Aspen density dynamics in western boreal mixedwood stands

by

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Abstract

Trembling aspen (*Populus tremuloides* Michx.) is a common species in Canadian boreal forests. As a shade intolerant and dynamic species (i.e., stand density and structure change over time), it naturally regenerates by root suckering and grows rapidly. Aspen has a short life compared to spruce or pine species, and experiences severe mortality derived from intraspecific competition, fungal diseases, and insect attacks. As a result, aspen stands often develop an irregular structure with age. In addition, if spruce is present in the stand, mixedwood stands may develop. In this thesis, I examine three aspects relating to aspen dynamics in pure and mixed stands.

The first study examined maximum size-density relationships (MSDR). I developed static and dynamic self-thinning lines for pure aspen stands in the boreal forest region of Alberta and Saskatchewan. Climate variables were included to examine effects of climates on both self-thinning lines. The results demonstrate that climate influences the slope and intercept of self-thinning lines, suggesting that increasing summer dryness related to climate change may decrease the carrying capacity and productivity of aspen stands in portions of this region.

For the second study, I investigated how age structure influences tree survival in aspen dominated stands and examined effects of stand factors, climate, and tree age on survival probability. Based on field data, I found a positive relationship between stand age and stand structure (i.e., structural diversity or stand age structure). Using data from 199 permanent sample plots, I examined effects of tree size, intraspecific competition, tree size diversity, and climate on survival probability. Results indicate that structural diversity and its effects on survival probability varied between stand age classes. In particular, deciduous basal area larger (i.e., sum of basal area of deciduous trees larger than a target tree) and tree size diversity were negatively related to tree survival and the magnitude of the negative impact varied between age groups (young, mature, and old stands). Tree size diversity was related to increasing stand level competition while deciduous basal area larger was effective as a measure of individual tree level competition. Under warmer conditions, competition variables (e.g., deciduous basal area larger and tree size diversity) had stronger effects on tree mortality, with magnitude of effects varying between age groups.

The third study examined whether overyielding occurs in young aspen-spruce mixtures and investigated which factors influence productivity of these mixtures. Overyielding is occurring in these young boreal mixedwood stands in western Canada. Relative productivity total (overyielding rate) varied from 0.921 to 1.537 among mixedwood treatments, and thinned aspen stands show higher productivity than unthinned aspen stands. Initial stand density (basal area) and initial quadratic mean diameter of aspen positively influenced mixing effect while initial quadratic mean diameter of spruce negatively influenced mixing effect. Consequently, a mixed species stand that has space partitioning and size inequality between species, which reduces competition and favours expression of the functional traits (e.g., shade tolerance) of each species, tends to have better productivity. The magnitude of overyielding declined with increasing growing season length and the relative productivity of aspen decreased with increasing site quality.

Preface

Through all chapters, with assistance and input from Dr. Phil Comeau, I undertook experimental design, data analysis, interpretation of results, manuscript composition, and edits.

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List of Abbreviations

AG	Age group
AHM	Annual heat moisture, (mean annual temperature+10)/(mean annual precipitation/1000)
Aw	Trembling aspen
CMI	Climate moisture index
DD5	Degree days above 5 ˚C
DBL	Deciduous basal area larger, (Sum of the basal areas of deciduous trees larger than a target tree)
FFP	Frost free period
MAP	Mean annual precipitation
MAT	Mean annual temperature
MCMT	Mean coldest month temperature
MSDR	Maximum size-density relationship
NSR	Natural sub-region
PAI	Periodic annual increment
PSP	Permanent Sample Plots
QMD	Quadratic mean diameter
RP	Relative productivity
SDI	Stand density index, (trees per hectare*(quadratic mean diameter/25.4)^1.605)
SFF	Stochastic frontier function
SHM	Summer heat moisture, (mean warmest month temperature)/(mean summer precipitation/1000)
SI	Site index
Sw	White spruce
TPH	Trees per hectare
TSD	Tree size diversity

Chapter 1: Introduction

1.1 Trembling aspen

Trembling aspen (*Populus tremuloides* Michx.) is a prominent and widespread tree species in North America, distributed from Newfoundland and Labrador west across Canada and from northwestern Alaska to the mountains of Mexico throughout the Western United States (Perala, 1990). This species grows on well drained, loamy, and high organic matter soils, and can also be found on shallow and rocky sands and heavy clays (Perala, 1990). Aspen is found in single species stands throughout its range, and in the Canadian boreal forest it is also found in mixture with conifers.

Figure 1.1 The distribution of trembling aspen in North America (from Little, 1971)
(retrieved from https://www.fs.fed.us/wildflowers/beauty/aspen/images/grow/poputrem_usgs_lg.gif)

Aspen provides a broad range of ecological and economic benefits. Aspen stands have been associated with a variety of habitats for wildlife and understory plants (Perala, 1990; Peterson and Peterson, 1992; Kuhn et al., 2011), and have positive effects on soil water retention and quality, increases in soil moisture and nutrients, and stabilizing soil carbon (DeByle and Winokur, 1985; LaMalfa and Ryle, 2008; Buck and St. Clair, 2012; Laganière et al., 2017). Productivity of aspen is high with a short rotation (e.g., 300 m^3/ha at age 55 for Ontario aspen on the best sites) and aspen provides a range of wood products (e.g., pulp, lumber, panelboard, plywood, biomass fuels, etc.) (Peterson and Peterson, 1992; Morley and Balatinecz, 1993).

As values of this natural resource have increased over the past four decades, aspen has seen increasing utilization, which is different from the past when aspen was considered to be a weed (Peterson and Peterson, 1992). Research on aspen and other poplar species has been conducted to better utilize and sustainably manage the natural resource in terms of silviculture, wood science, conservation, environmental science, physiology, biochemistry, pests, diseases, and genetics (Cooke and Rood, 2007).

Trembling aspen can regenerate from root suckers and stump sprouts, which together with root grafting results in individual trees being connected through an extensive root system (Peterson and Peterson, 1992; DesRochers and Lieffers, 2001; Jelínková et al., 2009). In addition, vegetative reproduction results in trees being genetically identical (Peterson and Peterson, 1992). Each aspen clone has typical leaf shape and size, bark character, branching habit, resistance to disease, time of flushing, and autumn leaf color, and these characteristics can be used to distinguish between clones (DeByle and Winokur, 1985; Peterson and Peterson, 1992). The sizes of single clones range from less than 0.01 hectare to more than 40 hectares in the American aspen stands (Steneker, 1973; Kemperman and Barnes, 1976), and clonal and genetic diversity also vary in a stand depending on site condition and history (Namroud et al., 2005; Namroud et al., 2006).

Clonal tree species have several advantages related to the root interconnection. Water and nutrients for shoot growth can be transferred through the root connection, which helps shoots grow faster than seedling origin aspen and faster than other associated species (Graham et al., 1963; Peterson and Peterson, 1992). Sharing carbohydrates through grafted roots has been reported as well (Fraser et al., 2006; Tarroux et al., 2010). Root connections belowground can mitigate impacts of defoliation and water stress and encourage radial growth of suppressed trees using resources from neighboring tree (Baret and DesRochers, 2011; Adonsou et al., 2016a; Adonsou et al., 2016b). For example, a sucker connected with other suckers had higher photosynthetic rates and larger specific leaf area than a disconnected sucker. In contrast to these benefits, disease or pathogens may be transmitted through a root system from tree to tree (Epstein, 1978; Lev-Yadun, 2011). These interactions belowground may influence aspen stand aboveground dynamics.

1.2 Aspen stand dynamics

Aspen is a shade intolerant and pioneering species, which regenerates in abundance from living roots left behind after stand replacing disturbances such as fire or harvesting. Aspen also regenerates from seed but this requires very particular seedbed, continuous moisture, and climatic conditions and is not always successful, despite there generally being an abundant seed supply in areas where aspen grows (Perala, 1990; Peterson and Peterson, 1995).

Aspen grows rapidly and dominates disturbed sites for several decades. Figure 1.2 illustrates the life cycle of an aspen stand over time. Due to the regeneration from root suckers, aspen sucker densities can exceed 100,000 stems per hectare at age 2 when conditions are suitable (Steneker, 1976; Bella, 1986). Given these high densities of regeneration, self-thinning begins at early ages due to the intraspecific competition for resources (light, water, and nutrients) and space, and densities are reduced to about 30,000 stems/ha by age 10 (Bokalo et al., 2007).

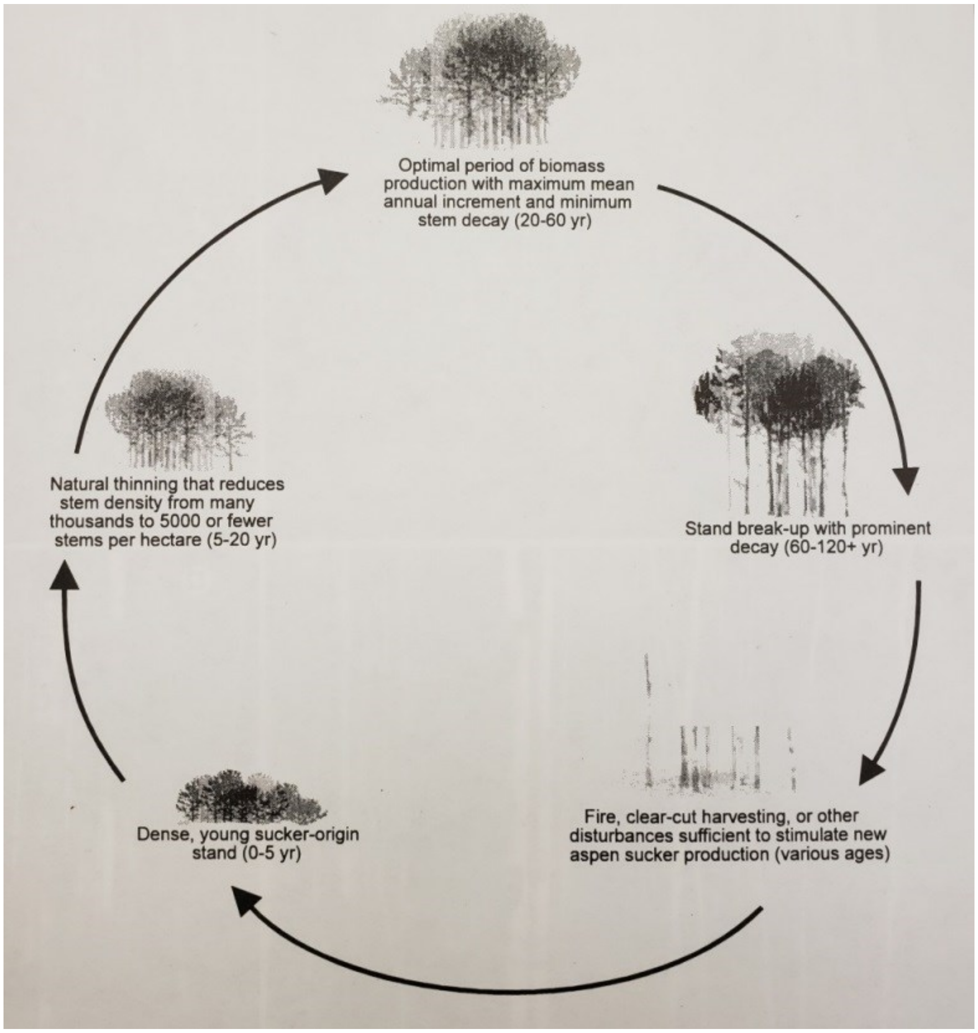


Figure 1.2 The life cycle of aspen stand development (from Peterson and Peterson, 1995).

Aspen productivity increases and aspen stands reach maximum mean annual increment at approximately age 60, which can vary with site condition (Peterson and Peterson, 1992). After aspen stands pass age 60, they start declining and stand breakup begins because of senescence, drought stress, stem disease fungi, and insect damage (Peterson and Peterson, 1992; Senecal et al., 2004; Frey et al., 2004). With stand breakup and tree mortality, new aspen suckers or shade tolerant tree species (e.g., white spruce (*Picea glauca* (Moench) Voss) regenerate or grow faster under aspen crown. Depending on the proportion of understory species, aspen stands can be maintained through gap dynamics or succeed to mixedwood stands or conifer dominated stands (Figure 1.3).

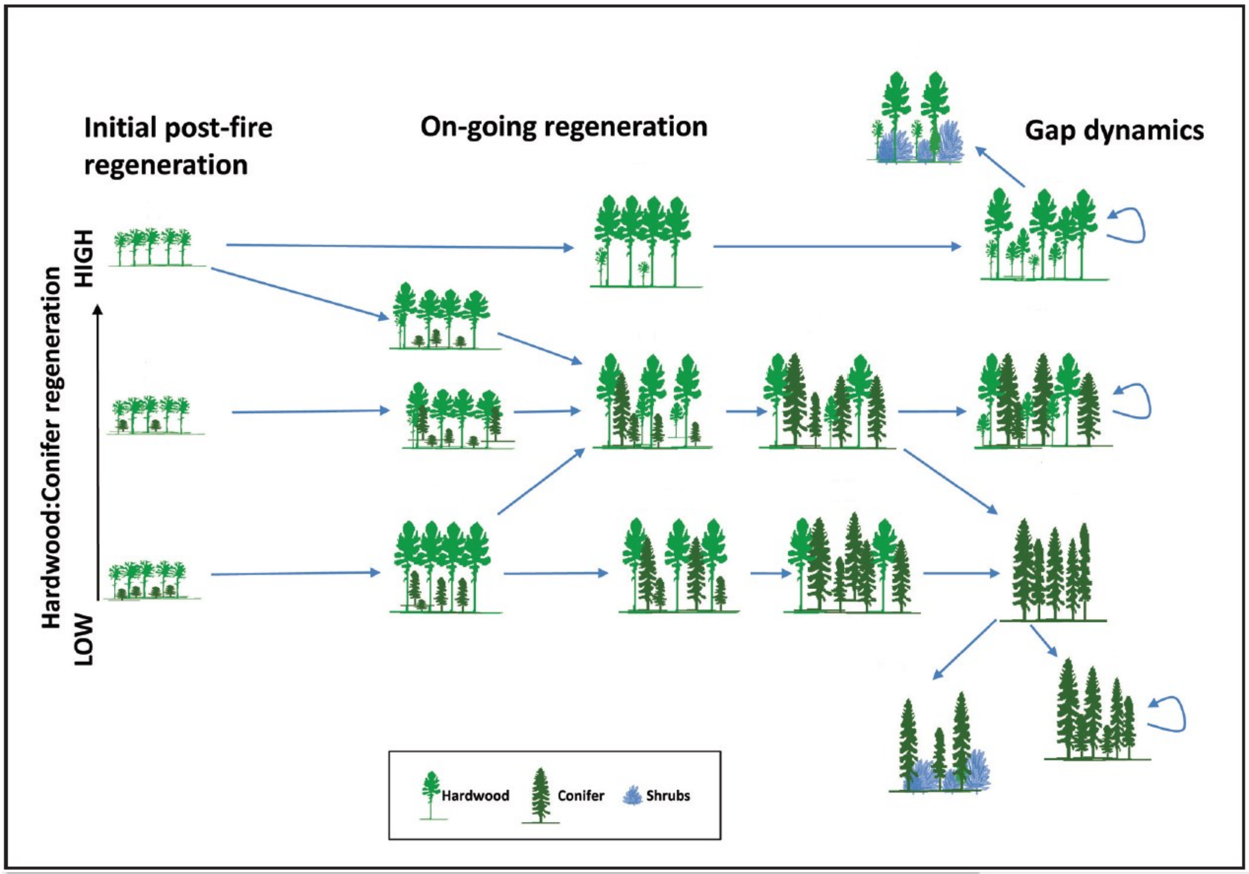


Figure 1.3 Mixedwood stand dynamics based on proportion of hardwood and coniferous trees after stand replacing disturbances (from Bergeron et al., 2014).

1.3 Mixtures of aspen and white spruce

Mixtures of aspen and white spruce are a prominent natural component of the boreal plains and a common forest type in Canada (Man and Lieffers, 1999). Increasing recognition of the economic and ecological values of mixed-species stands has led to increased interest in mixedwood management in contrast to the management of separate pure stands of white spruce and aspen in the past (Macdonald, 1995; Man and Lieffers, 1999; Chen and Popadiouk, 2002; Macdonald et al., 2010). In general, mixed-species stands can have higher productivity and produce more volume than monospecific stands (Condés et al., 2013; Liang et al., 2016). In addition, mixedwood stands may provide several ecological benefits, such as increased resistance to insects attack and disease (Bergeron et al., 1995; Cappuccino et al., 1998), protection from frost damage and overheating (Groot and Carlson, 1996; Pritchard and Comeau, 2004; Voicu and Comeau, 2006), reduced windthrow (Grover et al., 2015), increased nutrient cycling (Légaré et al., 2004; Jerabkova et al., 2006; Macdonald et al., 2010), and higher biodiversity (Macdonald et al., 2010; Cavard et al., 2011b).

White spruce establishes on exposed mineral soil following stand destroying disturbances, and also regenerates on rotted logs, organic layers, and moss beds under established stands (Nienstaedt and Zasada, 1990; DeLong et al., 1997). In contrast to aspen, white spruce is moderately shade tolerant and can survive and grow under aspen canopies with growth rates often improving after aspen starts declining at age 50 to 70 (Yang, 1991; Lieffers and Stadt, 1994; Filipescu and Comeau, 2007). In aspen-spruce mixed stands, aspen plays an important role as a nurse tree in protecting small young spruce trees from frost damage and winter injury (Groot and Carlson, 1996; Filipescu and Comeau, 2011). At the same time, however, shade from aspen does reduce the growth of white spruce (Filipescu and Comeau, 2007).

1.4 Maximum size-density relationships

The maximum number of trees that can be supported in a unit area generally depends on average tree size. Based on observed relationships between maximum stand density and average tree size, maximum size-density lines have been developed to define the maximum number of trees that can be supported in a stand when trees are any particular size. Representative size-density relationships widely used in forestry are Reineke's rule (Reineke, 1933) and the -3/2 power law (Yoda et al., 1963). Reineke's rule indicates the relationship between the maximum number of trees and their average size follows the straight-line on logarithmic scales, while Yoda's -3/2 power law follows the relationship between average plant weight and plant density in single-species crowded population. Since the size-density relationships were released, ecologists and foresters have applied size-density concepts to various species and different site conditions and have debated how best to formulate the concept.

The main debate was whether the slope and intercept values of the self-thinning line are static, and previous studies have shown that changes of slope and intercept occur depending on species (Weller, 1987; Pretzsch and Biber, 2005; Charru et al., 2012; Vospernik and Sterba, 2015), and are also influenced by stand origin (Weiskittel et al., 2009), site quality (Bi, 2001; Weiskittel et al., 2009), climate (DeBell et al., 1989; Comeau et al., 2010), and nutrient level (Morris, 2003; Reyes-Hernandez et al., 2013). Variation between species reflects differences in resource requirements (e.g., shade tolerance, drought tolerance, and packing capacity) (Zeide, 1985; Pretzsch and Biber, 2005; Charru et al., 2012). In general, shade tolerant species show higher "stockability" (i.e., for any given average size, maximum densities are higher) than shade intolerant species (Pretzsch and Biber, 2005; Charru et al., 2012). Plantation origin stands have been reported to have a lower intercept and a flatter slope than natural stands (Weiskittel et al., 2009; Charru et al., 2012). Increases in site quality or nutrient regime lead to increases in the intercept value (Westoby, 1984; Bi, 2001; Weiskittel et al., 2009; Reyes-Hernandez et al., 2013). DeBell et al. (1989) reported that climate can influence the stockability of loblolly pine (*Pinus taeda* L.) stands, with stands in Hawaii carrying higher density and basal area at any given sizes than stands in the southeastern United States.

Weller (1987) stated that the thinning rule should be considered an applicable rule instead of a quantitative law because the differences among slopes may reflect ecological differences among species. Zeide (1987) suggested a curve concave down for the self-thinning line, rather than a straight line because of crown dynamics. Furthermore, Weller (1990) suggested that a dynamic thinning line was applicable to each stand to describe stand dynamics influenced by population and site condition, whereas the static thinning line provided the general boundary limit for the species in a region. The dynamic thinning lines are useful to account for effects of site quality, silvicultural treatments and other factors on the position and slope of the self-thinning line (Westoby, 1984; Weller, 1990; VanderSchaaf and Burkhart, 2007). VanderSchaaf and Burkhart (2007; 2008; 2010) used a mixed effects model to better reflect the behavior of individual self-thinning stands and develop an average dynamic thinning line for loblolly pine. The self-thinning concept developed for pure and even-aged stands has been extended to mixed species stands (Puettmann et al., 1992) using more complex models and equations.

1.5 Stand breakup in aging aspen stands

Tree mortality creates gaps in the canopy and facilitates changes in stand composition and structure by providing opportunities for trees to establish and grow in the gaps (Franklin et al., 1987; Hill et al., 2005). It is important to understand the causes of tree mortality because the death and decline of numerous trees in a short time can have serious ecological and economic impacts (Hogg et al., 2008; Michaelian et al., 2011).

A high incidence of decay, stem breakage and tree death are often observed for aspen when stands exceed 80 years of age (Luo and Chen, 2011). The onset of stand breakup is, however, highly variable and appears to be influenced by climate, stand structure, composition, age, and other factors (Senecal et al., 2004; Luo and Chen, 2011; Bell et al., 2014). Self-thinning occurs during the early stages of stand development due to intraspecific competition for resources and space, while mortality in older stands results largely from disease and insect damage due to reduced resistance of older aspen (Senecal et al., 2004; Luo and Chen, 2011; Zegler et al., 2012; Bell et al., 2014). Specifically, Pothier et al. (2004) estimated that the average age for the onset of aspen decline was 64 years and identified an important increase of tree mortality and wood decay at around age 60 years in Quebec stands. Impacts of rising temperature and severe drought arising from climate change on tree mortality have been reported by several authors (Allen et al., 2010; Peng et al., 2011). Hogg et al. (2008) and Michaelian et al. (2011) showed that aspen mortality and dieback were closely related to drought severity in western Canada, and Bell et al. (2014) predicted that forest succession and conversion to conifer forests could be accelerated by warming and drying of aspen forests in the future. However, they concluded that the pattern of aspen mortality is better explained by forest stand structure, productivity, and age than climate. Luo and Chen (2013) found that young forests had higher sensitivity to warming and drought than old forests due to higher intensities of competition for resources and spaces. The intensity and frequency of insect and disease outbreaks are expected to increase in the future due to increases in drought stress and increased temperatures (Boland et al., 2004; Sturrock et al., 2011;

Bell et al., 2015). The agents of tree mortality are complex and the effects of climate change on tree survival may vary according to region, forest composition and structure, and site condition, so an improved overall understanding of forest ecosystem and stand dynamics is also needed.

1.6 Productivity and mixing effects in mixtures

Overyielding (i.e., greater productivity in mixtures than in monocultures) has been observed in many mixed forests (Beckage and Gross, 2006; Pretzsch and Schutze, 2009). Research on overyielding started in plant sciences in the 1950s and 1970s to assess productivity of mixtures of plants (Hector, 2006), and studies on overyielding in mixed species forests have been conducted as well (Pretzsch and Schutze, 2009; Pretzsch et al., 2010; Condés et al., 2013; Sapijanskas et al., 2013; Mason and Connolly, 2014; Pretzsch, 2014; Toïgo et al., 2015).

Higher production in mixtures results from the positive "mixing effect" (Pretzsch and Schütze, 2016), and increase in production results from the mixed environment encouraging species traits to surpass their behaviors in pure stands (Kelty, 2006; Forrester, 2014; Pretzsch, 2014). In general, competitive reduction and facilitation cause the mixing effect. Competitive reduction leads to complementarity though niche partitioning because species in mixtures do not need to compete with other species for resources (e.g., light, water, and nutrients) and space (Man and Lieffers, 1999; Kelty, 2006; Pretzsch and Schutze, 2009). For example, shade tolerant species in the understory have a better capacity for carbon fixation under low light than intolerant species (Givnish, 1988). This advantage makes shade intolerant species in the overstory get full light and results in a stand structure that more fully utilizes light over the growing season. In the case of conifer and deciduous mixed stands, differences in phenology of leaf development can also contribute to higher production of mixtures because they differ in utilization of light during the growing season (Constabel and Lieffers, 1996; Man and Lieffers, 1999). With regard to niche partitioning, mixed species stands support higher stocking and greater canopy stratification (Garber and Maguire, 2004; Condés et al., 2013; Pretzsch and Schütze, 2016). Shade tolerance and crown shapes of species may also allow stands to stock more trees in mixtures compared to monocultures (Pretzsch, 2014; Peer et al., 2018; Toïgo et al., 2018). When species occupy different crown layers, there can be an increase in stand leaf area index which may contribute to increased productivity in mixtures (Man and Lieffers, 1999; Kelty, 2006; Forrester and Albrecht, 2014; Forrester et al., 2018). However, the nature and magnitude of mixing effects depend on combinations of the component species, and may also be influenced by environmental conditions. Facilitation relates to certain species that improve the environment for other species (Hooper et al., 2005). Structural nursing increases productivity by maintaining higher humidity under canopy and reducing mortality rate or injury from frost, insect attacks, and wind (Taylor et al., 1996; Groot and Carlson, 1996; Man and Lieffers, 1999). Mixed species stands may also improve nutrient status and encourage microbial activity potentially resulting in overyielding (Pretzsch and Schutze, 2009; Forrester, 2014; Mason and Connolly, 2014).

Stand developmental stages can influence the productivity of mixtures because growth rates of each species can be different depending on age (del Río et al., 2016). Early successional species typically have rapid initial growth that reaches a maximum over a short period while late successional species often have slower early growth rates (Cavard et al., 2011a). As a result, the contribution of each species to total production varies over time and can influence whether overyielding occurs, when it occurs, and its magnitude.

Environmental conditions, such as site quality and climate, can influence the productivity of mixtures through effects on growth of the component species, nature and intensity of interactions, and potential stocking (Pretzsch et al., 2010; Paquette and Messier, 2011; Prior and Bowman, 2014; Potter and Woodall, 2014; Toïgo et al., 2015; Jucker et al., 2016; Peer et al., 2018; Mina et al., 2018). According to the stress gradient hypothesis, interactions among species tend to be more positive (i.e., interactions leading to increased growth) under poor or stressful conditions whereas under rich or moderate conditions weak positive or negative outcomes are more common (Callaway and Walker, 1997; Paquette and Messier, 2011; Toïgo et al., 2015). Where this is the case, overyielding would be expected to be of larger magnitude under more stressful conditions.

1.7 Thesis objectives

The overall objectives of this Ph.D. thesis are to examine maximum size density relationships in aspen stands, aspen stand breakup, and overyielding in young aspen-white spruce mixedwood stands.

Chapter number two of this Ph.D. thesis examines effects of climate on the intercept and slope of static and dynamic self-thinning lines. The hypothesis is that climate influences the intercept and slope of the self-thinning line in aspen stands. To test this, I: 1) develop static and dynamic self-thinning lines; and 2) examine effects of climate on both the static and dynamic self-thinning lines for trembling aspen.

In chapter three of this thesis, I address survival probability of aging aspen stands. I hypothesize that survival probability of aspen changes with age and drought stress accelerates aspen mortality.

Thus, I attempted to: 1) determine the survival probability of aspen based on stand age and stand structure; and 2) examine the effect of climate, stand characteristics, and tree age on survival probability.

In chapter four of this thesis, I hypothesize that mixed stands have higher productivity than pure stands, so I examine: 1) whether overyielding occurs in stands that are less than 30 years old; 2) the effects of species composition, stand density, proportion, and tree size on overyielding and productivity; and, 3) effects of climate and, site productivity (site index) on the magnitude of overyielding and productivity of two species.

Finally, chapter five presents the overall conclusion and provides recommendations for further studies.

Chapter 2: Effects of climate on maximum size-density relationships in western Canadian trembling aspen stands

2.1 Introduction

The relationship between tree size or weight and maximum density was simplified through the two concepts: Reineke's rule (Reineke, 1933) and the 3/2 power law (Yoda et al., 1963). The fact that the slope and intercept of this relationship fit on log-transformed data can vary between species (Pretzsch and Biber, 2005; Charru et al., 2012; Vospernik and Sterba, 2015) and are also influenced by stand origin (Weiskittel et al., 2009), site quality (Bi, 2001; Weiskittel et al., 2009), climate (DeBell et al., 1989; Comeau et al., 2010), and nutrient level (Morris, 2003; Reyes-Hernandez et al., 2013) has been demonstrated.

Analysis of maximum size-density relationships has focused primarily on static self-thinning lines defined using the upper boundary points from a large number of crowded stands (Osawa and Sugita, 1989; Weller, 1990). The self-thinning line provides a general boundary limit for the species in a region (Weller, 1990; VanderSchaaf and Burkhart, 2007). For this reason, the species boundary line has been used in developing stand density management diagrams, stocking guides, and in growth models (Drew and Flewelling, 1979; Weller, 1990; Jack and Long, 1996; Yang and Titus, 2002). In contrast, dynamic self-thinning lines use data from re-measurements of permanent sample plots to define the self-thinning line for each plot. The dynamic lines show the behavior of individual crowded stands over time (Weller, 1987) because these lines are more sensitive to effects of site quality, silvicultural treatments and other factors (Westoby, 1984; Weller, 1990; VanderSchaaf and Burkhart, 2007).

A few studies have examined maximum size-density relationships (MSDR) in western Canadian boreal forests. Lieffers and Campbell (1984) estimated the self-thinning line using biomass and density in young aspen stands and obtained a slope of -0.962 which differs from Yoda's boundary thinning line. Yang and Titus (2002) developed static maximum size-density functions for aspen, white spruce, and lodgepole pine (*Pinus contorta* var. *latifolia* Engelm) based on the self-thinning rule and Reineke's stand density index. They examined the effect of site quality and species with the size-density function and found no effect of site quality on the size-density relationship. Bokalo et al. (2007) developed size-density equations for young-regenerated aspen stands and found that the slope of the maximum density-quadratic mean root collar diameter line was -1.408. In a recent study, Reyes-Hernandez et al. (2013) estimated the static and dynamic self-thinning lines for mature mixed stands of aspen and white spruce and examined the effects of stand composition, age, and site quality indicators (soil moisture regime and soil nutrient regime). While they found that the slope of the static line became steeper as aspen proportion increased, there was no effect of site quality on the static line. With regard to the dynamic line, the intercept decreased with increasing proportion of aspen and increased with increasing nutrient regime.

Maximum size density lines have been developed for trembling aspen in this region and effects of stand age, site quality, and soil water and nutrient regime have been examined, but these studies have not examined effects of climate. Climate, particularly drought, is important to tree growth and survival (Suarez et al., 2004). Western Canadian boreal forests have short growing seasons and low mean annual precipitation ranging between 472 and 620 mm based on 1961-1990 climate normal data (Gray et al., 2011; Price et al., 2013). Drought stress is considered to be an important factor causing mortality of trembling aspen (Hogg et al., 2002; Allen et al., 2010; Michaelian et al., 2011; Peng et al., 2011; Hogg et al., 2013; Worrall et al., 2013).

The purpose of this study was to use data from Alberta and Saskatchewan to determine whether a single regional maximum size-density relationship can be used or if it is necessary to incorporate climate into the models. For the current study, the objective was to evaluate effects of climate on both the static and dynamic self-thinning lines for trembling aspen.

2.2 Material and Methods

2.2.1 Data

Data from permanent sample plots located in the boreal plains ecozone across Alberta and Saskatchewan (Figure 2.1) were used for this study. The Boreal plains ecozone has 0.2 ˚C mean annual temperature and 472 mm annual precipitation (Price et al., 2013), and despite the low precipitation this ecozone is considered to have a moist climate because of cold winters, moderately warm summers, with 67% (316 mm) of annual precipitation falling during the growing season (Wiken, 1986; Price et al., 2013). Gray Luvisolic soils predominate on forested sites in this region (Wiken, 1986; Lavkulich and Arocena, 2011). The boreal plains ecozone has a frost free period of 80 to 130 days and 1000 to 1250 degree-days above 5 ˚C for the growing season, where trembling aspen, balsam poplar, white birch, white and black spruce, jack pine and tamarack are found in pure or mixed stands (Wiken, 1986).

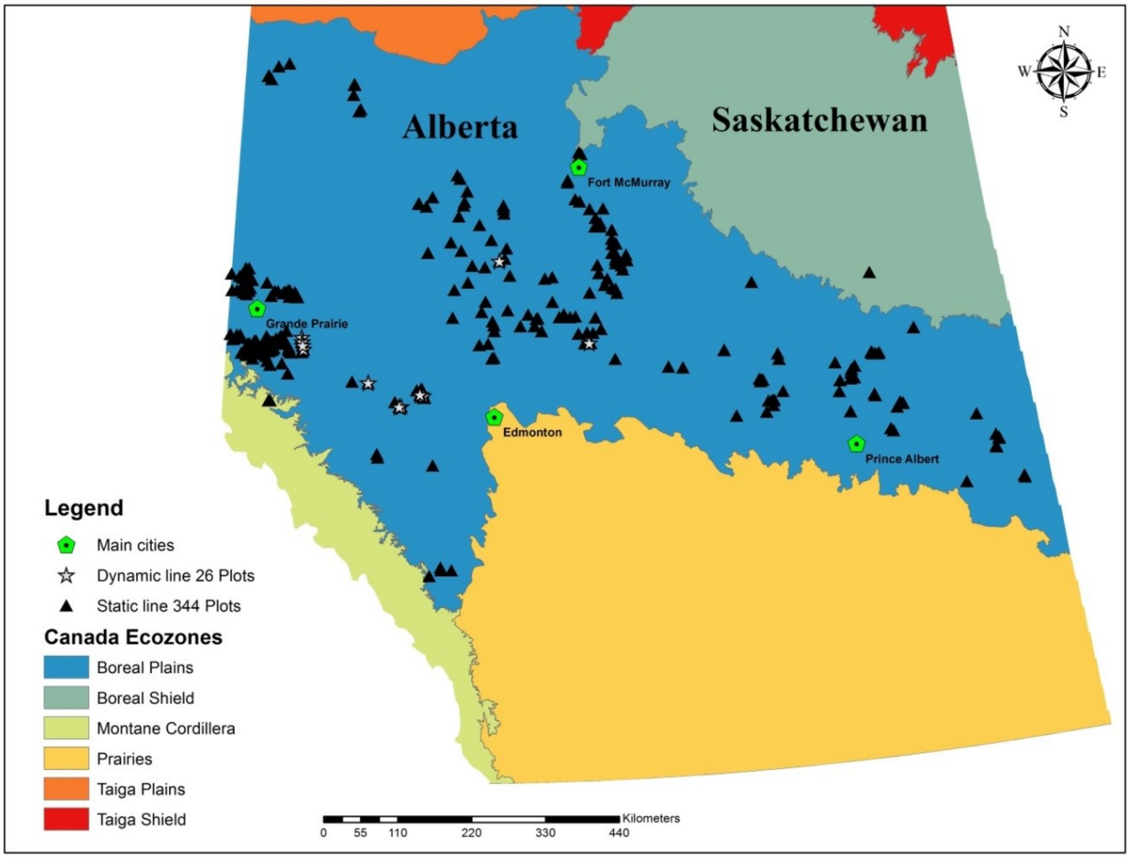


Figure 2.1 Locations of plots across Alberta and Saskatchewan used for this study (Stars indicate locations of the 26 permanent sample plots used for developing the dynamic self-thinning lines and triangles indicate locations of 344 permanent sample plots used for developing the static self-thinning line).

344 aspen dominated permanent sample plots were used for this analysis. These PSPs were established by government agencies and forest industry and were measured for the last one to four decades depending on agencies (Table 2.1). Alberta government (ESRD), Alberta-Pacific Forest Industries Inc. (ALPC), and Weyerhaeuser Company Ltd. (WEYR) PSP's meet the minimum standards of the Alberta Provincial Growth and Yield Initiative (PGYI). In general, trees where a diameter is bigger than 9.1 cm were measured in 400 m^2 and plot size varied from 400 to 1000 m^2 depending on agency. Saskatchewan government measures trees larger than 7.1

cm and plot size varies from 600 to 1000 m^2. In order to unify the dataset, only trees bigger than 9.1 cm were used for the analysis. In all of these plots, aspen comprised at least 80% of plot basal area. These permanent sample plots varied in elevation, tree size, and density and included between one and five measurements (Table 2.1).

Table 2.1 General information relating to the aspen dominated permanent sample plots used for this study.

Variables\Agencies		ESRD	ALPC	SK	WEYR	All
Number of plots		87	75	86	96	344
Measurement years		1965-2008	2004-2014	1979-2012	1982-2012	1965-2014
Elev. (m)	Mean	755.7	560.7	506.5	807.4	665.3
	SD	209.8	110.6	48.3	98.2	182.7
	Min.	320.8	260.0	315.0	593.0	260.0
	Max.	1536.1	766.9	669.0	1083.0	1536.1
QMD (cm)	Mean	24.5	20.9	21.3	26.5	23.5
	SD	7.6	5.2	5.2	7.2	6.9
	Min.	13.2	11.9	12.7	12.9	11.9
	Max.	46.3	36.9	33.0	43.6	46.3
HT (m)	Mean	22.1	22.1	20.8	22.7	21.9
	SD	3.9	3.4	3.5	4.3	3.9
	Min.	14.4	14.3	13.4	13.6	13.4
	Max.	30.0	29.4	29.2	32.4	32.4
SDI	Mean	619.8	678.3	580.9	534.2	598.9
	SD	148.1	143.9	138.7	175.9	161.4
	Min.	351.4	334.8	282.2	222.3	222.3
	Max.	1118.7	1088.5	972.4	1067.2	1118.7
TPH (trees/ha)	Mean	792.8	1039.6	860.2	607.1	811.7
	SD	453.9	486.3	405.3	421.0	465.0
	Min.	143.0	250.0	235.0	138.0	138.0
	Max.	1920.0	2742.0	2100.0	2325.0	2742.0
BA (m^2/ha)	Mean	29.7	30.7	26.5	26.3	28.2
	SD	7.4	6.8	6.5	8.8	7.7
	Min.	16.1	17.0	14.1	12.0	12.0
	Max.	50.2	47.3	43.8	55.0	55.0

ESRD, Alberta government; ALPC, Alberta-Pacific Forest Industries Inc.; SK, Saskatchewan government; WEYR, Weyerhaeuser Company Ltd.; Elev. Elevation; QMD, quadratic mean diameter; HT, mean tree height; SDI, stand density index (TPH*(QMD/25.4)^1.605); TPH, trees per hectare; BA, basal area.

2.2.2 The static self-thinning line

A maximum boundary line can be defined from the maximum obtainable number of trees for a particular tree size across all stands of a specific species within a particular region (Weller 1990). Corrected ordinary least squares (OLS), quantile regression (QR), and Stochastic frontier function (SFF) methods have been used in previous studies to determine the boundary line at various areas (Zhang et al., 2005). OLS can be used to yield a boundary line after relocating the line to the upper point indicating the highest stand density index or basal area, and QR is also useful in determining boundary lines for highly skewed distributions. Stochastic frontier analysis was used in this research because it can yield the line without any adjustments required when using OLS and because addition of covariates is possible with SFF.

Stochastic frontier function (SFF) directly determines boundary lines and accommodates inclusion of covariates (Bi et al., 2000; Zhang et al., 2005; Weiskittel et al., 2009; Reyes-Hernandez et al., 2013). The self-thinning boundary line was fit, using stand density (TPH) as the dependent variable and quadratic mean diameter (QMD) as the independent variable. Even though SFF allows observations to depart from the frontier line, low values for TPH on the left or right side can influence the estimates of slope and intercept. Consequently, measurements where relative density (Curtis, 1982) was below 0.2 were removed. This left 344 plots from 4 agencies for fitting the SFF (Table 2.2). For this analysis, only a single measurement (the highest measurement of basal area) was included for each plot to avoid issues arising from repeated measurements. The equation for the self-thinning boundary line is:

$$\ln(TPH) = \beta_0 + \beta_1 \times \ln(QMD) + \varepsilon\ (= v - u), \qquad \textbf{(2.1)}$$

where ln is the natural logarithm, TPH is trees/ha, QMD is quadratic mean diameter (cm), β_0 is the intercept value, and β_1 is the slope value. ε consists of two error terms where the first error term (v) is the effect of random factors influencing stand density, such as external disturbances or environmental influences and the second error term (u) is a non-negative random variable related to site occupancy (Bi et al., 2000; Bi, 2004; Zhang et al., 2005). Climate variables were added as separate variables to test the effects of climate on the intercept and also as interaction terms with ln(QMD) to evaluate their influence on the slope of the maximum size-density line. The equation is:

$$\begin{aligned}\ln(\mathrm{TPH}) = \beta_0 + \beta_1\times\ln(\mathrm{QMD}) + \beta_2\times\text{Climate variable} \\ + \beta_3\times\ln(\mathrm{QMD})\times\text{Climate variable} + \varepsilon,\end{aligned} \qquad \textbf{(2.2)}$$

where β_2 is the coefficient of climate variable and β_3 is the coefficient of the interaction term between ln(QMD) and climate variable. To develop better models, up to three climate variables were added with the interaction term (β_3) to the basic model. Parameters for stochastic frontier function were estimated using the frontier package (Coelli and Henningsen, 2013) of R version 3.0.3 (R Core Team, 2017).

Table 2.2 Characteristics of the measurements used in the maximum size-density relationship (MSDR) analyses.

Analysis	N	Variable	Mean	SD	Max.	Min.
MSDR static	344	Quadratic mean diameter (cm)	23.5	6.9	46.3	11.9
		Trees per hectare (TPH)	811.7	465.0	2742.0	138.0
		Basal area (m^2ha^{-1})	28.2	7.7	55.0	12.0
MSDR dynamic	26*	Quadratic mean diameter (cm)	23.3	3.0	30.1	18.3
		Trees per hectare (TPH)	699.1	173.7	1156.0	400.0
		Basal area (m^2ha^{-1})	28.9	5.5	43.7	20.4

*62 observations in 26 plots; N, Number of plots.

2.2.3 The dynamic self-thinning line

To assess dynamic self-thinning lines, at least 2 measurements of each plot are required to track the behavior of a stand. Out of the 407 plots (699 measurements) available for fitting of static lines, 41 plots had two or more measurements. Fifteen plots not undergoing self-thinning over time were removed (Reyes-Hernandez et al., 2013). 26 plots (62 observations) having two or more re-measurements were used to develop and evaluate dynamic self-thinning lines (Table 2.2). Dynamic maximum size-density lines were fit using logarithm of stand density (TPH) as the dependent variable and logarithm of quadratic mean diameter (QMD) as the independent variable, and plot and log-quadratic mean diameter were used as random intercept and slope. Because re-measurements of plots were correlated and all plots were independent, a linear mixed-effects model was used (VanderSchaaf and Burkhart, 2007; Vanderschaaf, 2010). An unstructured variance-covariance matrix was assumed for developing the model due to heterogeneous variances of errors and correlations among repeated measurements. A spatial-Gaussian variance-covariance matrix structure was applied for the random effects to deal with the issue of correlation derived from the unequally spaced time in measurements (Reyes-Hernandez et al., 2013). The equations were based on Reineke's rule and the effects of climate variables on the intercept and as interaction terms with ln(QMD) to test their influence on the slope of the average dynamic self-thinning line. The equations are:

$$\ln(\mathrm{TPH}) = (\beta_0 + u_{0i}) + (\beta_1 + u_{1i})\times\ln(\mathrm{QMD}) + \varepsilon, \tag{2.3}$$

$$\ln(\mathrm{TPH}) = (\beta_0 + u_{0i}) + (\beta_1 + u_{1i})\times\ln(\mathrm{QMD}) + \beta_2\times\text{Climate variable} + \beta_3\times\ln(\mathrm{QMD})\times\text{Climate variable} + \varepsilon, \tag{2.4}$$

where β_0 and β_1 are population-average parameters, u_{0i} and u_{1i} are cluster-specific random effects and assumed to be $N(0, \sigma_0^2)$ and $N(0, \sigma_1^2)$, respectively (Vanderschaaf, 2010). β_2 is the coefficient of climate variable, β_3 is the coefficient of the interaction term between ln(QMD) and climate variable, and ε is random error. Parameters for linear mixed-effects models were estimated using the nlme package (Pinheiro and Bates, 2000; Pinheiro et al., 2015) of R version 3.0.3 (R Core Team, 2017).

Data for the 26 plots which could be used for the evaluation of dynamic self-thinning lines came from only a small area in west-central Alberta. To make appropriate comparisons with the static lines, 46 plots from this same area were selected for fitting of a static maximum size-density line. Maximum likelihood method was used to compare models, and corrected AIC value was calculated to consider the small sample size.

2.2.4 Climate variables

Climate data were obtained from ClimateWNA (Climate for Western North America, Hamann et al., 2013). Climate normals for the 30 year period between 1981 and 2010 were used in the analysis of the static self-thinning line representing climate conditions of plots (Table 2.3). For the dynamic self-thinning line, periodic climate data were used to examine effects of climatic conditions during the interval between measurements on the behavior of individual stands. For the first measurement of each plot, the preceding 5-year mean climate data were used. For the subsequent measurements, the mean climate data for the interval between the two measurement years (first-second and second-third measurement years) was used. Mean annual temperature (MAT), degree-days above 5 ˚C (DD5), degree-days below 0 ˚C (DD_0), and frost free period (FFP) were tested as thermal variables because the variation of temperature influences tree growth, growing period, and evapotranspiration of forests (Way and Oren, 2010; Abtew and Melesse, 2013). Mean annual precipitation (MAP), mean summer (May to Sep.) precipitation (MSP), climate moisture index (CMI), climate moisture demand (CMD), annual heat moisture (AHM), summer heat moisture (SHM), and summer (Jun. to Aug.) precipitation (PPT_sm) were applied to the models to evaluate drought related effects on the size-density line because tree growth and survival rate are significantly influenced by moisture condition in forests.

Table 2.3 Means and ranges for climate variables for sites used for analyses of static and dynamic self-thinning lines.

	The static self-thinning line (n=344)				The dynamic self-thinning line (n=26)			
Variables	Mean	SD	Max.	Min.	Mean	SD	Max.	Min.
MAT (˚C)	1.4	1.0	3.0	-1.3	1.8	0.6	2. 7	0.1
DD5	1245.4	80.9	1482.0	844.0	1218.0	63.4	1324.0	1099.0
DD_0	1638.9	354.9	2398.0	999.0	1527.6	177.2	2027.2	1186.0
FFP	102.1	5.8	113.0	74.0	108.3	7.4	122.3	89.8
MAP (mm)	506.1	59.6	790.0	658.0	565.2	41.7	630.0	453.2
MSP (mm)	342.5	45.5	460.0	258.0	379.4	41.6	446.1	317.0
CMD (mm)	143.6	46.6	234.0	27.0	154.7	26.8	205.1	107.0
CMI (cm)	7.5	6.4	26.0	-5.0	13.2	4.9	20.7	0.03
AHM	22.7	1.7	28.4	17.3	21.5	1.6	25.5	19.0
SHM	47.5	7.8	65.2	29.6	44.3	7.1	56.7	33.8
PPT_sm (mm)	244.7	32.9	325.0	180.0	275.5	30.7	324.1	227.9
MWMT (˚C)	15.9	0.9	18.0	12.8	15.3	0.4	16.3	14.5
MCMT (˚C)	-14.9	3.5	-7.8	-21.1	-15.0	2.5	-10.8	-22.5
Tave_sm (˚C)	14.7	0.8	16.5	11.6	13.9	0.5	15.1	13.2
Tave_wt (˚C)	-13.1	2.9	-7.3	-18.3	-11.9	1.6	-8.8	-15.8

MAT, mean annual temperature; DD5, degree-days above 5 ˚C; DD0, degree-days below 0 ˚C; FFP, frost free period; MAP, mean annual precipitation; MSP, mean summer precipitation; CMD, climate moisture demand; CMI, climate moisture index, AHM, annual heat moisture ((MAT+10)/(MAP/1000)); SHM, summer heat moisture (MWMT/(MSP/1000)); PPT_sm, summer precipitation; MWMT, mean warmest month temperature; MCMT, mean coldest month temperature; Tave_sm, summer mean temperature; Tave_wt, winter mean temperature.

Climate moisture index was calculated using the formula provided by Hogg (1997), applied to monthly temperatures, annual precipitation, and elevation for each location. Mean warmest month temperature (MWMT), mean coldest month temperature (MCMT), summer mean temperature (Tave_sm), and winter mean temperature (Tave_wt) were also included as climate variables in order to determine the effects of climatic extremes and seasonal temperatures in the models (Hansen et al., 2012; Price et al., 2013).

2.3 Results

2.3.1 Stochastic frontier analysis for the static self-thinning line

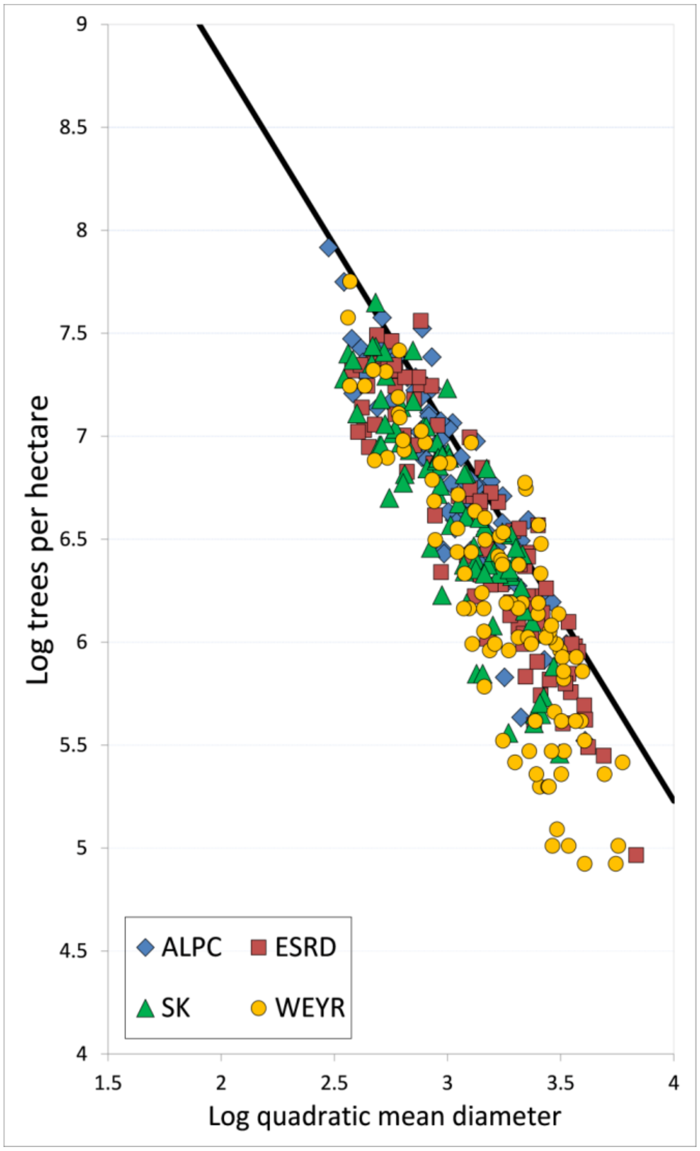


Figure 2.2 The static self-thinning line estimated by stochastic frontier function and plots of natural logarithm of trees per hectare over the natural logarithm of quadratic mean diameter. Data points are indicated by symbols (ALPC, Alberta-Pacific Forest Industries Inc.; ESRD, Alberta government; SK, Saskatchewan government; WEYR, Weyerhaeuser Company Ltd.). The maximum size-density line is shown in black and is described by the equation: ln(TPH) = 12.425 - 1.799×ln(QMD).

Stochastic frontier analysis produced the static self-thinning line using data from four agencies (Figure 2.2). The static line has a slope of -1.799 and is significantly different from Reineke's slope value of -1.605 according to likelihood ratio test (p-value < 0.001).

Table 2.4 Models for the static self-thinning line. A is the best model with only one climate variable, B is the best model with two climate variables, and C is the best model with three climate variables.

Variables	Models	σ^2	γ	AIC
Basic	$\ln(\mathrm{TPH}) = 12.425 - 1.799\times\ln(\mathrm{QMD})$	0.169	0.845	90.08
model	(0.159) (0.051)	(0.021)	(0.047)	
(A) FFP	$\ln(\mathrm{TPH}) = 13.251^{*} - 1.738\times\ln(\mathrm{QMD}) - 0.010\times\mathrm{FFP}$	0.159	0.843	72.92
	(0.250) (0.051) (0.002)	(0.019)	(0.046)	($p<0.001$)[1]
(B) FFP	$\ln(\mathrm{TPH}) = 13.644^{*} - 1.767\times\ln(\mathrm{QMD}) - 0.009\times\mathrm{FFP}$	0.161	0.854	70.28
AHM	(0.316) (0.052) (0.002)	(0.019)	(0.045)	($p=0.031$)[2]
	$- 0.018\times\mathrm{AHM}$			
	(0.008)			
(C) FFP	$\ln(\mathrm{TPH}) = 20.119^{*} - 3.977^{*}\times\ln(\mathrm{QMD}) - 0.081\times\mathrm{FFP}$	0.142	0.804	65.79
SHM	(3.754) (1.221) (0.034)	(0.019)	(0.069)	($p=0.014$)[3]
MCMT	$+ 0.103\times\mathrm{SHM} + 0.297\times\mathrm{MCMT}$			
	(0.049) (0.120)			
	$+ 0.023\times\ln(\mathrm{QMD})\times\mathrm{FFP} - 0.037\times\ln(\mathrm{QMD})\times\mathrm{SHM}$			
	(0.011) (0.016)			
	$- 0.105\times\ln(\mathrm{QMD})\times\mathrm{MCMT}$			
	(0.040)			

*Significantly different from the intercept or slope value of the basic model (12.425 or -1.799) at alpha = 0.05 (using likelihood ratio test); All parameters are significant; standard errors are shown in parentheses; FFP, frost free period; AHM, annual heat moisture; SHM, summer heat moisture; MCMT, mean coldest month temperature; $\sigma^2 = \sigma_v^2+\sigma_u^2$; $\gamma = \sigma_u^2/(\sigma_v^2+\sigma_u^2)$; AIC, Akaike's information criterion; P-values of likelihood ratio test [1]between basic model and model A, [2]between model A and model B, and [3]between model B and model C. Sample sizes and data ranges for each model are shown in Table 2.2.

FFP, AHM, SHM, and MCMT were significant in models as indicated in Table 2.4 and improved goodness of fit over the basic models for the static self-thinning line. According to the likelihood ratio test and the comparison of AIC values, model C was the best model and included FFP, SHM, and MCMT with the intercept of the self-thinning boundary line decreasing with increasing FFP and increasing with increases in SHM and MCMT. In addition, the slope increased with increasing FFP and decreased with increasing SHM and MCMT. Figure 2.3 illustrates the effects of the three climate variables included in model C. Effects of climate variables on both the intercept and slope of the static lines lead to different effects on maximum densities depending on tree size.

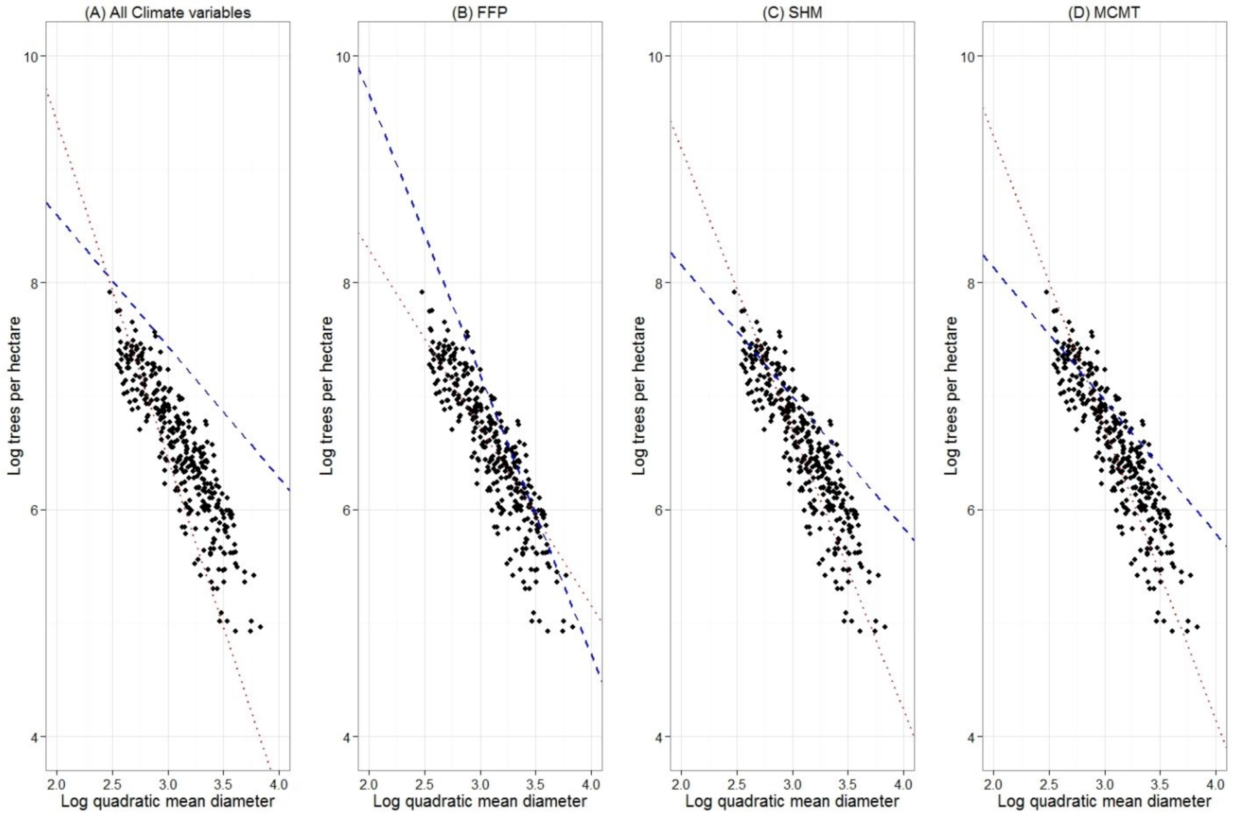


Figure 2.3 The scatter plots for the best model C of the static self-thinning line with climate variables. The blue dashed line indicates the minimum value for each climate variable and the red dotted line indicates the maximum value for each climate variable. Panel A includes all climate variables, panel B includes FFP (frost free period), panel C includes SHM (summer heat moisture), and panel D includes MCMT (mean coldest month temperature). See Table 2.4 for parameter estimates.

2.3.2 Dynamic self-thinning lines for trembling aspen

Dynamic thinning lines can represent behavior of individual stands using repeated measurements over time. A linear mixed-effects model was used to account for the serial correlation among observations in this study (Vanderschaaf, 2010). This model is also suitable to examining the effects of environmental differences on self-thinning lines. The resulting average dynamic self-thinning line had an intercept value of 11.680 and a slope of -1.644. Slope values for individual stands ranged from -1.851 to -1.437 and intercept values ranged from 11.046 to 12.315. In addition, the likelihood ratio test indicated that the random effect of the linear mixed-effects model was significant (p-value < 0.001). The slope for the fixed effects portion of the model was not significantly different from the Reineke's rule (-1.605) and the slope value obtained for the static self-thinning line (-1.799) (Figure 2.4 (A)). However, comparing the two lines could be problematic because of differences between the methods used to develop the two self-thinning lines. For this reason, a static thinning line was developed using 46 plots located in the areas for the 26 plots (Figure 2.4 (B)), and the static line was compared with the static self-thinning line from 344 plots to examine the effect of regional difference on the static thinning line. The resulting static self-thinning line (46 plots) has a slope value of -1.636 and an intercept value of 11.932, and these values were not significantly different from the values of the dynamic line (slope: p-value = 0.478, intercept: p-value = 0.230) and the static line from 344 plots (slope: p-value = 0.141, intercept: p-value = 0.146).

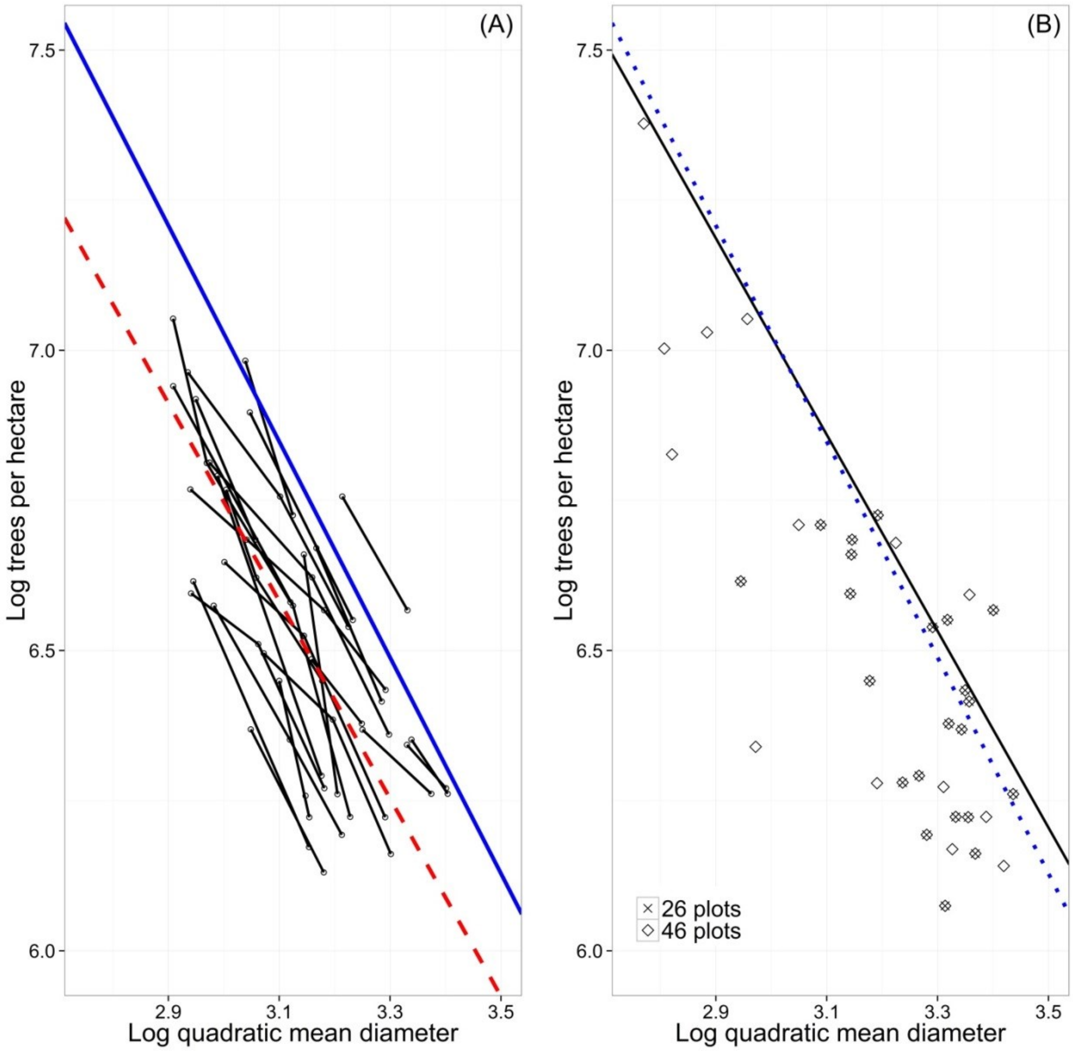


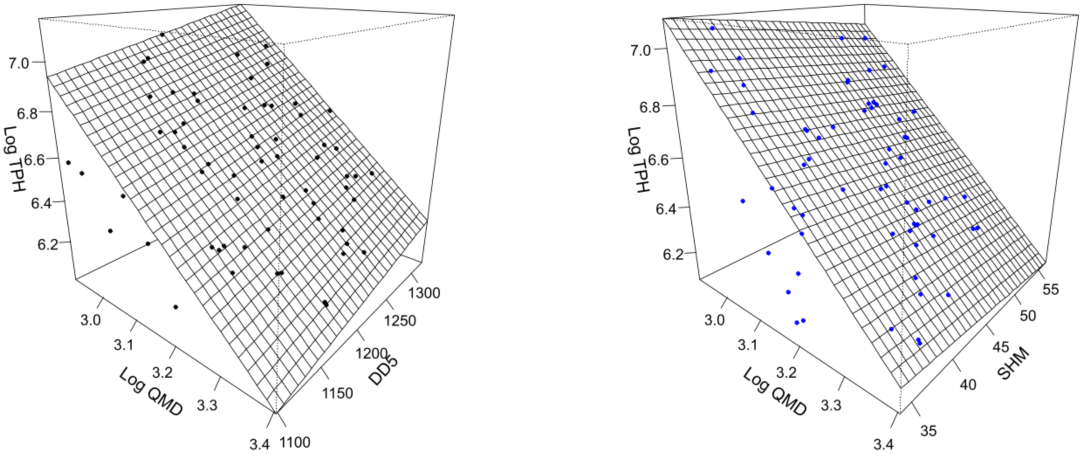
Figure 2.4 (A) Dynamic self-thinning lines for the 26 individual plots used in this analysis shown with the static self-thinning boundary line (blue solid line) and the average dynamic self-thinning line (red dashed line) fit without climate variables. The average dynamic thinning line is described by the equation: ln(TPH) = 11.680 - 1.644×ln(QMD). (B) The static self-thinning line estimated by 46 plots located in same areas with 26 plots (black solid line) and the static self-thinning line estimated by 344 plots (blue dotted line). The static line (black solid line) is described by the equation: ln(TPH) = 11.932 - 1.636×ln(QMD).

Several climatic variables were found to be significant when included in the analysis of the dynamic self-thinning line. The intercept of the dynamic self-thinning line was positively influenced by DD5 and MAT, and negatively influenced by SHM, AHM, and MCMT (Table 2.5). Although there is no interaction term influencing the slope, the slope value in model B differs from the basic model (Table 2.5). Among the models evaluated, best performance was achieved when DD5 and SHM are included in the model (Model B). Model B, which included DD5 and SHM, was considered to be the best model according to the lowest AIC and the likelihood ratio test. Inclusion of three climate variables resulted in increases in AIC compared to Model B. Figure 2.5a illustrates outcomes from model B and indicates that stockability (maximum density at any given tree size) increases as DD5 increases while Figure 2.5b indicates decreasing stockability with increasing SHM.

Table 2.5 Parameters estimated for the average dynamic self-thinning line fit using linear mixed-effects model and Equations 2.3 and 2.4 without and with covariates. A is the best model with one climate variable, B is the best model with two climate variables, and C is the best model with three climate variables.

Variables	Models	σ_0	σ_1	AICc
Basic model	ln(TPH) = 11.680 - 1.644×ln(QMD) (0.318) (0.103)	0.366	0.158	-69.74
(A) DD5	ln(TPH) = 10.622* - 1.821×ln(QMD) + 0.001×DD5 (0.391) (0.105) (0.000)	0.620	0.243	-82.08 ($p<0.001$)[1]
(B) DD5 SHM	ln(TPH) = 11.498 - 1.884*×ln(QMD) + 0.001×DD5 (0.502) (0.101) (0.0003) - 0.004×SHM (0.002)	0.659	0.249	-86.24 ($p=0.008$)[2]
(C) MAT AHM MCMT	ln(TPH) = 12.430* - 1.957×ln(QMD) + 0.165×MAT (0.354) (0.131) (0.035) - 0.015×AHM - 0.016×MCMT (0.006) (0.006)	0.646	0.250	-81.56 ($p=0.177$)[3]

*Significantly different from the intercept or slope value of the basic model (11.680 or -1.644) at alpha = 0.05 (using likelihood ratio test); All parameters are significant; standard errors are shown in parentheses; DD5, degree-days above 5 ˚C; SHM, summer heat moisture; MAT, mean annual temperature; AHM, annual heat moisture; MCMT, mean coldest month temperature; σ_0, σ_1, standard deviations of random effects of intercept and slope; AICc, corrected AIC (Akaike's information criterion); P-values of likelihood ratio test [1]between basic model and model A, [2]between model A and model B, and [3]between model B and model C. Sample sizes and data ranges for each model are shown in Table 2.2.



(A) DD5

(B) SHM

Figure 2.5 The overall (average) dynamic self-thinning line for trembling aspen with (A) degree-days above 5 ˚C (DD5) and (B) summer heat moisture (SHM). See Table 2.5 for parameter estimates.

2.4 Discussion

2.4.1 The static self-thinning line and effects of climate

The self-thinning boundary line represents the ecological limit on the number of trees that can be supported in stands of a certain average size. In this study, the static maximum size-density boundary line was developed for pure aspen stands, and effects of climate variables were examined (seasonal or annual temperature and precipitation) on the static boundary line using stochastic frontier function. The static boundary line had a slope that was steeper than -1.605. These aspen stands had a steeper slope than white spruce dominated stands and a shallower slope than mixed species stands examined by Reyes-Hernandez et al. (2013) in boreal forests.

The intercept of the static self-thinning line was influenced by climate variables associated with evapotranspiration and water balance. Increases in frost free period (FFP) and mean coldest month temperature (MCMT) are associated with warmer conditions. Longer frost free period and an associated longer growing season would increase the time over which stands are exposed to high temperatures and drought. Warmer winter temperatures and increasing annual temperatures could also lead to increases in potential evapotranspiration (Ramírez and Finnerty, 1996; Van Mantgem et al., 2009; Abtew and Melesse, 2013; Williams et al., 2013). Because of the climate effects, stands with a longer FFP have lower densities at particular tree sizes when ln(QMD) is below 3.5 (approximately 33 cm DBH), and Figure 2.3b is showing that high density stands are more affected by FFP than low density stands. Longer frost free period increases tree growth and associated competition, and self-thinning is more activated in crowded stands as tree size increases. MCMT also shows a similar trend with warmer conditions when ln(QMD) is above 2.7 (approximately 15 cm DBH) because warmer winter can accelerate dryness in the growing season. The drier condition caused by warmer winter makes larger trees more vulnerable (Figure 2.3 (D)).

Summer heat moisture (SHM=MWMT/MSP) also influenced the static maximum size-density relationship for these aspen stands. Increases in SHM indicate decreasing growing season moisture availability and are associated with lower densities for stands with ln(QMD) above 2.7 (approximately 15 cm DBH). The result is consistent with previous studies (Hogg et al., 2013; Worrall et al., 2013) where moisture balance has been identified as an important factor influencing aspen growth and mortality. However, Weiskittel et al. (2009) found that a dryness index positively influenced the intercept of the self-thinning boundary line for red alder. In

Weiskittel et al. (2009), study sites were located in humid oceanic areas, and since red alder is often associated with moist to wet lower slope positions, increasing dryness index (DD5/MAP) might increase stockability through reducing the duration of saturated soil conditions or through increases in temperature and solar radiation. The differences between studies highlight the need to consider effects of species, site and the range of climatic conditions included in the analysis of self-thinning relationships. Furthermore, Figure 2.3c indicates that larger trees are more vulnerable to dryness compared to small trees (Bennett et al., 2015). In general, lager trees are taller and older, so they suffer more than small trees during drought because of hydraulic resistance, and declining bigger trees are more likely to succumb to secondary attacks from insects and diseases (Worrall et al., 2013; Bennett et al., 2015).

Results from my study indicate significant effects of climate on both the slope and intercept of the static self-thinning line. Increases in frost free period are associated with reductions in the intercept and a shallower slope while increases in the ratio of summer temperature to precipitation (SHM) and mean coldest month temperature (MCMT) are associated with an increase in the intercept and a steeper slope across the region covered by the data. This supports the need for either including climate in these models, or developing static self-thinning lines for smaller regions.

2.4.2 The dynamic self-thinning lines and the differences from the static thinning line

My results show that the dynamic self-thinning line can vary below the static boundary line due to effects of climate. Other studies suggest that age, site quality and other factors may also influence the position of dynamic self-thinning lines (Weller, 1990; VanderSchaaf and Burkhart, 2007). In this study, the average slope for the dynamic lines does not differ from the slope values of Reineke (-1.605) and the static line (-1.799). A local static line was also developed for the second static line, using 46 plots located in the same area as the dynamic thinning lines. The resulting local static thinning line has similar slope and intercept values to the static self-thinning line from 344 plots.

Tracking the behavior of dynamic self-thinning lines for individual stands can provide insights into factors influencing maximum size-density relationships. Results from application of a mixed effects model indicate that degree-days above 5 ˚C (DD5) and summer heat moisture (SHM) have significant effects on the slope of the dynamic thinning line. Similar to results for the general static thinning line (from 344 plots), SHM has a negative influence on the dynamic thinning line. With regard to degree-days above 5 ˚C, results for the dynamic line differ from those obtained for the general static thinning line. While temperature negatively influences the static thinning line, growing degree-days positively influences the dynamic thinning lines. Climate data indicate that the 26 plots used to develop the dynamic thinning line had narrower ranges in temperature, precipitation and SHM than was the case for the 344 plots used for the static thinning line. Table 2.3 shows that mean precipitation is higher for the data used in fitting the dynamic line than was the case for the static thinning line and the minimum CMI is above 0. Thus, more growing degree-days in the 26 plots played a role in encouraging trees to grow more and led aspen stands to have larger tree sizes than stands with cooler conditions (Figure 2.5).

Due to limited data, dynamic self-thinning lines could only be fit for a portion of the study area that had a more limited range in growing conditions and drought stress than was the case for the static relationships. Nevertheless, DD5 and SHM were found to influence the slope of the dynamic line. The dynamic lines should be explored further when additional re-measurements become available. Influences of soil and site factors and stand productivity (e.g., site index) on dynamic self-thinning lines should also be examined in future studies.

2.4.3 Potential issues related to the maximum size-density relationship

Continuing increases in mean temperature and drought stress are predicted in western Canada's boreal forest (Gray et al., 2011; Price et al., 2013). My results indicate that increasing temperatures, frost free period and drought stress are likely to lead to reductions in maximum densities that stands in this region can support. This is consistent with results from other studies indicating that climate change is increasing aspen mortality (Hogg et al., 2008), and causing increases in tree mortality in many other parts of the world (Allen et al. 2010).

In addition to declines in stand density, warming temperatures and drought stress can increase the vulnerability of trees to secondary factors, such as insects, diseases, and forest fires (Hogg et al., 2002; Frey et al., 2004; Rouault et al., 2006). For example, forest tent caterpillar (*Malacosoma disstria* Hübner), which is a major defoliator of trembling aspen could be associated with mild winters and warm weather during spring and early summer (Cooke and Roland, 2003; Chen et al., 2018). Increases in impacts of this insect are anticipated as a result of climate change, and are expected to result in increased mortality and declines in aspen growth (Hogg et al., 2002; Sturrock et al., 2011; Worrall et al., 2013). Stem decay (*Phellinus tremulae*) is also common in aspen stands (Allen et al., 1996). Since its impact is influenced by environment and host condition, increases in climate induced stresses may lead to increases in decay and stem breakage. Increases in the frequency and size of forest fires are also anticipated as a result of continued warming in this region (Price et al., 2013).

2.5 Conclusions

A static self-thinning boundary line for trembling aspen stands was developed using data from Alberta and Saskatchewan. Frost free period (FFP), winter temperature (MCMT), and summer water availability (SHM) were significant in the model. The model indicates that, in general, declines in maximum stocking occur as temperature and FFP increase.

While the evaluation of dynamic thinning lines was limited by a small sample size, results were consistent with those for static lines. In addition, the dynamic self-thinning models show decreasing maximum densities with increasing summer drought stress. Results also indicate that the dynamic self-thinning line can better reflect effects of environmental factors. Through refined application with larger datasets and modeling at the stand level, development of dynamic self-thinning lines will be warranted.

Chapter 3: Effects of stand age, stand structure and other factors on survival probability of aspen

3.1 Introduction

Tree mortality facilitates changes in stand composition and structure by providing opportunities for trees to establish and grow in the gaps created by death of individuals (Franklin et al., 1987). Understanding the causes of tree mortality contributes to an understanding of stand dynamics and is important to sustainable forest management.

Aspen generally regenerates in large numbers, grows rapidly in early stages, and self-thinning occurs due to intraspecific competition (Peterson and Peterson, 1992). A high incidence of decay, stem breakage and tree death are often observed when aspen stands exceed 80 years of age (Luo and Chen, 2011) and is widely referred to as stand breakup. Stand breakup and gap formation in old stands are due to mortality caused by stem disease fungi, insect damage, and other factors (e.g., drought and windthrow) (Senecal et al., 2004; Franklin and Van Pelt, 2004; Frey et al., 2004; Zegler et al., 2012).

The onset of stand breakup is highly variable and appears to be influenced by stand age, climate, stand structure, species composition, site conditions, and other factors (Peterson and Peterson, 1992; Senecal et al., 2004; Frey et al., 2004; Hill et al., 2005; Luo and Chen, 2011; Bell et al., 2014). Pothier et al. (2004) identified an important increase of tree mortality and wood decay at around age 60 in Quebec stands. Hogg et al. (2008) and Michaelian et al. (2011) showed that aspen mortality and dieback were closely related to drought severity in western Canada. Bell et al. (2014) predicted that forest succession and conversion to conifer forests could be accelerated by warming and drying of aspen forests. However, they concluded that the pattern of aspen mortality is better explained by forest stand structure, productivity, and age than climate. Luo and Chen (2013) found that young forests had higher sensitivity to warming and drought than old forests due to higher intensities of competition for resources. With regard to disease and insect attack, the intensity and frequency of outbreaks could increase with climate change, due to increases in drought and heat stress (Boland et al., 2004; Sturrock et al., 2011; Bell et al., 2015). Since the effects of climate change on tree survival may vary according to region, forest age, composition, structure, site condition, and other factors, an understanding on how these factors interact is potentially useful in predicting mortality and subsequent changes.

Although aspen is frequently seen in even-aged stands with simple canopy structure that develop after stand replacing disturbances, aspen stands can develop age and size structure if allowed to reach ages in excess of 80 years (Cumming et al., 2000; Pothier et al., 2004; Kurzel et al., 2007; Binkley, 2008; LeBlanc, 2014; Binkley et al., 2014; Bergeron et al., 2014). In aging stands, mortality and the opening of the canopy provide opportunities for aspen regeneration in the understory and the development of stands with multiple cohorts. The existence of multiple cohorts, rather than universally assuming that aspen stands are even-aged should be considered in estimating survival probability since age and stand structure are important determinants of survival probability (Luo and Chen, 2011; Reyes-Hernández and Comeau, 2014; Cortini et al., 2017). In this study, the objectives were to: 1) determine survival probability of aspen in relation to stand age and stand structure; and 2) examine effects of climate, stand factors, and tree age on survival probability.

3.2 Material and methods

3.2.1 Study area and sites

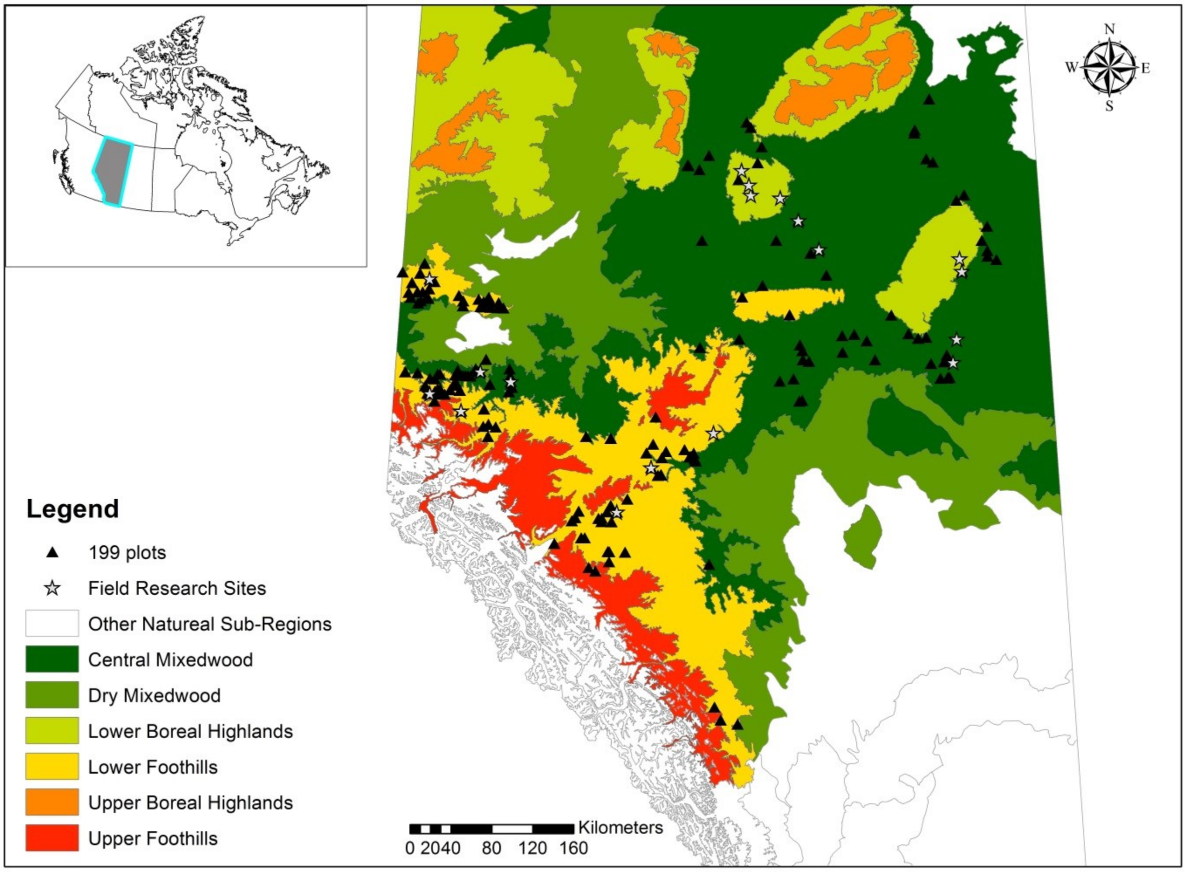


Figure 3.1 Study areas and field research sites used for this study (Triangles indicate locations of the 199 permanent sample plots used for this study while stars indicate the locations of the 18 permanent sample plots selected for detailed sampling to evaluate age class structure). Natural subregions (Downing and Pettapiece, 2006) are shown for reference and to illustrate the distribution of research sites across climatic conditions.

One hundred ninety nine permanent sample plots and 46785 trees (alive: 43725, dead: 3060) measured between 1962 and 2014 across Alberta were selected for the study (Figure 3.1). These plots were re-measured permanent sample plots (PSP) established and measured by the Alberta government and forestry companies, and they had 2 to 8 measurements of DBH and condition (live vs dead) for all trees in each plot. Plots established in pure aspen (i.e., proportion of aspen basal area higher than 0.8) or aspen dominated stands (i.e., proportion of aspen basal area higher than 0.5) were selected. Plot sizes varied between 0.006 ha and 0.2 ha and contained smaller subplots for measuring saplings and regeneration. For this study, trees less than 4 cm DBH were removed from the analysis because small trees were not measured in all plots. Most of the plots were located in the Central Mixedwood (22615 trees in 87 plots, ranged from 0.006 ha to 0.2 ha and measured between 1968 and 2014) and Lower Foothills (22633 trees in 103 plots, ranged from 0.006 ha to 0.2 ha and measured between 1962 and 2012) natural Subregions with some located in the Dry Mixedwood (547 trees in 5 plots, 0.08 ha and measured between 1984 and 2012) and Lower Boreal Highland (990 trees in 4 plots, 0.1 ha and measured between 1988 and 2013) subregions.

The largest natural subregion of Alberta is the Central Mixedwood which has short, warm summers and long, cold winters (mean annual temperature (MAT): 0.2 ˚C, mean annual precipitation (MAP): 478 mm, Downing and Pettapiece, 2006). The Dry Mixedwood subregion is warmer and drier (MAT: 1.1 ˚C, MAP: 461 mm) than the Central Mixedwood, and the Lower Boreal Highland subregion is colder and wetter (MAT: -1.0 ˚C, MAP: 495 mm, Downing and Pettapiece, 2006). The Lower Foothills subregion is warmer and wetter than the Central and Dry Mixedwood natural subregions, and has a mean annual temperature (MAT) of 1.8 ˚C and mean annual precipitation (MAP) of 632 mm (Wiken, 1986; Downing and Pettapiece, 2006). Gray Luvisolic soils prevail and aspen stands are common in these four natural subregions (Wiken, 1986; Downing and Pettapiece, 2006).

3.2.2 Increment core analysis and tree size diversity

Increment cores were collected in 2016 from trees in the buffer zones of 18 permanent sample plots randomly selected to confirm stand ages and determine age structure. Coring was conducted outside of each of these selected PSP’s within 30 m from the plot edges (the plot buffer area) in order to avoid damaging remeasured trees located within the remeasured PSP’s. 6 plots from the Central and Dry Mixedwood, 6 plots from the Lower Boreal Highlands, and 6 plots from the Lower Foothills with stand ages exceeding 70 years old were randomly selected from the PSP’s available in each subregion. Because aspen stands start declining at around age 60 and allow aspen regeneration, we collected cores in older stands to investigate age structure resulting from aging. Increment cores were collected from 5 or more trees in each crown class (dominant, codominant, and intermediate classes) for each plot. In addition, 5 of the largest diameter (DBH) trees were selected for coring. At the time of coring, DBH, height, crown class, and condition were measured and recorded for each tree.

Tree rings were counted using WinDENDRO software ver. 2017a (Regent Instruments Canada Inc., 2017), and a microscope was also used to confirm the WinDENDRO ring counts. 435 cores (81.9%) were available to directly determine total tree ages and reference data were used to increase the accuracy of tree age determination at each plot. Total age could not be determined for 96 cores due to internal stem decay or core damage and they were removed from the analysis.

Species composition, management activities, disturbance history, and other factors may cause differences in tree size diversity (Ozdemir et al., 2008). Age diversity could be represented by the diameter class distribution in a stand because tree size increases with tree age and measuring tree size is more efficient than determining tree age in stands (Leak, 1985; Lähde et al., 1999). In addition, use of tree size overcomes problems with determining tree and stand age when internal stem decay is common in the largest and oldest trees. To examine whether aging aspen stands have age diversity (age structure), we investigated the relationship between stand age, age variation, and tree size diversity using results from core analysis and field research.

Tree size diversity was calculated using Shannon's index (Shannon, 1948) which is widely used in forestry and there is no weight on a specific group (Varga et al., 2005; Lexerød and Eid, 2006). GINI coefficient (Gini, 1921) was also tested but found it explained less variation in age diversity than the Shannon's Index. Furthermore, Shannon's index can calculate tree size diversity based on diameter classes (5 cm DBH width) considering age classes and structural layers, while the Gini coefficient considers only individual tree class. Basal area was calculated for each 5 cm diameter class to reflect the change of tree size and the proportion of stand basal area in each diameter class was used in analysis. The equation for Shannon's index is:

$$\text{Tree size diversity (TSD)} = -\sum_{i=1}^{N} p_i \ln(p_i), \qquad \textbf{(3.1)}$$

where N is the total number of diameter classes and p_i is the proportion of stand basal area in the ith diameter class.

3.2.3 Potential predictor variables

Diameter at breast height (DBH) is closely related to growth rate, with large trees being more competitive than smaller trees (Monserud and Sterba, 1999). At the same time, as trees become larger the probability of death related to senescence, disease or insect injury may increase. To investigate the effects of tree size and age on survival probability, DBH and squared DBH were both included in the models as suggested by previous studies in this region (Yao et al., 2001; Yang et al., 2003; Cortini et al., 2017). While I attempted to estimate ages of all trees in all plots based on relationships between age and DBH developed using data from tree coring, this was not successful due to lack of data for young trees.

Competition is a significant factor influencing tree survival. Sum of the basal areas of trees larger than a target tree is a widely used competition index (Monserud and Sterba, 1999; Temesgen and Mitchell, 2005; Reyes-Hernández and Comeau, 2014; Cortini et al., 2017). In this study, only deciduous basal area larger (i.e., sum of the basal areas of deciduous trees larger than a target tree, DBL) was used for the analysis because all plots are aspen dominated stands (91.5% of plots are pure stands (>0.8)). While annual DBH increment is recognized as an indicator of tree vigor (Buchanan, 1983; Yao et al., 2001) and is included in many mortality models (Yao et al., 2001; Yang et al., 2003; Reyes-Hernández and Comeau, 2014), it has not been included in models in this study because it is generally strongly correlated with competition and tree diameter, which are already included in the models.

Stand age (years after stand establishment or years determined by felling and sectioning trees within the plot) is associated with vigor of trees in a stand. As a stand gets older, survival rate of trees decreases due to senescence. Because older stands generally have vertical layers and multiple cohorts (Cumming et al., 2000; Franklin and Van Pelt, 2004; Kurzel et al., 2007) and mortality of overtopped trees is expected to be higher than for dominant trees, stand structure (e.g., tree size diversity or age diversity) is also considered a predictor variable. However, stand age and tree size diversity were correlated and since tree size diversity performed better in logistic models, we excluded stand age in final models. Table 3.1 summarizes stand characteristics for each of the 3 age classes (young, mature, and old stands) examined in this study as well as for the entire dataset.

Table 3.1 A summary of tree and stand characteristics for PSP's in each of the three age groups and for all plots combined.

Age group	Young stands (age ≤ 60): 75 plots, 17180 trees (alive: 16478, dead: 702)						
	DBH (cm)	DBL (m^2/ha)	HT (m)	Age	TSD	BA (m^2/ha)	L
Mean	13.15	14.37	15.34	43.06	1.04	20.86	7.33
SD	5.40	9.25	4.57	12.27	0.35	8.66	4.06
Max.	47.90	51.98	30.50	60.00	1.97	42.02	31.00
Min.	4.09	0.00	3.50	9.00	0.00	0.14	2.00
Age group	Mature stands (60 <age ≤ 100): 127 plots, 19810 trees (alive: 18217, dead: 1593)						
	DBH (cm)	DBL (m^2/ha)	HT (m)	Age	TSD	BA (m^2/ha)	L
Mean	21.58	19.92	21.46	78.24	1.41	27.79	10.41
SD	7.22	10.60	3.96	11.58	0.23	7.82	3.81
Max.	65.90	65.90	35.09	100.00	2.01	66.52	25.00
Min.	4.40	0.00	1.70	60.40	0.00	0.35	3.00
Age group	Old stands (age > 100): 74 plots, 6436 trees (alive: 6159, dead: 277)						
	DBH (cm)	DBL (m^2/ha)	HT (m)	Age	TSD	BA (m^2/ha)	L
Mean	28.31	21.85	23.71	112.98	1.53	32.53	6.42
SD	8.96	11.67	4.60	10.21	0.23	8.91	2.80
Max.	63.40	56.57	36.50	167.00	2.15	55.01	15.00
Min.	4.10	0.00	2.22	100.57	0.00	0.41	1.00
Age group	All stands : 199 plots, 43426 trees (alive: 40854, dead: 2572)						
	DBH (cm)	DBL (m^2/ha)	HT (m)	Age	TSD	BA (m^2/ha)	L
Mean	19.24	18.01	19.37	69.47	1.28	25.75	8.66
SD	8.75	10.69	5.46	26.98	0.35	9.35	4.16
Max.	65.90	65.90	36.50	167.00	2.15	66.52	31.00
Min.	4.09	0.00	1.70	9.00	0.00	0.14	1.00

DBH, diameter at breast height; DBL, deciduous basal area larger; HT, tree height; Age, stand age (years after stand establishment); TSD, tree size diversity; BA, basal area of aspen at each plot; L, measurement interval length (year).

Environmental variables, such as site condition and climate, are also important to tree growth and survival. Because better sites encourage tree competition due to faster growth, it can lead to increases in tree mortality (Yao et al., 2001; Weiskittel et al., 2011). In this study I was only able to investigate the effect of climate on tree survival since consistent site information was not available for these plots. ClimateWNA (Hamann et al., 2013) was used to generate average climatic conditions during each measurement interval for each PSP. Mean annual temperature (MAT), degree days above 5 ˚C (DD5), and frost free period (FFP) were used to test the effect of the temperature variation on tree survival. Mean annual precipitation (MAP), mean summer precipitation (MSP), annual heat moisture (AMH), summer heat moisture (SHM), and climate moisture index (CMI) were used to examine the influence of water availability and, mean warmest month temperature (MWMT) and mean coldest month temperature (MCMT) were also applied to survival models to evaluate the effect of climatic extremes on tree survival. Climate moisture index was calculated using monthly temperatures, annual precipitation, and elevation for each plot (Hogg, 1997).

Table 3.2 Means and ranges in climate variables for all permanent sample plots (199 plots) used in the analysis.

Variables	MAT (˚C)	DD5	FFP	MAP (mm)	MSP (mm)	AHM	SHM	CMI (cm)	MWMT (˚C)	MCMT (˚C)
Mean	1.79	1215.43	102.76	534.19	366.16	22.72	45.11	9.94	15.51	-15.59
SD	0.84	79.39	8.01	74.04	58.03	2.48	9.39	7.64	0.76	2.99
Max.	3.46	1499.20	127.50	689.60	498.50	31.82	79.24	26.75	17.99	-6.52
Min.	-0.96	1003.12	70.00	364.80	233.40	18.00	29.26	-11.03	13.59	-23.43

MAT, mean annual temperature; DD5, growing degree days above 5 ˚C; FFP, frost free period; MAP, mean annual precipitation; MSP, mean summer precipitation; AHM, annual heat moisture ((MAT+10)/(MAP/1000)); SHM, summer heat moisture ((MWMT)/(MSP/1000)); CMI, climate moisture index; MWMT, mean warmest month temperature; MCMT, mean coldest month temperature.

3.2.4 Model development and data analysis

The relationship between stand age and tree size diversity was examined using collected field data, results from core analysis, and PSP data. For the analysis, a linear or nonlinear mixed effects model was used to consider effects of natural subregions (as a random effect).

To investigate the effects of potential predictor variables on survival probability depending on stand developmental stages (i.e., stand age), a categorical variable indicating three age groups (i.e., young (less than age 60), mature (from age 60 to 100), and old (higher than age 100) stands) was used. These age classes were selected based on published literature which indicates that aspen stands start declining after they reach maximum annual productivity at around age 60, and most of original trees start dying and being replaced by regenerating aspen or shrubs above age 100 (Peterson and Peterson, 1992; Mueggler, 1994; Bergeron et al., 2014).

Models were developed both with the categorical age-class variable and without the categorical variable. All measurements (2 to 8) were used for the model development. Tree size (DBH), deciduous basal area larger (DBL), tree size diversity (TSD), and climate from PSP dataset were selected as predictor variables in this analysis. The categorical variable (AG, three age groups) was included in the model (Equation 3.4) as an interaction term with other predictor variables. To evaluate the effect of the interaction term, a survival model without the interaction term was also developed (Equation 3.3). Logistic regression was used to deal with survival probability of individual tree using the function glm (R Core Team, 2017). The logistic models are:

$$\text{Ps (logistic)} = [\exp(c)/(1+\exp(c))]^{L}, \quad \textbf{(3.2)}$$

$$c = \beta_0 + \beta_1\times\text{DBH} + \beta_2\times\text{DBH}^2 + \beta_3\times\text{DBL} + \beta_4\times\text{TSD} + \beta_5\times\text{Climate}, \quad \textbf{(3.3)}$$

$$c = \beta_0 + \beta_1 \times DBH + \beta_2 \times DBH^2 + \beta_3 \times DBL + \beta_4 \times TSD + \beta_5 \times Climate + \beta_6 \times AG$$

$$+ \beta_7 \times DBH \times AG + \beta_8 \times DBH^2 \times AG + \beta_9 \times DBL \times AG + \beta_{10} \times TSD \times AG + \beta_{11} \times Climate \times AG, \quad \mathbf{(3.4)}$$

where Ps is survival probability, L is measurement interval length, c is natural log odds and the explanatory variable of a linear function, β_0 is the intercept, β_1 is the coefficient of DBH, β_2 is the coefficient of DBH^2, β_3 is the coefficient of DBL, β_4 is the coefficient of TSD, β_5 is the coefficient of climate, and β_6 is the coefficient of age group. In addition, β_7 - β_{11} are coefficients for the interaction terms between predictor variables and age group.

Mixed effects logistic regression was used to examine whether including natural subregions as a random effect can improve the model fit using the function glmer (Bates et al., 2015). The correlation structure in the mixed effects models was tested using the function glmmPQL (Venables and Ripley, 2002) because trees nested within plots and plots nested in natural subregions were repeatedly measured. The logistic random effects models are:

$$c = (\beta_0 + u_0) + \beta_1 \times DBH + \beta_2 \times DBH^2 + \beta_3 \times DBL + \beta_4 \times TSD + \beta_5 \times Climate, \quad \mathbf{(3.5)}$$

$$c = (\beta_0 + u_0) + \beta_1 \times DBH + \beta_2 \times DBH^2 + \beta_3 \times DBL + \beta_4 \times TSD + \beta_5 \times Climate + \beta_6 \times AG$$

$$+ \beta_7 \times DBH \times AG + \beta_8 \times DBH^2 \times AG + \beta_9 \times DBL \times AG + \beta_{10} \times TSD \times AG + \beta_{11} \times Climate \times AG, \quad \mathbf{(3.6)}$$

where u_0 is used to represent the random intercept (natural subregion) and other coefficients are same as Equation 3.4.

Akaike's information criterion (AIC) was used to compare models that have the same response variable, but different sets of independent variables. A model with lower AIC has better goodness of fit than others (Liu, 2016). Area under receiver operating characteristic (ROC) curve (AUC) was calculated to assess the predictive capacity of the model developed. AUC values higher than 0.8 are excellent and a value between 0.7 and 0.8 is acceptable (Hosmer and Lemeshow, 2000). Parameter estimation for the logistic/mixed effects logistic regression models and calculations for AUC values were conducted using R software, version 3.4.1 (R Core Team, 2017).

3.3 Results

3.3.1 Tree age and stand structure based on field research and core analysis

Based on analysis of increment cores from 18 plots and stand ages determined from the oldest tree age in each plot, positive relationships between age variation, stand age, and tree size diversity were evident (Figure 3.2). Results indicate that old stands have higher variation of tree ages and tree size diversity than younger stands.

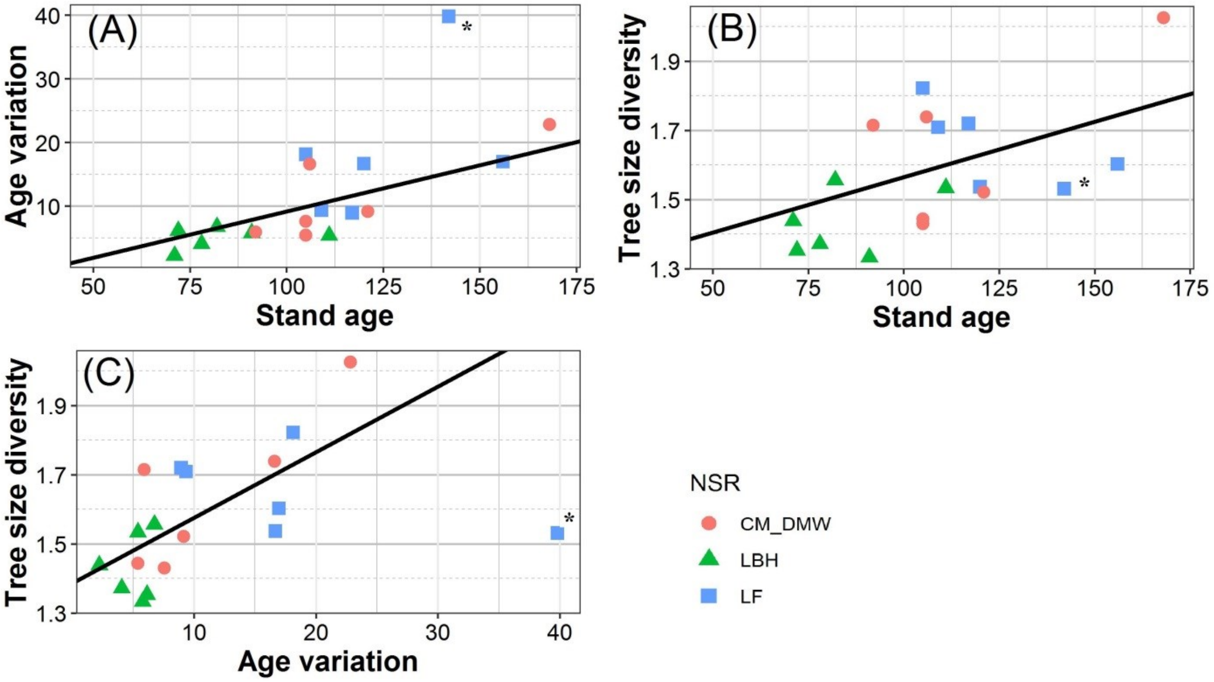


Figure 3.2 (A) Relationship between stand age (oldest tree age) and standard deviation of age (Age variation = -5.397 + 0.145×Stand age, R^2 = 0.47), relationships between tree size diversity and (B) stand age (TSD = 1.245 + 0.003×Stand age, R^2 = 0.23) or (C) standard deviation of age (TSD = 1.385 + 0.019×Age variation, R^2 = 0.46) for the 18 sampled plots. One outlier (*) departing from the line was removed from the analysis. R^2 is the marginal r-squared value associated with fixed effects. A linear mixed effects model was used to consider 3 natural subregions as random effects. All regression lines are significant at α=0.05 level. NSR refers to natural sub-regions (CM_DMW, Central and Dry Mixedwood; LBH, Lower Boreal Highland; LF, Lower Foothills).

3.3.2 Tree status and size diversity for PSP data

Tree status in each diameter class changed with age group (Table 3.3 and Figure 3.3) showing a shift in the distribution of dead tree proportion with increasing DBH and age for the PSP dataset (removed trees less than 4 cm diameter). In the old age group, there is also an increase in the number of young trees in the 4-5 cm DBH class compared to the mature age group, indicating increased numbers of surviving regenerated trees.

Table 3.3 Tree status in each diameter class and proportion of dead trees among three age groups (Prop. represents proportion of trees in the stand that are dead for each DBH class).

DBH class	Young stands (age≤60)			Mature stands (60<age≤100)			Old stands (age>100)		
	Alive	Dead	Prop.	Alive	Dead	Prop.	Alive	Dead	Prop.
4-5	513	42	0.070	2	1	0.330	38	0	0.000
5-10	3960	317	0.074	360	121	0.252	151	3	0.019
10-15	6941	247	0.034	2825	537	0.160	244	23	0.086
15-20	3387	69	0.020	4711	486	0.094	538	63	0.105
20-25	1155	15	0.013	4771	243	0.048	1093	65	0.056
25-30	368	8	0.021	3149	124	0.038	1483	53	0.035
30-35	94	4	0.041	1519	49	0.031	1294	38	0.029
35-40	43	0	0	610	20	0.032	792	14	0.017
40-45	14	0	0	203	9	0.042	328	9	0.027
45-50	3	0	0	57	3	0.050	123	6	0.047
50-	0	0	0	10	0	0	75	3	0.038
Total	16478	702	0.041	18217	1593	0.080	6159	277	0.043

Alive, alive trees; Dead, dead trees; Prop., proportion of dead trees over all trees.

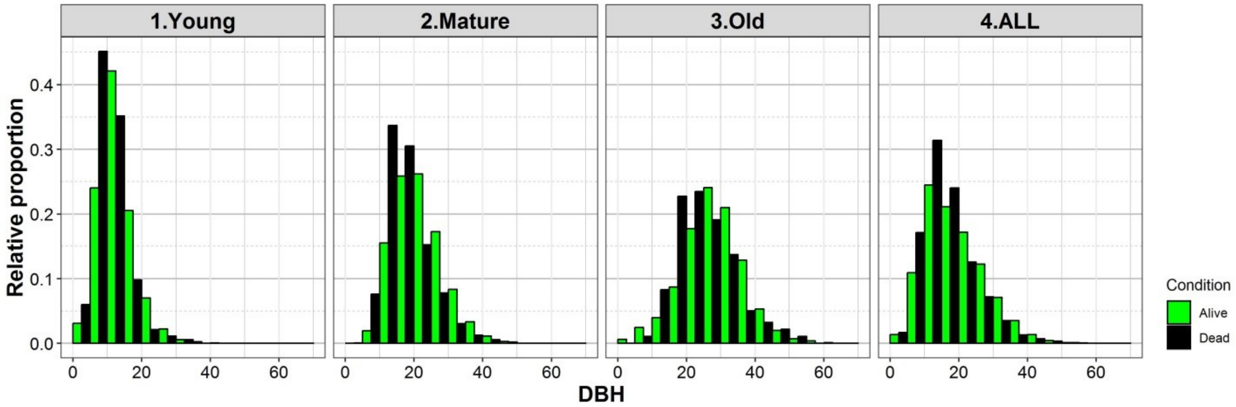


Figure 3.3 Distribution of live and dead trees among age groups (young (≤60), mature (60<age≤100), old (>100), and all age group).

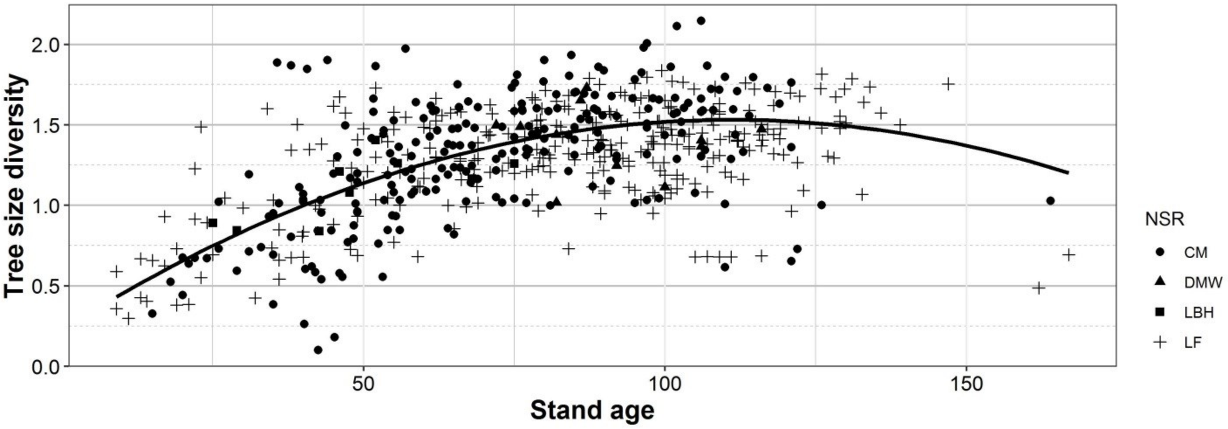


Figure 3.4 A nonlinear regression line showing the relationship between stand age and tree size diversity (Tree size diversity (TSD) = 0.228 + 0.023×Standage - 0.000106×Standage^2). The regression line is significant (α=0.05). A nonlinear mixed effects model was used to consider 4 natural subregions as random effects. NSR refers to natural subregions (CM, Central Mixedwood; DMW, Dry Mixedwood; LBH, Lower Boreal Highland; LF, Lower Foothills).

The general trend for the PSP dataset shown in Figure 3.4 indicates that tree size diversity increases up to about age 110 and decreases after age 120. Most stands from age 70 to age 150 had tree size diversity ranging from 1.0 to 2.0.

3.3.3 Model development for aspen survival probability

Table 3.4 shows effects of including the interaction term indicating age group (i.e., young, mature, and old stands) and natural subregion as random effects. Model 4 developed with the interaction term and random effects of subregion had better goodness of fit than other models tested for this study (Table 3.4).

Table 3.4 Comparison of candidate models based on AIC and AUC values.

Models	Applications	AIC	ΔAIC	AUC
Model 1 (Eq. 3.3)	No interaction term, no random effects $(Survival \sim DBH+DBH^2+DBL+TSD+MAT)$	17392	430	0.841
Model 2 (Eq. 3.4)	Interaction term, no random effects $(Survival \sim DBH+DBH^2+DBL+TSD+MAT+AG$ $+DBH\times AG+DBH^2\times AG+DBL\times AG+TSD\times AG+MAT\times AG)$	16985	23	0.844
Model 3 (Eq. 3.5)	No interaction term, random effects $(Survival \sim DBH+DBH^2+DBL+TSD+MAT+\mathbf{NSR})$	17320	358	0.843
Model 4 (Eq. 3.6)	Interaction term, random effects $(Survival \sim DBH+DBH^2+DBL+TSD+MAT+AG$ $+DBH\times AG+DBH^2\times AG+DBL\times AG+TSD\times AG+MAT\times AG+\mathbf{NSR})$	16962	0	0.846

DBH, diameter at breast height; DBH^2, squared diameter; DBL, deciduous basal area larger; TSD, tree size diversity; MAT, mean annual temperature; ×AG, interaction with age groups (young, mature, and old stands); **NSR**, natural subresions as random effects; AIC: Akaike's Information Criterion; ΔAIC: difference in AIC value compared to the best model in this analysis; AUC, area under ROC curve.

Four survival probability models were developed with selected variables, and the models developed using mean annual temperature (MAT) had better fit than models which used other climate variables from Table 3.2. For model 4, the young age group had a lower DBL coefficient and a higher MAT coefficient than the mature age group. The mature age group had a lower TSD coefficient than other groups, and the old age group had a lower DBH coefficient compared to other groups. When the data were analyzed separately for three age groups, only the parameter of TSD for the old age group was not significant.

Table 3.5 Parameter estimates of model 4 (Equation 3.6) including the interaction term (three age groups) and random effects considering 4 natural subregions.

Variable	Estimate (*Est. for each group*)	Standard error	*p*-value
Intercept	4.1650	0.2853	**0.000***
Young×Mature	0.0057 *(4.1707)*	0.3772	0.989
Young×Old	0.8425 *(5.0075)*	0.7691	0.273
DBH	0.2065	0.0299	**0.000***
DBH^2	-0.0036	0.0010	**0.000***
DBL	-0.0535	0.0047	**0.000***
TSD	-0.6914	0.1377	**0.000***
MAT	-0.6505	0.0552	**0.000***
DBH: Young×Mature	0.0591 *(0.2656)*	0.0347	0.089
DBH: Young×Old	-0.0822 *(0.1243)*	0.0416	**0.048***
DBH^2*: Young×Mature*	-0.00004 *(-0.0037)*	0.0011	0.971
DBH^2*: Young×Old*	0.0018 *(-0.0018)*	0.0011	0.115
DBL: Young×Mature	0.0183 *(-0.0352)*	0.0059	**0.002***
DBL: Young×Old	0.0126 *(-0.0409)*	0.0087	0.148
TSD: Young×Mature	-1.3410 *(-2.0324)*	0.2022	**0.000***
TSD: Young×Old	0.2000 *(-0.4914)*	0.3411	0.558
MAT: Young×Mature	-0.1603 *(-0.8108)*	0.0734	**0.029***
MAT: Young×Old	-0.2040 *(-0.8545)*	0.1317	0.121

DBH, diameter at breast height; DBH^2, squared DBH; DBL, deciduous basal area larger; TSD, tree size diversity; MAT, mean annual temperature; *Est. for each group*, estimate calculated for each variable of each age group; Young, young stands (age≤60); Mature, mature stands (60<age≤100); Old, old stands (age>100); star (*) indicates the statistical significance at α=0.05 level.

Table 3.5 and Figure 3.5 show that each age group has a different survival pattern with DBH. The young and mature age groups show steeper increases in survival probability with increasing DBH for trees smaller than 20 cm diameter than the old age class. The mature age group had lower survival probability than other groups for trees with diameter below 30 cm. The old age group had higher positive effect of DBH on survival probability and maintained higher survival probability than other groups.

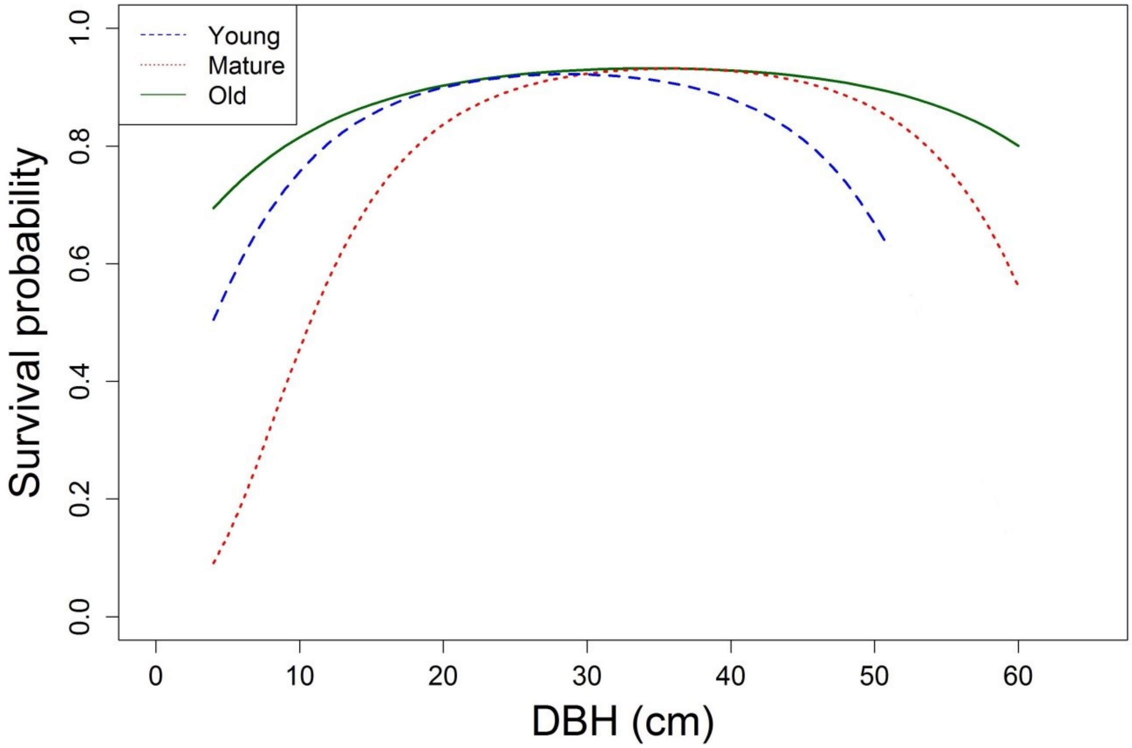
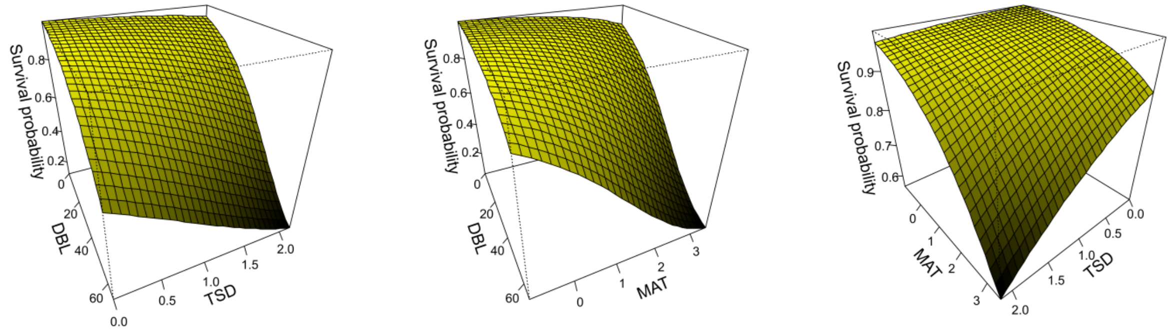


Figure 3.5 Changes in predicted survival probability with diameter (DBH) by age groups (young, blue dashed line; mature, red dotted line; old, dark green solid line) based on the model 4 (Equation 3.6). For these predictions, L was set to 5 years and average values were used for other variables (Table 3.1 and Table 3.2). Parameter values used for each age class were provided in Table 3.5.

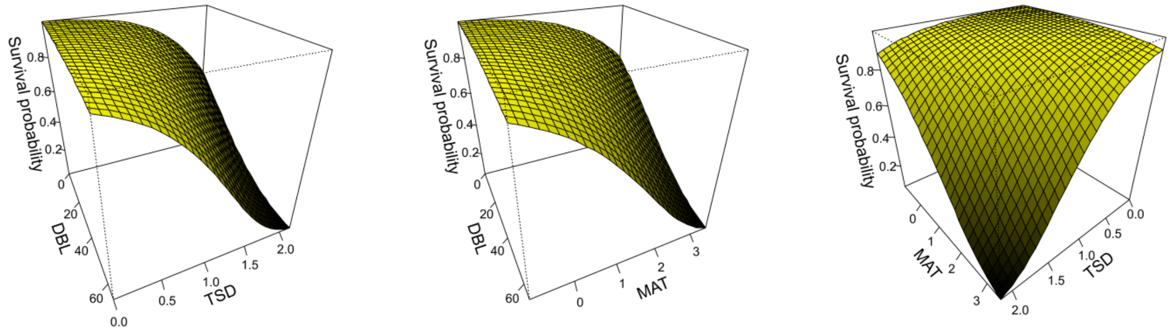
The effect of competition (i.e., deciduous basal area larger (DBL)) on survival was significant for all age groups and the magnitude of the negative influence varied among age groups in model 4 (Table 3.5). In the young age group, competition had a stronger negative influence on survival than in the mature age group. For tree size diversity, negative effects on survival were highest in the mature age group, and the effect was not significant in the old age group. The effect of climate on survival in the mature age group was more strongly negative than in the young age group.

Young stands



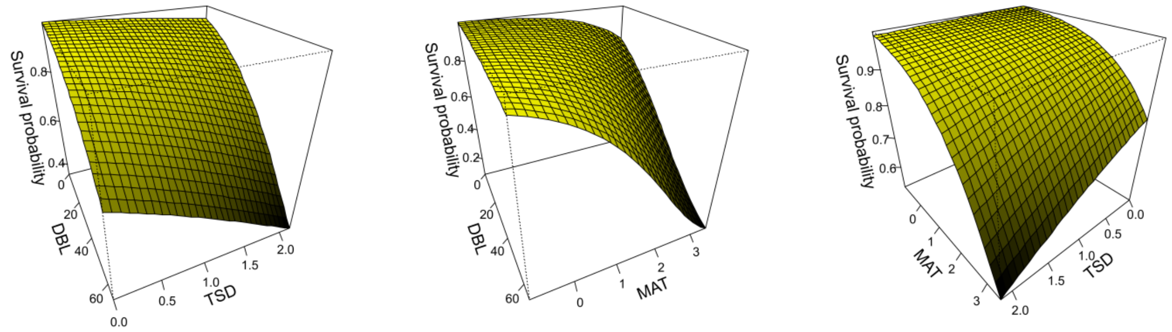
(a) DBL and TSD (b) DBL and MAT (c) TSD and MAT

Mature stands



(d) DBL and TSD (e) DBL and MAT (f) TSD and MAT

Old stands



(g) DBL and TSD (h) DBL and MAT (i) TSD and MAT

Figure 3.6 Relationships among deciduous basal area larger (DBL), tree size diversity (TSD), and mean annual temperature (MAT) by age groups from survival model 4 (Equation 3.6). For these predictions, L was set to 5 years and average values were used for variables (Tables 3.1 and 3.2). Parameter values used for each age class are provided in Table 3.5.

Predicted effects of competition, tree size diversity, and climate are shown in Figure 3.6 to illustrate how the predictor variables behave in each age group and how combinations of variables influence tree survival. The combined effect of DBL and TSD on mortality was weakest in the old stands (Figure 3.6g). The negative influence of MAT and DBL on survival was similar in all stands (Figure 3.6b, e, and h) while the negative influence of MAT and TSD on survival was strongest in the mature stands (Figure 3.6f). Increasing MAT also negatively influenced tree survival at the same DBL or TSD level, especially higher values of them.

3.4 Discussion

Franklin and Van Pelt (2004) stated that mortality changed from competition-based mortality in young stands to agent-based mortality (i.e., insects, diseases, and wind) in old stands. During the early stand developmental stage, large trees are more competitive and show higher survival than small trees while in later stages, intermediate size trees tend to have higher survival probability than larger trees (Harcombe, 1987; Yao et al., 2001; Yao et al., 2001; Luo and Chen, 2011; Moustakas and Evans, 2015; Cortini et al., 2017). For these reasons, trees generally show a U-shaped mortality pattern in relation to DBH (Harcombe, 1987; Monserud and Sterba, 1999). My results also demonstrate the positive effect of size up to a maximum at a DBH of 28 cm (Figure 3.5). In addition, this diameter-related trend in survival probability is linked to changes in stand characteristics (e.g., changes of competitive condition and stand structure) as stands age, and the trend varies between age groups. In general the survival probability of larger diameter trees is lower in older stands than in younger stands due to senescence and increases in agent-based mortality, but the survival probability of larger trees (>50 cm diameter) was higher in old stands than in mature stands in this study. This is likely due to the prevalence of agent-based mortality in old stands (Franklin et al., 1987; Franklin and Van Pelt, 2004) and the reduced effects of competition-based mortality.

Aspen is a shade intolerant species with both fast growth and severe intraspecific competition occurring when aspen stands are young (Peterson and Peterson, 1992). Thus, trees that can dominate the canopy first have higher survival probability, and small trees that are under the canopy have lower survival. Vigorous trees between 20 and 50 cm DBH maintained stable conditions, but their chances of survival decline with further increases in size (Figure 3.5). In general, very large trees are more likely to have physiological disorders and lower growth efficiency (e.g., aging cell tissue, less photosynthesis, and reductions in hydraulic transport) and are less able to withstand insect attacks, diseases, and drought (Franklin et al., 1987; Ryan et al., 1997; Ryan and Yoder, 1997; Bennett et al., 2015) largely due to their age. In addition, scars, stem breakage, branch death, and frost cracks are often evident on aspen stems and provide entry points for decay and disease fungi which may eventually lead to reduced vigor and death (Hiratsuka and Loman, 1984; Peterson and Peterson, 1992; Holmer et al., 1994).

My results indicate that competition from overtopping trees (DBL) was negatively associated with survival as has been shown by other studies (Temesgen and Mitchell, 2005; Reyes-Hernández and Comeau, 2014; Cortini et al., 2017). In particular, DBL had a stronger effect on survival in the young age group (Table 3.4) due to severe intraspecific competition during the stem exclusion stage. As a shade intolerant species, aspen stands close canopy and reach maximum leaf area index (LAI) at young stand ages (Peterson and Peterson, 1992; Lieffers et al., 2002). Early achievement of crown closure and maximum LAI leads to low levels of light transmission through the main canopy resulting in high rates of mortality of overtopped aspen trees (Peterson and Peterson, 1992; Lieffers et al., 2002).

Crown stratification begins to develop in young stands and becomes increasingly apparent in mature stands during the understory re-initiation stage (Peterson and Peterson, 1992; Oliver and Larson, 1996). In the study, tree size diversity (TSD) characterizes the degree of stratification and provides an indicator of stress. TSD was associated with increasing stand level competition while DBL represented competition at the individual tree level. For this reason, the mature age group had a stronger relationship with TSD than did the young and old age groups (Table 3.5). TSD generally increases with increasing stand age, but TSD declines in old stands (> age 120) where there are only a few large trees and many newly regenerated small trees (Table 3.3 and Figure 3.4). Variables representing stressful conditions (i.e., higher DBL, MAT or TSD) negatively influence aspen survival and they had their strongest effects on aspen survival under warmer conditions (Figure 3.6).

Mean annual temperature (MAT) had a negative effect on tree survival (Table 3.5 and Figure 3.6). This may be because increasing temperature is associated with decreasing water availability and increased intraspecific competition due to increases in tree growth rates (Luo and Chen, 2013; Kweon and Comeau, 2017). Results also indicate that climate can work differently in different stand development stages (Thorpe and Daniels, 2012; Luo and Chen, 2013; Bell et al., 2014). In this study increasing MAT under the same DBL level more negatively influenced tree survival in young stands while under the same TSD level, the negative effect of increasing MAT on survival was stronger in mature stands (Figure 3.6). These results are consistent with other studies which show that dense stands with high levels of competition are more vulnerable to increasing temperature (Luo and Chen, 2013; Zhang et al., 2015).

Models in the study correctly predicted aspen survival between 84.1% (AUC=0.841) and 84.6% (AUC=0.846) with four different models (i.e., logistic regression models with/without the interaction term of age groups and logistic mixed effects models with/without the interaction term of age groups) where tree size, competition, tree size diversity, and climate were the primary predictors (Table 3.4). Unexplained variation may be related to effects of site conditions (e.g., soil, site quality, slope, and aspect). Site conditions can influence the carrying capacity of stands and moderate effects of high temperatures and drought stress (Frey et al., 2004; Worrall et al., 2010). Unfortunately, because of the lack of available data (soil and site data were not available for many of these plots and data for calculation of site index were available for less than half of the plots), I could not test these variables in survival models. In addition, disturbances (e.g., insect attacks, drought, windthrow, and herbivores) and diseases (e.g., stem decay, hypoxylon canker, and root disease) can influence aspen mortality (Peterson and Peterson, 1992; Allen et al., 1996; Frey et al., 2004; Marchetti et al., 2011; Dudley et al., 2015). Incorporating these and other factors should be explored in future studies to improve predictions of survival.

3.5 Conclusions

Aspen stands are dynamic and develop stratified multicohort structure over time as trees experience mortality caused by endogenous (e.g., competition) and exogenous (e.g., drought, windthrow, insect attacks, and pathogens) stresses. Based on tree core analysis, a positive relationship between stand age and stand structure was found. Using age (i.e., young, mature, and old stands) groups as an interaction term, the effects of aspen age, tree size, competition, stand structure, and climate on tree survival were examined. This model appears to reflect the changes of survival probability with incresing tree size and changes in stand structure with age. This study showed that tree size diversity (i.e., stand age structure or diversity of diameter classes) was related to increasing stand level competition while deciduous basal area larger (i.e., sum of the basal area of deciduous trees larger than a target tree) was effective as a measure of individual tree level competition. Under warmer conditions, competition variables (e.g., deciduous basal area larger and tree size diversity) had stronger effects on tree mortality and the magnitude of temperature effects varied between age groups due to different stand conditions and structure.

Chapter 4: Factors influencing overyielding in young boreal mixedwood stands in western Canada

4.1 Introduction

Several studies have demonstrated the benefits of tree species diversity on forest productivity, resilience, wildlife habitat, and aesthetics (Macdonald, 1995; Hoffman and Palmer, 1996; Macdonald et al., 2010; Cavard et al., 2011b; Zhang et al., 2012; Pretzsch et al., 2013b; Liang et al., 2016; Ma and Chen, 2017). Increases in productivity are of interest since this is closely associated with carbon capture and economic values (Ruiz-Benito et al., 2014; Liang et al., 2016). When productivity is higher in mixtures than in associated monocultures, it is termed overyielding (Hector, 1998; Beckage and Gross, 2006; Pretzsch and Schutze, 2009). Overyielding may result from competitive reduction, facilitation or other factors and is often also termed the "mixing effect". In such cases, an increase in production results from the mixed environment encouraging species traits to surpass their behaviors in pure stands (Kelty, 2006; Forrester, 2014; Pretzsch, 2014).

Niche partitioning between species can lead to reductions in competition (Man and Lieffers, 1999; Hooper et al., 2005; Kelty, 2006; Pretzsch and Schutze, 2009). For example, shade tolerant species in the understory have a capacity for carbon fixation at low light levels (Givnish, 1988) with shade intolerant species in the overstory needing full light, and with mixtures of understory tolerant and overstory intolerant species resulting in a stand structure that more fully utilizes light over the growing season leading to higher net primary production. In the case of mixtures of coniferous and deciduous species, they can also differ in utilization of light during the growing season due to differences in phenology of leaf development (Constabel and Lieffers, 1996; Man and Lieffers, 1997; Man and Lieffers, 1999). Understory spruce can utilize light when overstory aspen does not have leaves in the spring and autumn. For example, young aspen stands (< 20 years old) allowed about 60% of full light to penetrate to 1.3 m in the spring and autumn but allowed about 20% of full light in the summer (Constabel and Lieffers, 1996). Understory spruce can utilize available light during the spring and autumn in photosynthesis and accumulate more carbon than would be the case if they were growing under an evergreen canopy (Man and Lieffers, 1997). Overyielding in mixtures also results from them supporting potentially higher stocking and canopy stratification (Garber and Maguire, 2004; Condés et al., 2013; Pretzsch and Schütze, 2016). Functional differences (e.g., shade tolerance) and traits (e.g. crown shapes of species) may allow stands to stock more trees in mixtures compared to monocultures (Pretzsch, 2014; Peer et al., 2018; Toïgo et al., 2018). When species occupy different crown layers, there can also be an increase in leaf area index which may contribute to higher productivity of the mixed stand (Man and Lieffers, 1999; Kelty, 2006; Forrester and Albrecht, 2014; Forrester et al., 2018).

Facilitation, which involves certain species improving the environment for other species (Hooper et al., 2005), may also contribute to overyielding (Pretzsch and Schutze, 2009; Forrester, 2014; Mason and Connolly, 2014). Increases in productivity could result from higher humidity in the understory, reductions in frost, insect attacks, and wind exposure (Taylor et al., 1996; Groot and Carlson, 1996; Man and Lieffers, 1999), and/or increases in nutrient availability.

Stand developmental stages can influence the mixing effect because growth rates of each species may differ with age (del Río et al., 2016). Early successional species, such as trembling aspen, typically have rapid initial growth that reaches a maximum over a short period while late successional species, such as white spruce, often have slow early growth rates (Cavard et al., 2011a). As a result, the contribution of each species to total production may vary with stand age and influence the magnitude and occurrence of overyielding.

Site quality and climate influence the productivity of mixtures through effects on growth of the component species, nature and intensity of interactions, and potential stocking (Pretzsch et al., 2010; Paquette and Messier, 2011; Prior and Bowman, 2014; Potter and Woodall, 2014; Toïgo et al., 2015; Jucker et al., 2016; Peer et al., 2018; Mina et al., 2018). The stress gradient hypothesis, suggests that interactions among species will tend to be more positive (i.e., interactions leading to increased growth) under poor or stressful conditions whereas under rich or moderate conditions weak positive or negative outcomes are more common (Callaway and Walker, 1997; Paquette and Messier, 2011; Toïgo et al., 2015).

Higher productivity of these aspen-spruce mixtures has been identified in mature natural forests (Man and Lieffers, 1999; MacPherson et al., 2001) and modelling studies (Comeau et al., 2005; Comeau, 2014) in western Canada, but overyielding has not been examined in young stands in this region. Groot et al. (2014) found no significant effect on production of mixtures in young aspen-spruce stands in eastern Canada, contrary to predictions derived from previous research.

The objectives of the study were to examine: 1) whether or not overyielding occurs in young (< 30 years old) mixed stands; 2) effects of species composition, stand density, proportion (i.e., the proportion of basal area of each species), and tree size on overyielding; and 3) effects of climate and site quality (Site index) on the magnitude of overyielding in these aspen-spruce mixedwood stands.

4.2 Material and methods

4.2.1 WESBOGY Long-Term Study and Data selection

Data from the Western Boreal Growth and Yield Association (WESBOGY) Long-Term Study (LTS) collected between 2006 and 2015 were used for these analyses. The WESBOGY LTS uses a randomized block design with 11 agencies and companies, and each agency or company involves one or two installations which differ in site quality (Superior and Median). Each installation originally contained two replicates of 15 treatment plots, however, one replicate was lost in the WFR Superior and WGP Medium installations. The 15 treatments include five monospecific stands of aspen (1500, 4000 trees/ha, and natural (initial mean density was more than 70,000 stems per hectare (Bokalo et al., 2007)) and white spruce (500 and 1000 trees/ha), as well as mixtures with spruce densities of 500 and 1000 trees per hectare and five aspen densities (200, 500, 1500, 4000 trees/ha, and natural). Spruce was planted at uniform spacing for the two spruce densities and aspen were also fairly uniformly distributed in these stands. At year 5 after planting of spruce and natural regeneration of aspen, spruce and aspen were thinned to these treatment densities. Each plot is square with 20 m × 20 m (0.04 ha). Diameter at breast height (DBH), tree height (HT), crown width, species age, and tree condition (e.g., dead or alive) have been measured over time. Four mixtures (spruce 500 trees/ha with aspen 200 and 500 trees/ha and spruce 1000 trees/ha with aspen 200 and 500 trees/ha) were excluded from this study because of the lack of reference pure aspen stands with theses densities (200 and 500 trees/ha).

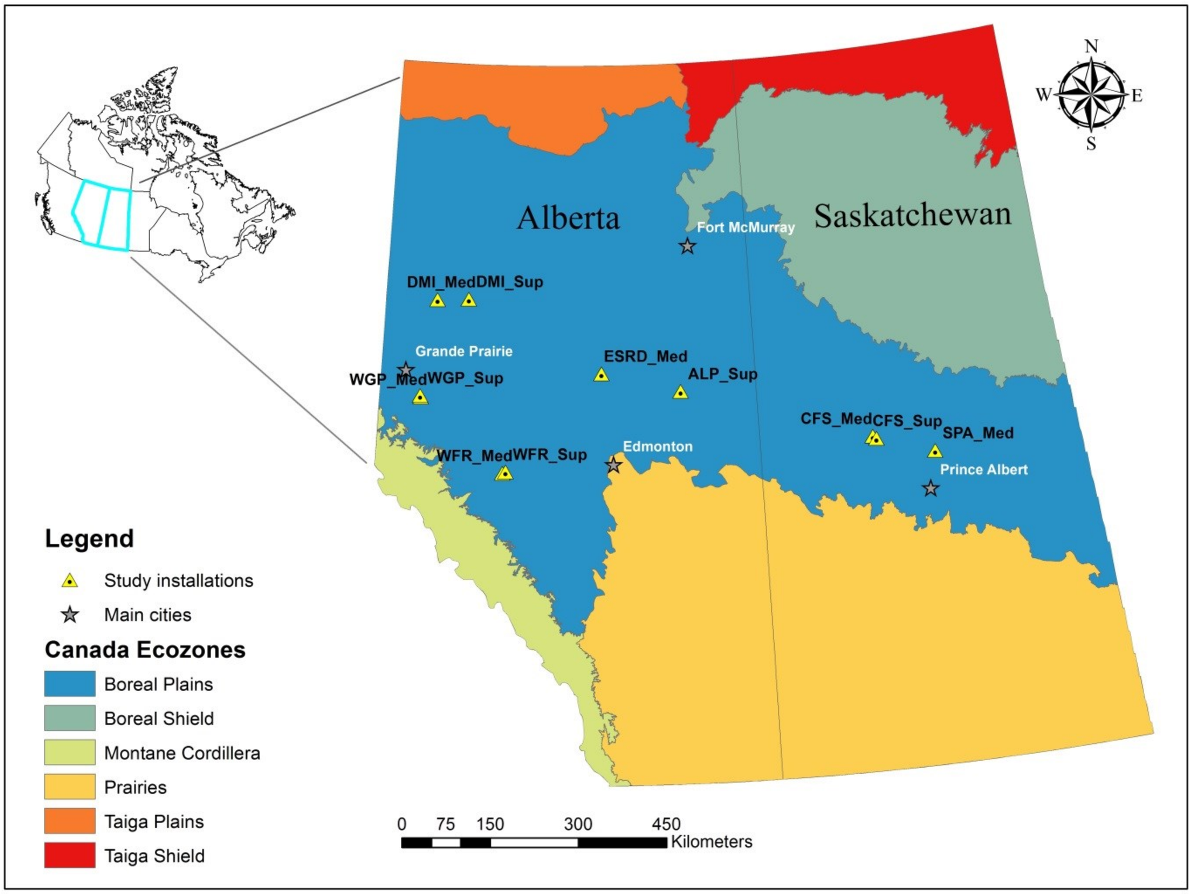


Figure 4.1 Ecozones and locations of study sites (7 agencies, 11 installations (ALP, Alberta-Pacific Forest Industries Inc.; CFS, Canadian Forest Service; DMI, Daishowa-Marubeni International Ltd.; ESRD, Government of Alberta; SPA, Saskatchewan Ministry of Environment; WFR, Alberta Plywood; WGP, Weyerhaeuser Company Ltd.; Sup, superior installation; Med, median installation) in total).

All study installations are located in the Boreal Plains ecozone (Figure 4.1) where mixed stands of trembling aspen and white spruce are naturally common. The Boreal plains ecozone has a mean annual temperature of 0.2 ˚C and annual precipitation of 472 mm (Price et al., 2013), and it has moderately warm summers with most precipitation occurring during the growing season. Gray Luvisolic soils are prevalent in forested areas in this region (Wiken, 1986; Lavkulich and Arocena, 2011).

This study utilized data from 7 agencies with trees taller than breast height (1.3 m). Alberta-Pacific Forest Industries Inc. (ALP), Daishowa-Marubeni International Ltd. (DMI), Government of Alberta (ESRD), Alberta Plywood (WFR), and Weyerhaeuser Company Ltd. (WGR) are located in Alberta, and Canadian Forest Service (CFS) and Saskatchewan Ministry of Environment (SPA) are from the province of Saskatchewan. In total, 11 installations, 20 replicates, and 220 treatments (20 replicates × 11 treatments) were used for the study (Table 4.1). The number of measurements ranges from 2 to 4 at each location, and years between successive measurements are 2 to 3 years. In this study, the data from the ages (Sw_age and Aw_age) indicated in Table 4.1 were used for the analysis.

Table 4.1 Locations and information on available data.

Location	INST	REPL	Trt	No.	Latitude/longitude	Elev. (m)	M_period	Sw_age	Aw_age
ALP	Sup	R1, R2	22	4	55˚00'N, 112˚00'W	568	2008-2014	16-22	15-21
CFS	Sup	R1, R2	22	2	54˚03'N, 106˚58'W	505	2008-2010	17-19	16-18
	Med	R1, R2	22	2	54˚05'N, 107˚03'W	515	2008-2010	17-19	16-18
DMI	Sup	R1, R2	22	4	56˚24'N, 117˚43'W	728	2006-2012	15-21	15-21
	Med	R1, R2	22	4	56˚23'N, 118˚35'W	788	2006-2012	15-21	15-21
ESRD	Med	R1, R2	22	4	55˚18'N, 114˚06'W	643	2006-2014	15-23	15-23
SPA	Med	R1, R2	22	3	53˚45'N, 105˚30'W	548	2006-2010	16-20	16-20
WFR	Sup	R2	11	4	53˚47'N, 116˚36'W	1085	2007-2013	13-20	18-25
	Med	R1, R2	22	4	53˚47'N, 116˚41'W	1050	2007-2013	15-22	17-24
WGP	Sup	R1, R2	22	3	54˚55'N, 118˚53'W	906	2010-2015	20-25	23-28
	Med	R1	11	3	54˚53'N, 118˚53'W	926	2010-2015	20-25	23-28

INST, installation; REPL, replicate; Trt, number of treatments (11 treatments×number of replicates at each installation); No., number of measurements; Elev., elevation; M_period, measurement periods; Sw_age, age of white spruce at last indicated measurement; Aw_age, age of trembling aspen at last indicated measurement.

4.2.2 Mixing effect and potential variables

Calculation of relative productivity total for mixing effect

The dry mass of stems in each stand was calculated based on Canadian national biomass equations (Ung et al., 2008) using diameter at breast height (DBH) and tree height (HT), and the equation is given as:

$$Biomass_{\mathrm{stem}} = \beta_{\mathrm{wood1}} DBH^{\beta\mathrm{wood2}} HT^{\beta\mathrm{wood3}} + \beta_{\mathrm{bark1}} DBH^{\beta\mathrm{bark2}}\ HT^{\beta\mathrm{bark3}}, \qquad \textbf{(4.1)}$$

where β_{wood1}=0.0143, β_{wood2}=1.9369, β_{wood3}=1.0579, β_{bark1}=0.0063, β_{bark2}=2.0744, and β_{bark3}=0.6691 for trembling aspen, and β_{wood1}=0.0252, β_{wood2}=1.7819, β_{wood3}=1.0022, β_{bark1}=0.0096, β_{bark2}=1.6901, and β_{bark3}=0.7393 for white spruce.

Based on calculated stem biomass for each stand, periodic annual increment (PAI) of stem biomass was computed for use as the response variable in examining overyielding. The equation is:

$$PAI_{total} = \frac{BM_{t2} - BM_{t1}}{t2 - t1}, \qquad \textbf{(4.2)}$$

where PAI_{total} is the total periodic annual increment of two species between two measurements at time t_1 and t_2 for a plot, and BM is the total stem biomass of two species. Specific PAI_{sw} and PAI_{aw} were also computed as response variables.

Relative Productivity Total (RPT) used in this study (Equation 4.3) is equal to the Land Equivalent Ratio (LER) and is useful in evaluating the effect of species mixing without considering the mixing proportions of species in mixture (Willey and Osiru, 1972; Forrester and

Pretzsch, 2015; Pretzsch et al., 2017). RPT means the required land area of the pure stand to produce the same yield as a mixture and is applicable to additive experimental designs where total densities and species proportions differ between treatments. Additive effects of two species in mixture were examined using relative productivity (e.g., RP=productivity of spruce or aspen in mixture/productivity of spruce or aspen in monoculture), and relative productivity total was calculated by summing up relative productivities of two species (i.e., RP_{sw} and RP_{aw}) at equivalent densities for each species. Relative productivity was calculated using PAI of each species. The equation is:

$$RPT_{sw,aw} = RPsw\left(\frac{PAI_{sw(aw)}}{PAI_{sw}}\right) + RPaw\left(\frac{PAI_{aw(sw)}}{PAI_{aw}}\right), \quad \textbf{(4.3)}$$

where PAI_{sw} and PAI_{aw} are periodic annual increment of each pure spruce or aspen stand, and $PAI_{sw(aw)}$ is the periodic annual increment of spruce in the mixed stand and $PAI_{aw(sw)}$ is the periodic annual increment of aspen in the mixed stand. A relative productivity total higher than 1, indicates an advantage of species mixing. The pure spruce plots (1000 and 500 trees/ha) and the pure aspen plots (1500, 4000 trees/ha, and unthinned natural plot) in each replicate were used as reference pure stands for each density combination.

Potential predictor variables

Stand density represents site occupancy by trees and is closely related to resources and growing space used by trees in a stand (del Río et al., 2016). Stem number, basal area, and stand density index per unit area are commonly used as measures of site occupancy, and this study also used these variables to quantify species-specific site occupancy of pure and mixed stands. Species proportion is often used as an indicator of composition of a mixed stand (del Río et al., 2016). In this study, basal area of aspen or spruce over total basal area was used to calculate species proportion.

Canopy stratification can influence the productivity of mixtures because it can reduce competition among species and increase light interception due to increasing leaf area index and better filling of canopy space (Seidel et al., 2013; del Río et al., 2016; Pretzsch and Schütze, 2016). Young aspen-spruce mixtures generally consist of two canopy layers because of differences in growth rates and shade tolerance. Thus, the difference of tree height between two species was used as a proxy variable for canopy stratification. Tree size is associated with stand structure in mixtures, so quadratic mean diameter (QMD) and mean tree height (HT) were also included as covariates.

Since environmental factors influence species interactions in mixtures and the interactions lead to changes in stand structure (Forrester et al., 2013; Huber et al., 2014; Toïgo et al., 2015), the effects of climate and site quality were also tested. Climate data were obtained from climate WNA (Hamann et al., 2013) and climate averages for intervals between two measurement years were used in this analysis. As representative climate variables, mean annual temperature (MAT), annual heat moisture (AHM), degree days above 5 ˚C (DD5), mean annual precipitation (MAP), mean summer precipitation (MSP), summer heat moisture (SHM), frost free period (FFP), and climate moisture index (CMI) were utilized. Climate moisture index was calculated using monthly temperatures, annual precipitation, and elevation for each location (Hogg, 1997). To examine the effect of site quality on mixing effect, site index considering the average productivity of a stand was used (Husch et al., 2003). Site index was calculated for aspen using tree heights measured in pure aspen plots (Huang et al., 2009) for each installation.

Table 4.2 Characteristics of variables used in the analysis.

Var.	QMD (cm)		HT (m)		BA (m^2/ha)		SDI		TPH (trees/ha)	
	Sw	Aw	Sw	Aw	Sw	Aw	Sw	Aw	Sw	Aw
Mean	4.07	7.08	3.7	8.23	1.00	11.21	39.00	376.6	649.6	3291.5
SD	1.58	1.98	1.05	1.96	0.88	4.49	29.23	134.2	274.0	1652.4
Max.	9.69	12.09	6.33	14.26	4.26	27.62	142.07	824.1	1175.0	9250.0
Min.	0.00	2.59	0.87	3.80	0.00	4.38	0.00	195.1	0.00	1075.0
Var.	RD		Proportion		Stem biomass (t/ha)			PAI (t/ha*year)		
	Sw	Aw	Sw	Aw	Sw	Aw	Total	Sw	Aw	Total
Mean	3.36	32.38	0.08	0.92	2.20	33.30	25.60	0.42	4.01	4.42
SD	2.51	11.52	0.07	0.07	2.06	18.18	13.51	0.39	2.16	2.27
Max.	12.21	70.74	0.34	1.00	10.82	122.38	88.78	2.29	11.79	12.26
Min.	0.00	16.77	0.00	0.66	0.00	9.54	7.04	0.00	0.08	0.37
Var.	SI (m)	MAT (˚C)	FFP	MAP (mm)	AHM	MSP (mm)	SHM	PPT_sm	DD5	CMI (cm)
Mean	21.07	1.71	107.1	498.4	23.80	336.7	49.85	246.8	1304.1	5.20
SD	2.64	0.81	6.7	51.9	2.26	46.3	7.43	38.5	98.7	6.00
Max.	27.13	3.10	121.0	607.7	28.30	426.7	63.80	326.0	1511.0	17.44
Min.	14.30	-0.05	93.5	388.0	19.35	262.0	34.15	176.5	1096.7	-4.43

Sw, white spruce; Aw, trembling aspen; QMD, initial quadratic mean diameter; HT, initial mean tree height; BA, initial basal area; SDI, initial stand density index; TPH, initial trees per hectare; RD, initial relative density; Proportion, initial spruce/aspen proportion; Biomass, stem biomass; PAI, periodic annual increment; SI, site index; MAT, mean annual temperature; FFP, frost free period; MAP, mean annual precipitation; AHM, annual heat moisture (MAT+10)/(MAP/1000); MSP, mean summer precipitation (May to Sep.); SHM, summer heat moisture (MWMT)/(MSP/1000); PPT_sm, summer precipitation (Jun. to Aug.); DD5, growing degree days above 5 ˚C; CMI, climate moisture index.

4.2.3 Data analysis

Comparison of aspen-spruce combinations

Stand characteristics (e.g., tree size, stand density, and productivity) among 11 treatments including pure stands were compared to investigate the responses of two species according to aspen-spruce combinations and to determine reasons causing the difference in mixing effect.

Effects of treatments (combination of spruce and aspen density) on relative productivity total (RPT) were tested using a linear mixed effects model to control for regional variation. Treatment was used as a fixed effect and replicate nested in installation nested in agency was used as a random effect. Because repeated measurements can be correlated over time, autocorrelation functions were tested and the order 1 autocorrelation function was selected. After developing the linear mixed effects model, Tukey's HSD (honestly significant difference) test was conducted to compare which treatments are different from others using the function lsmeans (Russell, 2016)

Density effects can be confounded with the effect of species mixing when under stocked stands are included in the data. In particular, under stocked aspen stands can allow understory spruce to grow better than in well stocked aspen stands in this study. To control for density effects, we investigated effects of stocking using both relative density (Curtis, 1982) and relative stand density index (SDI of aspen in mixture divided by maximum SDI of unthinned aspen stand). Relative density or relative stand density index of unthinned aspen stands experiencing self-thinning was higher than relative density=15 or relative SDI=0.3 respectively. Based on these values of aspen stocking, 32 plots considered to be under stocked and 22 plots having negative PAI values due to self-thinning were removed from 282 plots (6 treatments × number of replicates × number of repeated measurements at each agency). In addition, 35 outliers (15.4% of

228 plots) which were outside of the range of 2.5 - 97.5 standard normal quantiles were removed to achieve equal variance and normal distribution of residuals for all models developed in this analysis. Relative productivity total and periodic annual increment total used in the analysis are from the sum of aspen and spruce values (e.g., relative productivity or periodic annual increment of two species), so the errors of aspen and spruce values can cause increases in variation for coefficients in models with the total response variables. In addition, since the relative values (e.g., relative productivity=biomass of a species in a mixture/biomass of a species in a monoculture) were used in the analysis, the relative value can become extreme when tree mortality results in the biomass of a species in a monoculture being low relative to its biomass in a mixture. In particular, unthinned aspen stands showed wide variations of these response variables because self-thinning is active in these stands compared to thinned aspen stands. Log and Box-Cox transformation of data was also tested, but this did not resolve issues with extreme values.

Relationships between mixing effects and stand variables

To determine which factors influence relative productivity total (RPT), a linear mixed effects model was fit to the data. Fixed effects (species proportion, basal area, stand density index, tree size, age, canopy stratification, climate, and site index) and random effects (Agency, installation, and replicate) were used for the analysis. Correlations between fixed effects variables included in each model were examined and were found to be non-significant. Variables which were strongly collinear (e.g., Basal area and SDI) were not included together in any models. To better account for relationships between relative productivity and predictor variables, I examined how predictor variables influence PAI total and PAI for each of the two species in mixtures.

In addition, I selected four agencies (i.e., ALP (Alberta-Pacific Forest Industries Inc.), DMI (Daishowa-Marubeni International Ltd.), ESRD (Government of Alberta), and WGP (Weyerhaeuser Company Ltd.)) including at least 3 measurements to examine the effect of stocking (e.g., SDI and species proportion) on mixing effect over time. The analysis was conducted at the treatment plot level (6 subsets) instead of the replicate level because each treatment plot had different ranges and variation in stocking. Relative productivity total was used as the response variable and stand density index total and spruce proportion were used for predictor variables.

A first order autocorrelation function was included to control for correlation among repeated measurements (2 to 4 measurements for 3 to 9 years). Variance inflation factors (VIF) were tested to examine potential collinearity among predictor variables and models with VIF greater than 4 were excluded because higher VIF (e.g., VIF>5) often causes increases in variance for coefficients and decreases in the statistical power of the analysis (Mason et al., 2003; Sheather, 2009). The maximum likelihood method was used to compare models, and the best model was selected based on lowest AIC (Akaike Information Criterion) and the likelihood ratio test. All parameters were estimated using the nlme package (Pinheiro and Bates, 2000; Pinheiro et al., 2015) of R software, version 3.4.1 (R Core Team, 2017).

4.3 Results

4.3.1 Comparisons of stand characteristics between mixtures and monocultures

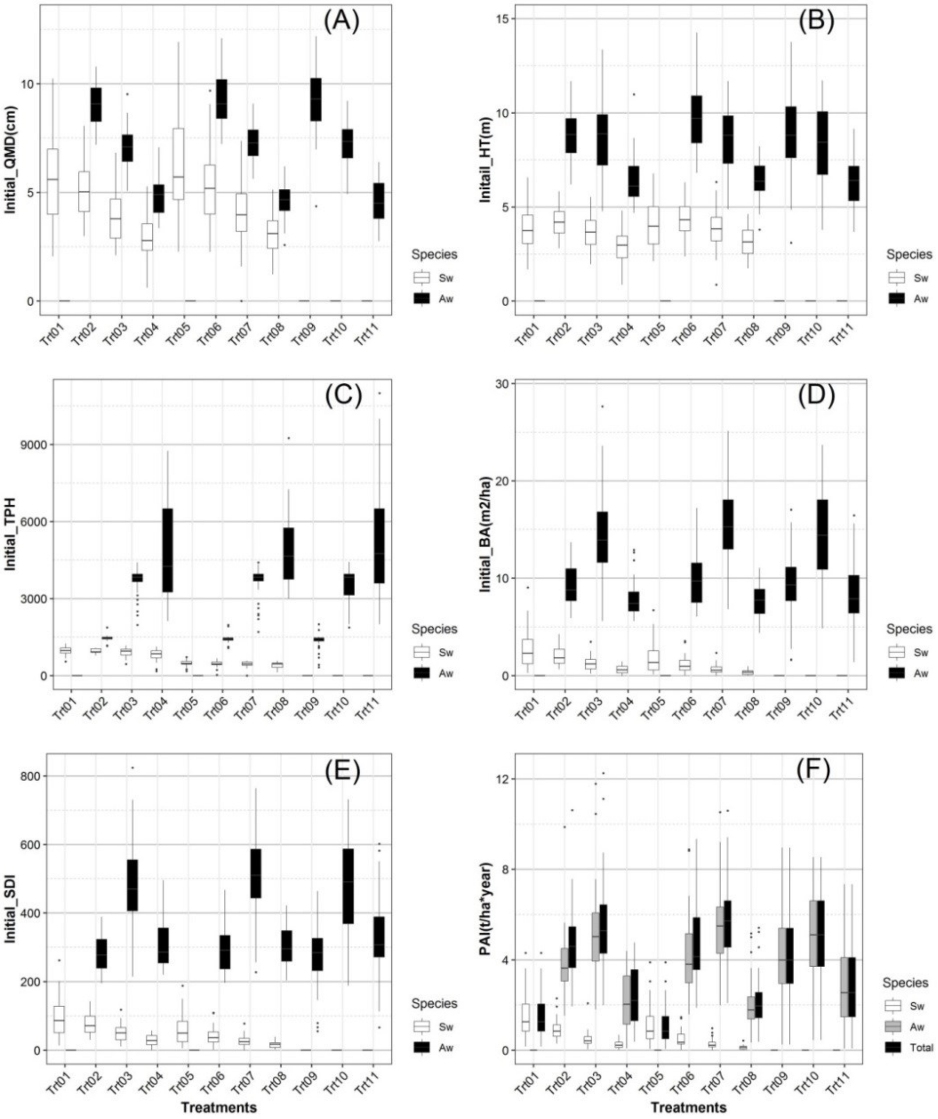


Figure 4.2 Comparisons of tree size, stand density, and productivity among 11 treatments in the WESBOGY Long-Term Study (Sw, white spruce; Aw, trembling aspen; Total, Sw+Aw; Initial_QMD, initial quadratic mean diameter; Initial_HT, initial mean tree height; Initial_TPH, initial trees per hectare; Initial_BA, initial basal area; Initial_SDI, initial stand density index; PAI, periodic annual increment; Trt01, Sw1000; Trt02, Sw1000/Aw1500; Trt03, Sw1000/Aw4000; Trt04, Sw1000/AwNatural; Trt05, Sw500; Trt06, Sw500/Aw1500; Trt07, Sw500/Aw4000; Trt08, Sw500/AwNatural; Trt 09, Aw1500; Trt10, Aw4000; Trt11, AwNatural). For the analysis, 193 experimental units were used.

Tree size (e.g. quadratic mean diameter and mean tree height), stand density (e.g. trees per hectare (tph), basal area, and stand density index), and periodic annual increment of stem biomass were compared among treatments including pure spruce and aspen treatments (Figure 4.2). The mean diameter of pure spruce stands (e.g., 500 or 1000 spruce tph without aspen) is largest compared to mean spruce diameter of other treatments. Among mixtures the combinations of either 500 or 1000 spruce tph with 1500 aspen tph have the largest mean aspen diameter and mean aspen diameter decreases as stem number increases. For mean tree height, however, the combinations of either 500 or 1000 spruce tph with either 1500 or 4000 aspen tph have similar heights. Mean tree height is substantially smaller at both spruce densities in the natural (unthinned) aspen densities. With regard to stand density, unthinned aspen treatments have higher numbers of trees and larger variation in the number of trees due to self-thinning, while thinned aspen treatments have narrower variation in the number of trees. For basal area, unthinned aspen treatments are lower than other treatments although stem numbers are higher than for other treatments. Stand density index is highest in the 4000 aspen tph treatments, and 1500 aspen tph treatments have a similar range of SDI to unthinned aspen treatments. Unthinned aspen treatments have lower PAI total than other treatments and 4000 aspen tph treatments with both spruce densities have the highest PAI total.

4.3.2 Evidence of overyielding in young mixedwood stands

Overall, 145 out of 193 (75.1%) plots had relative productivity total higher than one. The combination of 1000 spruce and 1500 aspen trees per hectare (tph) had the highest overyielding rate (96.5%, overyielding plots to stocked plots), whereas the combination of 500 spruce tph and unthinned aspen had the lowest overyielding rate (31.3%, overyielding plots to stocked plots) (Table 4.3). According to Tukey's test, thinned aspen stands with 1000 spruce and 500 spruce tph did not differ significantly, but were significantly different from the combinations of unthinned aspen stands with either 500 or 1000 spruce tph (Table 4.3).

Relative productivity total varied from 0.921 to 1.537 among mixedwood treatments. The combination of 1000 spruce tph and 1500 aspen tph had 53.7% higher productivity compared to pure stands. In addition, except for the combinations of unthinned aspen stands with 1000 spruce tph and 500 spruce tph, mixtures had significantly higher relative productivity totals than pure stands (RPT=1).

Table 4.3 The least square means of relative productivity total (RPT) among treatments.

Treatment (level)	Lsmean	SE	Df	Lower CL	Upper CL	T-test with μ=1	Overyielding rate
Sw1000/Aw1500 (a)	1.537	0.084	6	1.331	1.743	*P*-value=0.001*	96.5% (28/29)
Sw1000/Aw4000 (a)	1.349	0.078	6	1.160	1.539	*P*-value=0.004*	86.5% (32/37)
Sw1000/AwNat (b)	1.083	0.089	6	0.866	1.300	*P*-value=0.386	54.2% (13/24)
Sw500/Aw1500 (a)	1.483	0.083	6	1.280	1.685	*P*-value=0.002*	93.5% (29/31)
Sw500/Aw4000 (a)	1.420	0.076	6	1.235	1.606	*P*-value=0.001*	82.5% (33/40)
Sw500/AwNat (b)	0.921	0.081	6	0.722	1.120	*P*-value=0.370	31.3% (10/32)

*Significantly different from relative productivity total=1 (using likelihood ratio test α=0.05); Sw1000 or Sw500, 1000 spruce or 500 spruce trees per hectare; Aw1500 or Aw4000, 1500 aspen or 4000 aspen trees per hectare; AwNat, unthinned aspen stand; Overyielding rate, number of overyielding plots/number of available plots. For the analysis, 193 experimental units were used.

Figure 4.3 shows the contribution of each species to relative productivity total. Relative productivities of aspen were not significantly different from relative productivity=1 except for the combination of 500 spruce tph and unthinned aspen while all relative productivities of spruce were significantly lower than relative productivity=1. The result indicates that productivity of aspen in mixtures does not differ from that of pure aspen stands, but aspen suppresses spruce and increasing aspen density leads to reductions in productivity of spruce.

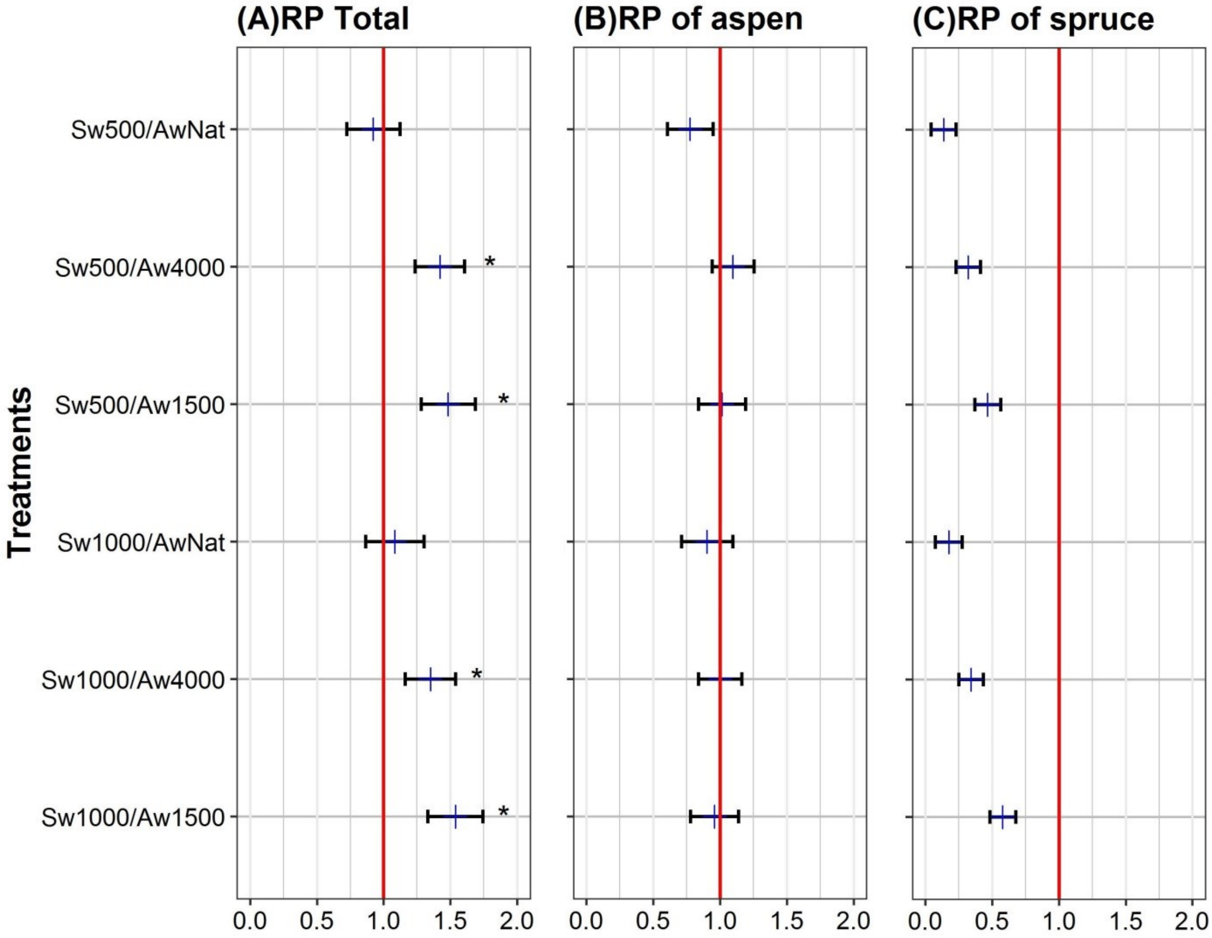


Figure 4.3 Comparisons of relative productivities among treatments. (A) Relative productivity total (sum of relative productivities of two species, Equation 4.3), (B) Relative productivity of aspen, and (C) Relative productivity of spruce. The red solid-vertical line represents that overyielding rate is equal to 1 (i.e. non-mixing effect) and star (*) represents significant overyielding.

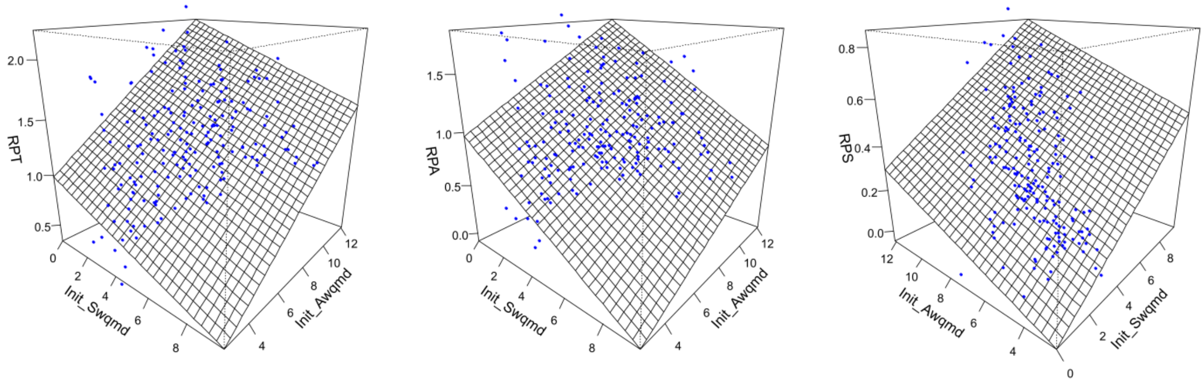
4.3.3 Factors influencing overyielding of mixtures among treatments

All variables in Table 4.2 (with the exception of biomass and PAI) were tested to examine relationships with relative productivity. As shown in Table 4.4, tree size (QMD), stand density (Basal area), site quality (site index), and climate significantly influence relative productivity. In general, initial stand density and tree size influenced relative productivity in spruce-aspen mixtures, and addition of site index and climate (e.g., DD5, degree days above 5 ˚C) led to a slight improvement in the goodness of fit of models. For relative productivity total (RPT), initial tree size (QMD) of the two species and DD5 provided the best model. Initial aspen size (QMD) positively influenced RPT while initial spruce size (QMD) and DD5 negatively influenced RPT (Figures 4.4 and 4.5). For relative productivity of aspen (RPA), the effect of tree size was the same as for the model of RPT, with RPA decreasing with increasing aspen site index (Figure 4.5). However, relative productivity of spruce (RPS) increased as initial spruce size (QMD) increased (Figure 4.4).

Table 4.4 Models developed with potential variables across treatments. Model 1 is the best for relative productivity total (RP_total), model 3 is the best for relative productivity of aspen (RP_Aspen), and model 5 is the best for relative productivity of spruce (RP_Spruce).

Models	AIC
1. RP_Total = 2.2112 - 0.0676 ×Init_SwQMD + 0.1303×Init_AwQMD - 0.0012×DD5	175*
(0.5357) (0.0237) (0.0170) (0.0004)	
2. RP_Total = 3.0733 + 0.0913×Init_SwBA + 0.0228×Init_AwBA - 0.0016×DD5	214
(0.6449) (0.0360) (0.0070) (0.0005)	
3. RP_Aspen = 1.5623 - 0.1083×Init_SwQMD + 0.0924×Init_AwQMD - 0.0396×SI	125*
(0.2719) (0.0193) (0.0150) (0.0128)	
4. RP_Aspen = 1.5683 - 0.0713×Init_SwBA + 0.0279×Init_AwBA - 0.0408×SI	137
(0.2668) (0.0282) (0.0057) (0.0129)	
5. RP_Spruce = - 0.1457 + 0.0582×Init_SwQMD + 0.0367×Init_AwQMD	-134*
(0.0507) (0.0109) (0.0079)	
6. RP_Spruce = 1.0984 + 0.0871×Init_SwBA - 0.0117×Init_AwBA	-120
(0.3921) (0.0208) (0.0031)	
+ 0.0649×Init_SwHT + 0.0234×Init_AwHT – 0.0009×DD5	
(0.0209) (0.0104) (0.0003)	

All estimates are significant at α=0.05 level and standard errors are shown in parentheses of estimates; RP_Total, relative productivity total; RP_Aspen, relative productivity aspen; RP_Spruce, relative productivity spruce; star (*) indicates the best model for each response variable; Init_SwQMD, initial quadratic mean diameter of spruce; Init_AwQMD, initial quadratic mean diameter of aspen; Init_SwBA, initial basal area of spruce; Init_AwBA, initial basal area of aspen; Init_SwHT, initial mean tree height of spruce; Init_AwHT, initial mean tree height of aspen; DD5, growing degree days above 5 ˚C; SI, site index; AIC, Akaike’s information criterion. For the analysis, 193 experimental units were used.



(A) RPT and tree sizes (B) RPA and tree sizes (C) RPS and tree sizes

Figure 4.4 Relationships between relative productivities and tree sizes for two species (i.e., Init_Swqmd, initial quadratic mean diameter of spruce; Init_Awqmd, initial quadratic mean diameter of aspen). (A) Relative productivity total (RPT) and tree sizes from model 1, (B) Relative productivity of aspen (RPA) and tree sizes from model 3, and (C) Relative productivity of spruce (RPS) and tree sizes from model 5. For degree days above 5 ˚C and site index, average values were used in the model (Table 4.2). See Table 4.4 for parameter estimates.

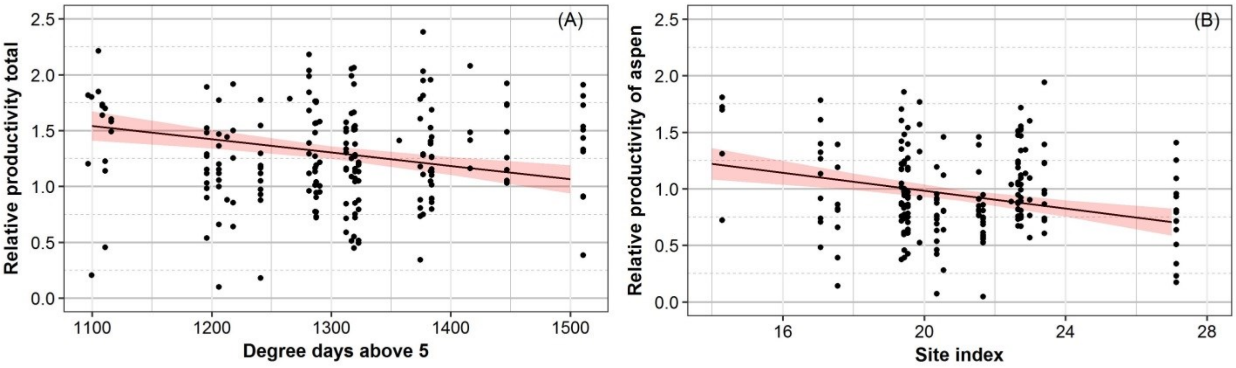


Figure 4.5 Effects of climate and Aspen site index on relative productivity. (A) Relative productivity total and degree days above 5 ˚C from model 1 (Table 4.4) and (B) Relative productivity of aspen and site index from model 3 (Table 4.4). For initial spruce QMD and aspen QMD, average values were used in the models (Table 4.2).

4.3.4 Relationships between productivity and stand factors (predictor variables) in mixtures

Table 4.5 shows relationships between predictor variables and PAI total, PAI aspen, and PAI spruce. Increases in stand density (e.g., Basal area and stand density index) and tree size (e.g., tree height) were associated with increases in total and aspen periodic annual increment. However, as stand density of aspen increased, spruce PAI decreased. Increases in climate moisture index (CMI) were associated with an increase in PAI, while increases in annual heat moisture (AHM) were associated with a decrease in PAI.

Table 4.5 Relationships between periodic annual increment total and two species and predictor variables in mixtures.

Models	AIC
PAI_Total = 3.6730 + 0.4265×Init_SwBA + 0.2452×Init_AwBA + 0.3110×Init_SwHT (1.4502) (0.1794) (0.0238) (0.1370) + 0.2699×Init_AwHT - 0.2564×AHM (0.0736) (0.0625)	719*
PAI_Total = - 4.2831 + 0.0129×Init_SwSDI + 0.0067×Init_AwSDI + 0.3425×Init_SwHT (0.5907) (0.0050) (0.0007) (0.1371) + 0.4347×Init_AwHT + 0.1024×CMI (0.0678) (0.0261)	731
PAI_Aspen = 3.2250 + 0.3163×Init_SwBA + 0.2547×Init_AwBA + 0.2926×Init_AwHT (1.3927) (0.1439) (0.0233) (0.0700) - 0.2136×AHM (0.0595)	709*
PAI_Aspen = - 4.3000 + 0.0071×Init_AwSDI + 0.3920×Init_SwHT + 0.4166×Init_AwHT (0.556) (0.0006) (0.1117) (0.0641) + 0.0963×CMI (0.0254)	714
PAI_Spruce = 0.3678 + 0.0104×Init_SwSDI - 0.0004×Init_AwSDI + 0.0170×Init_AwHT (0.1067) (0.0004) (0.0001) (0.0062) - 0.0153×AHM (0.0045)	-279*
PAI_Spruce = 0.3971 + 0.3756×Init_SwBA - 0.0099×Init_AwBA + 0.0161×Init_AwHT (0.1054) (0.0149) (0.0027) (0.0072) - 0.0160×AHM (0.0045)	-277

All estimates are significant at α=0.05 level and standard errors are shown in parentheses of estimates; PAI_Total, periodic annual increment total in stem biomass; PAI_Aspen, period annual increment of aspen in stem biomass; PAI_Spruce, periodic annual increment of spruce in stem biomass; star (*) indicates the best model for each response variable; Init_SwBA, initial basal area of spruce; Init_AwBA, initial basal area of aspen; Init_SwSDI, initial stand density index of spruce; Init_AwSDI, initial stand density index of aspen; Init_SwHT, initial mean tree height of spruce; Init_AwHT, initial mean tree height of aspen; AHM, annual heat moisture; CMI, climate moisture index; AIC, Akaike's information criterion. For the analysis, 193 experimental units were used.

4.3.5 Relationships between mixing effect and stand stocking over time

Figures 4.6 and 4.7 show the relationships between mixing effect and stand density index total or spruce proportion. As either SDI total or spruce proportion increased, relative productivity total tended to decrease. For SDI total, 4000 aspen tph treatments with both spruce densities and the natural aspen treatment with 500 spruce tph (Figure 4.6b, e, and f) showed significant trends in relative productivity total. In particular, Figure 4.6f (Sw 500 tph and Aw Natural) had a steeper declining slope than other treatments and a likelihood ratio test (α=0.05 level) indicated that the intercept of Figure 4.6f was higher than Figure 4.6b and c.

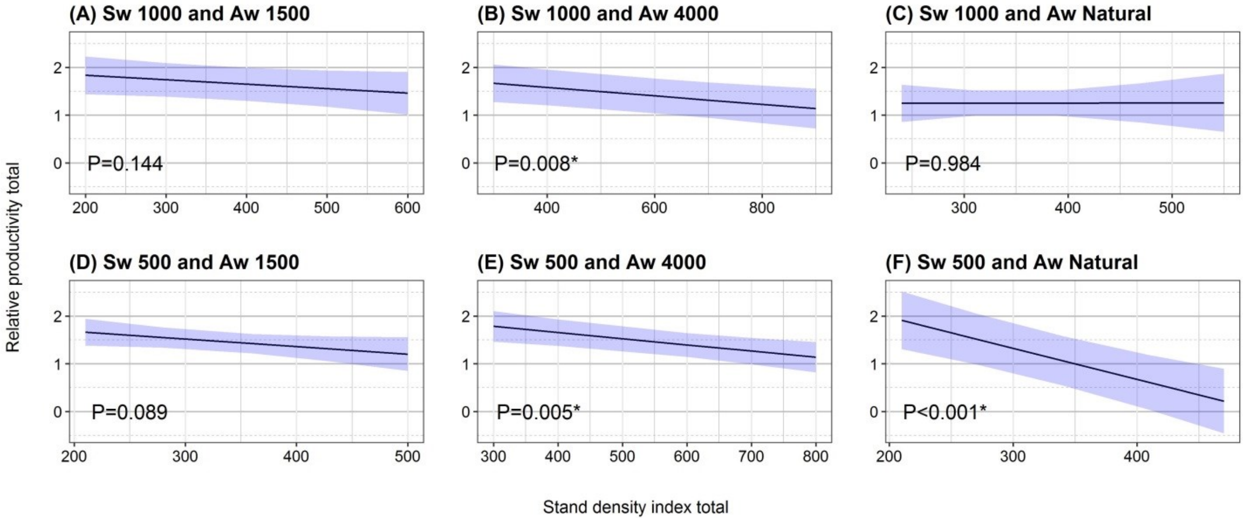


Figure 4.6 Relationships between stand density index and relative productivity total at each treatment. Star (*) indicates the significance of slope at each treatment and *p*-values were shown in each panel.

All thinned aspen treatments (with both spruce densities) and the natural aspen treatment with 500 spruce tph showed significant declining trends as spruce proportion increased. According to the likelihood ratio test (α=0.05 level), Figure 4.7b and f had steeper slopes than Figure 4.7c, and Figure 4.7a had a larger intercept than Figure 4.7c and d.

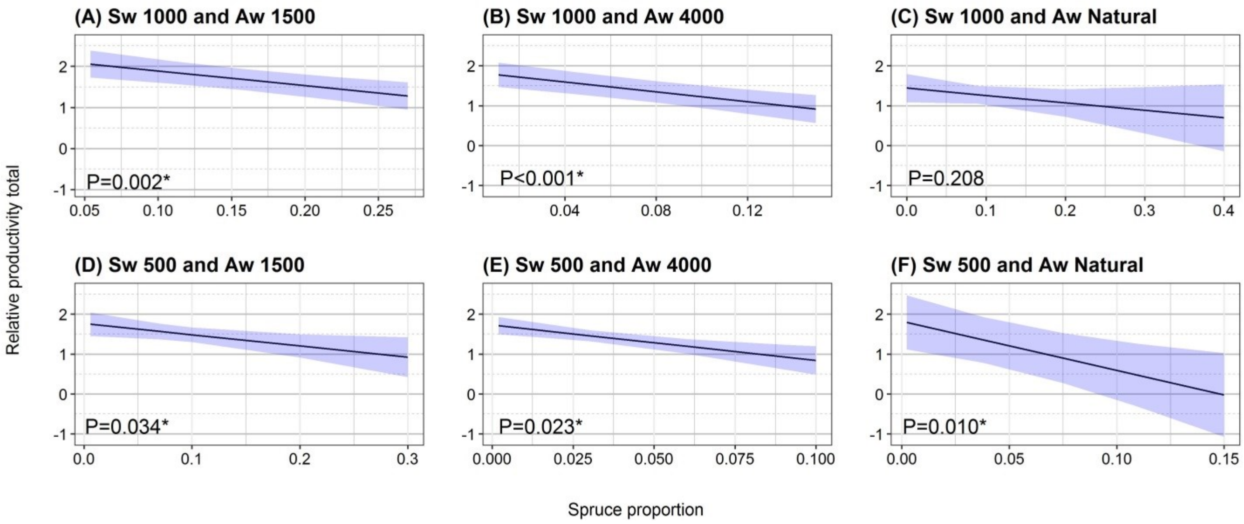


Figure 4.7 Relationships between spruce proportion and relative productivity total at each treatment. Star (*) indicates the significance of slope at each treatment and *p*-values were shown in each panel.

4.4 Discussion

Relative productivity was used to determine the mixing effect (i.e. overyielding) in mixtures and factors influencing overyielding were examined. Overyielding was evident in these young boreal mixedwood stands and species interactions varied with species composition and stand density. Adding spruce into thinned aspen stands was generally associated with maintaining aspen PAI in mixtures similar to that in pure aspen plots and adding extra spruce PAI, while treatments combining spruce with unthinned aspen had lower PAI for both species and less frequency of overyielding (Table 4.3 and Figure 4.3). This trend reflects shade tolerance of white spruce, effects of increasing understory light levels due to thinning of the aspen on growth of white spruce, and the effects of reducing intraspecific competition for aspen. This is consistent with results from other studies showing that light levels and growth of understory spruce decline with increasing aspen density (Comeau, 2001; Comeau et al., 2006; Filipescu and Comeau, 2007). 14

m^2/ha of aspen basal area (transmittance = 40%) can reduce the radial growth of spruce up to 51% and spruce mortality rapidly increases when aspen densities exceed 20 m^2/ha of basal area (Comeau, 2001). Spruce survival is low at 8% transmitted light or lower (Lieffers and Stadt, 1994; Comeau, 2001) but increases dramatically with increases in light levels. Spruce height growth shows an asymptotic trend and reaches a maximum at about 40% transmitted light (or BA of aspen below 14 m^2/ha).

My results indicate that tree size (e.g., diameter and height) and stand density (e.g., basal area and stand density index) were the main factors determining the yield of young trembling aspen-white spruce mixtures (Tables 4.4 and 4.5). In general, tree size is an important factor influencing productivity of a mixture since productivity will decline when two species compete. Consequently, a mixed species stand that has space partitioning and size inequality between species leads to competitive reduction and favours differences in functional traits (e.g. shade tolerance) between the component species (Pretzsch and Schütze, 2016; Toïgo et al., 2018; Forrester et al., 2018). In this study, interspecific competition between two species is less severe than observed in mature mixed stands because most spruce trees are still substantially shorter than the aspen. The shade tolerance of spruce enables spruce to survive under the aspen canopy and allows mixtures of aspen and spruce to maintain higher stocking (Man and Lieffers, 1999; Peer et al., 2018). In addition, model 1 from Table 4.4 indicates that the relationship between initial tree size and relative productivity total is also associated with intraspecific competition amongst aspen. Treatments with higher relative productivity total have bigger differences in tree size between two species and less intraspecific competition (Figure 4.4). Thus, thinned plots with larger aspen lead to higher basal area than unthinned plots and spruce are receiving higher light levels due to their larger tree height (Figure 4.2). In contrast, the mixing effect decreases when sizes of the two species are similar.

Species mixtures often support higher stocking than pure stands (Condés et al., 2013; Pretzsch and Biber, 2016; Pretzsch and Schütze, 2016) leading to increases in productivity. This is consistent with my results indicating that PAI total in mixtures increases as both spruce and aspen basal area increase (Table 4.5). Differences in species growth rates result in canopy stratification and increases in stocking in mixtures lead to increases in light capture and biomass production (Forrester et al., 2018). However, when aspen densities are high, understory light levels and spruce growth are low and lead to little or no overyielding. In the study, the combinations of spruce with unthinned aspen stands have relatively small tree sizes compared to the others (Figures 4.2a and b) and the mixing effect is also lower than others (Table 4.3). This also indicates the importance of tree size to the productivity of aspen-spruce mixtures.

The mixing effect is influenced by site quality and environmental conditions. Figure 4.5 indicates that relative productivity in mixtures declines as site index and degree days above 5 ˚C (DD5) increase. This is consistent with other studies (Pretzsch et al., 2010; Pretzsch et al., 2013a; Toïgo et al., 2015) which have shown that overyielding occurs more commonly on poor sites than good sites. Pretzsch et al. (2013a) state that species interactions change from facilitation to competition along a gradient of increasing site quality, and the result is supported by the stress gradient hypothesis that facilitation among species is more common under stressful conditions (Bertness and Callaway, 1994). As expected for a harsh boreal environment, stand mixing effect is negatively influenced by increasing growing season length (DD5), which appears to be primarily associated with increases in competition in this study (Table 4.4). For the relative productivity of aspen, as site index increases, intraspecific competition may lead to decreasing PAI and increasing interspecific competition, especially in unthinned aspen plots.

With regard to changes in mixing effects over time, it is expected that the mixing effect will decrease as stand stocking (e.g., stand density index and spruce proportion) increases (Figures 4.6 and 4.7). Increasing total stocking is expected to lead to increased resource utilization and increasing intraspecific competition among aspen trees, leading to reduced productivity of aspen. In addition, increasing aspen stocking can suppress the growth of understory spruce. For these reasons, treatments with higher stocking (i.e., 4000 aspen tph plots) might show more significant declines than treatments with lower stocking (Figure 4.6). However, in unthinned aspen treatments, relative productivity was irregular and variable (Figures 4.6 and 4.7) due to self-thinning (Figure 4.2c). Continued measurement of this study will be useful in evaluating trends over a longer period, beyond age 28.

In addition to these reasons for the positive mixing effect, faster nutrient cycling, low mortality rate of spruce, and differences in phenology between two species are expected to lead to increases in productivity in boreal mixedwood stands (Groot and Carlson, 1996; Taylor et al., 1996; Constabel and Lieffers, 1996; Man and Lieffers, 1997; Man and Lieffers, 1999; Macisaac and Krygier, 2009). Spruce roots are primarily located near the surface while aspen roots are most abundant between 15 cm and 40 cm (Strong and La Roi, 1983; Man and Lieffers, 1999;

Lawrence et al., 2012). This difference in the distribution of root systems is likely to contribute to niche separation between aspen and spruce and increases in total productivity. Further research is needed to evaluate contributions of these and other factors to overyielding and to increase our understanding of mixing effects.

4.5 Conclusions

This study focuses on productivity of mixtures and illustrates the occurrence of overyielding in young (13 to 28 year old) boreal mixedwood stands in western Canada. My results show that overyielding varies depending on species composition. Thinned aspen stands show higher production than unthinned aspen stands and also contain larger trees than unthinned stands. Overyielding ranges up to 1.537 in the stands studied and is greatest in mixtures with 1500 aspen tph and 1000 spruce tph at approximately 20 years of age. Initial stand densities (basal area) of two species and initial aspen size (QMD) positively influence mixing effect while initial spruce size (QMD) negatively influences mixing effect. In other words, a mixed species stand that has space partitioning and size inequality between species, which reduces competition and favours expression of the functional traits (e.g., shade tolerance) of each species, tends to have higher productivity. The magnitude of overyielding declines with increasing growing season length (DD5) and the relative productivity of aspen decreases with increasing site quality. Overyielding may decrease as these stands age and spruce become larger, indicating a need for ongoing measurement and monitoring of the WESBOGY LTS installations, and other related studies.

Chapter 5: Conclusions and recommendations

Forest ecosystems consist of biotic (e.g., plants, wildlife, microorganisms, etc.) and abiotic components (e.g., soil, water, nutrients, climate, etc.) which shape forest structure, and ecological processes and changes through the interactions of components over time (Kimmins, 2004). In addition, management regime, stand dynamics, or natural disturbances can change the structure of a forest ecosystem, and these changes in structure may influence various processes (Spies, 1998). These changes in processes and conditions may then also lead to further changes in structure (Spies, 1998). Thus, understanding forest structures, their attributes, and relationships with associated functions is important for sustainable forest management.

In western Canada, trembling aspen (*Populus tremuloides* Michx.) is a widely distributed and common species. This species naturally regenerates in large numbers from root suckers, with density subsequently declining due to effects of intra- or interspecific competition, aging, and disturbances (e.g., insects, diseases, windthrows, and herbivory). During the process of stand dynamics, aspen stand structure in pure aspen or mixedwood stands changes and the associated functions also change.

This dissertation has examined some changes in characteristics (e.g., stockability, tree survival, and productivity) of aspen dominated stands associated with aspen stand dynamics (e.g., structural changes: tree sizes, vertical structure, stand composition, and stand density). The specific research objectives for this study were as follows:

- To determine whether a single regional maximum size-density relationship (MSDR) applicable across Alberta and Saskatchewan can be developed for pure aspen stands;
- To evaluate effects of climate on the static and dynamic self-thinning lines developed;

- To determine survival probability of aspen trees in relation to stand age and stand structure in aspen dominated stands;
- To examine effects of climate, stand factors, and tree age on survival probability;
- To determine whether overyielding occurs in young aspen-white spruce mixed stands (< 30 years old);
- To examine effects of species composition, stand density, species proportion, and tree size on overyielding, and to evaluate effects of climate and site index on the magnitude of overyielding in mixed stands.

Research on maximum size-density relationship (MSDR) has been conducted for one century, and is still ongoing to better understand size-density relationship and manage forests through improving statistical methods (Weller, 1987; Bi et al., 2000; Zhang et al., 2005; VanderSchaaf and Burkhart, 2007) and adding covariates representing site conditions, nutrients regime, and species composition (DeBell et al., 1989; Morris, 2003; Weiskittel et al., 2009; Comeau et al., 2010; Reyes-Hernandez et al., 2013). Chapter 2 also tried to develop two types of self-thinning lines (i.e., the static boundary and dynamic self-thinning lines) using stochastic frontier regression and linear mixed effects regression. For covariates, three different categories of climate variables (i.e., temperature, moisture, and extreme climate) were applied to self-thinning lines as a new trial.

The results of chapter 2 support the inclusion of climate in Maximum Size Density models for aspen. The static self-thinning line was developed with three climate variables and it showed how the slope and intercept varied depending on climate variables in this region. Maximum stocking declines as winter temperature, summer dryness, and frost free period increase in aspen stands due to water availability (Hogg et al., 2013; Worrall et al., 2013; Williams et al., 2013). Even though the sample size was small (26 plots), the dynamic self-thinning lines illustrate behavior of individual aspen stands (Weller, 1987) and results demonstrated that the dynamic line can better reflect effects of changing climate (Weller, 1990; VanderSchaaf and Burkhart, 2007).

Site conditions such as soil and nutrient regimes, and site index were not included in this study due to lack of available data. These data should be examined together with climate in future studies since site conditions can moderate effects of extreme climate on aspen stands or more negatively influence stand stockability with warming temperature. Furthermore, research on simulating stands with changing climate will be helpful to understand the change of carrying capacity of stands.

With regard to results of this chapter, increasing drought stress associated with increases in mean temperature and growing season length in western Canada's boreal forest (Price et al., 2013) may cause continuing tree mortality in aspen stands. Increases in mortality of trembling aspen can lead to the loss of biomass and the increasing carbon emission from dead trees (Hogg et al., 2008; Hogg and Michaelian, 2015), and also influence aspen inventory and allowance cut. In addition aspen stands weakened by drought stress can be more vulnerable to secondary factors, such as insects and diseases (Frey et al., 2004; Rouault et al., 2006), which may make aspen stands difficult to regenerate or recover from the stresses (Hogg and Wein, 2005; Worrall et al., 2015). Ongoing monitoring of aspen stands in terms of aboveground and belowground biomass and productivity should be considered in order to provide data relating to influences of climate change, age and other factors.

Analyses and results of the third chapter demonstrated that aspen stands can develop stand structure (e.g., age diversity and tree size diversity) and stand structure has a positive relationship with stand age based on increment core analysis and field sampling. With regard to the effect of stand structure on aspen survival, this study suggested that the stand structure (i.e., tree size diversity) is associated with increasing stand level competition (i.e., providing stressful condition to aspen). The model with interaction term of age groups (i.e., young, mature, and old stands) showed how tree survival varies with tree size and stand development stage. The result is also consistent with previous studies indicating that tree survival follows an inverted U-shaped pattern with increasing DBH (Harcombe, 1987; Monserud and Sterba, 1999).

In addition, findings illustrate the effects of climate (e.g., mean annual temperature) on different age groups of stands. Warmer temperature more negatively influences tree survival in young dense stands with high level of competition (Luo and Chen, 2013; Zhang et al., 2015). Under warmer conditions, increasing tree level competition (i.e., sum of basal area of overtopped trees) and stand level competition (i.e., tree size diversity or structural diversity) negatively influence aspen survival. As stands age, other factors such as site conditions (e.g., soil, site quality, aspect, slope, and elevation), disturbances (e.g., insect attacks, drought, windthrow, and herbivores), and diseases (e.g., stem decay, hypoxylon canker, and root disease) can influence aspen mortality (Peterson and Peterson, 1992; Allen et al., 1996; Frey et al., 2004; Marchetti et al., 2011; Dudley et al., 2015). Consequently, incorporating these factors in survival models is essential to successfully modeling effects of climate change.

Chapter four demonstrated that overyielding in young aspen-white spruce stands (< 30 years old) is evident and overyielding varies depending on species composition. Compared to unthinned aspen stands with spruce, thinned aspen stands with spruce showed higher production. This result suggests that shade tolerance of white spruce, effects of increasing understory light levels on growth of white spruce associated with thinning aspen, and the effects of reducing intraspecific competition for aspen were associated with higher production.

Results from chapter 4 indicate that tree size (e.g., diameter and tree height) and stand density (e.g., basal area and stand density index) are important factors influencing productivity of mixed stands. Differences in tree size leading to less competition and increased canopy stratification in these young mixed stands favour the functional traits (e.g., shade tolerance) of each species and lead to higher productivity. In addition, total periodic annual increment (PAI) in mixtures increases as both spruce and aspen basal area increase. This is related to the fact that species mixtures support higher stocking (Condés et al., 2013; Pretzsch and Biber, 2016; Pretzsch and Schütze, 2016) than pure stands leading to increases in productivity. The overyielding rate declined with increasing site quality and increasing growing season length as shown in other studies (Pretzsch et al., 2010; Pretzsch et al., 2013a; Toïgo et al., 2015). In this study, overyielding may decrease as these stands age and spruce become larger. However, these stands are still young (<30 years old) and self-thinning is still occurring, so ongoing measurement and monitoring of the WESBOGY LTS installations are needed to support further studies.

This chapter shows that a variety of species combinations can provide different sizes of trees and productivities of stands, suggesting that the management application can vary with the objective. Intensively thinned aspen stands (1500 stems/ha) with spruce maximized tree size (e.g., diameter) of two species and moderately thinned aspen stands (4000 stems/ha) with spruce maximized productivity and production of mixtures, while unthinned aspen stands with spruce showed lower productivity and smaller tree size. In addition, better biomass accumulation in mixtures than in monocultures is likely to increase carbon capture (Ruiz-Benito et al., 2014). However, the contribution of aspen to the total production of mixture was much higher than that of spruce in these young (<30) stands and results may differ at the final harvest due to increasing spruce production among species combinations. For example, a previous study (Kabzems et al., 2016) predicted the final yield of these types of mixtures. Intensively thinned aspen stand (2000 stems/ha) with the higher density of spruce (1300 stems/ha) maximized spruce total volume (345 m^3/ha) among mixtures (e.g., 2000, 5000, and 10000 aspen stems/ha with 500 or 1300 spruce stems/ha) with single harvest at age 90 and provided higher mean annual increment of the mixture (4.6 m^3/ha·year) than that of pure spruce (4.2 m^3/ha·year) at age 90. For the understory protection harvest with two harvesting plans at age 60 and 90, moderately thinned aspen stand (5000 stems/ha) with higher density of spruce (1300 stems/ha) maximized mean annual increment (5.9 m^3/ha·year) among mixtures. Consequently, thinned aspen stands with spruce can provide better productivity and yield, and objectives to be achieved will be different depending on the degree or application of thinning. To support decisions relating to the optimal management plan for aspen-spruce mixtures, continuing monitoring of these mixtures and prediction comparing for various combinations are needed.

In addition to the higher productivity of mixtures, provision of diverse habitats for wildlife and plants according to stand types and ages (Macdonald et al., 2010; Cavard et al., 2011b) and ecosystem functions (e.g., aesthetics, carbon storage, forest resilience and resistance, nutrient cycling, etc.) associated with mixedwood stands (Hoffman and Palmer, 1996; Forrester et al., 2005; Pretzsch et al., 2013b; Ruiz-Benito et al., 2014; Thurm et al., 2016) should be considered.

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