

Modelling tree competition in a boreal mixedwood forest in Alberta

by

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Abstract

In boreal forests, tree competition has been widely considered as a key process contributing to forest dynamics including driving species turnover, succession and shaping stand-level structure. Understanding how the competition process in boreal forests regulates tree growth and survival is critical to both the ecology and management of boreal forests. In this thesis, I focused on several questions, essential for understanding the role that competition plays in maintaining boreal forests: (i) How do intraspecific and interspecific competition affect tree survival and growth in boreal forests? (ii) Is there a competition measure with universally superior performance? (iii) What is the maximum distance over which a tree affects the growth of its neighbours? (iv) How does difference in the size of neighbouring trees affect the intensity of competition between them?

To answer these questions, I investigated competition in a 1-hectare stem-mapped plot where all free-standing trees with a diameter at breast height ≥ 1 cm were censused in 2010 and again in 2015 in a boreal mixed-wood forest in George Lake, Edmonton, Alberta which is dominated by deciduous species (birch and aspen) and coniferous species (white spruce). Spatial distribution patterns in the plot were analyzed using an inhomogeneous pair-correlation function to infer competition effect on tree survival. Neighbourhood analysis was used to determine the relationship between neighbourhood density and individual tree survival. I also used likelihood-based non-linear regression models to quantify effects of neighbourhood competition on tree growth.

The analysis of the competition effect on both growth and survival of individual trees confirmed the importance of both inter- and intraspecific competition in regulating the study forest. Spatial analysis showed that the survival of coniferous trees was subjected to strong intraspecific crowding effect, while for deciduous trees, the effect of intraspecific competition was less detectable. However, spatial analysis indicated strong interspecific competition between coniferous and deciduous trees, suggesting that species replacement from deciduous to coniferous was occurring in the plot. Consistent with these results from the spatial analysis, coniferous trees showed lower survival rates in both the neighbourhood of denser conspecific and heterospecific stems. The coniferous trees had a slightly higher per capita effect on the survival of deciduous trees, suggesting the higher competitive ability of coniferous trees. The evidence of strong interspecific competition was also found from the neighbourhood analysis of individual tree growth, where crowding of both coniferous and deciduous trees has strong per capita effect on each other. However, the effect of intraspecific competition on growth of white spruce was weak.

Results also showed that individual tree model performance varied with different competition measurements. The commonly used neighbourhood competition index (NCI) was the best index for birch, while for aspen and white spruce, an index that is based on horizontal angles performed best. The estimated effective neighbourhood radius varied from 3 to 17 m, depending on the species identity of the target trees. Inclusion of the effective neighbour size ratio (a parameter to filter small-size neighbouring trees) improved the model likelihood for birch and white spruce but not for aspen. The estimated effective neighbour size ratio was close to 1 for both species, suggesting that target tree growth of birch and white spruce was more likely to be affected by larger neighbours.

This thesis highlights the importance of competition in driving dynamics and structure of boreal forests. Applying the effective neighbourhood radius and effective neighbour size to tree growth models allowed us to better investigate the effect of competition. Moreover, the analysis of competition effect on both tree growth and survival allowed us to quantify the competition and predict the dynamics of the forest.

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Chapter 1 Introduction

1.1 Background

1.1.1 Forest dynamics: disturbance, habitat heterogeneity, and biotic processes

The term “forest dynamics” describes changes in stand structure and species composition over different temporal and spatial scales (Frelich, 2016). Underlying these dynamics are many driving processes, such as disturbance, habitat filtering, dispersal, and competition. The operations of these processes and their interactions could leave their signatures in both stand structure and the species that comprise the forest. For example, the local disturbance created by fallen trees creates canopy gaps that allow for tree recruitment and promote gap dynamics. Such gap dynamics are considered as a major mechanism responsible for generating the variability in stand structure, including spatial variation of species distribution (Denslow, 1987; Kneeshaw et al., 1998; Hubbell et al., 1999). Ecologists have also recognized that the spatial structure of forest communities is strongly affected by habitat heterogeneity (Hubbell et al., 1999; Shen et al., 2009; Lin et al., 2011). For example, spatially heterogeneous habitats lead to more clustered hemlock seedling and can accelerate succession through faster plant growth on Vancouver Island (Getzin et al., 2008). In addition to the abiotic effects of disturbance and habitat heterogeneity on the spatial distribution of species, biotic processes such as dispersal (Luo et al., 2009; Pacala et al., 1996) and species interactions (Kenkel, 1988), notably competition, can also profoundly affect spatial patterns of species distribution (Luo et al., 2012; Zhang et al., 2009). For example, different spatial patterns of boreal species distributions can be attributed to contrasting seed dispersal strategies or competitive interaction between species (Pastor et al., 1999; Gray and He 2009). Most mechanistic models of forest successional dynamics include the effect of neighbourhood competition on tree growth and survival (Hubbell et al., 2001; Pacala et al., 1996; Canham et al., 2006). However, the effects of environmental heterogeneity may be confounded with those of seed dispersal and competition, leading to a mixture of spatial processes in plant communities (Getzin et al., 2008; Lin et al., 2011).

1.1.2 Dynamics of boreal forest ecosystems

Boreal forests comprise one of the most important terrestrial ecosystems on Earth, accounting for about 33% of global forest area (Bailey, 1996). In North America, Canadian boreal forests represent about 30% of the global boreal forest (CCFM, 2000) and feature varying canopy dominance of deciduous and coniferous trees. Boreal forests are characterized by a few plant species with distinct functional traits (Pastor et al., 1999). Boreal species are generally adapted to cold temperatures, a short growing season, low nutrient soils, and recurrent natural disturbances such as wildfire and insect infestation (Bhatii et al., 2002). In the absence of a major disturbance, the process of species succession takes place by the gradual replacement of deciduous species (e.g., *Betula*, *Populus*) by coniferous species (e.g., *Abies*, *Picea*) over a long period of time (Hornberg et al., 1995; Peterson and Squires, 1995a; Kneeshaw and Bergeron, 1998; Cumming et al., 2000). However, the occurrence of severe stand-replacing disturbances, such as fires, can return the stand to an early seral stage, where it is recolonized by shade-intolerant species more adapted to harsh conditions (Bergeron et al., 2014). In boreal forests, shade-intolerant (deciduous) species usually colonize and dominate canopy at early successional stages. Shade-tolerant (coniferous) species initially occupy the understory and gradually replace the pioneer species and dominate the stand in late-successional stages (Chen and Popadiouk, 2002). Over the course of this succession, forest structure and spatial distributions are influenced by several essential underlying biotic mechanisms including the mixed effects of seed dispersal and habitat heterogeneity and competitive interactions between species (Chen and Popadiouk, 2002). These mixed effects create different spatial distribution patterns in boreal plant communities over a range of temporal and spatial scales (Fraver et al., 2014).

1.1.3 Competition: the main driver of forest dynamics

Forest ecosystems in high latitude regions such as Western Canada are undergoing tremendous changes, which could plausibly be driven by increasing temperatures from global warming (Serreze et al., 2000; Peng et al., 2011; Zhang et al., 2015). Evidence has shown that tree mortality rates have increased markedly over the past five decades across the Canadian boreal zone (Peng et al., 2011; Lou and Chen 2013; Zhang et al., 2015) and across the temperate forests of the Western United States (Mantgem et al., 2009). Both endogenous (e.g., competition)

and exogenous (e.g., climate change) processes have contributed to the changes in forest dynamics (Zhang et al., 2015), especially the widespread mortality rate across global forests which was suggested to be a consequence of regional water deficiencies (Peng et al., 2011; Mantgem et al., 2009). However, it was more recently shown that competition is a dominant factor causing the long-term changes in tree mortality, growth, and recruitment in western Canada (Zhang et al., 2015).

Tree competition is a complex process that has profound and long-term effects on forest establishment, dynamics, and succession (Larocque et al., 2012). Competition is mainly caused by the limited availability of resources and can be partitioned into belowground competition for water and/or soil nutrients via roots and aboveground competition for light and/or crown space. Competition processes are a major cause of non-random mortality patterns and their strength depends on composition and spacing of near-neighbours (Aakala, 2012; Kenkel, 1988; Mack and Harper 1977). Density-dependent mortality is an example of this, which has been found in forests in most parts of the world (Getzin 2008; He and Duncan 2000; Lutz et al., 2014; Peters 2003). Trees in tropical forests are subjected to higher negative density-dependent mortality than in temperate forests, which could explain higher species diversity (LaManna et al., 2017). Strong intraspecific competition among species could lead to more regularly distributed survivors due to higher rates of mortality in the conspecific neighbourhood (He and Duncan 2000). Over the course of succession, the importance of intraspecific competition is expected to gradually shift from pioneer species to late-successional species (Gray and He 2009). The stronger interspecific competition between pioneer and late-successional species could also be detected during succession, because the plot would eventually be dominated by the most competitive species, which usually is the shade-tolerant, coniferous species.

1.1.4 The application of spatial analysis

With increasing attention being paid to spatial patterns and processes in forest ecology, it becomes possible to develop technologies to advance our understanding of species coexistence and community assembly. Spatial point pattern analysis makes inference of species' spatial arrangement using the distribution of distance between trees (Loosmore and Ford, 2006). Statistical neighbourhood analysis quantifies the performance of an individual tree (growth,

mortality, and recruitment) by relating it to the neighbourhood immediately around it with a scale estimated or defined (Uriarte et al., 2004a, b; Hubbell et al., 2001). Analyzing spatial patterns of fully stem-mapped plots at neighbourhood scales can provide insights into the competition processes underlying community assembly and dynamics (Wiegand et al., 2017).

1.2 Problem Statement

Abundant evidence has shown that intraspecific competition can strongly affect the growth and survival of early-seral species in the boreal plant community (Duncan 1991; Newton & Jolliffe 1998; Stadt et al., 2007; Filipescu and Comeau, 2007; Cortini and Comeau, 2008). In the basic routine of boreal succession, pioneer species, usually composed of deciduous, shade intolerant species, would be gradually replaced by late-successional, shade-tolerant species (Connell and Slatyer 1977; Oliver 1980; Peet and Christensen 1980; Finegan 1984; Pickett et al., 1987). Through the analysis of competition, we can investigate the extent to which interspecific competition between early- and late-successional species affects boreal species growth and survival in a specific stand. Species undergoing self-thinning, with higher rates of mortality in conspecific neighbourhoods, usually shift to a more regular pattern. Effects of self-thinning may vary over different life-stages of a species. By analysing neighbourhood competition, we can investigate which species are more likely to be affected by self-thinning effect. Although spatial point pattern analysis has been repeatedly shown as an effective approach for detecting negative density dependence (He and Duncan 2000, Getzin et al., 2008, Zhu et al., 2010), the spatial signatures left by density dependent processes may be difficult to detect due to the potential confounding factors. The results from spatial pattern analysis sometimes may show no evidence of density dependent effects even though the effect actually exists, as may be confounded by species habitat preference (Dovciak et al., 2001, McDonald et al., 2003). Using individual-based models to investigate neighbourhood competition on the survival or growth of subject trees can provide direct evidence of competition and clearer insights into the nature of competitive interactions. Previous studies used a series of methods to quantify the neighbourhood competition reflect the mechanistic links between the characteristics of neighbouring trees, the spatial structure of neighbouring trees and the strength of competition (Biging and Dobbertin, 1992, 1995; Canham et al., 2004; Contreras et al., 2011; Stadt et al., 2007).

Numerous competition indices have been developed to quantify competitive effects on the survival and growth of individual trees (Hegyi, 1974; Martin-Ek, 1984; Tomé and Burkhart, 1989; Holmes and Reed, 1991; Wykoff et al., 1982; De Luis et al., 1998; Reineke's, 1933), with each competition index based on an explicit assumption of the competitive relationship between neighbouring trees and the focal tree. Comparison of these competition indices of their effectiveness as predictors in individual tree growth models has been conducted for many tree species and forests (Biging and Dobbertin, 1992, 1995; Canham et al., 2004; Contreras et al., 2011; Stadt et al., 2007). No single type of competition index has been found to be the “best” (Contreras et al., 2011), as their performance depends on many conditions, e.g., species composition, stand age, and habitat heterogeneity. To better understand the competition effect between boreal species, it is necessary to find a competition index with the best performance for different species.

Moreover, determining a proper neighbourhood competition radius is essential to develop a more accurate growth model. Most previous studies have considered that neighbouring trees are within a circle with a fixed radius centred on the subject tree (usually spanning from 10 to 20 m). Canham et al. (2004) used a parameter as a fraction of 15 m to estimate the maximum radius of the neighbourhood of the target tree. Their analysis showed that the focal species hemlock and redcedar responded to neighbours within distances of 8 m and 13 m, respectively. However, it is unclear whether competitive effects between boreal tree species also occur within a certain distance, and what maximum distance between two trees can produce a competitive effect. We need to define the neighbourhood circle with a radius over which a tree produces negative effect to its neighbours and to select the neighbours which are considered “competitors” within this circle. However, few attempts have been made to detect the maximum effective neighbourhood distance together with the threshold of competitor tree size.

1.3 Thesis objectives and outline

In this thesis, my research focuses on exploring the role of tree competition in regulating community dynamics in a boreal forest ecosystem. To accomplish this, I investigated competition on the scale of the neighbourhood and the whole stand by evaluating the effect of competition on both tree survival and growth. The overall purpose of this study is to provide new perspectives about how to evaluate the importance of competition in regulating boreal forest and

to gain insights into the role of competition in affecting boreal forest structures and spatial patterns of species. All data sources used in my thesis were collected from a 1-hectare stem-mapped plot in a boreal, mixed-wood forest in George Lake, Edmonton, Alberta, in 2010 (first census) and 2015 (second census).

My thesis is organized as follows:

In **Chapter 2**, I investigate density-dependent effects on tree survival in the sample plot by analyzing both spatial patterns and the relationship between neighbourhood density and individual tree survival for the dominant species. Specifically, **Chapter 2** is divided into three complementary parts:

Part 1 tested the random mortality hypothesis for each species and compared the mortality pattern of those species among seedlings and adults. This part therefore explored whether the mortality pattern differed between seedlings and adults and whether density-dependent mortality varied among different species groups.

Part 2 examined the spatial associations between different species pairs and the seedling-adults spatial associations between conspecific pairs and heterospecific pairs. This part therefore explored whether seedlings are spatially attractive, repulsive, or randomly distributed with con- or heterospecific adults. It also allowed investigation of interspecific competition effects among different size-classes.

Part 3 applied autologistic regression to detect the independent effects of neighbourhood stem density of each species on tree survival. To adjust for spatial autocorrelation in the field data, I incorporated an additional term in the model to correct the potential biotic and abiotic effects of trees living closely to each other.

When competition is not strong enough, its effect on neighbouring trees would just cause reduction in growth instead of mortality. As **Chapter 2** used the spatial point pattern analysis with the neighbourhood analysis to explore the effects of competition on tree survival, in **Chapter 3** I focused on investigating how competition influenced neighbourhood tree growth.

Thus, in **Chapter 3**, I analyzed the effects of neighbourhood competition on tree growth for three dominant species in the sampling plot. This analysis used data from those individuals survived to 2015 and likelihood-based regression models. The purpose of this chapter was to provide insights into how dominant boreal species interact with each other and thus to gain a deeper understanding of how to accurately quantify the competitive interactions between species. Specifically, **Chapter 3** is divided into two parts:

In Part 1, I developed a likelihood-based model which was modified from previous studies (Uriarte et al., 2004 a, b) and which allowed estimates of the potential maximum tree growth as a function of tree species and size, and the species-specific competitive effects of neighbouring species on subject species growth as a function of species, tree size of both subject and competitors, and distance between subject and neighbours.

In Part 2, I compared several traditional competition indices to select the most effective index for predicting tree growth in the sample plot. Using this index, I calculated the parameter values of the likelihood model, and explained how those parameters varied with tree growth.

Finally, **Chapter 4** summarizes the main findings in **Chapters 2 and 3**, clarifying a number of caveats and suggesting directions for future research.

Chapter 2 Density-dependent effect on tree survival in a boreal mixedwood forest in Alberta

2.1 Introduction

Tree mortality in boreal forests is subjected to a wide variety of influences, with density-dependent competition acknowledged to be a key one (Peet and Christensen, 1987; Tilman, 1994; Keddy, 2001; Szwagrzyk and Szewczyk, 2001). There is abundant research demonstrating that negative density dependence plays a fundamental role in regulating tree spatial structure and species composition in forests (e.g., Cannell et al., 1984; Weiner, 1984; Peet & Christensen, 1987; Kenkel, 1988; Duncan, 1991; Newton & Jolliffe, 1998; Szwagrzyk and Szewczyk, 2001). Plants living within a neighbourhood with higher conspecific density have a higher risk of mortality because of the competition for resources and greater susceptibility to pathogens and predators (Janzen, 1970; Connell, 1971). Numerous field studies provide evidence that plant survival, growth and recruitment are negatively correlated with neighbourhood conspecific density, particularly in tropical forests (Condit et al., 1992; Wills et al., 1997; Hubbell et al., 2001; Peters, 2003; Uriarte et al., 2004). Density-dependent tree mortality has also been demonstrated in temperate (He and Duncan, 2000; Getzin et al., 2006) and subtropical forests (Chen et al., 2010; Zhu et al., 2010). However, some field studies have found that density-dependent effects were not prevalent in heterogeneous (Luo et al., 2012) and mature and old-growth stands (Aakala et al., 2012; Silver et al., 2013).

In empirical studies, forest ecologists usually infer density-dependent effects in plant communities from the spatial signature within the plant communities (Duncan et al., 1991; He and Duncan, 2000; Luo et al., 2012). For example, density-dependent competition between plants would result in tree mortality at neighbourhood scales. Through spatial pattern analysis over the whole scale of the tree community, a negative spatial association (a repulsive pattern) can be thus detected for plants. It is widely observed that density-dependent competition usually leaves some typical spatial signatures at the community level. Firstly, a strong negative conspecific density dependent effect would lead to an increasingly regular pattern of surviving

trees over time (Gray and He, 2009; Luo et al., 2012). Secondly, fewer seedlings occurred in the neighbourhood of adults over time because large trees suppress tree recruitments (Lutz et al., 2014). However, these kinds of spatial signatures could be confounded by other effects associated with life-stage and/or species habitat preference. Getzin et al. (2008) found that tree dynamics interacted with spatial heterogeneity, which might obscure the signatures of spatial changes of plants. Previous empirical studies have also provided evidence that density dependence is more likely to occur in seedlings (Norghauer et al., 2006; Luo et al., 2012), because trees tend to recruit in canopy gaps that form dense clusters of seedlings. Both the existence of habitat preferences and seedling dynamics could produce confounding effects on spatial signatures of negative density dependence. Therefore, it is preferable to examine the spatial arrangement within different tree size classes to account for possible confounding effect of habitat preference.

As the possible confounding effects mask spatial patterns, previous studies on the spatial pattern based on data from one census cannot provide direct evidence of density dependence. Investigating the correlation between the performance of individual trees (survival and growth) and the density of neighbouring plants can make up for this deficiency. He and Duncan (2000) used spatial pattern analysis combined with individual-based regression models to test for tree density dependency. However, their spatial analysis was based on one census and predictor variables in the regression model only accounted for neighbourhood crowding effects. Few studies have attempted to combine static data (that is, collected from one-census) and short period dynamic data to investigate density-dependent competition in boreal forest plots. It is preferable to integrate spatial pattern and neighbourhood analysis to analyze field sampling data to provide a clearer insight into any possible influence of density dependence on boreal forest dynamics.

There is abundant research in tropical forests indicating that the density-dependent effect plays a critical role in maintaining their high biodiversity at local scales. In contrast with tropical forests, boreal forests in Canada are composed of few tree species (usually dominated by the genera *Picea*, *Abies*, *Larix*, and *Pinus*). Density-dependent effects in boreal forests are however thought to be responsible for species turnover in succession (Gray and He, 2009). Boreal stands are usually colonized by shade intolerant deciduous species in the initial stage, while over the

path of succession, shade tolerant coniferous species gradually replace the deciduous pioneers through interspecific competition. The signal of intra- and interspecific competition can therefore be inferred from con- and hetero-specific density-dependent mortality.

Field sampling was conducted in two censuses in a 1-hectare stem-mapped boreal forest plot located in Central Alberta, Canada and provided the necessary data to investigate the importance of con- and hetero-specific density dependence between three common species (trembling aspen [*Populus tremuloides*], birch [*Betula spp.*], and white spruce [*Picea glauca*]). Aspen and birch are shade-intolerant pioneer species, usually forming the initial composition of the whole stands at early stage of succession. Over time, the shade tolerant species white spruce, is expected to replace the early-seral species and eventually comes to dominate the whole stand. Therefore, a strong negative spatial association is expected between the pioneer species aspen and birch and the late-seral species white spruce, and a more regular spatial distribution is expected to arise in all deciduous species over the period.

In this study, I aimed to assess the community dynamics in a mature, mixedwood boreal forest by seeking evidence of any density dependent effects through both spatial and local neighbourhood analysis. This study addresses the following four questions: (i) whether tree mortality is spatially random; (ii) how the spatial pattern of living stems has changed from seedlings to adults; (iii) how intra- and interspecific competition affect survival of early-seral and late-seral species; and (iv) how neighbourhood density of target trees affects tree survival?

2.2 Methods

2.2.1 Study site and data collection

Field sampling was conducted in a mature, natural mixedwood permanent forest plot (1 ha area, 100×100 m) located at the George Lake Field Station approximately 80 km northwest of the city of Edmonton in the province of Alberta, Canada (53°57'25.38"N, 114°7'27.52"W). This forest plot is in the transition zone between the aspen parkland and the western boreal forest (Rowe 1972) and includes several species of forest trees that are common in Central Alberta in one relatively small area. The forest surrounding the permanent plot comprises about 180 ha of continuous forest. In this forest region, hardwood species generally dominate sites during the

first 30-40 years after fire, but gradually succeeded to coniferous stands (Samoil, 1988). The climate in this region is characterized by long winters and short summers with a mean annual temperature of 4 °C and mean annual precipitation of 400 mm. The upper canopy is composed of birch (*Betula spp.*), aspen (*Populus tremuloides*), spruce (*Picea glauca*), tamarack (*Larix laricina*) and poplar (*Populus balsamifera*). Understory shrubs are mainly composed of beaked willow (*Salix bebbiana*), beaked hazelnut (*Corylus cornuta*), saskatoon berry (*Amelanchier alnifolia*), dogwood (*Cornus stolonifera*) and green alder (*Alnus crispa*). The permanent plot was established during the summer of 2010 by stem-mapping the distribution of all stems (alive and dead) greater than 1 cm in diameter at breast height (DBH) using laser total stations. The second measurement was conducted in the fall of 2015. Species identity, living status and DBH were recorded for each of the mapped stems in the plot. A total of 4318 trees were mapped in the plot, including 3308 (76.63%) trees that were alive at the time of first measurement (2010) and 2743 (63.52%) trees that were alive at the time of second measurement (2015).

2.2.2 Data analysis

2.2.2.1 Stand structure and composition

There were three dominant species in the 1-ha plot: birch, aspen and white spruce. However, Because of their low densities, the remaining species were lumped into the following groups: OD, other deciduous trees (including poplar and tamarack) and OS, other shrubs (including all shrub species)". The total number of both live and dead stems (N), their relative proportions (%), mean DBH (in cm) and nearest neighbour distance (i.e. the distance between the focal tree with its nearest neighbours, measured in meter) were counted for each species in the plot. Following Gray and He (2009), the following metrics were calculated for each species over the 5-year period between two censuses: proportion of mortality (the proportion of trees that died over the 5-year period for each species), intraspecific mortality (trees dying in a conspecific neighbourhood where more than 4 of the 5 nearest neighbours were the same species as the focal tree) and interspecific mortality (trees dying in a heterospecific neighbourhood where no more than 1 of the 5 nearest neighbours were the same species as the focal tree).

2.2.2.2 Spatial pattern analysis

The second-order characteristics of a homogeneous and isotropic point pattern utilizes the distribution of distance between events to make inference on spatial distribution patterns (Loosmore and Ford, 2006). A widely used second-order characteristic process is Ripley's K function (Ripley, 1976, 1977), which measures events in circles. The Ripley's K function is defined as:

$$k(r) = \lambda^{-1}E(\# \text{ of other events within distance } r \text{ of an arbitrary event})$$

where # means "the number of", $E()$ is the expectation operator and λ is the intensity of the event.

The pair correlation function $g(r)$ was derived from Ripley's K function and uses rings/annulus instead of circles, and it has the advantage of isolating distance classes (Wiegand and Moloney 2004). Therefore, I used the pair correlation function $g(r)$ to analyze changes in the spatial point pattern of tree distributions (Stoyan and Stoyan, 1994; Diggle, 2003; Illian et al., 2008).

The pair correlation function is defined as:

$$g(r) = \frac{k'(r)}{2\pi r}$$

where $k'(r)$ is the derivative of $k(r)$, the reduced second moment function (aka "Ripley's K function") of the point process (Ripley 1977). An unbiased Ripley's K function expression for stationary point processes is:

$$k(r) = \frac{1}{n(n-1)} \sum_{i=1}^n \sum_{j \neq i} I(\text{dist}_{ij} \leq r) * w_{ij}^{-1}$$

where n is the number of tree points and the sum is taken over all ordered pairs of tree points i and j ; dist_{ij} is the distance between the two points, and, $I(\text{dist}_{ij} \leq r)$ is an indicator function that equals 1 if the distance is less than or equal to r , and 0 otherwise. w_{ij}^{-1} is the edge correction weight. Ripley's isotropic edge correction weight is used to estimate the K function.

For those tree points located close to the plot edge, the isotropic edge correction weight is applied to unbiased results for values of the second-order statistics. For a pair of points x_i, x_j in a window W , the isotropic edge correction weight is

$$w(x_i, x_j) = \frac{2\pi||x_i - x_j||}{length(W \cap \partial b(x_i, ||x_i - x_j||))}$$

which is indicated by the perimeter of the circle with radius $||x_i - x_j||$ centered at point x_i divided by the boundary length on the window W intersected by the circle.

The univariate $g(r)$, as described above, was used to analyze intraspecific tree distributions. To quantify spatial relationships between two different tree species, i.e., points of species i and j , I used the bivariate $g_{i,j}(r)$, which is defined as:

$$g_{i,j}(r) = \frac{k'_{i,j}(r)}{2\pi r}$$

in which

$$k'_{i,j}(r) = \frac{1}{n_i n_j} \sum_{i=1}^n \sum_{j \neq i} I(dist_{ij} \leq r) * w_{ij}^{-1}$$

and used the multi-type $g_{i,\cdot}(r)$ to measure the relationships between points of type i and all other types.

The value of $g(r)$ indicates different spatial point patterns where:

$$g(r) \begin{cases} > 1, \text{spatial aggregation} \\ = 1, \text{complete spatial randomness (CSR)} \\ < 1, \text{spatial regularity} \end{cases}$$

To account for the effects of habitat heterogeneity, I used inhomogeneous pair correlation function to calculate $g(r)$, in which the intensity λ is not constant but varies with locations. It can be defined as:

$$g_{inhom} = \frac{k'_{inhom}(r)}{2\pi r}$$

in which

$$k'_{inhom}(r) = \frac{1}{\sum_i \hat{\lambda}_i^{-1}} \sum_i \sum_{j \neq i} \frac{I(dist_{ij} \leq r)}{\hat{\lambda}_i \hat{\lambda}_j} * w_{ij}^{-1}$$

in which the $\hat{\lambda}_i$ is an estimate of the intensity function for event i .

In this study, I used the Monte Carlo simulations to test significance of departure from an underlying null model. The pair correlation function of the observed spatial pattern was compared by approximating 95% simulation envelopes using the third lowest and highest values for the inhomogeneous pair correlation functions of data calculated using 99 simulations of appropriate null models. I used the package *spatstat* (Baddeley and Turner, 2005) in R statistical software (R Development Core Team 2017) to perform spatial pattern analysis in this study.

To assess the density-dependent effects on seedlings and adults, I specified trees with DBH < 5cm as “seedlings” and trees with DBH > 15cm as “adults”, I ignored all of the remaining trees with DBH between 5cm and 15cm, because those trees were not considered in this analysis. All spatial analysis is conducted for the tree patterns of “seedlings” and “adults” separately and for all life-stages pooled together.

Analysis 1: Univariate patterns and multi-type patterns for testing non-random mortality

To investigate the effects of density dependent mortality, I used a case-control design implemented with random labeling null models. Density dependent mortality is expected to cause the spatial distribution pattern of trees to be more regular over time (Lutz et al., 2014). Therefore, I quantified change in the pattern of surviving trees due to mortality over the 5-year period. The difference $g_{l,l}(r) - g_{d+l,d+l}(r)$ was calculated to test whether the mortality pattern was the same for pre- and post-mortality. The null model was constructed by random labelling of live and dead trees based on the pre-mortality pattern. Statistic values below the simulation envelop indicate that surviving trees became more uniform after mortality.

In addition, I used the difference $g_{d,d+l}(r) - g_{l,d+l}(r)$ to compare the initial neighbourhood density of dead trees with those of trees that survived by the second census. The test value of this statistic is expected to be zero under random mortality and a positive value of the statistic indicates density-dependent mortality among trees. I used a random labelling of dead trees in the pre-mortality pattern using the same number occurring in the post-mortality pattern as the null model. The procedure was simulated 99 times as described above to produce a simulation envelope for testing the significance of departure from random.

Analysis 2: Bivariate patterns for testing species spatial associations

To investigate the effects of density-dependent repulsion on the spatial association between seedlings (DBH ≤ 5 cm) and conspecific and heterospecific adults (DBH > 15 cm), I implemented the null model simulated by toroidal shift of the seedling populations with the bivariate pair correlation analysis function. If large diameter trees constrained the survival rates of seedlings, a spatially negative pattern would be observed. I tested the bivariate $g_{s,a}(r)$ where s indicates seedlings species (including aspen, birch, white spruce, other deciduous and other shrubs) and a indicated the species of adults (including aspen, birch and white spruce) to assess how dominant adult species spatially associated with ingrowth species. A hyperdispersed pattern between aspen/birch species and white spruce was expected as a result of interspecific competition between pioneer (shade intolerant) and late-seral (shade-tolerant) species during the process of forest succession.

To investigate the interaction between shade-intolerant pioneers (aspen and birch) and late-successional, shade-tolerant species (white spruce), I implemented null models simulated by toroidal shift of the second-order structure of both patterns relative to each other. If the interspecific competition effect is strong between the two species, a repulsive spatial pattern should be detected. I tested the bivariate $g_{sp1,sp2}(r)$ (where $sp1$ and $sp2$ indicates the different species pairs including aspen, birch, white spruce, other deciduous, and other shrubs) to assess different species interactions with each other. The interspecific competition between different shade-intolerant species was also of interest. A strong negative spatial association between shade-intolerant species would be considered to indicate which species has the advantage of competitive ability.

2.2.3 Neighbourhood analysis

Intra- and interspecific competition effects can be detected where the probability of tree survival becomes lower under the crowding effects from con- and hetero-specific neighbouring trees. Therefore, I tested the importance of the effects of stem density of each neighbouring species on focal species in the plot. Modelling neighbourhood effects on tree survival by autologistic regression allows us to account for potential spatial autocorrelation in tree survival, which can be caused by biotic and abiotic factors such as habitat heterogeneity (Hubbell et al., 2001; Luo et al., 2012). The toroidal method was used to reduce the influence of any bias caused by edge effects. To examine how far the neighbourhood crowding effect extended for a given tree, this analysis was conducted using neighbourhood radii of 5, 10, 15, and 20 m.

I used tree survival as the response variable in autologistic regression modelling. Survival is a binary variable Z_i that was assigned one if the plant was alive and zero if the plant was dead in 2015, where $Z_i \sim \text{Bernoulli}(p_i)$. Let p_i be the probability of survival of a plant i for a given stem density X_i . The logistic function for the probability of survival as a function of total stem density:

$$p_i = \frac{1}{1 + e^{-(\beta_0 + \beta_1 X_i)}}$$

the corresponding log odds $\pi(X_i)$, which indicates the log ratio of probability of tree survival to dead:

$$\pi(X_i) = \log\left(\frac{p_i}{1 - p_i}\right) = \beta_0 + \beta_1 X_i$$

Here, $\pi(X_i)$ measures the effect on the logit transform by increasing a stem to the total stem density X_i .

$$\pi(X_i + 1) - \pi(X_i) = \beta_1$$

The neighbourhood variables used in this analysis are the total stem density in the neighbourhood for each species. As the neighbourhood variables are assumed independent in this analysis, the generalized logistic model can be written as:

$$p_i = \frac{1}{1 + e^{-\beta^T X_i}}$$

where β is a vector containing p parameters which correspond to the p neighbourhood variables for plant i , and X_i is the vector containing neighbourhood attributes for plant i . The odds ratio (OR) was used to measure the partial contribution of each independent variables. The partial effects of j^{th} variables in X can be defined as:

$$OR_{\beta_j} = \exp(\beta_j) = \exp(\pi_j(X_j + 1) - \pi_j(X_j))$$

However, this model is not sufficient to test our hypothesis, because data of spatial tree points violates the assumption of independence. Tree survival can be spatially autocorrelated, because it can be affected by neighbourhood living tree density. Adding a parameter accounting for spatial autocorrelation allows us to accurately weigh the effect of each neighbourhood variable. A variable counting total living stems around the subject tree within a distance r was thus treated as the spatial autocorrelation term for the model. Therefore, the model for one observation becomes:

$$p_i = P(z_i = 1 | z_j (j \neq i), \beta, \gamma) = \frac{1}{1 + e^{-(\beta^T X_i + \gamma \sum_{j=1}^n z_j)}}$$

The next step is to maximize the corresponding likelihood function of each plant for the whole plot. The likelihood for one observation z_i can be written as:

$$L(z_i | \beta, \gamma) = p_i^{z_i} (1 - p_i)^{1 - z_i}$$

The likelihood for the entire observation $z_{i=1,2,\dots,N}$ becomes the product of the N individual likelihood contribution. With the log-odds function, the likelihood for the whole observation becomes:

$$L(Z | \beta, \gamma) = \prod_{i=1}^n \left(\frac{1}{1 + e^{-(\beta^T X_i + \gamma \sum_{j=1}^n z_j)}} \right)^{z_i} \left(\frac{1}{1 + e^{\beta^T X_i + \gamma \sum_{j=1}^n z_j}} \right)^{1 - z_i}$$

$$= \frac{e^{\sum_{i=1}^n z_i \beta^T X_i + \gamma \sum_{j=1}^n z_j}}{\prod_{i=1}^n (1 + e^{\beta^T X_i + \gamma \sum_{j=1}^n z_j})}$$

Bayes rule was used to infer the corresponding parameters of neighbourhood variables. In this case, independent priors for the components of the vector $\alpha = [\beta_0, \beta_1, \dots, \beta_p, \gamma]$ are specified as noninformative uniform distribution, which is $p(\alpha) \propto 1$. According to Bayes theorem, the posterior distribution of parameters α can be expressed as:

$$f(\alpha|Z) \propto L(Z|\alpha)p(\alpha)$$

This posterior distribution was estimated using Monte Carlo Markov Chain (MCMC) simulation. The Markov chain was simulated by the random walk Metropolis algorithm. I used the package MCMCpack (Martin et al., 2018) in R statistical software (R Development Core Team 2017) to conduct the simulation in this analysis.

2.3 Results

2.3.1 Stand structure

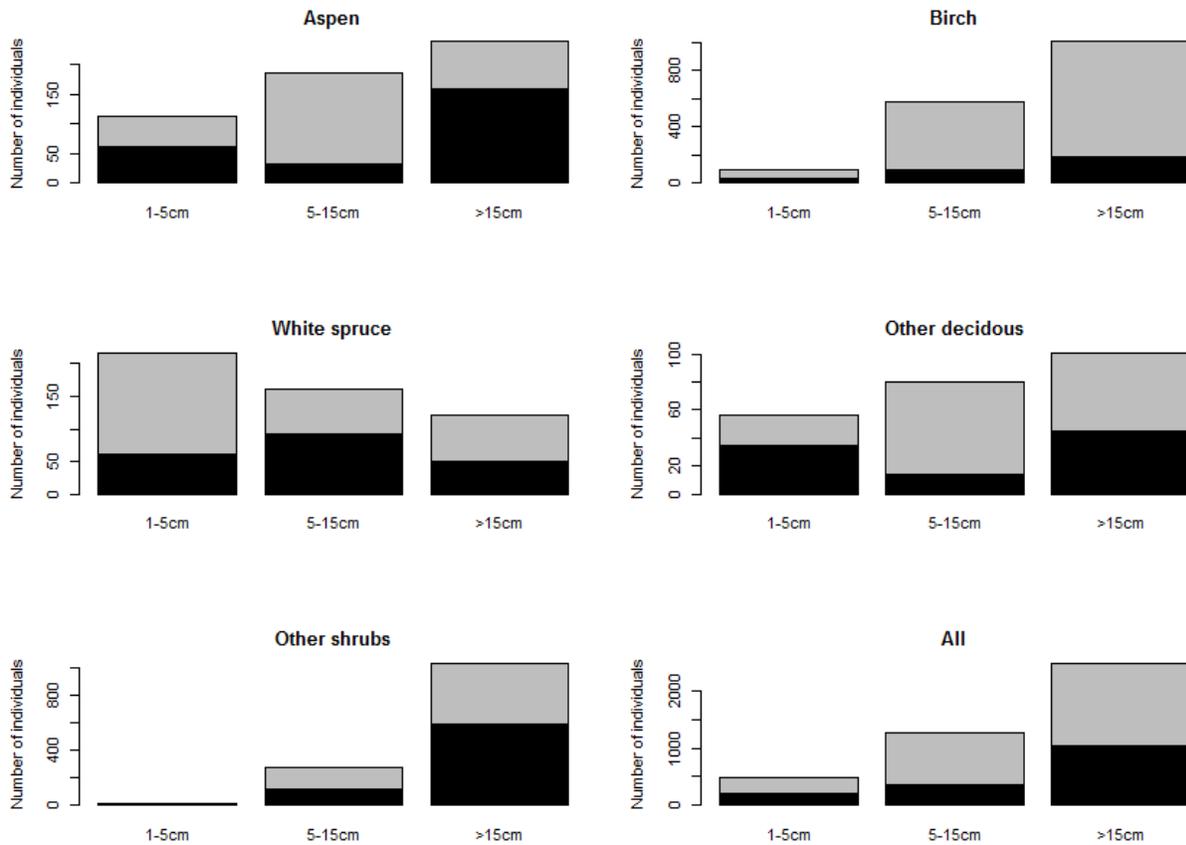
Through the results showed in Table 2.1, I observed a general picture that shows a summary of stem density, stem size, mortality rate and spatial structure of the five groups of species. For live and dead trees combined, the 1-ha plot mainly comprised birch (39.18%) and shrub species (30.82%), followed by aspen (12.68%) and white spruce (11.74%), which indicates that the plot was deciduous dominated. Although aspen and white spruce had fewer stems, they accounted for a large proportion of total basal area in the plot. The average DBH of white spruce was the largest among all species in the plot. The range of the mean nearest neighbour distance for each species was small (0.23-0.79 m). Shrubs were observed to have the highest mortality rate during the 5-year period, with most of the dead shrubs caused by intra-mortality. The mortality rate of shrubs was followed by white spruce, of which intra-mortality comprised the majority. Mortality rates for birch were the lowest, while most of its cases were composed of intra-mortality. Mortality rates of aspen were higher than birch, while most of its cases were inter-mortality. The situation for other deciduous tree was similar to that of aspens.

Table 2.1 Summary of density, mortality, and spatial structure of aspen, birch, white spruce, OD (other deciduous trees), OS (other shrubs). # stem = total number of stems; % stems = percentage of total stems in the stand; DBH = diameter at breast height (cm); NND = nearest neighbour distance (m); % mortality = percentage of dead stems occurred in the 5-year period; intra-mortality = proportion of dead trees located within conspecific neighbourhoods; inter-mortality = proportion of dead trees located within heterospecific neighbourhoods.

Species	#stems	% stems	Mean DBH	Mean NND	% mortality	Inter-mortality	Intra-mortality
Birch	1665	39.2%	5.59	0.36	9.35%	5.04%	83.45%
OS	1310	30.9%	3.47	0.23	33.78%	8.85%	69.51%
Aspen	539	12.7%	10.49	0.79	17.15%	59.32%	11.86%
White spruce	499	11.7%	16.11	0.76	25.32%	11.00%	62.00%
OD	237	5.6%	11.2	0.76	20.11%	50.00%	33.33%

The frequency distribution plots as shown in Fig. 2.1 reveals the mortality distributions in different size classes. For all species pooled together in Fig. 2.1, the graph reveals that most dead stems were distributed in the smallest size class and the dead stems decreased as size became larger. The size-class distributions of deciduous species (aspen, birch, other deciduous and other shrubs in Fig. 2.1) were mostly concentrated in the small size classes. In contrast, the coniferous species (white spruce) showed an inverse distribution, in which the proportion of tree stems increased with size. Most of the dead aspens were in the smallest size class, which was similar for shrub species. Most of the birches survived during the period. There were fewer dead birch than dead aspen, and they gradually decreased with size classes. For white spruce, the distribution of dead trees was symmetric with most of those found in the middle size class. Other deciduous trees also comprised a large number of dead trees in the small size class, followed by the large size class.

Figure 2.1 Frequency distribution of size classes of aspen, birch, white spruce, other deciduous species, other shrubs species, and all species. Size classes on the horizontal axis refer to diameter at breast height. The black area represents dead trees and the grey area represents live trees.



2.3.2 Spatial pattern analysis

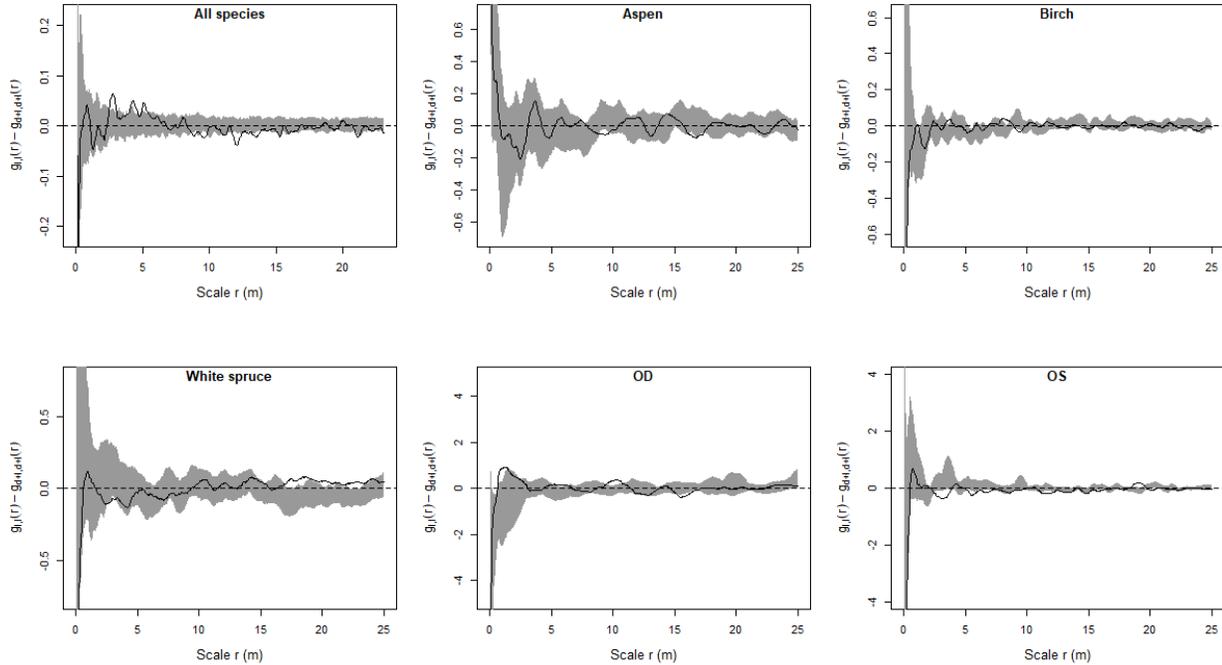
2.3.2.1 Analysis 1: Univariate and multi-type pattern

I compared the differences separately in the pattern of surviving trees (all live trees in 2015) and initial live trees (all live trees in 2010) for all species, and for each species and each life stage, using the random labelling null models (with the dead tree number equal to what it was in 2015) to test if the live pattern changed. In general, the univariate analysis showed an overall random mortality pattern, and a large number of tree patterns did not differ over the 5-year period.

Through the analysis of univariate pair correlation functions, I found little evidence of density-dependent effects. The surviving pattern of all species became significantly more regular in spatial distribution at distances from 9 to 14 m than in the pre-mortality pattern (Fig. 2.2 All species). The spatial pattern of surviving aspen trees shifted toward a more regular spatial pattern at distances from around 10 m and 16 m (Fig. 2.2 Aspen). Almost no significant spatial pattern changes were detected for the surviving pattern of post-mortality birch, for which I only found a marginally more clustered pattern at 7 m and a marginally more regular pattern at 9 m (Fig. 2.2 Birch). Mortality in white spruce was random for scales from 0 to 16 m, but the pattern of post-mortality was found to be even more clustered at scales around 16 to 24 m (Fig. 2.2 White spruce). The post-mortality pattern of other deciduous species was observed to become significantly more aggregated at distances from 10 to 11 m and significantly more regular between 16 to 18 m (Fig. 2.2 OD). The mortality pattern of shrubs was also non-random, with living shrubs more regularly distributed at scales of 3 m and from 11 to 14 m (Fig. 2.2 OS).

The density-dependent mortality pattern was partially different from seedlings to adults (Figs. A1 and A2), where almost all living adults, regardless of the species, did not change in spatial pattern over the 5-year period. However, the spatial distribution of survived seedlings had shifted toward a more regular pattern over time for birch at scales around 14 m, other deciduous, and shrubs across all scales. In contrast, for some species the spatial patterns of seedling survival became to be more aggregated, such as for white spruce (on scales less than 5 m) and aspen (on scales of 7 to 8 m). This kind of clustering was also represented by the change in spatial pattern of live seedlings for all species pooled together for scales less than 3 m (Fig. A2).

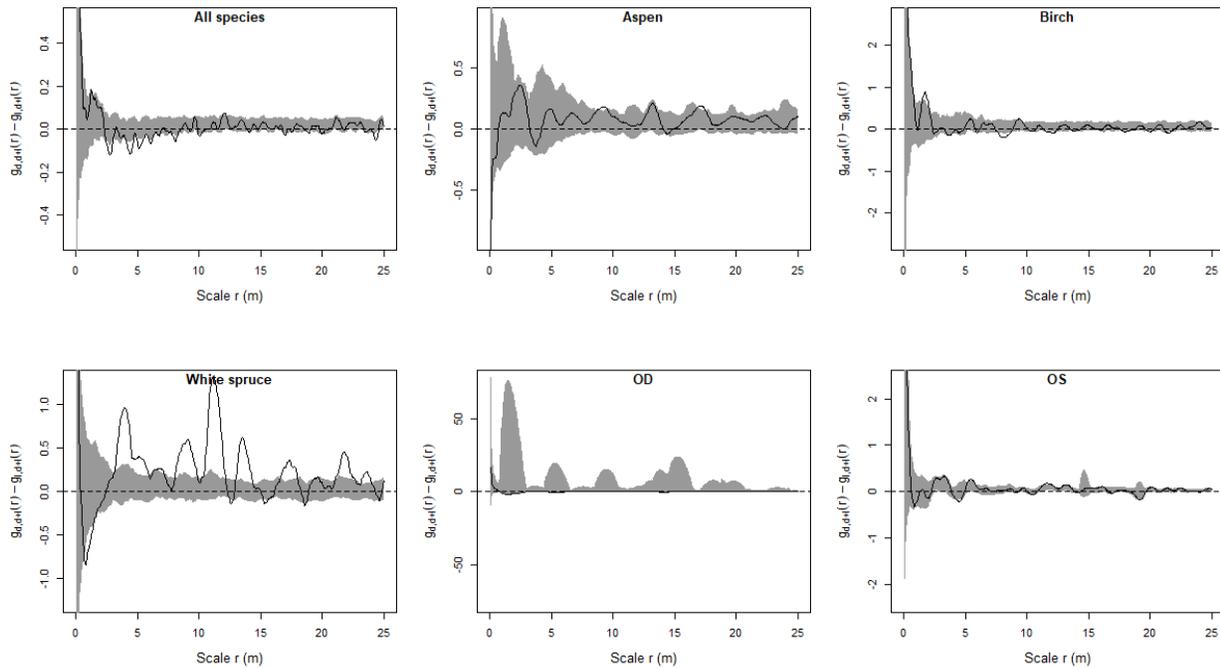
Figure 2.2 Univariate density-dependent mortality analysis for the change in living trees pattern using the random labelling null model. If the spatial pattern of living trees became more regular due to density-dependent mortality, the test statistic $g_{l,l}(r) - g_{d+l,d+l}(r) < 0$. Solid lines showed the observed values for test statistics and approximate 95% simulation envelopes (grey areas) were constructed using 99 null model simulations. The analysis was conducted for all species together and the five species groups Aspen, Birch, White spruce, OD (other deciduous trees), OS (other shrubs) separately.



To further assess density-dependent mortality, I investigated if the stem density in the initial neighbourhoods of surviving trees differed from that of trees that had died during the 5-year period. Contrary to my expectation, dead trees were shown to be surrounded by marginally and significantly fewer initial neighbours than those of survivors at scales from 3 to 6 m for all species pooled together (Fig. 2.3 All species). Although random mortality patterns were generally not detected for most deciduous species individually and for all species together, a strong density-dependent mortality pattern was observed for white spruce over all scales (Fig. 2.3 White spruce). There was slightly more crowding of birches that died during the study period at scales of 2 m (Fig. 2.3 Birch). For other deciduous and shrubs species, there was no significant departure from the null model envelope (Fig. 2.3 OD, OS). However, dead aspen tended to occur in denser neighbourhoods than surviving aspen, and a slightly significant departure from the null model was observed at 9 m and 17 m (Fig. 2.3 Aspen).

Similarly, density-dependent mortality was not prevalent for both seedlings and adults of each species (Figs. A3 and A4). However, adult trees were much less likely to be affected by neighbourhood density, as surviving adults are more spatially separated from the initial neighbourhood, except for adult white spruce which showed a significant aggregated pattern with initial neighbourhood.

Figure 2.3 Multi-type density-dependent mortality analysis comparing the initial neighbourhood of live and dead trees using a random labelling null model. If tree density around dead trees is larger than expected under random mortality, the test statistic $g_{d,d+l}(r) - g_{l,d+l}(r) > 0$. Solid lines show observed values of test statistics and approximate 95% simulation envelopes (grey areas) were constructed using 99 null model simulations. The analysis was conducted for all species together and five species groups Aspen, Birch, White spruce, OD (other deciduous trees), OS (other shrubs) separately.



2.3.2.2 Analysis 2: Bivariate pattern

Interspecies spatial association

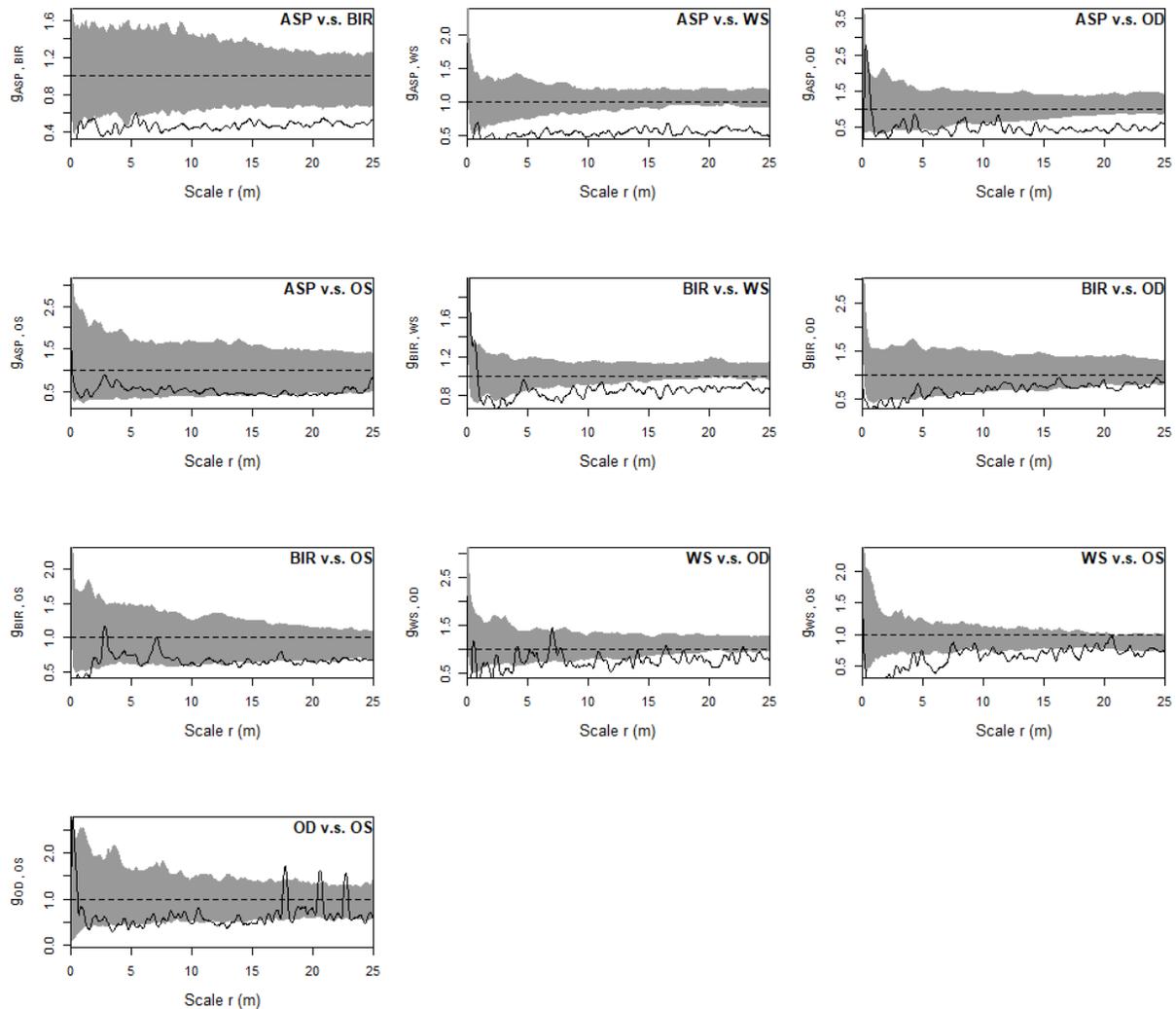
To investigate the spatial relationship between living trees of different species, I used bivariate pair correlation function $g_{sp1,sp2}(r)$. It is expected that under the interspecific competition of deciduous and coniferous species, a repulsion pattern (in which the observed

value of $g_{sp1,sp2}(r)$ would be below the simulated envelope) would be detected for the two species groups. The results from the bivariate analysis of spatial association between species of all life stages were consistent with this expectation. All comparisons of the dominant species resulted in significant downward departures from the null model, suggesting that the presence of each dominant species did affect the mortality of the other species. Particularly significant repulsive spatial relationships were shown between the shade tolerant late-successional species (white spruce) and shade intolerant pioneer species. For example, I found significant repulsion between white spruce and aspen (Fig. 2.4 ASP vs. WS) and between white spruce and birch (Fig. 2.4 BIR vs. WS). The results were similar for other deciduous (OD) and other shrubs (OS), which were repulsively associated with white spruce across a range of distances. Significant negative spatial associations were also displayed among different deciduous species. Negative spatial associations were detected between aspen and birch and between aspen and other deciduous trees. Birch also showed a marginal spatial separation with other deciduous trees.

Seedling-adult spatial association

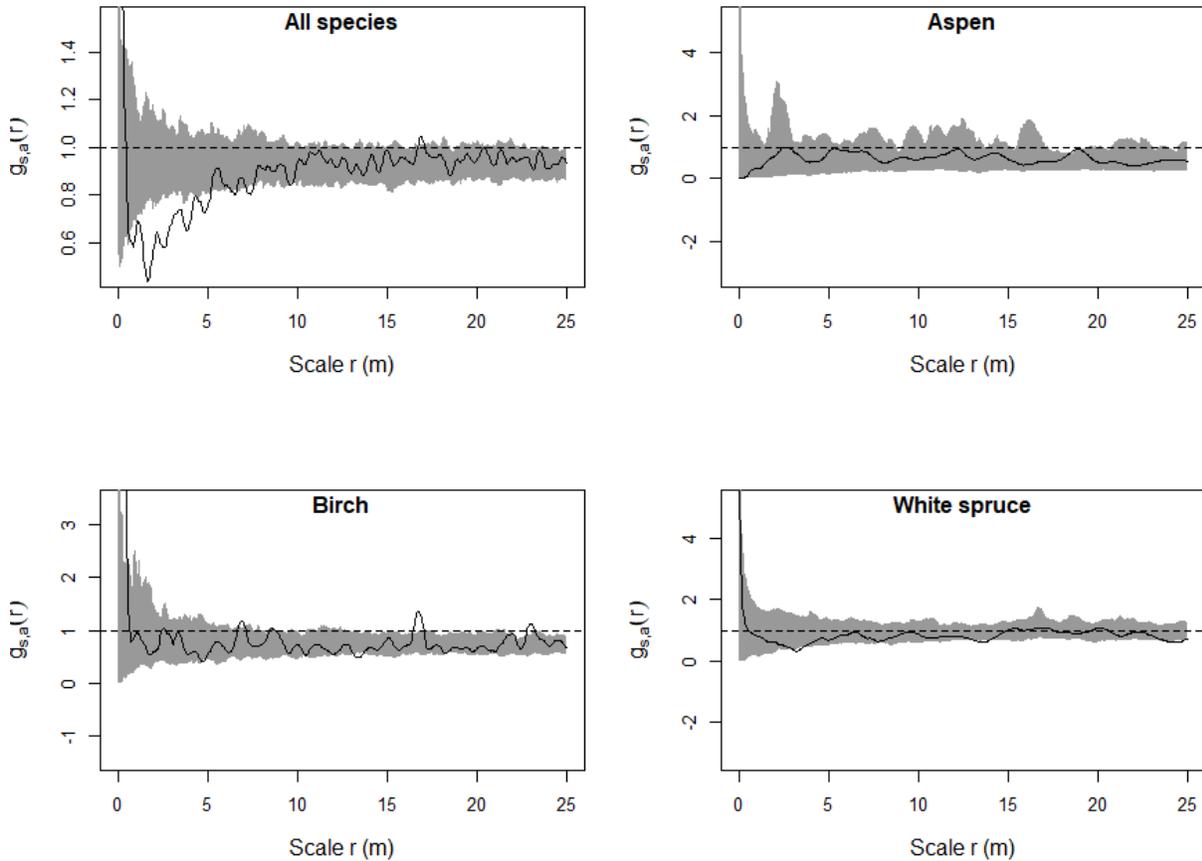
During the 5-year period between the two censuses, I found there were no new seedling recruitments recorded in the dataset. Therefore, I grouped all of the trees with a DBH less than 5 cm as seedlings in this analysis. In this first analysis of seedling-adult spatial associations, I investigated the spatial relationships of seedlings and adults of conspecific trees for three dominant species. The results from the rest of the groups of species were removed because of insufficient data. The seed dispersal strategy and the canopy suppression on recruitments should leave a signature in the spatial pattern of the seedling-adult association. However, the results of the bivariate analysis showed no significant shifts in spatial patterns for conspecific trees (Fig. 2.5). This suggests that seedlings are randomly distributed with conspecific adults and the constraints of conspecific large trees on seedlings was not strong enough to cause significant mortality. However, as the conspecific spatial association analysis showed a small-scale (from 0 – 6 m) significantly repulsive pattern between seedlings and adults for all species pooled together, the recruitment suppression from heterospecific adults was probably more important in this stand.

Figure 2.4 Bivariate analysis of spatial associations between species pairs. Interaction between species pairs compared to the toroidal shift null model. Values above (below) the simulation envelope indicate attraction (segregation) between the two species. Solid lines showed observed values of test statistics and a proximate 95% simulation envelopes (grey areas) were constructed using 99 null model simulations. Species abbreviations: ASP, aspen; BIR, birch; WS, white spruce; OD, other deciduous; OS, other shrubs.



Although the results from the heterospecific adult-seedling spatial association analysis indicates that most adult species did not significantly depart from the null model, I found significant negative spatial associations between adult white spruce and seedling birches and other deciduous species at small scales (Fig. A5).

Figure 2.5 Conspecific seedling–adult association analyses. Interaction between conspecific seedling and adult pairs compared to the toroidal shift null model. Values above (below) the simulation envelope indicate attraction (segregation) between seedlings and adults. Solid lines showed observed values of test statistics and approximate 95% simulation envelopes (grey areas) were constructed using 99 null model simulations. Species abbreviations: ASP, aspen; BIR, birch; WS, white spruce; OD, other deciduous; OS, other shrubs.



2.3.3 Neighbourhood analysis

Figure 2.6 illustrates how spatial autocorrelation in the survival of three dominant species (aspen, birch, and white spruce) change as a function of distance from a focal tree in the stand. It shows that tree survival was almost significantly spatially autocorrelated for all dominant species, but the effect of spatial autocorrelation declined as the distance to the focal tree increased and became negligible at the maximum distances (from 10 – 20 m). At distances < 5 m, survival of birch was more strongly spatially autocorrelated than aspen, while the spatial structure of the survival of white spruce was not significantly different from either of them.

Figure 2.7 illustrates how the survival odds ratios of three dominant species (aspen, birch, and white spruce) for the neighbourhood variables (stem density of each species) change as a function of distance from a focal tree in the stand. Odds ratios below unity indicate negative effects on tree survival, while values greater than unity represent positive effects on tree survival. All results in Fig 2.7 show negative effect from neighbourhood stem density on those target species, and those negative effects fades out spatially and become undetectable beyond 15 m (Fig. 2.7). Survival odds ratios of aspen did not significantly decline due to conspecific density effects (Fig. 2.7 A), while the odds ratios of survival for birch dropped almost 17% due to conspecific density effect within a radius of 5 m. The conspecific density effects were even stronger on the survival of white spruce, with survival odds ratio reduced by almost 17% within a 5-m radius and still significantly below unity as distance increased (Fig. 2.7 C). Negative heterogeneity density dependence was also found for most species over short scales. For example, survival odds ratio of aspen and birch dropped almost 8% and 11% when surrounded by white spruce (Fig. 2.7 C), but the survival odds ratio of white spruce did not significantly change when neighbored by aspen and dropped only 6% due to the density effect of birch within 5 m (Fig. 2.7 A and B). The crowding effect of aspen significantly reduced by 10% the survival odds ratio of birch. Inversely, the density of birch significantly made the survival odds ratio 8% lower (Fig. 2.7 A and B). The density of other deciduous species (OD) only had significantly negative effects on the survival odds ratios of birch within a 5-m radius (Fig 2.7 D and E). Density effects from shrubs also exerted a significant but weak negative effect on the survival of dominant trees (Fig 2.7 E).

Figure 2.6 Spatial autocorrelation (the coefficient gamma) in tree survival as a function of distance (m) at 5, 10, 15, and 20 m radius from focal plants. Error bars represent 95% Bayesian confidence intervals.

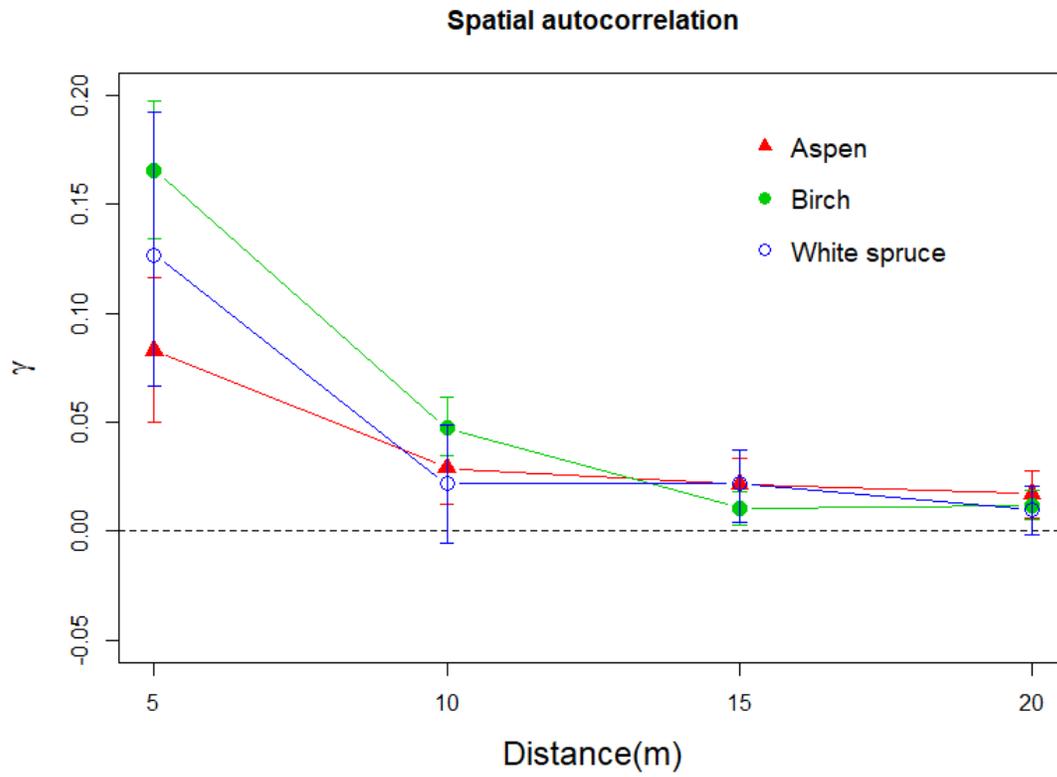
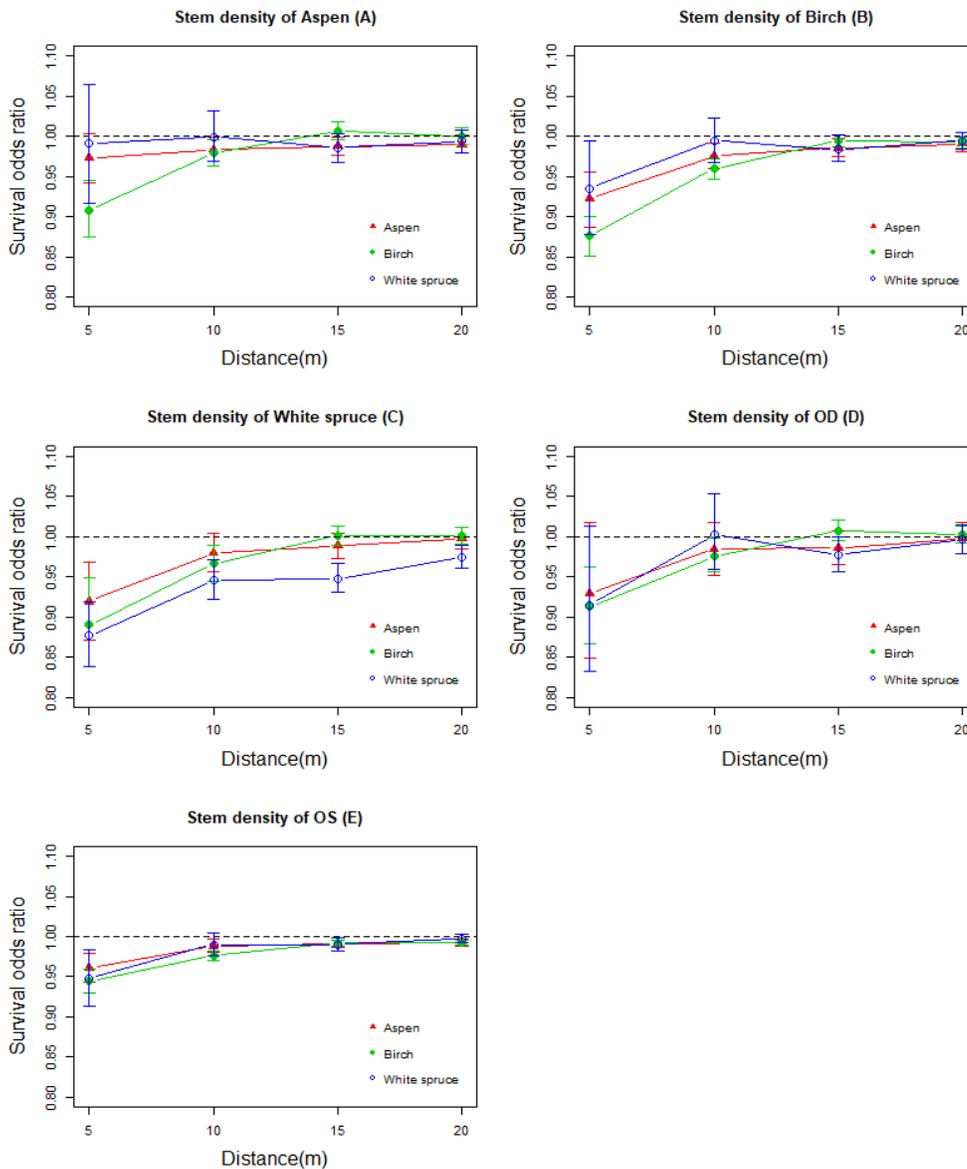


Figure 2.7 Odds ratios of tree survival within successive increasing radii for each species. Spatial decay of the crowding effects of neighbourhood species (A - E) as a function of distance (m) at 5, 10, 15 and 20 m from focal plants. Error bars represent 95% Bayesian confidence intervals.



2.4 Discussion

Spatial patterns and neighbourhood analyses for testing density-dependent mortality of trees have been studied over many years (Condit et al., 2000; He and Duncan 2000; Getzin et

al.,2006; Getzin et al., 2008; Yu et al., 2009; Luo et al., 2012). In my thesis, the spatial pattern analysis using data from two censuses and Bayesian regression analysis of the neighbourhood crowding effect on tree survival allows a clearer understanding of the importance of density-dependent effects on tree survival in the boreal forest. The random mortality hypothesis predicts that the spatial patterns of post mortality (living trees only) remain unchanged if all trees in the field have an equal probability of mortality. If density-dependent effects decrease the survival rate of conspecific trees, the post-mortality pattern becomes more regular than the pre-mortality pattern (Pielou 1962; Antonovics and Levin 1980; Stoll and Bergius 2005; Getzin et al., 2006). If light gaps in the canopy promote recruitment and higher survival rates for shade-intolerant species, the post-mortality pattern would become more aggregated than the pre-mortality pattern (He and Duncan 2000).

Both spatial and neighbourhood analyses suggested strong intra- and interspecific density-dependent effects on tree survival. The significant density-dependent mortality pattern of white spruce (particularly for adults) and the significantly lower survival rates in conspecific neighbourhoods provided evidence for the self-thinning effect on white spruce, which is consistent with the results are shown in Table 2.1. This result is same as the study in the northwest America (Cortini et al., 2017). However, self-thinning was less detectable for most deciduous species in the plot. There was inconspicuous evidence of intra-specific competition among aspen, as a large percentage of aspen mortality occurred in inter-specific neighbourhoods, as shown in Table 2.1. The results of spatial pattern analyses also supported a lack of conspecific density dependence for aspen, because there was no obvious change toward a more regular spatial pattern for surviving aspen trees. In contrast, aspens were undergoing greater inter-specific competition during the 5-year interval, as indicated by the significant repulsive pattern with birch, white spruce, and other deciduous trees (Fig. 2.4). Results from neighbourhood analysis also showed that the density effect of birch and white spruce had a significant negative effect on the survival of aspen. The mortality rate of birch was lowest among all species, and most of the dead birches were caused by intra-mortality (Table 2.1). Although the spatial pattern of birch was not significantly changed due to its mortality, my neighbourhood analysis provided other evidence to support a great effect of intra-specific competition (Fig. 2.4). The survival rate of birch was significantly lower under the stem density effects of itself. The bivariate analysis showed a significantly repulsive pattern between birch and other species, particularly for aspen

and white spruce. My neighbourhood analysis showed consistent results for the effects of the intra-specific competition effect on the survival of birch, which was reduced significantly due to density effects from aspen and white spruce. The negative density effect from other deciduous trees and other shrubs on the survival of birch was also significant, which is consistent with the marginal spatial repulsive pattern between birch and other deciduous trees and other shrubs. A large portion of other deciduous trees and other shrubs died during the 5-year survey period. However, the negative density-dependent effects from those species only slightly lowered the survival rate of the dominant species (Fig. 2.7), while the survival rate of other deciduous trees was strongly influenced by the dominant species (Fig. 2.4). Other shrubs were undergoing strong intra-specific competition (Table 2.1) and suppression effects that mainly arose from white spruce and its shade intolerance. For spruce, conspecific competition is widely shown to have stronger effects on survival and growth than interspecific (Stadt et al. 2007), this has often been attributed to stronger effects of spruce on light levels (Filipescu and Comeau, 2007).

Although the overall results from the spatial pattern and neighbourhood analysis showed consistency and supported density dependency, a few unexpected spatial patterns that contradicted the evidence of the density-dependent effect occurred. For example, patterns of all surviving trees shifted towards more aggregated patterns at small scales, and surviving trees had a denser initial neighbourhood than dead trees for all species pooled together (Figs. 2.2 and 2.3). Further, the surviving seedlings (particularly for white spruce) became more clustered in the post-mortality pattern. The unexpected seedling patterns could be explained by the possible confounding effect of habitat preference and seed dispersal limits, as recruits were more likely to grow under the open canopy, leading to a spatially aggregated pattern (Pielou 1960; Chapin et al., 1989; Wilson 1991; Duncan 1995; Bagchi et al., 2011). Failing to account for potential confounding effects on the stand might also lead to an incorrect result. Therefore, I suggest that measuring topographic data is necessary for future inventory work on the George Lake sampling plot.

Neighbourhood analysis provided more information on the neighbourhood density-dependent effects on tree survival as it is based on individual models of tree survival and incorporates species basal areas as neighbourhood variables (Hubbell and Foster, 1986; Hubbell et al., 2001), which allows us to represent competition more precisely. The results from

neighbourhood analysis suggested strong interspecific competition between the pioneer species (birch and aspen) and late-seral species (white spruce) over small scales, as expected from interspecific competition. As white spruce is shade tolerant, it can grow under the dense canopy whereas shade intolerant species like aspen and birch can only recruit from canopy gaps. The results from neighbourhood analysis indicate the density effect of white spruce reduced the survival odds ratios for aspen and birch more than the opposite effect from white spruce (Fig. 3.2 A-C). Spatial pattern analysis shows a similar result, in which a strong negative spatial association was present between white spruce and deciduous species including aspen, birch, other deciduous, and other shrubs. Stadt et al 2007 and Cortini et al 2017 also indicate that spruce is a stronger competitor than aspen. Intraspecific competitive effects on the survival of the late-successional species white spruce showed a similar correlation with conspecific density dependence, as shown in spatial analysis.

Through the seedling-adult association patterns, adult white spruce was found to be separated from seedling birch and other deciduous, which corresponded to the reduction of the survival rate for birch under the density effects of white spruce. Contrary to expectation, the results showed no significant repulsion patterns for conspecific seedlings and adult trees. This scenario is inconsistent with the Janzen–Connell hypothesis, which considers conspecific adults to constrain recruitment within the vicinity (Janzen 1970, Connell 1971). This suggests that the negative density dependence from the conspecific parent trees was not strong enough to kill the seedlings, and most seedlings were tending to be suppressed by heterospecific adults in boreal forests.

2.5 Conclusion

This study confirmed the importance of both inter- and intraspecific density-dependent effects in regulating mature boreal forest structures. It was shown that intra-specific competition was an important process in regulating the distribution of late-successional species (white spruce). Furthermore, the analysis suggested that interspecific competition plays an important role in species turnover during the boreal forest succession, including strong interspecific competition between pioneer and late-successional species, negative density dependence between two shade intolerant dominant species (aspen and birch), and negative spatial association between seedling birches and adult white spruce.

Chapter 3 A neighbourhood analysis of the competition effect on tree growth in a boreal mixedwood forest in Alberta

3.1 Introduction

Tree competition is an important process driving long-term forest dynamics and shaping forest community structures (Barnes et al., 1998; Harper, 1977; He and Duncan, 2000; Pacala et al., 1996; Zhang et al., 2015). Understanding the competitive interactions among boreal forest trees is important to understanding boreal forest community structure and dynamics, and to the development of sustainable management of boreal forest. Neighbourhood competition has potentially dramatic effects on the growth and survival of adjacent trees. Competition primarily reduces neighbouring tree growth and can cause tree death during successional processes. If the effect of competition is not great enough to cause neighbourhood tree mortality, it could cause reduction in tree growth. Understanding how neighbourhood competition affects tree growth is therefore necessary for predicting and understanding the development of mixedwood boreal forests.

Competition is difficult to measure due to its complex underlying mechanisms. To better quantify the effect of competition, forest ecologists have developed approaches that essentially reflect the mechanistic links between the characteristics of neighbouring trees and the strength of competition (Coates et al., 2009; Larocque, 2002). Therefore, a series of competition indices have been developed to quantify competitive effects on the survival and growth of individual trees (Hegyi, 1974; Martin-Ek, 1984; Tomé and Burkhart, 1989; Holmes and Reed, 1991; Wykoff et al., 1982; De Luis et al., 1998; Reineke's, 1933), with each competition index based on an explicit assumption of the competitive relationship between neighbouring trees and the focal tree. Most of the traditional competition indices can be grouped into either non-spatially explicit (distance-independent) or spatially explicit (distance-dependent), which respectively assume that competition intensity is not dependent or dependent on the spatial configuration of

neighbouring trees. A commonly used non-spatially explicit index, basal area (BA), was found the best index in growth models of white fir in Northern California (Biging and Dobbertin, 1995). However, BA did not perform well in predicting tree growth for the mixed conifers species in Northern California (Biging and Dobbertin, 1992). A similar index, basal area of large trees (BAL), assumes asymmetric competition in which neighbours only have competitive effects if the size of the target tree is smaller. The traditional spatially explicit indices usually represent competition as a function of the size of, and the distance to, neighbouring trees (e.g., Hegyi, 1974; Lorimer, 1983; Biging and Dobbertin, 1992, 1995; Wimberly and Bare, 1996; Vettenranta, 1999; Berger and Hildenbrandt, 2000). Most of these indices do not differentiate competitive effects among species. Canham et al. (2004) used a neighbourhood competition index (NCI) which allowed estimation of the relative competitive effects of neighbourhood species, separately and used a scaling effect for size and distance from neighbours of target trees that contrasted with traditional competition indices which set these parameters arbitrarily.

Comparison of these competition indices regarding their effectiveness as predictors in individual tree growth models has been conducted for many tree species and forests (Biging and Dobbertin, 1992, 1995; Canham et al., 2004; Contreras et al., 2011; Stadt et al., 2007). No single type of competition index has been found to be the “best” (Contreras et al., 2011), as their performance depends on many conditions, e.g., species composition, stand age, and habitat heterogeneity. Some argue that model performance of the distance-dependent approach is generally stronger than the distance-independent approach in mixed-species, uneven-aged forest stands, as these models reflect spatially explicit variations in the strength of competition (Contreras et al., 2011; Canham et al., 2004). Some previous studies (Stadt et al., 2007; Filipescu and Comeau, 2007) showed that simple competition indices based on density are limited in their ability to predict tree growth in boreal mixedwoods, while distance-dependent competition indices were more superior in the predictive abilities.

In forests with a more complex structure, competition varies in different habitat conditions, and individual-based, spatially explicit models appear to be a more powerful tool for predicting the performance of a tree by capturing these competitive interactions within a neighbourhood. A widely applicable approach has been to use neighbourhood analysis of the growth and survival of an individual as a function of the distribution and abundance of its

neighbours (Uriarte et al., 2004 a, b; Canham et al., 2004), measuring competition using a neighbourhood competition index (NCI). However, it is unknown whether NCI is a superior measure of competition compared with other commonly used indices.

Determining a proper neighbourhood competition radius is essential to develop a more accurate growth model. Most previous studies have considered that neighbouring trees are within a circle with a fixed radius centred on the subject tree (usually spanning from 10 to 20 m). Canham et al. (2004) used a parameter as a fraction of 15 m to estimate the maximum radius of the neighbourhood of the target tree. Their analysis showed that the focal species hemlock and redcedar responded to neighbours within distances from 8 m to 13 m, respectively. However, it is still unclear whether competitive effects between boreal tree species occur within a certain distance, and what maximum distance between two trees can produce a competitive effect.

There is a difference when calculating competition indices with a condition imposed, such as excluding the neighbours with a smaller size than the focal tree. For example, the competition index of BA was superior to BAL in growth modelling of white fir (Biging and Dobbertin, 1995). Similarly, the growth model of spruce was better predicted using equations incorporating BA than BAL (Stadt et al., 2007). However, BAL showed a better performance in modelling the growth of birch, poplar, and pine in mature boreal mixed forests (Stadt et al., 2007). An angle-based competition index developed by Rouvinen and Kuuluvainen (1997) also showed the growth model that combined the index including a size threshold had a higher correlation coefficient value than those without size thresholds (Shi and Zhang, 2003). But the results from Filipescu and Comeau (2007) showed that the competition index BA performed poorly in the ability to predict growth of spruce species in boreal mixedwood area.

The strength of competition also depends on the competing species. Many previous studies have demonstrated that competing species have distinct per capita effects on subject species and support the existence of competitive hierarchies among forest species (Canham et al., 2004; Uriarte et al., 2004; Papaik et al., 2006). Some have suggested that these competition hierarchies would be reflected by differences in the relative abundance of species (Howard & Goldberg, 2001). Dominant species usually have either the strongest competitive ability or minimal competitive response to neighbours (Goldberg, 1990; Goldberg & Landa, 1991).

However, some have argued that hierarchies of interspecific competitive abilities are not the sole factor explaining the species' relative abundance in plant communities (Hubbell et al., 2001), other factors such as soil nutrients, soil moisture, treefall gaps can also affect the growth or survival of different species. Therefore, it is necessary to consider species-specific competitive effects in the model and compare the results of modelling and empirical observations of forest species compositions.

In this study, I developed an extension of a spatially explicit tree competition model from previous studies (Canham et al., 2004, Uriarte et al., 2004a, b) to analyze tree competition within a 1-ha sample plot in a mature, mixedwood boreal forest in Alberta. The model allows estimation of individual tree growth of a given species as a function of the maximum potential tree growth and the magnitude of the competitive effect from neighbouring trees on target tree growth. Moreover, by incorporating the distinct parameters for each neighbouring species, this model allows estimation of species-specific competitive effects on the target species.

The objectives of this study were: (i) Compare the competition indices shown in Table 3.2 and identify the “best” index for predicting tree growth for each target species in a 1-ha sample boreal forest plot; (ii) Determine the maximum distance of detectable competitive effect between competing trees and determine the tree size competition threshold for each of the dominant species; (iii) Empirically estimate the strength of intra- and interspecific competitive effects on target tree growth.

3.2 Material and methods

3.2.1 Study site and data collection

Field sampling was conducted in a mature, natural mixedwood permanent forest plot (1 ha area) located at the George Lake Field Station approximately 80 km northwest of the city of Edmonton in the province of Alberta, Canada (53°57'25.38"N, 114°7'27.52"W). This forest plot is in the transition zone between the aspen parkland and the western boreal forest (Rowe 1972) and includes several species of forest trees that are common in Central Alberta in one relatively small area. The forest surrounding the permanent plot comprises about 180 ha of continuous forest. In this forest region, hardwood species generally dominate sites during the first 30-40

years after fire, but gradually succeed to coniferous stands (Samoil, 1988). The permanent plot was established during the summer of 2010 by stem-mapping the distribution of all stems (alive and dead) greater than 1 cm in diameter at breast height (DBH). A second measurement was conducted in the fall of 2015. Species identity and DBH were recorded for each of the mapped stems in the plot. A total of 4318 trees were mapped in the plot, including 3308 (76.63%) trees alive at the time of first measurement (2010) and 2743 (63.52%) trees alive at the time of second measurement (2015). For growth modelling, I used data of live trees from the second measurement. Table 3.1 lists number of stems, mean DBH, and maximum DBH of each species from the second census. Due to their abundance, aspen, birch and white spruce were selected as subject tree species. All shrub species, including green alder (*Alnus crispa*), saskatoon berry (*Amelanchier alnifolia*), dogwood (*Cornus stolonifera*), hazelnut (*Corylus cornuta*), beaked willow (*Salix bebbiana*), balsam willow (*Salix pyrifolia*) and the remaining deciduous tree species of tamarack (*Larix laricina*) and balsam poplar (*Populus balsamifera*) were grouped as OS (other shrubs) and OD (other deciduous), respectively.

Table 3.1 A summary of total number of stems (No. stem), percentage of stems (% stem), mean and max diameter at breast height (DBH, cm), and mean annual diameter growth (dg, cm/year).

Species	No. stem	% stems	$\overline{\text{DBH}}$	Max DBH	$\overline{\text{dg}}$
Birch	1045	53.73%	6.52	48.5	0.18
Other shrubs (OS)	357	18.35%	3.94	5.1	0.1
Aspen	226	11.62%	12.14	45.1	0.23
White spruce	208	10.69%	19.04	20.2	0.18
Other deciduous (OD)	109	5.60%	12.04	59.6	0.26

3.2.2 Data analysis

3.2.2.1 A maximum-likelihood model of neighbourhood competition

I used data from the 1-ha sampling plot to develop and test a spatially explicit, maximum-likelihood neighbourhood model of target tree growth for three dominant target species on the site. The growth model assumes that each target tree has an average maximum potential growth rate, which is adjusted to account for the effect of initial size and crowding by neighbouring trees:

$$\widehat{dg} = f(dbh) * g(competition)$$

The effect of initial subject tree size on growth was indicated by $f(dbh)$, which assumes the maximal potential tree growth varied with the target tree size. I used a lognormal function based on theoretical and empirical evidence (Uritarte et al., 2004; Canham et al., 2006) for the shape of the size effect:

$$f(dbh) = M \times \exp\left(-\frac{1}{2} \left(\frac{\ln\left(\frac{dbh}{X_0}\right)}{X_b}\right)^2\right)$$

where M is the expected potential optimum growth that a tree can achieve with no competitive effect (measured in cm/year; can be visualized as the point at the peak of the lognormal shape), X_0 is the DBH (of target trees) at which the potential optimum growth occurs, and, X_b determines the breadth of the function. This functional form is flexible enough that for the effective range of trees, the shape can be monotonically increasing (i.e., when X_0 is very large) or decreasing (i.e., when X_0 is very small) or have a single “hump” and a skew to the left when X_0 is within the normal range of DBH.

The predicted growth of target trees was assumed to decline monotonically as the competition effect increases. In this study, I used a negative exponential function $g(ci)$ to describe the shape of the crowding effect, where ci represents the competition effect measured by a given competition index:

$$g(ci) = \exp\left(-C \times \frac{ci_i^D}{ci_{max}^D}\right)$$

where C and D are species-specific estimated parameters, ci_i is the chosen competition index for target tree i , and ci_{max} is the maximum value of the ci for all neighbour trees of the target tree. The use of ci_{max} standardizes the competition effect term and facilitates comparisons across species. Parameters C and D are the two inflection points of the function that defines the effect of competition on growth: parameter C defines the sharpness of the decline in growth due to an

increment in ci , whereas parameter D determines whether there is a threshold at which the decline in growth takes effect.

3.2.2.2 Neighbourhood competition effects as measured by competition indices

The analysis of neighbourhood competition in this study follows traditional distance-independent and distance-dependent analyses of competition, in which neighbourhood crowding effects are measured as a function of the sizes with or without distances (e.g., Bella 1971; Hegyi 1974; Lorimer 1983; Biging and Dobbertin 1995; Wimberly and Bare 1996; Wagner and Radosevich 1998; Vettenranta 1999; Berger and Hildenbrandt 2000; Canham et al., 2004; Uriarte et al., 2004a, b; Filipescu and Comeau 2007a,b; Stadt et al. 2007). A competition index basically assumes that negative effects from neighbouring competitors are increased with the neighbour's size and decline with the distance to the target trees. In this study, two distance-independent competition indices (that do not utilize spatial information explicitly in their formulation); and five distance-dependent indices (that incorporate distance between competing trees) were used as alternative indices to incorporate into the model (Table 3.2). The performance of each alternative model was compared to find out the most effective competition index, which was used in the following procedure on neighbourhood effect analysis.

Basal area (BA) combines both tree size and density of a stand. It basically assumes that greater living biomass leads to greater competition intensity (Dale et al., 1985). Lorimer's index(L) is a ratio of the sum of neighbouring DBH to the subject tree and assumes that the larger the subject tree size the smaller the competition stress from others.

For most distance-dependent indices, the value of competition indices increases with closer distances between competing trees, assuming inter-tree distance is a main factor affecting competition. Hegyi's index (H) is the sum of the ratio of neighbouring tree sizes to the focus tree size weighted by the distance between them (Hegyi, 1974). RK_{1-2} are indices calculating the sum of horizontal angles originating from the centre of the focal tree and spanning the diameter of each neighbour tree at breast height, where RK_2 assumes neighbourhood competition depends on the size ratio of subject tree and neighbour trees. The neighbourhood competition index (NCI) is a simple size- and distance-dependent index that is basically evaluated by the sum of neighbouring tree sizes weighted by distance, in which the effect of tree size and distance are

scaled by power parameters α and β , respectively (Canham et al., 2004; Uriarte et al., 2004). The scaling parameters in NCI were used to determine the shape of the effect of the DBH and distance to neighbours. However, whether the NCI incorporating scaling parameters performed universally better than the NCI without the scaling parameters is still unclear. Therefore, I used NCI₀ as a special case of NCI where all the scaling parameters are set as 1 to detect the effect of tree size and/or distance scaling by any values.

Table 3.2 Sources and mathematical formulas of competition indices. i represents i th subject tree, j indicates j th neighbouring tree, and s indicates s th neighbouring tree.

Competition Indices	Source	Equation
Distance-independent indices		
Basal area (BA)	(Biging & Dobbertin, 1995)	$\sum_{j=1}^n DBH_j^2 \times \pi/4$
Lorimer (L)	(Lorimer, 1983)	$\sum_{i \neq j} \frac{DBH_j}{DBH_i}$
Distance-dependent indices		
Hegyi (H)	(Hegyi, 1974)	$\sum_{i \neq j} \frac{DBH_j}{DBH_i \times dist_{ij}}$
RK ₁	(Rouvinen & Kuuluvainen, 1997)	$\sum_{i \neq j} \tan^{-1} \frac{DBH_j}{dist_{ij}}$
RK ₂	(Rouvinen & Kuuluvainen, 1997)	$\sum_{i \neq j} \frac{DBH_j}{DBH_i} \tan^{-1} \frac{DBH_j}{dist_{ij}}$
Neighbourhood competition index (NCI ₀)		$\sum_{i \neq j} \frac{DBH_j}{dist_{ij}}$
Neighbourhood competition index (NCI)	(Canham et al., 2004)	$\sum_{i \neq j} \frac{DBH_j^\alpha}{dist_{ij}^\beta}$

3.2.2.3 Species-specific parameter λ

In this analysis, the net effect of an individual neighbour is multiplied by a species-specific scalar λ that ranges from zero to one and allows for differences among species in their competitive effects on a target tree species. Then, for $i = 1, \dots, s$ species and $j = 1, \dots, n$ neighbours of species s within a maximum radius (R) of the target tree, a competition index (ci) specifying the net competitive effect of the neighbours on the target tree is given by

$$ci_s = \sum_{i=1}^s \sum_{j=1}^n \lambda_i \times ci_{ij}$$

3.2.2.4 Selecting appropriate neighbouring trees

I calculated all competition indices used in this study by summing the effects of all neighbouring trees within a specific radius of the focal tree. Some previous studies used a fraction of a specified initial maximum radius usually ranging from 15 to 20 m (Canham et al., 2004; Uriarte et al., 2004) to specify the neighbourhood radius. In this analysis, I used a parameter R representing a numeric value of the neighbourhood radius to select the possible competitors. Furthermore, I used an additional parameter X representing a size ratio of the focal tree to a neighbour to select the possible competitors.

Effective neighbourhood radius (R)

An effective neighbourhood searching radius (R) was incorporated in every model tested in this study. It was defined as the maximum searching radius surrounding subject trees that allows us to select all trees within this radius.

$$dist_{ij} \leq R$$

Growth models incorporating R , $G_1(size, ci, R, \lambda_j)$ were evaluated firstly.

Effective neighbourhood size ratio (X)

I also used the effective neighbourhood size ratio (X) to filter neighbour trees that are assumed not large enough to produce competition effects on subject trees. In other word, this parameter allows us to select those neighbouring trees with a diameter larger than X times of the subject tree's diameter.

$$DBH_i \leq X * DBH_j$$

Following the evaluation of growth models $G_1(size, ci, R, \lambda_j)$, growth models estimating both R and X , $G_2(size, ci, R, X, \lambda_j)$ were then fitted. Through the comparison of both model G_1

and G_2 , we can see whether the prediction ability improved by adding those ‘filtering parameters’ into the model.

3.2.2.5 Edge effects correction

Trees near the plot border can have neighbouring trees located outside the plot. This study used the toroidal method (Yamada and Rogerson, 2003) to reduce the influence of the possible bias caused by edge effect.

3.2.2.6 Likelihood estimation, hypothesis testing, and comparison of alternative models

I used simulated annealing, a global optimization procedure (Goffe et al., 1994), to determine the parameters that maximize the log likelihood for the observed data using C++ and R programmes written specifically for this study. I ran each algorithm for at least 10^7 iterations and considered it to have converged if it did not change in likelihood after the initial 10^7 iterations. In general, models with a larger number of parameters converged after a greater number of iterations than simpler models. Table 3.3 provides a complete list of all model parameters with initial values and ranges. Parameter ranges were established to provide maximum flexibility while staying within biologically realistic values.

Table 3.3 List and range of parameters included in growth model.

Parameters	Range
Maximum potential growth (M)	0-2
Size (X_0)	0-100
Variance (X_b)	0-10
Coefficient of neighbourhood effect (C)	0-10
Coefficient of neighbourhood effect (D)	0-5
Effect of neighbour size on target growth (α)	0-4
Effect of neighbour size on target growth (β)	0-4
Effective neighbourhood radius (R)	0-20
Effective neighbourhood size ratio (X)	0-3

Alternate models were compared using Akaike’s Information Criterion (AIC_c) corrected for small sample size:

$$AIC_c = -2 \log(\text{likelihood}) + 2k \left(\frac{n}{n - k - 1} \right)$$

where n is the total number of observations and k is the number of estimated parameters in the model. The best candidate model is the one with the lowest AIC_c . The square of coefficient of correlation (R^2) between observed tree diameter annual increment and predicted increment was used to measure goodness of fit.

I used asymptotic support limits for each parameter by holding all other parameters at their maximum likelihood values, systematically increasing and decreasing the parameter of interest until the likelihood changed by two units. A two-unit support interval is roughly equivalent to a 95% support limit defined using a likelihood ratio test (Hilborn and Mangel 1997).

Alternate models were compared using likelihood ratio tests (Hilborn and Mangel 1997), with degrees of freedom equal to the difference in the number of parameters between the two models. This method tests whether the improvement (if any) in likelihood from the inclusion of additional parameters in the model results in a significant improvement in the likelihood of the resulting model.

3.3 Results

3.3.1 Likelihood and goodness of fit of alternate models and a comparison of competition indices

I first estimated maximum likelihood parameter values for a series of alternative models without the parameter X (effective neighborhood size ratio, i.e., size threshold) in Table 3.2 and then estimated the values for those models incorporating the parameter X . As shown in Table 3.3 and Table 3.4, the most effective competition index for aspen is RK1, an index that depends on horizontal angles scaling to neighbour trees, which declines as the distance to neighbour increases or the neighbour size decreases. Adding the parameter X into the same model did not improve the model likelihood for aspen. However, incorporating the parameter X improves the model performance for both white spruce and birch. The neighbourhood competition index (NCI) was the most effective index in modelling growth of birch, and RK1 performed even better than NCI in modelling tree growth of white spruce.

The models produced unbiased estimates of diameter growth, with a 1:1 relationship between predicted and observed and symmetrically distributed residuals (Fig 3.1). The percentage of variance explained by the best models ranged from 20% to 29%. Neither the likelihood estimation methods that I used to fit the models nor the likelihood ratio statistics that I used to compare the models are particularly sensitive to heteroscedasticity, so I did not attempt to transform the growth rates to homogenize the variance before fitting the models (Canham et al., 2004).

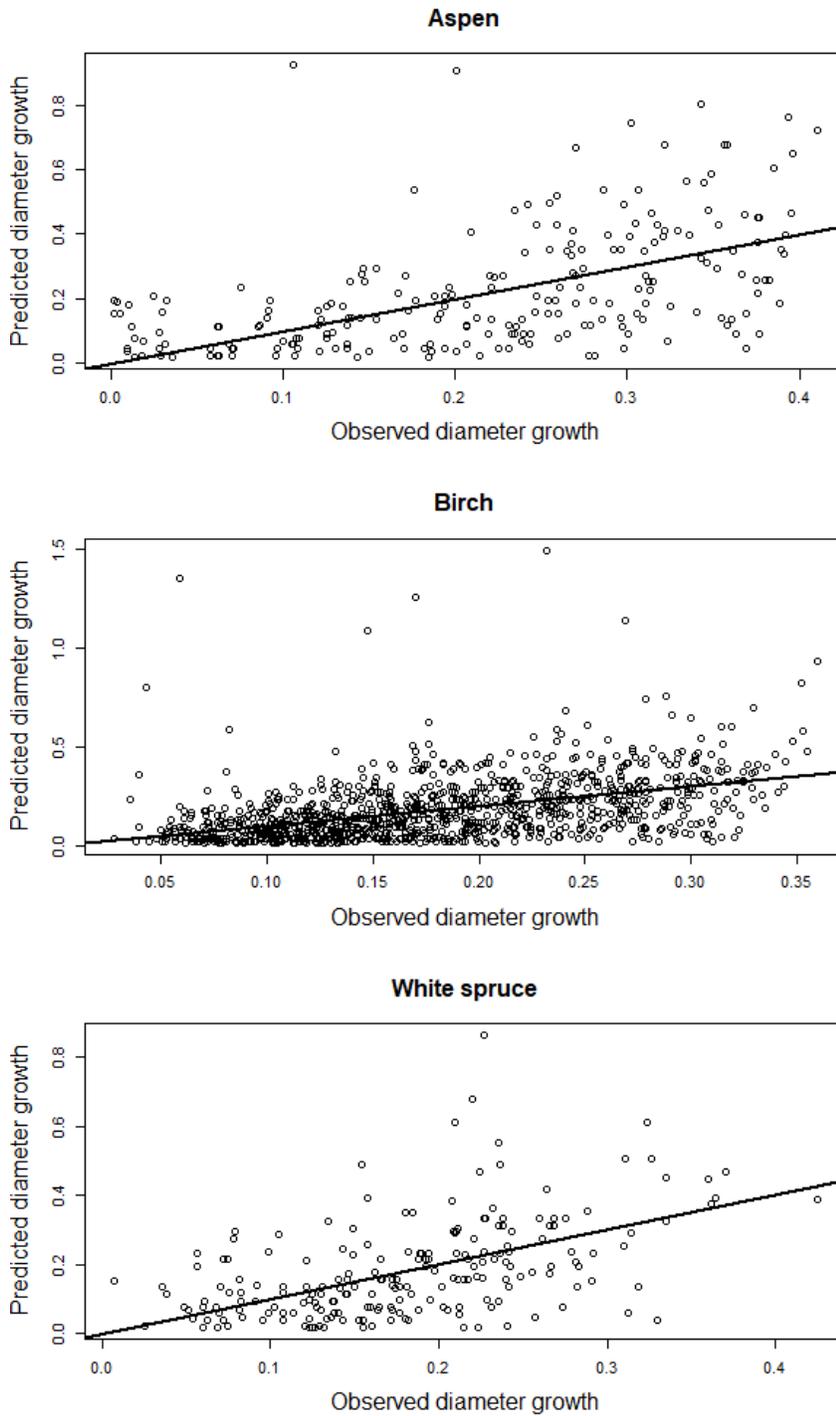
Table 3.3 AICc values and R2 for alternate models of G₁ (as mentioned in section 3.2.2.4).
The model with the lowest AIC_c is highlighted in bold.

Distance dependence	Competition index	Number of parameters	Aspen		Birch		White spruce	
			AIC _c	R ²	AIC _c	R ²	AIC _c	R ²
Distance independent	BA	12	-157.25	0.26	-1035.67	0.15	-244.67	0.21
	L	12	-161.55	0.28	-1037.24	0.15	-222.42	0.13
Distance dependent	H	12	-158.78	0.27	-1021.81	0.14	-216.55	0.10
	RK ₁	12	-168.41	0.29	-1009.24	0.13	-221.11	0.11
	RK ₂	12	-161.47	0.28	-1047.98	0.16	-228.72	0.17
	NCI ₀	12	-159.13	0.27	-1029.53	0.15	-232.31	0.16
	NCI	14	-162.36	0.29	-1048.9	0.17	-247.64	0.23

Table 3.4 AICc values and R2 for alternate models of G₂ (as mentioned in section 3.2.2.4).
The model with the lowest AIC_c is highlighted in bold.

Distance dependence	Competition index	Number of parameters	Aspen		Birch		White spruce	
			AIC _c	R ²	AIC _c	R ²	AIC _c	R ²
Distance independent	BA	13	-157.79	0.27	-1035.37	0.15	-249.96	0.24
	L	13	-159.09	0.27	-1061.97	0.18	-222.09	0.13
Distance dependent	H	13	-160.11	0.27	-1033.21	0.16	-223.43	0.14
	RK ₁	13	-159.68	0.27	-1079.81	0.19	-259.27	0.27
	RK ₂	13	-157.45	0.26	-1069.54	0.19	-234.31	0.20
	NCI ₀	13	-157.02	0.26	-1071.28	0.18	-249.02	0.23
	NCI	15	-152.56	0.27	-1096.43	0.20	-256.81	0.28

Figure 3.1 Goodness of fit of the best-fitting models for aspen, birch, and white spruce. Lines are a 1:1 relationship between predicted and observed radial growth.



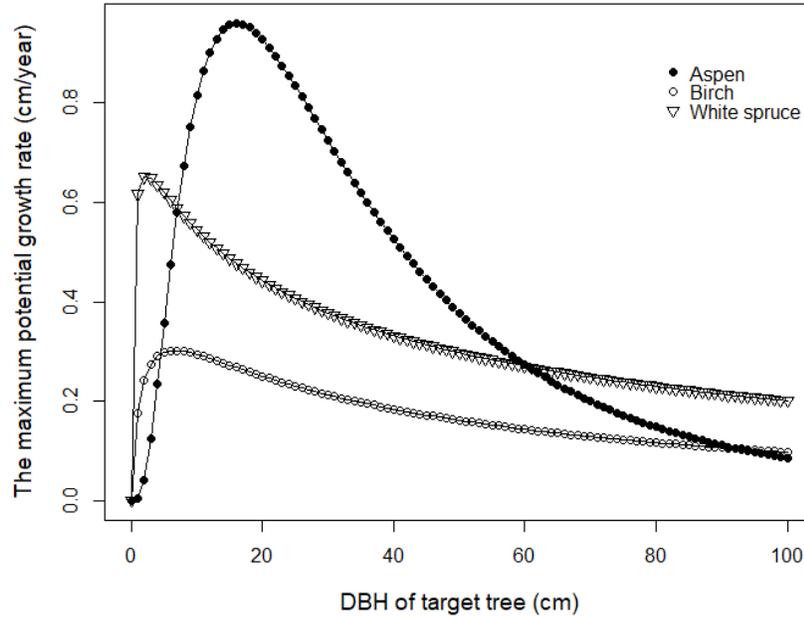
3.3.2 Effects of DBH on potential diameter growth

I estimated the average potential diameter growth of a tree (in the absence of any competitors) as a function of tree initial DBH for three target species. Fig. 3.2 shows shapes of relationship that are controlled by three of the estimated parameters in Table 3.5: M , which determines the height of the peak; X_0 , which determines the DBH at which peak growth occurs; and X_b , which determines the function breadth (Uriarte et al., 2004). The optimum diameter growth of aspen is predicted to be the highest ($M = 0.96$ cm/year, Table 3.6) among all three species, and it occurs at a relatively large tree size ($X_0 = 16.09$ cm) and then declines rapidly as size increases ($X_b = 0.83$). White spruce is predicted to achieve maximum annual growth at a relatively small size ($X_0 = 2.28$ cm) with the second highest growth rate ($M = 0.62$ cm/year). Afterwards, it declines rapidly as tree size increases ($X_b = 2.46$). The maximum growth ($M = 0.3$ cm/year) of birch occurs at a larger size ($X_0 = 6.60$ cm) than white spruce, and rapidly declines when tree size increases ($X_b = 1.81$).

Table 3.5 Maximum likelihood parameter estimates and 95% support interval in parentheses for the best-fitting models for each target species. λ_i indicates the species-specific effect of neighbours, *asp*=aspen, *bir*=birch, *ws*= white spruce, *OS* = deciduous shrubs, *OD*=other deciduous.

Parameter	Aspen	Birch	White spruce
M	0.96(0.88-1.05)	0.30(0.29-0.32)	0.62(0.60-0.71)
X_0	16.09(14.72-17.59)	6.60(5.25 -8.27)	2.28(1.78-2.94)
X_b	0.83(0.75-0.92)	1.81(1.49-2.37)	2.46(2.23-2.74)
C	1.57(1.42-1.74)	2.00(1.76-2.26)	4.53(4.08-5.05)
D	1.76(1.46-2.06)	0.73(0.66-0.80)	1.00(0.93-1.07)
R	17.08(16.54-17.67)	3.36(3.34-3.54)	8.43(8.33-8.57)
X	NA	1.36(1.35-1.37)	0.77(0.75-0.81)
λ_{asp}	0.07(0.01-0.15)	0.89(0.31-1.00)	0.26(0.06-0.52)
λ_{bir}	1.00(0.77-1.00)	0.79(0.24-1.00)	0.71(0.60-0.84)
λ_{ws}	0.37(0.27-0.45)	0.98(0.62-1.00)	0.07(0.02-0.15)
λ_{OS}	0.28(0.14-0.52)	0.00(0.00-0.24)	0.79(0.68-0.91)
λ_{OD}	0.00(0.00-0.21)	0.66(0.10-1.00)	0.72(0.36-1.00)
σ	0.16(0.14-0.17)	0.14(0.14-0.15)	0.12(0.11-0.13)
α	NA	0.28(0.05-0.50)	NA
β	NA	0.27(0.02-0.49)	NA

Figure 3.2 Estimated potential diameter growth for aspen, birch and white spruce as a function of tree initial DBH.



3.3.3 Effects of neighbouring tree distance and size on degree of crowding

The competition indices in this analysis sum the effects of all competitors in the neighbourhood, which is defined as a circle with an estimated radius (R) surrounding the focal trees (Table 3.5). Our analysis shows that the growth of subject aspen responded to neighbours within a distance of 17.08 m. The effective neighbourhood radii of birch and white spruce are much smaller (approx. 3.4 m and 8.1 m, respectively).

Previous studies usually use two scaling parameters (α and β) of the neighbourhood competition index (NCI) to determine the effect of distance between neighbours and subject trees and the effect of neighbour size on the same index. Although results from Table 3.4 and Table 3.5 showed that neither NCI nor NCI_0 is the best competition index for all species, comparing these two indices revealed that adding the scaling parameters can improve the model likelihood. Through comparing the growth model G_2 of three species fitted using NCI in Table 3.5, I found some variation in the effect controlled by the two scaling parameters for different species (Table 3.6; Fig 3.3; Fig 3.4). For instance, the effects of neighbours on the growth of aspen declined less

than linearly with distance to neighbours ($\beta = 0.74$), while the effect shows a much smaller decline with distance to neighbours for white spruce ($\beta = 0.32$) and for birch ($\beta = 0.27$). The competition effects of neighbours were scaled to the DBH for white spruce ($\alpha = 0.96$), while the effects were scaled to less than half of DBH for aspen and birch ($\alpha = 0.22$ and 0.28 respectively) (Fig 3.3 and Fig 3.4).

Table 3.6 Maximum likelihood parameter estimates and 95% support interval in parentheses for models using NCI for each target species. λ_i indicates the species-specific effect of neighbours, *asp*=aspen, *bir*=birch, *ws*= white spruce, *OS* = deciduous shrubs, *OD*=other deciduous.

Parameter	Aspen	Birch	White spruce
<i>M</i>	0.43(0.39-0.47)	0.30(0.29-0.32)	0.39(0.35-0.42)
<i>X₀</i>	15.64(14.31-17.03)	6.60(5.25 -8.27)	4.10(2.96-5.81)
<i>X_b</i>	0.80(0.71-0.89)	1.81(1.49-2.37)	2.47(2.11-2.98)
<i>C</i>	2.43(1.11-4.31)	2.00(1.76-2.26)	4.62(3.85-5.54)
<i>D</i>	0.84(0.61-1.28)	0.73(0.66-0.80)	1.12(1.02-1.24)
<i>R</i>	1.53(1.41-1.62)	3.36(3.34-3.54)	8.54(8.28-8.91)
<i>X</i>	0.47(0.45-0.54)	1.36(1.35-1.37)	1.01(1.00-1.04)
λ_{asp}	0.00(0.00-0.03)	0.89(0.31-1.00)	0.08(0.00-0.23)
λ_{bir}	0.23(0.15-1.00)	0.79(0.24-1.00)	0.38(0.28-0.49)
λ_{ws}	0.81(0.25-0.97)	0.98(0.62-1.00)	0.09(0.02-0.18)
λ_{OS}	0.71(0.35-1.00)	0.00(0.00-0.24)	0.91(0.73-1.00)
λ_{OD}	0.00(0.00-0.33)	0.66(0.10-1.00)	0.59(0.29-1.00)
σ	0.16(0.14-0.18)	0.14(0.14-0.15)	0.12(0.11-0.13)
α	0.22(0.00-0.84)	0.28(0.05-0.50)	0.96(0.79-1.00)
β	0.74(0.34-1.29)	0.27(0.02-0.49)	0.32(0.00-0.67)

Figure 3.3 Predicted shape of the effect of neighbour size on NCI using growth model G_1 and parameters reported in Table 3.6.

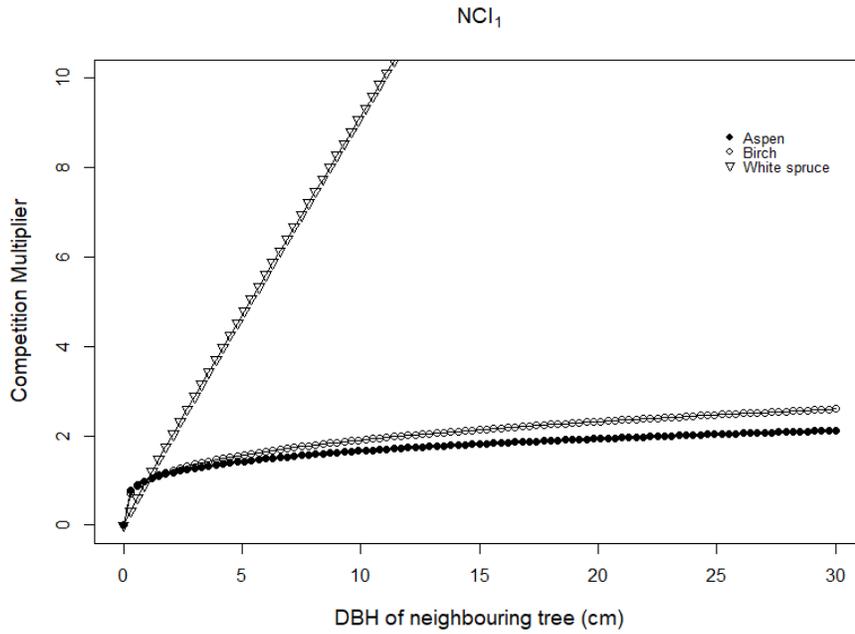
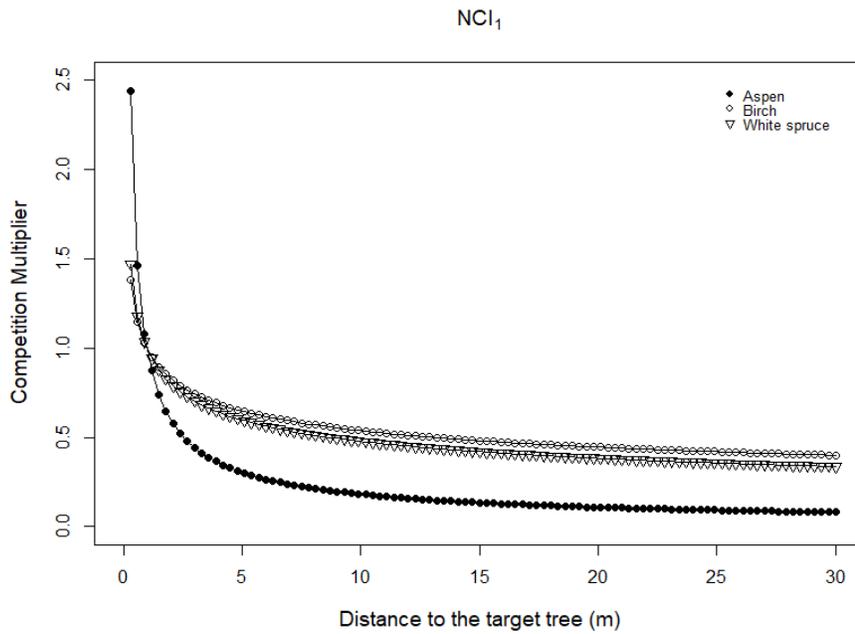


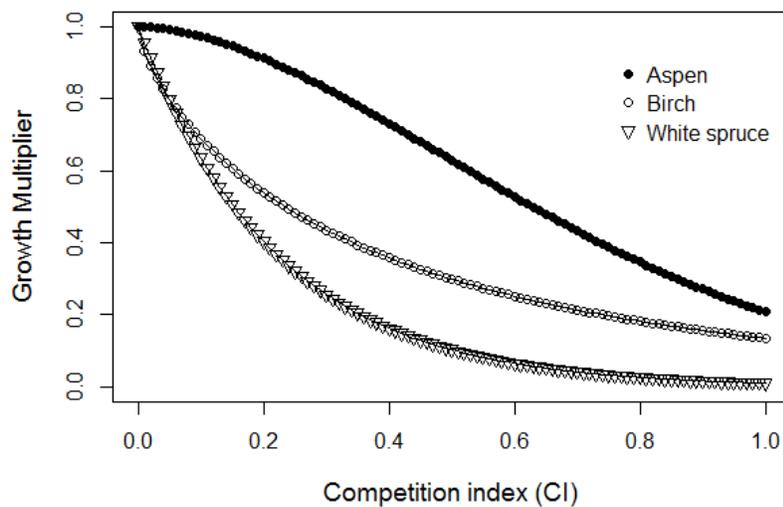
Figure 3.4 Predicted shape of the effect of neighbour distance to the target tree on NCI using growth model G_1 and parameters reported in Table 3.6.



3.3.4 Relative effects of crowding on tree growth

The magnitudes of the C and D parameters (Table 3.5) provide an approximate measure of the amount of reduction in growth due to an incremental increase in crowding (CI). The parameter C determines the steepness of the decline in growth with an increase in CI , while D determines the degree of crowding at which the decline becomes more marked (Fig. 3.3). For white spruce and birch, the growth declined as an exponential function of the competition index (D is close to 1), while white spruce declined more sharply than birch ($C = 4.53$). Growth of aspen initially declined slowly as an exponential function of crowding ($D = 1.76$), and then dropped off exponentially with a slower rate ($C = 1.57$).

Figure 3.5 Predicted decline in growth as a function of Neighbourhood Competition Index (NCI) and parameters reported in Table 3.5

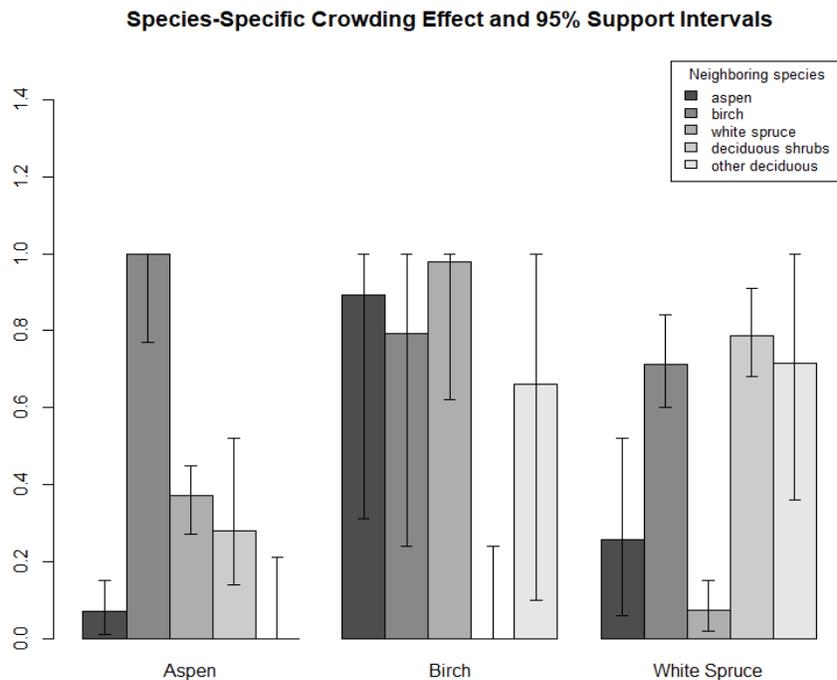


3.3.5 Interspecific versus intraspecific competition

As measured by λ (the parameter calibrating species-specific competitive effects, with a higher value corresponding to a stronger competitive effect), my analysis shows apparent variation in the crowding effects of inter- and intraspecies, depending on the identity of both the focal tree and neighbours (Table 3.5; Fig 3.4). In general, the conspecific crowding effect on growth of birch was highest among all species, whereas the conspecific crowding effect on

growth of aspen and white spruce was negligible (λ close to zero). I also detected a strong interspecific crowding effect between birch and aspen and between birch and white spruce (λ close to 1). Aspen was undergoing significantly greater interspecific competition than intraspecific competition. The greatest competitive effect on growth of aspen was produced by birch (λ close to 1), while the suppression effect from white spruce or shrubs was much lower. The interspecific competition effect on birch was equivalent to the intraspecific competition; both aspen and white spruce produce a large competitive effect on growth of birch. For white spruce, the conspecific suppression on growth was almost negligible while the crowding effect from deciduous species was greater on its growth. The crowding effect from shrubs on growth of the deciduous species (aspen and birch) was negligible but shrubs had much greater on growth of coniferous (white spruce). For white spruce and birch, the crowding effect of other deciduous species on their growth was much larger than on growth of aspen. Small sample sizes resulted in very large confidence intervals on the estimates of λ . The results showed generally greater interspecific competition between those dominant species than intraspecific competition.

Figure 3.6 Comparison of species-specific competition effect (the parameter λ) on subject tree growth and 95% support intervals.



3.4 Discussion

The likelihood method used in this study shows a great potential for modelling tree growth in the boreal forest. The goodness of fit of the growth model (R^2) varied from 20% to 27% for the target species examined, suggesting over 20% of the variation can be explained by the fitted model. The result is not as high as results obtained by studies in tropical forests (Uriarte et al., 2004). Additionally, there was a great difference between some fitted parameters (e.g. R , λ) of selected best-fitting competition index and the alternative competition index NCI (Table 3.5 and 3.6), indicating those estimated parameters could lack of reliability and further variation among the original data could be ignored. However, Unlike the traditional regression method applied in modelling tree growth, the estimated parameters and associated 95% support limits in this analysis showed greater flexibility and allowed the testing of hypotheses about the nature of the competitive interactions (Canham et al., 2004). In this study, the best distance-dependent competition index was better in modelling growth than the best distance-independent competition index for each species. For birch, the neighbourhood competition index (NCI) appeared to be the most effective index. However, for both aspen and white spruce, my analysis showed a marginally higher effectiveness of a competition index based on the horizontal angles scaling to neighbours (RK_1). Although NCI is not always the best-performing index, I found that the scaling parameters it incorporated significantly improved the model likelihood through comparing it with NCI_0 (Tables 3.4 and 3.5), indicating that the competitive effects responded differently to the distance and neighbour size for each species. My study showed an improvement in predictive ability by using RK_1 in modelling tree growth, suggesting the NCI index that most previous studies used in neighbourhood analysis (Canham et al., 2004, Uriarte et al., 2004a, b; Canham et al., 2006, Coates et al., 2009; Gomez-aparicio et al. 2011; Buechling et al., 2017) could be replaced by RK_1 to improve the model performance.

Incorporating the thresholds of tree size ratio (X) into the model improved the model likelihood for both birch and white spruce, suggesting a better way for future works on tree growth modeling. In contrast, for aspen, results from Table 3.3 and Table 3.4 showed that adding the size threshold (parameter X) even decreased the likelihood of models with RK_{1-2} and NCI_{0-1} , which may be because aspen was not sensitive to neighbour size. Similarly, results from Table 3.6 showed that the estimated value of α for aspen was close to 0.2, indicating that the

competition increased slowly with the DBH of aspen. Those results also suggested that birch was still more likely to be affected by larger neighbours and the scaling parameter needs to be further corrected in future work (e.g., setting those parameters to be species-specific). The effective neighbourhood distance is another case reflecting the flexibility of the likelihood approach. The results from Table 3.5 suggested that the maximum competition distance depends on the target species identity. For aspen, the effective neighbourhood distance was much longer than that of white spruce, followed by birch. In addition, no previous studies have ever estimated the effective neighbouring size. There were many evidences showed asymmetric interspecific density-dependence in boreal forests (He and Duncan, 2000; Thorpe et al., 2010; Luo and Chen, 2011), adding a neighbouring size threshold allows us to test the size-asymmetric competition hypothesis and estimate accurately the size ratio of target and neighbours.

As most studies of neighbourhood competition (Canham et al., 2004, Uriarte et al., 2004a, b; Canham et al., 2006, Coates et al., 2009; Gomez-aporicio et al. 2011; Buechling et al., 2017), this study assumes a maximum potential tree growth in the optimum condition (that is, without competitors and affected by no other stress), which is reduced by the effect of competition of neighbours. However, despite its importance, competition is not the only factor affecting tree growth. Other factors including soil, climate, pathogens and insects can affect tree growth increments. As a result, the pattern of scatter of predicted growth shown in Fig. 3.1 indicates that any of those confounding effect may contribute to the variance of the predicted growth value.

Through the model selection, the growth of shade-intolerant focal aspens was inhibited more by the shade-intolerant neighbour birches than by the shade-tolerant species white spruce, which may be because of the ecological proximity between aspen and birch. Previous studies in tropical forests also found that taxonomic proximity strengthens the interactions between neighbouring species (Connell et al. 1984; Hubbell et al. 1990; Peters 2003; Uriarte et al., 2004 b).

The results from estimated species-specific coefficient (λ) provided evidences of great variation in the strength of the competitive effects from different neighbourhood species on the target species. Other studies use similar methods in both tropical (Uriarte et al., 2004) and boreal (Canham et al. 2004) also showed striking variation among species. However, the interspecific competition effects are consistently strong on the growth of the target species, regardless which

the competitor species is. This suggests that the stand might be undergoing the process of species turnover, i.e. the stand would be gradually dominated by species that are highly competitive, as interspecific competition was considered as a vital mechanism driving species turnover during forest succession (Kneeshaw and Bergeron, 1998; Gray and He, 2009). The results also showed a dramatic asymmetry in the strength of interspecific competition between three dominant species. Crowding by birch has a strong per capita effect on all species, suggesting that the highly competitive ability of birch in competitive hierarchies. Crowding by aspen has a slight effect on white spruce, while the effect was very strong on birch, suggesting that interspecific competitive interactions were strong between deciduous species in the plot. Crowding by white spruce has a strong effect on birch but much less of an effect on aspen, suggesting the interspecific competition between coniferous and deciduous species was also important in this boreal plot. Although another similar study in mature boreal mixedwood forest showed the competitive ability of birch and white spruce were approximately same, and both of them are higher than aspen. It should be noted that the estimated coefficient may lack of reliability due to some confounding effect on the original data (e.g. the wind disturbance, insects outbreaks). The magnitude of interspecific competition effects among the three dominant species as indicated by the species-specific coefficient (λ) provides valuable information on the implications of forest management and development of silvicultural systems that optimize yield by managing for species (Coates et al. 2004; Comeau et al., 2005).

Chapter 4 Conclusions and Future Work

4.1 Overall conclusions

This thesis provided further demonstrations of the importance of competition in driving stand dynamics and structure of mixedwood boreal forests. Through investigating density-dependent effects on tree survival using second order spatial point-pattern analysis with statistical neighbourhood modelling in Chapter 2 and modelling individual tree growth using different competition indices in Chapter 3, I found generally consistent results. The main findings of this study are presented as follows:

Strong intraspecific competition effect on the survival of the late-successional species

White spruce, the only shade-tolerant, coniferous and late-successional species in the study plot, was shown to be under great pressure from conspecific tree density. More than half of the dead white spruce occurred in conspecific neighbourhoods, and the spatial pattern of surviving trees shifted toward more regular patterns due to self-thinning. Results from neighbourhood analysis of density effects on tree survival similarly showed a significantly lower survival rate under the effect of conspecific stem density of white spruce. However, in Chapter 3, the results from the analysis of competition effects on tree growth showed that the growth of white spruce was only slightly affected by intraspecific competition. Most dead white spruce were concentrated in the middle size class and fewer dead white spruce were seedlings (Fig. 2.1), suggesting that juvenile and adult white spruce were more likely to be affected by conspecific below-ground density dependence.

Interspecific competition and the competition hierarchies

The bivariate spatial pair correlation analysis showed a significant spatial repulsion between late-successional and pioneer species. Results of this analysis were similar to that from neighbourhood analysis, showing that the neighbourhood stem density of white spruce significantly reduced the survival probability of aspen and birch over small scales. However, the inverse effect was relatively less influential on the survival rate of white spruce, which showed a

stronger competition ability of late-successional than pioneer species. The neighbourhood analysis of tree growth showed similar results of a strong interspecific competition effect between coniferous and deciduous species on tree growth, while competitive hierarchies were not significantly detectable (Fig 3.5). This scenario is consistent with the usual species turnover path in boreal communities, in which coniferous species gradually replace the deciduous species in succession. In contrast to the assumption that more abundant species are more competitive, the species of the highest abundance (birch) in the sample plot did not show a superior competitive ability over white spruce. The evidence showed that the importance of intraspecific competition declined over succession for deciduous species, while it increased for coniferous species.

Prediction using multi-model inference

In Chapter 3, I compared a series of competition indices to find the “best” index for predicting tree growth. The result demonstrated that the most capable competition index is distance dependent and based on the sum of horizontal angles scaling from the focal tree to the diameter of neighbouring trees within the circle with the effective neighbourhood radius. The approach provided flexibility in finding the most effective ways to predict tree growth in a given stand. Moreover, by incorporating parameters like the effective neighbourhood radius and the species-specific competition parameters to the model, we can test specific hypotheses about the nature of competitive interactions. In Chapter 3, I found that the effective neighbourhood radius varies with the focal species and using the same competition index but excluding those neighbours smaller than the target works better for birch and white spruce. These results indicate competitive hierarchies and strong asymmetries in species interactions.

4.2 Future research

This study provided strong evidence that competition plays an essential role in driving boreal forest dynamics. However, there are some limitations of the approaches used in this study. One such limitation is due to the 1-ha plot sampling data lack of plot replications compared with other previous field studies (Getzin et al., 2008; Gray and He 2009; Zhang et al., 2009; Luo et al., 2012). I suggest using multi-plot sampling data in future research on tree competition in boreal forests to increase the robustness of the results produced from individual plots.

In addition, topographic and climate data were not included in the dataset. The importance of including topographic data in the individual tree model has been demonstrated by many forest ecologists, although the study plot is very flat and may not have the same degree of topographic variations as other studies. It is necessary to note that reductions on the growth of white spruce across Alberta was intensified during the recent drought condition from 2014 to 2015. Moreover, the potential role of insects and pathogens (e.g., forest tent caterpillar to aspen; spruce beetle and spruce budworm to white spruce) could be major drivers causing tree mortality and declining tree growth. Failing to consider the effects of topography and other factors could result in inaccurate results. It should be note that the remarkably high rates of mortality in Table 2.1, especially for white spruce, which is much greater than the reported long-term mortality of white spruce in plot networks across western Canada is <2% per year (Fig. 2 of Zhang et al. 2015; Fig. 2 of Luo and Chen 2013). The potential role of wind throw as a disturbance type may influence the interpretation of the effects of tree competition in this study. Also, the interaction of climate change and tree neighbourhood competition is likely to be a significant factor that influences tree growth and mortality and the forest community dynamics (Dwyer et al., 2010; Cortini et al. 2017). Incorporating the contributions of climate effects with the competition effect on tree growth and survival will be necessary for understanding the current and future boreal forest dynamics.

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Appendix

Figure A1 Univariate density-dependent mortality analysis for the change in living adult trees (DBH >15cm) pattern with random labeling null model. If the spatial pattern of living trees became more regular due to density-dependent mortality, the test statistic $g_{l,l}(r) - g_{d+l,d+l}(r) < 0$. The solid lines showed observed values of test statistics. Approximately 95% simulation envelopes (grey areas) were constructed using 99 times simulations of the null model. The analysis was conducted for all species together and five species groups Aspen, Birch, White spruce, OD (other deciduous trees), OS (other shrubs) separately.

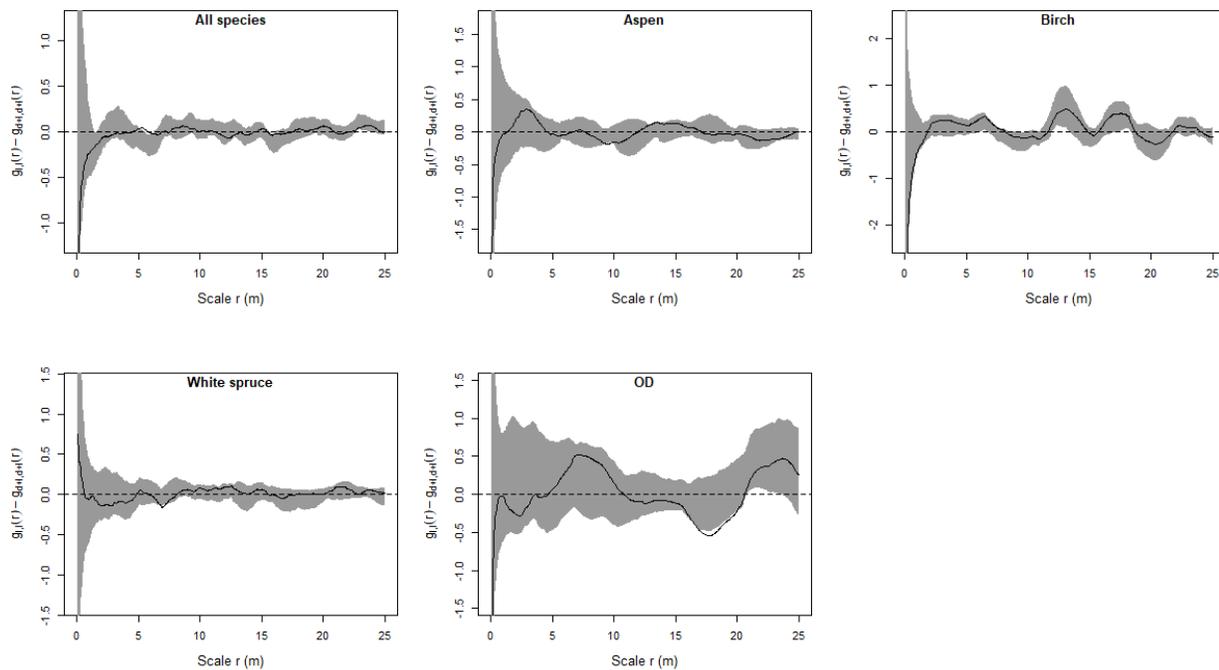


Figure A2 Univariate density-dependent mortality analysis for the change in living seedling trees (DBH ≤ 5 cm) pattern with random labeling null model. If the spatial pattern of living trees became more regular due to density-dependent mortality, the test statistic $g_{l,l}(r) - g_{d+l,d+l}(r) < 0$. The solid lines showed observed values of test statistics. Approximately 95% simulation envelopes (grey areas) were constructed using 99 times simulations of the null model. The analysis was conducted for all species together and five species groups Aspen, Birch, White spruce, OD (other deciduous trees), OS (other shrubs) separately.

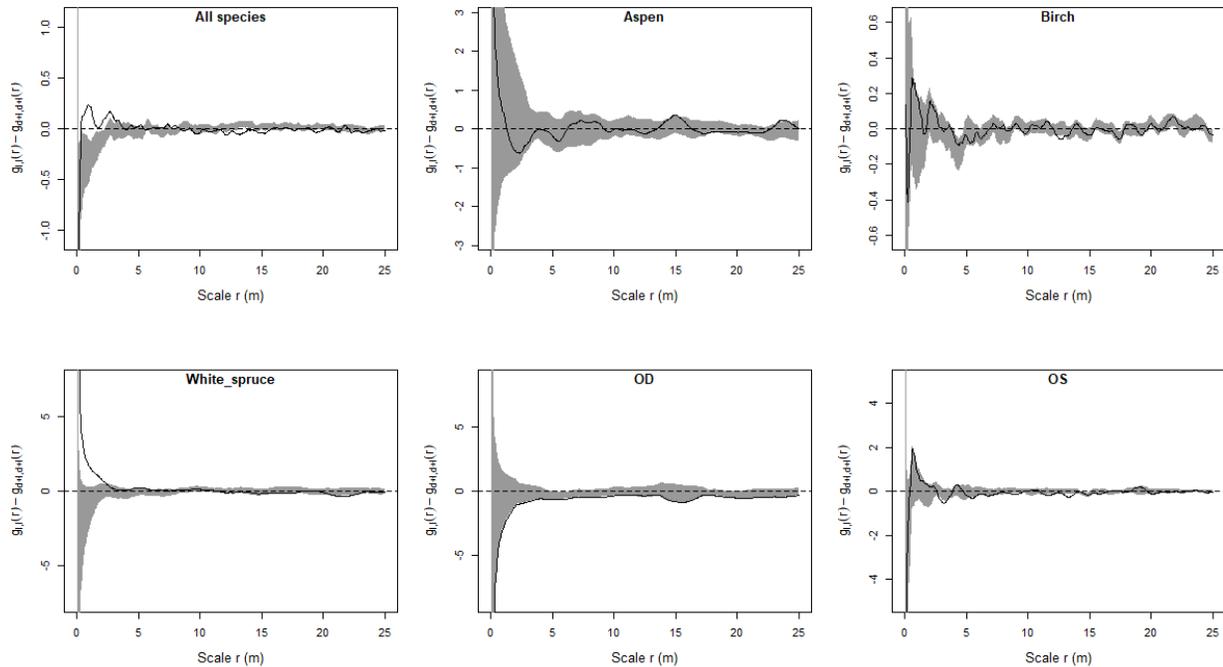


Figure A3 Multi-type density-dependent mortality analysis for comparison of initial neighbourhood of live and dead adult trees (DBH > 15cm) with random labeling null model. If tree density around dead trees is larger than expected under random mortality, the test statistic $g_{d,d+l}(r) - g_{l,d+l}(r) > 0$. The solid lines showed observed values of test statistics. Approximately 95% simulation envelopes (grey areas) were constructed using 99 times simulations of the null model. The analysis was conducted for all species together and five species groups Aspen, Birch, White spruce, OD (other deciduous trees), OS (other shrubs) separately. (The last graph is not showed because of the insufficient data)

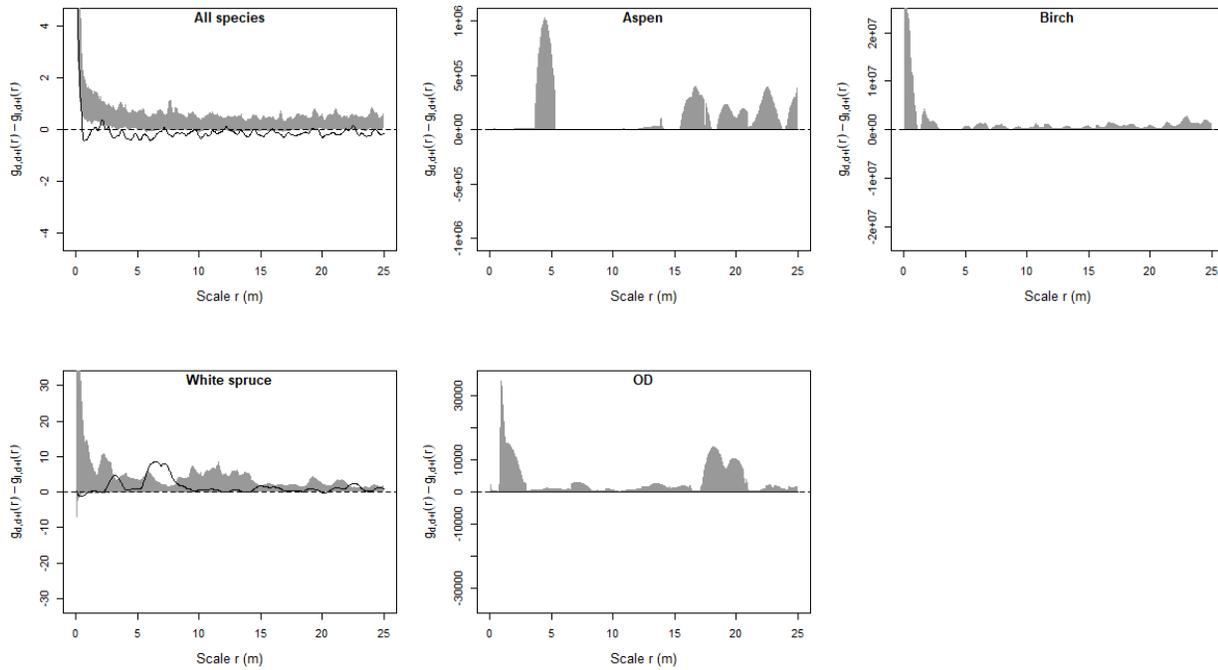


Figure A4 Multi-type density-dependent mortality analysis for comparison of initial neighbourhood of live and dead seedling trees (DBH \leq 5cm) with random labeling null model. If tree density around dead trees is larger than expected under random mortality, the test statistic $g_{d,d+l}(r) - g_{l,d+l}(r) > 0$. The solid lines showed observed values of test statistics. Approximately 95% simulation envelopes (grey areas) were constructed using 99 times simulations of the null model. The analysis was conducted for all species together and five species groups Aspen, Birch, White spruce, OD (other deciduous trees), OS (other shrubs) separately. (The last graph is not showed because of the insufficient data)

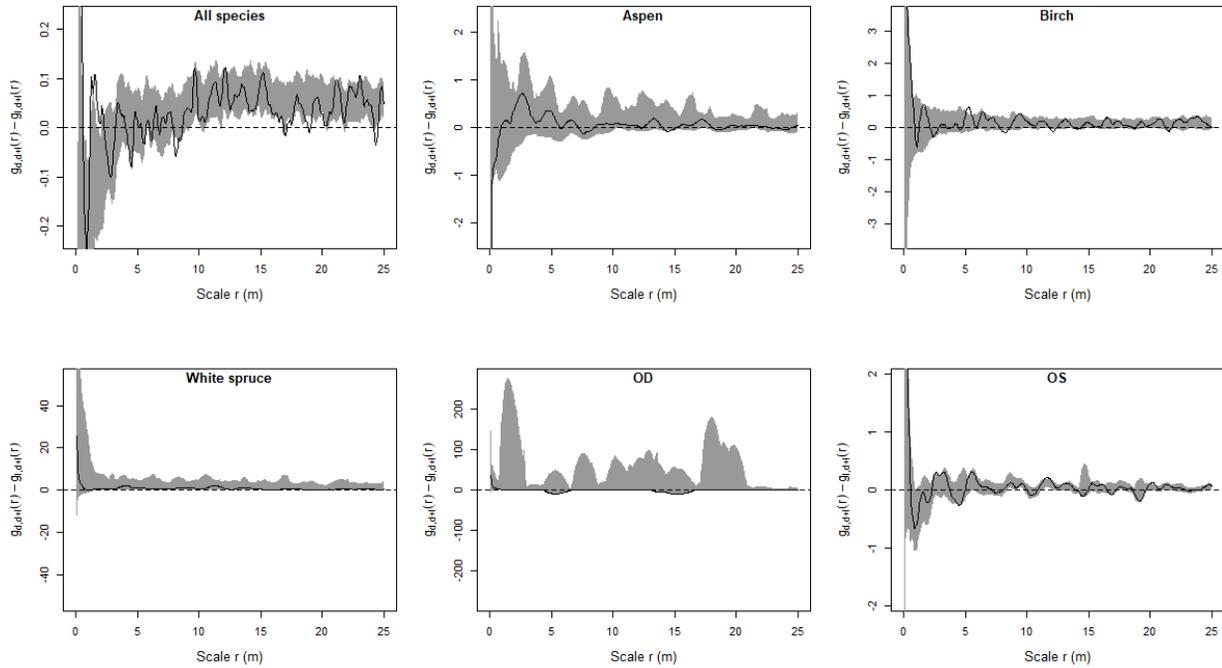


Figure A5 Heterospecific seedling–adult association analyses. Interaction between heterospecific seedling-adult pairs compared to the toroidal shift null model. Values above (below) the simulation envelope indicate attraction (segregation) between seedlings and adults. The solid lines showed observed values of test statistics. Approximately 95% simulation envelopes (grey areas) were constructed using 99 times simulations of the null model. Species abbreviations: ASP, aspen; BIR, birch; WS, white spruce; OD, other deciduous; OS, other shrubs.

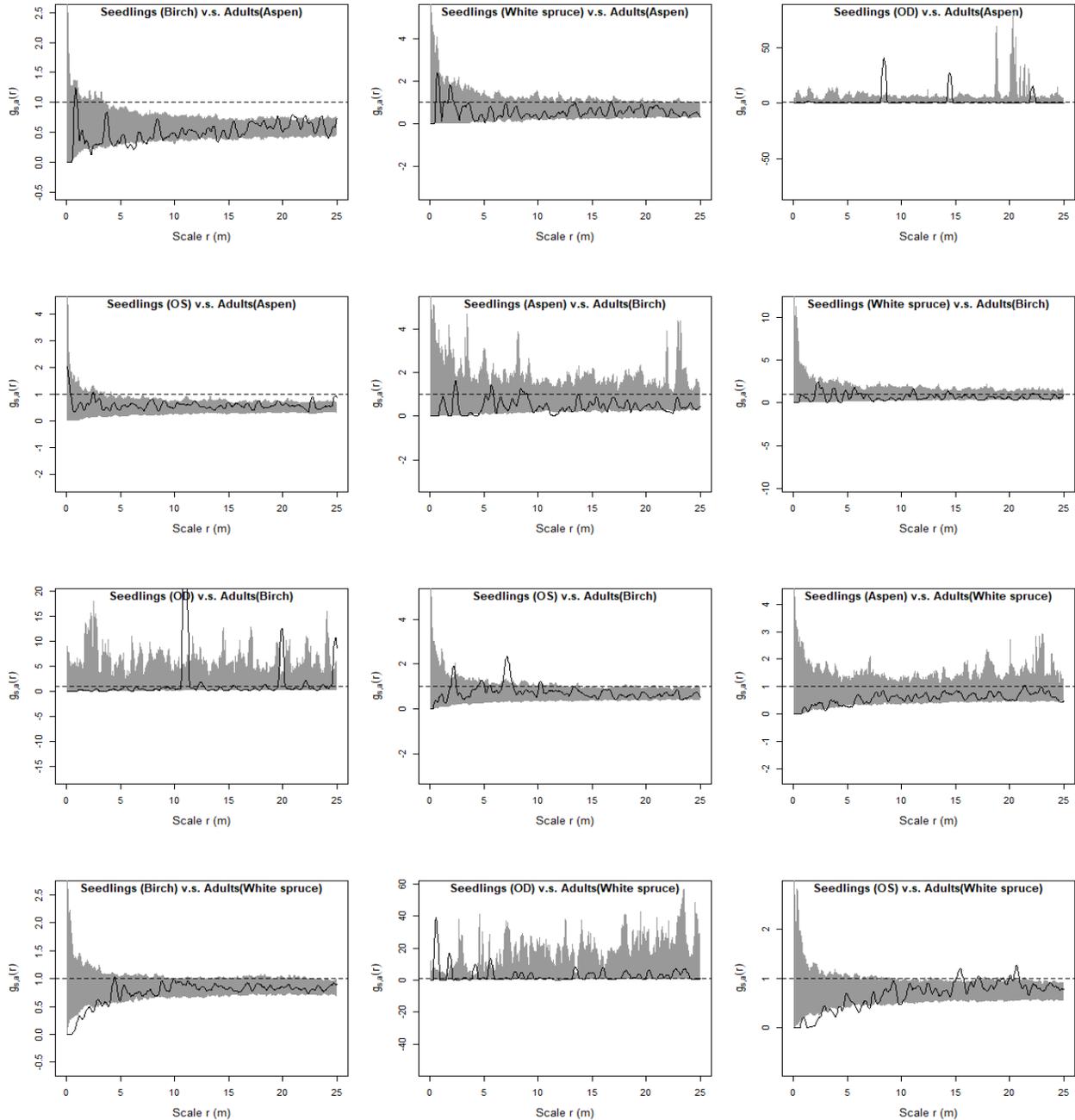
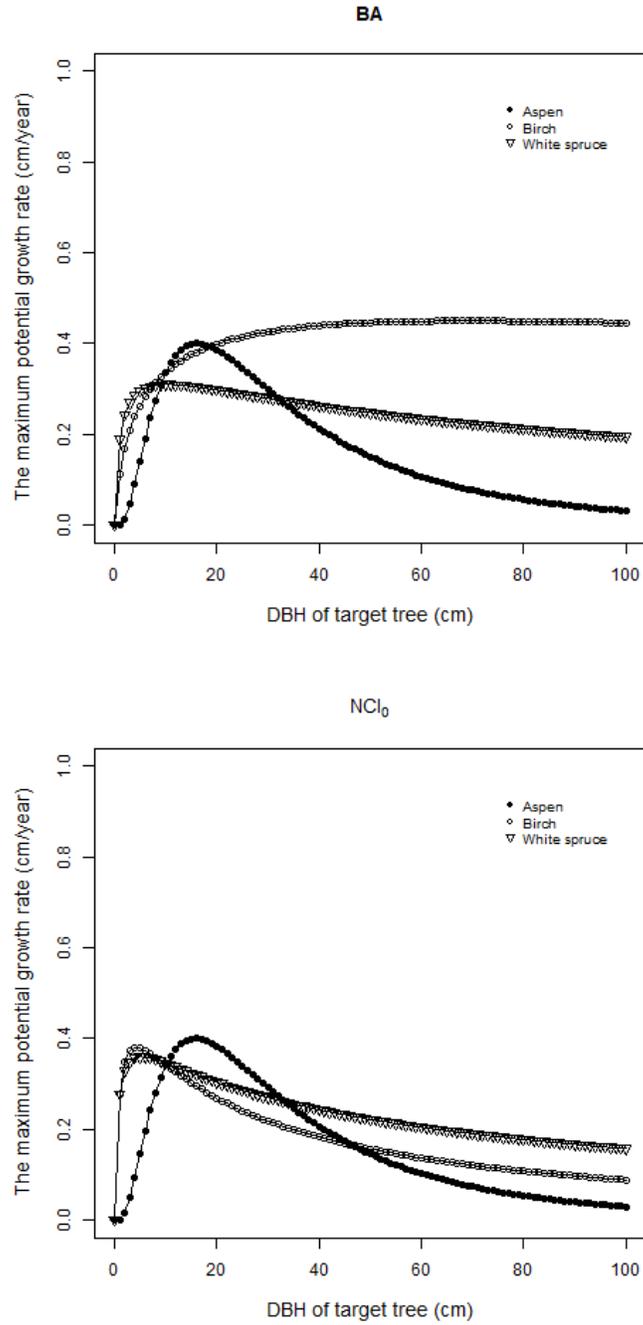
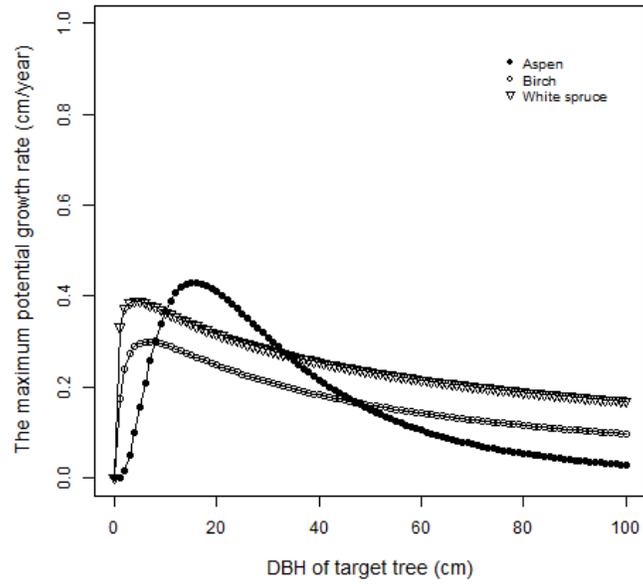


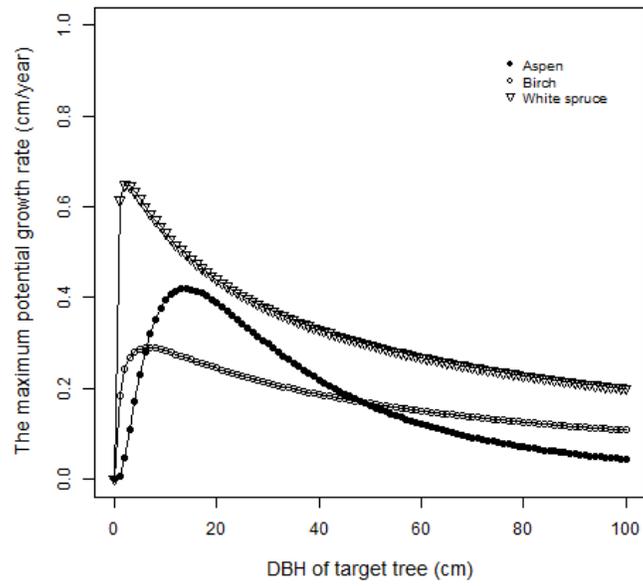
Figure A6 Estimated potential diameter growth for aspen, birch and white spruce as a function of tree initial DBH using competition indices from Table 3.4



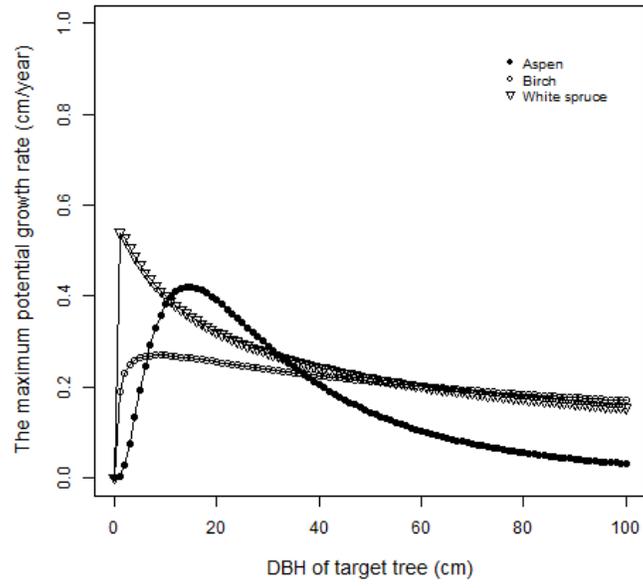
NCI₁



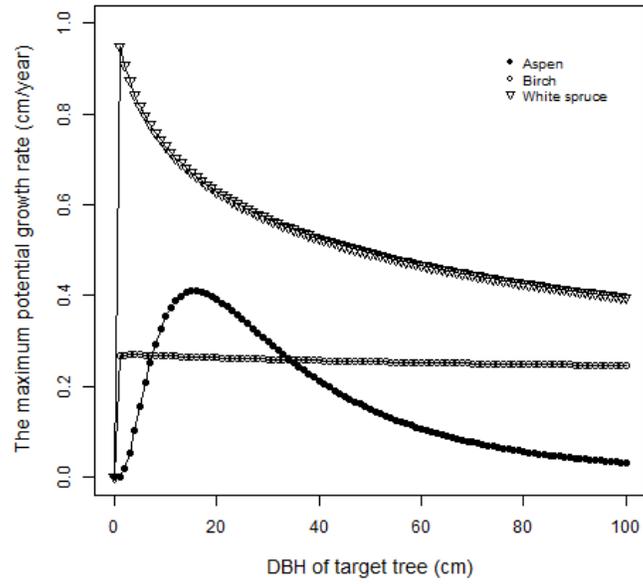
RK₁



RK₂



H



L

