

University of Alberta

Dynamics of competition in boreal mixedwood stands

by

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Abstract

This dissertation investigated selected aspects of competition dynamics in boreal mixedwood stands of trembling aspen and white spruce. Results indicated that competition indices are effective for predicting the availability of light in the understory of young boreal mixedwood stands of variable density. However, these indices appear less suited to predict understory light in natural stands aged 20-60 years with a more narrow density gradient. Simple indices such as Lorimer's and basal area provided similar predictions compared to indices based on crown measurements. Relationships between aspen basal area and light transmittance differed significantly between geographical locations. Models suggested that incorporating the distance between subject trees and competitors did not improve predictions of spruce growth as a function of competition indices. The addition of initial spruce size significantly increased the predictive power of growth models.

I examined whether a single relationship can be applied across a broad range of locations and across stands of different ages. Results indicated that models of spruce growth differ with geographical location and stand age. It appears that the balance between competition and facilitation may shift from location to location and with stand age. This implies that changes in the occurrence and relative importance of each contributing factor add to the variation in relationships between growth and competition indices.

I investigated whether morphological attributes of spruce can be substituted to competition indices to predict spruce growth. Results showed some promise in using simple attributes such as height to diameter ratio for evaluating the vigour and growth of spruce seedlings.

Finally, I evaluated the impact of density reduction on frost incidence in young boreal mixedwood stands. It appears that aspen cover provided protection against frost, and more importantly these effects are site specific and depend on local site characteristics. The differential frost regime contributed to the variation in growth relationships.

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Chapter 1 General introduction

1.1 Stand development and succession in boreal mixedwood stands

Competition and disturbance are major factors that influence the dynamics of boreal mixedwood stands (Chen and Popadiuk 2002). These stands are comprised mainly of white spruce (*Picea glauca* (Moench) Voss) and trembling aspen (*Populus tremuloides* Michx.), with variable proportions of other species like balsam poplar (*Populus balsamifera* L.), white birch (*Betula papyrifera* Marsh.), black spruce (*Picea mariana* (Mill.) BSP), and balsam fir (*Abies balsamea* (L.) Mill.). Boreal mixedwoods occupy the majority of upland mesic sites in the western boreal forest (Rowe 1972).

Boreal mixedwood stands represent a spatially and temporally dynamic mosaic owing to adaptations to a complex disturbance regime (Andison and Kimmins 1999; Chen and Popadiuk 2002). There are two classes of disturbance in the boreal forest: *i*) those that affect mainly the overstory (e.g., insect outbreaks and wind-induced stem-breakage); and *ii*) those that affect both the overstory and the advance regeneration and soil organic layers (e.g., fire) (Bergeron et al. 1999). Wildfires and insect outbreaks are considered the main disturbances in the boreal forest (Johnson et al. 2003).

Large fires (over 1000 ha) are responsible for regenerating and structuring most of the boreal forest, with fires smaller than 1000 ha accounting for less than 10% of total burned area (Bergeron et al. 2002). Severe fires that induce the mortality of most trees while leaving isolated islands to serve as seed source play an important role in stand establishment. Fire suppression, as well as recent climate change, make it difficult to estimate the mean fire cycle, however it is believed to be around 150 years in Quebec, shorter in Western Canada (50-75 years), and as long as 500 years in the more humid climate on the East Coast. The replacement of fire with clearcutting can have very different ecological effects (i.e., soil organic matter does not burn and there are no snags left). Such differences can be partially compensated by site preparation and variable retention of dead standing wood to mimic the natural disturbance (Bergeron et al. 1999).

Boreal mixedwood stands follow the same four stages of development as every forested ecosystem: stand initiation, stem exclusion, canopy transition, and gap dynamics

(Chen and Popadiuk 2002). Gap dynamics is considered the last development stage, with gaps being reported to occupy between 3 and 16% of stand area in mature aspen stands increasing with stand age in a linear fashion (Cumming et al. 2000).

The severity of disturbance to the forest floor and availability of seed sources or vegetative reproductive organs are the main factors influencing the early development of mixedwood stands (Lieffers et al. 1996). In the absence of nearby seed sources and of exposed mineral soil as a result of deeply burned forest floor, aspen and other herbaceous sprouting species invade the site.

Root suckers lead to high initial densities in aspen stands, though these stands begin to self-thin very soon owing to natural mortality (Peterson and Peterson 1995). Spruce may regenerate immediately after fire or in the later development stages (Peters et al. 2002). Aspen stands experience a period of optimal biomass accumulation between the ages of 20 and 60 years, followed by a declining stage with reduced growth and vitality. Stand break-up seems to be determined by heart rot, and deterioration, once started, evolves very quickly and could take as little as 3-4 years (Peterson and Peterson 1992). The break-up stage of the aspen overstory coincides with spruce generally outgrowing the aspen, with both species co-dominating in the overstory. In the absence of major stand disturbance, the stand may evolve to a more stable forest community dominated by spruce to which other species, such as balsam fir, may be added later (Lieffers et al. 1996). In the absence of spruce regeneration, aspen may regenerate in the understory as the aspen canopy breaks up, resulting in a multiple-aged aspen stand (Bergeron 2004; Haeussler et al. 2007). If a well-developed shrub layer is present, such as beaked hazelnut (*Corylus cornuta* Marsh.), this may also inhibit aspen regeneration and lead to a shrub dominated ecosystem.

Succession mechanisms converge towards dominance by conifers, owing to their higher tolerance to shade. Accumulation of woody debris favors conifer regeneration on decayed logs, while the increase of humus depth may lead to a decrease in aspen recruitment (Bergeron 2000). In the absence of fire reverting stands to earlier succession stages, insects play an important role in regulating stand composition. In Quebec and

Ontario, mortality of balsam fir owing to budworm defoliation may allow the spruce to recover and maintain its overstory presence (Holling 1992).

Wind damage and windthrow has been studied much less than fire, possibly owing to the rare occurrence of catastrophic windthrows in the boreal forest, sometimes at intervals greater than 1000 years (Pastor and Mladenoff 1992).

In conclusion, depending on the disturbance regime, seed sources and seedbed availability, boreal mixedwood stands may follow multiple successional pathways (Lieffers et al. 1996; Bergeron et al. 2002; Chen and Popadiuk 2002): *i*) cyclic pathway – aspen invades the area, followed by spruce and ends with a spruce and balsam fir overstory; a stand-replacing fire reverts the site back to aspen; *ii*) convergent pathway – aspen and birch stands converge into spruce stands; *iii*) divergent pathway – aspen stands develop into spruce or birch stands; *iv*) aspen stands can develop into uneven-aged aspen stands; and *v*) aspen stands may develop into shrub dominated communities.

1.2 Evidence of competition in boreal mixedwood stands

Following stand replacing disturbances (e.g., wildfire and clearcutting) aspen dominates the main canopy owing to abundant regeneration and faster growth than spruce. Complementarities in regeneration strategies, initial growth rates, shade tolerance and longevity make possible the co-existence of aspen and white spruce in mixed stands (Lieffers et al. 1996).

White spruce is a species of high ecological and economic importance, and covers an impressive transcontinental range from Newfoundland and Labrador into Western Canada, Northwest Territories and Yukon (Burns and Honkala 1990). Natural regeneration of spruce is dependent on the coinciding existence of seed availability and suitable microsites (Purdy et al. 2002). Following a history of exploitative removal of large white spruce during the first half of the twentieth century and a gradual replacement of wildfire with clearcutting, regeneration and recruitment of white spruce are one of the main challenges in the establishment and management of boreal mixedwood stands (Lieffers and Beck 1994; Comeau et al. 2005).

Researchers, as well as field foresters and managers, have long observed the significant increase of white spruce growth following release from aspen competition (Cayford 1957; Lees 1966; Eis 1967; Stenecker 1967). However, interest in understanding and managing the competition processes in boreal mixedwood stands is relatively recent. Competition is a major factor that influences spruce growth, while also being one of the few factors that can be influenced by silviculture (Comeau et al. 2005; Bokalo et al. 2007). Other factors that limit spruce growth and survival in the western boreal forest include cold and flooded soil conditions in the spring, frost during the active growing season, summer droughts, nutrient deficient sites, and short growing season (Grossnickle 2000).

Competition in the boreal mixedwood forest is driven mainly by light and it has received extensive attention in numerous recent studies (Wright et al. 1998; Coates and Burton 1999; Lieffers et al. 1999; Messier et al. 1999; Comeau and Heineman 2003; Stadt et al. 2005). However, there is an increasing amount of evidence suggesting that competition for resources other than light (i.e., nutrients and water) should also be considered in boreal mixedwood stands (Staples et al. 1999; Hangs et al. 2002; Voicu and Comeau 2006; Matsushima and Chang 2007; Man et al. 2008).

Reduced growth and survival of spruce owing to competition from aspen and other hardwoods is well documented. Recent studies have examined competition effects on spruce performance: *i*) spruce growth in the understory of aspen dominated mixedwoods in Alberta (Lieffers and Stadt 1994) and Ontario (Groot and Carlson 1996); *ii*) competition effects of aspen and tall shrubs on spruce growth, light, and nitrogen availability in Quebec (Jobidon 2000); *iii*) spruce growth and light conditions in gaps of variable size in aspen dominated stands in Alberta (Pritchard 2003); *iv*) spruce growth and associated conditions (light, air and soil temperature, soil moisture) in openings adjacent to young aspen stands (Voicu and Comeau 2006); *v*) spruce growth in young mixedwoods of variable density dominated by paper birch (Comeau et al. 2003) or aspen (Bokalo et al. 2007; Filipescu and Comeau 2007; Kabzems et al. 2007); *vi*) growth of spruce underplanted beneath spaced aspen stands in the Northern Interior of British Columbia (Comeau et al. 2004, 2009).

While many competition studies have focused on interactions between aspen and white spruce, there is increasing evidence that shorter vegetation (grasses and shrubs) also plays an important role in the competitive environment affecting white spruce performance (Lieffers and Stadt 1994; Voicu and Comeau 2006; Cortini and Comeau 2008; Man et al. 2008). *Calamagrostis canadensis* is a particularly aggressive competitor that may invade boreal sites after disturbance (Lieffers et al. 1993; Landhäusser et al. 1996; Matshushima and Chang 2007; Man et al. 2008).

1.3 Competition and facilitation – two sides of the same coin?

Competition and facilitation usually occur together and may result in complex interactions (Berkowitz et al. 1995; Greenlee and Callaway 1996; Callaway and Walker 1997; Holmgren et al. 1997; Brooker et al. 2008). Competition and facilitation have also been observed to occur simultaneously in boreal forests (Simard and Vyse 2006). Understanding and separating the effects of co-occurring competition and facilitation on plant performance is difficult owing to their disjunctive influences that may vary spatially, temporally and at different scales within a certain ecosystem (Powell and Bork 2004; Dickie et al. 2005). Therefore, depending on the relative influence of individual processes, the end-result may be perceived as net competition, net facilitation, or neutral (balanced) effects.

One aspect that has received attention in the recent literature is whether mixed stands of aspen and spruce are more productive than pure stands of either species. Mixtures of species with different ecological requirements and tolerances, particularly mixtures that have intolerant overstory and tolerant understory species are expected to be more productive owing to niche complementarity (Kelty 1992). Model simulations have suggested that mixed stands would produce higher yield than pure spruce stands, but less than pure aspen stands (Wang et al. 1995). In contrast, other studies have shown that mixed stands may indeed be more productive than pure aspen stands and have speculated that higher productivity could be attributed, at least in part, to direct facilitative effects (MacPherson et al. 2001). Some of these effects may be explained by a reduction of competition owing to the vertical stratification of aspen and spruce in mixed stands

leading to a more efficient use of the growing space. In addition, there is also a phenological separation with significant amount of light available to understory spruce in the spring and fall when the aspen overstory is leafless (Constabel and Lieffers 1996; Comeau et al. 2009). Nevertheless, direct facilitative effects appear to play an important role through better litter decomposition and nutrient cycling rates, amelioration of environmental extremes, reduction of competition from invasive grasses and shrubs, and reduced incidence of insect damage (Lieffers and Stadt 1994; Taylor et al. 1996; Groot and Carlson 1996; Man and Lieffers 1999; Pritchard and Comeau 2004; Voicu and Comeau 2006; Man et al. 2008).

It was also theorized that the balance between competition and facilitation varies along resource gradients. Competition is believed to increase with increasing productivity (Grime 1979), while facilitation is more evident under extreme environmental conditions (Holmgren et al. 1997). Currently, there is an ongoing debate on the complementarity of these theories of plant competition across productivity gradients (Craine 2005). Limited evidence is available to support these theories for boreal mixedwood stands and more thorough studies are needed to test hypotheses of interplay between competition and facilitation.

1.4 Competition measurement and dynamics

Competition is determined by the partitioning of resources available in limited supply; as a process, it results in reduced fitness of competing individuals (e.g., growth, reproduction, survival). Since competition is difficult to measure directly, competition indices have been proposed and developed to quantify the effects of competition on plant performance (Weigelt and Jolliffe 2003). Most competition indices assume that there should be a relationship between the proximity and size of competitors and the availability of resources (Wagner and Radosovich 1991). Competition indices focus mainly on aboveground competition, assuming that the intensity of shading in forest stands is likely to be correlated with the intensity of root competition (Coomes and Grubb 2000).

The predictive ability of competition indices is tested by evaluating the fit of regression models of growth rates against competition levels (i.e., how much variation in the growth response could be accounted for by competition). Numerous studies (Daniels 1976; Alemdag 1978; Lorimer 1983; Daniels et al. 1986; Tomé and Burkhart 1989) have concluded that there are some indices better suited to certain species or conditions than other indices. Nevertheless, the performance of a particular index appears to be dependent on the stage of stand development or silvicultural treatment, and no index has been proven to be universally superior (Daniels et al. 1986).

The static nature of most competition indices, when in fact competition is dynamic and changes with stand age and development, limits their application (Burton 1993; Wagner 1993). In addition, most competition studies have focused primarily on the early stages of development and over short periods. Generalization of findings is difficult owing to space and time limitations of competition studies with little or no replication across larger geographical areas or over several years (Goldberg and Barton 1992).

Competition may vary across a range of conditions owing to the complexity and multiplicity of competitive and facilitative interactions and effects of climate and site factors on interactions between broadleaf and conifer components in the boreal mixedwood forest (Green 2004). However, there is limited information on how and if competition changes with site conditions and local environment. There are also plenty of unanswered questions regarding the temporal dynamics of competition. Competitive abilities of perennial plants change over time and may influence species composition and abundance in grassland communities (Lamb and Cahill 2006). In forest ecosystems, the predictive ability of growth models may increase by adjusting for age (Wagner and Radosevich 1991) or by making competition indices independent of age (Lorimer 1983). Simard et al. (2004) examined competitive processes along an age sequence of mixed stands of paper birch and conifers in British Columbia, concluding that the importance and intensity of competition may differ between young and older age classes.

Forest industry has witnessed a significant change in the management of western boreal mixedwoods during the last few decades. Several new strategies have been proposed and developed, however limited knowledge about their long-term effects

increase the uncertainty regarding these new approaches (Lieffers et al. 1996; Comeau et al. 2005). Economic, social, and ecological issues have to be integrated into these management plans (Bergeron et al. 1999; Greene et al. 2002). In this respect, growth models are important tools that provide managers and researchers with additional information on alternative strategies.

Competition has long been considered one of the main factors reducing forest growth (Vanclay 1994). Considerable debate surrounds the concepts of competition, ways to measure it (Brooker et al. 2005) and ways to include competition in forest growth models (Lieffers et al. 2008). Reliable growth models are needed to support the decision-making process and the development and implementation of viable management strategies.

1.5 Thesis outline and objectives

This research was prompted by the lack of verified information on the geographical and temporal changes of competition in boreal mixedwood stands. Rigorous hypothesis testing is needed to determine the processes and mechanisms that influence the dynamics of competition in these stands.

The research contained in this thesis is presented in four main sections, followed by a concluding chapter. In chapter 2, I examine the effectiveness of several competition indices (density, distance-dependent and independent size ratio, and crown based indices) to predict the understory light availability and growth of spruce across a gradient of competition environments (i.e., young mixedwood stands spaced to variable density) at four geographical locations in Alberta and Saskatchewan. The objectives were to determine which competition indices are reliable predictors of light and spruce growth across a larger geographical area and to test whether these models differ with location.

In chapter 3, I address the temporal changes of competition using an age sequence of boreal mixedwood stands between 10 and 60 years old located in Alberta. The objective was to apply a unified approach to testing competition indices across stands of different ages. I test whether relationships between spruce growth and competition indices change with stand age.

In chapter 4, I explore the potential of using morphological attributes as alternatives to competition indices to predict spruce growth across a gradient of competition environments of spaced young mixedwood stands. In addition, I use empirical data to examine several aspects of growth allocation under variable competition.

In chapter 5, I investigate the incidence and occurrence of frost in young mixedwood stands of variable density, followed by a description of air and soil temperature regime during the active growing season. I also discuss facilitative effects regarding frost protection and practical implications for management of young boreal mixedwoods.

I conclude the thesis with a review of my main findings, of implications for mixedwood management, and a discussion of topics requiring further research.

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Chapter 2 Aspen competition affects light and white spruce growth across several boreal locations in western Canada [‡]

2.1 Introduction

Trembling aspen (*Populus tremuloides* Michx.) is a prominent, widespread, and important competitor with white spruce (*Picea glauca* (Moench) Voss) following disturbance of spruce or mixedwood sites in the boreal forests of North America. Aspen regenerates abundantly, with initial sucker densities sometimes exceeding 100 000 stems·ha⁻¹. By age 10, aspen densities drop to about 10 000 stems·ha⁻¹, due to self-thinning (Peterson and Peterson 1992). After fire or clearcutting aspen grows more rapidly in height than spruce, leading to aspen-dominated stands for the first 40-60 years (Chen and Popadiouk 2002). Meanwhile, spruce may persist in the understory due to its ability to survive and grow slowly under aspen canopies at light levels as low as 10% of full sunlight (Lieffers and Stadt 1994). However, tending can be used to increase spruce growth and survival (Comeau et al. 2005).

Competition for light has been considered the major mechanism by which aspen influences spruce growth in the boreal forest (Burton 1993). Light availability may be improved by manipulating the overstory canopy, and several recent studies have shown that understory light can be predicted by various stand characteristics, especially basal area (Comeau et al. 2003; Comeau et al. 2006). Spruce needles and shoots experience photosynthetic saturation at light levels between 40% and 60% of full sunlight (Coates and Burton 1999), and maximum height growth of seedlings may occur at around 40% of full sunlight (Lieffers and Stadt 1994). Nevertheless, diameter and stem volume growth of spruce and other conifer saplings typically increase with light levels up to full sunlight (Wright et al. 1998).

Competition indices have been widely used to quantify and interpret the effects of plant competition (Weigelt and Jolliffe 2003). Numerous competition indices have been proposed and tested in studies of forest competition. Indices based on the size ratio

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between competitors and the subject tree adjusted by distance, initially proposed by Hegyi (1974) and Daniels (1976), have been modified and evaluated in numerous studies (Alemdag 1978; Martin and Ek 1984; Tomé and Burkhart 1989). Since application of distance-dependent indices is limited by the requirement for measurement of intertree distances, distance-independent indices have been more widely applied for evaluating competitive effects (Lorimer 1983; Daniels et al. 1986; Holmes and Reed 1991). Crown-based competition indices have been proposed as alternatives to indices based on more commonly collected height and diameter measurements (Hix and Lorimer 1990; Biging and Dobbertin 1992). Incorporating crown size may include biological information more meaningful to explaining competitive interactions, such as the amount of light intercepted by subject trees and the use of other resources (i.e., water and nutrients). While some indices work better than others under particular sets of conditions, the vast literature on the subject does not indicate any index as being the best under all conditions.

Despite the extensive and successful use of competition indices, there is still criticism of their use. One of the main shortcomings is that competition indices provide a static quantification of competition within a dynamic and changing system (Burton 1993). In addition, most competition studies are limited in space and time (Goldberg and Barton 1992), with little replication across larger geographical areas or across several years, which limits generalization of findings.

Previous studies of aspen competition indicate that simple distance-independent competition indices such as basal area and density can be as effective as more detailed indices in spruce plantations (Steneker and Jarvis 1963; Alemdag 1978; MacIsaac and Navratil 1996). Comeau et al. (2003) reported that basal area and light transmittance provide predictions of white spruce growth similar to those obtained using distance-independent or -dependent size ratio indices of paper birch (*Betula papyrifera* Marsh.) competition, suggesting little benefit from including proximity in a competition index.

Crown-based competition indices have not been tested for their application to the aspen-spruce combination. In addition, there are no published studies designed to examine whether the same relationships between growth and competition apply across a range of locations. This paper evaluates the effectiveness of several competition indices

(density, distance-dependent and -independent size ratio, and crown-based indices) for predicting light transmittance and examines the use of these indices together with initial size for describing variation in growth of spruce across a gradient of densities following spacing treatments at four locations. My objectives were to evaluate the influence of aspen density on light and growth of spruce and to identify which competition indices provide the most reliable predictions. A second objective was to test for differences in these relationships between four geographical locations (i.e., can a single relationship be applied across a broad range of locations?).

2.2 Materials and methods

This study used selected field installations established by the Western Boreal Growth and Yield association (WESBOGY) as part of a Long-Term Study (LTS) of growth and development of tended mixtures of white spruce and trembling aspen. Ten forest companies and government agencies from western Canada are involved, and each member established one block with two installations, one for a superior site and one medium (site quality was determined prior to establishment based on field observations and previous stand information). The LTS consists of plots with different combinations of aspen and spruce densities, randomly assigned in each of the two replicates. Each measurement plot is 20 m x 20 m with a 5 or 10 m treated buffer around the plot. More details on the experimental design and establishment and maintenance of the LTS can be found in WESBOGY (2004).

My study utilized the four oldest WESBOGY LTS blocks located near Peace River, Grande Prairie, and Edson in Alberta and near Prince Albert in Saskatchewan (table 2-1). Both the medium and superior installations for Peace River (abbreviated hereon as PRm and PRs) and Prince Albert (PAm and PAs) have two complete replications. The medium installation for Edson (EDm) includes two complete replications, while at the superior installation (EDs), there is only one replication. At the Grande Prairie (GP) block, the plots have recently been characterized as having very similar site quality; therefore, GP currently has three replications, as one of the initial four replications was damaged by oil and gas development.

For each installation, plots with five levels of aspen density (0, 500, 1500, and 4000 stems·ha⁻¹ and natural unthinned) and two levels of spruce density (500 and 1000 stems·ha⁻¹) were used. Given the size of spruce (0.7 - 2.6 m height) at the time of the study, intraspecific competition is unlikely to influence growth of individual spruce trees at the present time; therefore, the two levels of spruce density were treated as extra replicates of aspen density. A total of 140 plots were used in this study (5 aspen densities x 2 spruce densities x 2 replicates x 2 site quality levels x 4 locations = 160 plots, less 10 plots lost in Edson and 10 in Grande Prairie).

Sites were generally flat, with slopes less than 5%, with soil drainage ranging from moderate to well drained (table 2-1). All sites were characterized as low-bush cranberry ecosites, with mesic moisture regime and medium nutrient regime (Beckingham and Archibald 1996, Beckingham et al. 1996a, 1996b). Soil parent materials were morainal, glaciolacustrine, and glaciofluvial, with medium to moderately fine texture, and a variety of clay, clay-loam and sandy loam textures, usually with less than 10% coarse fragments. Precipitation during the study period (2002-2003) was below climatic normals (table 2-1).

In each plot, three spruce seedlings located closest to gridpoints established 5m north, 5m southeast, and 5m southwest of the plot center were selected. Selection of subject trees aimed to ensure their independence from each other, no edge influences, and no overlap between the aspen competition zones. Root collar diameter, total height, leader length, and crown radii in four cardinal directions were measured for each spruce in May 2002, May 2003, and September 2003. These measurements provided: (1) growth information on diameter, height, and stem volume (spruce stem volume was calculated using the formula for a cone) during the 2-year measurement period (2002-2003), and (2) data on initial spruce size (diameter, height, and crown size; crown volume and surface area were calculated using the formula for a cone) at the beginning of the growing period (2002).

During the summer of 2002, aspen competition was assessed within a 3.99 m radius plot centered at each selected spruce. While search radius has been shown to impact the effectiveness of competition measures (Hynynen and Ojansuu 2003), a 3.99 m

radius is expected to be optimal for competition quantification based on similar studies conducted in stands of comparable age (Comeau et al. 1998; Simard and Sachs 2004). Diameter at breast height was measured for all aspen in the 3.99 m radius plot. The assessment plot was divided into four quadrants and in each of them, the closest dominant or codominant aspen was determined and the intertree distance (aspen-spruce) was measured in addition to height, height to crown base, and crown radii (in four cardinal directions). In each competition plot, 10-15 representative aspen were systematically selected across the range of sizes and measured in greater detail (height, height to crown, and crown radii). Regression equations were developed for each treatment plot to estimate height, average crown radius, and crown length as a function of breast height diameter for all aspen. Aspen crown form was assumed to be a prolate ellipsoid (a rotation ellipse around the major axis, crown length, with average crown diameter as the minor axis). Crown surface area, cross-sectional area, and volume were also calculated.

The fraction of full sunlight (transmittance) reaching each subject tree was measured during the summers of 2002 and 2003 using LAI-2000 plant canopy analyzers (Li-COR Inc., Lincoln, Nebraska). Previous studies showed that LAI-2000 sensors provide consistent estimates of light transmittance throughout the growing season (Gendron et al. 1998). In a concurrent study at the GP and PR WESBOGY field locations, Voicu (2005) observed that the instantaneous LAI-2000 measurements were highly correlated with photosynthetic photon flux density integrated over the growing season. Light was measured at the top of the spruce seedlings and at midcrown height with the sensor oriented pointing away from the crown of the subject tree and paired subsequently with another simultaneous measurement taken in an adjacent open area at the same height. The sensors were fitted with 180° view restrictors, with one reading taken facing west in the morning and a second reading taken facing east in the afternoon to avoid direct light in the sensor view. For the midcrown measurement, the sensor was located just outside the canopy edge so that it did not include the influence of the subject tree on light levels at this height. The sky portion below 31.9° above the horizon was

ignored, and only values from rings 1-4 of the LAI-2000 sensor were used, to avoid the influence of plot edges.

My objectives were to evaluate indices that can be calculated from measurements commonly and readily collected in the field. This guided the selection of indices included in this study (table 2-2). Competition indices used for predicting understory light incorporated only aspen characteristics and were kept independent of spruce size (i.e., spruce size in Lorimer's and Hegyi's indices was set to 1), except for the spacing factor that was adjusted with the height at which light was measured. Similar indices were used for explaining variation of spruce growth. Indices LOR1, VCR1, SCR1, and SCROS1 included only characteristics of aspen as opposed to LOR2, VCR2, SCR2, and SCROS2, which also included the size of subject spruce. This differentiation was based on concerns that size ratio indices may artificially inflate the coefficient of determination in the regression models by incorporating subject tree size in the competition index. Distance-dependent indices (HEG4, VCR4, SCR4, and SCROS4) were based on data collected only from the four closest competitors and adjusted with the number of trees per assessment plot. Spacing factor indices were also used in two forms, one (SF_T) adjusted with spruce height, which considers the intertree distance as a ratio of the difference in height between the competitor and subject trees, and another (SF_{AW}) that uses only aspen height. For plots with aspen density of zero, values of 0.001 were assigned to competition indices that otherwise would have been 0 in order to allow for different models to be tested.

Simple and multiple nonlinear regression models were developed for each installation (medium and superior) and location to predict (i) understory light as a function of competition indices:

$$[1] \quad DIFM = a + b \ln CI; DIFT = a + b \ln CI$$

$$[2] \quad DIFM = a CI^b; DIFT = a CI^b$$

$$[3] \quad DIFM = a e^{b CI}; DIFT = a e^{b CI}$$

where transmittance was measured at midcrown (DIFM) and topcrown (DIFT) and CI is competition index as defined in table 2-2; (ii) spruce growth as a function of competition indices:

$$[4] \quad \text{SWgr} = a + b \ln \text{CI}$$

$$[5] \quad \text{SWgr} = a \text{CI}^b$$

$$[6] \quad \text{SWgr} = a e^{b \text{CI}},$$

where spruce growth measurements (SWgr) tested were diameter, height, height allocation ratio (the latter as defined in Comeau et al. 2003), and stem volume increment; and (iii) spruce growth as a function of competition indices and initial size:

$$[7] \quad \text{SWgr} = a \text{CI}^b \text{IS}^c$$

$$[8] \quad \text{SWgr} = a e^{b \text{CI}} e^{c \text{IS}}$$

$$[9] \quad \text{SWgr} = a \text{CI}^b e^{c \text{IS}}$$

$$[10] \quad \text{SWgr} = a e^{b \text{CI}} \text{IS}^c$$

where the initial spruce size (IS) was tested in the form of initial diameter, height, crown volume and crown surface area, a , b , and c are model parameters.

Model parameters were estimated using least-squares nonlinear regression. Data analysis was completed using the SAS statistical package for Windows (version 8.2) (SAS Institute Inc., Cary, North Carolina). Validity of the underlying assumptions for tested models and evaluation of model fit was based on analysis of residuals plotted against predicted values with the goal of minimizing the residual mean square (Bates and Watts 1988). The adjusted values of the coefficient of determination (R^2_{adj}) were calculated to account for differences in sample size and model complexity (i.e., number of parameters). Despite criticism of using R^2 for nonlinear models (Ratkowsky 1990), R^2 represents a robust tool in deciding on model fit and provides an effective method for comparing the degree to which different independent variables explain variation in a dependent variable (Draper and Smith 1981). The R^2 values also offer additional information on the importance of competition for a particular location (Welden and Slauson 1986). Extra sum of squares testing with indicator variables (Ott 1997) was used to evaluate whether data could be combined into a single equation for medium and superior sites at each location and for all four geographical locations.

2.3 Results

Significant relationships ($p < 0.001$) were found between transmittance and competition indices at all study locations (table 2-3). Consistently better results were obtained for predicting understory light measured at white spruce midcrown as opposed to light measured at the top of the spruce; therefore, results are presented for midcrown measurements. Exponential models provided superior prediction and fit the data sets better than other tested models (power and logarithmic). Predictive ability varied with location and competition index, with values of the coefficient of determination (R^2_{adj}) ranging between 0.41 and 0.94. At each field installation, differences between all of the competition indices except trembling aspen density were small (density was generally one of the poorer indices). The group of indices based on crown size performed better than other indices, and amongst the crown indices, SCR1 was generally superior. Crown indices were followed by a second group of indices comprising basal area, LOR1, and HEG4, of which basal area was marginally better.

Extra sum of squares tests of regression fit to data from different locations showed significant differences for relationships between understory light and aspen basal area or crown surface (table 2-4, results shown for basal area). Since there were no significant differences between medium and superior sites at PR and PA (i.e., no significant differences were detected between PRs and PRm and between PAs and PAm, respectively), data for different site qualities at each location could be pooled. However, significant differences were detected between the medium and superior sites at ED. With the exception of PR with EDm and GP with EDs, all the other combinations indicated significant differences (figure 2-1). Parameter estimates for these relationships are provided in table 2-5.

Significant relationships between spruce growth and competition indices were obtained. Stem volume increment provided consistently better results than diameter and height growth; hence, presentation of my results is focused mainly on relationships between stem volume growth and competition indices. As expected, spruce growth increased with available resources (e.g., light) and aspen spacing (figure 2-2). When considered by itself, competition explained less than 60% of the variation of stem growth

(table 2-6) and the importance of competition (expressed as R^2_{adj} values) was lower for GP ($R^2_{\text{adj}} \leq 0.16$) and ED ($R^2_{\text{adj}} \leq 0.34$) and was highest at PR ($R^2_{\text{adj}} \leq 0.60$).

Importance is defined as the relative impact of competition versus other environmental conditions and it is represented by the amount of total variation explained by competition (Welden and Slauson 1986). The performance of competition indices varied from location to location, with basal area and midcrown light transmittance (DIFM) offering some of the best results. Indices that included spruce tree size (LOR2, VCR2, SCR2, and SCROS2) provided only a small increase of predictive ability as opposed to indices that did not include subject tree size (LOR1, VCR1, SCR1, and SCROS1). Distance-dependent indices (HEG4, VCR4, SCR4, and SCROS4) provided slightly inferior results compared with distance-independent indices (LOR2, VCR2, SCR2, and SCR2). Both spacing factor and density consistently ranked low in terms of predictive ability.

Tests for difference between models predicting spruce growth as a function of light transmittance showed significant differences between locations (table 2-7). The medium and superior sites for both PA and ED allowed data pooling (no significant difference was detected between PAm and PAs and between EDm and EDs, respectively).

The addition of initial size as a second explanatory variable in multiple nonlinear regression models increased R^2_{adj} values. Several measures of initial spruce size were tested, including initial stem diameter, stem height, volume, and surface area of crown. For example, at PRm, adding spruce crown volume to aspen basal area explained 74% of the variation, crown surface area 74%, height 74%, and diameter 79%, whereas for PRs, crown volume combined with basal area explained 80% of the variation, crown surface area 84%, height 85%, and diameter 86%, respectively; similar trends were observed for the other study locations. Thus, results are presented for the best models obtained when initial spruce diameter was added to competition indices (table 2-6). Multiple regression models including competition indices and initial diameter explained between 63% and 93% of the variation in stem volume increment. The best predictive models across the range of locations included aspen basal area and initial spruce diameter followed by

models combining light transmittance and diameter. These relationships are illustrated in figures 2-3 and 2-4.

Models predicting spruce volume increment as a function of aspen basal area and initial spruce diameter were tested for differences between locations and installations (table 2-8). These tests indicated no significant differences between medium and superior installations at each location but indicated that the PR location differed significantly from the other three locations (PA, ED, and GP). Similar differences were obtained when other initial spruce size measures (e.g., height or crown volume) were used in addition to basal area or transmittance.

Predictive models of stem volume increment were superior to models predicting diameter and height increment. Nevertheless, diameter and height increment of spruce were also well predicted by competition indices and initial spruce size. Selected models for the Peace River location are presented in table 2-9.

2.4 Discussion

Results demonstrate the effectiveness of competition indices based on trembling aspen characteristics for predicting understory light in western boreal mixedwoods. While indices based on crown characteristics provided slightly better predictions, other indices, readily obtained from common field measurement such as stem diameter (i.e., Lorimer's index) or basal area, are also effective for predicting light across a broad range of aspen densities and locations. Results are consistent with findings of previous studies (Comeau et al. 2003; Comeau et al. 2006). Predictions of transmittance were better at white spruce midcrown than at the top position owing to this location being more consistently located below the base of the live aspen canopy. Observations obtained from examination of vertical light profiles suggest a substantial increase in variability of light conditions and a declining influence of basal area as measurement positions move up through the live aspen canopy (Pritchard and Comeau 2004; Comeau et al. 2006). Equations for estimating transmittance developed in this study should only be applied to situations where the spruce midcrown point is below the base of the aspen canopy.

Differences in parameter values between locations may be related to the influence of climatic and site factors, particularly soil moisture, on relationships between leaf area index and basal area or crown cover. Messier et al. (1998) suggested this as the reason for differences in understory light levels for stands with similar basal area in Quebec and Alberta. Comeau et al. (2006) also reported regional differences in parameter values for models relating transmittance to aspen basal area that appear to be related to climate. Lower precipitation and soil moisture levels as a result of regional and year to year variation appear to lead to reduced aspen leaf area index and increased light availability in the understory.

Data in this study were collected from a range of aspen densities 5 - 7 years following spacing, and it is likely that differences in rates of crown and leaf area development between locations influence results. Temporal and spatial variations in leaf area index attributed to forest management and site factors have been observed in temperate deciduous forests (Le Dantec et al. 2000). Moreover, rates of leaf area index recovery following thinning seem to be site specific owing to differences in productivity (Jokela et al. 2004). Further studies are needed to determine if relationships between transmittance and basal area (or other competition measures) change over time as a reflection of annual growing conditions, time after treatment, and other factors.

Although crown-based indices are expected to perform better than other indices (Biging and Dobbertin 1992), we have found that the performance of stem diameter based indices was only slightly inferior, raising the question of whether the more difficult and expensive field measurements associated with crown indices are justified by the small gain in predictive power. The relatively small difference between indices within individual locations may be explained in part by the strong correlation between aspen measures and leaf area (Pinno et al. 2001). The number of stems performed reasonably well, with better performance at some locations than at others. Similar results are reported in a study of effects of aspen competition on growth of lodgepole pine (*Pinus contorta* Dougl. ex Loud) in central British Columbia (Newsome et al. 2003). The coefficient of determination for models using number of stems as the competition index was higher for installations with fairly uniform and well-stocked aspen stands than at

installations with heterogeneous stands having larger size differentiation. At the same time, basal area appears to serve as a consistently good predictor of both light and spruce growth. Basal area may be more desirable for general application, since it incorporates both aspen diameter, which is correlated with leaf area of individual trees, and the number of trees.

The group of indices that included crop tree size (LOR2, VCR2, SCR2, and SCROS2) offered only a slight improvement over indices that did not include crop tree size (LOR1, VCR1, SCR1, and SCROS1); therefore, concerns over artificially inflating predictive power through including crop tree size in size ratio indices were partially alleviated for the particular stand structure in this study (i.e., young mixedwoods with planted spruce under spaced aspen). Another controversial aspect is whether to incorporate distance between crop tree and competitors in competition indices (Daniels et al. 1986; Tomé and Burkhart 1989). In my study, distance-dependent indices (HEG4, VCR4, SCR4, and SCROS4) provided inferior predictions to distance-independent indices, confirming previous findings for juvenile mixtures of spruce and aspen or paper birch (Alemdag 1978; Comeau et al. 2003). My versions of distance-dependent indices were based on spatial information from only the four closest competitors, given practical methodological limitations, while the search radius was 3.99 m (see Materials and Methods). However, it is still possible that distance-dependent indices could perform better than distance-independent indices in more heterogeneous stands where larger competition plots are used.

My results are consistent with the expectation (e.g., Wright et al. 1998; Coates and Burton 1999) that increases in available resources are associated with positive spruce growth responses. However, the measures of competition explain less than 60% of the variation in spruce stem increment, suggesting that aspen competition is only one of many factors affecting growth. R^2_{adj} values are lower for GP, ED, and PA than for PR, which may reflect the effects of microclimatic extremes (frost), wildlife, and competition from other vegetation (i.e., grasses and shrubs). In addition, my findings show that there are differences in growth-competition relationships between locations. Other studies indicate that competitive effects may vary as a function of climate, availability of

resources, and influences of other limiting factors. Both the most effective competition measure and the relationships between lodgepole pine growth and competition were found to vary with study location (Newsome et al. 2003). Pritchard (2003) and Voicu and Comeau (2006) also found significant location differences in relationships between white spruce growth and transmittance. Green and Hawkins (2005) suggested that competitive interactions may differ between north-facing and south-facing slopes in subboreal mixedwood stands owing to changes in environmental conditions.

There are few plant competition studies that examined the influence of environmental factors on competition. An extensive literature search and meta-analysis of results from plant competition studies suggested that the magnitude of competition does not depend on site, but authors did not find it conclusive given the very limited number of studies testing site influences (Goldberg and Barton 1992). Moreover, the same meta-analysis indicated that outcomes of competition studies are sometimes conflicting; for example, findings from natural density studies are not consistent with results from experimentally created gradients.

Another aspect often neglected when interpreting competition effects is that competition and facilitation usually occur together and can result in very complex interactions (Holmgren et al. 1997). Broadleaf overstory manipulation simultaneously impacts competitive and facilitative interactions (Simard and Vyse 2006). Facilitative effects of aspen in the boreal forest may include reduced photorespiration and photoinhibition of understory spruce (Singsaas et al. 2000; Langvall and Örlander 2001), reduced grass and shrub competition (Lieffers and Stadt 1994), reduction of frost (Groot and Carlson 1996; Pritchard and Comeau 2004), and reduced incidence of insect damage (Taylor et al. 1996). Separating the influences of competition and facilitation on tree performance is difficult, and facilitation may be overshadowed by the importance of competition for light. Nevertheless, the balance between competition and facilitation may shift from site to site owing to variation in the relative occurrence and importance of each factor (Callaway 1998) and may offer another explanation for variation in relationships between growth and competition indices. For example, frost occurrence and intensity and

the incidence of insect damage were observed to be site specific in boreal mixedwood sites (Voicu and Comeau 2006).

Although competition for light seems to be the driving factor affecting spruce growth, other interactions are also likely to be occurring at the same time, such as competition for other resources (water and nutrients), physical interaction (e.g., leader whipping), microclimatic effects (soil and air temperature), and other interactions (DeLong 1991). The differential availability of resources and their interplay influence sapling growth in the understory (Finzi and Canham 2000). In addition, local site characteristics may affect growth relationships (Kobe 1996).

Adding initial size as a second explanatory variable increased the predictive power of spruce growth models. The ability of competition indices to explain growth variation seems to be limited and the use of initial size as an additional variable is recommended by several studies (Morris and MacDonald 1991; MacFarlane and Kobe 2006). While competition indices incorporate present growth conditions, subject tree size at the beginning of the growing period is considered to account for past factors, acting as the “tree memory” of previous external and internal influences (Hatch et al. 1975). Subject tree size may also provide a surrogate measurement of tree leaf area, which will have an important influence on the amount of light being absorbed and utilized by the tree (Pritchard 2003).

In this study, initial diameter performed better for describing variation in spruce growth than other initial size measures. This is consistent with the pipe model theory (Waring et al. 1982; Chiba 1998), suggesting that stem conducting cross-sectional area is strongly correlated with tree leaf area. In some cases, other measures of tree size such as crown surface area have been more closely related to growth than diameter or height (Pritchard 2003; Voicu and Comeau 2006). Variation in the effectiveness of tree measures may be influenced by the ability to represent variation in leaf area, as well as by site, relative position in the canopy, or other characteristics that may influence tree growth.

This study indicates that several types of competition indices can be used to predict understory transmittance and spruce growth. Simple indices such as basal area or

Lorimer's had very close predictive ability to those of more complex indices based on crown measurements. Selection of which index to use in certain conditions should be based on desired levels of precision and resources available to collect and process field data. Indices tested in my study may have direct application in traditional growth and yield models and may facilitate the transition of growth modeling from the juvenile stage to intermediate and mature stands (Vanclay 1994). Moreover, some of the indices in this study may provide a link to other types of models. For example, basal area may facilitate incorporating light into empirical growth and yield models, whereas crown size may offer a link to other hybrid and process-based models.

2.5 Conclusions

Results indicate that distance-independent competition indices (basal area and Lorimer's) work as well or better than distance-dependent indices for characterizing trembling aspen competition with white spruce in young mixedwood boreal stands in western Canada. Crown competition indices provide only a small gain over simpler indices readily obtained from common field measurements. Relationships between aspen competition indices and either light or spruce growth vary from location to location, making region-specific calibration of these relationships necessary. Further study is needed to understand the factors contributing to this variation.

2.6 References

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Table 2-1 Location and site information for the study installations

| Location | Latitude and longitude | Elevation (m asl) | Natural subregion ^a | Soil subgroup | Year planted | Total annual precipitation (mm) | | | Growing season precipitation ^b (mm) | | |
|------------------------------|------------------------|-------------------|--------------------------------|-------------------------|--------------|---------------------------------|------|---------------------|--|------|--------|
| | | | | | | 2002 | 2003 | Normal ^c | 2002 | 2003 | Normal |
| Peace River Medium (PRm) | 56°55'N 118°30'W | 800 | Boreal Mixedwood | Orthic Gray Luvisol | 1992 | 256 | 363 | 402 | 170 | 195 | 269 |
| Peace River Superior (PRs) | 56°41'N 117°72'W | 731 | | | | | | | | | |
| Grande Prairie (GP) | 54°55'N 118°30'W | 762 | Boreal Mixedwood | Orthic Gray Luvisol | 1991 | 399 | 392 | 447 | 255 | 175 | 288 |
| Edson Medium (EDm) | 53°46'N 116°41'W | 1060 | Lower Foothills | Brunisolic Gray Luvisol | 1992 | 327 | 451 | 562 | 196 | 234 | 415 |
| Edson Superior (EDs) | 53°48'N 116°38'W | 1120 | | | | | | | | | |
| Prince Albert Medium (PAm) | 53°45'N 105°30'W | 552 | Mid-Boreal Upland | Orthic Gray Luvisol | 1990 | 332 | 315 | 424 | 248 | 235 | 295 |
| Prince Albert Superior (PAs) | 53°40'N 105°56'W | 549 | | Brunisolic Gray Luvisol | | | | | | | |

Note: ^a From Beckingham and Archibald (1996), Beckingham et al. (1996a, 1996b)

^b Growing season considered May to September; ^c Normal values represent averages for the interval 1971-2000 (source National Climate Data, Environment Canada)

Table 2-2 Formulas used to calculate competition indices (including abbreviations)

| Competition index | Formula (description) |
|--|---|
| Number of trees | N (stems/ha) |
| Basal area | BA (m ² /ha) |
| Lorimer's 1 | $\text{LOR1} = \sum_{i=1}^n DBH_{AWi} \text{ (cm)}$ |
| Lorimer's 2 | $\text{LOR2} = \sum_{i=1}^n DBH_{AWi} / D_{SW}$ |
| Crown volume 1 | $\text{VCR1} = \sum_{i=1}^n VCr_{AWi} \text{ (m}^3\text{)}$ |
| Crown volume 2 | $\text{VCR2} = \sum_{i=1}^n VCr_{AWi} / CrV_{SW}$ |
| Crown surface area 1 | $\text{SCR1} = \sum_{i=1}^n SCr_{AWi} \text{ (m}^2\text{)}$ |
| Crown surface area 2 | $\text{SCR2} = \sum_{i=1}^n SCr_{AWi} / CSA_{SW}$ |
| Crown sectional area 1 | $\text{SCROS1} = \sum_{i=1}^n SCros_{AWi} \text{ (m}^2\text{)}$ |
| Crown sectional area 2 | $\text{SCROS2} = \sum_{i=1}^n SCros_{AWi} / SCros_{SW}$ |
| Hegyi's (based on 4 closest aspen) | $\text{HEG4} = \left(\sum_{i=1}^4 DBH_{AWi} / D_{SW} * dist_i \right) * Npl / 4$ |
| Crown volume (based on 4 closest aspen) | $\text{VCR4} = \left(\sum_{i=1}^4 VCr_{AWi} / CrV_{SW} * dist_i \right) * Npl / 4$ |
| Crown surface area (based on 4 closest aspen) | $\text{SCR4} = \left(\sum_{i=1}^4 SCr_{AWi} / CSA_{SW} * dist_i \right) * Npl / 4$ |
| Crown sectional area (based on 4 closest aspen) | $\text{SCROS4} = \left(\sum_{i=1}^4 SCros_{AWi} / SCros_{SW} * dist_i \right) * Npl / 4$ |
| Light transmittance (at spruce midcrown) | DIFM (%) |
| Light transmittance (at spruce top) | DIFT (%) |
| Spacing factor (top of spruce) | $\text{SF}_T = 10000 / (H_{AW} - H_{SW}) * \sqrt{N} \text{ (%)}$ |
| Spacing factor (aspen) | $\text{SF}_{AW} = 10000 / H_{AW} * \sqrt{N} \text{ (%)}$ |

Note: DBH_{AWi} , basal diameter of the i th aspen tree; D_{SW} , root collar diameter of the subject spruce tree; VCr_{AWi} , crown volume of the i th aspen tree; CrV_{SW} , crown volume of

the subject spruce tree; SCr_{AWi} , crown surface area of the i th aspen tree; CSA_{SW} , crown surface area of the subject spruce tree; $SCros_{AWi}$, area of the crown horizontal section of the i th aspen tree; $SCros_{SW}$, area of the horizontal section at crown base of the subject spruce tree; $dist_i$, intertree distance between the subject spruce and the i th aspen tree; N_{pl} , number of aspen trees per plot of competition assessment; H_{AW} , dominant height of aspen; H_{SW} , height of subject spruce tree; N , number of aspen trees per hectare; light transmittance was averaged for the 2002 and 2003 growing seasons.

Table 2-3 Predictive ability of light transmittance (measured at white spruce midcrown) by competition indices (R^2_{adj} values)

| Location | Installation | Competition index | | | | | | | | | | |
|----------------|--------------|-------------------|------|------|------|------|--------|------|------|------|--------|-----------------|
| | | N | BA | LOR1 | VCR1 | SCR1 | SCROS1 | HEG4 | VCR4 | SCR4 | SCROS4 | SF _T |
| Peace River | Medium | 0.80 | 0.92 | 0.90 | 0.89 | 0.94 | 0.93 | 0.85 | 0.94 | 0.92 | 0.92 | 0.86 |
| | Superior | 0.81 | 0.86 | 0.86 | 0.86 | 0.87 | 0.88 | 0.87 | 0.87 | 0.88 | 0.88 | 0.77 |
| Prince Albert | Medium | 0.68 | 0.80 | 0.78 | 0.76 | 0.78 | 0.78 | 0.75 | 0.73 | 0.75 | 0.75 | 0.73 |
| | Superior | 0.65 | 0.67 | 0.68 | 0.64 | 0.68 | 0.67 | 0.70 | 0.70 | 0.71 | 0.70 | 0.59 |
| Edson | Medium | 0.85 | 0.82 | 0.86 | 0.81 | 0.85 | 0.85 | 0.81 | 0.82 | 0.83 | 0.85 | 0.70 |
| | Superior | 0.92 | 0.94 | 0.95 | 0.93 | 0.96 | 0.95 | 0.91 | 0.92 | 0.92 | 0.93 | 0.74 |
| Grande Prairie | | 0.46 | 0.51 | 0.54 | 0.52 | 0.55 | 0.54 | 0.51 | 0.52 | 0.53 | 0.51 | 0.53 |

Note: All values shown are for statistically significant models ($p < 0.001$) and are based on nonlinear regressions fit to data using the exponential equation $DIFM = a e^{(b \cdot CI)}$ where DIFM is light transmittance in the understory, CI is competition index as defined in table 2-2, and a and b are model parameters.

Table 2-4 Test of difference between locations and installations for models predicting light transmittance as a function of basal area of the overtopping trembling aspen (p values)

| | | Peace River | Prince Albert | Edson | | Grande Prairie |
|----------------|----------|-------------|---------------|--------|----------|----------------|
| | | | | Medium | Superior | |
| Peace River | | | 0.042* | 0.238 | 0.0004* | 0.0001* |
| Prince Albert | | | | 0.039* | 0.00058* | 0.0001* |
| Edson | Medium | | | | 0.008* | 0.00056* |
| | Superior | | | | | 0.6208 |
| Grande Prairie | | | | | | |

Note: Indicator variable tests (extra sum of squares methods) for differences between locations and installations were performed using the model $DIFM = a e^{(b BA)}$ where $DIFM$ is light transmittance in the understory, BA is basal area of the overtopping aspen, and a and b are model parameters; the asterisk associated with the p values indicates a significant difference ($p < 0.05$). For Peace River and Prince Albert, there was no significant difference between the medium and superior installations.

Table 2-5 Parameter estimates for models of light transmittance as a function of aspen basal area

| Location | <i>n</i> | MS _{res} | R ² _{adj} | <i>a</i> | <i>b</i> |
|--------------------------------|----------|-------------------|-------------------------------|-----------------------------|--------------------------------|
| Peace River medium | 60 | 0.00774 | 0.92 | 0.9817 (0.9409 - 1.0225) | -0.1413 (-0.1564 - -0.1262) |
| Peace River superior | 60 | 0.0134 | 0.86 | 1.0237 (0.9705 - 1.0768) | -0.1480 (-0.1691 - -0.1269) |
| Peace River (data pooled) | 120 | 0.0105 | 0.89 | 1.0032 (0.9701 - 1.0363) | -0.1445 (-0.1572 - -0.1318) |
| Prince Albert medium | 55 | 0.0151 | 0.80 | 0.9513 (0.8928 - 1.0098) | -0.1283 (-0.1503 - -0.1064) |
| Prince Albert superior | 54 | 0.0226 | 0.67 | 0.8831 (0.8125 - 0.9536) | -0.0924 (-0.1153 - -0.0694) |
| Prince Albert (data pooled) | 109 | 0.0194 | 0.73 | 0.9155 (0.8695 - 0.9615) | -0.1089 (-0.1250 - -0.0929) |
| Edson medium | 60 | 0.00545 | 0.82 | 0.7266 (0.6991 - 0.7541) | -0.0876 (-0.1014 - -0.0739) |
| Edson superior | 30 | 0.0029 | 0.94 | 0.7989 (0.7708 - 0.8629) | -0.1437 (-0.1652 - -0.1221) |
| Grande Prairie | 86 | 0.0252 | 0.51 | 0.7308 (0.6696 - 0.7921) | -0.1345 (-0.1661 - -0.1030) |

Note: Models shown are significant ($p < 0.001$) and represent nonlinear regressions fit to data based on the exponential equation $DIFM = a e^{(b BA)}$ where DIFM is light transmittance in the understory measured at white spruce midcrown, BA is basal area of the overtopping aspen, and *a* and *b* are model parameters reported with 95% confidence limits. For Peace River and Prince Albert, there was no significant difference detected between models for the medium and superior sites, allowing for data pooling.

Table 2-6 Predictive ability of white spruce stem volume increment by competition indices and initial diameter (R^2 adj values)

| Loc | Inst | Model type | Competition index | | | | | | | | | | | | | | | | SF _{AW} | |
|----------------|------|---------------|-------------------|------|----------|----------|----------|----------|----------|----------|------------|------------|----------|----------|----------|------------|------|------|------------------|-----------------|
| | | | N | BA | LOR 1 | LOR 2 | VCR 1 | VCR 2 | SCR 1 | SCR 2 | SCROS 1 | SCROS 2 | HEG 4 | VCR 4 | SCR 4 | SCROS 4 | DIFM | DIFT | | SF _T |
| Peace | Med | M1 | 0.51 | 0.52 | 0.53 | 0.59 | 0.47 | 0.58 | 0.52 | 0.60 | 0.51 | 0.57 | 0.58 | 0.59 | 0.59 | 0.56 | 0.57 | 0.48 | 0.44 | 0.43 |
| | | M2 | 0.78 | 0.79 | 0.79 | 0.79 | 0.78 | 0.79 | 0.79 | 0.79 | 0.78 | 0.79 | 0.78 | 0.79 | 0.79 | 0.78 | 0.80 | 0.77 | 0.77 | 0.79 |
| River | Sup | M1 | 0.36 | 0.41 | 0.40 | 0.45 | 0.40 | 0.53 | 0.40 | 0.51 | 0.41 | 0.50 | 0.42 | 0.50 | 0.47 | 0.46 | 0.44 | 0.46 | 0.38 | 0.31 |
| | | M2 | 0.85 | 0.86 | 0.86 | 0.85 | 0.86 | 0.86 | 0.86 | 0.86 | 0.86 | 0.86 | 0.85 | 0.85 | 0.85 | 0.85 | 0.87 | 0.86 | 0.86 | 0.85 |
| Prince | Med | M1 | 0.11 | 0.17 | 0.14 | 0.19 | 0.14 | 0.30 | 0.14 | 0.25 | 0.13 | 0.25 | 0.16 | 0.26 | 0.21 | 0.21 | 0.21 | 0.16 | 0.20 | 0.17 |
| | | M2 | 0.93 | 0.93 | 0.93 | 0.93 | 0.93 | 0.93 | 0.93 | 0.93 | 0.93 | 0.93 | 0.93 | 0.93 | 0.93 | 0.93 | 0.93 | 0.93 | 0.93 | 0.93 |
| Albert | Sup | M1 | 0.36 | 0.38 | 0.38 | 0.42 | 0.39 | 0.53 | 0.39 | 0.50 | 0.39 | 0.50 | 0.38 | 0.49 | 0.46 | 0.46 | 0.37 | 0.33 | 0.44 | 0.42 |
| | | M2 | 0.64 | 0.64 | 0.64 | 0.64 | 0.64 | 0.66 | 0.64 | 0.66 | 0.64 | 0.65 | 0.63 | 0.65 | 0.65 | 0.64 | 0.64 | 0.63 | 0.64 | 0.64 |
| Edson | Me | M1 | 0.22 | 0.23 | 0.23 | 0.26 | 0.23 | 0.33 | 0.23 | 0.31 | 0.22 | 0.31 | 0.26 | 0.31 | 0.28 | 0.30 | 0.22 | 0.24 | 0.21 | 0.21 |
| | | M2 | 0.78 | 0.79 | 0.78 | 0.78 | 0.80 | 0.78 | 0.80 | 0.78 | 0.79 | 0.78 | 0.77 | 0.78 | 0.78 | 0.78 | 0.78 | 0.78 | 0.79 | 0.80 |
| | Sup | M1 | 0.20 | 0.24 | 0.22 | 0.27 | 0.28 | 0.36 | 0.26 | 0.34 | 0.27 | 0.33 | 0.27 | 0.35 | 0.32 | 0.33 | 0.29 | 0.30 | 0.22 | 0.17 |
| | | M2 | 0.89 | 0.88 | 0.89 | 0.89 | 0.88 | 0.88 | 0.89 | 0.88 | 0.89 | 0.88 | 0.88 | 0.87 | 0.87 | 0.87 | 0.87 | 0.86 | 0.86 | 0.85 |
| Grande Prairie | | M1 | 0.04 | 0.05 | 0.04 | 0.09 | 0.04 | 0.18 | 0.05 | 0.15 | 0.05 | 0.16 | 0.06 | 0.14 | 0.11 | 0.11 | 0.10 | 0.07 | 0.03 | 0.02 |
| | | M2 | 0.75 | 0.75 | 0.75 | 0.75 | 0.75 | 0.75 | 0.75 | 0.75 | 0.75 | 0.75 | 0.75 | 0.75 | 0.75 | 0.75 | 0.75 | 0.75 | 0.75 | 0.75 |

Note: All values presented are for statistically significant models ($p < 0.001$). Model 1 is $SVI = a e^{(b CI)}$ for $CI = N$ to SCROS4 and $SVI = a (CI)^b$ for $CI = DIFM, DIFT, SF_T,$ and SF_{AW} ; Model 2 is $SVI = a e^{(b CI)} (Dsw)^c$ for $CI = N$ to SCROS4 and $SVI = a (CI)^b (Dsw)^c$ for $CI = DIFM, DIFT, SF_T,$ and SF_{AW} . SVI is stem volume increment of spruce, CI is competition index as defined in table 2-2, Dsw is initial stem diameter of spruce, and $a, b,$ and c are model parameters.

Table 2-7 Test of difference between locations and installations for models predicting stem volume increment of white spruce as a function of transmittance (p values)

| | | Peace River | | Prince Albert | Edson | Grande Prairie |
|----------------|----------|-------------|----------|---------------|---------|----------------|
| | | Medium | Superior | | | |
| Peace River | Medium | | 0.003* | 0.0001* | 0.0001* | 0.0001* |
| | Superior | | | 0.043* | 0.0001* | 0.0001* |
| Prince Albert | | | | | 0.069 | 0.0001* |
| Edson | | | | | | 0.0001* |
| Grande Prairie | | | | | | |

Note: Indicator variable tests (extra sum of squares methods) for differences between locations and installations were performed using the model $SVI = a (DIFM)^b$, where SVI is stem volume increment of spruce, DIFM is light transmittance in the understory measured at the spruce midcrown, and a and b are model parameters; the asterisk associated with the p values indicates a significant difference ($p < 0.05$). For Prince Albert and Edson, there was no significant difference between the medium and superior installations.

Table 2-8 Test of difference between locations and installations for models predicting stem volume increment of white spruce as a function of basal area of overtopping trembling aspen and initial stem diameter of spruce (p values)

| | Peace River | Prince Albert | Edson | Grande Prairie |
|----------------|-------------|---------------|---------|----------------|
| Peace River | | 0.0001* | 0.0001* | 0.0001* |
| Prince Albert | | | 0.706 | 0.283 |
| Edson | | | | 0.068 |
| Grande Prairie | | | | |

Note: Indicator variable tests (extra sum of squares methods) for differences between locations and installations were performed using the model $SVI = a e^{(b BA)} (Dsw)^c$, where SVI is stem volume increment of spruce, BA is basal area of overtopping aspen, Dsw is initial stem diameter of spruce, and a , b , and c are model parameters; the asterisk associated to the p values indicates a significant difference ($p < 0.05$). For all locations, there was no significant difference between the medium and superior installations.

Table 2-9 Selected models and parameter estimates for predicting diameter and height increment of white spruce during the 2-year measurement period (2002-2003)

| Location | Model | <i>n</i> | MS _{res} | R ² _{adj} | <i>a</i> | <i>b</i> | <i>c</i> |
|-------------------------|-----------------------------------|----------|-------------------|-------------------------------|----------|----------|----------|
| Peace River medium | $DI = a * e^{b * BA} * D_{sw}^c$ | 60 | 3.34 | 0.68 | 3.9293 | -0.0597 | 0.6912 |
| | $DI = a * DIFM^b * D_{sw}^c$ | 60 | 3.25 | 0.69 | 4.5163 | 0.3948 | 0.6243 |
| | $HI = a * e^{b * BA} * Ht_{sw}^c$ | 60 | 103.2 | 0.46 | 31.509 | -0.0413 | 0.6945 |
| | $HI = a * DIFM^b * Ht_{sw}^c$ | 60 | 100.7 | 0.47 | 33.1195 | 0.26 | 0.6617 |
| Peace River superior | $DI = a * e^{b * BA} * D_{sw}^c$ | 60 | 1.8118 | 0.81 | 2.1262 | -0.0712 | 1.1546 |
| | $DI = a * DIFM^b * D_{sw}^c$ | 60 | 1.6756 | 0.82 | 2.4244 | 0.4156 | 1.0728 |
| | $HI = a * e^{b * BA} * Ht_{sw}^c$ | 60 | 42.9459 | 0.63 | 27.6686 | -0.0432 | 0.8773 |
| | $HI = a * DIFM^b * Ht_{sw}^c$ | 60 | 44.5677 | 0.62 | 28.8024 | 0.2316 | 0.8097 |

Note: All models are significant ($p < 0.0001$), where DI is spruce diameter increment (mm/yr), HI is spruce height increment (cm/yr), BA is basal area of overstory aspen, DIFM is light transmittance at spruce midcrown, D_{sw} is initial root collar diameter of spruce (2002), Ht_{sw} is initial height of spruce (2002), and *a*, *b*, and *c* are parameter estimates.

Figure 2-1 Relationships between light transmittance (DIFM) and basal area of overstory trembling aspen (*Populus tremuloides*) for the studied locations. Lines shown are based on nonlinear regressions fit to data using the exponential model $DIFM = a e^{(b BA)}$. Parameters values and statistics are provided in table 2-5. All models are statistically significant ($p < 0.001$). For the Peace River and Prince Albert locations, data were pooled owing to no significant difference detected between the models for the medium and superior sites. PR, Peace River; PA, Prince Albert; GP, Grande Prairie; EDm, Edson medium; EDs, Edson superior.

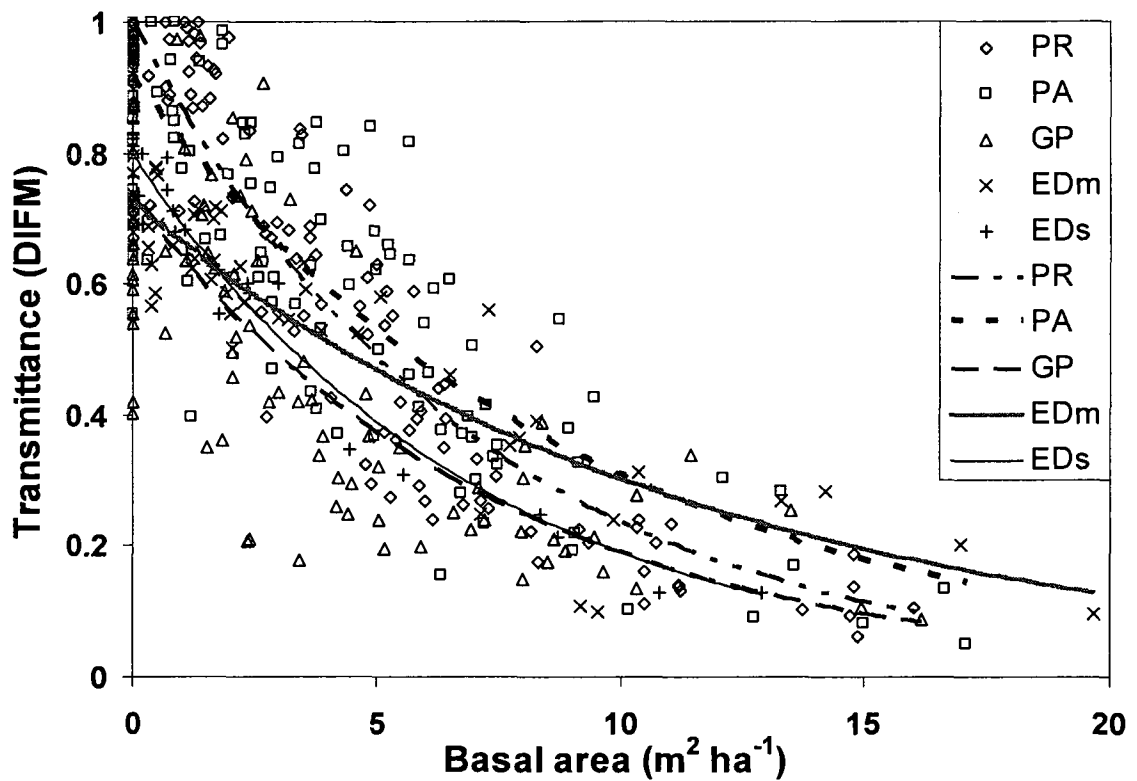


Figure 2-2 Relationships between stem volume increment of white spruce (*Picea glauca*) during the 2-year measurement period (2002 – 2003) for (a and c) Peace River medium and (b and d) Peace River superior and (a and b) transmittance and (c and d) trembling aspen basal area. Lines shown on the graphs are based on nonlinear regressions fit to data: (a) $SVI = 5299.85 \text{ DIFM}^{1.0067}$ ($n = 60$, $MS_{\text{res}} = 6.623$, $R^2_{\text{adj}} = 0.57$); (b) $SVI = 3424.8 \text{ DIFM}^{0.9349}$ ($n = 60$, $MS_{\text{res}} = 4.9430$, $R^2_{\text{adj}} = 0.44$); (c) $SVI = 4598.65 e^{-0.1433 \text{ BA}}$ ($n = 60$, $MS_{\text{res}} = 7.3865$, $R^2_{\text{adj}} = 0.52$); (d) $SVI = 3269.5 e^{-0.1704 \text{ BA}}$ ($n = 60$, $MS_{\text{res}} = 5.2110$, $R^2_{\text{adj}} = 0.41$)

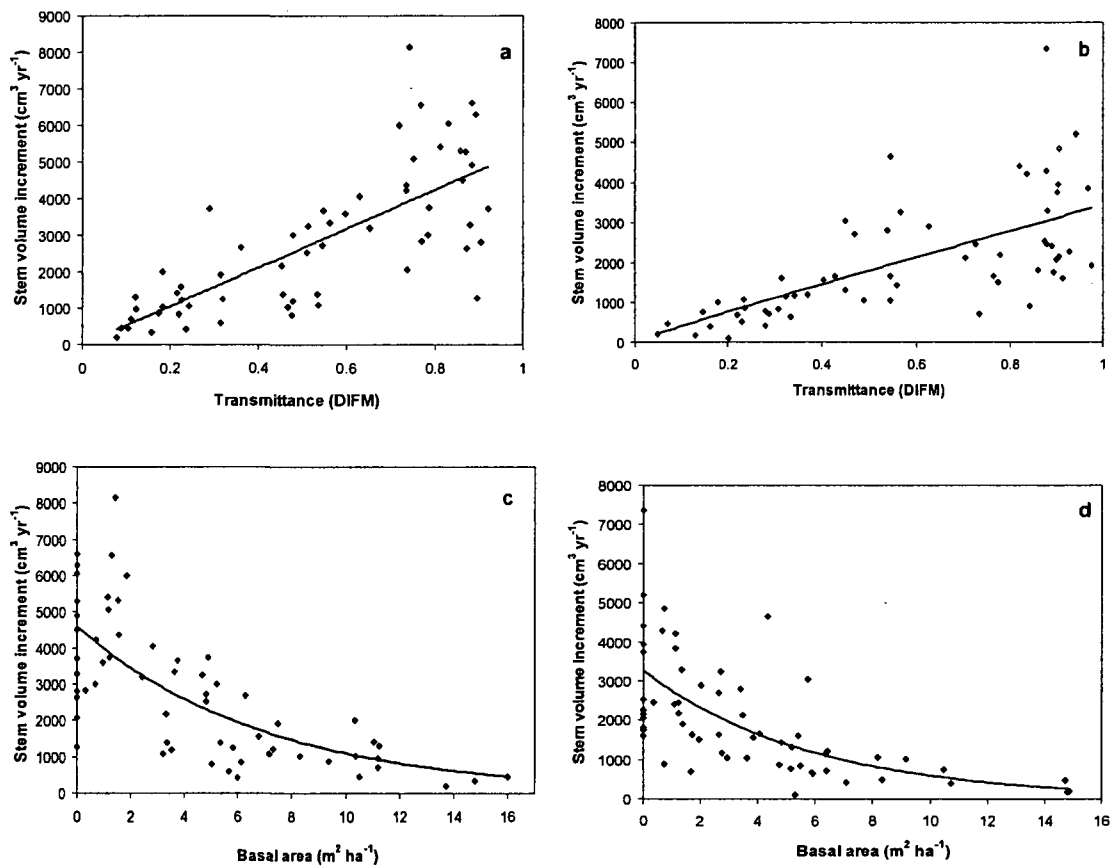


Figure 2-3 Relationships between stem volume increment of white spruce during the 2-year measurement period (2002-2003) for (a and b) Peace River medium and (c and d) Peace River superior and aspen basal area and initial spruce diameter (2002). Lines shown are based on nonlinear regressions fit to data using the independent variable shown on the x-axis and with values of the second independent variable set to three different values selected to illustrate the range of variation in this variable as indicated in the legend below each graph. Regression models: (a and b) $SVI = 271.75 e^{-0.0620 BA} D_{sw}^{1.9539}$ ($n = 60$, $MS_{res} = 3.2906$, $R^2_{adj} = 0.79$); (c and d) $SVI = 59.5 e^{-0.0522 BA} D_{sw}^{2.9912}$ ($n = 60$, $MS_{res} = 1.2416$, $R^2_{adj} = 0.86$)

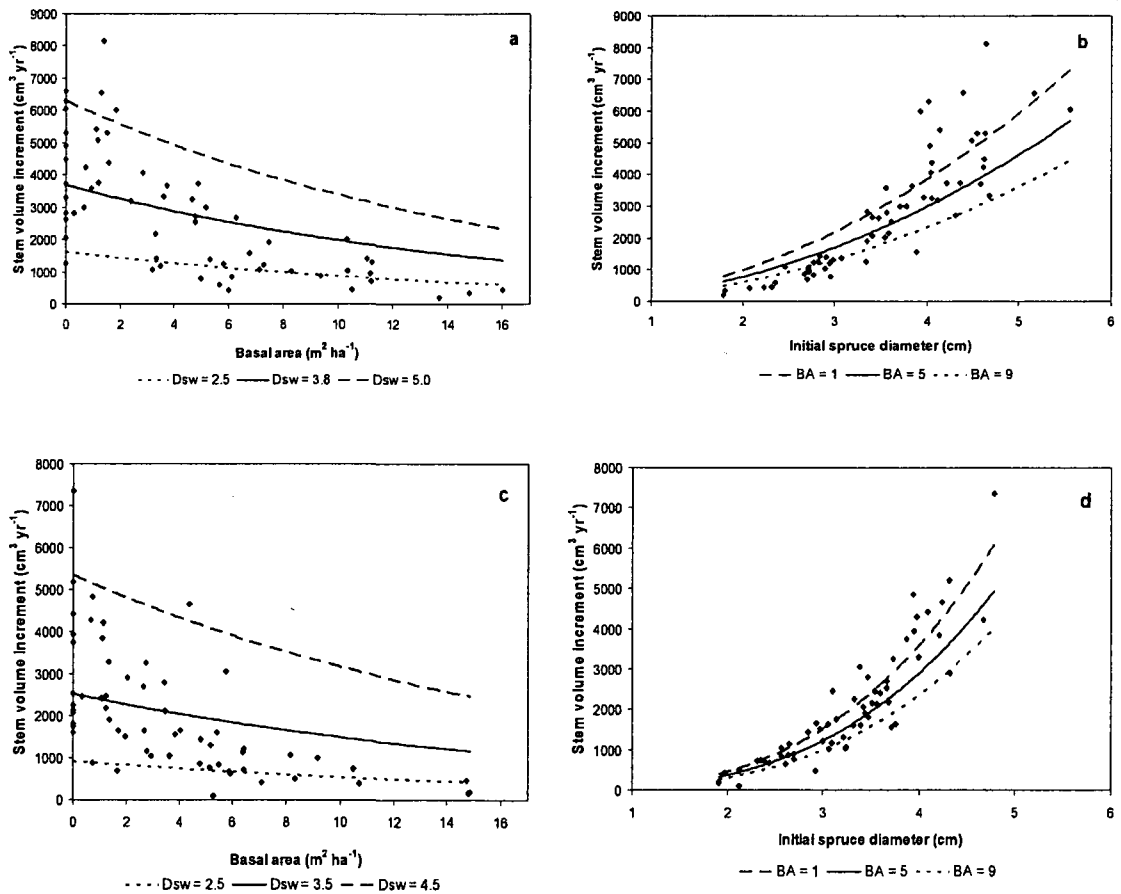
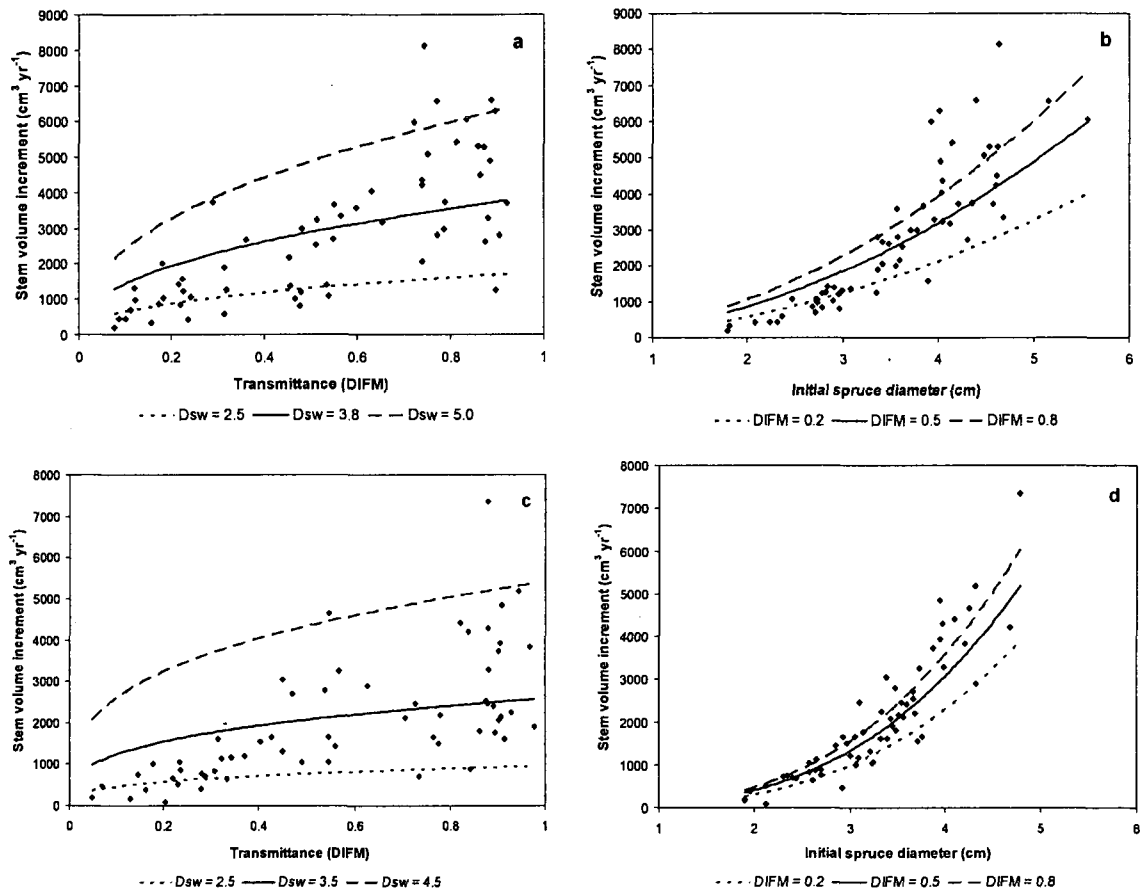


Figure 2-4 Relationships between stem volume increment of white spruce during the 2-year measurement period (2002-2003) for (a and b) Peace River medium and (c and d) Peace River superior and light transmittance and initial spruce diameter (2002). Lines shown are based on nonlinear regressions fit to data using the independent variable shown on the x-axis and with values of the second independent variable set to three different values selected to illustrate the range of variation in this variable as indicated in the legend below each graph. Regression models: (a and b) $SVI = 312.1 \text{ DIFM}^{0.4382} \text{ Dsw}^{1.8968}$ ($n = 60$, $MS_{\text{res}} = 3.1749$, $R^2_{\text{adj}} = 0.80$); (c and d) $SVI = 65.5 \text{ DIFM}^{0.3205} \text{ Dsw}^{2.9363}$ ($n = 60$, $MS_{\text{res}} = 1.2054$, $R^2_{\text{adj}} = 0.87$)



Chapter 3 Competitive interactions between aspen and white spruce vary with stand age in boreal mixedwoods [§]

3.1 Introduction

During the last few decades there has been a gradual shift in perspectives and management strategies for boreal mixedwood forests (Andison and Kimmins 1999). Multiple-use forestry and the increasing need for both aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench) Voss) fibre, coupled with a shrinking land base available for commercial forestry, a desire to reduce reforestation and early tending costs and public concerns over maintaining species and structural diversity are stimulating the development of new silvicultural prescriptions (Lieffers et al. 1996; Comeau et al. 2005). However, few of these new management options have been tested and their long-term implications are not fully understood.

At the stand and landscape level, boreal mixedwood forests represent a complex natural mosaic of patches of pure aspen, patches of pure white spruce and patches with both species intimately mixed (Wang et al. 1995a). Maintaining mixed-species stands as opposed to converting them to pure stands presents several advantages including: the potential for increase in productivity (Man and Lieffers 1999; MacPherson et al. 2001); the opportunity to meet broader biodiversity and aesthetics goals; reduced effects of climatic extremes (Pritchard and Comeau 2004), and reduced competition from understory (Lieffers and Stadt 1994).

Disturbance and competition are generally considered major ecological processes influencing the dynamics of boreal mixedwoods (Chen and Popadiuk 2002). Following disturbances (e.g., wildfire, clearcutting) that return stands to early seral stages, competition exerted by aspen reduces spruce growth and survival for the first several decades of stand development. Competition as a process is difficult to measure directly, therefore competition indices are used to quantify and interpret the competitive effects in

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the form of growth response of crop trees. Numerous competition studies have proposed and tested indices based on the size ratio between competitor and subject trees, without including spatial information (Lorimer 1983; Holmes and Reed 1991), or adjusted with the distance to competitors (Hegyi 1974; Daniels 1976; Alemdag 1978; Tomé and Burkhardt 1989). In addition to simple indices based on density, such as number of trees, basal area or spacing factor, another group of indices based on crown measures has been proposed and suggested to be more meaningful for explaining competitive interactions (Hix and Lorimer 1990; Biging and Dobbertin 1992; Bravo et al. 2001). Crown size includes biological information (i.e., capture and use of resources) relevant to explaining competitive interactions and growth response. Although competition indices have been used extensively, no index has been shown to perform consistently better than others under various conditions. In addition, competition indices provide a relatively static quantification of a dynamic system with conditions changing over time (Burton 1993).

Past competition studies have focused primarily on interactions during early stages of stand development. Moreover, existing published studies have presented results obtained using competition gradients from individual sites or from a limited range of sites. While these studies provide useful insight into the expected effect of competition on growth when other factors (e.g., environment and stand age) are held relatively constant, results from such studies can not be widely applied.

Previous studies have suggested that stand age influences tree growth and interacts with competition. Wagner and Radosevich (1991) found that the addition of an age-adjusted component of competition increased the predictive ability of stem-diameter growth equations. Lorimer (1983) also suggested making competition indices independent of age by relating the search radius of competitors to the mean crown radius of overstory trees that increase with time.

There is limited or no information on how competition changes with age, and whether observed relationships between spruce growth and measures of aspen competition vary with changes in age or site. Further studies are required to examine how relationships change and why the negative effects of competition appear to be cumulative in time (Wagner and Radosevich 1998). Knowing if and how interactions change is

important to the understanding of mixedwood stand dynamics and to the development of growth models and crop plans for boreal mixedwood systems.

The objective of this study was to develop and test models for estimating growth of white spruce as a function of competition indices and tree size across an age sequence of boreal mixedwood stands. A second objective was to examine whether relationships between spruce growth and competition indices change with stand age (i.e., can a single relationship be applied across a range of stand ages?).

3.2 Materials and methods

The study used a neighbourhood approach to examine competition across an age sequence of mixedwood stands. Nine stands were located on similar ecosites, three for each of the three age classes considered (class 1: 10-20 years, class 2: 21-40 years, and class 3: 41-60 years), in the southeastern area of Boreal Mixedwood ecological subregion of Alberta (table 3-1).

Stand selection was based on several criteria: (1) aspen stands with a component of spruce in the understory, at least 4 ha in area and with a minimum width of 200m; (2) naturally regenerated stands, of fire origin, located on ecologically similar sites (mesic soil moisture and medium nutrient regime); and (3) untended stands with no previous history of human disturbance. Owing to difficulties encountered during stand selection, especially for young stands in the 10-20 year age class, it was necessary to include two stands that regenerated naturally after harvesting (sites B and L) and two stands where white spruce were planted (sites A and L).

Increment cores were collected at 30 to 50 cm above the ground level from 15-20 dominant aspen trees in each stand to provide information on stand age. The increment cores confirmed that aspen were still sound (i.e., no heart rot) and vigorous. Height of these trees was also measured for information on site quality (Huang et al. 1997). Within each selected stand, there was a reasonable gradient of natural density and the selected stands were relatively homogeneous in aspen site index, with values ranging between 20 and 24 (table 3-1). Spruce age was considered equal to aspen age, recent evidence suggesting that spruce regeneration usually occurs within 4 years after disturbance

(Peters et al. 2002), as seedbeds are receptive for only the first three to five years after disturbance, and receptivity declines rapidly soon after fire (Purdy et al. 2002).

In each of the nine selected stands, 30 focus spruce trees were selected closest to 30 systematically located grid points along random bearings. Selected trees were located far enough apart so that neighbourhood assessment plots would not overlap and meet the requirement of sample independence. Trees influenced by factors other than aspen competition (i.e., competition from shrubs and other vegetation, wildlife browsing) were discarded and other trees were selected to replace them.

Initial detailed measurements were collected before the start of the growing season in the spring of 2003. Current total height, height to crown base and the past 3-year height growth (2000-2002) were measured. Crown radii in four directions (north, south, east, and west), and stem diameter at 0.3 m above ground level were also measured. Diameter measurements were made at 0.3 m to avoid the basal stem swelling at root collar. Diameter at breast height (dbh) was measured for trees taller than 2 m, however only two out of nine selected stands had the majority of spruce trees taller than 2 m. Crown volume and surface area were calculated using the formula for a cone. Height and stem diameter were remeasured at the end of the growing season in the fall of 2005.

Competition was assessed during 2003 by recording the number and dbh of aspen trees within a series of concentric circular plots centered at each focus spruce tree. All aspen trees with dbh less than or equal to 8 cm were measured in a 3.99 m radius plot (0.005 ha), aspen trees larger than 8 cm but less than or equal to 16 cm were measured in a 5.64 m radius plot (0.01 ha) and aspen trees larger than 16 cm dbh were measured in a 7.98 m radius plot (0.02 ha). This sampling approach has been used by other studies (Zhao et al. 2004) and allows for a unified and efficient assessment of competition across the age sequence. At the same time, it reduces the effects of a variable plot radius on estimation of competition levels. Distance from each focus spruce tree to the nearest dominant or codominant competitor aspen in each of the four quadrants of the circular plot was also measured. For these four closest aspen, crown radii were measured in four directions (north, south, east, and west), and total height and height to crown base were also recorded.

Light levels were determined for each selected spruce tree during midsummer of 2003 at midcrown height using LAI-2000 plant canopy analyzers (LI-Cor Inc., Lincoln, Nebraska). The sensors were fitted with 180° view restrictors and were located at the edge of the spruce crown pointing away from the focus tree. For trees taller than 5m an extension cable was used and the sensor was fixed to a rigid extendable height pole. Two measurements were taken in the morning and late afternoon to avoid the presence of direct light within the sensor view. A second LAI-2000 sensor was used to obtain measurements at each 30-s interval in an adjacent open area and the closest measurements in time were subsequently matched to provide information on light transmittance.

The study was designed to evaluate competition indices that can be calculated from measurements commonly and readily collected in the field. These indices (table 3-2) were based on: (1) density (number of trees, basal area); (2) size ratio distance-independent indices (Lorimer's) with and without the size of subject spruce (LOR1 and LOR2), owing to concerns that including spruce size may artificially increase the amount of variation accounted for; (3) size ratio distance-dependent indices, based on spatial data collected only from the 4 closest competitors and adjusted with basal area (Hegyi's and crown indices – aspen crown was assumed to be a prolate ellipsoid); (4) spacing factor, in two forms, SF_S adjusted with spruce height, which considers the intertree distance as a ratio of the difference in height between the competitor and half the height of subject tree, and SF_A which uses only aspen height; and (5) light transmittance at spruce midcrown.

Simple and multiple regression models were developed for each stand to predict:

- understory light transmittance as a function of competition indices:

$$[1] \quad \text{Transmittance} = f(\text{CI})$$

where transmittance was measured at midcrown, and CI is a competition index as defined in table 3-2;

- spruce growth as a function of competition indices:

$$[2] \quad \text{Spruce growth} = f(\text{CI})$$

where spruce growth measurements tested were diameter increment (for the interval 2003-2005), and height increment (2003-2005 and 2000-2005);

- spruce growth as a function of competition indices and size of spruce:

$$[3] \quad \text{Spruce growth} = f(\text{CI}) g(\text{size})$$

where the initial spruce size was tested in form of initial diameter (2003), height (2003 and 2000), crown volume and crown surface area (2003).

Several types and combinations of models were tested for each stand. Model parameters were estimated using least-squares nonlinear regression. Data analysis was completed with PROC NLIN of the SAS statistical package for Windows (version 9.1) (SAS Institute Inc., Cary, North Carolina). Validity of the underlying assumptions for the tested models and evaluation of model fit was based on analysis of residuals plotted against predicted values with the goal of minimizing the residual mean square (Bates and Watts 1988). The adjusted values of the coefficient of determination (R^2_{adj}) were calculated to account for differences in sample size and model complexity (i.e., number of parameters). Additional sum of squares methods with indicator variables (Draper and Smith 1981; Ott 1997) were used to test for coincidence of regression equations between stands in the same age class, and between age classes.

3.3 Results

Significant relationships ($p < 0.05$) between competition indices and transmittance were obtained only for 15 out of 81 combinations of nine stands and nine indices. These models were obtained only for stands from age class 1 (< 20 years), with indices based on density (number of trees, basal area, Lorimer's, and spacing factor) and R^2_{adj} values between 0.14 and 0.42. Extra sum of squares tests indicated that transmittance data could not be pooled across sites within each of the three age classes into one relationship.

Relationships between spruce growth and competition indices were evaluated separately for each selected stand. Models obtained for diameter increment were significant ($p < 0.05$) for the majority of stands and indices (table 3-3). Some exceptions were observed for N, LOR1, BA, spacing factor (both SF_A and SF_S), and transmittance. For stand V, none of the indices provided significant models of diameter increment. Similar significant models were obtained for height increment measured over 3 years

(2003-2005) and 6 years (2000-2005) with slightly better results for the latter. The 3-year results are presented in table 3-4, and the 6-year results in table 3-5. The inclusion of spruce size in the size ratio indices (LOR2 vs. LOR1) resulted in superior predictive ability. Some of the best and most consistent indices for predicting spruce growth across all stands were LOR2 and HEG4 for diameter increment and LOR2 and VCR4 for height increment.

Adding initial size (measured at the beginning of the growing period) to competition indices as a second predictive variable increased the amount of variation explained by the models of spruce growth. At the same time, the difference between indices within each individual stand was reduced. Initial diameter, height, crown volume and surface area were used as variables to represent initial size. Diameter increment was most consistently predicted by competition indices and initial diameter, and height increment by competition indices and initial height. Hence, results are presented only for these combinations of explanatory variables (models M2 in tables 3-3, 3-4 and 3-5).

The most consistent regression models of diameter and height increment were selected to test for parameter differences between stands and age classes using extra sum of squares methods. These tests indicated that pooling data into a single model for all stands and age classes was not possible (table 3-6). For models predicting diameter increment and height increment as a function of competition indices (LOR2, HEG4, and LOR2, VCR4, respectively), parameters for stand B were significantly different from those for stands A and L combined in age class 1. Data from age classes 2 and 3 could be combined into a single relationship, while both stands B and stands A+L were significantly different from age classes 2 and 3 pooled together. These differences in diameter and height increment as a function of LOR2 index are illustrated in figure 3-1. For multiple regression models including both competition (expressed as LOR1) and initial size even more combinations resulted and data from the three age classes could not be combined into a single relationship. Nevertheless, when transmittance (DIFM) was used as a measure of competition alongside initial size to predict spruce growth, data could be pooled into a single relationship within each of the three age classes, and one

model could combine data from age classes 2 and 3. However, age class 1 could not be combined with age classes 2 and 3 into a single model.

Notwithstanding these differences, growth data from all stands and age classes were combined into a single relationship to explore the implications of data pooling. Plotting model residuals against predicted values (figure 3-2) illustrates that pooling all data into a single relationship results in overprediction of growth for smaller trees and increasing variation with tree size and stand age.

3.4 Discussion

Results contradicted the expectation that competition indices are effective in predicting light transmittance available to understory spruce. Several recent studies have indicated that stand characteristics and competition indices can be useful for predicting transmittance (Comeau et al. 2003; Comeau et al. 2006; Filipescu and Comeau 2007). However, these other studies used a wider gradient of stand densities with understory light levels up to full sunlight, whereas in this study transmittance had a more limited range (0.04 to 0.58, with the majority of values below 0.3). The high variability at the low end of the transmittance gradient in natural stands seems to limit the sensitivity of competition indices for predicting understory light.

The majority of competition indices tested provided significant models for explaining variation in white spruce growth. However, some of the simple indices based on density, such as number of trees (N), Lorimer's (LOR1), basal area (BA) and spacing factor (SF_A and SF_S) were not as effective, resulting in lower R^2_{adj} values, and even non-significant models ($p > 0.05$) for some stands. Light transmittance (DIFM) provided similarly poor results for some stands. In natural untended stands, with full or close to full site occupancy, competition for water and nutrients may also become important (Mitchell et al. 1993; Simard and Sachs 2004). It is likely that simple indices do not provide adequate quantification of competition in natural stands. In addition, factors other than competition can influence growth and their resultant effect may not be fully represented by these simple models.

Overall, my results suggest little improvement to using distance-dependent over distance-independent competition indices. In the last few decades, there has been ongoing debate on whether to incorporate distance between crop tree and competitors in competition indices (Lorimer 1983; Daniels et al. 1986; Tomé and Burkhardt 1989). Natural stands selected for this study presented relatively uniform spatial arrangements of trees; therefore, spatial information may not be as important as in more heterogeneous stands where it is possible that distance-dependent indices perform better. However, one should note that this study used simplified versions of distance-dependent indices owing to practical field limitations on data collection.

Furthermore, indices that incorporated additional information (i.e., initial size – diameter for LOR2, HEG4, or crown measures for VCR4, SCR4, and SCros4) were more effective in predicting spruce growth. Accounting for initial tree size in growth models has been recommended by several previous studies (MacDonald et al. 1990; Wyckoff and Clark 2005; MacFarlane and Kobe 2006). Initial size is correlated with tree leaf area (Comeau et al. 1993) and will be related to resource acquisition, carbon fixation and growth. In addition, initial size includes information on previous growing conditions and genetics of subject trees. Size is a cumulative measure that can provide a more reliable reflection of exposure to prolonged periods of competition and to other environmental factors. However, collinearity may become an issue when size is included both in the competition index and as a second independent variable. It may be desirable to represent the effects of initial tree size separately from the effects of competition through the use of multiple regression models.

My study provided better results for models of height growth over a 6-year measurement period (2000-2005) compared with a 3-year measurement period (2003-2005). The influence of various factors affecting height growth seems to be more balanced over longer periods of time resulting in reduced growth variability and better predictive models.

Results show that data from the three stands in age class 1 can not be combined into a single model. Stand B differs from stands A and L, with several possible explanations being offered: (1) difference in age (stand B was 13 years old, while both

stands A and L were 19 years old); (2) spruce origin was different, resulting in difference of size and growth patterns (stand B was naturally regenerated, while spruce were planted in stands A and L); (3) it is possible that in early stages boreal mixedwoods still reflect post-disturbance conditions; and (4) the effects of other limiting factors (e.g., site, competition from shrubs, herbs and grasses, winter injury, summer frost) may have a greater impact in young stands, therefore affecting competition-growth relationships to a greater extent. The influence of early differences may become less important as stands age and develop.

Data from stands within age classes 2 and 3 could be pooled into a single relationship when growth was predicted only as a function of competition indices. In multiple regression models (i.e., with initial subject tree size included as an explanatory variable), one relationship for both age classes 2 and 3 was possible when using transmittance (DIFM) as a measure of competition, whereas different models were needed when Lorimer's index (LOR1) was used. While competition for other resources (water and nutrients) may also influence growth relationships, transmittance seems to be a more general measure of competition than size ratio indices, with fewer model combinations across sites and age classes. However, data from stands in age class 1 still can not be combined with data from age classes 2 and 3 into a single equation of spruce growth as a function of transmittance and initial size. Including initial size increases the amount of variation explained by the models and also appears to increase model sensitivity to age and location differences.

Forest research studies have long been concerned with changes taking place over time. Careful selection of stands to meet predefined criteria may provide a series of stands of different ages, supposed to have evolved similarly over time and which are presumed to be similar in all features except age. However, there is always a chance that variability in all influencing factors may not be accounted for. In this study, factors such as frost, Chinook injury, other competing vegetation, and terrain characteristics were not controlled for.

Simultaneous occurrence of competition and facilitation results in complex species interactions (Callaway and Walker 1997; Simard and Vyse 2006). Results

presented by Filipescu and Comeau (2007) suggested that the interplay of competition and facilitation may result in changes in relationships between spruce growth and aspen competition from one site to another. It is possible that changes in the occurrence and importance of each contributing factor also happen as stands develop, resulting in different competition-growth relationships over time.

Temporal changes in overstory biomass and nutrient distribution (Ruark and Bockheim 1988; Wang et al. 1995*b*) are complemented by changes in the composition and cover of understory vegetation (MacLean and Wein 1977; De Grandpré et al. 1993). Competitive interactions between understory and overstory may also change over time (Alifragis et al. 2001), as well as light availability. Lieffers et al. (2002) suggested that light levels under fully stocked boreal mixedwoods reach minimum levels between 10 and 25 years, and subsequently increase with age. Recent studies show that light levels can reach minimum values (below 10%) within 2 years after disturbance owing to the combined influence of both aspen and understory vegetation (P. Comeau, unpublished). Stand development may cause a shift in resource availability and a change in competition processes, leading to different growth relationships for understory spruce.

Most competition studies are limited in space and time (Goldberg and Barton 1992), and studies that consider changes of competition with time are even more limited. Results from Simard et al. (2004) examining competition along a sequence of age classes of mixed stands of paper birch (*Betula papyrifera* Marsh) and conifer species in interior British Columbia indicated that the importance and intensity of competition may differ between young and older age classes. Results show that in some cases data from age classes 2 (20-40 years) and 3 (40-60 years) can be pooled into a single model, being in agreement with findings of Simard and Sachs (2004) who found that competition processes were similar in the 25- and 50-year old stands, but were different from those in the 11-year old stands they examined.

Results indicate that older mixedwoods do not necessarily have larger understory spruce trees. For example, spruce were generally smaller in age class 2 than in age class 1. A change in size is believed to result in different growth strategies by understory conifers, owing to morphological and physiological changes (Claveau et al. 2002). Other

studies have suggested that tree size may influence relative growth rates more than age (Kironko and Mason 2003), while growth-size relationships may change significantly over time (Hokka and Groot 1999).

Relationships presented in this paper can be applied in modeling growth of understory spruce in mixedwoods younger than 60 years. In this respect, a number of competition indices can be used, with better results warranted by indices that include initial spruce size. Most importantly though, my study shows that no competition index can be used universally across an age sequence, and suggests that applying growth-competition relationships across stands of different ages should be done with caution. Further studies are needed to provide a better understanding of the factors and processes governing the change of relationships with stand development.

3.5 Conclusions

Results from my study indicate that simple competition indices based on density (basal area, Lorimer's, and spacing factor) are limited in their ability to predict the growth of understory spruce trees in untended boreal mixedwoods. Distance-dependent indices provide little or no improvement over simpler distance-independent indices in these stands. Indices or models that include a measure of initial size of spruce trees provide better results. Relationships between aspen competition indices and spruce growth vary with age, making age and/or size specific calibration of these relationships necessary. In addition, this study also suggests that relationships between spruce growth and aspen competition are site specific in stands that are less than 20 years of age.

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Table 3-1 Location and site information

| Stand | Origin/ Spruce | Latitude and Longitude | Elevation (m asl) | Age (yrs.) | Spruce height 2003 (m) | Aspen basal area (m ² /ha) | Aspen top height (m) | Aspen SI ₅₀ (m) |
|-------|-------------------|---------------------------|----------------------|---------------|------------------------------|--|-------------------------------|-------------------------------|
| B | H / N | 55°13'N 113°23'W | 649 | 13 | 0.73 - 3.42 | 4.2 - 14.8 | 7.5 | 20 |
| A | F / P | 55°00'N 113°54'W | 679 | 19 | 1.45 - 5.98 | 9.7 - 25.4 | 11.6 | 22 |
| L | H / P | 55°15'N 113°07'W | 627 | 19 | 1.37 - 4.6 | 12.4 - 31.9 | 12.0 | 23 |
| SL | F / N | 55°11'N 114°48'W | 768 | 33 | 0.74 - 4.4 | 14.1 - 37.6 | 17.5 | 22 |
| K | F / N | 55°18'N 113°15'W | 614 | 30 | 0.47 - 1.95 | 15.5 - 36.3 | 18.0 | 24 |
| R | F / N | 55°07'N 112°55'W | 588 | 34 | 1.1 - 3.31 | 16.2 - 34.4 | 16.1 | 21 |
| LB | F / N | 55°04'N 111°45'W | 614 | 54 | 1.71 - 7.65 | 23.2 - 63.8 | 25.1 | 24 |
| V | F / N | 55°06'N 113°13'W | 597 | 54 | 1.99 - 19.38 | 20.9 - 50.7 | 23.6 | 23 |
| O | F / N | 55°16'N 112°58'W | 650 | 45 | 0.69 - 11.9 | 17.2 - 45.7 | 22.9 | 24 |

Note: Stand origin – F (fire), H (harvesting); Spruce regeneration – N (natural), P (planted); SI₅₀ – site index at age 50.

Table 3-2 Competition indices tested (abbreviations and formulas)

| Competition index | Formula (description) |
|--|--|
| Number of trees | N (stems/ha) |
| Basal area | BA (m ² /ha) |
| Lorimer's 1 | $LOR1 = \sum_{i=1}^n DBH_{AWi} \text{ (cm)}$ |
| Lorimer's 2 | $LOR2 = \sum_{i=1}^n DBH_{AWi} / D_{SW}$ |
| Hegyi's (based on 4 closest aspen) | $HEG4 = \left(\sum_{i=1}^4 DBH_{AWi} / D_{SW} * dist_i \right) * BA / BA_4$ |
| Crown volume (based on 4 closest aspen) | $VCR4 = \left(\sum_{i=1}^4 VCr_{AWi} / CrV_{SW} * dist_i \right) * BA / BA_4$ |
| Crown surface area (based on 4 closest aspen) | $SCR4 = \left(\sum_{i=1}^4 SCr_{AWi} / CSA_{SW} * dist_i \right) * BA / BA_4$ |
| Crown sectional area (based on 4 closest aspen) | $SCROS4 = \left(\sum_{i=1}^4 SCros_{AWi} / SCros_{SW} * dist_i \right) * BA / BA_4$ |
| Spacing factor (aspen) | $SF_A = 10000 / H_{AW} * \sqrt{N} \text{ (\%)} $ |
| Spacing factor (spruce midcrown) | $SF_S = 10000 / (H_{AW} - H_{SW} / 2) * \sqrt{N} \text{ (\%)} $ |
| Light transmittance (at spruce midcrown) | DIFM (%) |

Note: DBH_{AWi} – basal diameter of the i th aspen tree; D_{SW} – stem diameter of spruce tree at 0.3m; VCr_{AWi} – crown volume of the i th aspen tree; CrV_{SW} – crown volume of spruce tree; SCr_{AWi} – crown surface area of the i th aspen tree; CSA_{SW} – crown surface area of spruce tree; $SCros_{AWi}$ – area of the crown horizontal section of the i th aspen tree; $SCros_{SW}$ – area of the horizontal section at crown base of spruce tree; $dist_i$ – inter-tree distance between spruce and the i th aspen tree; BA_4 – basal area of the 4 closest aspen; H_{AW} – dominant height of aspen; H_{SW} – height of spruce tree.

Table 3-3 Predictive ability (R^2_{adj}) of average diameter increment (2003-2005) by competition indices

| Index/ Stands | Model | N | LOR1 | LOR2 | BA | HEG4 | VCR4 | SCR4 | SCros4 | SFa | SFs | DIFM |
|------------------|-------|------|------|------|------|------|------|------|--------|------|------|------|
| B | M1 | - | 0.22 | 0.72 | 0.15 | 0.31 | 0.49 | 0.41 | 0.35 | 0.35 | 0.55 | 0.51 |
| | M2 | 0.78 | 0.79 | 0.79 | 0.79 | 0.70 | 0.70 | 0.70 | 0.70 | 0.80 | 0.79 | 0.80 |
| A | M1 | - | - | 0.50 | 0.39 | 0.53 | 0.61 | 0.62 | 0.52 | - | - | 0.17 |
| | M2 | 0.67 | 0.68 | 0.68 | 0.69 | 0.70 | 0.70 | 0.71 | 0.68 | 0.67 | 0.68 | 0.69 |
| L | M1 | - | - | 0.32 | - | 0.59 | 0.40 | 0.52 | 0.49 | - | - | - |
| | M2 | 0.29 | 0.31 | 0.31 | 0.31 | 0.65 | 0.38 | 0.54 | 0.50 | 0.27 | 0.27 | 0.29 |
| SL | M1 | 0.26 | 0.31 | 0.39 | 0.21 | 0.32 | 0.36 | 0.37 | 0.30 | - | 0.17 | 0.48 |
| | M2 | 0.41 | 0.41 | 0.41 | 0.41 | 0.40 | 0.40 | 0.41 | 0.41 | 0.42 | 0.42 | 0.68 |
| K | M1 | - | - | 0.16 | - | 0.20 | 0.27 | 0.28 | 0.26 | - | - | - |
| | M2 | 0.33 | 0.28 | 0.28 | 0.25 | 0.26 | 0.29 | 0.29 | 0.27 | 0.32 | 0.32 | 0.25 |
| R | M1 | - | - | 0.43 | - | 0.28 | 0.33 | 0.29 | 0.27 | - | - | - |
| | M2 | 0.43 | 0.45 | 0.44 | 0.44 | 0.49 | 0.44 | 0.46 | 0.45 | 0.43 | 0.44 | 0.43 |
| LB | M1 | 0.20 | - | 0.34 | - | 0.48 | 0.41 | 0.46 | 0.34 | 0.15 | 0.23 | 0.33 |
| | M2 | 0.50 | 0.39 | 0.39 | 0.44 | 0.53 | 0.49 | 0.54 | 0.44 | 0.48 | 0.48 | 0.61 |
| V | M1 | - | - | - | - | - | - | - | - | - | - | - |
| | M2 | 0.07 | 0.05 | 0.05 | 0.06 | 0.05 | 0.05 | 0.05 | 0.05 | 0.06 | 0.05 | 0.06 |
| O | M1 | 0.22 | 0.24 | 0.72 | 0.18 | 0.55 | 0.68 | 0.64 | 0.59 | 0.26 | 0.42 | - |
| | M2 | 0.70 | 0.70 | 0.70 | 0.69 | 0.71 | 0.70 | 0.70 | 0.70 | 0.70 | 0.70 | 0.73 |

Note: Values presented are for statistically significant models ($p < 0.05$). Missing values indicate non-significant models ($p > 0.05$). Models tested were: M1 – $Dinc = a + b \ln(CI)$; M2 – $Dinc = a (CI)^b (Dsw)^c$; where Dinc – average diameter increment (2003-2005), CI – competition indices as in table 3-2, Dsw – initial spruce diameter (2003), a , b , and c – model parameters.

Table 3-4 Predictive ability (R^2_{adj}) of average height increment (2003-2005) by competition indices

| Indices/ Stands | Model | N | LOR1 | LOR2 | BA | HEG4 | VCR4 | SCR4 | SCros4 | SFa | SFs | DIFM |
|--------------------|-------|------|------|------|------|------|------|------|--------|------|------|------|
| B | M1 | - | 0.19 | 0.76 | 0.15 | 0.44 | 0.72 | 0.67 | 0.46 | 0.32 | 0.53 | 0.41 |
| | M2 | 0.78 | 0.78 | 0.80 | 0.80 | 0.77 | 0.78 | 0.76 | 0.77 | 0.78 | 0.77 | 0.75 |
| A | M1 | - | 0.15 | 0.50 | 0.33 | 0.40 | 0.49 | 0.48 | 0.42 | - | 0.19 | 0.28 |
| | M2 | 0.60 | 0.64 | 0.64 | 0.66 | 0.63 | 0.61 | 0.61 | 0.62 | 0.61 | 0.62 | 0.70 |
| L | M1 | - | - | 0.28 | - | 0.14 | 0.43 | 0.33 | 0.30 | - | - | - |
| | M2 | 0.39 | 0.39 | 0.41 | 0.39 | 0.43 | 0.47 | 0.45 | 0.47 | 0.39 | 0.39 | 0.40 |
| SL | M1 | 0.24 | 0.43 | 0.64 | 0.36 | 0.61 | 0.67 | 0.69 | 0.62 | - | 0.22 | 0.37 |
| | M2 | 0.85 | 0.83 | 0.84 | 0.84 | 0.83 | 0.85 | 0.83 | 0.85 | 0.89 | 0.90 | 0.93 |
| K | M1 | - | - | 0.46 | - | 0.43 | 0.63 | 0.60 | 0.53 | - | - | - |
| | M2 | 0.69 | 0.70 | 0.69 | 0.70 | 0.67 | 0.68 | 0.68 | 0.68 | 0.69 | 0.69 | 0.67 |
| R | M1 | - | - | 0.57 | - | 0.17 | 0.52 | 0.35 | 0.31 | - | - | - |
| | M2 | 0.83 | 0.84 | 0.84 | 0.84 | 0.84 | 0.84 | 0.84 | 0.84 | 0.84 | 0.84 | 0.85 |
| LB | M1 | - | - | 0.26 | - | 0.29 | 0.28 | 0.30 | 0.18 | - | 0.19 | - |
| | M2 | 0.36 | 0.34 | 0.34 | 0.39 | 0.36 | 0.34 | 0.35 | 0.34 | 0.36 | 0.36 | 0.36 |
| V | M1 | - | - | 0.29 | - | 0.15 | 0.29 | 0.23 | 0.22 | - | 0.14 | 0.18 |
| | M2 | 0.32 | 0.32 | 0.32 | 0.32 | 0.32 | 0.32 | 0.32 | 0.32 | 0.33 | 0.33 | 0.36 |
| O | M1 | 0.28 | 0.26 | 0.56 | 0.18 | 0.37 | 0.49 | 0.48 | 0.41 | 0.27 | 0.41 | 0.07 |
| | M2 | 0.63 | 0.60 | 0.62 | 0.58 | 0.62 | 0.64 | 0.63 | 0.63 | 0.61 | 0.61 | 0.59 |

Note: Values presented are for statistically significant models ($p < 0.05$). Missing values indicate non-significant models ($p > 0.05$). Models tested were: M1 – $Hinc = a + b \ln(CI)$; M2 – $Hinc = a (CI)^b (Hsw)^c$; where Hinc – average height increment (2003-2005), CI – competition indices as in table 3-2, Hsw – initial spruce height (2003), a , b , and c – model parameters.

Table 3-5 Predictive ability (R^2_{adj}) of average height increment (2000-2005) by competition indices

| Indices/ Stands | Model | N | LOR1 | LOR2 | BA | HEG4 | VCR4 | SCR4 | SCros4 | SFa | SFs | DIFM |
|--------------------|-------|------|------|------|------|------|------|------|--------|------|------|------|
| B | M1 | - | - | 0.53 | 0.27 | 0.36 | 0.58 | 0.53 | 0.44 | - | 0.24 | 0.26 |
| | M2 | 0.65 | 0.66 | 0.67 | 0.66 | 0.66 | 0.66 | 0.66 | 0.66 | 0.66 | 0.68 | 0.73 |
| A | M1 | - | 0.15 | 0.80 | - | 0.49 | 0.71 | 0.62 | 0.53 | 0.28 | 0.53 | 0.45 |
| | M2 | 0.88 | 0.86 | 0.90 | 0.90 | 0.89 | 0.89 | 0.88 | 0.88 | 0.88 | 0.88 | 0.88 |
| L | M1 | - | - | 0.42 | - | 0.19 | 0.59 | 0.45 | 0.41 | - | - | - |
| | M2 | 0.40 | 0.43 | 0.51 | 0.44 | 0.50 | 0.62 | 0.56 | 0.59 | 0.40 | 0.41 | 0.40 |
| SL | M1 | 0.30 | 0.49 | 0.68 | 0.41 | 0.64 | 0.68 | 0.70 | 0.63 | 0.17 | 0.28 | 0.33 |
| | M2 | 0.76 | 0.77 | 0.77 | 0.76 | 0.79 | 0.76 | 0.79 | 0.76 | 0.80 | 0.80 | 0.91 |
| K | M1 | - | - | 0.46 | - | 0.47 | 0.69 | 0.66 | 0.56 | - | - | - |
| | M2 | 0.64 | 0.67 | 0.60 | 0.66 | 0.62 | 0.70 | 0.67 | 0.64 | 0.63 | 0.62 | 0.60 |
| R | M1 | - | - | 0.58 | - | 0.16 | 0.50 | 0.33 | 0.27 | - | - | - |
| | M2 | 0.84 | 0.85 | 0.86 | 0.86 | 0.86 | 0.85 | 0.85 | 0.85 | 0.85 | 0.85 | 0.85 |
| LB | M1 | - | - | 0.30 | - | 0.35 | 0.34 | 0.37 | 0.22 | - | 0.21 | - |
| | M2 | 0.31 | 0.28 | 0.30 | 0.35 | 0.37 | 0.34 | 0.37 | 0.30 | 0.32 | 0.33 | 0.37 |
| V | M1 | - | - | 0.23 | - | - | 0.23 | 0.18 | 0.18 | - | - | 0.17 |
| | M2 | 0.20 | 0.19 | 0.22 | 0.19 | 0.19 | 0.22 | 0.19 | 0.20 | 0.21 | 0.21 | 0.27 |
| O | M1 | 0.30 | 0.32 | 0.72 | 0.25 | 0.51 | 0.66 | 0.64 | 0.56 | 0.33 | 0.51 | - |
| | M2 | 0.75 | 0.71 | 0.76 | 0.71 | 0.73 | 0.72 | 0.72 | 0.73 | 0.74 | 0.73 | 0.72 |

Note: Values presented are for statistically significant models ($p < 0.05$). Missing values indicate non-significant models ($p > 0.05$). Models tested were: M1 – $Hinc = a + b \ln(CI)$; M2 – $Hinc = a (CI)^b (Hsw)^c$; where Hinc – average height increment (2000-2005), CI – competition indices as in table 3-2, Hsw – initial spruce height (2000), a , b , and c – model parameters.

Table 3-6 Selected models and parameter estimates for predicting diameter increment (cm yr⁻¹) and height increment (m yr⁻¹) for spruce

| Age class/ Stand | Model | <i>n</i> | MS _{res} | R ² _{adj} | <i>a</i> | <i>b</i> | <i>c</i> |
|------------------------------|---|----------|-------------------|-------------------------------|----------|----------|----------|
| 1 / B | Dinc = $a + b \ln(\text{LOR2})$ | 30 | 0.0427 | 0.72 | 1.9968 | -0.1681 | |
| 1 / A, L | | 60 | 0.0988 | 0.43 | 2.1447 | -0.1922 | |
| 2, 3 / SL, K, R, LB, V, O | | 179 | 0.0954 | 0.50 | 1.1142 | -0.0903 | |
| 1 / B | Dinc = $a + b \ln(\text{HEG4})$ | 30 | 0.1048 | 0.31 | 1.0913 | -0.088 | |
| 1 / A, L | | 60 | 0.0773 | 0.55 | 1.5758 | -0.1427 | |
| 2, 3 / SL, K, R, LB, V, O | | 179 | 0.1058 | 0.45 | 0.8676 | -0.0715 | |
| 1 / B | Dinc = $a (\text{LOR1})^b (\text{Dsw})^c$ | 30 | 0.0332 | 0.79 | 8.0386 | -0.35 | 0.6429 |
| 1 / A, L | | 60 | 0.0857 | 0.51 | 2.0981 | -0.2664 | 0.7435 |
| 2 / SL, K, R | | 90 | 0.0381 | 0.41 | 0.4482 | -0.0989 | 0.4642 |
| 3 / LB, V, O | | 89 | 0.1543 | 0.27 | 0.7728 | -0.115 | 0.2347 |
| 1 / B, A, L | Dinc = $a (\text{DIFM})^b (\text{Dsw})^c$ | 90 | 0.0691 | 0.60 | 0.3183 | 0.3339 | 0.5897 |
| 2, 3 / SL, K, R, LB, V, O | | 179 | 0.0927 | 0.52 | 0.4212 | 0.3389 | 0.2544 |
| 1 / B | Hinc = $a + b \ln(\text{LOR2})$ | 30 | 0.0929 | 0.80 | 1.7617 | -0.1525 | |
| 1 / A, L | | 60 | 0.2005 | 0.51 | 1.7889 | -0.1602 | |
| 2, 3 / SL, K, R, LB, V, O | | 179 | 0.1384 | 0.71 | 0.9766 | -0.085 | |
| 1 / B | Hinc = $a + b \ln(\text{VCR4})$ | 30 | 0.1338 | 0.71 | 0.9876 | -0.0653 | |
| 1 / A, L | | 60 | 0.1676 | 0.59 | 1.067 | -0.0759 | |
| 2, 3 / SL, K, R, LB, V, O | | 179 | 0.2295 | 0.50 | 0.6037 | -0.0387 | |
| 1 / B | Hinc = $a (\text{LOR1})^b (\text{Hsw})^c$ | 30 | 0.0656 | 0.86 | 8.1853 | -0.3437 | 1.0204 |
| 1 / A, L | | 60 | 0.1843 | 0.55 | 2.6574 | -0.2668 | 0.6996 |
| 2 / SL, K, R | | 90 | 0.0339 | 0.79 | 0.2793 | -0.0885 | 0.8712 |
| 3 / LB, V, O | | 89 | 0.2447 | 0.47 | 0.8541 | -0.1509 | 0.2846 |
| 1 / B, A, L | Hinc = $a (\text{DIFM})^b (\text{Hsw})^c$ | 90 | 0.138 | 0.71 | 0.4026 | 0.4135 | 0.6275 |
| 2, 3 / SL, K, R, LB, V, O | | 179 | 0.16 | 0.67 | 0.3095 | 0.3421 | 0.3366 |

Note: All models presented are statistically significant ($p < 0.05$). Indicator variable tests were performed to allow data pooling across multiple stands and age classes; where possible, stands were grouped. Dinc – average diameter increment of spruce (2003-2005); Hinc – average height increment of spruce (2000-2005); LOR2, HEG4, VCR4, DIFM – competition indices as in table 3-2; Dsw – initial stem diameter of spruce (2003), Hsw – initial height of spruce (2000).

Figure 3-1 Relationships between diameter increment (2003-2005) and competition (Lorimer's index) (*a* and *b*) and height increment (2000-2005) and competition (Lorimer's index) (*c* and *d*) for age class 1 (stands B vs. A and L – *a* and *c*) and age class 1 (stands A and L) vs. age classes 2 and 3 (AC2+3, *b* and *d*). Data were pooled where possible based on indicator variable tests. Lines shown on the graphs (B pred, A+L pred, and AC2+3 pred) are based on nonlinear regressions fit to data (models provided in table 3-6).

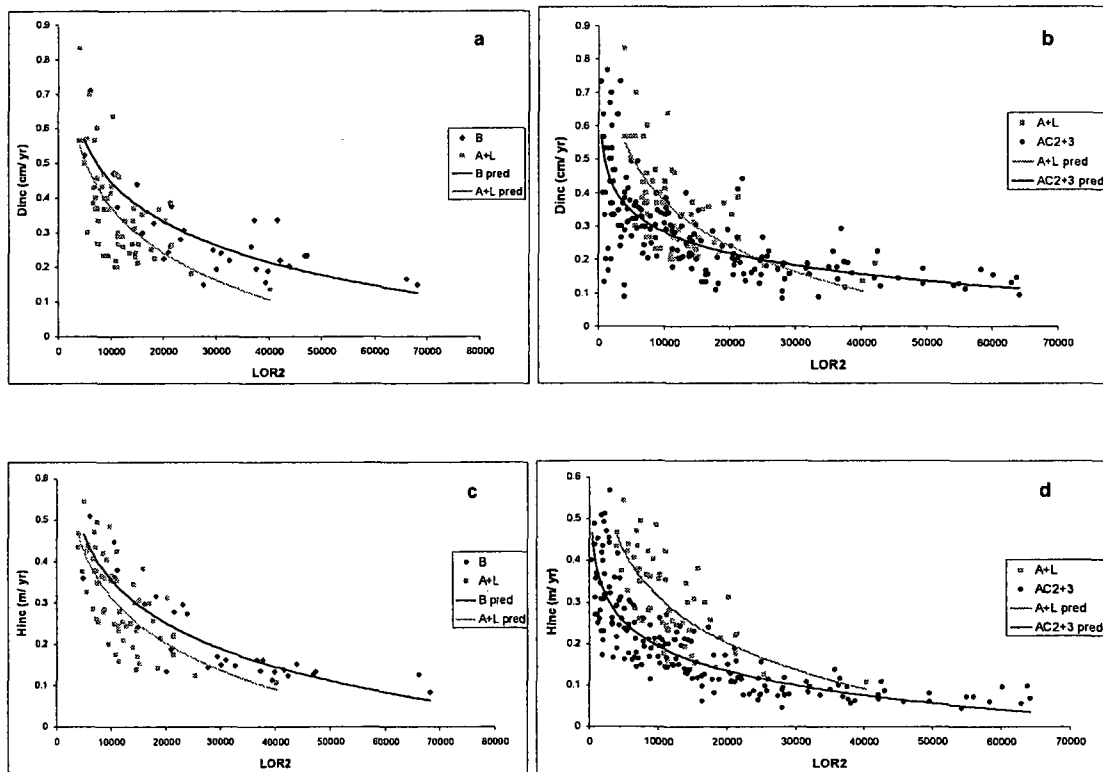
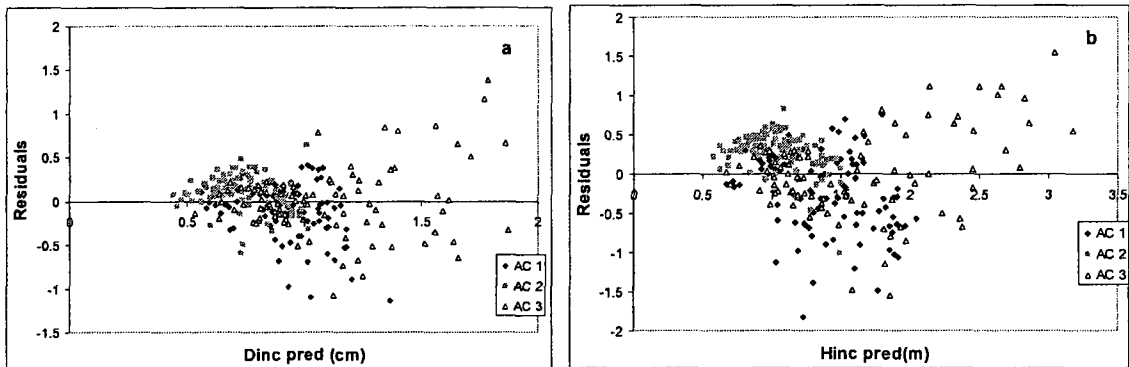


Figure 3-2 Distribution of residuals against predicted values (Dinc pred and Hinc pred) for models predicting diameter increment (*a*) and height increment (*b*) as a function of competition index and initial size. Data were pooled across all stands and age classes, ignoring previously detected differences. Residuals were provided by the following models: *a* – $\text{Dinc} = 0.4686 * (\text{Lor1})^{0.0247} * (\text{Dsw})^{0.3468}$ ($n=269$, $\text{MS}_{\text{res}}=0.1091$, $R^2_{\text{adj}}=0.43$); *b* – $\text{Hinc} = 0.1713 * (\text{Lor1})^{0.1695} * (\text{Hsw})^{0.4314}$ ($n=269$, $\text{MS}_{\text{res}}=0.2518$, $R^2_{\text{adj}}=0.52$), where Dinc – average diameter increment of spruce (2003-2005); Hinc – average height increment of spruce (2000-2005); LOR1– Lorimer’s competition index as in table 3-2; Dsw – initial stem diameter of spruce (2003), Hsw – initial height of spruce (2000). AC 1 – age class 1 (10-20 years), AC 2 – age class 2 (20-40 years), AC 3 – age class 3 (40-60 years).



Chapter 4 Morphological attributes of white spruce as potential indicators of competition and growth allocation

4.1 Introduction

Morphological attributes such as the ratio of height to diameter are simple and easily measurable tree characteristics that reflect the adaptation of seedlings and saplings to their growing environment (Claveau et al. 2002; Stancioiu and O'Hara 2006). These attributes may also express genetic characteristics that could influence the response to changes in resource availability or other factors (Chmura et al. 2007).

The mixedwood boreal forest is prominent in western Canada where it usually occupies the most productive sites (Rowe 1972), being dominated by two main species: trembling aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench) Voss). These two species present complementary characteristics that make their growth in mixture possible: regeneration and recruitment strategies, initial growth rates, and differences in shade tolerance, longevity, and time to maturity (Lieffers et al. 1996). In young mixtures, aspen is typically situated in the overstory, whereas spruce is moderately shade tolerant, grows more slowly, and is located in the understory. Therefore, abundant regeneration and faster initial growth of aspen can limit spruce access to resources, and may lead to reduced spruce growth and survival (Jobidon 2000).

Growth models require quantification of growth potential given certain conditions (e.g., species, age, site), and competition is widely recognized as a major cause of growth reduction (Vanclay 1994). Models develop and test mathematical equations that describe growth, regeneration and recruitment, and mortality; therefore, competition is also quantified in a mathematical form. Several competition indices have been formulated for use in estimating the intensity of tree competition. While some indices may consider a stand-level approach, most indices were formulated based on an individual-tree approach, with or without spatial information included. Lorimer (1983) noted that three main groups may be distinguished: (1) indices that measure the amount of overlap of hypothetical "zones of influence" among neighboring trees, (2) indices that consider the area potentially available to each tree, and (3) indices that incorporate relative diameters

and distances between subject trees and competitors. Predicting spruce growth response based on aspen competition indices is a viable option, previous studies suggesting that simple indices such as basal area or density may work as well or better than more complex indices (Steneker and Jarvis 1963; Alemdag 1978; MacIsaac and Navratil 1996).

Competition indices can help explain competitive interactions, however there has been much debate and controversy over their use. Some indices seem to be better suited to certain species than others and the index performance may be dependent on the stand age, therefore no index can be considered universally superior (Daniels et al. 1986). Moreover, some studies suggest that relationships between growth and competition are site-specific (Green 2004; Filipescu and Comeau 2007). In a dynamic system with conditions changing over time, most competition indices provide only a static quantification (Burton 1993), limiting the application of results to stands of different ages.

The rationale supporting the use of morphological attributes as indicators of competition is that trees are able to prioritize different types of growth (e.g., roots versus shoots; height versus diameter; vertical growth versus lateral crown development) and alter their morphology when resources become scarce (Morgan and Cannell 1988; Messier et al. 1999). Understory trees attempt to increase light interception and reduce physiological losses (mainly by respiration), while trying to compensate for limited availability of light through better acquisition and efficiency of using other resources, such as nutrients and water (Kohyama 1987; King 1990, 1991).

Morphological attributes that are used to assess seedling vigour and growth potential include stem height, live crown ratio (crown length divided by total height), crown form and size, stem height to diameter ratio, apical dominance ratio (leader length divided by the length of the longest top whorl branch), and number of branches or number of buds (Duchesneau et al. 2001; Ruel et al. 2000).

Species shade tolerance influences the morphological and physiological plasticity of young trees growing under variable light environments. In this respect, more shade-tolerant species have an advantage over less shade-tolerant ones, while coniferous seedlings are considered more adaptable than deciduous seedlings (Claveau et al. 2002;

Beaudet and Messier 1998). Size also appears to play a role in morphological plasticity, with stronger influence in larger size classes (Duchesneau et al. 2001), whereas other studies suggest that size has only a limited effect on morphological characteristics (Williams et al. 1999).

Previous studies have focused on morphological attributes of advance regeneration and the ability of understory saplings to respond to release from mature canopies (Messier et al. 1999; Ruel et al. 2000). Nevertheless, there is an increasing interest in the use of morphological characteristics in young boreal mixedwoods where broadleaf pioneer species overtop coniferous seedlings. Regulating competition through overstory density reduction to promote growth and survival of understory conifers is one option to establish and maintain boreal mixedwood stands (Comeau et al. 2005; Bokalo et al. 2007).

Height to diameter ratio (HDR) is a sensitive indicator of crop tree vigour for newly established conifer stands that experience competition from hardwood or herbaceous species (Tesch et al. 1993; Wagner et al. 1996, 1999). Moreover, height and diameter, the input variables for HDR, are easily measured response variables of seedling growth that may express the potential of future biomass production.

Height and diameter growth are influenced by a combination of genetic factors and physiological and morphological response to environmental factors (Opio et al. 2000). However, increasing levels of competition affect diameter increment more (Richardson et al. 1999), as height allocation is favoured over diameter for better positioning to capture light, resulting in slender etiolated stems (i.e., priority is given to height growth over diameter growth). Further, for many conifers height growth is determinate and uses currently available resources during the beginning of the growing season. Cambial growth starts later, having a lower priority in photosynthate allocation, it is not determinate and may continue for the remainder of the growing season (Lanner 1985).

The apical dominance ratio (ADR), also known as leader to lateral branch growth ratio, may also serve as an indicator of tree vigour and competition environment (Williams et al. 1999). Defined as the inhibition of a lateral branch by the shoots above it,

apical control appears to be influenced by several hormones, however the exact mechanisms are still unclear (Wilson 2000). It is considered that the higher the ADR (i.e., the stronger the control of the apical bud on lateral buds and branches), the more vigorous the seedling. Apical control may inhibit the growth of lateral branches to the benefit of the main shoot, with important implications for crown architecture (Wilson 1998). While both light and phytohormones play an important role in apical dominance, it is not clear yet whether they affect the morphological response independently, or whether hormones are involved in a series of processes initiated by photoreceptor excitation (Chory and Li 1997).

The number and size of buds on shoots and on the terminal leader are also influenced by competition (Harrington and Tappeiner II 1991; Lieffers and Stadt 1994). Bud production is a photosynthate sink that may indicate the level of available resources, mainly light, during the previous year. Nevertheless, for Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) bud production and subsequent seedling growth were strongly correlated (Tappeiner II et al. 1987), suggesting a compounded effect over time (i.e., lower competition increases bud production that in turn leads to more photosynthetic tissue and increased growth rates). Therefore, the number of buds was suggested to be a good representation of competition. However, interwhorl bud production may prove more responsive to competition reduction than leader and whorl bud production (Tappeiner II et al. 1987). The interwhorl buds play an important role, as the short-lived nonnodal (interwhorl) branches may support up to half of the total foliage, while accounting only for 10% of woody supporting tissue (Jensen and Long 1983).

Early growth performance was linked to long-term success in reaching the canopy, suggesting that growth models should account for individual growth history (Landis and Peart 2005). Morphological attributes are less data intensive and less expensive to acquire than most other competition measures. At the same time, they may provide a direct link between tree morphological expression and growth response. This chapter explores the potential of using morphological attributes to predict spruce growth response across a gradient of competition environments following spacing treatments in young boreal mixedwoods. The objectives are to evaluate the correlation between

morphological attributes and competition indices, and to test the ability of morphological attributes to predict subsequent spruce growth.

4.2 Methods

The site conditions, experimental design, and field data collection are described in detail in chapter 2 and summarized briefly here. Field installations consisting of young aspen-spruce mixedwoods of variable density were used. Western Boreal Growth and Yield Association (WESBOGY) established blocks for medium and superior sites and this study used data from four installations located near Peace River, Alberta (medium site PRm 56°55'N and 118°30'W, superior site PRs 56°41'N and 117°72'W), near Edson, Alberta (medium site EDm 53°46'N and 116°41'W, superior site EDs 53°48'N and 116°38'W), Prince Albert, Saskatchewan (medium site PAm 53°45'N and 105°30'W, superior site PAs 53°40'N and 105°56'W), and Grande Prairie, Alberta (GP 54°55'N and 118°30'W, there was no differentiation made between medium and superior sites at this location).

Spruce trees were selected at each installation in plots with five levels of aspen density (0, 500, 1500, 4000 stems/ha, and natural unspaced). Spruce seedlings were measured to provide growth information over 2 years (2002-2003). Additional measurements were collected in May 2002 to determine several morphological attributes: leader length (i.e., stem height growth for previous year) and the length of the longest top whorl branch to determine the apical dominance ratio (ADR); the number of buds on the current stem leader; crown volume and crown surface area were computed based on crown length and average crown radii; stem height to diameter ratio (HDR) was based on current measurements of height and diameter. For each selected spruce the number of branches at each whorl were counted and since there were no trends across the gradient of aspen density or over time, this was not considered further.

During the summer of 2002 aspen competition was assessed by collecting detailed measurements within a 3.99 m radius plot centered at each selected spruce. In addition, light transmittance was measured at midcrown and topcrown position of spruce using LAI-2000 plant canopy analyzers (Li-COR Inc., Lincoln, Nebraska). Several competition

indices calculated from measurements commonly collected in the field were evaluated (table 4-1).

Regression models were developed for each location and installation (medium and superior) to explore relationships between: (i) morphological attributes and competition indices; and (ii) spruce growth (as stem volume increment) and morphological attributes. These attributes included: apical dominance ratio, number of buds on the leader, height to diameter ratio, and size attributes (height, crown volume and crown surface area).

Least-squares linear and nonlinear regression was used to estimate model parameters within the SAS statistical package for Windows (version 9.1) (SAS Institute Inc., Cary, North Carolina). Evaluation of model fit and validity of model assumptions were based on analysis of residuals plotted against predicted values. To account for differences in sample size, the adjusted values of the coefficient of determination (R^2_{adj}) were calculated.

4.3 Results

Apical dominance ratio showed virtually no relationship with competition indices or with spruce growth. The number of buds on the terminal leader showed weak correlation with competition indices (R^2_{adj} generally lower than 0.2), while providing poor prediction of spruce growth (R^2_{adj} values between 0.05 and 0.26). Height to diameter ratio measured in the spring of 2002 was a relatively poor predictor of average spruce growth over 2 growing seasons 2002-2003 (R^2_{adj} lower than 0.35), though it was generally well correlated with competition indices, with R^2_{adj} values higher than 0.4, except for Prince Albert and Edson locations where relationships were not as strong (table 4-2). Morphological attributes based solely on size (i.e., height, crown volume, and crown surface area) were very poorly correlated with competition indices (R^2_{adj} lower than 0.1), while being consistently good predictors of spruce growth (table 4-3). Examples of these relationships between morphological attributes, competition indices and spruce growth are illustrated in figure 4-1.

Relationships between growth allocation ratios, as defined by Comeau et al. (2003) (i.e., the ratio of height increment to volume increment and the ratio of height increment to diameter increment – based on average growth over 2002-2003), and selected competition indices (e.g., basal area, Lorimer's, transmittance, and spacing factor) were also explored. Additional relationships between growth ratios and several combinations of competition indices and initial spruce size or HDR were examined. These models provided inconsistent results and behaviour, and in many cases parameter estimation failed to converge. Additional problems were revealed by the analysis of residuals. Selected models that proved reliable are illustrated in figure 4-2.

Aspen basal area was a competition index consistently correlated with HDR. In addition, basal area is a simple index, easily measured in the field or obtained from traditional growth and yield models. It is also widely used and readily understood by field foresters. Therefore, relationships between basal area and HDR were evaluated further, with parameter estimates for these models included in table 4-4. For each location, there was no significant difference between medium and superior sites, allowing for data pooling. Examining the 95% confidence limits of parameter estimates showed that relationships between HDR and basal area were similar across the four geographical locations included in the study (figure 4-3).

Changes over time in HDR values were also examined (table 4-5). Relative to 2002, the HDR change for individual trees ranged up to 48% in 2003 and 32% in 2004. However, within each location average changes of HDR over time were much smaller (under 10%). In addition, temporal changes of spruce HDR do not appear to be influenced by levels of aspen density (figure 4-4). Seasonal weather data from the closest climate stations is provided for the growing seasons 2001-2003 for Peace River, Grande Prairie, and Prince Albert (table 4-6). Climate data from Edson was not available from Environment Canada. No consistent relationships between HDR and seasonal weather data were observed.

Significant relationships between spruce growth (diameter and height relative growth – calculated as average increment for 2002-2003 divided by initial diameter or height in the spring of 2002) and aspen basal area were obtained for all installations

(table 4-7), except for Grande Prairie and Prince Albert medium. At each installation linear regressions fit to data resulted in models with similar slopes of relative increment for both diameter and height (figure 4-5).

4.4 Discussion

Results from my study provide further evidence on the potential of morphological attributes to represent the competition environment and growth of spruce seedlings in young boreal mixedwoods.

Apical dominance ratio and the number of buds on the terminal leader displayed poor or no relationships with competition indices and growth of spruce. Previous studies (Lieffers and Stadt 1994; Ruel et al. 2000) suggested that ADR and number of buds are related to the competition environment; in my study however, it seems that other factors may have a stronger influence. The apical dominance may be disrupted by damage from a variety of factors, including herbivore attacks (Aarssen 1995). Personal field observations showed that damage from insects, frost, and non-flush of the terminal bud owing to dry and cold spring weather may affect apical dominance of spruce seedlings. The number of buds on the terminal leader also seemed to be controlled by other factors (e.g., spring weather). In addition, light levels under deciduous cover may not be sufficiently low or low for sufficient duration to cause as full a range of responses as may occur under conifer canopies.

Morphological attributes based on spruce size (height, crown volume and surface area) were consistently strong predictors of subsequent growth. Current size is an effective representation of tree growth potential in terms of access to limiting resources and ability to use them through the foliar apparatus (as discussed in detail in chapters 2 and 3). As competition levels decrease, growth becomes even more dependent on size (Weiner and Thomas 1992). Nevertheless, current size is a compounded response to past competition levels over longer periods, explaining the poor correlation between size and competition indices observed in my study. Other factors such as herbivore attacks and frost may have had a differential effect on current size.

Height to diameter ratio was generally well correlated with other competition measures owing to the allometrical plasticity of young spruce seedlings and findings from my study are in agreement with previous studies (Lieffers and Stadt 1994; Coopersmith and Hall 1999; Opio et al. 2000; Bokalo et al. 2007). HDR seems to represent the competition environment effectively in the absence of other influencing factors (e.g., aggressive understory at Prince Albert or moose browsing at Edson where relationships were not as strong). However, HDR was a relatively poor predictor of spruce growth, possibly because HDR is a relative measure well correlated with competition indices, while trees with similar HDR but of different absolute size grow differently. As shown in chapters 2 and 3, competition indices are strong predictors of spruce growth, and HDR is correlated with these indices. Nevertheless, competition indices are preferable to HDR, which reflects the cumulative effect of competition. In addition, using HDR alongside initial size to predict spruce growth could be problematic owing to self-correlation (i.e., both are based on same spruce measures). HDR may be a reliable indicator of past competition, without providing much information on current and future conditions. Therefore, to include this information I suggest reliance on other competition measures for making reliable predictions of spruce growth (Filipescu and Comeau 2007).

It is generally considered that 60 (55-70) is the HDR threshold value separating stressed from unstressed seedlings, however this is based mostly on empirical observation of growth rates. Despite the abundance of empirical evidence on the effectiveness of HDR to represent competition, in general the literature stops short of discussing the exact mechanisms and processes that control HDR.

Differences in allometric relationships between individuals from crowded as opposed to uncrowded populations are well documented, as trees are able to adapt their metabolic rates and structure to availability of resources (Weiner and Fishman 1994; Reich et al. 2005). In addition to height having higher allocation priority over diameter with increasing competition, it seems that less windy conditions in more dense stands may also affect stem morphology. Trees prevented from swaying grew less in diameter in the lower part of the trunk than free-swaying trees (Jacobs 1954), while suppressed understory saplings presented slender, etiolated stems in sheltered conditions (King

1986). Meng et al. (2006) showed that height growth of tall lodgepole pine (*Pinus contorta* Dougl. ex Loud) increases with a reduction in stem bending. Nonetheless, increased variability in height-diameter allometry for understory species (O'Brien 1995) suggests that in less windy understory there should be other factors affecting morphological responses. For example, lateral shade was found to influence height-diameter allometry more than reduced wind sway (Holbrook and Putz 1989). Light quality differences in terms of lower ratios of red to far-red radiation leads to stronger apical dominance and promotes shoot elongation and internode length (Morgan et al. 1983; Schmitt 1997; Smith and Whitelam 1997).

Stand development and tree size may also influence HDR, changes in height-diameter allometry being triggered by diameter growth increasing faster than height growth (Niklas 1995). As trees grow higher into the canopy, stem diameter increases to minimize the risk of buckling owing to addition of crown width (Henry and Aarssen 1999). Therefore, evaluating relationships between stem diameter and crown width may be more appropriate than modeling height-diameter allometry. In addition, static relationships between height and diameter may not provide reliable insight into the effects of age or neighbours, since these are confounded (Henry and Aarssen 1999).

Size has a mediating role between biomechanical constraints and resource requirements at differing levels of resource availability (Niklas 1994). While an increase in size generally leads to increased access to resources, at the same time it may result in increases in vascular hydrodynamic resistance hindering the supply of water and nutrients to the crown (Ryan and Yoder 1997). Using principles of fractal geometry, West, Brown and Enquist developed a general allometry model based on optimization of hydrodynamic resistance and whole-stem architecture (West et al. 1999; Enquist 2002). The model adequately explains empirical allometrical relationships; however, it may have several limiting assumptions, such as the use of a terminal unit (Nygren and Pallardy 2008) or ignoring the importance of competition when accounting for growth variability (Coomes and Allen 2007).

The nondestructive setup of my study as part of a long-term, large scale experiment precluded detailed evaluation of biomass allocation patterns, apart from

empirical data on HDR variation with competition. The 'functional equilibrium' theory predicts that trees react to change in resource availability by capturing the resources most limited (i.e., a plant would increase allocation to shoots and leaves when aboveground resources decrease, and increase allocation to roots when belowground resources decrease). Light and water may have a larger effect on relative growth than on biomass partitioning, while nutrients may have a larger effect on biomass allocation (Poorter and Nagel 2000). Following release, suppressed seedlings were observed to allocate more to roots than stem diameter or height in order to capture soil resources (Kneeshaw et al. 2002; Claveau et al. 2006). Increased allocation to roots may also be explained by increased exposure to open conditions (Ruel et al. 2003). In addition, biomass allocation to roots seems to be species-specific when resources are limited (Canham et al. 1996).

The use of growth allocation ratios was problematic with my data. In contrast, Comeau et al. (2003) successfully developed relationships between growth ratios and competition indices. Several aspects may have had an impact, such as size variability of spruce trees, regeneration differences, and experiment setup. It is also possible that the response variability and amplitude of treatment effects on spruce growth in my study was smaller than the one reported by Comeau et al. (2003), therefore inducing problems with the testability of growth ratios (Jasieński and Bazzaz 1999).

Influences of the geographical location on HDR have been reported by comparing results from competition studies across British Columbia (Mustard and Harper 1998), suggesting that differences in growing conditions (e.g., climate) would result in HDR differences at similar competition levels. My results showed that across the four geographical locations examined (3 in Alberta and 1 in Saskatchewan) HDR values and relationships between HDR and competition (quantified as the basal area of the overtopping aspen) are similar. As a possible explanation, it could be argued that the uniform experimental design and less pronounced climatic differences in the boreal region I examined resulted in comparable relationships as opposed to the ones reported by Mustard and Harper (1998) with data from different experiments across a more variable climatic area. However, growth-competition relationships were found to differ with the geographical location (as discussed in chapter 2).

Relationships between relative diameter and height growth of spruce with aspen basal area revealed very similar relationships, suggesting that growth patterns have stabilized and trees allocated variable resources available to growth proportional with their size. However, when other factors are present (such as frost and insect damage at the Grande Prairie site and aggressive shrub competition at the Prince Albert medium site), relationships are no longer similar. In my study the influence of understory was ignored, however understory vegetation may explain growth variation in spruce plantations (Cortini and Comeau 2008).

While my results provide a starting point for discussing morphological attributes in relation to the competition environment and ability to predict subsequent growth, several aspects need further exploration. More verified evidence is needed on the effects of environmental factors and their seasonal variation (during the growing season and from year to year) on the growth of white spruce. The interplay of various types of resources and the priority of biomass allocation to roots versus shoots, stem versus foliage, and height versus diameter require additional examination to understand better the mechanisms and processes regulating spruce growth in boreal mixedwoods.

4.5 Conclusions

Results from my study indicate that morphological attributes have the potential to represent the competition environment and predict subsequent spruce growth. Some morphological attributes (e.g., apical dominance ratio, number of buds) were very weakly correlated with competition indices, while others (e.g., height to diameter ratio and size attributes) provided strong relationships of competition indices and growth. Despite their demonstrated potential, caution is recommended with morphological attributes and the use of combined indicators is suggested.

4.6 References

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Table 4-1 Formulas and abbreviations of competition indices

| Competition index | Formula (description) |
|--|--|
| Number of trees | N (stems/ha) |
| Basal area | BA (m ² /ha) |
| Lorimer's | $\mathbf{Lor} = \sum_{i=1}^n DBH_{AWi} \text{ (cm)}$ |
| Crown volume | $\mathbf{VCr} = \sum_{i=1}^n VCr_{AWi} \text{ (m}^3\text{)}$ |
| Crown surface area | $\mathbf{SCr} = \sum_{i=1}^n SCr_{AWi} \text{ (m}^2\text{)}$ |
| Crown sectional area | $\mathbf{SCros} = \sum_{i=1}^n SCros_{AWi} \text{ (m}^2\text{)}$ |
| Hegy's (based on 4 closest aspen) | $\mathbf{Heg4} = \left(\sum_{i=1}^4 DBH_{AWi} / dist_i \right) * Npl / 4$ |
| Crown volume (based on 4 closest aspen) | $\mathbf{VCr4} = \left(\sum_{i=1}^4 VCr_{AWi} / dist_i \right) * Npl / 4$ |
| Crown surface area (based on 4 closest aspen) | $\mathbf{SCr4} = \left(\sum_{i=1}^4 SCr_{AWi} / dist_i \right) * Npl / 4$ |
| Crown sectional area (based on 4 closest aspen) | $\mathbf{Scros4} = \left(\sum_{i=1}^4 SCros_{AWi} / dist_i \right) * Npl / 4$ |
| Spacing factor | $\mathbf{SF} = 10000 / H_{AW} * \sqrt{N} \text{ (\%)} $ |
| Light transmittance (at spruce midcrown) | DIFMid (%) |
| Light transmittance (at spruce topcrown) | DIFTop (%) |

Note: DBH_{AWi} is basal diameter of the i th aspen; VCr_{AWi} is total crown volume of the i th aspen; SCr_{AWi} is total crown surface of the i th aspen; $SCros_{AWi}$ is surface area of the crown horizontal section of the i th aspen; $dist_i$ is inter-tree distance between the selected spruce and the i th aspen; Npl is number of aspen per competition assessment plot; H_{AW} is dominant height of aspen; N is number of aspen stems per ha.

Table 4-2 Predictive ability of relationships between spruce height to diameter ratio and competition indices (R^2_{adj} values)

| Sites / CI | Peace River | | Prince Albert | | Edson | | Grande Prairie |
|---------------|-------------|------|---------------|------|-------|------|-------------------|
| | Med | Sup | Med | Sup | Med | Sup | |
| N | 0.59 | 0.57 | 0.20 | 0.08 | 0.65 | 0.31 | 0.43 |
| BA | 0.67 | 0.61 | 0.32 | 0.27 | 0.57 | 0.62 | 0.53 |
| Lor | 0.68 | 0.61 | 0.29 | 0.12 | 0.63 | 0.35 | 0.50 |
| VCr | 0.45 | 0.61 | 0.29 | 0.11 | 0.55 | 0.35 | 0.41 |
| SCr | 0.62 | 0.65 | 0.30 | 0.12 | 0.63 | 0.35 | 0.48 |
| SCros | 0.60 | 0.63 | 0.30 | 0.10 | 0.59 | 0.34 | 0.47 |
| Heg4 | 0.63 | 0.50 | 0.20 | 0.08 | 0.55 | 0.28 | 0.42 |
| VCr4 | 0.58 | 0.51 | 0.18 | 0.10 | 0.61 | 0.31 | 0.39 |
| SCr4 | 0.64 | 0.54 | 0.20 | 0.10 | 0.61 | 0.32 | 0.41 |
| SCros4 | 0.65 | 0.52 | 0.20 | 0.07 | 0.61 | 0.31 | 0.39 |
| SF | 0.66 | 0.69 | 0.34 | 0.17 | 0.56 | 0.23 | 0.46 |
| DIFMid | 0.66 | 0.52 | 0.29 | 0.12 | 0.56 | 0.40 | 0.49 |
| DIFTop | 0.56 | 0.34 | 0.27 | 0.15 | 0.56 | 0.37 | 0.34 |

Note: Values shown are for statistically significant models ($p < 0.05$), and are based on regressions fit to data using the equations: $HDR = a + b \text{ CI}$ for $\text{CI} = \text{N, BA, ..., SCros4}$; $HDR = a + b \ln \text{ CI}$ for $\text{CI} = \text{DIFMid, DIFTop}$; and $HDR = a \text{ CI}^b$ for $\text{CI} = \text{SF}$; HDR is height to diameter ratio; CI is competition index as in table 4-1; a , and b are model parameters.

Table 4-3 Predictive ability of relationships between spruce stem volume increment (average 2002-2003) and morphological attributes (R^2_{adj} values)

| Sites / MA | Peace River | | Prince Albert | | Edson | | Grande Prairie |
|---------------|-------------|----------|---------------|----------|--------|----------|-------------------|
| | Medium | Superior | Medium | Superior | Medium | Superior | |
| HT | 0.43 | 0.35 | 0.69 | 0.50 | 0.36 | 0.69 | 0.51 |
| CV | 0.44 | 0.38 | 0.82 | 0.53 | 0.45 | 0.69 | 0.67 |
| CSA | 0.46 | 0.39 | 0.81 | 0.54 | 0.44 | 0.70 | 0.66 |

Note: Values shown are for statistically significant models ($p < 0.05$), and are based on nonlinear regressions fit to data using the equation: $SVI = a \text{ MA }^b$; SVI is stem volume increment of spruce – average 2002-2003; MA is morphological attribute based on size measured in spring of 2002: height (HT), crown volume (CV) and crown surface area (CSA); a , and b are model parameters.

Table 4-4 Parameter estimates for models predicting spruce height to diameter ratio as a function of aspen basal area

| Location | <i>n</i> | MS _{res} | R ² _{adj} | <i>a</i> | <i>b</i> |
|----------------------------------|----------|-------------------|-------------------------------|--------------------------|-----------------------|
| Peace River medium | 60 | 29.34 | 0.67 | 46.44 (44.40 - 48.49) | 1.82 (1.49 - 2.16) |
| Peace River superior | 60 | 34.48 | 0.61 | 44.51 (42.37 - 46.65) | 1.91 (1.51 - 2.31) |
| Peace River (data pooled) | 120 | 32.03 | 0.64 | 45.41 (43.94 - 46.87) | 1.88 (1.63 - 2.14) |
| Prince Albert medium | 54 | 62.54 | 0.32 | 47.94 (44.82 - 51.06) | 1.48 (0.89 - 2.08) |
| Prince Albert superior | 54 | 83.47 | 0.27 | 47.45 (43.86 - 51.04) | 1.35 (0.75 - 1.95) |
| Prince Albert (data pooled) | 108 | 71.97 | 0.29 | 47.75 (42.42 - 50.08) | 1.40 (0.99 - 1.81) |
| Edson medium | 60 | 50.46 | 0.57 | 44.77 (42.47 - 47.07) | 1.79 (1.38 - 2.20) |
| Edson superior | 30 | 42.67 | 0.62 | 44.94 (41.97 - 47.91) | 2.43 (1.72 - 3.14) |
| Edson (data pooled) | 90 | 48.87 | 0.57 | 44.97 (43.16 - 46.78) | 1.91 (1.56 - 2.26) |
| Grande Prairie | 85 | 65.97 | 0.53 | 42.13 (39.63 - 44.63) | 2.34 (1.87 - 2.82) |
| General model (all locations) | 403 | 54.88 | 0.50 | 45.21 (44.21 - 46.22) | 1.85 (1.67 - 2.04) |

Note: Models shown are significant ($p < 0.05$), and are based on linear regressions fit to data $HDR = a + b BA$; HDR is spruce height to diameter ratio; BA is aspen basal area; a , and b are model parameters reported with 95% confidence limits; for Peace River, Prince Albert and Edson there was no significant difference detected between model parameters for the medium and superior sites, allowing for data pooling at the same location.

Table 4-5 Percentage of change in spruce height to diameter ratios relative to 2002

| Location | 2003 | 2004 |
|------------------------|--------------------|--------------------|
| Peace River medium | -12.9 - 47.7 (7.2) | -21.4 - 18.7 (6.9) |
| Peace River superior | -8.1 - 17.3 (7.3) | -10.2 - 31.8 (6.2) |
| Prince Albert medium | -19.7 - 23.3 (7.7) | -28.5 - 21.8 (8.2) |
| Prince Albert superior | -16.4 - 17.2 (6.8) | -17.6 - 22.7 (7.7) |
| Edson medium | -43.9 - 12.5 (6.9) | -36.6 - 15.6 (8.6) |
| Edson superior | -16.0 - 14.8 (6.9) | -18.3 - 19.1 (7.0) |
| Grande Prairie | -14.5 - 18.8 (6.5) | -18.6 - 24.9 (7.2) |

Note: Values represent absolute ranges of change with averages provided within brackets.

Table 4-6 Climate data for the studied sites – monthly air temperature and precipitation averages for the growing seasons of 2001-2003

| Location | Year | Mean temperature ($^{\circ}\text{C}$) | | | | | Mean precipitation (mm) | | | | |
|----------------|------|---|------|------|------|------|-------------------------|------|-------|-------|------|
| | | May | Jun | Jul | Aug | Sept | May | Jun | Jul | Aug | Sept |
| Peace River | 2001 | 9.9 | 14.0 | 16.5 | 16.4 | 11.1 | 44.2 | 57.8 | 64.1 | 21.4 | 15.3 |
| | 2002 | 8.1 | 15.6 | 16.1 | 14.9 | 8.3 | 19.3 | 16.3 | 44.0 | 16.6 | 74.2 |
| | 2003 | 9.0 | 13.5 | 16.6 | 14.8 | 9.1 | 34.2 | 56.6 | 32.4 | 47.4 | 24.4 |
| Grande Prairie | 2001 | 10.0 | 13.8 | 16.1 | 16.0 | 11.0 | 40.6 | 48.7 | 110.1 | 47.4 | 14.4 |
| | 2002 | 7.9 | 15.7 | 16.3 | 15.2 | 8.8 | 43.3 | 43.5 | 77.1 | 24.2 | 67.3 |
| | 2003 | 9.2 | 14.5 | 17.1 | 15.3 | 10.1 | 20.4 | 57.2 | 30.8 | 45.4 | 21.2 |
| Prince Albert | 2001 | 11.6 | 14.8 | 18.7 | 18.7 | 12.8 | 19.4 | 37.2 | 66.4 | 5.8 | 10.8 |
| | 2002 | 7.6 | 17.4 | 20.3 | 16.2 | 10.2 | 16.8 | 29.2 | 24.2 | 126.0 | 51.2 |
| | 2003 | 11.7 | 15.7 | 18.5 | 19.6 | 10.1 | 27.0 | 45.8 | 103.6 | 40.0 | 18.4 |

Table 4-7 Parameter estimates for models relating spruce relative increment (diameter and height) to aspen basal area

| Location | Relative increment | <i>n</i> | MS _{res} | R ² _{adj} | <i>a</i> | <i>b</i> |
|------------------------|--------------------|----------|--------------------------------------|-------------------------------|----------|----------|
| Peace River medium | Diameter | 60 | 0.00232 | 0.35 | 0.2462 | -0.00841 |
| | Height | 60 | 0.00287 | 0.29 | 0.2557 | -0.00820 |
| Peace River superior | Diameter | 60 | 0.00199 | 0.48 | 0.2471 | -0.01140 |
| | Height | 60 | 0.00152 | 0.44 | 0.2587 | -0.00920 |
| Prince Albert medium | Diameter | 54 | Model not significant ($p > 0.05$) | | | |
| | Height | 54 | 0.00311 | 0.08 | 0.1756 | -0.00502 |
| Prince Albert superior | Diameter | 54 | 0.00397 | 0.15 | 0.2018 | -0.00663 |
| | Height | 54 | 0.00284 | 0.25 | 0.2044 | -0.00748 |
| Edson medium | Diameter | 60 | 0.00374 | 0.28 | 0.2460 | -0.00866 |
| | Height | 60 | 0.00268 | 0.30 | 0.2086 | -0.00755 |
| Edson superior | Diameter | 30 | 0.00222 | 0.41 | 0.2666 | -0.01156 |
| | Height | 30 | 0.00394 | 0.26 | 0.2481 | -0.01121 |
| Grande Prairie | Diameter | 85 | Model not significant ($p > 0.05$) | | | |
| | Height | 85 | Model not significant ($p > 0.05$) | | | |

Note: Models shown are significant ($p < 0.05$), and are based on linear regressions fit to data $\text{RelInc} = a + b \text{ BA}$; RelInc is spruce relative increment (calculated as average 2002-2003 diameter or height increment divided by 2002 initial diameter or height); BA is aspen basal area.

Figure 4-1 Relationships between morphological attributes, competition and spruce volume growth averaged for 2002-2003 (examples for the Peace River medium site) (a) spruce height to diameter ratio measured in spring of 2002 (HDR) as a function of aspen basal area (BA): $\text{HDR} = 46.44 + 1.82 \text{ BA}$ ($n = 60$, $\text{MS}_{\text{res}} = 29.34$, $R^2_{\text{adj}} = 0.67$); (b) average 2002-2003 spruce stem volume increment (SVI) as a function of HDR: $\text{SVI} = 68.01 e^{-0.0471 \text{ HDR}}$ ($n = 60$, $\text{MS}_{\text{res}} = 9.83$, $R^2_{\text{adj}} = 0.35$); (c) spruce height (Ht) as a function of BA: $\text{Ht} = 1.99 - 0.024 \text{ BA}$ ($n = 60$, $\text{MS}_{\text{res}} = 0.093$, $R^2_{\text{adj}} = 0.09$); (d) SVI as a function of Ht: $\text{SVI} = 1.102 (\text{Ht})^{2.505}$ ($n = 60$, $\text{MS}_{\text{res}} = 8.68$, $R^2_{\text{adj}} = 0.43$).

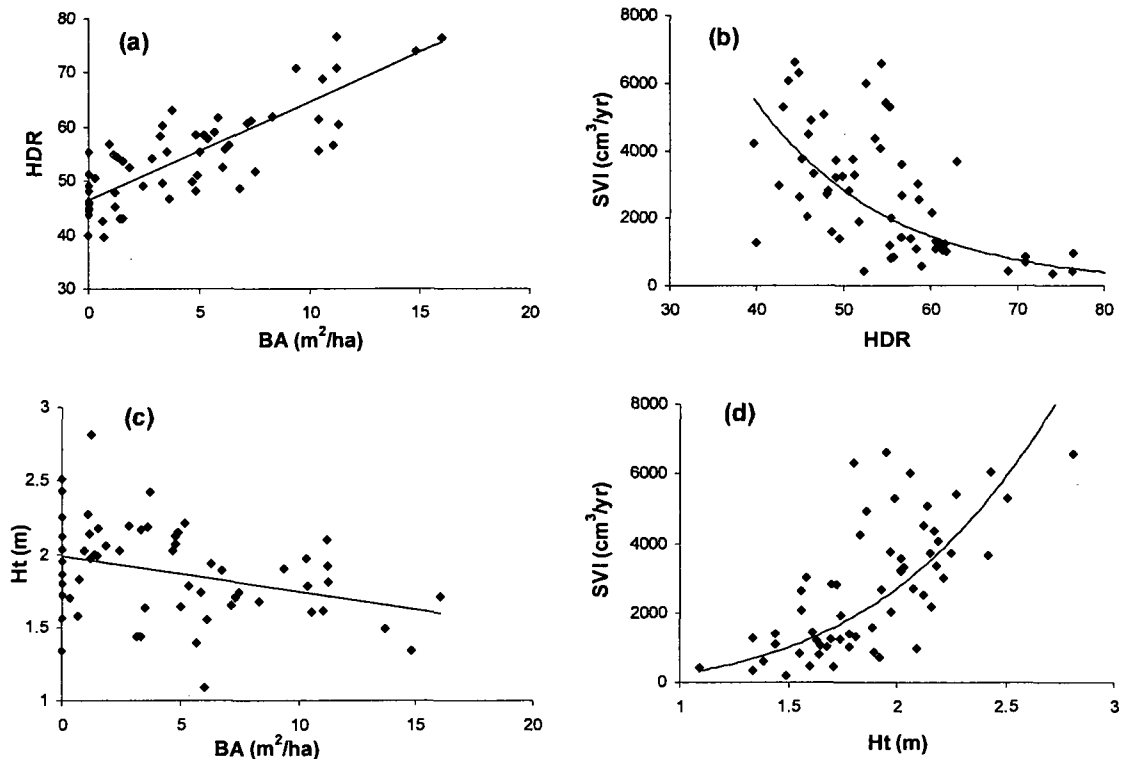


Figure 4-2 Relationships between spruce growth allocation ratios based on averages 2002-2003 and competition (examples for the Peace River medium site) (a) spruce height to volume increment ratio (HtoVinc) as a function of aspen basal area (BA): $HtoVinc = 13.64 e^{0.00929 BA}$ ($n = 60$, $MS_{res} = 119.4$, $R^2_{adj} = 0.50$); (b) HtoVinc as a function of transmittance (DIFM): $HtoVinc = 12.379 (DIFM)^{-0.602}$ ($n = 60$, $MS_{res} = 109.1$, $R^2_{adj} = 0.55$).

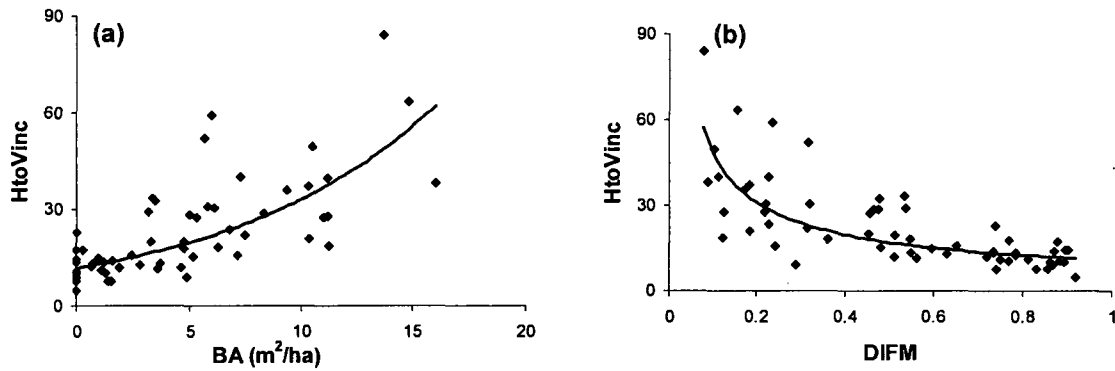


Figure 4-3 Relationships between spruce height to diameter ratio (HDR) and aspen basal area (BA) measured in 2002 for the studied sites (PR – Peace River, PA – Prince Albert, ED – Edson, GP – Grande Prairie). No significant difference for model parameters was detected between medium and superior sites at Peace River, Prince Albert and Edson, allowing for data pooling at each location.

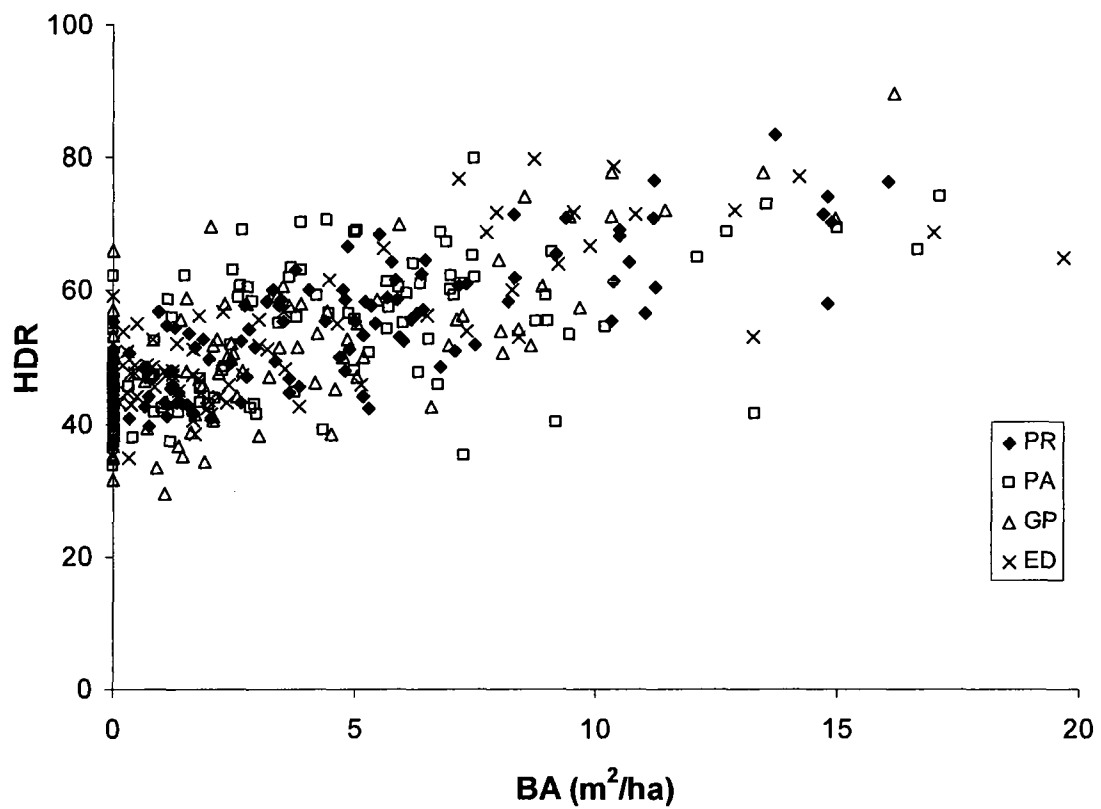


Figure 4-4 Illustration of change over time (for 2002, 2003, and 2004) in spruce height to diameter ratio (HDR) against aspen basal area (BA in 2002).

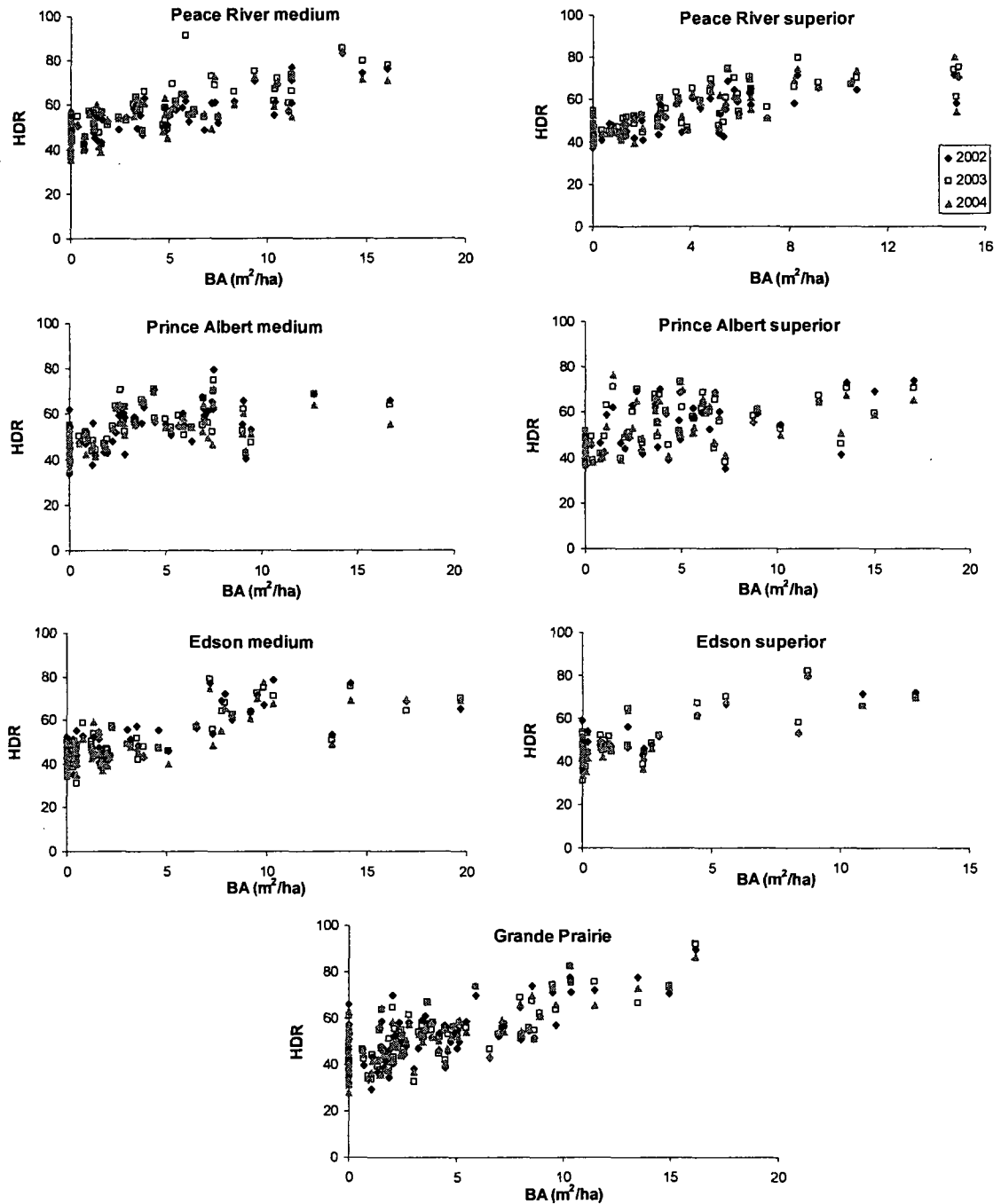
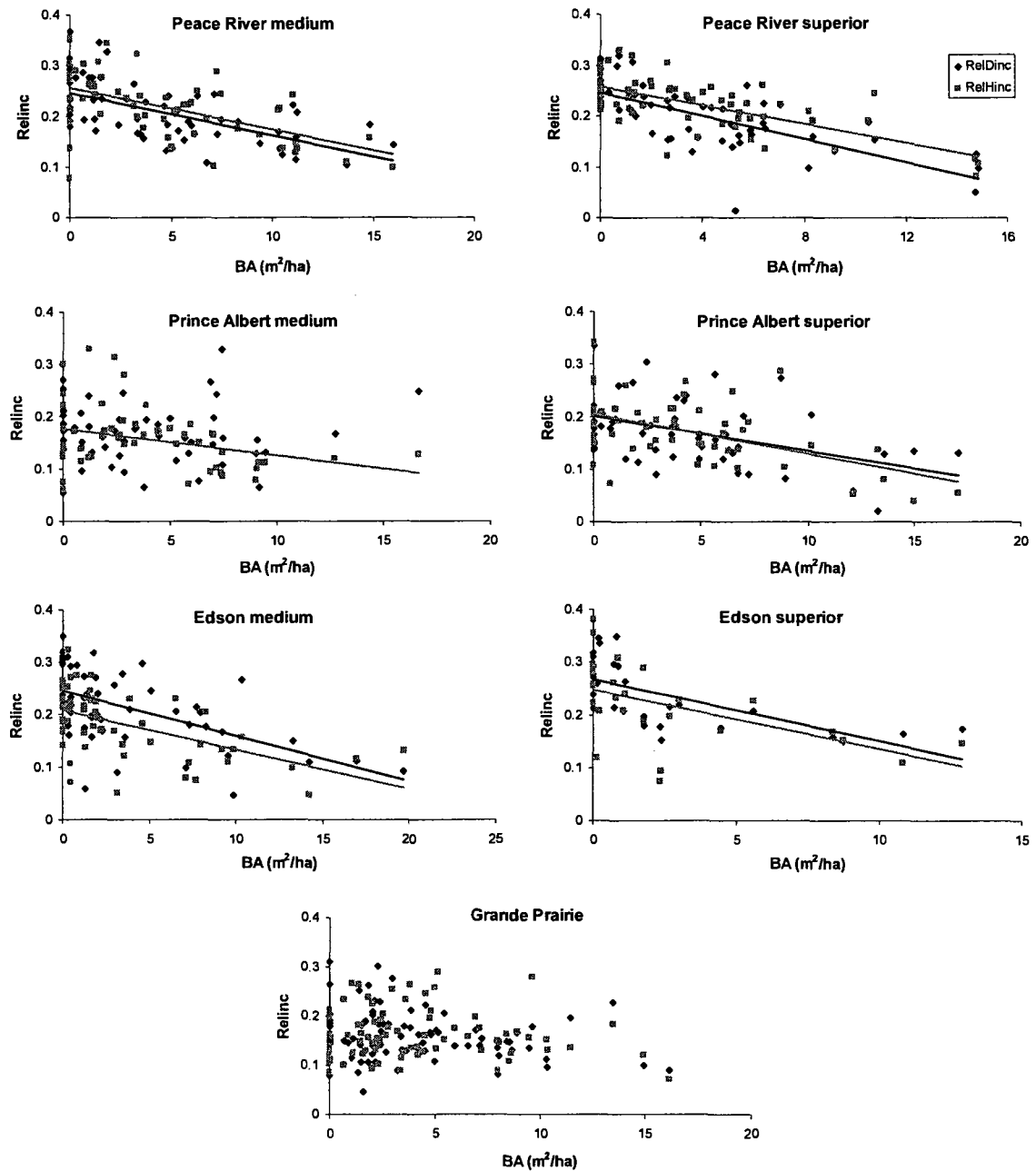


Figure 4-5 Relationships between spruce relative increment average 2002-2003 (Relinc) and aspen basal area (BA) for the studied sites; lines are based on linear regressions fit to data, with models provided in table 4-7. RelDinc is spruce relative diameter increment, RelHinc is spruce relative height increment (calculated as average 2002-2003 diameter or height increment divided by 2002 initial diameter or height). For Prince Albert (RelDinc) and Grande Prairie (both RelDinc and RelHinc) models were not significant ($p > 0.05$).



Chapter 5 Differential effects of aspen density on air and soil temperature

5.1 Introduction

Temperature is an important ecological factor that regulates several physiological processes (Kimmmins 1997). These processes are reflected on plants performance (i.e., growth and survival) to environment. Plants have evolved to function optimally within certain ranges of temperature and have developed morphological and physiological adaptations to environment stress (Gillies and Vidaver 1990; Larcher 2003). These adaptations become increasingly important in the boreal climate where the growing season is short and freezing temperatures may occur at any time of the year. Frost during the active growing season has a higher impact during the early stages of stand establishment and is a major cause of poor performance and mortality in young forest plantations (Stathers 1989).

Frost may result from two different processes: *i) radiation frosts* occur in open areas during calm, clear nights when plant or ground surfaces cool owing to heat being radiated toward the atmosphere and not replaced by the re-radiation back that would occur under otherwise covered conditions; and *ii) advection frosts* occur when cold air cooled at another location moves onto a site (Spittlehouse and Stathers 1990). Chances of frost occurrence are higher at the end and beginning of the growing season, during May and September, owing to lower air temperature and longer nights (Grossnickle and Major 1994).

Frost damage to young conifer seedlings occurs when the air temperature drops below -2 to -5°C during the active growing season. The water outside the cell wall and inside the cell freezes and forms ice particles, resulting in damage (Stathers 1989). Freezing tolerance however depends on the type of tissue being affected, as young foliage and buds are usually more susceptible to damage than older plant parts (Bigras and Hébert 1996). Grossnickle (2000) noted that bud development may be stopped by frost damage occurring during the initial stages of activity in the spring. Therefore, buds may look healthy but may not break dormancy. Emerging shoots are succulent and more susceptible to frost damage than mature shoots; following frost, they turn brown in 1-2

weeks and needles are shed. Consequently, the leader is lost and may be replaced in subsequent years by one or more lateral branches resulting in forked top or other crown deformations.

In addition to visible damage, frost may also cause invisible damage to young seedlings. Reduced photosynthesis rates have been reported for conifer species following frost exposure (DeLucia and Smith 1987; Dang et al. 1992; Ryyppo et al. 1997). Moreover, frosty nights are often followed by clear mornings and intense light may lead to additional damage of the photosynthetic apparatus through photoinhibition (Örlander 1993; Gillies and Binder 1996).

Over the past two decades there has been increasing interest in the management of boreal mixedwood stands comprised of trembling aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench) Voss). While aspen regenerates more abundantly and grows faster initially, density manipulation of the aspen overstory in order to promote spruce growth and survival is considered a viable option for managing boreal mixedwood stands (Comeau et al. 2005).

Reducing aspen cover improves growth conditions (i.e., light availability) for understory spruce (Filipescu and Comeau 2007), but at the same time may lead to increased likelihood of frost occurrence. The occurrence of frost increased with the size of circular openings in young aspen stands; however, height and density of surrounding aspen have also been found to influence frost occurrence in these stands (Pritchard and Comeau 2004). Young dense aspen stands may provide growing season frost protection into adjacent openings up to one tree length from the edge (Voicu and Comeau 2006). Minimum air temperature decreased with the sky view factor (the proportion of total long-wave radiation received directly from the sky) in a 40-year old mixedwood stand in Ontario (Groot and Carlson 1996).

This study evaluates how manipulating aspen cover may affect the temperature regime in boreal mixedwood stands of variable density. The main objective was to evaluate the incidence and occurrence of frost across a gradient of aspen densities following spacing treatments at two boreal locations, while a second objective was to

characterize the overall regime of air and soil temperature during the active growing season.

5.2 Methods

The study used two field installations established by the Western Boreal Growth and Yield association (WESBOGY), as part of a long-term study of growth and development of tended mixtures of aspen and white spruce. Experimental blocks consist of permanent plots of variable density. A more complete description of the study sites and experimental design is provided in chapter 2. In my study, I used two field locations near Peace River (56°55'N and 118°30'W) and Grande Prairie (54°55'N and 118°30'W) in Alberta. Aspen regenerated naturally after harvesting, and plots were spaced to target densities at age 5. When my study was initiated in 2002, aspen were 11 years old with height ranging between 3.2 and 6.4 m. At each of the two locations one plot was selected for each of four aspen densities (0, 500, and 1500 stems/ha and natural untreated). In the natural untreated plots density at age 11 ranged between 6,000 and 9,000 stems/ha.

To measure air temperature, clusters of three custom-built chromel-constantan (fine wire) thermocouples were installed near the centre of each plot to avoid edge influence. These sensors were not shielded in order to increase the detection sensitivity to radiative cooling. Soil temperature was measured using custom-built chromel-constantan thermocouples at the same three clustered locations in each selected plot. Sensors were installed at two soil depths, 5 cm and 20 cm. These sensors were connected to CR-10X dataloggers (Campbell Scientific Canada Corp., Edmonton) through AM 16/32-XT multiplexers (Campbell Scientific Canada Corp., Edmonton). Measurements were taken and recorded every 10 minutes, with hourly averages and daily minimum and maximum values also stored. For both the Peace River and Grande Prairie locations, temperature was monitored continuously during the active growing seasons of 2002, 2003, and 2004. In 2002 difficulties with equipment delayed the establishment of the study until late June, while for 2003 and 2004 data recording started in early to mid May, and continued until mid or late September. For comparison purposes across sites and from year to year, data

was processed and analyzed for the intervals of July 1 – August 31 in 2002, and June 1 – August 31 in 2003 and 2004, unless mentioned otherwise.

Owing to limited availability of equipment and other logistics conflicts, plot density was not replicated; instead I opted to monitor the effects of density on temperature at two study locations. The lack of replication for plot density at each location precluded more in-depth statistical analysis (i.e., significance tests of differences between levels of aspen density were not possible).

5.3 Results

Frost events were recorded during the growing season in 2002, 2003, and 2004 for the Grande Prairie site, and only in 2002 at the Peace River site. A typical frost event during the morning of July 3, 2002 is illustrated in figure 5-1. Temperature dropped to lower levels and for a longer interval in the no aspen plot compared to the intermediate densities and the natural untreated. The lowest levels of freezing temperature were recorded in the early morning, a common characteristic of radiative frosts, at -1.5°C for the natural plot, -2.3°C for the 500 stems/ha plot, -2.4°C for the 1500 stems/ha and -3.1°C for the no aspen plot.

Reduction of aspen density led to increases in both frost-hour sum (sum of average hourly temperatures $< 0^{\circ}\text{C}$) and number of hours with negative temperature over the growing season (table 5-1). While frost events were recorded for the natural untreated plots, these were less frequent and of less total duration compared with the no aspen plots. The intermediate densities (500 and 1500 stems/ha) had similar values for frost-hour sum and number of hours of frosts to which understory spruce were subjected. When the monitoring period was extended beyond the June 1 – Aug 31 interval by including the months of May and September, the incidence of frost events increased substantially for one of the two study sites (figure 5-2 summarizes the frost incidence between May 8 – September 30, 2003). There was a clear distinction between the Grande Prairie site where the reduction of aspen cover resulted in increased frost (increased number of frost hours and frost-hour sum) and the Peace River site where frost incidence

was rare and similar across the range of aspen leaf area index (LAI). Linear relationships described the increase of frost with reduced aspen LAI at Grande Prairie (figure 5-2).

The amount of accumulated heat during the growing season, expressed as growing degree hours (GDH), was inversely related to aspen cover. During the period of study, the Grande Prairie site showed larger values of accumulated heat than the Peace River site. The trend of increased GDH with reduced aspen cover was similar at both sites across the three years that air and soil temperature was monitored (table 5-2).

During the growing season, daily maximum air and soil temperature increased with the reduction of aspen density (table 5-3). For example, maxima averaged up to 2.3°C for air, 6.7°C for soil at 5 cm depth, and 3.7°C for soil at 20 cm depth higher in the no aspen plots than in the untreated plots. Daily minimum air temperature were lower in the no aspen plots than in the natural aspen plots, while for soil minima averaged more in the no aspen compared with natural plots (table 5-4).

The general trend in maximum and minimum air and soil temperature was uniform across the growing season for all density treatments. There was a similar pattern for both sites during the three years of the study (figure 5-3 illustrates the distribution of daily extremes for 2004 at Grande Prairie). The reduction in aspen density from natural untreated to zero aspen leads to increased extremes in temperature.

5.4 Discussion

My study provides evidence that frost increases with the reduction of overstory density. Results show that the number of frost events and the frost-hour sum are inversely related to aspen cover (e.g., density and leaf area index) at one site but not at another. My findings are consistent with previous studies in the boreal forest (Groot and Carlson 1996; Pritchard and Comeau 2004; Voicu and Comeau 2006).

Exposure to frost may affect current seedling growth, as well as growth during subsequent seasons. Grossnickle (2000) reported that exposure to a -4°C frost had no effect on new leader growth, but reduced the shoot and root biomass produced in the next growing season, while exposure to -6°C led to a large reduction of the overall biomass production. In my study, -3°C was the lowest negative temperature reached on several occasions during the three growing seasons temperature was monitored. However, in

addition to resulting in lower minimum temperatures during the growing season, removal of aspen also led to longer duration of freezing temperatures. Frost damage is thought to be more strongly influenced by the duration of frost rather than the actual minimum temperature (Spittlehouse and Stathers 1990).

Field observations indicated that visible frost damage was practically non-existent at the Peace River site, and only minimal incidence was observed at the Grande Prairie site. The most prevalent frost damage was failure of terminal buds to flush, leading to forked crowns. In my study non-visible damage was not assessed, however it is likely that freezing nights followed by mornings of intense light may have led to reduced photosynthesis rates through photoinhibition. Maintaining partial cover could be beneficial by maintaining higher nocturnal air temperature and shading the day after the frost event, leading to reduced visible and physiological damage (Lundmark and Hällgren 1987; Langvall and Örlander 2001).

Results from my study revealed that frosts at Grande Prairie occurred more often and were more intense than frosts at Peace River. In addition, at Grande Prairie frost occurrence increased with the reduction of aspen cover in a linear fashion, while no such effect was observed at Peace River. In addition, it should be noted that the Peace River site is located 2° latitude farther North than the Grande Prairie site. Topographic characteristics may explain these differences, as the Grande Prairie site is located in a low-lying basin at the base of a gradual slope, while the Peace River site is located on a relative topographic rise that seems to have more wind and air mixing. Local characteristics and differences in respect to frost may be one of the reasons competitive relationships between spruce growth and aspen competition indices were observed to be site specific (Filipescu and Comeau 2007).

In northern climates, low temperature may be a serious limitation during the growing season (Grossnickle 2000). Cold soil temperature during spring, especially when complemented by flooded conditions, may lead to significant reduction in physiological response and growth of seedlings (DeLucia 1986; Grossnickle 1987). My results indicate that the amount of accumulated heat for air and soil is inversely related to aspen density. Accumulated heat may influence the growth of white spruce, as suggested by

experiments of site preparation in Northern Interior of British Columbia (Bedford et al. 2000). In my study, differences in accumulated heat do not appear to be large; however, given that the growing season is short, even small differences may become important. Study limitations made it impossible to quantify their potential effects, but they remain to be examined in future studies. While there is an increased risk of damage owing to radiative frost, growth conditions may be improved where temperature is a limitative factor. The amount of accumulated heat was lower at Peace River, which is located north of Grande Prairie.

The differences in minimum air temperature during frost nights between natural untreated plots and no aspen plots were 1.5-2°C, while differences in average minima varied more with year and site. Groot and Carlson (1996) showed that the difference in minimum temperature between clearcut conditions and shelterwoods in boreal mixedwoods in Ontario averaged almost 3°C during the growing season. The distribution pattern of daily minimum and maximum temperature in my study was similar across densities except for the amplitude of extremes. Results constitute further evidence that maintaining partial cover leads to the amelioration of temperature extremes, as described by Coopersmith et al. (2000) for a similar mixedwood experiment in the Northern Interior of British Columbia.

My study indicates that aspen overstory may play a role in frost protection. These results will be useful in refining guidelines and prescriptions for the establishment and management of young mixedwood stands. In addition, data may be useful in calibrating and validating hybrid and process-based models of spruce growth as a function of several factors, including air and soil temperature.

A number of factors affect the chance of frost occurrence (Stathers 1989) and include:

- *Air temperature and humidity* - through processes of heat loss and absorption and emittance of longwave radiation;
- *Wind speed* - through mixing warmer air near the ground surface;
- *Cloud cover* - through emittance of longwave radiation toward the ground surface;

- *Slope angle and position* - through the drainage and transfer of cold air;
- *Aspect* - through the amount of solar radiation, heat storage and time of the day sites become cold;
- *Topography* - through effects on wind speed, drainage, and accumulation of cold air.

Careful site selection to avoid frost prone-sites (e.g., high elevation areas, valleys, low-lying terrain) may help managing the risk of frost occurrence (Stathers 1989). Other strategies may include: *i*) selection of planting spots in suitable microsites (e.g., the vicinity of logs, stumps, and higher areas); *ii*) site preparation treatments that alter the seedling microenvironment, such as soil properties, and the overall energy balance; and *iii*) maintaining some degree of woody vegetation cover, which may result in reduced temperature extremes owing to reduced daytime solar heating and longwave radiative cooling at night, also daytime shading to reduce problems with photoinhibition. Vegetation cover shifts the surface where radiative transfer occurs from the soil surface into the vegetation canopy, where the air is usually well mixed and warmer than the air near the ground (Spittlehouse and Stathers 1990).

On sites with high risk of frost, selection of more frost resistant species (e.g., black spruce) and planting on raised microsites or mounds with an exposed mineral surface are potential options. Young seedlings are particularly susceptible during the beginning of the growing season, consequently, delaying planting until later in the season and planting larger seedlings may help reduce the chance of frost damage. In intimate mixtures, thinning of aspen overstory may be delayed until spruce is established (3 to 5 years after planting) and becomes less susceptible to frost damage. In addition, provenances with late budbreak in the spring and adapted to earlier dormancy in the fall would avoid some of the potentially damaging frosts at the beginning and the end of the growing season. While there are no studies comparing the risk of frost in plantations as opposed to naturally regenerated stands, there are reasons to believe that natural regeneration should be more resistant to frost damage. Nevertheless, the issues discussed in this chapter should also be considered when and where natural regeneration is viable and financially possible.

5.5 Conclusions

This study further supports that maintaining partial aspen cover may provide frost protection in young boreal mixedwoods. However, these benefits may only be apparent on those sites where there is an actual risk of frost injury occurring. Establishment of young mixedwoods needs thorough planning and assessment of frost injury risk and its impacts. Reducing aspen cover may also lead to increased accumulated heat during the growing season and to increased air and soil temperature extremes. More in-depth studies are needed to provide further information on the impact of non-visible effects of frost and interaction with other microclimatic conditions and site factors.

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Table 5-1 Frost-hour sum (sum of average hourly temperatures $< 0^{\circ}\text{C}$, also referred to as the number of degree hours of negative temperature) for the two study locations

| Location | Plot | Year | | |
|----------------|---------------|------------|------------|------------|
| | | 2002 | 2003 | 2004 |
| Grande Prairie | zero aspen | 30.51 (35) | 31.43 (29) | 31.72 (32) |
| | 500 stems/ha | 21.48 (25) | 15.85 (19) | 10.59 (21) |
| | 1500 stems/ha | 17.74 (25) | 22.68 (22) | 15.14 (23) |
| | natural aspen | 4.25 (9) | 7.76 (13) | 4.36 (11) |
| Peace River | zero aspen | 3.82 (6) | 0 | 0 |
| | 500 stems/ha | 0.16 (1) | 0 | 0 |
| | 1500 stems/ha | 0.47 (1) | 0 | 0 |
| | natural aspen | 0.32 (1) | 0 | 0 |

Note: The period monitored represents July 1 – August 31 for 2002, and June 1 – August 31 for 2003 and 2004. Values in brackets are number of hours with average temperature below 0°C . Number of frost events for Grande Prairie was 11 in 2002, 9 in 2003, and 8 in 2004, while for Peace River only 1 in 2002 and no frosts were recorded during the monitored intervals in 2003 and 2004.

Table 5-2 Growing degree hours (sum of hourly average temperatures > 5°C) for the two study locations

| Location | Plot | Year | | | | | | | | |
|-------------------|------------------|-------|-------------|--------------|-------|-------------|--------------|-------|-------------|--------------|
| | | 2002 | | | 2003 | | | 2004 | | |
| | | Air | Soil 5cm | Soil 20cm | Air | Soil 5cm | Soil 20cm | Air | Soil 5cm | Soil 20cm |
| Grande Prairie | zero aspen | 13708 | 12854 | 11599 | 19526 | 18906 | 16850 | 19859 | 18423 | 17412 |
| | 500 stems/ha | 13639 | 11153 | 10140 | 19455 | 15835 | 14076 | 20181 | 18039 | 16423 |
| | 1500 stems/ha | 13510 | 10744 | 9550 | 19354 | 14763 | 12735 | 19722 | 16935 | 15034 |
| | natural aspen | 13425 | 10495 | 9761 | 19077 | 14611 | 13271 | 19459 | 15810 | 14720 |
| Peace River | zero aspen | 12073 | 10355 | 9046 | 18176 | 13907 | 11606 | 19300 | 17374 | 15855 |
| | 500 stems/ha | 11961 | 9103 | 7591 | 18218 | 12357 | 9730 | 19274 | 14400 | 11960 |
| | 1500 stems/ha | 11392 | 8813 | 7135 | 17103 | 11783 | 8971 | 18364 | 14103 | 11419 |
| | natural aspen | 11384 | 7216 | 5795 | 17459 | 10321 | 7939 | 18728 | 12249 | 9998 |

Note: The period monitored represents July 1 – August 31 for 2002, and June 1 – August 31 for 2003 and 2004.

Table 5-3 Growing season average of daily maximum temperatures for the two study locations

| Location | Plot | Year | | | | | | | | |
|-------------------|------------------|-------|-------------|--------------|-------|-------------|--------------|-------|-------------|--------------|
| | | 2002 | | | 2003 | | | 2004 | | |
| | | Air | Soil 5cm | Soil 20cm | Air | Soil 5cm | Soil 20cm | Air | Soil 5cm | Soil 20cm |
| Grande Prairie | zero aspen | 23.06 | 16.38 | 14.96 | 22.7 | 16.54 | 14.95 | 23.16 | 15.35 | 14.74 |
| | 500 stems/ha | 22.68 | 14.67 | 13.49 | 22.98 | 14.32 | 12.90 | 22.80 | 14.98 | 13.69 |
| | 1500 stems/ha | 23.28 | 13.03 | 12.29 | 23.40 | 12.35 | 11.54 | 22.31 | 12.98 | 12.33 |
| | natural aspen | 21.71 | 9.90 | 12.79 | 21.81 | 9.81 | 12.08 | 20.79 | 13.56 | 12.74 |
| Peace River | zero aspen | 20.86 | 13.59 | 12.90 | 21.65 | 12.99 | 12.09 | 21.12 | 14.86 | 13.90 |
| | 500 stems/ha | 21.14 | 11.92 | 10.82 | 21.82 | 11.04 | 9.85 | 21.56 | 11.99 | 10.86 |
| | 1500 stems/ha | 19.51 | 13.07 | 10.97 | 19.61 | 11.90 | 10.05 | 19.70 | 12.74 | 10.90 |
| | natural aspen | 19.24 | 7.23 | 9.66 | 19.61 | 7.78 | 9.18 | 19.54 | 9.23 | 10.23 |

Note: The period monitored represents July 1 – August 31 for 2002, and June 1 – August 31 for 2003 and 2004.

Table 5-4 Growing season average of daily minimum temperatures for the two study locations

| Location | Plot | Year | | | | | | | | |
|-------------------|------------------|-------|-------------|--------------|-------|-------------|--------------|-------|-------------|--------------|
| | | 2002 | | | 2003 | | | 2004 | | |
| | | Air | Soil 5cm | Soil 20cm | Air | Soil 5cm | Soil 20cm | Air | Soil 5cm | Soil 20cm |
| Grande Prairie | zero aspen | 4.09 | 11.87 | 11.68 | 3.97 | 11.88 | 11.58 | 4.99 | 10.5 | 10.28 |
| | 500 stems/ha | 4.53 | 11.37 | 10.33 | 4.40 | 10.70 | 9.75 | 5.61 | 11.86 | 10.91 |
| | 1500 stems/ha | 4.58 | 9.42 | 9.09 | 4.31 | 9.40 | 8.93 | 5.69 | 10.21 | 9.84 |
| | natural aspen | 13.45 | 5.69 | 9.56 | 12.9 | 5.34 | 9.36 | 6.42 | 10.65 | 10.18 |
| Peace River | zero aspen | 6.05 | 10.71 | 9.94 | 5.88 | 10.41 | 9.57 | 7.58 | 10.43 | 9.93 |
| | 500 stems/ha | 6.63 | 7.89 | 7.40 | 6.58 | 8.17 | 7.45 | 7.61 | 9.48 | 8.80 |
| | 1500 stems/ha | 6.66 | 8.88 | 7.54 | 6.69 | 8.73 | 7.13 | 7.71 | 10.17 | 8.60 |
| | natural aspen | 11.29 | 7.01 | 6.49 | 10.89 | 6.98 | 5.04 | 11.94 | 8.12 | 8.19 |

Note: The period monitored represents July 1 – August 31 for 2002, and June 1 – August 31 for 2003 and 2004.

Figure 5-1 Frost event at the Grande Prairie location during the night of July 3, 2002

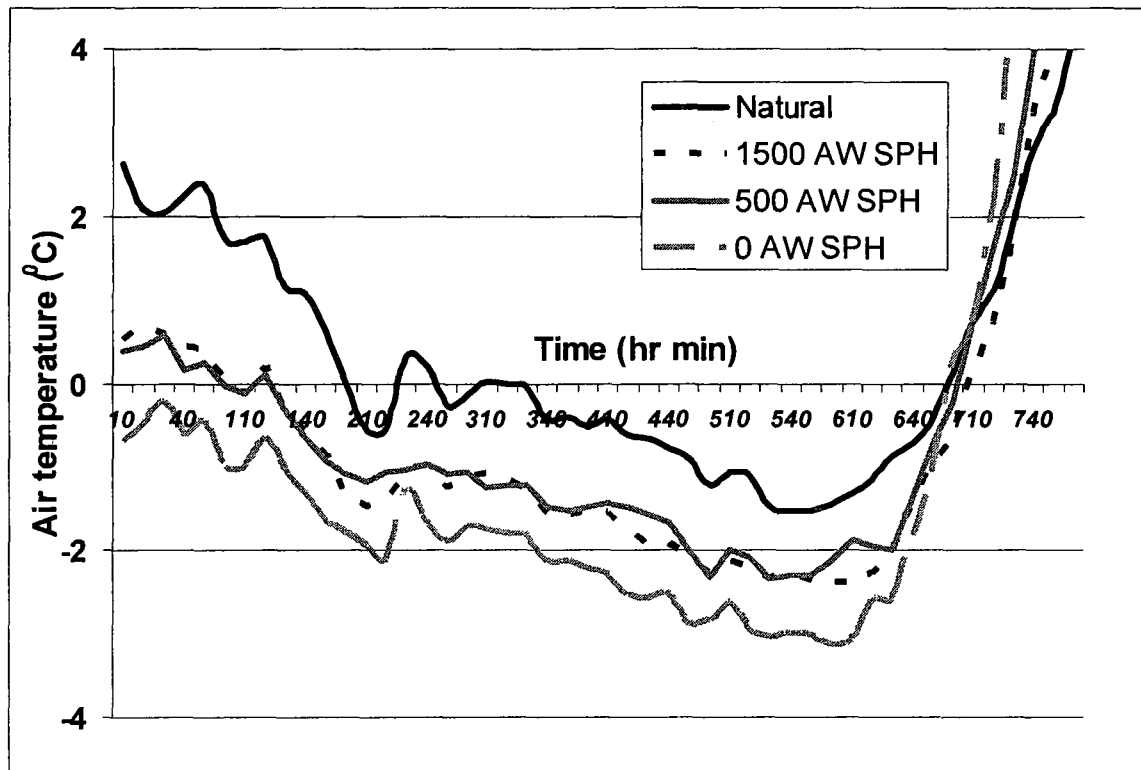


Figure 5-2 Relationships between aspen leaf area index (LAI) and frost occurrence at the two study locations (May 8 – September 30, 2003). The lines are described by linear regression: a) No hrs = $-14.42 \text{ LAI} + 206.93$ ($n=12$, $R^2_{\text{adj}}=0.86$); b) No degr = $-47.22 \text{ LAI} + 450.79$ ($n=12$, $R^2_{\text{adj}}=0.83$). For Peace River relationships were not significant.

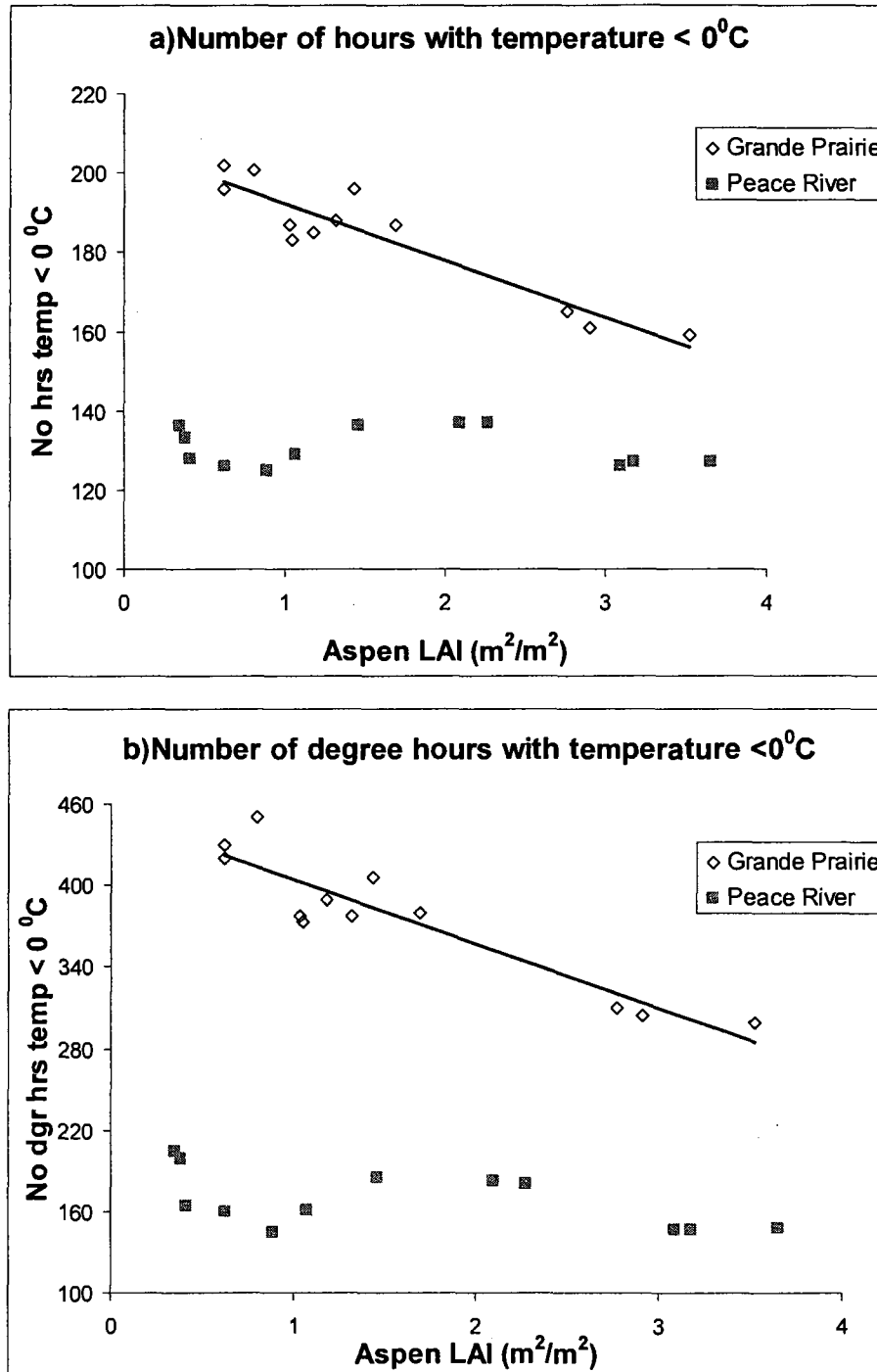
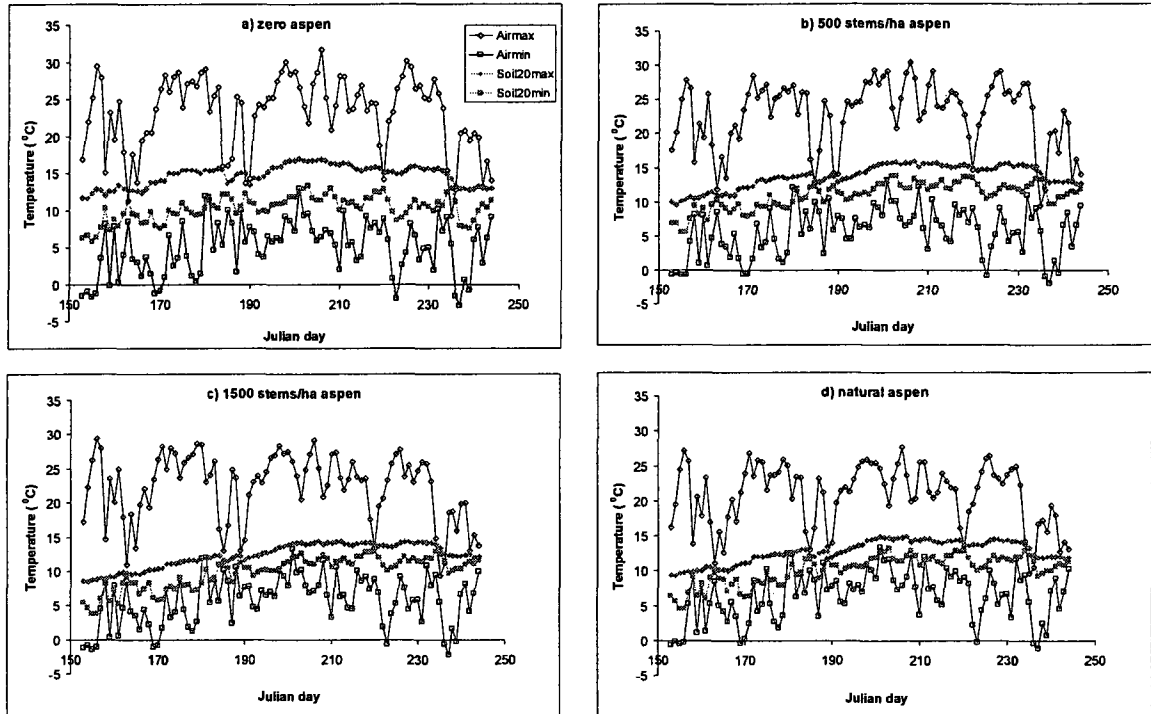


Figure 5-3 Daily minimum and maximum air and soil temperatures at Grande Prairie
(June 1 – August 31, 2004)



Chapter 6 General discussion and conclusions

The research presented in this thesis has focused on the dynamics of competition in boreal mixedwood stands dominated by trembling aspen (*Populus tremuloides* Michx.) with an understory component of white spruce (*Picea glauca* (Moench) Voss).

Specifically, the following research objectives were addressed:

- Evaluate the effectiveness of competition indices for estimating light availability and spruce growth in young mixedwood stands of variable density; also similar competition indices were tested for their ability to explain variation in spruce growth across an age sequence of boreal mixedwood stands;
- Determine whether models predicting spruce growth as a function of competition indices can be applied across a broad range of locations, and across stands of different ages;
- Investigate the possibility of substituting competition indices with simple morphological attributes for modeling spruce growth in young mixedwood stands;
- Document the incidence and occurrence of frost in young boreal mixedwood stands of variable density and describe the air and soil temperature regime in these stands during the active growing season.

Results in chapter 2 indicate that competition indices are effective for predicting the availability of light in the understory of young boreal mixedwoods of variable density. Indices based on crown characteristics provided slightly better predictions than other indices such as Lorimer's or basal area that are based on simple field measurements such as stem diameter. However, it seems that these indices are not as effective for predicting understory light in natural stands. Results presented in chapter 3 (that examined a more narrow density gradient) suggest that high variability in transmittance limits the usefulness of competition indices for predicting understory light. It is noteworthy that models of light transmittance measured at spruce midcrown were better than those at the top of trees. Other studies (Pritchard and Comeau 2004; Comeau et al.

2006) have also indicated an increase in variability of light conditions as measurement positions move up into the aspen canopy.

Relationships between basal area and light transmittance differed significantly between study locations. It appears that climate (i.e., precipitation and soil moisture) may play a role in regional differences owing to effects on leaf area and crown development (Messier et al. 1998; Comeau et al. 2006). In addition, temporal and spatial variations in leaf area development and recovery after spacing treatments may also influence relationships between light and basal area.

Incorporating the distance between subject trees and competitors into competition indices is a controversial issue that has received extensive attention in previous research (Lorimer 1983; Daniels et al. 1986; Tomé and Burkhart 1989; Biging and Dobbertin 1992; Laroque 2002). Results presented in chapters 2 and 3 indicate that distance-dependent indices provide inferior predictions of white spruce growth compared to distance independent indices, in agreement with previous studies in young boreal mixedwood stands (Alemdag 1978; Comeau et al. 2003).

The addition of initial size as explanatory variable to models of spruce growth as a function of competition indices resulted in significant increase of predictive power, as discussed in chapters 2 and 3. Tree size at the beginning of the growing period may account for past factors and growing conditions, while also being related to leaf area (Morris and MacDonald 1991; MacFarlane and Kobe 2006).

Relationships between spruce growth and competition indices were significantly different between locations and age classes. The vast majority of competition studies are limited in space and time (Goldberg and Barton 1992), which makes it difficult to interpret the implications of competitive effects over larger geographical areas and longer periods. Field installations established by the Western Boreal Growth and Yield Association allowed for a unified evaluation of competition across several locations.

The differences in competition relationships with location and age are perhaps some of the most indicative findings in my thesis. The balance between competition and facilitation shifts from location to location and with stand age. Changes in the occurrence and relative importance of each contributing factor add to the variation in relationships

between growth and competition indices. These findings have important implications for our understanding of competition and for how we manage and predict competitive outcomes. Modeling spruce growth as a function of competition indices across broader geographical areas and across age classes may require developing region and age specific models. In addition, more studies are needed to determine whether alternative approaches such as hybrid or process based models are more generally applicable than traditional growth models based on empirical evidence.

Previous studies have discussed limitations of competition indices and suggested the use of morphological attributes such as height to diameter ratio for evaluating the vigour and growth of coniferous seedlings (Claveau et al. 2002; Stancioiu and O'Hara 2006). Results from chapter 4 show some promise in using simple morphological attributes to predict subsequent growth response. Moreover, height to diameter ratio (HDR) provides further insight into how trees react to changes in the competition environment owing to their allometrical plasticity. Relationships between spruce HDR and aspen basal area do not seem to differ across the geographical locations examined. In addition, changes in HDR values from year to year appear to stabilize several years after spacing treatments, suggesting that HDR may have a wider applicability in evaluating competitive effects. However, since HDR is a relative measure, it has limited usefulness for predicting spruce growth.

Reduction of frost incidence by aspen overstory is one of many facilitative effects in boreal mixedwood stands. Results in chapter 5 provide evidence of frost protection by aspen cover, in agreement with previous studies (Groot and Carlson 1996; Pritchard and Comeau 2004; Voicu and Comeau 2006). More importantly though, it appears that frost occurrence and incidence is location specific and depends on site characteristics. I suggest that the differences in frost regime contribute to the variation in growth relationships and it may partially explain regional differences between competition models. Moreover, the overall air and soil temperature regime is influenced by reducing the density of the aspen overstory, leading to increased accumulated heat over the active growing season. At the same time, temperature extremes are also inversely related to aspen density. Effects on temperature regime may lead to differential response to

availability of resources. However, it should be noted that temperature may be influenced by a number of topographic, site and soil factors as well as by vegetation cover.

In this thesis, I have focused on light as the main driver of competition in boreal mixedwood stands. However, resources other than light (i.e., water and nutrients) are simultaneously affected by manipulation of aspen density and further studies are needed to evaluate the relative importance of these resources in influencing competition outcomes. At the same time, regional, site-to-site, and year-to-year variations, as well as the influence of stand development, necessitate further investigation. Moreover, studies presented in this thesis have focused on interactions between aspen and white spruce, without much consideration given to other competition layers such as grasses and shrubs. While recent studies have documented these aspects (Cortini and Comeau 2008; Man et al. 2008), I consider that more detailed studies are required to provide an integrated and broad perspective on competition dynamics.

The main findings of my thesis suggest that relationships between growth and competition indices are location specific. While I speculated on potential causes and explanations, I consider that a more detailed examination of processes and mechanisms underlying these differences is needed. Results discussed in chapter 3 showed that competition models in stands younger than 20 years were different from stands between 20 and 60 years, suggesting that initial differences may disappear over time. Therefore, it is important to determine if regional differences will disappear with time. Moreover, further studies will determine whether these differences will influence the final yield of mixedwood stands of variable density.

Traditional growth models based on empirical evidence appear to be less generally applicable than previously considered. Alternatives to these models, such as hybrid and process-based models need to be developed and tested further to determine the applicability and generalization of predictions. Understanding and quantifying the influence of contributing factors may increase the predictive ability of growth models based on competition dynamics.

Competition indices are useful ways to represent and model competition mechanisms, effects and outcomes at individual and population levels (Weigelt and

Jolliffe 2003). Currently, there is a need for more detailed indices of plant competition (Wilson 2007). These indices will advance ecological knowledge and provide a more thorough understanding of the role competition plays relative to other factors (Brooker and Kikvidze 2008).

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