EVALUATING THE IMPACT OF STAND COMPOSITION AND COMPETITION ON WHITE SPRUCE AND ASPEN WOOD ATTRIBUTES IN THE BOREAL MIXEDWOOD

by

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Abstract

I evaluated how intra- and inter-specific competition affects the development of eleven wood attributes of trembling aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench) Voss) over 34 years. My analysis was conducted in a mixedwood trial site in Northern British Columbia, Canada, that included treatments consisting of 0, 1000, 2000, 5000, and 10000 stems per hectare of aspen. Competition was found to negatively influence wood attribute development in aspen and positively impact spruce (at low levels of competition). Plot level competition indices were the best predictor of variation in aspen wood attributes, while stand level competition (population density) best explained the majority of spruce wood attributes. Maintaining aspen at lower densities in intimate mixture can have a positive effect on spruce wood quality, while incurring relatively small reductions in spruce volume production and also retaining the ecological benefits associated with managing for mixed stands.

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1. Introduction

1.1 Boreal forest introduction and overview

Boreal forests are frequently composed of broadleaf and conifer trees interacting and competing for limited resources. These forests are among the most productive and diverse forest ecosystems in North America (Chen and Popadiouk 2002). Aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench) Voss) are the predominant components of the Western Canadian boreal mixedwood forest and competition driven succession between these species is the primary process of forest composition shift (Jiang et al. 2018). The forest industry in western Canada has largely focused on the utilization of softwood, however, reductions in the predicted midterm supply, pine beetle infestation, projected future climate change, and a shift towards the valuation of products such as carbon storage all portend to an increased use of hardwood species (McCulloch and Kabzems 2009; Mbogga et al. 2010; Dhar et al. 2016). Previous studies have evaluated the challenges and benefits of growing various mixed stands have primarily focused on stand productivity, nutrient cycling, over yielding potential, pest and fire mitigation, and resistance to climate change (Brassard et al. 2008; Girardin and Terrier 2015; Laganière et al. 2015; Kweon and Comeau 2019). Many of the studies focusing on wood quality in mixedwoods have focused on basal area increment or biomass productivity. However, recently within wood attributes such as wood density, and modulus of elasticity (MOE), have become a subject of interest in both aspen and spruce due to the increased economic appeal of aspen products and softwood value-added forest products. The objective of this thesis is to examine the effect of competition on the within wood attributes of both aspen and white spruce.

1.2 Mixedwood stand dynamics

Historically, aspen has been viewed as a weed, undesirable and inhibiting of preferred conifer growth (Carleton and Maycock 1981). Aspen is frequently the primary tree species to grow in post-disturbance landscapes, following destructive fire, beetle infestation or clear-cut through asexual root suckering (Comeau et al. 2005; Frey et al. 2011; Smith et al. 2011). Aspen is shade intolerant and displays fast initial growth rates, which allows it to quickly dominate the forest canopy, compared to the seed-sowed and slow juvenile growth rates of spruce (Lieffers et al. 1996). Aspen, however, has a short lifespan (50 – 60 years), and reaches the age of senescence earlier than most conifers (250 – 300 years). Canopy openings from this senescence allows for establishment or release of more shade tolerant, slow-growing conifer species, including spruce (Brassard and Chen 2006). Competition is particularly critical for mixedwood stand development in the stem exclusion or self-thinning phase (20-40 years of stand age) where resources such as light, soil moisture and nutrients become scarce as the trees expand in size, leading to logarithmic decreases in stem density (Lieffers et al. 2002; Chen and Popadiouk 2002). Although spruce is a shade tolerant species, studies have shown a strong response in radial and height growth to increases in light, and poor conifer height growth under dense hardwood canopies with light levels below 20% of full sunlight (Lieffers and Stadt 1994).

1.3 Combining abilities of mixed stands

Management objectives have been biased towards conifer growth as softwoods offer superior properties for both pulp and lumber, however, recent studies have demonstrated the ecological and economic benefits of growing white spruce in conjunction with aspen. As such, the novel silviculture technique of planting spruce under developing or mature aspen has been shown to effectively create boreal mixedwood establishment (Kabzems et al. 2016). Managing for mixtures can vary with site fertility, but, can also positively impact the diversification of each species functional traits, which, maximizes growing space (Pretzsch et al. 2013). Species diversity can increase ecosystem function through habitat creation and through increased nutrient cycling leading to productivity and carbon sequestration (Brassard et al. 2008; Laganière et al. 2015; Payne et al. 2019). Competition is the driving force of stand diversity in mixedwood stands as it strongly influences successional trajectory (Filipescu and Comeau 2007). This successional trajectory contributes to the landscape patchwork age-class distribution, which in turn, mitigates fire and insect outbreak (Comeau et al. 2005; Girardin and Terrier 2015).

Since the early 2000's, utilization of aspen increased and is now the main fibre source for several oriented strand board (OSB) and veneer mills. Support for mixedwood management options, including aspen utilization, has the potential to diversify forest silviculture and lower costs of traditionally intensive silviculture practices while creating more resilient forests in B.C. Also, the delayed maturation age of spruce relative to aspen allows for multiple entry partial harvest, thereby allowing constant timber supply, while preserving biodiversity and habitat continuation (Man and Lieffers 1999).

One of the distinct benefits of mixedwood forests is the potential for overyielding, or the increase in productivity of a mixed species stand compared to a monoculture (Hector 1998). Overyielding can occur when managing for space partitioning and size inequality between spruce and aspen (Hector 1998; Kweon and Comeau 2019). The potential for overyielding in boreal aspen spruce mixtures has been identified (Man and Lieffers 1999; Kabzems et al. 2007). However, an increase in volume is only desirable when it corresponds with merchantable timber. The characterization of wood attributes along with cost effective land use management is at the forefront of the boreal forest industry's fundamental shift from traditional wood products to multiple value-added forest products (Chen et al. 2017).

1.4 Wood attribute overview

Mixed species stands have been found to differ from pure stands in terms of growth (Comeau et al. 2004; Pretzsch et al. 2013), tree shape (Pretzsch 2019), resource use efficiency (Carr et al. 2020), and resistance to disturbance (Hansen et al. 2016). Much less is known on the effect of tree mixtures on individual tree wood attribute development, especially in the boreal mixedwood. Mixedwood stands provide opportunities to apply variation in silviculture techniques such as planting densities and thinning treatments to manage for desired combinations of wood properties and yield (Comeau 2021). Wood attributes (Table 1.1) within both soft and hardwoods have impacts on tree survivability and the grade of economic viability.

Table 1.1 A summary of each of the wood attributes that were analyzed in this study

Wood Attribute	Description	Economic Value	History
Modulus of Elasticity (MOE)	A measure of stress compared to strain within wood, and often varies with MFA (Evans and Ilic 2001)	Stiffness of wood increases resistance to trunk breakage, xylem explosion and increases stem stability (Hacke et al. 2001)	Previous studies have shown that MOE is the best representation of wood stiffness (Antony et al. 2012a; Sattler et al. 2014)
Microfibril Angle (MFA)	The orientation of the crystalline cellulose in the secondary cell wall (S2) wood along the fibre axis (Cave 1966).(Varies with age as juvenile (core) wood has larger MFA, mature wood has lower MFA (Barnett and Bonham 2004).	Low MFA leads to higher dimensional stability in lumber and tensile strength in paper. As MFA increases, stiffness and compressive strength decrease (Aziz 2013).	Previous studies have shown that MFA varies most with age (De Araujo et al. 2015).

Wood Attribute	Description	Economic Value	History
Density	Wood density is defined as the ratio of the oven-dry weight of a sample to the weight of a volume of water equal to the volume of the sample at a specified moisture content (green, air-dry, or oven-dry).	Wood density influences lumber strength (determining lumber grade), pulp yield, pulp quality, timber shrinkage, stiffness, hardness, heating value, machinability, and energy requirement of the pulping process (Jozsa and Middleton 1994). Denser wood is associated with lowered trunk breakage, xylem implosion and increased stem stability (Hacke et al. 2001).	Previous study has shown that there was no effect of mixed vs pure competition having an effect on wood density (De Araujo et al. 2015)
Ring area	Related to ring width	Fibre morphology and cell wall structure directly influences fibre flexibility, plasticity and resistance to processing	Height (rather than diameter) preferred growth in competitive environments has resulted in a lower ring width in aspen and spruce (Coopersmith and Hall 1999)
Specific surface area	Fibre perimeter divided by coarseness (See methods equation 3).	Tensile strength	
Ring width	Ring width represents the interannual variability in several factors both endogenous and exogenous. Variations in climate, site conditions, competition, and disturbance lead to differences in observed ring widths (Fritts 1976)	Lower ring width can indicate increased density and impact other wood attributes	Height (rather than diameter) preferred growth in competitive environments has resulted in a lower ring width in aspen and spruce (Coopersmith and Hall 1999)
Tangential Diameter	Tracheid length parallel, or tangent, to growth rings.	Tracheid length, diameter and wall thickness not only affect tensile and tear strength, but also impact the optical and printing properties of paper (Macdonald and Hubert 2002).	Longer fibres have been reported for mixed white spruce and aspen sites compared to pure stands (De Araujo et al. 2015).
Radial Diameter	Tracheid length that is perpendicular to growth rings.	Fibre morphology and cell wall structure directly influences fibre flexibility, plasticity and resistance to processing	Longer fibres have been reported for mixed white spruce and aspen sites compared to pure stands (De Araujo et al. 2015).

Wood Attribute	Description	Economic Value	History
Coarseness	Defined as the weight per unit length of the wood fibres (methods equation 3)	Lower Coarseness means higher tear strength, greater bonding area, and more fibres per tonne of pulp, which are important to papermaking (Watson and Bradley 2009)	Higher coarseness has been reported for mixed white spruce and aspen sites compared to pure stands (De Araujo et al. 2015).
Wall Thickness	The thickness of xylem cell walls.	Influences fibre collapsibility during paper making	Thickness in the cell wall may change in response to long term ecological factors such as wind, exposure and climate, thereby changing MFA and resultant wood properties (Hein and Lima 2012).

Within angiosperms (aspen) and gymnosperms (spruce), xylem cells are necessary for structural integrity and for water transport within the tree. Gymnosperm tracheids are characterized by many bordered pits in their radial walls, and are also much longer than angiosperm fibres (Barnett and Bonham 2004). The orientation and magnitude of certain characteristics within the tracheid reflects the influence of external forcing which can include competition, or environmental conditions such as temperature changes, nutrient availability, precipitation, increased wind stress or snowpack (Speer 2012).

Traditionally, density has been considered the most important industry wood trait as it affects wood quality as well as the tear strength and burst of paper (Zobel and Jett 1995). Studies have shown that ecologically, a denser wood is associated with lowered trunk breakage, xylem implosion, and increased stem stability (Hacke et al. 2001).

However, it has been shown that the longitudinal modulus of elasticity (MOE) which is a measure of stress compared to strain within wood, is in fact the best representation of wood stiffness which is both desirable ecologically and for industry application (Antony et al. 2012b; Sattler et al. 2014). Microfibril angle (MFA) is defined as the orientation of the crystalline cellulose in the secondary cell wall (S2) wood along the fibre axis (Cave 1966). The MFA is measured within the S2 layer of the secondary cell wall since the thickness of the S2 layer is much greater than that of the primary S1 or S3 layers. Furthermore, MFA varies with age as juvenile (core) wood has a larger MFA where-as mature (outer) wood displays a low MFA (Barnett and Bonham 2004). As MFA increases in the wood, the stiffness and compressive strength decrease (Aziz 2013). In general, low MFA leads to higher dimensional stability in lumber and tensile strength in paper. Thickness in the cell wall may change in response to exterior forces such as wind and thunderstorm, thereby changing the MFA and the resultant wood properties (Hein and Lima 2012). Studies have found that Microfibril Angle (MFA) is the best predictor of MOE, whereby MFA alone accounts for 86% of the variation observed in MOE, and together with wood density describe 96% of the variation in MOE (Evans and Ilic 2001).

Fibre wall thickness in conjunction with fibre width influences fibre collapsibility during paper making. Coarseness is defined as the weight per unit length of the wood fibres. Lower coarseness means higher tensile sheet strength, greater bonding area, and more fibres per tonne of pulp, all of which are highly prized by papermakers (Watson and Bradley 2009). Ring width represents the interannual variability in several factors both endogenous and exogenous. Variations in climate, site conditions, competition, and disturbance lead to differences in observed ring widths (Fritts 1976). Lower ring width can indicate increased density and other desirable attributes.

1.5 Competition in the mixedwood

Studies of how competition influences wood attributes within mixedwood systems have been limited. Competition indices enable the quantitative analysis of relationships between stand composition and wood attributes. Competition indices are numerical expressions that describe how much each tree is affected by its neighbours. Two main types of competition indices are often considered: distance-independent and distance-dependent. Distance-independent indices are typically easier to calculate as they require less data, and have performed similarly to distance-dependent indices in previous modelling applications (Kahriman et al. 2018). However, much of the study of competition indices has been confined to models relating exterior tree growth characteristics or mortality, and there is currently a lack of research concerning the resolution required for finer wood attributes (Kahriman et al. 2018; Sun et al. 2019). Within mixed forest plantations in Eastern Quebec, distance independent indices have successfully quantified the competition effect on basal area increment growth in planted white spruce, while distance-independent indices worked best for ingrown or non-planted species (Bérubé-Deschênes 2017). In an analysis of permanent sample plots that included pure and mixed stands of aspen and white spruce of varying age in Central Alberta, wood density and carbohydrate content was found to be consistent across sites, while MFA was lower within aspen sampled in pure stands and fibre characteristics were higher in the pure site for both species (De Araujo et al. 2015). Previous studies have been limited due to sampling uneven age stands with inconsistent measures of treatment density. This study builds on previous work by analyzing the effect of competition on wood attribute development in managed aspen and spruce stands with homogenous site conditions.

1.6 Thesis Objectives

The purpose of this study was to characterize eleven wood attributes (Table 1.1) of both white spruce and trembling aspen grown in various levels of competition within a mixedwood trial site where tree ages and other ecological conditions were uniform. The specific objectives were:

1. To determine if there was a difference in wood attribute response to stand level competition between species.
2. To determine if aspen and white spruce display similar responses to stand level competition over time.
3. To analyze if there are any economic benefits observed in wood attributes with increasing aspen treatment density.
4. To compare spruce and aspen wood attribute response to inter- and intra-specific competition.
5. To utilize plot data and formulate neighbourhood level competition indices. Then to determine which neighbourhood level competition indices best improved a model for wood attributes in both aspen and spruce.
6. To determine the competition resolution required for the wood attributes of both spruce and aspen.

In addition to the introductory chapter, this thesis contains two chapters written as stand-alone manuscripts that address the above objectives, as well as a concluding chapter which synthesizes the conclusions from each of the two manuscripts. The following chapter (Chapter 2) explored objectives 1 through 3, by applying a mixed effect model approach to tree core data collected to characterize eleven wood attributes across different competition regimes. Chapter 3 builds on the mixed effect model of Chapter 2, by utilizing plot data from the study site to increase the competition resolution in order to explore objectives 4 to 6.

2. Evaluating the impact of stand composition and competition on Spruce and Aspen wood attributes in mixedwood stands

2.1 ABSTRACT

In this study, we sampled 50 aspen (*Populus tremuloides*) and 70 white spruce (*Picea glauca*) in northern British Columbia. We analyzed 11 wood attributes (microfibril angle, density, modulus of elasticity, cell wall thickness, coarseness, ring width, cell population, specific surface area, ring area, tangential diameter, and radial diameter) over five population densities (0, 1000, 2000, 5000, and 10,000 stems per hectare (sph) aspen) to evaluate the impact of competition on wood attributes. Through a mixed effects model framework, two thresholds emerged from our analysis. First, the largest effect on spruce wood attribute development occurred when aspen was grown in intimate mixture with spruce compared to spruce grown without aspen. Second, was the variation observed in the 10,000 sph aspen treatment compared to the treatments with lesser densities of aspen. Our results indicate that desirable wood attributes are generally increased when spruce is grown with aspen competitors. Further, our results show that desirable traits within aspen decrease with increasing levels of competition. Therefore, maintaining aspen at lower densities in intimate mixture can increase spruce wood quality, production and also provide the ecological benefits of aspen and their potential positive impacts on forest resilience, while incurring some reductions in spruce volume.

2.2 INTRODUCTION

Mixedwood forests are some of the most productive and diverse forest ecosystems in North American boreal forests (Chen and Popadiouk 2002), and support a range of ecosystem services such as reducing the risk of insect/pathogen/fire outbreaks and improving resilience to climate change (Bergeron et al. 2014). Mixedwood forests can also facilitate forest productivity (Reyes-Hernández and Comeau 2015), and are a source of lumber and various value added forest products (McCulloch and Kabzems 2009). Aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench) Voss) are the primary components of the Western Canadian boreal mixed forest and competition driven succession between these species is the primary process of forest composition shift (Jiang et al. 2018). Previous studies have shown that various levels of competition between species in a mixed stand can influence yield, biomass production, and exterior growth characteristics (Comeau et al. 2005; Kabzems et al. 2007). These findings have influenced forest management techniques, but knowledge gaps remain with regard to how stand composition and neighbourhood competition impacts spruce and aspen wood attributes and by extension economic value.

The forest industry in western Canada has largely focused on the utilization of conifers, however, reductions in the predicted midterm timber supply, pine beetle infestation, projected future climate change, and a shift towards the valuation of ecosystem services such as carbon storage all portend to an increased use of broadleaf species (McCulloch and Kabzems 2009; Mbogga et al. 2010; Dhar et al. 2016). Historically, aspen has been viewed as a weed, undesirable and inhibiting of preferred conifer growth (Carleton and Maycock 1981). Past management objectives were biased towards conifer growth as they offered superior properties for both pulp and lumber production, based on industrial scale processes available at the time.

Although the majority of current industrial application relies on conifer growth, the benefits of more holistic forest management plans which incorporate a diversity of tree species are increasingly recognized (Macdonald et al. 2010). For instance, the silviculture technique of planting spruce under developing or mature aspen has been shown to effectively establish boreal mixedwood conditions (Kabzems et al. 2016). Overyielding, or the increase in productivity of a mixed species stand compared to a monoculture, can occur when managing for space partitioning and size inequality between spruce and aspen (Hector 1998; Kweon and Comeau 2019). Within a mixed stand, an aspen density of 2000 – 5000 stems per hectare (sph) and white spruce at 1300 sph allows for overyielding with 21% more volume produced than monocultures of either (Kabzems et al. 2007). Also, the delayed maturation age of spruce relative to aspen allows for multiple-entry partial harvest, thereby enabling more consistent timber supply, while preserving biodiversity and habitat continuation (Man and Lieffers 1999). As a result, there has been increased interest in managing for intimate mixtures of aspen and spruce.

Developing a more thorough understanding of the complex interactions of the mixedwood system, and specifically how competition between overstory trees may influence tree growth and wood properties, is vital to the effective future management of these forests. Within angiosperms (aspen) and gymnosperms (spruce), xylem cells are important for structural integrity and for water transport within the tree. Gymnosperm tracheids are characterized by many bordered pits in their radial walls, and are also, often, longer than angiosperm fibres (Barnett and Bonham 2004). The orientation and magnitude of certain characteristics within the tracheid reflects the influence of external forcing which can include competition, or environmental conditions such as temperature changes, nutrient availability, precipitation, increased wind stress or snowpack (Speer 2012). Wood density, modulus of elasticity (MOE), microfibril angle (MFA), and other wood attributes (Table 1.1) are potentially responsive to changes in a trees neighbourhood composition, stand structure, and the type and intensity of competition that a tree experiences (Pretzsch and Rais 2016).

The primary objective of this study is to characterize the wood attributes of both white spruce and trembling aspen grown within an established mixedwood research experiment with variable aspen densities where tree ages and ecological conditions are uniform. The first sub-objective is to determine if there is a difference observed in wood attribute variation between species. The second sub-objective is to determine if there is a difference observed in wood attribute response to competition between species. The third and final sub-objective is to determine if spruce and aspen wood attributes display similar responses to competition, and whether those differences can be translated into discernable economic benefits. To achieve these sub-objectives, three hypotheses were formulated. The first hypothesis is that spruce and aspen display differences in their wood attributes which will be tested through the evaluation of a linear mixed effect model. Spruce has been shown to display physiological differences as well as variation in basal area increment growth in response to competition, so it is likely that spruce will also display differences in other wood attributes. Aspen is shade intolerant, and therefore will likely have a more pronounced reaction to competition than spruce. Therefore, the second hypothesis is that there is a difference in wood attribute response to competition between species. Finally, the third hypothesis is that spruce and aspen will display different responses to competition that will translate to benefits (or detriments) in wood quality. Evaluation of this third hypothesis will be critical to understanding the role that competition plays on wood quality in the boreal mixedwood.

2.3 MATERIALS AND METHODS

2.3.1 Study Site

The study site is located 45 km northeast of Fort St. John, British Columbia (Figure 2.1) in the moist warm subzone of the Boreal White and Black Spruce biogeoclimatic zone (BWBSmw, DeLong et al. 2011).

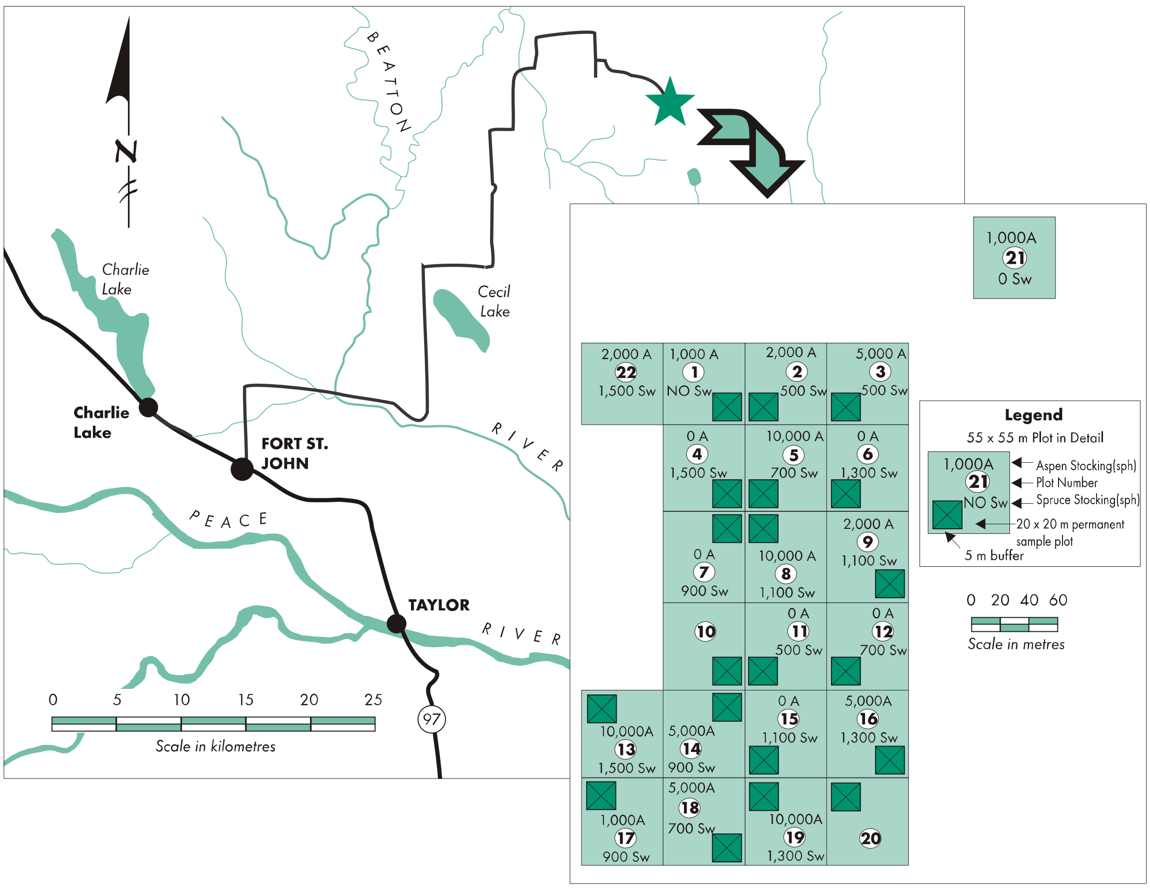


Figure 2.1 A map of Siphon Creek trial site with the treatment map (Richard Kabzems)

The site is characterized by a mesic to sub hygric moisture regime and rich nutrient regime (Kabzems et al. 2007). The soils underlying the study area are fine-textured Gray Luvisols, moderately well drained, with a thick, gray Ae horizon over a more fine-textured Bt horizon (Lord and Green 1986).

The area was selectively logged for conifers in 1968. The remaining aspen trees and existing vegetation were sheared and windrowed in the early winter of 1984/85. In 1985, the site was planted with three-year-old bareroot white spruce seedlings at 1480 stems per hectare, which were sampled for this study at 33 years of age. The study site was established in 1989 as part of Ministry of Forests Experimental Project 1077, and plots were laid out in 1990. Twenty plots with varying densities of aspen (0, 5000, and 10,000 stems per hectare) combined with a second planting of white spruce (0, 500, 700, 900, 1100, 1300 and 1500 stems per hectare) were laid out. In 1990, the aspen regeneration was manually thinned to target densities of 0, 5000, and 10,000 stems per hectare and all other tree and tall shrub species manually removed, similar to a juvenile spacing treatment. Repeated manual brushings were applied until 2000 to maintain the 0-aspen treatment. In the summer of 2000, two additional aspen treatments (1000 and 2000 stems per hectare) were created by reducing existing densities in previously established plots (Kabzems et al. 2015).

2.3.2 Data Collection

Samples were obtained in 2018 from trees within the 0, 1000, 2000, 5000, and 10,000 sph aspen treatment units (Table 2.1). A total of five undamaged spruce trees (i.e., those with no mechanical damage, forked tops, or other obvious growth issues), were sampled within each treatment. All sampled spruce trees within a treatment replicate were separated by a minimum 10-meter distance to ensure distribution over the plot. For each sampled spruce tree, one aspen was deemed to be ‘paired’ with the spruce and sampled. The aspen ‘pair’ was the nearest healthy, canopy dominant aspen stem within 1-2 meters of the sampled spruce tree.

Table 2.1Descriptive statistics of sampled trees. Diameter at breast height (DBH) means are shown with standard deviations in parentheses.

Treatment (aspen sph)	Spruce DBH (cm)	Aspen DBH (cm)	Number of spruce samples	Number of aspen samples
0	17.3 (2.3)	NA	20	0
1000	16.2 (3.1)	15.7 (4.2)	5	5
2000	15.0 (5.2)	14.4 (3.9)	5	5
s5000	12.1 (1.5)	13.7 (2.8)	20	20
10000	11.1 (2.1)	11.6 (1.8)	20	20

Using an increment borer, a 12 mm core was collected at breast height (1.3m), from each tree selected. Core position was chosen to minimize effects of slope on the ring patterns and to facilitate optimal cross dating. The cores were placed in paper tubes for protection and allowed to air dry prior to preparation. The condition and growth form of each sampled tree was noted along with any indications of historic abiotic or biotic damage. Height and diameter at breast height (DBH) were measured for the selected tree and for all neighborhood trees within a 3.99-meter radius of the targeted spruce and aspen stems. Competitive trees were deemed to be those greater than 1.3 m in height. The species and the distance of the competitive tree to the target tree were also recorded.

2.3.3 Sample Preparation

Tree core samples were air-dried and prepared for analysis in the University of Northern BC (UNBC) Dendrochronology Laboratory. An important factor controlling density in wood is resin. Since resin is unevenly distributed within the wood and it has different properties than the wood itself, it must be removed (Speer 2012). Samples were soaked in acetone for 8 hours, before being passed through a Soxhlet apparatus for a further 8 hours (Rydval et al. 2014). Within the Soxhlet apparatus, the acetone boils, and the steam will rise until it hits a condenser, then drips into the core chamber. When the acetone reaches a maximum height, the chamber is drained and the process is repeated, thereby extracting the resins. Once the samples were removed of all resins, they were sent to FPInnovations for SilviScan® analysis.

FPInnovations in Vancouver, Canada, further prepared the 12 mm cores collected. Cores were air-dried and then cut into strips of 2 x 7 mm (tangentially x longitudinally) using a twin-blade saw. Resulting laths were scanned using SilviScan® technology. Each strip was scanned for radial and tangential cell dimensions using optical microscopy, wood density using x-ray densitometry, and microfibril angle (MFA) using x-ray diffractometry. The analysis performed measured wood properties every 25 μm across the wood lath, with the exception of microfibril angle, which was measured every 5 mm. Properties measured included ring density, radial and tangential diameters, and microfibril angle. Coarseness (Cr), cell wall thickness (CWT), and Specific Surface Area (SSA) values were calculated as a function of other measured variables through the following equations:

[1] $$Cr = R \times T \times D_w$$

[2] $$CWT = \frac{P}{8}\left(1 - \sqrt{1 - \frac{16Cr}{P^2 D_w}}\right)$$

[3] $$SSA = P/Cr$$

Where: $P = 2\,(R + T)$

And, R and T are the radial and tangential tracheid diameters, respectively, P is fibre perimeter, and D_w is the cell wall density (Tong 2019).

2.3.4 Data analysis

The wood attributes analysed included: wood density (kg/m^3), radial diameter (μm), tangential diameter (μm), coarseness (μg/m), cell population (#/mm^2), microfibril angle (MFA, degree), modulus of elasticity (MOE, Gpa), wall thickness (μm), specific surface area (m^2/kg), ring width (mm), and ring area (mm^2). For each of the wood properties analysed, a mean value was calculated for each ring in order to determine if significant differences occurred between trees from varying treatments. Intra-annual differences were observed, but exceed the scope of this paper, as they did not exhibit clear increasing or decreasing trend over one ring width. The significance level selected for all levels of the statistical analysis was $\alpha = 0.05$ (95% confidence level). Residuals were checked visually with quantile-quantile plots using the ggpubr package (Kassambara 2020) and were found to not differ from normal at every stage of the analysis. A comparison of linear and 3rd, 4th, and 5th order polynomials, as well as exponential equations was used in order to observe the change in a given wood property over time for each species in each treatment. Akaike's information criterion (AIC value) was used to evaluate the goodness of fit of the various line types. All wood attribute variation approximated linear change at approximately 10 years.

A linear mixed model (equation 4), with tree as the random factor, and ring (cambial age), species, and treatment as the fixed factors, was utilized to investigate differences in wood attributes. The linear mixed model was created using the lme function within the nlme package (Pinheiro et al. 2020) in R (version 3.4.3)(R Development Core Team 2017). The dredge function within the MuMIn package (Barton 2020) for model selection was used to rank the best model (based on variable inclusion of the model terms) through Akaike's Information Criterion (AIC) value. The global model included both aspen and white spruce samples, in order to determine that there was a difference in wood attribute variation between species. Next, in order to determine if the observed wood attributes varied within species and between treatments, a linear mixed model separated by sample species was run (lme: ring, and treatment with tree as the random effect). An analysis of variance (ANOVA) was then used to determine significant effects of each species separated model. Post-hoc analysis of significant treatment effects were conducted by the pairwise comparison of contrasts from the lsmeans (Lenth 2016) package with a Bonferroni adjustment applied to p-values. Although p-values can be the subject of controversy when used as an indicator of significance in mixed effect models, and in scientific hypothesis testing in general, the application of the conservative Bonferroni adjustment can mitigate the potential of Type 1 error. Also, in this instance, the results of the multi model inference agreed with the same analysis comparing significant model terms based on p-values (Appendix Table 6.2). So, beyond the initial model selection test, p-values were used to represent significance. The goal of this portion of the study was not to create a predictive model, nor maximize R^2 of each model, but rather answer ecological questions through these statistics.

$$Y_j=\beta_0+\beta_1 x_j+\beta_2 x_j+\mu_1+\varepsilon_j, \quad [4]$$

Where Y_j and x_j represent fibre property for year j; β_0, β_1 and β_2 are the fixed effects. μ_{i1} is the random effect of tree and u_{i2} is the random slope; ε_{ij} is the error term.

Finally, an "improvement" heatmap was created by normalizing the aspen and spruce means for each property in each treatment to the mean within the 1000 sph aspen treatment. An improvement was termed to be either an increase or decrease in the value of each wood property as per Canadian wood fibre standards (Canadian Wood Fibre Centre et al. 2010). An important caveat is that these criteria for improvement could change depending on the properties required for the desired end product. For this study, improvements were defined as the treatments that displayed lesser values for coarseness, ring width, and MFA relative to the mean. The remaining wood attributes (density, MOE, ring area, specific surface area, cell population, tangential and radial diameter) were considered to have positive improvement if they increased between treatments relative to the mean. The years 10-34 were used in this comparison, to omit the variation observed in early age wood.

2.4 RESULTS

2.4.1 Linear mixed effect models

Table 2.2 shows the results of the multi model inference, where the global model that was tested included the terms: ring (cambial age), species, and treatment. This method chose the 'best model' (listed first for each wood attribute) based on lowest AIC score, which minimizes information loss of the model. Displayed in Table 2.2 is the 'best model' for each wood attribute and the next highest-ranking model until the change (delta) in AIC > 2, indicating a significant difference between models. The results of this analysis show that for all wood attributes, there is an important difference observed between species, as well as a difference observed between treatments.

Table 2.2 Summarized results of the multi model inference analysis of the global model (linear model = Ring + species + treatment + |tree).Loglik is the log likelihood, AIC is Akaike's information criterion, and delta is the difference in AIC for best performing

Wood attribute	(Intercept)	Ring	species	treatment	df	logLik	AICc	delta	weight
Ring Width	3.77	-0.0581	NA	+	8	-4169.12	8354.29	0.00	0.73
	3.75	-0.0581	+	+	9	-4169.09	8356.24	1.95	0.27
	2.83	-0.0580	+	NA	5	-4204.51	8419.04	64.75	0.00
Density	393.11	NA	+	+	8	-15803.80	31623.65	0.00	0.45
	396.28	NA	+	NA	4	-15808.32	31624.66	1.00	0.27
	392.80	0.0205	+	+	9	-15803.77	31625.60	1.94	0.17
	395.99	0.0194	+	NA	5	-15808.29	31626.60	2.95	0.10
MFA	23.15	-0.6538	+	+	9	-8835.62	17689.30	0.00	0.90

Wood attribute	(Intercept)	Ring	species	treatment	df	logLik	AICc	delta	weight
	20.77	-0.6539	+	NA	5	-8841.83	17693.68	4.38	0.10
MOE	8.14	0.2956	+	+	9	-5388.85	10795.75	0.00	0.93
	9.45	0.2956	+	NA	5	-5395.53	10801.08	5.33	0.07
Coarseness	542.70	2.3385	+	+	9	-18223.71	36465.47	0.00	0.99
	506.81	2.3359	+	NA	5	-18232.75	36475.52	10.05	0.01
Tangential Diameter	40.53	0.0520	+	+	9	-7820.46	15658.97	0.00	0.99
	39.29	0.0519	+	NA	5	-7829.07	15668.17	9.19	0.01
Radial Diameter	28.59	0.1495	+	+	9	-7283.05	14584.16	0.00	1.00
	27.27	0.1503	NA	+	8	-7290.68	14597.41	13.25	0.00
Specific Surface Area	263.46	-1.0999	+	+	9	-15900.29	31818.65	0.00	0.99
	283.86	-1.0987	+	NA	5	-15909.59	31829.21	10.56	0.01
Ring Area	491.55	17.8545	NA	+	8	-21516.34	43048.72	0.00	0.65
	460.56	17.8685	+	+	9	-21515.96	43049.97	1.25	0.35
	98.51	17.8805	+	NA	5	-21547.01	43104.04	55.32	0.00
Cell Population	905.31	-10.2019	+	+	9	-20622.59	41263.24	0.00	1.00
	1068.51	-10.2034	+	NA	5	-20639.18	41288.38	25.15	0.00
Wall Thickness	2.82	0.0083	+	+	9	-907.37	1832.81	0.00	0.97
	2.72	0.0083	+	NA	5	-914.87	1839.77	6.96	0.03

Next, in order to determine if there were differences in wood attribute variation between treatments and within species, the same model structure was applied to aspen and spruce samples separately. There was a significant effect of treatment in all wood attributes except for MFA (both aspen and spruce), and MOE (aspen) (Table 2.3).

Table 2.3. Results of species separated ANOVA of model terms for each species (Full results for each wood attribute in Chapter 2 Supplementary Appendix).

	Aspen Samples		Spruce Samples	
Wood Property	Cambial Age (Ring)	treatment	Cambial Age (Ring)	treatment
Ring Width	$F(1, 1421) = 367.21$, $p < 0.001$	$F(3, 46) = 3.30$, $p = 0.0284$	$F(1, 1621) = 488.01$, $p < 0.001$	$F(4, 65) = 24.43$, $p < 0.001$
Density	$F(1, 1421) = 113.28$, $p < 0.001$	$F(3, 46) = 3.86$, $p = 0.0151$	$F(1, 1621) = 90.97$, $p < 0.001$	$F(4, 65) = 2.56$, $p = 0.046$
Microfibril Angle	$F(1, 1421) = 3393.59$, $p <0.001$	**$F(3, 46) = 1.04$, $p = 0.3822$**	$F(1, 1621) = 7768.49$, $p < 0.001$	**$F(4, 65) = 2.22$, $p = 0.076$**
Modulus of Elasticity	$F(1, 1421) = 3930.35$, $p < 0.001$	**$F(3, 46) = 1.17$, $p = 0.3299$**	$F(1, 1621) = 10809.77$, $p <0.001$	$F(4, 65) = 3.42$, $p = 0.0135$
Coarseness	$F(1, 1421) = 39.4$, $p < 0.001$	$F(3, 46) = 6.19$, $p = 0.0013$	$F(1, 1621) = 339.61$, $p < 0.001$	$F(4, 65) = 10.44$, $p < 0.001$
Tangential Diameter	$F(1, 1421) = 13.71$, $p < 0.001$	$F(3, 46) = 5.67$, $p = 0.0022$	$F(1, 1621) = 68.08$, $p < 0.001$	$F(4,65) = 9.25$, $p < 0.001$
Radial Diameter	$F(1, 1421) = 6.39$, $p = 0.012$	$F(3, 46) = 3.82$, $p = 0.016$	$F(1, 1621) = 3411.57$, $p < 0.001$	$F(4,65) = 9.06$, $p < 0.001$
Specific Surface	$F(1, 1421) = 109.60$, $p < 0.001$	$F(3, 46) = 6.55$, $p < 0.001$	$F(1, 1621) = 90.64$, $p < 0.001$	$F(4, 65) = 5.55$, $p < 0.001$
Ring Area	$F(1, 1421) = 489.03$, $p < 0.001$	$F(3, 46) = 2.96$, $p = 0.042$	$F(1, 1621) = 1110.89$, $p < 0.001$	$F(4, 65) = 19.98$, $p < 0.001$
Cell Population	$F(1, 1421) = 17.14$, $p < 0.001$	$F(3, 46) = 4.45$, $p = 0.0079$	$F(1, 1621) = 1682.25$, $p < 0.001$	$F(4, 65) = 11.64$, $p < 0.001$
Wall Thickness	$F(1, 1421) = 74.01$, $p < 0.001$	$F(3,46) = 5.72$, $p = 0.0021$	$F(1, 1621) = 59.91$, $p < 0.001$	$F(4, 65) = 4.38$, $p = 0.0034$

Significant effects were explored through pairwise comparison (summarized in table 2.4, complete post hoc results in Appendix Tables 6.3 and 6.4). The contrasts that displayed significant differences between treatments are shown in Table 2.4. From this analysis, two thresholds became evident. First, for aspen samples, all of the significant treatment effects were driven by differences in the highest aspen density (10,000 sph) contrasted with lower aspen densities. The second threshold was that for spruce, most of the significant treatment effects were driven by contrasts between the treatment without aspen (0sph) and treatments where spruce was grown in mixture with aspen (i.e., > 0sph aspen). This analysis confirmed the hypothesis that aspen and spruce wood attributes would vary with competition. Also, boxplots show the variation for each wood attribute separated by species and treatment (Figure 2.3, Figures for each wood attribute found at the start of each wood attribute analysis chapter in Chapter 2 Supplementary Appendix).

Table 2.4. The results of species separated two-way analysis of variance (ANOVA) of the effects of treatment (aspen population density) and cambial age on each wood attribute. For significant treatment effects, pairwise post hoc testing (Bonferroni adjusted) determined contrasts between treatments. For full contrast table, consult appendix (Tables 6.3 and 6.4).

Figure Wood Property	Species	Treatment p-value	Post Hoc: Significant Contrasts
Ring Width	Aspen	0.0284	None
	Spruce	p < 0.001	0-2000, 1000-5000, 1000-10000
Density	Aspen	0.0151	2000-10000
	Spruce	0.0466	None
Microfibril Angle	Aspen	0.3822	N/A
	Spruce	0.076	N/a
Modulus of Elasticity	Aspen	0.3299	N/A
	Spruce	0.0135	0-5000, 0-10000
Coarseness	Aspen	0.0013	2000-10000, 5000-10000
	Spruce	p < 0.001	0-2000, 0-5000, 0-10000
Tangential Diameter	Aspen	0.0022	1000-10000, 2000-10000
	Spruce	p < 0.001	0-5000, 0-10000
Radial Diameter	Aspen	0.016	1000-10000
	Spruce	p < 0.001	0-5000, 0-10000
Specific Surface	Aspen	p < 0.001	2000-10000, 5000-10000
	Spruce	p < 0.001	0-2000, 0-10000
Ring Area	Aspen	0.0418	None
	Spruce	p < 0.001	0-2000, 1000-5000, 1000-10000
Cell Population	Aspen	0.0079	1000-10000
	Spruce	p < 0.001	0-5000, 0-10000
Wall Thickness	Aspen	0.0021	2000-10000, 5000-10000
	Spruce	0.0034	0k-2k, 0k-10k, 2k-5k, 5k-10k

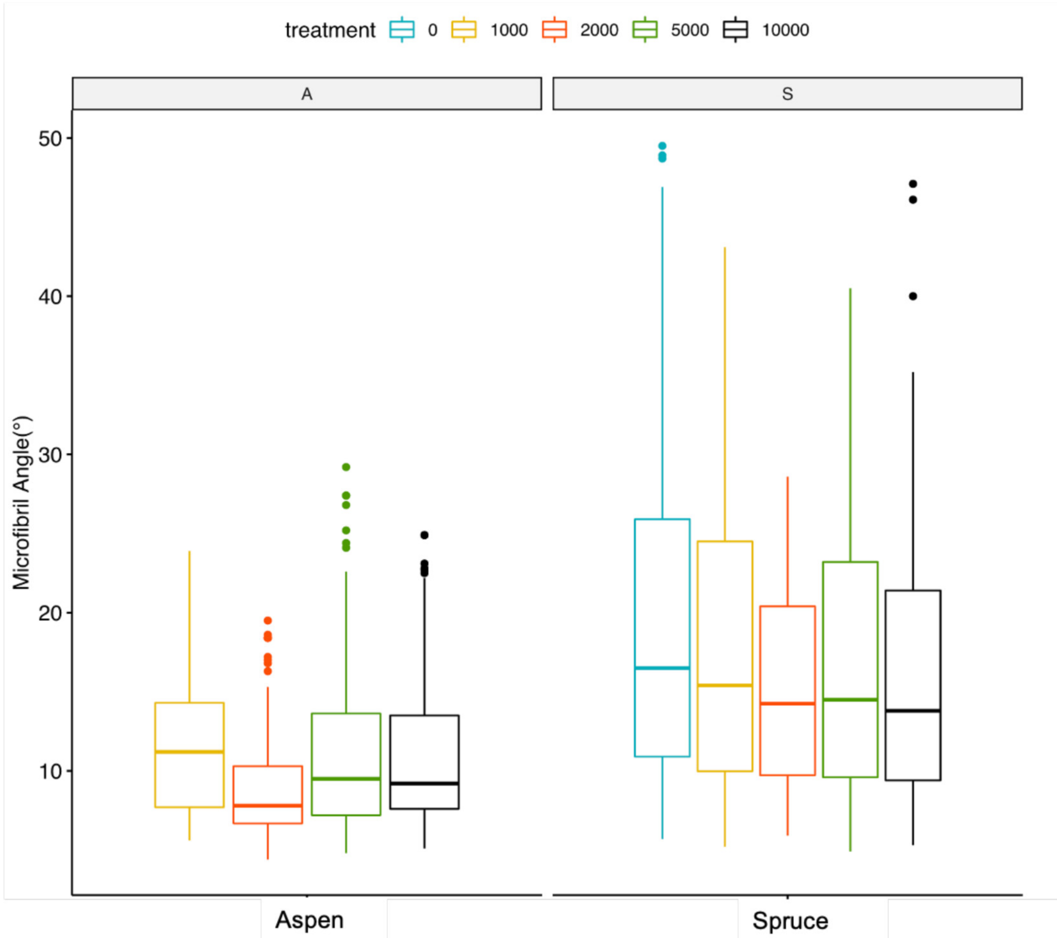


Figure 2.2 Boxplot showing the microfibril angle variation between aspen and spruce in each treatment. This is figure is shown as an example of the variation between species, for figures of all wood attributes consult Chapter 2 Supplementary Appendix.

2.4.2 Wood attribute variation over time

In order to show wood attribute change over time, we tested the fits of several line types for each treatment and the results indicate that all spruce attributes exhibit non-linear changes as the trees develop, with the largest changes in properties being distinguished by differences in establishing tree (cambial age 0-5 years), and older trees (cambial age 5-30 years) (Figures 2.3, 2.4, 2.5). While developmental changes in most wood attributes were best statistically described by 4th or 5th order polynomial, most approximated linear changes in the attributes between 5 and 30 years.

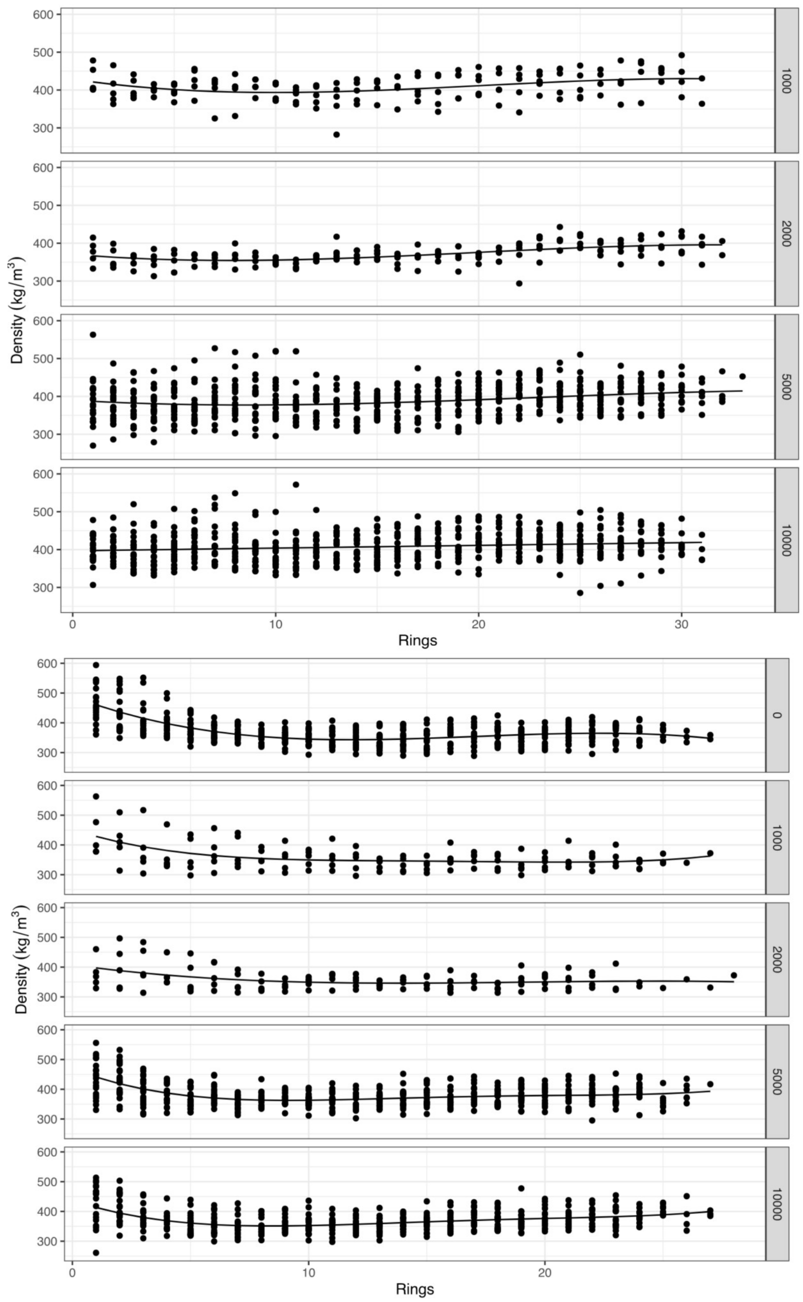


Figure 2.3 Density change over time with separated aspen (top) spruce (bottom) and treatment.

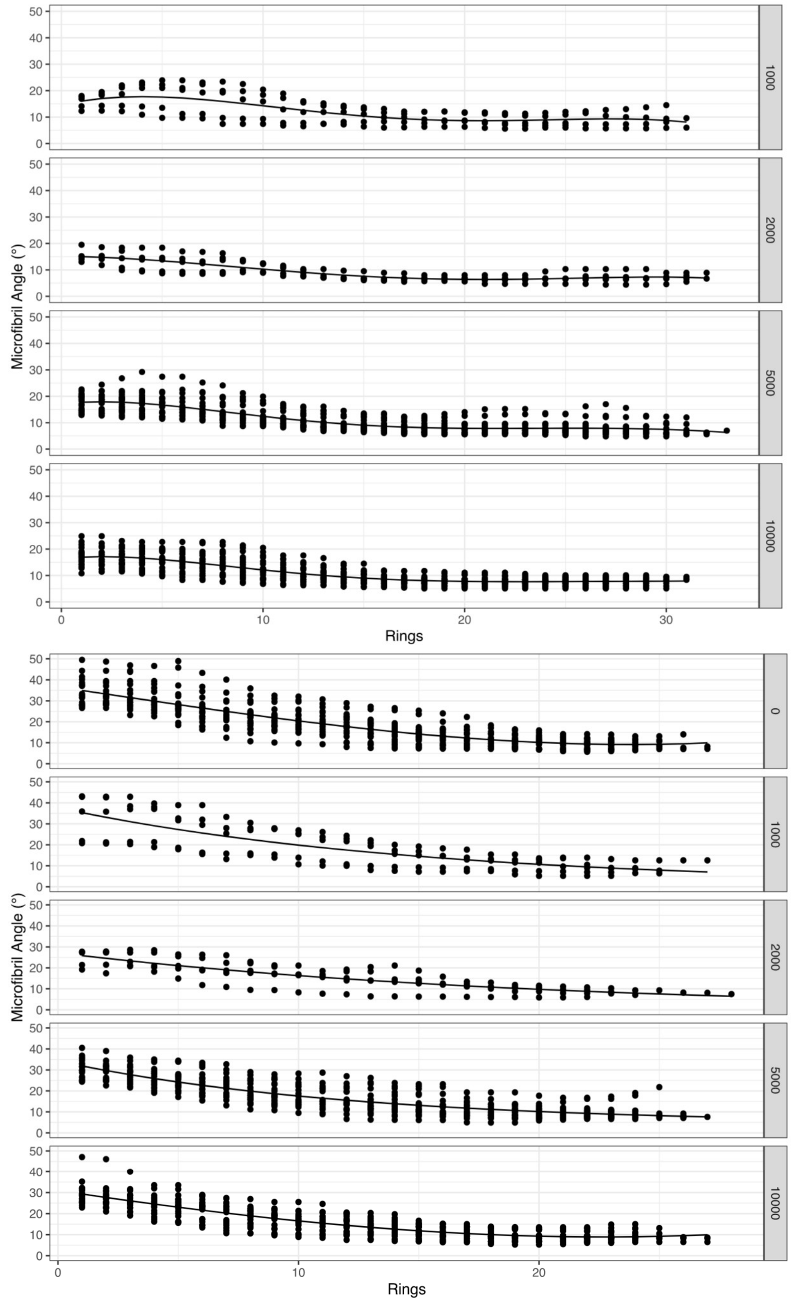


Figure 2.4 Microfibril angle change over time with separated (a, left) aspen, and (b, right) spruce and treatments.

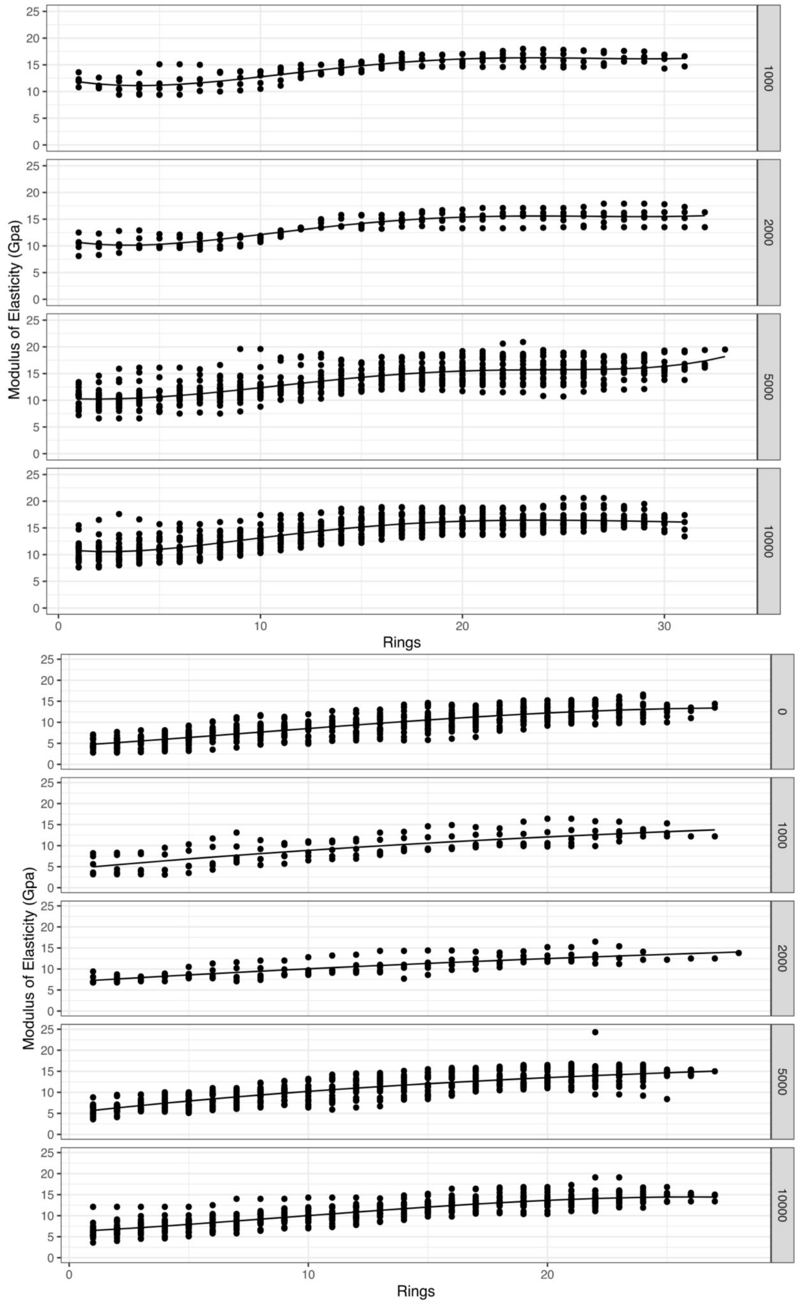


Figure 2.5 Modulus of Elasticity change over time with separated (a, left) aspen, and (b, right) spruce and treatments.

2.4.3 Heatmap

Figures 2.6 and 2.7 show the results of an "improvement" heatmap where a positive improvement meant a reduction in ring width, coarseness, and microfibril angle, and a maximization of all other wood attributes. In general, aspen wood quality (as previously defined) was diminished with increasing levels of treatment and spruce wood quality was improved. The only common improvement was ring width which was minimized with increasing aspen treatment density. Aspen wall thickness was improved in the 10,000 sph treatment and displayed a negative effect in other treatments. Radial diameter and tangential diameter improved with increasing aspen density. Coarseness was minimized with increasing aspen treatment density. MOE was most desirable in 10k treatment, while minimized in the other densities of aspen. MFA showed positive improvement in all densities relative to 1000 sph treatment. Wood density was negatively associated with increasing aspen population density. Ring width improved with aspen population density. Within spruce, most desirable wood traits were maximized in spruce with increasing aspen density. Tangential and radial diameter both did not display improvements as they decreased with increasing treatment density. Modulus of elasticity and density were maximized in the 5000 sph treatment. MFA, coarseness and ring width all improved with increasing aspen population density.

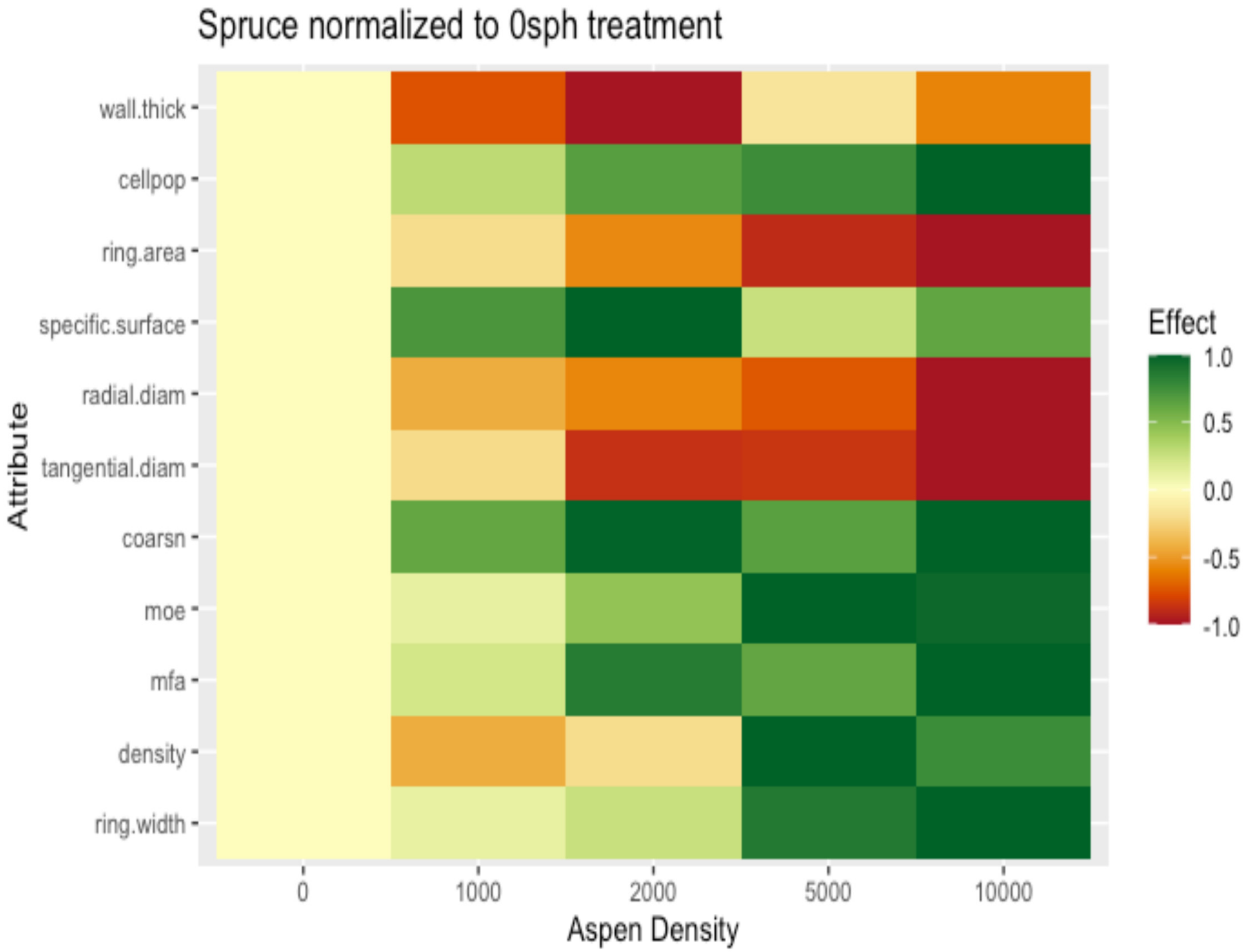


Figure 2.6 A relative improvement heatmap for all 11 wood attributes within spruce and their response to increasing levels of aspen treatment density (relative to control treatment).

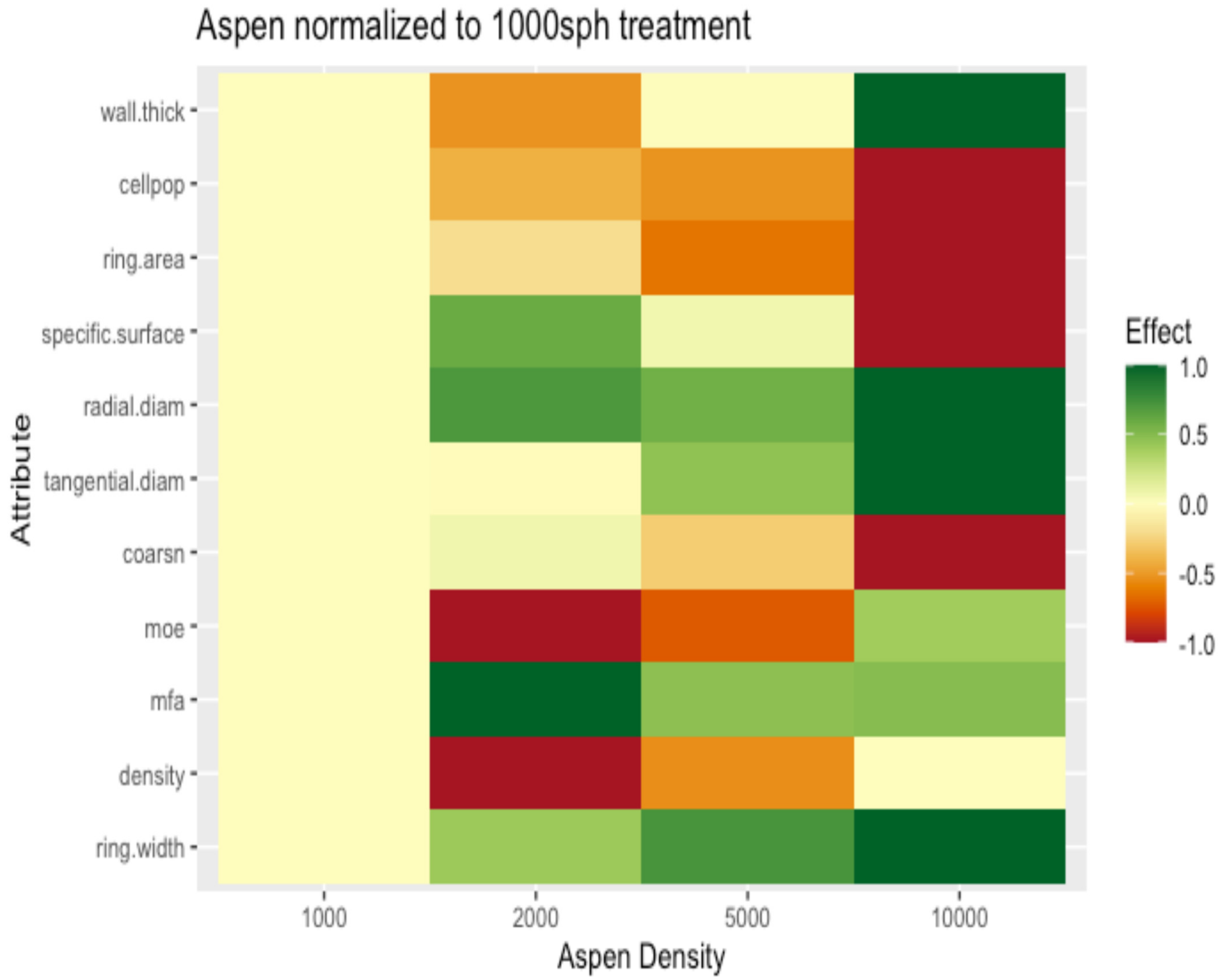


Figure 2.7 A relative improvement heatmap for all 11 wood attributes within aspen and their response to increasing levels of aspen treatment density (relative to 1000 sph aspen treatment).

2.5 DISCUSSION

Significant differences between spruce and aspen were observed for all wood attributes with the exception of ring width and ring area. A lack of difference between species for ring width and ring area is consistent with previous studies that have observed that for both species tree height to diameter ratio in mixed stands increases with competition (Lanner 1985; Coopersmith and Hall 1999). Both spruce and aspen exhibit increased slenderness with competition, which corresponds with reduced ring width and ring area. For all other wood traits, the distinct differences between species reflects the intrinsic anatomical differences of each species (Pretzsch and Rais 2016) as well as variations in their growth preferences such as shade tolerance (Man and Lieffers 1999). For both spruce and aspen, we found that aspen treatment density influenced most wood properties (Table 2.3), but that the sampled species responded differently to increases in aspen treatment density. Microfibril angle (MFA) in spruce and aspen, as well as modulus of elasticity in aspen, was not significantly impacted by aspen density. Our finding that MFA is insensitive to competition is consistent with previous studies from boreal mixedwood stands in Western Canada (De Araujo et al. 2015). The age of wood, and whether or not it is juvenile or mature is the greatest determinant of MFA, with large MFA's in juvenile, and smaller in mature wood (Barnett and Bonham 2004). It has been shown that the normal decrease in MFA from pith to bark can be interrupted by surge in growth rate such as that which may occur following the thinning and removal of competitor trees (Herman et al. 1999). We did observe a distinct increase in spruce MFA (Figure 2.5b) following the thinning that occurred in the sample plots in 1990, 8 years into the spruce growth (3-year-old planted spruce in 1985). We also observed high variation in the MFA in spruce for all samples (Figures 2.2 and 2.4) which could partially account for a significant treatment effect not being found. Further, MOE in aspen (Figure 2.5), displays greater variation than the spruce (Figure 2.5), and could explain some of the lack of significance between treatments. Also, since MFA did not exhibit a difference between treatments, and MFA can explain up to 86% of the variation in MOE it could be expected that MOE will follow a similar trend. However, within spruce cores, MOE did in fact display a significant effect of treatment. This could be explained by a dominant effect of wood density on MOE as it varied between treatments. Approximately ~10% of the variation in MOE can be explained by variation observed within wood density (Evans and Ilic 2001).

For most of the wood attributes that we measured (ring width, MOE, coarseness, tangential diameter, radial diameter, specific surface area, ring area, cell population, and wall thickness), two thresholds consistently emerged from our analysis. First, the largest effect on spruce growth occurred when aspen was grown in densities greater than zero with the spruce. Ninety percent of the significant differences within spruce wood properties, and between treatments, were attributed to the presence of aspen in the stand. Aspen growing in mixture with spruce will impact the availability of key limiting resources with regard to light, water and nutrients (Filipescu and Comeau 2007; Kabzems et al. 2015). Past studies have demonstrated that modifications to spruce's growing environment influence absolute growth as well as gross growth characteristics such as height-to-diameter ratio (Kabzems et al. 2015). Our findings build on this previous work by demonstrating that spruce wood attributes are different for spruce growing in pure stands (at lower density) compared to spruce grown in mixture.

The second threshold that emerged from our results was the impact of an aspen treatment density of 10,000 sph, on aspen wood characteristics. Differences between the 10,000 sph treatment and those with lower densities of aspen accounted for all of the significance observed in aspen wood attributes (Table 2.4). Growth of trembling aspen has been shown to be significantly affected by inter- and intraspecific competition (Jiang et al. 2018).

An outlier from these two thresholds is wood density. Both aspen and spruce displayed a significant effect of treatment, but upon post-hoc testing, only aspen wood density exhibited significant differences between 2000 – 10,000 sph (Table 2.4) treatments. The significant effect of the overall model term without significant post-hoc treatment contrasts, could be attributed to the low sample sizes, and an overly conservative result from the Bonferroni correction. This could further be explored through additional sampling. The finding that wood attributes of both aspen and spruce are affected by treatment compares to previous studies involving wood density and mixtures of white spruce and aspen (De Araujo et al. 2015), where no significant differences between mixed and pure stand wood density were found in either species. A possible explanation for the overall treatment significance observed in aspen and spruce cores in this study is that the Siphon Creek research plots provide a higher resolution as they were sampled from plots with the same ecological conditions, consist of controlled densities, and have the same age across plots. Since all other environmental variables are held constant, the differences in density were more readily apparent from the data collected at the research site than the geographically separate permanent sample plots in previous studies.

Furthermore, our work indicates that all spruce wood attributes exhibit non-linear changes as the trees develop, with the largest changes in properties being distinguished by the differences in establishing tree (age 0-5 years), compared to older trees (5-30 years). While developmental changes in most wood attributes were statistically best described by a third or fourth order polynomial, most approximated linear changes in the attributes between 5 and 30 years. This variation is consistent with previous observations of change in wood attribute development as trees age (Amarasekara 2002).

In this study we aspired to evaluate if there were discernable economic improvements in wood attribute value with increasing levels of competition. Our experimental framework does not allow us to explicitly tease apart the relative impact of increased interspecific competition compared to overall competition, on spruce wood attributes. However, our results indicate that desirable spruce wood attributes are generally increased when spruce is grown with aspen competitors (Figure 2.6). In general, spruce grown in intimate mixture with 5000 sph aspen density seemed to offer relative improvements in wood properties that are considered the most important for lumber products. Increased wood density, larger MOE, lower MFA, larger ring width, and increased wall thickness are the benefits observed in spruce grown in the 5000 sph treatment which constitute either best or second-best improvements to wood quality, relative to other treatments. Aspen densities of 5k and 10k are due to juvenile spacing of five-year-old aspen, while the 1k and 2k aspen have had two juvenile spacing treatments at 5 and 15 years. Thus, the aspen represents dominant and codominant individuals at the time of spacing treatment.

Density may be less important for lumber products in the future due to the increased production of value added engineered wood products, as they are often made stronger and stiffer by laminating a low-density wood to a higher-density wood (Canadian Wood Fibre Centre et al. 2010). However, density is still important for bioenergy, which values the higher energy content of dense wood.

MOE has been shown to be the best predictor of wood stiffness, which is desirable both for tree survivability, and lumber considerations when maximized (as evident in the increase between treatments in Figures 2.5, and the resultant heat map improvement in Figures 2.6 and 2.7).

Further, depending on the intended use, radial and tangential diameter can either be maximized or minimized. In this case length maximized was viewed as desirable in the improvement heatmap value as longer fibre results in stronger paper sheets, which resulted in negative improvement on the heatmap. However, thinner fibre tends to form better quality sheets of higher tensile strength and greater bonding area (Watson and Bradley 2009), so again, it depends on intended use. Increased water availability has been linked to formation of wider tracheids particularly in the radial direction (Vysotskaya and Vaganov 1989; Wilpert 1991). Since the treatments without aspen have a lower density of trees in general, there is likely to be more water available, allowing for the discrepancy in radial diameter observed between treatments (Kerhoulas et al. 2013).

In contrast to spruce wood attributes, our results indicate that most desirable traits (MOE, density, and MFA) within aspen decrease with increasing levels of aspen competition (Figure 2.7). Lower values for MOE and density increase the risk of trunk breakage, xylem implosion and decreased stem stability (Hacke et al. 2001). Effectively, in this instance, the increased competition is weakening the aspen, and accelerating the stand dynamics typical of mixedwood forests (Bergeron et al. 2014) . However, the majority of the negative associations for the remaining wood attributes are related to the 10,000 sph aspen treatment, suggesting that, aspen wood attributes are not significantly affected until densities are increased past a certain threshold.

Previous studies have shown that increases in maximum stand stem density can lead to an increase in productivity in mixed species forest stands when space partitioning allows for the favourable expression of the functional traits of each species (Reyes-Hernández and Comeau

2015). For both aspen and spruce samples, we found that the increased stockability of the managed 1000-5000 sph treatments, had very few negative effects on wood attribute values. Therefore, it is a conclusion of this study that some of the benefits of maintaining aspen in a stand are realized even at relatively low aspen densities (between 1000 and 5000 sph). This suggests that maintaining aspen at lower densities in intimate mixture can increase spruce wood quality and maintain the ecological benefits of aspen and their potential positive impacts of forest resilience (Macdonald et al. 2010). Changes in measures of productivity for the spruce and aspen components of a mixture will vary with management choices and desired outcomes (Comeau 2021). Increased competition from aspen may have a negative impact on spruce volume growth (Cortini et al. 2012), even though intimate mixture stands often exhibit similar total volume production (spruce and aspen volume growth combined) or potentially increased total yield (Kweon and Comeau 2019). Forest managers focused on conifer production must therefore consider the beneficial impacts of a managed aspen component on spruce wood attributes and increase in overall volume in the context of the concomitant reductions in spruce volume production.

3. A mixed effect approach to evaluating the impacts of stand composition, age and neighbourhood competition on the wood attributes of spruce and aspen grown in mixedwood stands

3.1 ABSTRACT

The influence of stand composition, neighbourhood competition, and stand level competition, on the development of wood attributes of aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench) Voss) were examined. Data was collected from a silvicultural trial site in British Columbia, Canada. Eleven wood attributes (wood density, radial diameter, tangential diameter, coarseness, cell population, microfibril angle (MFA), modulus of elasticity (MOE), cell wall thickness, specific surface area, ring width, and ring area) were analysed from 120 sample trees (70 spruce and 50 aspen). Four distance-independent and four distance-dependent competition indices were tested in order to determine the dominant effect, and competition resolution required for each wood attribute in each species. Aspen neighbourhood level (within 3.99m plot radius) competition was best described by a distance-dependent index, while spruce was best described by a distance-independent competition index. Neighbourhood level competition resolution is necessary for determining the wood attributes of ring area, ring width, radial diameter, cell population, and coarseness in aspen, but relatively unimportant in spruce. For spruce samples, stand level competition (treatment density) had a dominant effect on wood density, ring area, ring width, tangential diameter, radial diameter and cell population. Age was the dominant effect for MFA and MOE variation in both spruce and aspen. Our models explained up to 75% and 91% of the variation observed in aspen and spruce wood attributes respectively.

3.2 INTRODUCTION

Aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench) Voss) are the dominant tree species found in the Western Canadian boreal mixed forest and competition driven succession between these species is the primary process of forest composition shift (Jiang et al. 2018). Studies have shown that mixedwood competition at various levels can influence yield, biomass production, and exterior growth characteristics (Comeau et al. 2005; Kabzems et al. 2007). These findings have influenced forest management techniques, but knowledge gaps remain with regard to how stand composition and neighbourhood competition impacts spruce and aspen wood attributes, and by extension, economic value.

Both inter and intra-specific competition play important roles in affecting forest growth, composition, structure and succession in the boreal mixedwood. Aspen is frequently the primary tree species to grow in post-disturbance landscapes, following destructive fire, beetle infestation or clear-cut through asexual root suckering (Comeau et al. 2005; Frey et al. 2011; Smith et al. 2011). Aspen is shade intolerant and displays fast initial growth rates, which allow it to quickly dominate the forest canopy, compared to the seed-sowed and slow juvenile growth rates of spruce (Lieffers et al. 1996). Aspen, however, has a short lifespan (50–60 years), and reaches the age of senescence earlier than most conifers (250-350 years). Canopy openings from this senescence allow for establishment or release of more shade tolerant, slow-growing conifer species, including spruce (Brassard and Chen 2006). Competition is particularly critical for mixedwood stand development in the stem exclusion or self-thinning phase (20-40 years of stand age) where resources such as light, soil moisture and nutrients become scarce as the trees expand in size, leading to logarithmic decreases in stand density as trees compete for these resources (Lieffers et al. 2002; Chen and Popadiouk 2002). Although spruce is a shade tolerant species, studies have shown a strong response in radial and height growth to increases in light, and poor conifer height growth under dense hardwood canopies with light levels below 20% of full sunlight (Lieffers and Stadt 1994). Intra-specific competition has been shown to have a stronger effect on oak and beech growth than inter-specific competition, which shows the importance of the diversification of each species functional traits in order to maximize growing space (Pretzsch et al. 2013). Since competition can have an effect on radial and height growth, it is hypothesized that there will be an effect on the wood attributes of both spruce and aspen as well.

Competition indices enable the quantitative analysis of relationships between stand composition and wood attributes. Competition indices are numerical expressions that describe how much each tree is affected by its neighbours, and there are two main types: distance-independent (Wykoff et al. 1982) and distance-dependent (Martin and Ek 1984). Distance-independent indices are typically easier to calculate as they require less data, and have performed similarly compared to distance-dependent indices when the performance of each competition index and its contribution to a growth model were assessed by the mean square error reduction (Kahriman et al. 2018). However, much of the study of competition indices has been confined to models relating exterior tree growth characteristics or mortality, and there is currently a lack of research concerning the resolution required for finer wood attributes (Kahriman et al. 2018; Sun et al. 2019). In this study, both distance-dependent and distance-independent competition indices were used to characterize neighbourhood competition regime.

One of the distinct benefits of managing for competition in a mixedwood forest is overyielding, or the increase in productivity of a mixed species stand compared to a monoculture (Hector 1998). Overyielding can occur when managing for space partitioning and size inequality between spruce and aspen (Hector 1998; Kweon and Comeau 2019). The potential for overyielding in boreal aspen spruce mixtures has been identified (Man and Lieffers 1999; Kabzems et al. 2007). However, an increase in volume is only desirable when it corresponds with merchantable timber. The characterization of wood attributes along with cost effective land use management is at the forefront of the boreal forest industry's fundamental shift from traditional wood products to multiple value-added forest products (Chen et al. 2017).

Wood attributes within both broadleaves and conifers have impacts on tree survivability and the grade of economic viability (Table 1.1). Within angiosperms (aspen) and gymnosperms (spruce), xylem cells are important for structural integrity and for water transport within the tree. Gymnosperm tracheids are characterized by many bordered pits in their radial walls, and can be much longer than angiosperm fibres (Barnett and Bonham 2004). The orientation and magnitude of certain characteristics within each tracheid reflects the influence of external forcing which can include competition, or environmental conditions such as temperature changes, nutrient availability, precipitation, increased wind stress or snowpack (Speer 2012). Therefore, developing a thorough understanding of the complex interactions of the mixedwood system, and how, specifically competition between overstory trees may influence tree growth and wood properties, is vital to the effective future management of these forests.

In this study, the primary objective is to characterize the wood attributes of both white spruce and trembling aspen grown in varying levels of competition. The first sub-objective is to compare spruce and aspen wood attribute response to inter- and intra-specific competition. The second objective is to determine which wood attributes of which species varied with the tested distance-dependent or distance-independent competition indices. The third and final objective is to compare the responses of wood properties to neighbourhood and stand level competition. To achieve these sub-objectives, three hypotheses were formulated. The first hypothesis is that aspen wood attribute response will be most affected by intra specific competition, since aspen is a shade intolerant species and can grow in close proximity with other aspen. Alternatively, spruce was planted at prescribed densities, and as such will likely be affected by inter-specific competition (i.e., competition from in-grown aspen). The variation in shade tolerance, as well as below ground root behaviours between species leads to the second hypothesis that aspen neighbourhood level competition will best be described by a distance dependent index and spruce sample neighbourhood competition will best be described by a distance-independent index. The final hypothesis is that aspen wood attributes will be most influenced by neighbourhood competition while spruce will be most affected by stand level competition.

3.3 MATERIALS AND METHODS

3.3.1 Study Site

See section 2.3.1.

3.3.2 Data Collection

See section 2.3.2.

3.3.3 Sample Preparation

See section 2.3.3

3.3.4 Data analysis

The fibre attributes analysed included: wood density (kg/m^3), radial diameter (μm), tangential diameter (μm), coarseness (μg/m), cell population (#/mm^2), microfibril angle (MFA, degree), modulus of elasticity (MOE, Gpa), cell wall thickness (μm), specific surface area (m^2/kg), ring width (mm), and ring area (mm^2). For each of the fibre properties analysed, a mean value was calculated for each ring in order to determine if significant differences occurred between trees from varying treatments. Intra-annual differences were observed, but exceed the scope of this paper, as they did not exhibit clear increasing or decreasing trend over one ring width. The data analysis was comprised of three main parts: competition index calculation, neighbourhood competition model term selection, and mixed effect model evaluation. The null hypothesis was that wood attribute development is consistent across all trees of the same species, regardless of their competition index. The significance level selected for all levels of the statistical analysis was $\alpha = 0.05$ (95% confidence level).

Based on the plot data for each sample, four competition indices were calculated for each tree. The first, basal area (denoted BA, Equation 4) is a common distance-independent competition index that describes the average amount of an area (hectare) occupied by tree stems (m^2). The second competition index, basal area of larger trees (denoted BAL, equation 5) was calculated in the same way to equation 4, except that only the competitors with a larger diameter at breast height than the diameter at breast height of the sample were included. This is a commonly used index where it is assumed that neighbouring trees that are smaller than sample tree do not place the sample tree at a competitive disadvantage (Wykoff et al. 1982; Sun et al. 2019).

The Martin and Ek index (denoted MNE, Equation 6, (Martin and Ek 1984)) was chosen as the distance dependent index as it was shown to perform well in similar stand conditions in previous research (Kahriman et al. 2018). The MNE index places a larger "competitive weight", on neighbouring trees that are larger, and closer to the sample tree. The fourth competition index was another iteration of the Martin and Ek index, with the same size restriction imposed in the determination of BAL, where only the competitors that had a larger diameter at breast height than the diameter at breast height of the sample were included (denoted as MNEL, Equation 7).

[4] $\mathrm{BA} = (\pi \times \left(\frac{d_j}{200}\right)^2)$

Where *d* is in cm, to give BA in m^2/ha.

[5] $\mathrm{BAL} = (\pi \times \left(\frac{(d_j > d_i)}{200}\right)^2)$

Where *i* is subject tree; *j,* competitor*; d,* Diameter at breast height (cm), to give BAL in m^2/ha; $(d_j > d_i)$, those competitors that are greater in dbh than the dbh of the sample (Wykoff et al. 1982).

[6] $\mathrm{MNE} = \sum_{j=1}^{n}(\frac{d_j}{d_i}) \times e^{(16 \times L_{ij})/(d_i + d_j)}$

Where *i* is subject tree; *j,* competitor*; d,* Diameter at breast height (cm); L_{ij},distance of subject tree *I* to competitor *j* (m) (Martin and Ek 1984).

[7] $\mathrm{MNEL} = \sum_{j=1}^{n}(\frac{(d_j > d_i)}{d_i}) \times e^{(16 \times L_{ij})/(d_i + (d_j > d_i))}$

Where *i* is subject tree; *j,* competitor*; d,* Diameter at breast height (cm); L_{ij}, distance of subject tree i to competitor *j* (m). $(d_j > d_i)$, those competitors that are greater in dbh than the dbh of the sample.

Additionally, two iterations of each of the four competition indices aforementioned (BA, BAL, MNE, MNEL), were run in order to determine the effect of intra- vs inter-specific competition. The first iteration included both aspen and spruce competitors combined (denoted BA, BAL, MNE, MNEL). The second iteration separated aspen and spruce competitors into two terms (BA.aspen, BA.spruce, BAL.aspen, BAL.spruce, etc) but included both in the model in order to have the same cumulative competition index value as the combined competitor term. Therefore, eight indices were tested in total: BA, BA.aspen & BA.spruce, BAL, BAL.aspen & BAL.spruce, MNE, MNE.aspen & MNE.spruce, MNEL, MNEL.aspen & MNEL.spruce (where the L denotes a model with the size restriction).

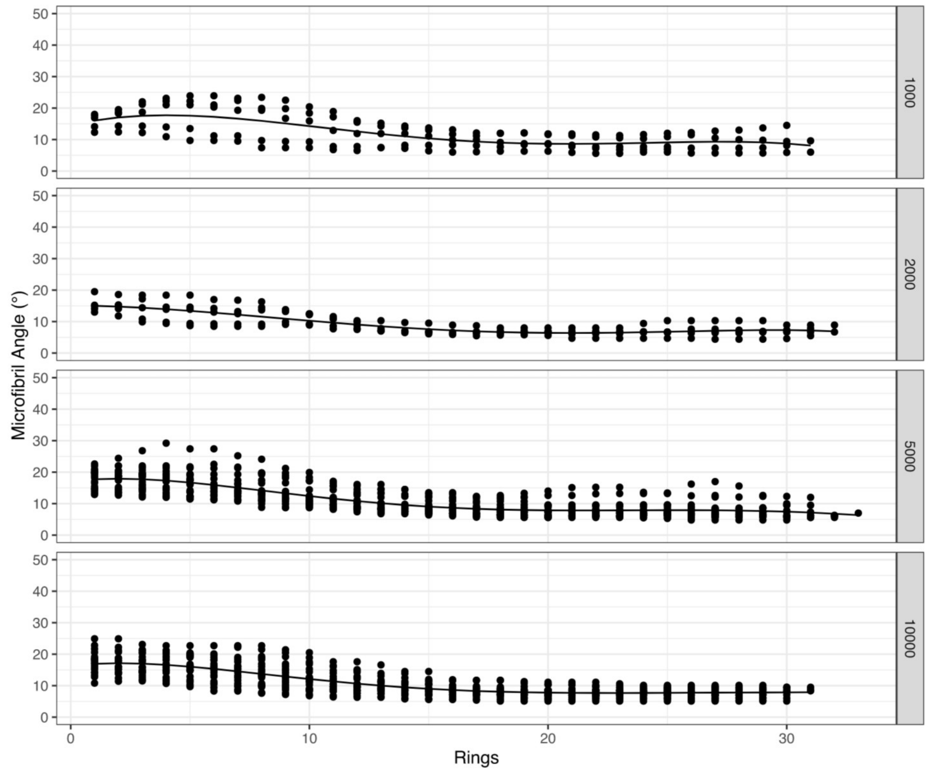
In order to determine which of the competition indices would be used as the neighbourhood competition term for the mixed effect model for each species, Akaike's Information Criterion (AIC value) was used to rank each model for each wood property. For each of the eleven wood attributes for each species, the best competition index was determined as that with the lowest AIC score for the most wood attributes. The competition index that described the most wood attributes for each species was then used as the neighbourhood competition term in the mixed effect model.

A linear mixed effect model (Equation 8), with tree as the random factor, and ring (cambial age), stand level competition (treatment) and neighbourhood level competition (one of the eight competition indices) as the fixed factors, was conducted to investigate differences in fibre attributes.

$$[8] \qquad Y_j=\beta_0+\beta_1 x_j+\beta_2 x_j+ (\beta_1\ \beta_2)+ \mu_1 +\varepsilon_j,$$

Where Y_j and x_j represent fibre property for year j; β_0, β_1 and β_2 are the fixed effects. μ_{i1} is the random effect of tree and u_{i2} is the random slope; ε_{ij} is the error term.

This portion of the analysis was completed using the lme function within the nlme statistical package (Pinheiro et al. 2020) in R (version 3.4.3) (R Development Core Team 2017). The relationships between growth levels and competition have been shown to vary between young and old stands, resulting in the need to parameterize models that characterize growth as a function of competition (Filipescu and Comeau 2007). The parameterization applied to this study was that measurements corresponding with a cambial age less than year 15 were omitted, to reduce the variation evident in early age wood attributes (Figure 3.1).



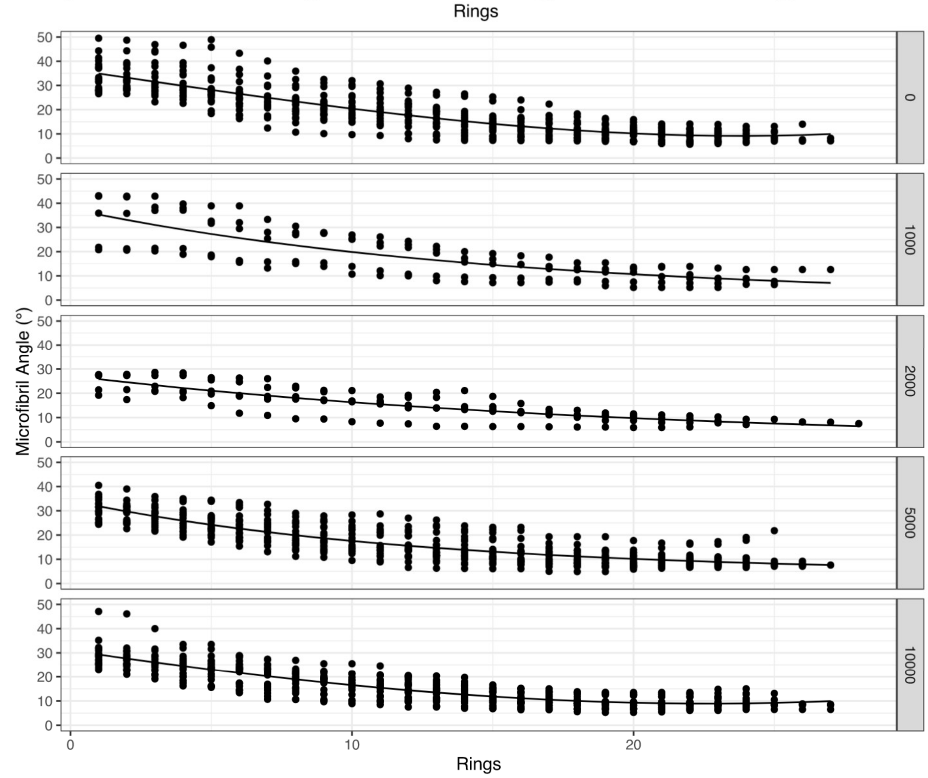


Figure 3.1 Microfibril angle change over time for aspen samples (top), and spruce samples (bottom), separated by treatments.This figure is shown as an example of the fluctuation of values between years 0 and 10 in both spruce and aspen samples and demonstrates that both approximate linear changes after year 15. This trend throughout wood attributes provided the basis for paramaterization. For the figures for each wood attribute and species, consult Chapter 2 Supplementry Appendix.

The R_β^2 statistic was calculated using the Kenward-Roger approach within the r2glmm (method = “kr”) function in R (Halekoh and Højsgaard 2014). The linear mixed model lmer function within the lme4 package (Bates et al. 2015) was used for the calculation of effect size, as the rbeta function does not work with the lme function in the nlme package. This statistic estimates the R^2 value for mixed effect models in the R environment. Tukey’s test for significant differences (TukeyHSD function in “stats” package (R Development Core Team 2017)) was used to determine differences between relative contributions of aspen and spruce competitors to the overall competition index.

3.4 RESULTS

3.4.1 Inter- vs intra specific competition

Table 3.1 summarizes the results of Tables 3.2 and 3.3, which show the results of the mixed effect model analysis that included cambial age, and neighbourhood level competition terms in the form of either a combined species “both” term or separated “aspen” and “spruce” terms. Building on results of the Chapter 2, we reviewed differences between treatment for each wood attribute. This analysis builds on the previous model by including plot level (3.99m) competition index terms. Due to the vast amount of information included in model outputs for each wood attribute, the results of these analyses have been synthesized into several summary tables. Full statistical results can be found in “Chapter 3 Supplementary Appendix” attached.

In order to test the first hypothesis, that aspen is more affected by intra-specific competition and that spruce is more affected by inter-specific competition, the number of significant results for species combined competition indices were tallied and compared to those indices which separated aspen and spruce (Table 3.1, 3.2 and 3.3). The first result is that, out of the species separated competition terms, the aspen term was more often significant than the spruce term, indicating that aspen is more susceptible to intra-specific competition, while spruce is more susceptible to inter-specific competition. Further, comparing the total number of significant neighbourhood level terms show that aspen wood attributes were determined to be more sensitive to neighbourhood level competition compared to white spruce. Finally, these results indicate that both spruce and aspen samples are more affected by competition models that included a combined "both" term rather than separated aspen and spruce terms. This shows that defining the overall competitive environment is more important than separating competitor species.

Table 3.1 A summary of the results from the evaluation of the neighbourhood level competition index mixed effect models ($\alpha < 0.05$) Percentages used for ease of interpretation (dividing the number of significant observations of either "both" "aspen" or "spruce" by the total number of significant observations of each species). For full statistical results, consult Table 3.2 and Table 3.3 as well as Chapter 3 supplementary Appendix.

	Aspen significance summary			
	Both	**Aspen**	**Spruce**	**total**
Overall % significant	55%	39%	6%	
Number of significant observations	18	13	2	33

	Spruce significance summary			
	Both	**Aspen**	**Spruce**	**Total**
Overall % significant	52%	30%	17%	
Number of significant observations	12	7	4	23

Table 3.2 Summarized aspen sample tree p-value results for the competition index term of each mixed effect model iteration (Full model results in Chapter 3 Supplementary Appendix). Each column represents a distinct model iteration (which included age, treatment, one of the competition index terms, and the random effect of tree). Bolded values correspond with lowest AIC value for each wood attribute. Significant interactions are denoted as follows: age (a), treatment: 1k (b), treatment: 2k (c), treatment: 5k (d), treatment: 10k (e).

Wood attribute	**BA**	**BA. aspen**	**BA. spruce**	**BAL**	**BAL. aspen**	**BAL. spruce**	**MNE**	**MNE. aspen**	**MNE. spruce**	**MNEL**	**MNEL. aspen**	**MNEL. spruce**
MOE	0.933	0.992	0.554	0.933^{a}	0.591^{a}	0.448	**0.628**	0.833	0.972	0.958^{a}	0.455^{a}	0.372
MFA	0.061^{a}	0.035^{a}	0.5144	**0.002**	0.003^{a}	0.227^{c}	$0.0213^{c,e}$	$0.273^{a,c,e}$	0.929^{a}	$0.0081^{a,c,d,e}$	0.123^{a}	0.411
Density	0.154	0.17	0.429	$\mathbf{0.072^{e}}$	0.191	0.169	0.597	$0.778^{c,d,e}$	0.559	0.912^{e}	0.465	0.299
Ring area	0.134^{a}	0.121^{a}	$0.872^{a,c}$	$\mathbf{<0.001^{a,c}}$	$<0.001^{a}$	$<0.001^{a}$	$0.0012^{a,d,e}$	0.462^{a}	0.295^{c}	$<0.001^{a,d,e}$	0.019^{a}	0.138
Ring width	0.147	0.132	0.9^{d}	$\mathbf{<0.001^{a}}$	$<0.001^{a}$	$<0.001^{e}$	$<0.001^{d,e}$	0.47	0.137^{c}	$<0.001^{a,d,e}$	0.003^{a}	0.08^{e}
Tangential Diameter	0.741^{a}	0.653^{a}	0.538	0.091	0.108	0.539	**0.053**	0.071	0.373	0.74	0.054	0.534
Radial Diameter	0.194	0.15	0.673	0.01	0.012	0.404	0.006	0.194	0.884	**0.005**	0.033	0.816
Specific surface area	0.439	0.528	0.246	0.768	0.885	0.399	**0.054**	0.385^{a}	0.904	0.212^{a}	0.054	0.237
Cell Population	0.334	0.27	0.572	0.013	0.018	0.343	0.009	0.068	0.598	**0.009**	0.022	0.843
Coarseness	0.965	0.844	0.358	0.249	0.189	0.971	**0.005**	0.167^{a}	0.949^{a}	0.019	0.016^{a}	0.51^{a}
Wall Thickness	0.579	0.672	0.318	0.932	0.681	0.588	**0.023**	0.421	0.699	0.089	0.039^{a}	0.372

Table 3.3 Summarized spruce sample tree p-value results for the competition index term of each mixed effect model iteration (Full model results in Chapter 3 Supplementary Appendix). Each column represents a distinct model iteration (which included age, treatment, one of the competition index terms, and the random effect of tree). Bolded values correspond with lowest AIC value for each wood attribute. Significant interactions are denoted as follows: age (a), treatment: 1k (b), treatment: 2k (c), treatment: 5k (d), treatment: 10k (e).

Wood attribute	**BA**	**BA. aspen**	**BA. spruce**	**BAL**	**BAL. aspen**	**BAL. spruce**	**MNE**	**MNE. aspen**	**MNE. spruce**	**MNEL**	**MNEL. aspen**	**MNEL. spruce**
MOE	0.523	0.973	0.105	0.591^{b}	0.994	0.37	0.876^{a}	**0.048**^{a}	**0.015**	0.997^{a,b}	0.912^{a}	0.9002^{b}
MFA	0.119	0.253^{a}	0.17^{a}	0.347^{b}	0.175	0.766	0.4^{a}	**0.062**^{a}	**0.004**	0.228^{a,b}	0.804^{a}	0.511^{a}
Density	0.322	0.084	0.224	**0.0091**	0.031	0.161	0.241^{a}	0.202	0.581	0.033^{a,c}	0.366^{a}	0.514
Ring area	0.44	0.148	0.243^{a}	<0.001^{d,e}	**0.015**	**<0.001**^{a}	0.08	0.488	0.54^{e}	0.034^{c,d,e}	0.97^{a}	0.08^{a,b,d,e}
Ring width	0.166^{a}	0.083^{a}	0.754	**<0.001**	0.019^{a}	0.0012^{a}	0.1^{a}	0.337^{a}	0.821	0.046^{a,c,d,e}	0.988^{a}	0.116^{a,b,d,e}
Tangential Diameter	0.989^{a}	0.581^{a}	0.232	**0.056**	0.062	0.534	0.556	0.431^{a}	0.162	0.21	0.395	0.998
Radial Diameter	0.371^{a,d}	0.056^{a}	0.0722	**0.002**^{a}	0.012^{a}	0.08	0.005^{a}	0.167^{a}	0.499	0.006^{d,e}	0.235	0.37^{e}
Specific surface area	**0.332**	0.265	0.992	0.342	0.447	0.6	0.9^{a}	0.287^{a}	0.177	0.588	0.882	0.8
Cell Population	0.556^{a,d}	0.107^{a}	0.055^{a}	**0.003**	0.006	0.233	0.016	0.569^{a}	0.188^{a}	0.005	0.112	0.694
Coarseness	0.829^{a}	0.887^{a}	0.412^{b}	0.372^{a}	0.409^{a}	0.727	**0.243**^{a}	0.639^{a}	0.135	0.395^{a}	0.644^{a}	0.896
Wall Thickness	0.515^{a}	0.4	0.848	**0.345**	0.513^{a}	0.505	0.942^{a}	0.315^{a}	0.215	0.506^{a}	0.892^{a}	0.716

There were distinct differences in the type of competition index that best described neighbourhood level competition for each of aspen and spruce (Table 3.4). Table 3.4 is the summary of table 3.5, which shows the AIC rankings of each neighbourhood competition index included in the mixed effect model for each wood property.

Table 3.4 The best neighbourhood competition term was determined by comparing the eight competition index terms, for each of the eleven wood attributes, for both aspen and spruce samples. Percentages show the number of times each competition index was chosen as the best term for each wood attribute divided by the total number of fibre properties (11).

Aspen AIC results		
Competition index	**Number of fibre properties**	**Percentage**
MNE	5	45%
BAL	4	36%
MNEL	2	18%

Spruce AIC results		
Competition Index	**Number of fibre properties**	**Percentage**
BAL	6	55%
MNE.aspen.spruce	2	18%
MNE	1	9%
BAL.aspen.spruce	1	9%
BA	1	9%

For aspen, no models which separated spruce and aspen competition terms improved model performance. The distance-dependent Martin and Ek competition index (MNE) yielded the lowest AIC score for five of the eleven aspen wood attribute models. There was more variety observed in the spruce samples, where several models displayed low AIC scores (Table 3.4). However, the distance-independent BAL (basal area where dbh competitor > dbh sample) yielded the lowest score for six out of eleven wood attributes in spruce so it was chosen as the best index for spruce. MNE was used as the neighbourhood competition term for the following iterations of the mixed effect models for aspen, and BAL was used for spruce mixed effect models in order to separate the effects of age, competition index and stand level competition.

Table 3.5 The best neighbourhood competition term was determined by comparing the eight competition index terms, for each of the eleven wood attributes, for both aspen and spruce sample, and ranked by AIC value.

	Aspen			Spruce		
Wood attribute	**Model**	**df**	**AIC**	**Model**	**df**	**AIC**
Ring Width	lme.BAL.a	8	1324.418	lme.BAL.s	9	790.0412
	lme.BAL.aspen.spruce.a	9	1325.607	lme.BAL.aspen.spruce.s	10	790.2578
	lme.MNEL.a	8	1333.212	lme.MNEL.s	9	800.5454
	lme.MNEL.aspen.spruce.a	9	1334.793	lme.MNEL.aspen.spruce.s	10	800.9915
	lme.MNE.a	8	1341.907	lme.MNE.s	9	801.7944
	lme.MNE.aspen.spruce.a	9	1343.009	lme.BA.s	9	802.6489
	lme.BA.a	8	1355.271	lme.BA.aspen.spruce.s	10	803.3094
	lme.BA.aspen.spruce.a	9	1357.051	lme.MNE.aspen.spruce.s	10	803.7911
	lme1.a	5	1749.084	lme1.s	6	1222.7332
Density	lme.BAL.a	8	7167.262	lme.BAL.s	9	6419.25
	lme.BA.a	8	7168.487	lme.BAL.aspen.spruce.s	10	6421.236
	lme.BAL.aspen.spruce.a	9	7168.962	lme.MNEL.s	9	6421.528
	lme.MNE.a	8	7170.278	lme.BA.aspen.spruce.s	10	6423.314
	lme.BA.aspen.spruce.a	9	7170.415	lme.MNEL.aspen.spruce.s	10	6423.454
	lme.MNEL.a	8	7170.55	lme.MNE.s	9	6424.786

Wood attribute	Model	df	AIC	Model	df	AIC
	lme.MNEL.aspen.spruce.a	9	7171.448	lme.BA.s	9	6425.188
	lme.MNE.aspen.spruce.a	9	7172.005	lme.MNE.aspen.spruce.s	10	6426.195
	lme1.a	5	7732.726	lme1.s	6	6854.024
MFA	lme.BAL.a	8	1965.562	lme.MNE.aspen.spruce.s	10	2734.74
	lme.BAL.aspen.spruce.a	9	1967.315	lme.BA.s	9	2738.692
	lme.MNEL.a	8	1968.172	lme.MNEL.s	9	2739.686
	lme.MNE.a	8	1969.939	lme.BA.aspen.spruce.s	10	2740.197
	lme.MNEL.aspen.spruce.a	9	1970.108	lme.BAL.s	9	2740.267
	lme.BA.aspen.spruce.a	9	1971.504	lme.MNE.s	9	2740.448
	lme.BA.a	8	1971.778	lme.BAL.aspen.spruce.s	10	2741.236
	lme.MNE.aspen.spruce.a	9	1971.884	lme.MNEL.aspen.spruce.s	10	2741.48
	lme1.a	5	3284.046	lme1.s	6	3730.14
MOE	lme.MNE.a	8	1941.123	lme.MNE.aspen.spruce.s	10	1901.319
	lme.BAL.a	8	1941.355	lme.BA.aspen.spruce.s	10	1904.728

Wood attribute	Model	df	AIC	Model	df	AIC
	lme.BA.a	8	1941.355	lme.BA.s	9	1905.025
	lme.MNEL.a	8	1941.359	lme.BAL.s	9	1905.146
	lme.BAL.aspen.spruce.a	9	1942.479	lme.MNE.s	9	1905.416
	lme.MNEL.aspen.spruce.a	9	1942.486	lme.MNEL.s	9	1905.44
	lme.BA.aspen.spruce.a	9	1942.981	lme.BAL.aspen.spruce.s	10	1906.62
	lme.MNE.aspen.spruce.a	9	1943.122	lme.MNEL.aspen.spruce.s	10	1907.424
	lme1.a	5	3021.362	lme1.s	6	2979.759
Coarseness	lme.MNE.a	8	8640.239	lme.MNE.s	9	6512.454
	lme.MNE.aspen.spruce.a	9	8642.127	lme.MNE.aspen.spruce.s	10	6512.676
	lme.MNEL.a	8	8642.599	lme.BAL.s	9	6513.03
	lme.MNEL.aspen.spruce.a	9	8643.152	lme.MNEL.s	9	6513.109
	lme.BAL.a	8	8646.848	lme.BA.s	9	6513.795
	lme.BA.a	8	8648.203	lme.BAL.aspen.spruce.s	10	6514.993
	lme.BAL.aspen.spruce.a	9	8648.438	lme.MNEL.aspen.spruce.s	10	6515.108
	lme.BA.aspen.spruce.a	9	8649.159	lme.BA.aspen.spruce.s	10	6515.11
	lme1.a	5	9228.614	lme1.s	6	7200.806
Tangential Diameter	lme.MNE.a	8	3457.947	lme.BAL.s	9	2252.067

Wood attribute	Model	df	AIC	Model	df	AIC
	lme.MNEL.a	8	3458.519	lme.BAL.aspen.spruce.s	10	2253.732
	lme.MNE.aspen.spruce.a	9	3458.556	lme.MNEL.s	9	2254.194
	lme.BAL.a	8	3458.871	lme.MNE.s	9	2255.447
	lme.MNEL.aspen.spruce.a	9	3459.442	lme.MNE.aspen.spruce.s	10	2255.668
	lme.BAL.aspen.spruce.a	9	3460.787	lme.BA.s	9	2255.8
	lme.BA.a	8	3461.678	lme.BA.aspen.spruce.s	10	2255.911
	lme.BA.aspen.spruce.a	9	3463.021	lme.MNEL.aspen.spruce.s	10	2256.141
	lme1.a	5	3970.028	lme1.s	6	2694.796
Radial Diameter	lme.MNEL.a	8	3105.711	lme.BAL.s	9	2408.213
	lme.MNE.a	8	3106.02	lme.MNE.s	9	2410.153
	lme.BAL.a	8	3107.104	lme.MNEL.s	9	2410.198
	lme.MNEL.aspen.spruce.a	9	3107.551	lme.BAL.aspen.spruce.s	10	2410.212
	lme.MNE.aspen.spruce.a	9	3107.958	lme.MNEL.aspen.spruce.s	10	2412.033
	lme.BAL.aspen.spruce.a	9	3108.751	lme.MNE.aspen.spruce.s	10	2412.113

Wood attribute	Model	df	AIC	Model	df	AIC
	lme.BA.a	8	3112.174	lme.BA.aspen.spruce.s	10	2412.577
	lme.BA.aspen.spruce.a	9	3113.162	lme.BA.s	9	2417.235
	lme1.a	5	3650.971	lme1.s	6	3084.568
Specific Surface Area	lme.MNE.a	8	6874.273	lme.BA.s	9	6324.396
	lme.MNEL.aspen.spruce.a	9	6876.251	lme.BAL.s	9	6324.437
	lme.MNE.aspen.spruce.a	9	6876.252	lme.MNEL.s	9	6325.056
	lme.MNEL.a	8	6876.486	lme.MNE.s	9	6325.339
	lme.BA.a	8	6877.462	lme.MNE.aspen.spruce.s	10	6325.482
	lme.BAL.a	8	6877.984	lme.BA.aspen.spruce.s	10	6326.076
	lme.BA.aspen.spruce.a	9	6878.564	lme.BAL.aspen.spruce.s	10	6326.437
	lme.BAL.aspen.spruce.a	9	6879.325	lme.MNEL.aspen.spruce.s	10	6327.03
	lme1.a	5	7448.818	lme1.s	6	6906.066
Ring Area	lme.BAL.a	8	10478.41	lme.BAL.aspen.spruce.s	10	9164.62
	lme.BAL.aspen.spruce.a	9	10479.54	lme.BAL.s	9	9165.148
	lme.MNEL.a	8	10496.82	lme.MNEL.s	9	9176.824

Wood attribute	Model	df	AIC	Model	df	AIC
	lme.MNEL.aspen.spruce.a	9	10498.49	lme.MNEL.aspen.spruce.s	10	9176.898
	lme.MNE.a	8	10503.15	lme.MNE.s	9	9178.302
	lme.MNE.aspen.spruce.a	9	10504.79	lme.BA.aspen.spruce.s	10	9179.621
	lme.BA.a	8	10511.61	lme.MNE.aspen.spruce.s	10	9180.197
	lme.BA.aspen.spruce.a	9	10513.4	lme.BA.s	9	9180.817
	lme1.a	5	11124.87	lme1.s	6	9913.561
Cell Population	lme.MNEL.a	8	9106.109	lme.BAL.s	9	8266.978
	lme.MNE.a	8	9106.221	lme.MNEL.s	9	8268.079
	lme.BAL.a	8	9106.83	lme.BAL.aspen.spruce.s	10	8268.533
	lme.MNE.aspen.spruce.a	9	9107.394	lme.MNEL.aspen.spruce.s	10	8270.064
	lme.MNEL.aspen.spruce.a	9	9107.475	lme.MNE.s	9	8270.154
	lme.BAL.aspen.spruce.a	9	9108.669	lme.BA.aspen.spruce.s	10	8271.236
	lme.BA.a	8	9112.244	lme.MNE.aspen.spruce.s	10	8271.29
	lme.BA.aspen.spruce.a	9	9113.212	lme.BA.s	9	8275.697

Wood attribute	Model	df	AIC	Model	df	AIC
	lme1.a	5	9691.333	lme1.s	6	8940.39
Wall Thickness	lme.MNE.a	8	16.16111	lme.BAL.s	9	-747.3024
	lme.MNE.aspen.spruce.a	9	18.15581	lme.MNEL.s	9	-746.8433
	lme.MNEL.a	8	18.49016	lme.BA.s	9	-746.8255
	lme.MNEL.aspen.spruce.a	9	18.8117	lme.MNE.s	9	-746.3988
	lme.BA.a	8	21.12628	lme.MNE.aspen.spruce.s	10	-745.975
	lme.BAL.a	8	21.43247	lme.BAL.aspen.spruce.s	10	-745.3287
	lme.BA.aspen.spruce.a	9	22.38627	lme.BA.aspen.spruce.s	10	-745.1763
	lme.BAL.aspen.spruce.a	9	22.96613	lme.MNEL.aspen.spruce.s	10	-744.9067
	lme1.a	5	618.64595	lme1.s	6	-214.5255

3.4.2 Competition index

The competition index terms varied in the relative contributions of each competitor species across treatments (Figure 3.2). In both spruce and aspen samples, the main contributor to the overall index value was aspen competitors, as the “A” value (defined as aspen competition) never differed significantly from the combined “both” indices (competition from both spruce and aspen). Alternatively, spruce competitors differed from the combined index and the aspen competitor contribution.

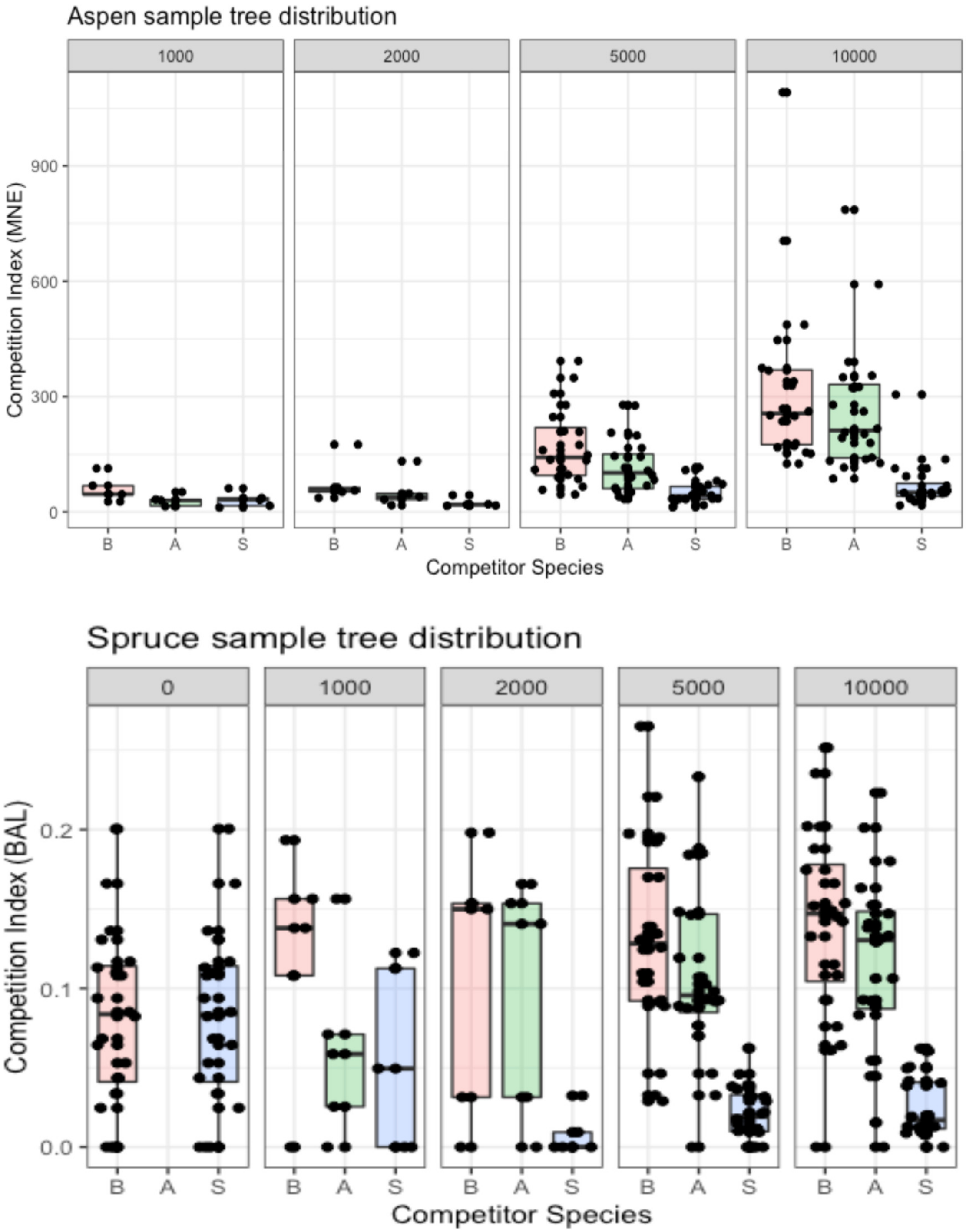


Figure 3.2 Aspen and MNE (top) with spruce and BAL (bottom)) showing the proportion that each competitor species, aspen (A), and spruce (S), contributes to the overall index, both (B).

3.4.3 Effect size (R_β^2)

The Kenward-Roger approach for calculating the R_β^2 (effect size) statistic, was utilized to determine relative effects of each of the model terms. Overall, the models for each wood attribute were effective in describing the variation observed in both aspen samples: 23% – 75%, and spruce samples: 54% – 90% (Table 3.3). The R_β^2 approximates an R^2 value for mixed effect models and indicates the fit of the model compared to the data. The terms for each wood attribute model are represented in the columns for each species. The "model" column shows the overall fit of the model, and each further column shows the relative contribution of each term to the model's performance. The remainder of the variation explained by the model, but not tabulated is the effect described by the random tree term in the model, but was excluded, in order to focus on the proportion of the variance explained by fixed effects. The neighbourhood competition model was chosen for each species based on which performed best for each sample species. For aspen sample wood attributes, the distance dependent competition index by Martin and Ek (1984) (denoted MNE) best described neighbourhood level competition variation observed. For spruce wood attributes, the distance independent competition index of basal area of larger trees (denoted BAL, where the size of the competitor > size of the sample tree diameter at breast height) best described neighbourhood level competition variation. The "stand level competition" column describes the effect attributed to the competitive environment as defined by stems per hectare aspen (0, 1000, 2000, 5000, or 10000 stems per hectare). This approach to determining effect size of terms in the model was used rather than global model simplification, as this form of study answers the question of which model terms are most important for each species and wood attribute, when the best competition index is included for each species.

The model terms for spruce and aspen samples differed in their responses. Each wood attribute model included four terms: age, neighbourhood level competition (competition index), stand level competition (treatment measured in aspen stems per hectare), and the random effect of tree. For each of the eleven wood attributes measured (and for each sample species), one dominant effect was chosen as the model term that explained the most variation out of the chosen model terms. Aspen and spruce differed in their dominant effects. In aspen samples, ring area, ring width, radial diameter, cell population and coarseness variation were all best explained by the neighbourhood level competition term. In spruce, none of the wood property variation was explained by the neighbourhood competition term. In both aspen and spruce, age was the dominant effect for MOE and MFA. However, no other aspen attributes were explained by age, while specific surface area, coarseness and cell wall thickness were all explained by age in spruce samples. Stand level competition was the main factor in the variation of density and tangential diameter in both spruce and aspen. The majority of the wood attribute variation in spruce was best explained by stand level competition (density, ring area, ring width, tangential diameter, radial diameter, and cell population) (Table 3.6).

Table 3.6 A summary of the R^2 values calculated by *the effect size (R_β^2) statistic results. Complete results can be found in Chapter 3 Supplementary Appendix (Page 192).*

	Aspen Samples				Spruce Samples			
Wood attribute	**model**	**Age**	**Neighbourhood Competition (MNE)**	**Stand Level Competition**	**model**	**Age**	**Neighbourhood Competition (BAL)**	**Stand Level Competition**
MOE	0.747	0.206	0.005	0.044	0.905	0.559	0.0042	0.108
MFA	0.639	0.127	0.102	0.087	0.873	0.479	0.0125	0.327
Density	0.611	0.115	0.006	0.129	0.591	0.064	0.093	0.163
Ring area	0.481	0.045	0.194	0.072	0.54	0.005	0.207	0.455
Ring width	0.602	0.076	0.267	0.138	0.811	0.302	0.186	0.441
Tangential Diameter	0.237	0.000008	0.074	0.129	0.732	0.223	0.052	0.351
Radial Diameter	0.363	0.025	0.145	0.079	0.598	0.091	0.131	0.364
Specific surface area	0.681	0.139	0.073	0.155	0.734	0.26	0.013	0.15
Cell Population	0.342	0.0159	0.129	0.102	0.79	0.276	0.121	0.441
Coarseness	0.56	0.069	0.147	0.136	0.836	0.387	0.012	0.295
Wall Thickness	0.662	0.126	0.1	0.139	0.729	0.255	0.013	0.131

3.5 DISCUSSION

Our analysis indicated that aspen is more sensitive to neighbourhood level competition than spruce (Table 3.1). Out of the 88 iterations (11 wood properties x 8 competition index models) for each species, 38% of the time, neighbourhood competition terms significantly explained the variation in aspen wood attributes and 26% of the time in spruce. Our results correspond with the trees life-history characteristics as aspen is shade intolerant and reacts negatively to competition (Farmer 1963), compared to spruce which (under aspen canopy) exhibits linear height increment growth in light levels up to 40%, with negligible gain in height increment exhibited between 40% and 100% (Lieffers and Stadt 1994; Groot 1999).

Aspen was found to be more affected by competition from other aspen than from spruce, based on the observed significance in the models with separated species terms (BA.aspen & BA.spruce, BAL.aspen & BAL.spruce, etc.) (Table 3.4). Intra-specific competition is often more detrimental to non-shade tolerant species due to increased leaf area index and canopy closure from competition from the same species (Pretzsch and Biber 2016). Conversely, in accordance with previous studies documenting the negative effect of broadleaf competition on white spruce growth, sampled spruce were more affected by inter specific competition (Bérubé-Deschênes 2017). However, our results suggest that competition from both spruce and aspen needs to be considered when assessing how wood properties are impacted by competition at the neighbourhood stand level. This finding could be a reflection of the uneven number of aspen competitors (~70%) in this study. In this case, the sheer amount of aspen in each treatment drives the competition index value in the combined "both" term (Figure 3.2). Therefore, since the competition index that included a combined term for aspen and spruce preformed best for each wood attribute model, our results indicate that differentiating the competitor species is less important than defining the overall competitive environment.

As hypothesized, there was a difference between best neighbourhood level competition index for aspen and spruce (Table 3.4). For aspen, the distance dependent MNE index best described the majority of wood attribute variation with neighbourhood competition environment (Table 6.1). Aspen typically develop large crowns, are shade intolerant and as such, require more growing space than a shade tolerant species. Since broadleaves are often more susceptible to competition, issues related to developing large crown radii can result in a larger importance placed on proximity to a competing tree (Pretzsch 2019). Alternatively, for spruce samples, the distance-independent BAL (basal area where $DBH_{competitor} > DBH_{sample}$) index best described the majority of wood attribute variation. BAL has also been found to effectively describe the neighbourhood competition effect on basal area increment growth of white spruce (Bérubé-Deschênes 2017) and other conifers (Kahriman et al. 2018). This could be explained by the fact that shade tolerant species have been found to be less sensitive to competition (Canham et al. 2006). Interestingly, the best models for both spruce and aspen included a size term (MNE size ratio term, and BAL size cut-off) further demonstrating that plant size can influence the intensity of competition (Canham et al. 2004).

Through the calculation of the R_{β}^2 statistic, each modeled wood attribute was determined to be most affected by one of the three model terms: (i) age, (ii) neighbourhood level competition (MNE/BAL), or (iii) stand level competition (treatment) (Table 3.6). For aspen samples, the dominant model term for the tested model structure for each wood attribute was one of the two competition terms whereas the majority of spruce wood attributes were dominated by the age and stand level terms.

Within aspen samples, the neighborhood competition effect (MNE index) was the dominant effect in ring width, ring area, radial diameter, cell population, and coarseness (Table 3.6). Ring width (and ring area which is directly related) was negatively impacted by increased competition levels in aspen samples. This is consistent with the exterior growth characteristics observed in trees in competitive environments, whereby height, rather than diameter growth is preferred (Coopersmith and Hall 1999; Carr et al. 2020). Aspen coarseness values have been shown to be statistically different and larger in pure stands than mixed stands (De Araujo et al. 2015). Our results expand on this finding as they indicate that stands with an increased proportion of aspen leads to higher values of coarseness. Coarseness is an important consideration for paper manufacturing but varies in desirability depending on end use. If a paper with improved density, strength and optical properties is the desired end product, then low coarseness is desirable as it generates higher fibre collapsibility (low aspen treatment densities). If high porosity paper is the desired end product, then higher coarseness values are necessary (high aspen treatment densities) (Seth and Kingsland 1990).

Stand level competition (treatment) was the dominant effect for density, tangential diameter, specific surface area and cell wall thickness in aspen samples. Density and cell wall thickness often vary together as density is the proportion of material in the cell which depends on the ratio of cell wall thickness and cell diameter (Lundgren 2004; Carrillo et al. 2015). Thickness in the cell wall has been shown to respond to external factors, such as exposure and climate (Hein and Lima 2012). A possible explanation for the change in density is that variation in competition regime can influence the sensitivity to these factors, thereby changing the cell wall thickness and density. The effect of stand composition on wood density in aspen was documented by De Araujo et al. (2015), but no difference between density in mixed and pure stands were found. The differences observed in our study could be a result of comparing various managed levels of treatments in homogenous growing conditions and even aged stands rather than unmanaged uneven sites.

The dominant model terms within spruce wood attributes were split between age and stand level competition (Table 3.6). The lack of neighbourhood level competition effect could be due to spruce's shade tolerance and relative (to aspen in this study) insensitivity to competition. The variation observed in MOE, MFA, specific surface area, coarseness and wall thickness were best described by age in spruce samples. It was surprising that cell wall thickness was more affected by age and not competition as thickness in the cell wall has shown to change with growth rates from fertilization (Lundgren 2004). However, it has been shown that age of conifers play an important role in the timings and duration of xylem formation: cell production in the cambial zone, cell expansion and cell wall thickening (Zeng et al. 2018). A possible explanation for why cell wall thickness was best described by age in this study, is that some of the strongest variation in growth rates between treatments were observed (and removed from our parameterization) early in stand development (< 15 years). This variation stabilized over time to similar values regardless of treatment.

Stand level competition was the dominant model term for density, ring area, ring width, tangential diameter, radial diameter and cell population in spruce. Ring width and ring area can vary with competition as discussed previously with the preferential height to diameter growth in increasing competition regimes. Water availability changes in microsite competitive environments, and has been linked to the formation of wider tracheids, which could explain the strong competition signal in radial diameter (Vysotskaya and Vaganov 1989; Wilpert 1991; Kerhoulas et al. 2013).

The main similarity between aspen and spruce was that MOE and MFA were best described by the age term for both species. MOE and MFA are two terms that often vary together and are typically associated with the age of the tree (Barnett and Bonham 2004). Up to 86% of the variation in MOE can be explained by variation in MFA (Evans and Ilic 2001). Microfibril angle is the orientation of the crystalline cellulose in the secondary cell wall (S2) wood along the fibre axis, and this orientation is driven by growth rate of the tree (Cave 1966). Typically, high MFA values result from fast initial growth rates as the tree develops resulting in the inversely proportional low MOE, allowing the stem to bend without breaking. As the tree ages, it must support the crown and weight of branches, and stiffens, resulting in a low MFA and high MOE (Barnett and Bonham 2004). In this study, while age was the most important determinant for MFA in both spruce and aspen, neighbourhood level, and stand level competition for both spruce and aspen respectively were next best terms (Table 3.6). In spruce samples, one of the best performing models across wood attributes, was in fact the model for MFA, which explained 87% of the variation, and age together with stand level competition explained 80%, with around 6% of the variation attributed to the random effect of tree. This competition effect would likely be pronounced if the entire age of the tree was used (rather the < 15-year cut-off) as there is a large variation in the initial values of MFA in the early development (age 0-5) of spruce. These variations corresponding with lower MFA's with increasing levels of treatment, indicating faster growth rates with increasingly competitive environments (Figure 3.1). Thus, while age was the most important factor in the model that described MFA change over time, stand level competition is also an important consideration for a comprehensive model.

3.6 CONCLUSION

We examined eleven wood attributes of aspen and white spruce sampled at a Northern British Columbia trial site and developed individual tree models to elucidate the effects of competition on wood attribute development. Our results demonstrated that differentiating the competition by species was less important than defining the overall competitive environment for both aspen and spruce wood attributes. We tested four neighbourhood competition indices and found that aspen wood attribute variation was best described by a distance dependent index, while spruce was best described by a distance independent index. Both of the neighbourhood competition indices included a size term, indicating that the size of the competitors was important for both species wood attribute development. Moreover, we developed a mixed effect model to describe each wood attribute development that included cambial age, neighbourhood competition, and stand level competition. Our results indicated that defining the neighbourhood level competition regime was most important for aspen but was relatively unimportant in spruce where cambial age and treatment were most important. Two of the most important wood attributes, microfibril angle and modulus of elasticity were best described by age and not competition in both spruce and aspen. These preliminary models lay the foundation for further studies that can make recommendations to forest managers based on desired end product. Since this study was conducted with samples from a managed trial site, the next step would be to sample natural even aged stands and compare wood attribute development across a number of sites. This would require careful consideration in order to find adequately comparable sites from an age and ecological perspective.

4. Conclusions and Future work

4.1 Conclusions

The key finding of my thesis is that wood attributes of white spruce and trembling aspen vary with competition and differ in their response to competition between species. Characterizing the effect that competition has on aspen and spruce wood attribute development is essential in order to effectively balance the benefits and shortcomings of managing for pure or mixed stands of aspen and white spruce. In this concluding chapter, I synthesize the main findings from each of the previous chapters, while I discuss the implications for management techniques, and recommend future research directions.

In Chapter 2, *Evaluating the impact of stand composition and competition on Spruce and Aspen wood attributes in mixedwood stands,* the objectives were threefold; (i) to determine if there was a difference in wood attribute response to stand level competition between species, (ii) to determine if aspen and white spruce display similar responses to stand level competition over time, and (iii) to analyze if there are any economic benefits observed in wood attributes with increasing aspen treatment density. First, my results indicated that aspen treatment density had a significant effect on most wood attributes in aspen and spruce samples and that each sampled species showed differences in their response. Second, my results indicated that all spruce wood attributes exhibit non-linear change as the trees develop (cambial age 0-5 years), and approximate linear change in older trees (cambial age 5-30 years). Finally, I developed a framework for visualizing change in industrial desirability of wood attribute as they vary with increasing levels of competition.

For most of the wood attributes that I measured (ring width, density, MOE, coarseness, tangential diameter, radial diameter, specific surface area, ring area, cell population, and wall thickness), two thresholds consistently emerged from the analysis.

First, the largest effect on spruce growth occurred when aspen was grown in densities greater than zero with the spruce (i.e., treatments of > 0 sph). Ninety percent of the significant differences within spruce wood properties, and between treatments, were attributed to the presence of aspen in the stand. This result was expected as aspen growing in mixture with spruce has been shown to impact the availability of key limiting resources with regards to light, water and nutrients (Filipescu and Comeau 2007; Kabzems et al. 2015). Additionally, past studies have demonstrated that modifications to spruce's growing environment influence absolute growth as well as gross growth characteristics such as height-to-diameter ratio (Kabzems et al. 2015).

The second threshold that emerged from my results was the impact of an aspen treatment density of 10,000 sph, on aspen wood characteristics. Differences between the 10,000 sph treatment and those with lower densities of aspen accounted for all of the significance observed in aspen wood attributes.

The final objective of Chapter 2 was to determine potential industrial desirability of each wood attribute as a function of competition for both spruce and aspen**.** As the desirability of certain wood attributes depend entirely on the end product, this section serves only as a general framework and not a guide for determining economic suitability with changing competition. The criteria for desirability were based on the typical uses of each wood attribute as defined by natural resource Canada, I found that spruce wood attributes are generally increased when spruce is grown in mixture with aspen. Increased wood density, larger MOE, lower MFA, larger ring width, and increased wall thickness are the benefits observed in spruce grown in the 5000 sph treatment which constitute either best or second-best improvements to wood quality, relative to other treatments. Managing for higher MOE can be desirable since MOE is the best predictor of wood stiffness. Although density may be less important for lumber products in the future due to the increased production of value added engineered wood products, density is still important for bioenergy, which values the higher energy content of dense wood (Canadian Wood Fibre Centre et al. 2010). These results indicate that there are multiple benefits to spruce wood attribute development up to 5000 sph treatment of aspen.

In contrast to spruce wood attributes, our results indicate that most desirable traits (MOE, density, and MFA) within aspen decrease with increasing levels of aspen competition (Figure 2.8). Lower values for MOE and density increase the risk of trunk breakage, xylem implosion and decreased stem stability (Hacke et al. 2001). Effectively, in this instance, the increased competition is weakening the aspen, and accelerating the stand dynamics typical of mixedwood forests (Bergeron et al. 2014). However, the majority of the negative associations for the remaining wood attributes are related to the 10,000 sph aspen treatment, suggesting that, aspen wood attributes are not significantly affected until densities are increased past a certain threshold.

In Chapter 3, *A mixed effect approach to evaluating the impacts of stand composition, age and neighbourhood competition on the wood attributes of spruce and aspen grown in mixedwood stands*, the mixed effect model of Chapter 2 was expanded by the inclusion of 3.99m plot data that incorporated information about each competitor and formed the basis for neighbourhood level competition indices. The objectives were again, threefold; (i) to compare spruce and aspen wood attribute response to inter- and intra- specific competition, (ii) to determine which neighbourhood level competition indices best improved a model for wood attributes in both aspen and spruce, and finally, (iii) To determine the competition resolution required for modelling wood attributes of both spruce and aspen. First, my results indicate that aspen is more sensitive to neighbourhood competition than spruce, which is similar to previous findings. The results also suggest that defining the overall competitive environment is more important for both spruce and aspen, rather than determining inter- vs intra-specific competition, which is also consistent with the literature (Bérubé-Deschênes 2017). Aspen wood attribute variation attributed to neighbourhood level competition was best described by the distance dependent index MNE, while spruce was best described by the distance independent BAL index. Finally, our results indicate that for aspen samples, most of the variation in wood attributes were best explained by one of the two competition terms (neighbourhood or stand level) in the model, while spruce sample variation was best described by age and stand level competition terms. These preliminary models lay the foundation for further studies that can make recommendations to forest managers based on desired end product.

4.2 Limitations and future work

In this section, I outline the limitations that apply to both of Chapter 2 and Chapter 3 as well as provide suggestions for improvements and future work.

The first limitation is that the conclusions of this study are based off a single managed trial site. Although the single sampling site offered a unique opportunity to compare various levels of competition in analogous site conditions, my analysis was restricted to one site, so my results may not accurately depict the effect competition has on wood attribute variation within aspen and white spruce throughout the boreal mixedwood forest. Further, since the sample site is a managed trial site that was maintained to target densities and not a natural stand, the within wood trends observed in this study may not mimic those found in natural stands. Our study also was limited in sample size due to budget restrictions associated with sending 120 samples for the in-depth Silviscan analysis. Finally, although our methods were such that we sampled trees that were greater than ten meters away from each other, aspen is a clonal species, and as such, the sampling process may have captured samples that originate from a single individual. While this is unlikely due to spatial distribution of samples, it would also likely not have a detrimental impact to the study as each sampled tree was grown in a unique competition environment. However, there could still be a small amount of variation attributed to the potential clonality of aspen.

The previous limitations could all be improved by selecting even-aged stands of similar site conditions and applying the same study framework. Multiple sites would increase the predictive nature of the study as well as remove the potential clonality influence of aspen and the results could then be applied to broader regions with confidence. Also, studying natural stands would increase the applicability of the study to forest managers. However, finding natural even-aged stands with similar site conditions is both time consuming and difficult, and as such has been a limitation of previous research on the topic as well.

5. Bibliography

Amarasekara, H. 2002. Effects of crown size on wood characteristics of Corsican pine in relation to definitions of juvenile wood, crown formed wood and core wood. Forestry **75**(1): 51–61. doi:10.1093/forestry/75.1.51.

Antony, F., Schimleck, L.R., Jordan, L., Daniels, R.F., and Clark, A. 2012a. Modeling the effect of initial planting density on within tree variation of stiffness in loblolly pine. Annals of Forest Science **69**(5): 641–650. doi:10.1007/s13595-011-0180-1.

Antony, F., Schimleck, L.R., Jordan, L., Daniels, R.F., and Clark, A. 2012b. Modeling the effect of initial planting density on within tree variation of stiffness in loblolly pine. Annals of Forest Science **69**(5): 641–650. doi:10.1007/s13595-011-0180-1.

Aziz, T.A.T. and F.A. 2013. Cellulose Microfibril Angle in Wood and Its Dynamic Mechanical Significance. Cellulose - Fundamental Aspects. doi:10.5772/51105.

Barnett, J.R., and Bonham, V.A. 2004. Cellulose microfibril angle in the cell wall of wood fibres. Biological Reviews **79**(2): 461–472. doi:10.1017/S1464793103006377.

Barton, K. 2020. Package "MuMIn." Available from https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf.

Bates, D., Mächler, M., Bolker, B., and Walker, S. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software **67**(1): 1–48. doi:10.18637/jss.v067.i01.

Bergeron, Y., Chen, H.Y.H., Kenkel, N.C., Leduc, A.L., and Macdonald, S.E. 2014. Boreal mixedwood stand dynamics: ecological processes underlying multiple pathways. The Forestry Chronicle **90**(02): 202–213. doi:10.5558/tfc2014-039.

Bérubé-Deschênes, A. 2017. Quantifying competition in white spruce (Picea glauca) plantations. Annals of Forest Science: 15.

Brandt, J.P., Flannigan, M.D., Maynard, D.G., Thompson, I.D., and Volney, W.J.A. 2013. An introduction to Canada's boreal zone: ecosystem processes, health, sustainability, and environmental issues. Environmental Reviews **21**(4): 207–226. doi:10.1139/er-2013-0040.

Brassard, B.W., and Chen, H.Y.H. 2006. Stand Structural Dynamics of North American Boreal Forests. Critical Reviews in Plant Sciences **25**(2): 115–137. doi:10.1080/07352680500348857.

Brassard, B.W., Chen, H.Y.H., Wang, J.R., and Duinker, P.N. 2008. Effects of time since stand-replacing fire and overstory composition on live-tree structural diversity in the boreal forest of central Canada. Can. J. For. Res. **38**(1): 52–62. doi:10.1139/X07-125.

Canadian Wood Fibre Centre, Canada, and Natural Resources Canada. 2010. The principal attributes of Canadian wood fibre. Natural Resources Canada, Ottawa. Available from http://publications.gc.ca/site/eng/381584/publication.html [accessed 2 April 2020].

Canham, C.D., LePage, P.T., and Coates, K.D. 2004. A neighborhood analysis of canopy tree competition: effects of shading versus crowding. Canadian Journal of Forest Research **34**(4): 778–787. Canadian Science Publishing NRC Research Press, Ottawa, Canada.

Canham, C.D., Papaik, M.J., Uriarte, M., McWilliams, W.H., Jenkins, J.C., and Twery, M.J. 2006. Neighborhood analyses of canopy tree competition along environmental gradients in New England forests. Ecol Appl **16**(2): 540–554. doi:10.1890/1051-0761(2006)016[0540:naoctc]2.0.co;2.

Carleton, T.J., and Maycock, P.F. 1981. Understorey–canopy affinities in boreal forest vegetation. Canadian Journal of Botany **59**(9): 1709–1716. doi:10.1139/b81-229.

Carr, S., Larocque, G.R., Luckai, N., and Bell, F.W. 2020. Effect of competition on individual white spruce production in young boreal mixedwood forests. Can. J. For. Res. **50**(8): 726–735. doi:10.1139/cjfr-2019-0395.

Carrillo, I., Aguayo, M.G., Valenzuela, S., Mendonça, R.T., and Elissetche, J.P. 2015. Variations in wood anatomy and fiber biometry of Eucalyptus globulus genotypes with different wood density. Wood Research **60**: 10.

Cave, I.D. 1966. Theory of X-ray measurement of microfibril angle in wood. Forest Products Journal **16**(10): 37–42.

Chen, H.Y.H., and Popadiouk, R.V. 2002. Dynamics of North American boreal mixedwoods. Environmental Reviews; Ottawa **10**(3): 137–166.

Chen, S., Shahi, C., Chen, H.Y.H., and McLaren, B. 2017. Economic analysis of forest management alternatives: Compositional objectives, rotation ages, and harvest methods in boreal forests. Forest Policy and Economics **85**: 124–134. doi:10.1016/j.forpol.2017.09.006.

Comeau, P.G. 2021. Effects of Thinning on Dynamics and Drought Resistance of Aspen-White Spruce Mixtures: Results From Two Study Sites in Saskatchewan. Front. For. Glob. Change **3**: 621752. doi:10.3389/ffgc.2020.621752.

Comeau, P.G., Filipescu, C.N., Kabzems, R., and DeLong, C. 2004. Early growth of white spruce underplanted beneath spaced and unspaced aspen stands in northeastern British Columbia. Canadian Journal of Forest Research **34**(11): 2277–2283. doi:10.1139/x04-105.

Comeau, P.G., Kabzems, R., McClarnon, J., and Heineman, J.L. 2005. Implications of selected approaches for regenerating and managing western boreal mixedwoods. The Forestry Chronicle **81**(4): 559–574. doi:10.5558/tfc81559-4.

Coopersmith, D., and Hall, E. 1999. Experimental Project 1077 – The Siphon Creek Mixedwood Trial: BC Ministry of Forests: 10.

Cortini, F., Comeau, P.G., and Bokalo, M. 2012. Trembling aspen competition and climate effects on white spruce growth in boreal mixtures of Western Canada. Forest Ecology and Management **277**: 67–73. doi:10.1016/j.foreco.2012.04.022.

De Araujo, F., Hart, J., and Mansfield, S. 2015. Variation in Trembling Aspen and White Spruce Wood Quality Grown in Mixed and Single Species Stands in the Boreal Mixedwood Forest. Forests **6**(12): 1628–1648. doi:10.3390/f6051628.

DeLong, C.S., Banner, A., Mackenzie, W.H., Kaytor, B., and Rogers, B.J. 2011. A field guide to ecosystem identification for the boreal white and black spruce zone of British Columbia. Ministry of Forests and Range, Forest Science Program, Victoria, B.C.

Dhar, A., Parrott, L., and Hawkins, C. 2016. Aftermath of Mountain Pine Beetle Outbreak in British Columbia: Stand Dynamics, Management Response and Ecosystem Resilience. Forests **7**(12): 171. doi:10.3390/f7080171.

Evans, R., and Ilic, J. 2001. Rapid prediction of wood stiffness from microfibril angle and density. Forest Products Journal **51**: 53–57.

Farmer, R.E. 1963. Effect of Light Intensity on Growth of Populus tremuloides Cuttings Under Two Temperature Regimes. Ecology **44**(2): 409–411. Ecological Society of America. doi:10.2307/1932193.

Filipescu, C.N., and Comeau, P.G. 2007. Competitive interactions between aspen and white spruce vary with stand age in boreal mixedwoods. Forest Ecology and Management **247**(1–3): 175–184. doi:10.1016/j.foreco.2007.04.038.

Frey, B.R., Lieffers, V.J., Landhäusser, S.M., Comeau, P.G., and Greenway, K.J. 2011. An analysis of sucker regeneration of trembling aspen. Canadian Journal of Forest Research. NRC Research Press Ottawa, Canada. doi:10.1139/x03-053.

Fritts, H.C. 1976. Tree rings and climate. Academic Press, London ; New York.

Girardin, M.P., and Terrier, A. 2015. Mitigating risks of future wildfires by management of the forest composition: an analysis of the offsetting potential through boreal Canada. Climatic Change **130**(4): 587–601. doi:10.1007/s10584-015-1373-7.

Groot, A. 1999. Effects of shelter and competition on the early growth of planted white spruce (Picea glauca). Canadian Journal of Forest Research. NRC Research Press Ottawa, Canada. doi:10.1139/x99-064.

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.

Halekoh, U., and Højsgaard, S. 2014. A Kenward-Roger Approximation and Parametric Bootstrap Methods for Tests in Linear Mixed Models - The R Package pbkrtest. J. Stat. Soft. **59**(9). doi:10.18637/jss.v059.i09.

Hansen, W.D., Chapin, F.S., Naughton, H.T., Rupp, T.S., and Verbyla, D. 2016. Forest-landscape structure mediates effects of a spruce bark beetle (Dendroctonus rufipennis) outbreak on subsequent likelihood of burning in Alaskan boreal forest. Forest Ecology and Management **369**: 38–46. doi:10.1016/j.foreco.2016.03.036.

Hector, A. 1998. The Effect of Diversity on Productivity: Detecting the Role of Species Complementarity. Oikos **82**(3): 597–599. [Nordic Society Oikos, Wiley]. doi:10.2307/3546380.

Hein, and Lima, J. 2012. Relationships between microfibril angle, modulus of elasticity and compressive strength in Eucalyptus wood. Maderas. Ciencia y tecnología **14**(3): 267–274. doi:10.4067/S0718-221X2012005000002.

Herman, M., Dutilleul, P., and Avella-Shaw, T. 1999. Growth Rate Effects on Intra-Ring and Inter-Ring Trajectories of Microfibril Angle in Norway Spruce (Picea Abies). IAWA J **20**(1): 3–21. doi:10.1163/22941932-90001542.

Jiang, X., Huang, J.-G., Cheng, J., Dawson, A., Stadt, K.J., Comeau, P.G., and Chen, H.Y.H. 2018. Interspecific variation in growth responses to tree size, competition and climate of western Canadian boreal mixed forests. Science of The Total Environment **631–632**: 1070–1078. doi:10.1016/j.scitotenv.2018.03.099.

Jozsa, L.A., and Middleton, G.R. 1994. A discussion of wood quality attributes and their practical implications. : 51.

Kabzems, R., Bokalo, M., Comeau, P., and MacIsaac, D. 2015. Managed Mixtures of Aspen and White Spruce 21 to 25 Years after Establishment. Forests **7**(12): 5. doi:10.3390/f7010005.

Kabzems, R., Comeau, P.G., Filipescu, C.N., Rogers, B., and Linnell Nemec, A.F. 2016. Creating boreal mixedwoods by planting spruce under aspen: successful establishment in uncertain future climates. Canadian Journal of Forest Research **46**(10): 1217–1223. doi:10.1139/cjfr-2015-0440.

Kabzems, R., Nemec, A.L., and Farnden, C. 2007. Growing trembling aspen and white spruce intimate mixtures. BC Journal of Ecosystems and Management **8**(1): 15.

Kahriman, A., Şahin, A., Sönmez, T., and Yavuz, M. 2018. A novel approach to selecting a competition index: the effect of competition on individual-tree diameter growth of Calabrian pine. Can. J. For. Res. **48**(10): 1217–1226. doi:10.1139/cjfr-2018-0092.

Kassambara, A. 2020. ggpubr: "ggplot2" Based Publication Ready Plots. Available from https://CRAN.R-project.org/package=ggpubr [accessed 22 April 2021].

Kerhoulas, L.P., Kolb, T.E., and Koch, G.W. 2013. Tree size, stand density, and the source of water used across seasons by ponderosa pine in northern Arizona. Forest Ecology and Management: 10.

Kweon, D., and Comeau, P.G. 2019. Factors influencing overyielding in young boreal mixedwood stands in western Canada. Forest Ecology and Management **432**: 546–557. doi:10.1016/j.foreco.2018.09.053.

Laganière, J., Cavard, X., Brassard, B.W., Paré, D., Bergeron, Y., and Chen, H.Y.H. 2015. The influence of boreal tree species mixtures on ecosystem carbon storage and fluxes. Forest Ecology and Management **354**: 119–129. doi:10.1016/j.foreco.2015.06.029.

Lanner, R.M. 1985. On the insensitivity of height growth to spacing. doi:10.1016/0378-1127(85)90030-1.

Lenth, R.V. 2016. Least-Squares Means: The R Package lsmeans. Journal of Statistical Software **69**(1): 1–33. doi:10.18637/jss.v069.i01.

Lieffers, V.J., Pinno, B.D., and Stadt, K.J. 2002. Light dynamics and free-to-grow standards in aspen-dominated mixedwood forests. The Forestry Chronicle **78**(1): 137–145. doi:10.5558/tfc78137-1.

Lieffers, V.J., and Stadt, K.J. 1994. Growth of understory Piceaglauca, Calamagrostiscanadensis, and Epilobiumangustifolium in relation to overstory light transmission. Canadian Journal of Forest Research. NRC Research Press Ottawa, Canada. doi:10.1139/x94-157.

Lieffers, V.J., Stewart, J.D., Macmillan, R.B., Macpherson, D., and Branter, K. 1996. Semi-natural and intensive silvicultural systems for the boreal mixedwood forest. The Forestry Chronicle **72**(3): 286–292. doi:10.5558/tfc72286-3.

Lord, T., and Green, A. 1986. Soils of the Fort St. John ~ Dawson Creek area, British Columbia. Available from http://www.env.gov.bc.ca/esd/distdata/ecosystems/Soils_Reports/bc42_report.pdf [accessed 12 November 2018].

Lundgren, C. 2004. Cell wall thickness and tangential and radial cell diameter of fertilized and irrigated Norway spruce. Silva Fennica **38**(1). doi:10.14214/sf.438.

Macdonald, E., and Hubert, J. 2002. A review of the effects of silviculture on timber quality of Sitka spruce. Forestry (Lond) **75**(2): 107–138. Oxford Academic. doi:10.1093/forestry/75.2.107.

Macdonald, E., Lecomte, Nicolas, Bergeron, Y., Brais, S., Chen, H., Comeau, P., Drapeau, P., Lieffers, V., Quideau, S., Spence, J., and Work, T. 2010. Ecological implications of changing the composition of boreal mixedwood forests: a state of knowledge report. Sustainable Forest Management Network, Edmonton, Alta. Available from https://www.deslibris.ca/ID/226979 [accessed 24 February 2021].

Man, R., and Lieffers, V.J. 1999. Are mixtures of aspen and white spruce more productive than single species stands? The Forestry Chronicle **75**(3): 505–513. doi:10.5558/tfc75505-3.

Martin, G.L., and Ek, A.R. 1984. A Comparison of Competition Measures and Growth Models for Predicting Plantation Red Pine Diameter and Height Growth. Forest Science **30**(3): 731–743. doi:10.1093/forestscience/30.3.731.

Mbogga, M.S., Wang, X., and Hamann, A. 2010. Bioclimate envelope model predictions for natural resource management: dealing with uncertainty. Journal of Applied Ecology **47**(4): 731–740. doi:10.1111/j.1365-2664.2010.01830.x.

McCulloch, L., and Kabzems, R. 2009. British Columbia's Northeastern Forests: Aspen Complex Stand Establishment Decision Aid. Journal of Ecosystems and Management **10**(2). Available from http://jem-online.org/index.php/jem/article/view/419 [accessed 18 October 2018].

Payne, N.J., Allan Cameron, D., Leblanc, J.-D., and Morrison, I.K. 2019. Carbon storage and net primary productivity in Canadian boreal mixedwood stands. J. For. Res. **30**(5): 1667–1678. doi:10.1007/s11676-019-00886-0.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S., Van Willigen, B., and Ranke, J. 2020. nlme: Linear and Nonlinear Mixed Effects Models. Available from https://CRAN.R-project.org/package=nlme [accessed 7 January 2021].

Pretzsch, H. 2019. The Effect of Tree Crown Allometry on Community Dynamics in Mixed-Species Stands versus Monocultures. A Review and Perspectives for Modeling and Silvicultural Regulation. Forests **10**(9): 810. doi:10.3390/f10090810.

Pretzsch, H., and Biber, P. 2016. Tree species mixing can increase maximum stand density. Canadian Journal of Forest Research **46**(10): 1179–1194. NRC Research Press. doi:10.1139/cjfr-2015-0413.

Pretzsch, H., Bielak, K., Block, J., Bruchwald, A., Dieler, J., Ehrhart, H.-P., Kohnle, U., Nagel, J., Spellmann, H., Zasada, M., and Zingg, A. 2013. Productivity of mixed versus pure stands of oak (Quercus petraea (Matt.) Liebl. and Quercus robur L.) and European beech (Fagus sylvatica L.) along an ecological gradient. Eur J Forest Res **132**(2): 263–280. doi:10.1007/s10342-012-0673-y.

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.

Reyes-Hernández, V.J., and Comeau, P.G. 2015. The Influence of Stocking and Stand Composition on Productivity of Boreal Trembling Aspen-White Spruce Stands. Forests **6**(12): 4573–4587. Multidisciplinary Digital Publishing Institute. doi:10.3390/f6124387.

Rydval, M., Larsson, L.-Å., McGlynn, L., Gunnarson, B.E., Loader, N.J., Young, G.H.F., and Wilson, R. 2014. Blue intensity for dendroclimatology: Should we have the blues? Experiments from Scotland. Dendrochronologia **32**(3): 191–204. doi:10.1016/j.dendro.2014.04.003.

Sattler, D.F., Comeau, P.G., and Achim, A. 2014. Within-tree patterns of wood stiffness for white spruce (Picea glauca) and trembling aspen (Populus tremuloides) (1). Canadian Journal of Forest Research **44**(2): 162-.

Seth, R.S., and Kingsland, M.A. 1990. The reinforcing properties of softwood kraft pulps. Pulp & Paper Canada **91**(7): 68–75.

Smith, E.A., O'Loughlin, D., Buck, J.R., and St. Clair, S.B. 2011. The influences of conifer succession, physiographic conditions and herbivory on quaking aspen regeneration after fire. Forest Ecology and Management **262**(3): 325–330. doi:10.1016/j.foreco.2011.03.038.

Speer, J.H. 2012. Fundamentals of Tree-Ring Research. University of Arizona Press: 522.

Sun, S., Cao, Q.V., and Cao, T. 2019. Evaluation of distance-independent competition indices in predicting tree survival and diameter growth. Canadian Journal of Forest Research **49**(5): 440–447. NRC Research Press. doi:10.1139/cjfr-2018-0344.
Vysotskaya, L.G., and Vaganov, E.A. 1989. Components of the Variability of Radial Cell Size in Tree Rings of Conifers. IAWA Journal **10**(4): 417–426. Brill. doi:10.1163/22941932-90001134.
Watson, P., and Bradley, M. 2009. Canadian pulp fibre morphology: Superiority and considerations for end use potential. The Forestry Chronicle **85**(3): 401–408. doi:10.5558/tfc85401-3.
Wilpert, K. von. 1991, April 27. Intraannual variation of radial tracheid diameters as monitor of site specific water stress. Available from https://eurekamag.com/research/002/416/002416079.php [accessed 24 March 2020].
Wykoff, W., Crookston, N.L., Stage, A.R., and Intermountain Forest and Range Experiment Station (Ogden, U. 1982. User’s guide to the stand prognosis model. U.S. Dept. of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah : Available from https://www.biodiversitylibrary.org/item/191561.
Zeng, Q., Rossi, S., and Yang, B. 2018. Effects of Age and Size on Xylem Phenology in Two Conifers of Northwestern China. Front. Plant Sci. **8**. Frontiers. doi:10.3389/fpls.2017.02264.
Zobel, B.J., and Jett, J.B. 1995. The Importance of Wood Density (Specific Gravity) and Its Component Parts. *In* Genetics of Wood Production. *Edited by* B.J. Zobel and J.B. Jett. Springer Berlin Heidelberg, Berlin, Heidelberg. pp. 78–97. doi:10.1007/978-3-642-79514-5_4.

6. Appendix

Table 6.1. Full results of the MuMIn analysis that forms the basis for table 2.2. Multi model inference analysis of the global model (linear model = Ring + species + treatment + |tree) where Loglik is the log likelihood, AIC is Akaike's information criterion, and delta is the difference in AIC for best performing model and next best.

Wood attribute	(Intercept)	Ring	species	treatment	df	logLik	AICc	delta	weight
Ring Width	3.77	-0.058	NA	+	8	-4169.122	8354.3	0.00	7.26E-01
	3.75	-0.058	+	+	9	-4169.091	8356.2	1.95	2.74E-01
	2.83	-0.058	+	NA	5	-4204.512	8419.0	64.75	6.31E-15
	3.00	-0.058	NA	NA	4	-4208.129	8424.3	69.98	4.63E-16
	2.87	NA	+	+	8	-4542.668	9101.4	747.09	4.29E-163
	3.04	NA	NA	+	7	-4544.708	9103.5	749.16	1.52E-163
	1.95	NA	+	NA	4	-4576.558	9161.1	806.84	4.55E-176
	2.20	NA	NA	NA	3	-4584.712	9175.4	821.14	3.57E-179
Density	393.11	NA	+	+	8	-15803.8	31623.7	0.00	4.52E-01
	396.28	NA	+	NA	4	-15808.32	31624.7	1.00	2.73E-01
	392.80	0.020	+	+	9	-15803.77	31625.6	1.94	1.71E-01
	395.99	0.019	+	NA	5	-15808.29	31626.6	2.95	1.03E-01
	367.72	NA	NA	+	7	-15816.98	31648.0	24.34	2.34E-06
	367.28	0.035	NA	+	8	-15816.88	31649.8	26.15	9.47E-07
	381.02	NA	NA	NA	3	-15823.37	31652.8	29.10	2.17E-07

	(Intercept)	Ring	species	treatment	df	logLik	AICc	delta	weight
Density	380.54	0.035	NA	NA	4	-15823.27	31654.6	30.90	8.82E-08
MFA	23.15	-0.654	+	+	9	-8835.623	17689.3	0.00	8.99E-01
	20.77	-0.654	+	NA	5	-8841.831	17693.7	4.38	1.01E-01
	27.00	-0.655	NA	+	8	-8851.43	17718.9	29.60	3.35E-07
	23.41	-0.656	NA	NA	4	-8863.718	17735.5	46.14	8.58E-11
	13.26	NA	+	+	8	-10464.935	20945.9	3256.61	0.00E+00
	10.81	NA	+	NA	4	-10471.872	20951.8	3262.45	0.00E+00
	18.80	NA	NA	+	7	-10496.844	21007.7	3318.42	0.00E+00
	14.43	NA	NA	NA	3	-10511.176	21028.4	3339.06	0.00E+00
MOE	8.14	0.296	+	+	9	-5388.845	10795.8	0.00	9.35E-01
	9.45	0.296	+	NA	5	-5395.529	10801.1	5.33	6.51E-02
	5.67	0.296	NA	+	8	-5416.273	10848.6	52.84	3.13E-12
	7.79	0.296	NA	NA	4	-5430.869	10869.8	74.00	7.96E-17
	12.61	NA	+	+	8	-7696.901	15409.9	4614.10	0.00E+00
	13.95	NA	+	NA	4	-7703.76	15415.5	4619.78	0.00E+00
	9.37	NA	NA	+	7	-7740.604	15495.2	4699.50	0.00E+00
	11.84	NA	NA	NA	3	-7756.135	15518.3	4722.53	0.00E+00

Wood attribute	(Intercept)	Ring	species	treatment	df	logLik	AICc	delta	weight
Coarseness	542.70	2.339	+	+	9	-18223.71	36465.5	0.00	9.93E-01
	506.81	2.336	+	NA	5	-18232.75	36475.5	10.05	6.52E-03
	578.11	NA	+	+	8	-18318.71	36653.5	188.00	1.49E-41
	542.37	NA	+	NA	4	-18327.53	36663.1	197.59	1.23E-43
	301.70	2.370	NA	+	8	-18323.99	36664.0	198.56	7.60E-44
	372.13	2.370	NA	NA	4	-18328.99	36666.0	200.52	2.84E-44
	331.38	NA	NA	+	7	-18421.52	36857.1	391.60	9.19E-86
	404.57	NA	NA	NA	3	-18426.56	36859.1	393.66	3.27E-86
Tangential Diameter	40.53	0.052	+	+	9	-7820.458	15659.0	0.00	9.90E-01
	39.29	0.052	+	NA	5	-7829.074	15668.2	9.19	9.99E-03
	41.32	NA	+	+	8	-7854.339	15724.7	65.75	5.22E-15
	40.08	NA	+	NA	4	-7862.818	15733.7	74.68	6.03E-17
	26.73	0.053	NA	+	8	-7985.163	15986.4	327.40	7.98E-72
	31.45	0.053	NA	NA	4	-7991.461	15990.9	331.96	8.15E-73
	27.39	NA	NA	+	7	-8020.34	16054.7	395.74	1.15E-86
	32.17	NA	NA	NA	3	-8026.665	16059.3	400.37	1.14E-87
Radial Diameter	28.59	0.150	+	+	9	-7283.053	14584.2	0.00	9.99E-01

Wood attribute	(Intercept)	Ring	species	treatment	df	logLik	AICc	delta	weight
Radial Diameter	27.27	0.150	NA	+	8	-7290.684	14597.4	13.25	1.33E-03
	26.28	0.150	+	NA	5	-7296.345	14602.7	18.54	9.38E-05
	25.90	0.150	NA	NA	4	-7298.178	14604.4	20.20	4.09E-05
	30.85	NA	+	+	8	-7640.389	15296.8	712.66	1.77E-155
	28.55	NA	+	NA	4	-7653.621	15315.3	731.09	1.76E-159
	29.15	NA	NA	+	7	-7652.896	15319.8	735.66	1.79E-160
	27.95	NA	NA	NA	3	-7658.331	15322.7	738.51	4.31E-161
Specific Surface	263.46	-1.100	+	+	9	-15900.29	31818.7	0.00	9.95E-01
	283.86	-1.099	+	NA	5	-15909.59	31829.2	10.56	5.06E-03
	246.80	NA	+	+	8	-15991.13	31998.3	179.65	9.69E-40
	267.14	NA	+	NA	4	-16000.2	32008.4	189.77	6.17E-42
	343.51	-1.116	NA	NA	4	-16005.9	32019.8	201.17	2.06E-44
	371.47	-1.115	NA	+	8	-16002.03	32020.1	201.45	1.79E-44
	328.24	NA	NA	NA	3	-16099.32	32204.7	386.00	1.51E-84
	357.51	NA	NA	+	7	-16095.37	32204.8	386.13	1.41E-84
Ring Area	491.55	17.855	NA	+	8	-21516.34	43048.7	0.00	6.52E-01
	460.56	17.869	+	+	9	-21515.96	43050.0	1.25	3.48E-01
	98.51	17.880	+	NA	5	-21547.01	43104.0	55.32	6.32E-13
	177.16	17.841	NA	NA	4	-21551.84	43111.7	62.97	1.38E-14

Wood attribute	(Intercept)	Ring	species	treatment	df	logLik	AICc	delta	weight
Ring area	715.12	NA	NA	+	7	-22107.41	44228.9	1180.15	3.54E-257
	730.88	NA	+	+	8	-22107.31	44230.7	1181.95	1.43E-257
	370.68	NA	+	NA	4	-22139.14	44286.3	1237.58	1.19E-269
	421.30	NA	NA	NA	3	-22141.25	44288.5	1239.79	3.96E-270
Cell Population	905.31	-10.202	+	+	9	-20622.59	41263.2	0.00	1.00E+00
	1068.51	-10.203	+	NA	5	-20639.18	41288.4	25.15	3.46E-06
	1363.40	-10.284	NA	NA	4	-20742.49	41493.0	229.75	1.29E-50
	1457.18	-10.281	NA	+	8	-20740.99	41498.0	234.80	1.03E-51
	750.85	NA	+	+	8	-20982.28	41980.6	717.37	1.68E-156
	913.18	NA	+	NA	4	-20998.87	42005.8	742.52	5.80E-162
	1222.60	NA	NA	NA	3	-21108.26	42222.5	959.30	4.91E-209
	1328.40	NA	NA	+	7	-21106.55	42227.1	963.89	4.94E-210
Wall Thickness	2.82	0.008	+	+	9	-907.3739	1832.8	0.00	9.70E-01
	2.72	0.008	+	NA	5	-914.874	1839.8	6.96	2.99E-02
	2.94	NA	+	+	8	-975.1697	1966.4	133.58	9.56E-30
	2.84	NA	+	NA	4	-982.4607	1972.9	140.13	3.62E-31
	2.05	0.008	NA	+	8	-985.5927	1987.2	154.43	2.84E-34
	2.28	0.008	NA	NA	4	-990.9849	1990.0	157.18	7.18E-35
	2.15	NA	NA	+	7	-1055.7946	2125.6	292.82	2.52E-64
	2.40	NA	NA	NA	3	-1061.2184	2128.4	295.64	6.16E-65

Table 6.2 The results of the analysis of variance of the effects of treatment (aspen population density), cambial age and species on each wood attribute. This test was conducted to corroborate results from the MuMIn anlaysis (Figure 6.1) and justify the use of p-values for hypothesis testing.

Wood Property	Cambial Age (Ring)	treatment	species
Ring Width	$F(1, 3043) = 861.13$, $p < 0.001$	$F(4, 114) = 27.31$, $p < 0.001$	**$F(1, 114) = 0.062$, $p = 0.802$**
Density	**$F(1, 3043) = .288$, $p = 0.59$**	$F(4, 114) = 4.18$, $p = 0.003$	$F(1, 114) = 29.2$, $p < 0.001$
Microfibril Angle	$F(1, 3043) = 5899$, $p < 0.001$	$F(4, 114) = 8.87$, $p < 0.001$	$F(1, 114) = 36.13$, $p < 0.001$
Modulus of Elasticity	$F(1, 3043) = 10896$, $p < 0.001$	$F(4, 114) = 13.03$, $p < 0.001$	$F(1, 114) = 69.42$, $p < 0.001$
Coarseness	$F(1, 3043) = 226.07$, $p < 0.001$	$F(4, 114) = 13.88$, $p < 0.001$	$F(1, 114) = 514.82$, $p < 0.001$
Tangential Diameter	$F(1, 3043) = 112.97$, $p < 0.001$	$F(4, 114) = 51.68$, $p < 0.001$	$F(1, 114) = 1731$, $p < 0.001$
Radial Diameter	$F(1, 3043) = 811.08$, $p < 0.001$	$F(4, 114) = 4.52$, $p = 0.002$	$F(1, 114) = 16.24$, $p < 0.001$
Specific Surface	$F(1, 3043) = 219.69$, $p < 0.001$	$F(4, 114) = 10.95$, $p < 0.001$	$F(1, 114) = 531.97$, $p < 0.001$
Ring Area	$F(1, 3043) = 1434.54$, $p < 0.001$	$F(4, 114) = 24.29$, $p < 0.001$	**$F(1, 114) = 0.76$, $p = 0.39$**
Cell Population	$F(1, 3043) = 891.21$, $p < 0.001$	$F(4, 114) = 5.55$, $p < 0.001$	$F(1, 114) = 742.48$, $p < 0.001$
Wall Thickness	$F(1, 3043) = 159.32$, $p < 0.001$	$F(4, 114) = 10.38$, $p < 0.001$	$F(1, 114) = 319.99$, $p < 0.001$

Table 6.3 Aspen results table of complete post-hoc test of species separated linear mixed model results (summarized in Figure 2.3). Lsmeans pairwise comparison to establish contrasts, p-value adjusted by Bonferroni method.

Wood Property	contrast	estimate	SE	df	t.ratio	p.value
Ring Width	1000 - 2000	0.078	0.274	46	0.2845	0.7773
	1000 - 5000	0.2788	0.2171	46	1.2841	0.2055
	1000 - 10000	0.5488	0.2172	46	2.5266	0.015
	2000 - 5000	0.2008	0.2163	46	0.9286	0.3579
	2000 - 10000	0.4708	0.2164	46	2.1759	0.0347
	5000 - 10000	0.27	0.1374	46	1.965	0.0555
Density	1000 - 2000	37.4002	16.649	46	2.2464	0.0295
	1000 - 5000	19.7303	13.1705	46	1.4981	0.1409
	1000 - 10000	-0.0497	13.1719	46	-0.0038	0.997
	2000 - 5000	-17.6699	13.1564	46	-1.3431	0.1858
	2000 - 10000	-37.4499	13.1581	46	-2.8462	0.0066
	5000 - 10000	-19.78	8.3309	46	-2.3743	0.0218
MFA	No significant effect of treatment					
MOE	No significant effect of treatment					
Coarseness	1000 - 2000	29.609	43.7801	46	0.6763	0.5022
	1000 - 5000	-19.2998	34.6432	46	-0.5571	0.5802
	1000 - 10000	-89.1754	34.6489	46	-2.5737	0.0133
	2000 - 5000	-48.9089	34.589	46	-1.414	0.1641

Wood Property	contrast	estimate	SE	df	t.ratio	p.value
	2000 - 10000	-118.7844	34.5955	46	-3.4335	0.0013
	5000 - 10000	-69.8755	21.915	46	-3.1885	0.0026
Tangential Diameter	1000 - 2000	0.4259	1.3173	46	0.3233	0.7479
	1000 - 5000	-1.3026	1.0423	46	-1.2498	0.2177
	1000 - 10000	-2.9991	1.0425	46	-2.877	0.0061
	2000 - 5000	-1.7285	1.0408	46	-1.6608	0.1036
	2000 - 10000	-3.425	1.041	46	-3.2902	0.0019
	5000 - 10000	-1.6965	0.6593	46	-2.573	0.0134
Radial Diameter	1000 - 2000	-1.4275	0.9353	46	-1.5263	0.1338
	1000 - 5000	-1.3656	0.7403	46	-1.8446	0.0715
	1000 - 10000	-2.3451	0.7405	46	-3.1669	0.0027
	2000 - 5000	0.0619	0.7388	46	0.0838	0.9336
	2000 - 10000	-0.9176	0.7389	46	-1.2417	0.2206
	5000 - 10000	-0.9795	0.4684	46	-2.0913	0.0421
Specific Surface Area	1000 - 2000	-23.3402	14.5948	46	-1.5992	0.1166
	1000 - 5000	-7.2824	11.5478	46	-0.6306	0.5314
	1000 - 10000	18.6077	11.5494	46	1.6111	0.114
	2000 - 5000	16.0579	11.5316	46	1.3925	0.1705

Wood Property	contrast	estimate	SE	df	t.ratio	p.value
	2000 - 10000	41.9479	11.5335	46	3.637	0.0007
	5000 - 10000	25.89	7.3048	46	3.5442	0.0009
Ring Area	1000 - 2000	23.9787	115.4942	46	0.2076	0.8364
	1000 - 5000	115.3324	91.3691	46	1.2623	0.2132
	1000 - 10000	217.5375	91.3803	46	2.3806	0.0215
	2000 - 5000	91.3537	91.2624	46	1.001	0.3221
	2000 - 10000	193.5588	91.2752	46	2.1206	0.0394
	5000 - 10000	102.2051	57.7961	46	1.7684	0.0836
Cell Population	1000 - 2000	34.0495	54.8124	46	0.6212	0.5375
	1000 - 5000	62.0499	43.3708	46	1.4307	0.1593
	1000 - 10000	130.7563	43.3775	46	3.0144	0.0042
	2000 - 5000	28.0004	43.3068	46	0.6466	0.5211
	2000 - 10000	96.7068	43.3144	46	2.2327	0.0305
	5000 - 10000	68.7064	27.4356	46	2.5043	0.0159
Wall Thickness	1000 - 2000	0.2374	0.1708	46	1.3903	0.1711
	1000 - 5000	0.0415	0.1351	46	0.3074	0.7599
	1000 - 10000	-0.2315	0.1351	46	-1.7131	0.0934
	2000 - 5000	-0.1959	0.1349	46	-1.4518	0.1534
	2000 - 10000	-0.4689	0.1349	46	-3.4748	0.0011

Wood Property	contrast	estimate	SE	df	t.ratio	p.value
	5000 - 10000	-0.273	0.0855	46	-3.1944	0.0025

Table 6.4 Spruce results table of complete post-hoc test of species separated linear mixed model results (summarized in Figure 2.3). Lsmeans pairwise comparison to establish contrasts, p-value adjusted by Bonferroni method.

Wood Property	contrast	estimate	SE	df	t.ratio	p.value
Ring Width	0 - 1000	0.2499	0.1967	65	1.2707	0.2084
	0 - 2000	0.6628	0.1975	65	3.3569	0.0013
	0 - 5000	0.9481	0.1246	65	7.6098	< 0.001
	0 - 10000	1.1053	0.1247	65	8.8669	< 0.001
	1000 - 2000	0.4129	0.2492	65	1.6568	0.1024
	1000 - 5000	0.6982	0.1966	65	3.5511	0.0007
	1000 - 10000	0.8554	0.1967	65	4.3497	< 0.001
	2000 - 5000	0.2853	0.1974	65	1.445	0.1533
	2000 - 10000	0.4425	0.1975	65	2.2409	0.0285
	5000 - 10000	0.1572	0.1246	65	1.2618	0.2115
Density	0 - 1000	9.7875	9.4269	65	1.0382	0.303
	0 - 2000	11.8164	9.4583	65	1.2493	0.216
	0 - 5000	-11.8251	5.9704	65	-1.9806	0.0519
	0 - 10000	-1.7975	5.973	65	-0.3009	0.7644
	1000 - 2000	2.0289	11.9437	65	0.1699	0.8656
	1000 - 5000	-21.6126	9.4252	65	-2.2931	0.0251
	1000 - 10000	-11.585	9.4269	65	-1.2289	0.2235
	2000 - 5000	-23.6415	9.4567	65	-2.5	0.015

Wood Property	contrast	estimate	SE	df	t.ratio	p.value
	2000 - 10000	-13.6139	9.4583	65	-1.4394	0.1548
	5000 - 10000	10.0277	5.9703	65	1.6796	0.0978
MFA	No significant effect of treatment					
MOE	0 - 1000	-0.1738	0.7592	65	-0.2289	0.8197
	0 - 2000	-1.2728	0.7596	65	-1.6756	0.0986
	0 - 5000	-1.4354	0.4803	65	-2.9887	0.004
	0 - 10000	-1.4623	0.4803	65	-3.0447	0.0034
	1000 - 2000	-1.099	0.9606	65	-1.1441	0.2568
	1000 - 5000	-1.2616	0.7592	65	-1.6617	0.1014
	1000 - 10000	-1.2886	0.7592	65	-1.6972	0.0944
	2000 - 5000	-0.1626	0.7595	65	-0.2141	0.8312
	2000 - 10000	-0.1896	0.7596	65	-0.2496	0.8037
	5000 - 10000	-0.027	0.4803	65	-0.0562	0.9554
Coarseness	0 - 1000	25.5604	11.3826	65	2.2456	0.0281
	0 - 2000	43.1356	11.4279	65	3.7746	< 0.001
	0 - 5000	28.6305	7.211	65	3.9704	< 0.001
	0 - 10000	44.2045	7.2147	65	6.127	< 0.001
	1000 - 2000	17.5752	14.426	65	1.2183	0.2275
	1000 - 5000	3.07	11.38	65	0.2698	0.7882
	1000 - 10000	18.6441	11.3825	65	1.638	0.1063
	2000 - 5000	-14.5052	11.4256	65	-1.2695	0.2088
	2000 - 10000	1.0689	11.4279	65	0.0935	0.9258

Wood Property	contrast	estimate	SE	df	t.ratio	p.value
	5000 - 10000	15.574	7.2108	65	2.1598	0.0345
Tangential Diameter	0 - 1000	0.1889	0.4386	65	0.4307	0.6681
	0 - 2000	1.2584	0.4425	65	2.8438	0.006
	0 - 5000	1.3478	0.2785	65	4.84	< 0.001
	0 - 10000	1.4168	0.2788	65	5.0822	< 0.001
	1000 - 2000	1.0695	0.5572	65	1.9194	0.0593
	1000 - 5000	1.1588	0.4384	65	2.6434	0.0103
	1000 - 10000	1.2279	0.4386	65	2.7996	0.0067
	2000 - 5000	0.0894	0.4423	65	0.202	0.8405
	2000 - 10000	0.1584	0.4425	65	0.358	0.7215
	5000 - 10000	0.0691	0.2784	65	0.2481	0.8049
Radial Diameter	0 - 1000	1.3694	0.7861	65	1.742	0.0862
	0 - 2000	1.6556	0.7868	65	2.1041	0.0392
	0 - 5000	2.2055	0.4974	65	4.4343	< 0.001
	0 - 10000	2.8468	0.4974	65	5.7229	< 0.001
	1000 - 2000	0.2863	0.9948	65	0.2878	0.7744
	1000 - 5000	0.8361	0.7861	65	1.0637	0.2914
	1000 - 10000	1.4774	0.7861	65	1.8794	0.0647
	2000 - 5000	0.5499	0.7868	65	0.6989	0.4871
	2000 - 10000	1.1911	0.7868	65	1.5138	0.1349
	5000 - 10000	0.6412	0.4974	65	1.2893	0.2019
Specific Surface Area	0 - 1000	-23.4501	10.2854	65	-2.2799	0.0259
	0 - 2000	-33.5114	10.3201	65	-3.2472	0.0018
	0 - 5000	-10.694	6.5142	65	-1.6416	0.1055

Wood Property	contrast	estimate	SE	df	t.ratio	p.value
	0 - 10000	-26.1929	6.5171	65	-4.0191	0.0002
	1000 - 2000	-10.0614	13.0316	65	-0.7721	0.4429
	1000 - 5000	12.7561	10.2834	65	1.2405	0.2193
	1000 - 10000	-2.7429	10.2853	65	-0.2667	0.7906
	2000 - 5000	22.8174	10.3183	65	2.2114	0.0305
	2000 - 10000	7.3185	10.3201	65	0.7092	0.4808
	5000 - 10000	-15.499	6.5141	65	-2.3793	0.0203
Ring Area	0 - 1000	112.182	84.8913	65	1.3215	0.191
	0 - 2000	282.1284	84.9941	65	3.3194	0.0015
	0 - 5000	382.9638	53.7168	65	7.1293	< 0.001
	0 - 10000	424.3377	53.7254	65	7.8983	< 0.001
	1000 - 2000	169.9464	107.4439	65	1.5817	0.1186
	1000 - 5000	270.7818	84.8856	65	3.19	0.0022
	1000 - 10000	312.1557	84.8913	65	3.6771	0.0005
	2000 - 5000	100.8355	84.9889	65	1.1865	0.2398
	2000 - 10000	142.2093	84.9941	65	1.6732	0.0991
	5000 - 10000	41.3739	53.7168	65	0.7702	0.444
Cell Population	0 - 1000	-62.6329	49.7296	65	-1.2595	0.2124
	0 - 2000	-133.2715	49.8366	65	-2.6742	0.0095
	0 - 5000	-165.5025	31.4798	65	-5.2574	< 0.001
	0 - 10000	-195.9866	31.4887	65	-6.224	< 0.001
	1000 - 2000	-70.6385	62.97	65	-1.1218	0.2661
	1000 - 5000	-102.8695	49.7236	65	-2.0688	0.0425
	1000 - 10000	-133.3537	49.7295	65	-2.6816	0.0093
	2000 - 5000	-32.231	49.8311	65	-0.6468	0.52
	2000 - 10000	-62.7152	49.8365	65	-1.2584	0.2127
	5000 - 10000	-30.4842	31.4797	65	-0.9684	0.3364

Wood Property	contrast	estimate	SE	df	t.ratio	p.value
Wall Thickness	0 - 1000	0.1152	0.0611	65	1.8845	0.064
	0 - 2000	0.1805	0.0614	65	2.9405	0.0045
	0 - 5000	0.0476	0.0387	65	1.2281	0.2238
	0 - 10000	0.135	0.0388	65	3.4837	0.0009
	1000 - 2000	0.0653	0.0775	65	0.8429	0.4024
	1000 - 5000	-0.0676	0.0611	65	-1.1067	0.2725
	1000 - 10000	0.0198	0.0611	65	0.3239	0.7471
	2000 - 5000	-0.133	0.0614	65	-2.1661	0.034
	2000 - 10000	-0.0455	0.0614	65	-0.7414	0.4611
	5000 - 10000	0.0874	0.0387	65	2.2575	0.0273