horizontal and vertical forest structure to mimic or recreate the structure characteristic of older coastal Douglas-fir stands with complex forest structure. These stands developed in the absence of stand replacing disturbances for hundreds to thousands of years, creating a mosaic of species, age classes and subsequent stand structure. Recreating these stand structures through silviculture would necessitate additional retention at the next rotation to accelerate the development of complex stand structure. I did not consider this scenario in this dissertation; however, additional retention would likely further decrease the value of a future stand. A second and equally plausible scenario is one where the retention is harvested at the next entry. This scenario may dampen the reduction in volume but would not continue to meet social and ecological management objectives.

The use of engineered wood products has been increasing. In engineered wood products, defects such as corewood, grain, wood density and knot size and distribution are less important (Shmulsky and Jones 2011). Concerns regarding these properties will likely become less important as we increasingly use engineered wood products in everyday applications. The simulation approach developed in this dissertation can be used to provide realtime lumber recovery estimates in standing forests. This capacity would be particularly powerful if LiDAR of digital aerial photogrammetry (DAP) data were able to initialize a TASS simulation and provide an estimate of lumber recovery.

Sawmill product specifications are often transmitted to harvesters and processing equipment working on a harvest site. The potential exists for silviculturists to use this simulation tool in a similar manner, using realtime product specifications and prices to target stand entries and harvests that may be financially optimal during the annual planning horizon.

# 5.3 Closing statement

The major contribution of this dissertation is a better understanding of the influence of retained stand structure on the distribution and architecture of knots within a stem, the vertical and horizontal pattern of wood density and the tradeoffs between alternative silviculture systems and lumber recovery. Alternative silviculture systems are distinguished by a gradient of stand edge and gaps. Simply put, silviculture systems are defined by the variability of stand structure and its interaction with growing space. Simulating lumber recovery in alternative silviculture systems must be spatially explicit if the true effects of changing stand structure on lumber recovery are to be understood. Though this is not the first simulated study of lumber recovery in retention systems, the methods developed and used in the chapters herein represent the first attempt at investigating lumber recovery and wood quality using a modeling framework that is spatially explicit from end to end. The first step towards a spatially explicit lumber recovery framework will allow scientists and managers to answer questions related to complex stand structures comprised of different ages and species and ultimately guide the financial and silvicultural implications of sustainable forest management.

# References

- Abdel-Gadir, A.Y., and Krahmer, R.L. 2007. Estimating the Age of Demarcation of Juvenile and Mature Wood in Douglas-Fir. Wood Fiber Sci. **25**(3): 242–249.
- Abdel-Gadir, A.Y., Krahmer, R.L., and McKimmy, M.D. 2007. Relationships between intra-ring variables in mature douglas-fir trees from provenance plantations. Wood Fiber Sci. 25(2): 182–191.
- Abdel-Gadir, Y. 1993. Genetic variation in the age of demarcation between juvenile and mature wood in Douglas-fir. **25**(4): 384–394.
- Acker, S.A., Zenner, E.K., and Emmingham, W.H. 1998. Structure and yield of two-aged stands on the Willamette National Forest, Oregon: implications for green tree retention. Can. J. For. Res. 28(5): 749–758. doi:10.1139/x98-039.
- Agostinelli, C., and Lund, U. 2017. R package circular: Circular Statistics (version 0.4-93). CA: Department of Environmental Sciences, Informatics and Statistics, Ca' Foscari University, Venice, Italy. UL: Department of Statistics, California Polytechnic State University, San Luis Obispo, California, USA. Available from https://r-forge.rproject.org/projects/circular/.
- Akaike, H. 1974. A new look at the statistical model identification. IEEE Trans. Autom. Control **19**(6): 716–723.
- An, Y., and Schajer, G.S. 2014. Geometry-based CT scanner for measuring logs in sawmills. Comput. Electron. Agric. 105: 66–73. doi:10.1016/j.compag.2014.03.007.

- Ashton, M.S., and Kelty, M.J. 2018. The practice of silviculture : applied forest ecology. *In* 10th edition. John Wiley & Sons, Inc., Oxford.
- Assmann, E. 1970. The Principles of Forest Yield Study: Studies in the Organic Production, Structure, Increment and Yield of Forest Stands. Elsevier Science.
- Aubry, C.A., Adams, W.T., and Fahey, T.D. 1998. Determination of relative economic weights for multitrait selection in coastal Douglas-fir. Can. J. For. Res. 28(8): 1164–1170. doi:10.1139/x98-084.
- Aubry, K.B., Halpern, C.B., and Peterson, C.E. 2009. Variable-retention harvests in the Pacific Northwest: A review of short-term findings from the DEMO study. For. Ecol. Manag.
  258(4): 398–408. doi:10.1016/j.foreco.2009.03.013.
- Aussenac, G., and Granier, A. 1988. Effects of thinning on water stress and growth in Douglasfir. Can. J. For. Res. **18**(1): 100–105. doi:10.1139/x88-015.
- Auty, D., and Achim, A. 2014. StatSAW: modelling lumber product assortment using zeroinflated Poisson regression. Can. J. For. Res. **44**: 638–647.
- Auty, D., Achim, A., Macdonald, E., Cameron, A.D., and Gardiner, B.A. 2014. Models for predicting wood density variation in Scots pine. Forestry 0: 1–10. doi:10.1093/forestry/cpu005.
- Baker, S.C., Halpern, C.B., Wardlaw, T.J., Crawford, R.L., Bigley, R.E., Edgar, G.J., Evans,
  S.A., Franklin, J.F., Jordan, G.J., Karpievitch, Y., Spies, T.A., and Thomson, R.J. 2015.
  Short- and long-term benefits for forest biodiversity of retaining unlogged patches in harvested areas. For. Ecol. Manag. 353: 187–195. doi:10.1016/j.foreco.2015.05.021.

- Barbour, R.J., Marshall, D.D., and Lowell, E.C. 2003. Managing for Wood Quality. *In*Compatible Forest Management, Vol. 8. Springer, Netherlands. pp. 299–336.
- Bates, D., Mächler, M., Bolker, B., and Walker, S. 2015. Fitting Linear Mixed-Effects Models Using lme4. J. Stat. Softw. 67(1). doi:10.18637/jss.v067.i01.
- Belley, D. 2014. Évaluation Du Volume Et Des Pertes De Qualité Causées Par Les Principaux Défauts Des Tiges D ' Épinette Blanche Et De Pin Gris. Université Laval, Quebec City, Quebec.
- Birch, K.R., and Johnson, K.N. 1992. Technical Commentary: Stand-Level Wood-Production Costs of Leaving Live, Mature Trees at Regeneration Harvest in Coastal Douglas-fir Stands. West. J. Appl. For. 7(3): 65–68. doi:10.1093/wjaf/7.3.65.
- Björklund, J., Seftigen, K., Schweingruber, F., Fonti, P., von Arx, G., Bryukhanova, M.V., Cuny,
  H.E., Carrer, M., Castagneri, D., and Frank, D.C. 2017. Cell size and wall dimensions
  drive distinct variability of earlywood and latewood density in Northern Hemisphere
  conifers. New Phytol. 216(3): 728–740. doi:10.1111/nph.14639.
- Briggs, D. 2010. Enhancing Forest Value Productivity through Fiber Quality. J For **108**(4): 174–182.
- Briggs, D., Ingaramo, L., and Turnblom, E. 2007. Number and diameter of breast-height region branches in a Douglas-fir spacing trial and linkage to log quality. For. Prod. J. **57**(9): 28.
- Briggs, D.G. 1995. Pruning in relation to forest inventory, wood quality and products. *In* Forest pruning and wood quality of western North American conifers. *Edited by* D. Hanley, C. Oliver, D. Maguire, D.G. Briggs, and R. Fight. College of Forest Resources, University of Washington, Seattle, WA. pp. 21–35.

- Brix, H. 1981. Effects of thinning and nitrogen fertilization on branch and foliage production in Douglas-fir. Can. J. For. Res. 11(3): 502–511.
- Brix, H. 1983. Effects of thinning and nitrogen fertilization on growth of Douglas-fir: relative contribution of foliage quantity and efficiency. Can. J. For. Res. 11(3): 167–175. doi:10.1139/x83-023.
- Brix, H., and Mitchell, A.K. 1986. Thinning and nitrogen fertilization effects on soil and tree water stress in a Douglas-fir stand. Can. J. For. Res. **16**: 1334–1338.
- Brokaw, N.V., and Lent, R.A. 1999. Vertical Structure. *In* Maintaining Biodiversity in Forest Ecosystems. Cambridge University Press, Port Chester, US. pp. 373–399.
- Bruce, D. 1981. Consistent Height-Growth and Growth-Rate Estimates for Remeasured Plots. For. Sci. **27**(4): 711–725.
- Brunner, A. 1998. A light model for spatially explicit forest stand models. For. Ecol. Manag. **107**: 19–46. doi:10.1016/S0378-1127(97)00325-3.
- Burdon, R.D., Kibblewhite, R.P., Walker, J.C.F., Megraw, R.A., Evans, R., and 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(4): 399–415.
- Cartenì, F., Deslauriers, A., Rossi, S., Morin, H., De Micco, V., Mazzoleni, S., and Giannino, F.
  2018. The Physiological Mechanisms Behind the Earlywood-To-Latewood Transition: A
  Process-Based Modeling Approach. Front. Plant Sci. 9. doi:10.3389/fpls.2018.01053.

- Chen, L., and Sumida, A. 2018. Effects of light on branch growth and death vary at different organization levels of branching units in Sakhalin spruce. Trees **32**(4): 1123–1134. doi:10.1007/s00468-018-1700-5.
- Christensen-Dalsgaard, K.K., Ennos, A.R., and Fournier, M. 2008. Are radial changes in vascular anatomy mechanically induced or an ageing process? Evidence from observations on buttressed tree root systems. Trees 22(4): 543–550. doi:10.1007/s00468-008-0214-y.
- Cochrane, L.A., and Ford, E.D. 1978. Growth of a Sitka Spruce Plantation: Analysis and
  Stochastic Description of the Development of the Branching Structure. J. Appl. Ecol.
  15(1): 227. doi:10.2307/2402933.
- Curtis, R.O., DeBell, D.S., Miller, R.E., Newton, M., St. Clair, J.B., and Stein, W.I. 2007.
  Silvicultural research and the evolution of forest practices in the Douglas-fir region /.
  General Technical Report, U.S. Department of Agriculture, Forest Service, Pacific
  Northwest Forest and Range Experiment Station., Portland, OR. Available from
  http://hdl.handle.net/2027/umn.31951d02974976p.
- Dalla-Salda, G., Martinez-Meier, A., Cochard, H., and Rozenberg, P. 2011. Genetic variation of xylem hydraulic properties shows that wood density is involved in adaptation to drought in Douglas-fir (Pseudotsuga menziesii (Mirb.)). Ann. For. Sci. 68(4): 747–757. Springer-Verlag. doi:10.1007/s13595-011-0091-1.
- DeBell, D.S., and Curtis, R.O. 1993. Silviculture and new forestry in the pacific northwest. J. For. **91**(12): 26–30.

- Devine, W.D., and Harrington, C.A. 2009. Relationships Among Foliar Phenology, Radial Growth Rate, and Xylem Density in a Young Douglas-Fir Plantation. Wood Fiber Sci. 41(3): 300–312.
- Di Lucca, C.M. 1989. Juvenile-mature wood transition. *In* Second growth Douglas-fir; its management and conversion for value. Forintek Canada Corp, Vancouver, B.C. pp. 22– 38.
- Di Lucca, C.M. 1998. TASS, SYLVER, TIPSY: Systems for predicting the impact of silvicultural practices on yield, lumber value, economic return and other benefits. *In* Stand Density Management Conference: Using the Planning Tools. *Edited by* C.R. Bamsey. Edmonton, AB. pp. 7–16.
- Diaz, D., Loreno, S., Ettl, G., and Davies, B. 2018. Tradeoffs in Timber, Carbon, and Cash Flow under Alternative Management Systems for Douglas-Fir in the Pacific Northwest. Forests 9(8): 447. doi:10.3390/f9080447.
- DiLucca, C.M. 1989. Juvenile-mature wood transition. *In* Second-growth Douglas-fir: its management and conversion for value. Forintek Canada Corp, Vancouver, B.C. pp. 59– 65.
- Domec, J.-C., and Gartner, B.L. 2002. How do water transport and water storage differ in coniferous earlywood and latewood? J. Exp. Bot. **53**(379): 2369–2379. doi:10.1093/jxb/erf100.
- Doruska, P.F., and Burkhart, H.E. 1994. Modeling the diameter and locational distribution of branches within the crowns of loblolly pine trees in unthinned plantations. Can. J. For. Res. 24: 2362–2376.

- Drew, D.M., and Downes, G.M. 2009. The use of precision dendrometers in research on daily stem size and wood property variation: A review. Dendrochronologia 27(2): 159–172. doi:10.1016/j.dendro.2009.06.008.
- Duchateau, E., Auty, D., Mothe, F., Longuetaud, F., Ung, C.H., and Achim, A. 2015. Models of knot and stem development in black spruce trees indicate a shift in allocation priority to branches when growth is limited. PeerJ 3: e873. doi:10.7717/peerj.873.
- Duchesne, I., Pitt, D.G., and Tanguay, F. 2013. Effects of precommercial thinning on the forest value chain in northwestern New Brunswick: Part 4-Lumber production, quality and value. For. Chron. 89(4): 474–489. doi:10.5558/tfc2013-089.
- Erickson, H.D., and Harrison, a. T. 1974. Douglas-fir wood quality studies part I: Effects of age and stimulated growth on wood density and anatomy. Wood Sci. Technol. 8(3): 207–226. doi:10.1007/BF00352024.
- Fabris, S. 2000. Influence of cambial ageing, initial spacing, stem taper and growth rate on the wood quality of three coastal conifers. The University of British Columbia, Vancouver, B.C.
- Fahey, T.D., Cahill, J.M., Snellgrove, T.A., and Heath, L.S. 1991. Lumber and Veneer Recovery from Intensively Managed Young-Growth Douglas-Fir. Research Paper PNW-RP-437, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station., Portland, OR.
- Filipescu, C.N., Lowell, E.C., Koppenaal, R., and Mitchell, A.K. 2014. Modeling regional and climatic variation of wood density and ring width in intensively managed Douglas-fir.
  Can. J. For. Res. 44(3): 220–229. doi:10.1139/cjfr-2013-0275.

- Franklin, J.F., Berg, D.R., Thornburgh, D.A., and Tappeiner, J.C. 1997. Alternative silvicultural approaches to timber harvesting: variable retention harvest systems. *In* Creating a Forestry for the 21st Century: The Science of Ecosystem Management. Island Press, Washington, D.C. pp. 111–140.
- Fredrikssona, M., Johansson, E., and Berglund, A. 2014. Rotating Pinus sylvestris sawlogs by projecting knots from X-ray computed tomography images onto a plane. BioResources 9(1): 816–827.
- Garber, S.M., and Maguire, D.A. 2005. Vertical trends in maximum branch diameter in two mixed-species spacing trials in the central Oregon Cascades. Can. J. For. Res. 35(2): 295–307. doi:10.1139/x04-164.
- Garcia, O., and Batho, A. 2005. Top Height Estimation in Lodgepole Pine Sample Plots. West. J. Appl. For. **20**(1): 64–68.
- Gartner, B.L. 2007. Does Photosynthetic Bark have a Role in the Production of Core vs. Outer Wood? Wood Fiber Sci. **28**(1): 53–61.
- Gartner, B.L., North, E.M., Johnson, G.R., and Singleton, R. 2002. Effects of live crown on vertical patterns of wood density and growth in Douglas-fir. Can. J. For. Res. 32(3): 439– 447. doi:10.1139/x01-218.
- Gartner, B.L., Robbins, J.M., and Newton, M. 2007. Effects of Pruning on Wood Density and Tracheid Length in Young Douglas-Fir. Wood Fiber Sci. **37**(2): 304–313.
- Gerland, P., Raftery, A.E., Ševčíková, H., Li, N., Gu, D., Spoorenberg, T., Alkema, L., Fosdick,B.K., Chunn, J., Lalic, N., Bay, G., Buettner, T., Heilig, G.K., and Wilmoth, J. 2014.

World population stabilization unlikely this century. Science **346**(6206): 234–237. doi:10.1126/science.1257469.

- Gilmore, A., Boyce, S., and Ryker, R. 1966. The relationship of specific gravity of loblolly pine to environmental factors in southern illinois. For. Sci. **12**(4): 399–405.
- Giudiceandrea, F., Ursella, E., and Vicaro, E. 2011. A high speed CT scanner for the sawmill industry. *In* Proceedings of the 17th international non destructive testing and evaluation of wood symposium. University of West Hungary, Sopron, Hungary.
- Gonzalez, J.S., and Richards, J. 1988. Early selection for wood density in young coastal Douglas-fir trees. Can. J. For. Res. **18**(9): 1182–1185. doi:10.1139/x88-181.
- Goulet, P. 2006. Optitek: User's Manual. Doc E-4130 Forintek Can. Corp Quebec City Quebec Can.
- Gustafsson, L., Baker, S.C., Bauhus, J., Beese, W.J., Brodie, A., Kouki, J., Lindenmayer, D.B.,
  Lõhmus, A., Pastur, G.M., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A.,
  Volney, W.J.A., Wayne, A., and Franklin, J.F. 2012. Retention Forestry to Maintain
  Multifunctional Forests: A World Perspective. BioScience 62(7): 633–645.
  doi:10.1525/bio.2012.62.7.6.
- Gustavsson, L., and Sathre, R. 2006. Variability in energy and carbon dioxide balances of wood and concrete building materials. Build. Environ. 41(7): 940–951.
  doi:10.1016/j.buildenv.2005.04.008.
- Hacke, U.G., Sperry, J.S., Pockman, W.T., Davis, S.D., and McCulloh, K. a. 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. Oecologia 126(4): 457–461. doi:10.1007/s004420100628.

Hann, D.W. 2011. ORGANON User's Manual Edition 9.1.

- Hansen, A.J., Garman, S.L., Weigand, J.F., Urban, D.L., McComb, W.C., and Raphael, M.G.
  1995. Alternative Silvicultural Regimes in the Pacific-Northwest Simulations of
  Ecological and Economic-Effects. Ecol. Appl. 5(3): 535–554. doi:10.2307/1941965.
- Hein, S., Weiskittel, A.R., and Kohnle, U. 2008a. Effect of wide spacing on tree growth, branch and sapwood properties of young Douglas-fir [Pseudotsuga menziesii (Mirb.) Franco] in south-western Germany. Eur. J. For. Res. **127**(6): 481–493. doi:10.1007/s10342-008-0231-9.
- Hein, S., Weiskittel, A.R., and Kohnle, U. 2008b. Branch characteristics of widely spaced
  Douglas-fir in south-western Germany : Comparisons of modelling approaches and
  geographic regions. For. Ecol. Manag. 256: 1064–1079.
  doi:10.1016/j.foreco.2008.06.009.
- Johnson, G.R., and Gartner, B.L. 2006. Genetic variation in basic density and modulus of elasticity of coastal Douglas-fir. Tree Genet. Genomes **3**(1): 25–33. doi:10.1007/s11295-006-0054-0.
- Johnson, J.W., and Kunesh, R.H. 1975. Tensile strength of special Douglas-fir and hem-fir 2inch dimension lumber. Wood Fiber Sci. **6**(4): 305–3018.

Jozsa, L.A. 1995. An overview of forest pruning and wood quality in British Columbia. Forest pruning and wood quality. *In* Forest pruning and wood quality of western North American conifers. *Edited by* D. Hanley, C. Oliver, D. Maguire, D.G. Briggs, and R. Fight. College of Forest Resources, University of Washington, Seattle, WA. pp. 36–64.

- Jozsa, L.A., and Brix, H. 1989. The effects of fertilization and thinning on wood quality of a 24year-old Douglas-fir stand. Can. J. For. Res. **19**: 1137–1145. doi:10.1139/x89-172.
- Jozsa, L.A., and Middleton, G.R. 1994. A discussion of wood quality attributes and their practical implications. Spec. Publ. No SP-34: Special Publication No. SP-34.
- Kantavichai, R., Briggs, D., and Turnblom, E. 2010. Modeling effects of soil, climate, and silviculture on growth ring specific gravity of Douglas-fir on a drought-prone site in Western Washington. For. Ecol. Manag. 259(6): 1085–1092. doi:10.1016/j.foreco.2009.12.017.
- Kellog, R.M. 1989. Second growth Douglas-fir: its management and conversion for value. Special Publication, Forintek Canada Corporation, Vancouver, B.C.
- Kimberley, M.O., Cown, D.J., McKinley, R.B., Moore, J.R., and Dowling, L.J. 2015. Modelling variation in wood density within and among trees in stands of New Zealand-grown radiata pine. N. Z. J. For. Sci. 45(1): 1–13. doi:10.1186/s40490-015-0053-8.
- Kimberley, M.O., McKinley, R.B., Cown, D.J., and Moore, J.R. 2017. Modelling the variation in wood density of New Zealand-grown Douglas-fir. N. Z. J. For. Sci. 47(1): 15. doi:10.1186/s40490-017-0096-0.
- Kucera, B. 1994. A hypothesis relating current annual height increment to juvenile wood formation in Norway spruce. Wood Fiber Sci. 26(1): 152–167.
- Lachenbruch, B., Johnson, G.R., Downes, G.M., and Evans, R. 2010. Relationships of density, microfibril angle, and sound velocity with stiffness and strength in mature wood of Douglas-fir. Can. J. For. Res. 40(1): 55–64. doi:10.1139/X09-174.

- Lachenbruch, B., Moore, J.R., and Evans, R. 2011. Radial Variation in Wood Structure and Function in Woody Plants, and Hypotheses for Its Occurrence. *In Size-* and Age-Related Changes in Tree Structure and Function. *Edited by* F.C. Meinzer, B. Lachenbruch, and T.E. Dawson. Springer Netherlands, Dordrecht. pp. 121–164. doi:10.1007/978-94-007-1242-3\_5.
- Lam, T.Y., and Maguire, D. a. 2011. Thirteen-Year Height and Diameter Growth of Douglas-Fir Seedlings under Alternative Regeneration Cuts in Pacific Northwest. West. J. Appl. For. 26(2): 57–63.
- Larson, P.R. 1960. A physiological consideration of the spring-wood summerwood transition in red pine. For. Sci. **6**: 110–122.
- Larson, P.R. 1963. Stem Form Development of Forest Trees. For. Sci. 9(suppl\_2): a0001-42. doi:10.1093/forestscience/9.s2.a0001.
- Larson, P.R. 1969. Wood formation and the concept of wood quality. Bulletin, Yale University, New Haven.
- Lassen, L.E., and Okkonen, E.A. 1969. Effect of Rainfall and Elevation on Specific Gravity of Coast Douglas-Fir. Wood Fiber Sci. 1(3): 227–235.
- Leemis, L.M. 1991. Nonparametric estimation of the cumulative intensity function for a nonhomogenous poisson process. Manag. Sci. **37**(7): 886–900.

Lindenmayer, D.B., Franklin, J.F., Lõhmus, A., Baker, S.C., Bauhus, J., Beese, W., Brodie, A.,Kiehl, B., Kouki, J., Pastur, G.M., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, J., Wayne, A., and Gustafsson, L. 2012. A major shift to the

retention approach for forestry can help resolve some global forest sustainability issues. Conserv. Lett. **5**(6): 421–431. doi:10.1111/j.1755-263X.2012.00257.x.

- Little, C.H.A., and Wareing, P.F. 1981. Control of cambial activity and dormancy in *Picea sitchensis* by indol-3-ylacetic and abscisic acids. Can. J. Bot. **59**(8): 1480–1493. doi:10.1139/b81-202.
- Lowell, E.C., Maguire, D.A., Briggs, D.G., Turnblom, E.C., Jayawickrama, K.J.S., and Bryce, J. 2014a. Effects of silviculture and genetics on branch/knot attributes of coastal Pacific Northwest Douglas-fir and implications for wood quality-a synthesis. Forests 5(7): 1717–1736. doi:10.3390/f5071717.
- Lowell, E.C., Maguire, D.A., Briggs, D.G., Turnblom, E.C., Jayawickrama, K.J.S., and Bryce, J.
  2014b. Effects of silviculture and genetics on branch/knot attributes of coastal pacific northwest douglas-fir and implications for wood quality-a synthesis. Forests 5(7): 1717–1736. doi:10.3390/f5071717.
- Macdonald, P., and Du, with contributions from J. 2018. mixdist: Finite Mixture Distribution Models. Available from https://CRAN.R-project.org/package=mixdist.
- Maguire, D. a, Johnston, S.R., and Cahill, J. 1999. Predicting branch diameters on secondgrowth Douglas-fir from tree-level descriptors. Can. J. For. Res. **29**(12): 1829–1840. doi:10.1139/x99-147.
- Maguire, D. a, Kershaw, J. a, and Hann, D.W. 1991. Predicting the effects of silvicultural regime on branch size and crown wood core in Douglas-Fir. For. Sci. **37**(5): 1409–1428.

- Maguire, D. a., Moeur, M., and Bennett, W.S. 1994. Models for describing basal diameter and vertical distribution of primary branches in young Douglas-fir. For. Ecol. Manag. 63: 23–55. doi:10.1016/0378-1127(94)90245-3.
- Maguire, D.A. 1994. Branch mortality and potential litterfall from Douglas-fir trees in stands of varying density. For. Ecol. Manag. **70**(1–3): 41–53. doi:10.1016/0378-1127(94)90073-6.
- Maguire, D.A., and Halpern, C.B. 2006. Stand dynamics after variable-retention harvesting in mature Douglas-Fir forests of Western North America. Allg. Forst Jagdztg. 177(6/7): 120–131.
- Maguire, D.A., Halpern, C.B., and Phillips, D.L. 2007. Changes in forest structure following variable-retention harvests in Douglas-fir dominated forests. For. Ecol. Manag. 242(2–3): 708–726. doi:10.1016/j.foreco.2007.02.004.
- Malcolm Knapp Research Forest. 2019. Available from
  - https://www.mkrf.forestry.ubc.ca/about/location-and-ecology/ [accessed 20 June 2019].
- Martinez-Meier, A., Sanchez, L., Pastorino, M., Gallo, L., and Rozenberg, P. 2008. What is hot in tree rings? The wood density of surviving Douglas-firs to the 2003 drought and heat wave. For. Ecol. Manag. 256(4): 837–843. doi:10.1016/j.foreco.2008.05.041.
- Ministry of Forests, Lands, Natural Resource Operations, and Rural Development. 2011. Timber Scaling Manual - Province of British Columbia. Available from https://www2.gov.bc.ca/gov/content/industry/forestry/competitive-forest-industry/timberpricing/timber-scaling/timber-scaling-manual [accessed 22 June 2019].
- Mitchell, K.J. 1969. Simulation of the growth of even-aged stands of white spruce. **75**. Available from http://cfs.nrcan.gc.ca/publications?id=27973 [accessed 25 August 2016].

- Mitchell, K.J. 1975a. Dynamics and simulated yield of Douglas-fir. For. Sci. Monogr. **17**(4): 1–39.
- Mitchell, K.J. 1975b. Stand Description and Growth Simulation from Low-level Stereo Photos of Tree Crowns. J. For. **73**(1): 12–45. doi:10.1093/jof/73.1.12.
- Montwé, D., Spiecker, H., and Hamann, A. 2015. Five decades of growth in a genetic field trial of Douglas-fir reveal trade-offs between productivity and drought tolerance. Tree Genet. Genomes **11**(2): 1–11. doi:10.1007/s11295-015-0854-1.
- Nemec, A.F., Parish, R., and Goudie, J.W. 2012. Modelling number, vertical distribution, and size of live branches on coniferous tree species in British Columbia. Can. J. For. Res.
  42(6): 1072–1090. doi:10.1139/x2012-060.
- Newton, M., Lachenbruch, B., Robbins, J.M., and Cole, E.C. 2012. Branch diameter and longevity linked to plantation spacing and rectangularity in young Douglas-fir. For. Ecol. Manag. 266: 75–82. doi:10.1016/j.foreco.2011.11.009.

NLGA. 2014. Standard grading rules for canadian lumber. National Lumber Grades Authority.

Nyvold, U., Dawson, J.K., and Hickey, J.E. 2005. An assessment of timber values from alternative silvicultural systems tested in wet Eucalyptus obliqua forest in Tasmania. Tasforests **16**(December): 19.

Oliver, C.D., and Larson, B.C. 1996. Stand Dynamics. John Wiley & Sons, Inc., New York, NY.

Pallardy, S.G. 2010. Physiology of Woody Plants. Academic Press.

Pastur, G.M., Lencinas, M.V., Cellini, J.M., Peri, P.L., and Soler Esteban, R. 2009. Timber management with variable retention in Nothofagus pumilio forests of Southern
Patagonia. For. Ecol. Manag. 258(4): 436–443. doi:10.1016/j.foreco.2009.01.048.

- Pernkopf, M., Riegler, M., and Gronalt, M. 2019. Profitability gain expectations for computed tomography of sawn logs. Eur. J. Wood Wood Prod. 77(4). doi:10.1007/s00107-019-01414-x.
- Pewsey, A., Neuhäuser, M., and Ruxton, G.D. 2013. Circular statistics in R. *In* First edition. Oxford University Press, Oxford ; New York.
- Pienaar, L.V., and Turnbull, K.J. 1973. The Chapman-Richards Generalization of Von Bertalanffy's Growth Model for Basal Area Growth and Yield in Even - Aged Stands.
  For. Sci. 19(1): 2–22. doi:10.1093/forestscience/19.1.2.
- Pitt, D.G., Bicho, P., Portillo, E., Yuen, B., and Yan, D. 2013. Effects of precommercial thinning on the forest value chain in northwestern New Brunswick: Part 1 - Roundwood production and stumpage value. For. Chron. 89(4): 446–457. doi:10.5558/tfc2013-086.
- Pojar, J., Klinka, K., and Meidinger, D.V. 1987. Biogeoclimatic ecosystem classification in British Columbia. For. Ecol. Manag. 22(1): 119–154. doi:10.1016/0378-1127(87)90100-9.
- Pretzsch, H., and Rais, A. 2016. Wood quality in complex forests versus even-aged monocultures: review and perspectives. Wood Sci. Technol. 50(4): 845–880. doi:10.1007/s00226-016-0827-z.
- Punches, J.W., and Puettmann, K.J. 2018. Distribution of epicormic branches and foliage on
  Douglas-fir as influenced by adjacent canopy gaps. Can. J. For. Res. 48(11): 1320–1330.
  doi:10.1139/cjfr-2018-0071.
- R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. doi:3-900051-07-0.

- Rais, A., Poschenrieder, W., Pretzsch, H., and Van De Kuilen, J.W.G. 2014. Influence of initial plant density on sawn timber properties for Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco). Ann. For. Sci. 71(5): 617–626. doi:10.1007/s13595-014-0362-8.
- Renninger, H.J., Gartner, B.L., and Grotta, A.T. 2006. No correlation between latewood formation and leader growth in Douglas-fir saplings. IAWA J. **27**(2): 183–191.
- Robbins, J.M. 2000. Influence of spacing and crown recession on wood quality of intensivelymanaged young-growth Douglas-fir. Oregon State University, Corvallis, OR.
- Rouvinen, S., and Kuuluvainen, T. 1997. Structure and asymmetry of tree crowns in relation to local competition in a natural mature Scots pine forest. Can. J. For. Res. 27(6): 890–902. doi:10.1139/x97-012.
- Samson, M. 1993. Modelling of knots in logs. Wood Sci. Technol. **27**(6): 429–437. doi:10.1007/BF00193865.
- Sattler, D.F., Finlay, C., and Stewart, J.D. 2014. Annual ring density for lodgepole pine as derived from models for earlywood density, latewood density and latewood proportion. Forestry 88(5): 622–632. doi:10.1093/forestry/cpv030.
- Schajer, G.S. 2016. Wood machining: Past achievements, present capabilities, future opportunities. Wood Mater. Sci. Eng. 11(3): 127–134. doi:10.1080/17480272.2015.1112833.
- Sekhon, J.S. 2011. Multivariate and Propensity Score Matching Software with Automated Balance Optimization: The Matching package for R. J. Stat. Softw. 42(1): 1–52. doi:10.18637/jss.v042.i07.

- Sheppard, S.R.J., Achiam, C., and D'Eon, R.G. 2004. Aesthetics: Are We Neglecting a Critical Issue in Certification for Sustainable Forest Management? J. For. **102**(5): 6–11.
- Shmulsky, R., and Jones, P.D. 2011. Forest products and wood science: An introduction. Wiley-Blackwell, Oxford, UK. doi:10.1002/9780470960035.
- Skog, K.E., Wegner, T.H., Bilek, E.M., and Michler, C.H. 2014. Desirable properties of wood for sustainable development in the twenty-first century. Ann. For. Sci. doi:10.1007/s13595-014-0406-0.
- Smith, J.H.G., and Kennedy, R.W. 1983. Effect of stand management on tree, log and wood quality of Douglas-fir. IAWA Bull. **4**(1): 1–12.
- Sprugel, D.G. 2002. When branch autonomy fails: Milton's Law of resource availability and allocation. Tree Physiol. **22**(15–16): 1119–1124. doi:10.1093/treephys/22.15-16.1119.
- Sprugel, D.G., Hinckley, T.M., and Schaap, W. 1991. The Theory and Practice of Branch Autonomy. Annu. Rev. Ecol. Syst. 22(1): 309–334. doi:10.1146/annurev.es.22.110191.001521.
- St. Clair, J.B. 1994. Genetic variation in tree structure and its relation to size in Douglas-fir. II. Crown form, branch characters, and foliage characters. Can. J. For. Res. 24(6): 1236– 1247. doi:10.1139/x94-162.
- Stevens, J.A., and Barbour, R.James. 2000. Managing the stands of the future based on the lessons of the past: estimating western timber species product recovery by using historical data. Res. Note PNW-RN-528., U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR.

- Stoehr, M.U., Ukrainetz, N.K., Hayton, L.K., and Yanchuk, A.D. 2009. Current and future trends in juvenile wood density for coastal Douglas-fir. Can. J. For. Res. 39(7): 1415–1419. doi:10.1139/X09-059.
- Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M., and Jeltsch, F. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J. Biogeogr. **31**(1): 79–92. doi:10.1046/j.0305-0270.2003.00994.x.
- Thomas, J.W. 1997. Forward. *In* Creating a forestry for the 21st century. *Edited by* K.A. Kohm and J.F. Franklin. Island Press/Center for Resource Economics, Washington, D.C. pp. 1– 6.
- Todoroki, C.L. 1990. AUTOSAW system for sawing simulation. N. Z. J. For. Sci. **20**(3): 332–348.
- Todoroki, C.L., Monserud, R.A., and Parry, D.L. 2005. Predicting internal lumber grade from log surface knots: Actual and simulated results. For. Prod. J. **55**(6): 38–47.
- Toman, M.A., and Ashton, P.Mark.S. 1996. Sustainable Forest Ecosystems and Management : A Review Article. For. Sci. **42**(3): 366–377.
- Trincado, G., and Burkhart, H.E. 2009. A framework for modeling the dynamics of first-order branches and spatial distribution of knots in loblolly pine trees. Can. J. For. Res. 39(3): 566–579. doi:10.1139/X08-189.
- Tyree, M.T., and Zimmermann, M.H. 2002. Xylem Structure and the Ascent of Sap. *In* 2nd edition. Springer-Verlag, Berlin Heidelberg.

- Ukrainetz, N.K., Kang, K.-Y., Aitken, S.N., Stoehr, M., and Mansfield, S.D. 2008. Heritability and phenotypic and genetic correlations of coastal Douglas-fir (Pseudotsuga menziesii) wood quality traits. Can. J. For. Res. **38**(6): 1536–1546. doi:10.1139/X07-234.
- Umeki, K. 1997. Effect of Crown Asymmetry on Size–Structure Dynamics of Plant Populations. Ann. Bot. **79**(6): 631–641. doi:10.1006/anbo.1996.0388.
- Vargas-Hernandez, J., and Adams, W. 1991. Genetic variation of wood density components in young coastal Douglas-fir: implications for tree breeding. Can. J. For. Res. 21: 1801– 1807.
- Waring, R., and Franklin, J. 1979. Evergreen coniferous forests of the pacific northwest. Science **204**: 1380–1386.
- Wegner, T., Skog, K.E., Ince, P.J., and Michler, C.J. 2010. Uses and Desirable Properties of Wood in the 21st Century. J. For. **108**(4): 165–173.
- Weiskittel, A.R., Maguire, D.A., and Monserud, R.A. 2007. Modeling crown structural responses to competing vegetation control, thinning, fertilization, and Swiss needle cast in coastal Douglas-fir of the Pacific Northwest, USA. For. Ecol. Manag. 245(1–3): 96– 109. doi:10.1016/j.foreco.2007.04.002.
- Wellwood, R.W. 1952. The effect of several variables on the specific gravity of second-growth Douglas fir. For. Chron. **28**(3): 34–44. doi:10.5558/tfc28034-3.
- Williams, H., Messier, C., and Kneeshaw, D.D. 1999. Effects of light availability and sapling size on the growth and crown morphology of understory Douglas-fir and lodgepole pine.
  29: 10.

- Zenner, E.K., Acker, S.A., and Emmingham, W.H. 1998. Growth reduction in harvest-age, coniferous forests with residual trees in the western central Cascade Range of Oregon.
  For. Ecol. Manag. 102(1): 75–88. Elsevier. doi:10.1016/S0378-1127(97)00108-4.
- Zielke, K., Bancroft, B., Sw, K., and Turner, J. 2008. British Columbia's Coastal ForestsVariable Retention Decision Aid for Biodiversity and Habitat Retention. J. Ecosyst.Manag. 9(2). [accessed 31 August 2016].
- Zobel, B.J., and van Buijtenen, J. 2012. Wood variation: its causes and control. Springer-Verlag, Berlin.