University of Alberta

Spatial Patterning of Tree Distributions and Density-Dependent Competition in a Boreal Forest of Alberta

By

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ABSTRACT

Although competition has been considered as one of the most fundamental ecological processes regulating population dynamics, survival, growth and species coexistence, few studies have used spatial patterns of tree distribution for inferring the effect of competition on tree mortality and stand development of boreal forests. Here, I studied point patterns of trees and competition in a chronosequence consisting of four stands in northwest Alberta. Spatial point-pattern analyses found intraspecific competition to be an important mechanism influencing stand development throughout succession. However, these analyses revealed that interspecific competition was not important, suggesting that interspecific competition may not be strong enough to cause significant tree mortality. Logistic regression of mortality further supported the point-pattern results and identified the neighborhood density of large (DBH>25 cm), small (DBH<10 cm) and dead trees as significant factors in the mortality of both deciduous and coniferous trees. My research highlighted the effect of competition over succession in the boreal forest.

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Chapter 1: Introduction to the thesis

1.1 RESEARCH RATIONALE and THESIS INTRODUCTION

The boreal forest is Canada's largest ecosystem, occupying nearly half of Canada's land area and 90% of Canada's total productive forest (Pruitt and Baskin 2004, Brassard and Chen 2006). Distinct from other forested landscapes in Canada, the western boreal forest has escaped major development disturbances until recently. Current exploration of oil and gas in Alberta has rapidly fragmented the boreal forest jeopardizing the livelihood of many species that rely on this forest to survive (Timoney and Lee 2001). Along with this development, the recently increased use of hardwood species in pulp production in addition to the traditional softwood timber operations has caused a decline in mature boreal forests (Timoney and Lee 2001). Facing these situations, there is a compelling incentive for forest managers to strengthen and adopt sustainable management practices.

In western Canada's boreal forest, fire disturbances have a significant role in determining forest structure and dynamics (Rowe 1956, Strauss et al. 1989, Hornberg et al. 1995, Freedman et al. 1996). Infrequent, high-intensity crown fires initiate secondary succession which creates a forest mosaic composed of patches of trees of different age classes (Kneeshaspen and Bergeron 1998). In Alberta, the current forest management practice is based on the paradigm to mimic the effects of natural disturbances, whether that disturbance is wildfire burn, wind blow down, or, single tree mortality.

While fire is considered the major disturbance regime affecting stand structure of boreal forests, in the absence of fire or during the period between more intense fire activity, density-dependent intra- and interspecific competition are critical mechanisms contributing to stand dynamics and tree mortality, particularly in high-density boreal forest stands.

Intra- and interspecific competition occurs when individuals of the same species and different species, respectively, within a community are forced to compete for limited resources, such as soil nutrients, water or light. Although other agents (e.g., disease, pathogens, insects, and wind disturbances) might contribute to tree death, the ability to successfully obtain these limited resources significantly affects the growth potential and prospects of survival of individual trees (Peet and Christensen 1987). Canopy gaps created from single or multiple overstory-tree mortality provide opportunity for newly established seedlings to be recruited into the canopy as resources, such as light, become more available (Kneeshaspen and Bergeron 1998). Intraspecific competition has been found particularly important for pioneer tree species which often grow in higher densities within these disturbed openings. In dense patches, pioneer trees face higher mortality rates and undergo self-thinning resulting in regularly spaced survivors (Yeaton and Cody 1976, Weiner 1984, Peet and Christensen 1987, Kenkel 1988, Duncan 1991, He and Duncan 2000). Interspecific competition can be a major mechanism limiting the establishment of shade-tolerant and late successional species in young stands, because the stand canopy is dominated by shade-intolerant pioneer species which reduce the availability of resources, suppressing the growth and survivorship of the understorey (Chapin et al. 1989, He and Duncan 2000). Thus, interspecific competition can slow down the replacement of pioneer species by late-successional species within a forest stand (Armesto et al. 1986, Chapin et al. 1989). As a result of interspecific competition, late-successional species are often found to be aggregated and negatively spatially associated with large pioneer trees in stands dominated by pioneer species (Williamson 1975, Stewart 1986).

The tradition pathway of succession for the mixedwood boreal forest is well understood (Kneeshaspen and Bergeron 1998, Brassard and Chen 2006). After the occurrence of fire a barren site is quickly colonized by aspen *(Populus tremuloides)* and to a much lower extent, white spruce *(Picea glauca)* (Rowe 1956). Although it is present in the understory, white spruce is generally thought to be unable to out-compete the canopy-dominant aspen, until aspen begins to self-thin at 70-90 years (Cumming et al. 1996). At this stage of succession, it is believed that white spruce start to out-compete aspen, and if time permits white spruce will eventually dominate the canopy. The increasing dominance of white spruce will cause a shift from a deciduous dominated stand to a mixedwood and eventually a shade-tolerant conifer dominated stand (Kneeshaspen and Bergeron 1998).

Research on the role of interspecific competition in successional change has resulted in evidence that both supports and challenges the importance of density-dependence in species replacement (Armesto et al. 1986, Chapin et al. 1989, Hornberg et al. 1995, Peterson and Squires 1995a, Halpern et al. 1997). Some studies have shown that changes in species composition may simply reflect the difference in life history traits, such as shade-tolerance, of the pioneer and late-successional species (Walker and Chapin 1987, Chapin et al. 1989). In this case, interspecific interactions may just affect the magnitude or timing of the change (Chapin et al. 1989). In other studies, competition for resources is considered to be an underlying mechanism controlling species replacement (Halpern et al. 1997). Although the importance of interspecific competition may vary, the general conclusion is that shifts in species composition and stand structure are at least partially driven by interspecific competition.

Natural disturbances cause abrupt changes in stand structure at larger spatial and temporal scales. In contrast, competition is a localized mechanism affecting stand structure over longer periods of time. As a result, understanding how competition impacts stand structure can be challenging because data of long-term observations are often not available. Facing this difficulty, a widely used approach is to use space-to-time substitution to infer competition and its role in driving succession. For stem-mapping data, this means comparing spatial distributions of neighboring live+dead trees against the distributions of live trees. If neighborhood competition is a primary mechanism for mortality, it is expected that the post-mortality patterns would be more regular (evenly spaced) than pre-mortality patterns (Figure 1-1). Although this method has been widely used to infer competition and has become a standard method for analyzing stem-mapped data (Duncan 1991, Moeur 1993, Getzin et al. 2006), it is important to recognize its potential limitation. Since stem-mapped data are snapshot data in which the time of mortality is not actually recorded but rather implied to have previously occurred, there is a potential risk that the observed patterns only reflect the current situation rather then the true interactions within the community. Thus, precaution is needed for interpreting the results of point pattern analysis.

Over the past two decades, much progress has been made about tree competition and the role it plays in determining stand structure and dynamics in boreal forests globally (Szwagrzyk and Czerwczak 1993, Hara et al. 1995, Kubota and Hara 1995, Kuuluvainen and Rouvinen 2000, Little 2002, Yang et al. 2003). A recent study has provided some insight into the spatial relationship and competitive interactions between aspen *(Populus tremuloides)* and jack pine *(Pinus banksiana)* at both the mature and juvenile stages within a deciduous dominated stand in Alberta (Little 2002). However, despite these studies in boreal forests, there is a lack of research focusing on the spatial dynamics of plant-to-plant competition in the later stage of boreal succession. Still less is known about the variation in the intensity of competition from deciduous dominated to mixedwood to conifer dominated forests and how competition would affect stand structure over this succession gradient.

Since analyzing a true boreal succession would require data collected from a single stand over a century long census, in this thesis I investigated a chronosequence consisting of four stands, each one representing a successional stage. This approach has been previously used to analyze the effect of density-dependent competition on stand structure over succession in a coastal temperate forest on Vancouver Island, British Columbia (Getzin et al. 2006). Although a true temporal scale cannot be analyzed using a chronosequence, this method provides a realistic approximation of a successional trajectory and thus is appropriate for this study.

I used a spatial point pattern analysis to determine the role intra- and interspecific competition played in the development of stand structure throughout succession of a boreal forest in Alberta. I evaluated the spatial pattern of 3 dominant boreal tree species, trembling aspen, balsam poplar, and white spruce, to try and detect spatial repulsion among individuals within each respective population and between species. Once the effect of competition was recognized, I used logistic regression to develop tree mortality models that would possibly identify attributes of neighbouring trees that significantly contribute to either deciduous or conifer mortality throughout succession. If identified, these attributes would be useful for improving mortality prediction accuracy, which is essential for modeling growth and yield (Monserud 1976). This thesis contributes to further understanding the effect of competition on the successional development of boreal forests of Alberta and highlights the importance of density-dependent effects in shaping boreal forest structure.

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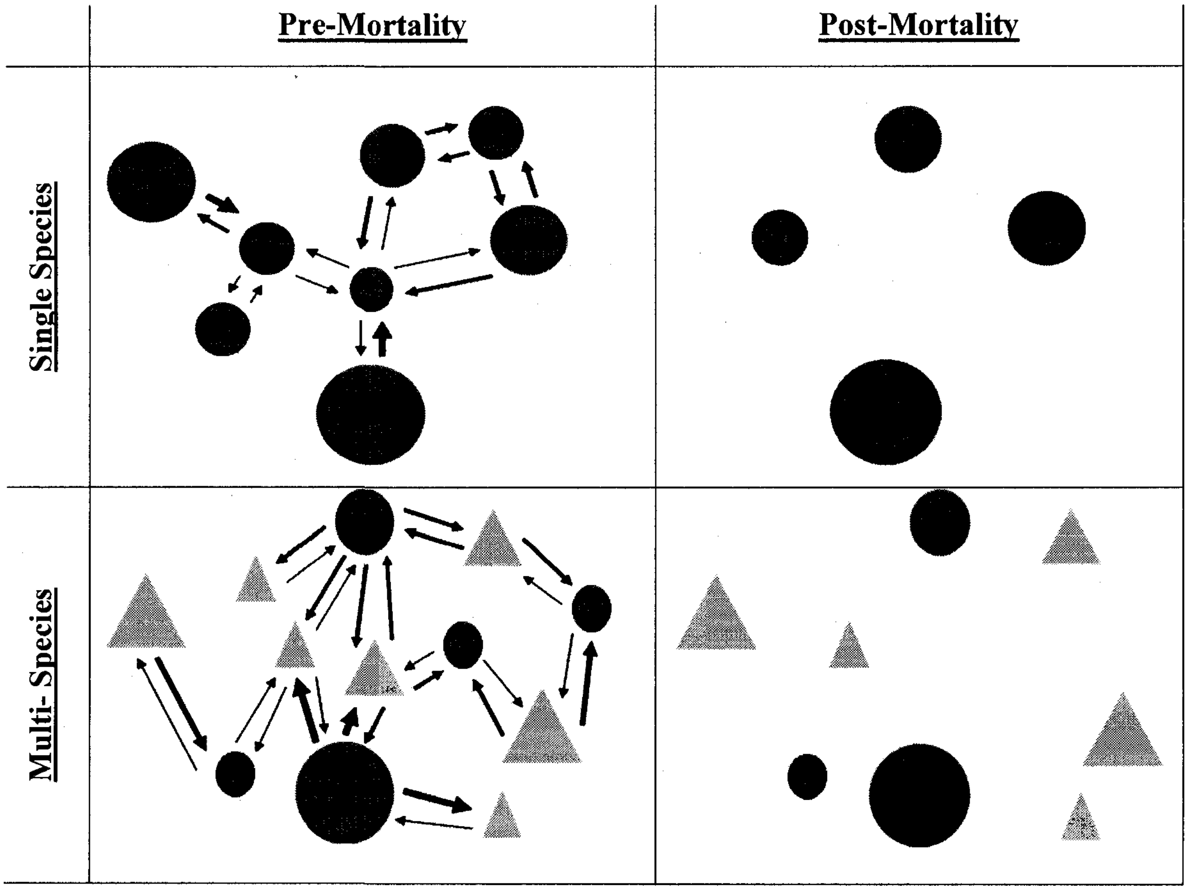
1.3 FIGURES

Figure 1-1. Illustrating the effect of density-dependent competition for single and multiple species populations within a stand. Larger, dominant trees will out-compete younger, weaker trees within a close proximity. This will shift the spatial pattern of stems towards a more regular (evenly-spaced) pattern in a single species population or negative spatial association among species in multiple species populations.



Chapter 2: Spatial point-pattern analysis for detecting density-dependent competition in a boreal forest of Alberta

2.1 INTRODUCTION

Competition is a fundamental ecological process regulating population dynamics, survival, growth and coexistence of species (Peet and Christensen 1987, Tilman 1994, Keddy 2001, Szwagrzyk and Szewczyk 2001). In boreal forests, in the absence of major disturbances such as fire, density-dependent competition is considered to be a vital mechanism driving species turnover and successional dynamics and shaping stand-level structure (Kneeshaspen and Bergeron 1998). Therefore, understanding competition is critical for predicting succession and the resulting effect on forest stand structure (Peet and Christensen 1980, Pacala and Deutschman 1995, Keddy 2001, Coates et al. 2003). Moreover, understanding competition has important management applications. Much of the foundation of silviculture is based on the idea of competition – how to maintain a stock that would minimize the negative effect of competition yet maximize the utility of resources so that the density of the stock would follow the trajectory of -3/2 thinning line (Yoda et al. 1963) or the recently revised -4/3 rule (Enquist et al. 1998). Understanding competition is especially important if the management goal is to mimic the dynamics of natural ecosystems (Attiwill 1994, Galindo-Leal and Bunnell 1995, Bergeron and Harvey 1997, Chen and Popadiouk 2002, Harvey et al. 2002).

Although additive or removal experimental manipulations are possible for studying competition of small and short-lived plants, this approach is practically infeasible for studying tree competition. Since competition is a process primarily occurring among neighboring trees, the spatial locations of trees provide essential information for inferring competition in field conditions. Growth reduction is expected if there is neighborhood competition, and the intensity of competition is often assessed by using a competition coefficient that is derived from basal area increment or a ratio of height growth and distance between neighboring trees (Wagner and Radosevich 1998, Bell et al. 2000, Weigelt and Jolliffe 2003, Woodall et al. 2003, Canham et al. 2004, Dolezal et al. 2004). In the absence of growth data, competition is often inferred from analyzing the spatial patterns of observed tree mortality (Laessle 1965, Antonovics and Levin 1980, Smith and Grant 1986, Kenkel 1988, Stoll and Bergius 2005). This approach is based on the assumption that mortality is not a random process but that trees having closer and bigger neighbors would suffer higher mortality rates. This is stronger evidence of competition because competition must be more severe to cause mortality rather than just reduce growth. In this study, I will analyze the spatial pattern of observed tree mortality to infer competition in four stands representing a chronosequence of boreal mixedwood forests in Alberta.

Analyzing the spatial patterns of trees has had notable success in investigating competitive interactions among trees within a forest stand (Yeaton and Cody 1976, Weiner 1984, Kenkel 1988, Duncan 1991, He and Duncan 2000). Mechanisms, such as life history traits, are known to significantly impact the rate of survivorship among competing trees (Hustonand and Smith 1987), but competition for resources (primarily light) are responsible for tree mortality (Halpern et al. 1997), thus leading to negative spatial association among trees. It is therefore widely accepted that the occurrence of a regular (evenly spaced) spatial pattern within a population provides strong empirical evidence of intraspecific competition (Pielou 1962, Antonovics and Levin 1980, Stoll and

Bergius 2005). The same inference can be made for interspecific competition if there is evidence of spatial segregation between species.

Investigating the effect of competition on succession is difficult because a full succession cycle can take centuries to conclude, making data collection unrealistic (Gavrikov and Stoyan 1995, He and Duncan 2000). A simple method for investigating competition over succession is to compare the spatial patterns of dominant species in subsequent stages of a chronosequence. The succession pathway of the boreal forests in western Canada is well documented (Hornberg et al. 1995, Peterson and Squires 1995a, Kneeshaspen and Bergeron 1998, Cumming et al. 2000). In the earliest stage of boreal succession, deciduous pioneer species such as trembling aspen (*Populus tremuloides*) and balsam poplar *(Populus balsamifera)* dominate the canopy. Over succession, late-successional conifer species such as white spruce (*Picea glauca*) begin to colonize the understory (Kneeshaspen and Bergeron 1998). The species composition then shifts to a mixedwood forest and, finally emerges as conifer dominated forest (Kneeshaspen and Bergeron 1998).

Comparing the pre- (live and dead trees together) and post mortality (live trees only) spatial patterns of trees in each chronosequence stage provides a simple evaluation of the random mortality hypothesis, which states that if mortality is a random event and every tree within the stand has an equal probability of death, there should be no change in the post-mortality spatial pattern of the community. Thus, a post-mortality shift in the spatial distribution of trees would suggest that plant-to-plant competition contributes to selective tree mortality within the stand (Sterner et al. 1986, Getzin et al. 2006). However, it has been widely observed that trees in high density stands often suffered elevated mortality as a result of higher levels of competition within dense neighbours. As a result, the post-mortality spatial pattern of surviving trees shifts towards a more regularly (evenly) spaced pattern (Figure 1-1), providing strong evidence of density-dependent competition. This shift has been observed in uneven-aged mixed coniferous forests (Duncan 1991, He and Duncan 2000) and can be reliably used to infer intra- and interspecific interactions in mixedwood boreal stands (Little 2002). Moreover, if density-dependent competition is an important mechanism in the development of stand structure throughout succession, regularity among older trees should increase over succession as individuals become larger, more intense competitors (Getzin et al. 2006).

However, failure to detect a shift towards a regularly spaced pattern does not necessarily nullify the importance of competition within a stand. Competitive interaction may simply not be strong enough to cause significant mortality, but rather cause a reduction in growth. In this case, a correlation between tree size and neighbourhood density can provide a measure for the relative importance of competition in a stand (Shackleton 2002, Getzin et al. 2006).

Although density-dependent competition has been considered a primary force driving the species turnover and the succession pathway of boreal forests (Kneeshaspen and Bergeron 1998), it is not yet clear how the importance of intra-and interspecific competition changes over succession, as deciduous trees are replaced by coniferous trees, and how competition would induce mortality and contribute to the development of stand structure of boreal forests. In this study I analyzed fine-scale spatial distributions of two dominant deciduous species, trembling aspen (*Populus tremuloides*) and balsam poplar (*Populus balsamifera),* and a single dominant coniferous species, white spruce (*Picea* *glauca*), in a successional chronosequence to address these questions. On the basis of the presented arguments I hypothesize that 1) intraspecific competition will cause the spatial pattern of all species to become more regular over succession, 2) interspecific competition will result in significant spatial repulsion between dominant deciduous and coniferous species, and 3) there will be a significant correlation between tree size and spatial distribution.

2.2 METHODS

2.1.1 STUDY SITES and DATA COLLECTION

Data were collected at the EMEND (Ecosystem Management Emulating Natural Disturbance) research site, located approximately 50 km North West of Peace River, Alberta (56° 46' 13" N -118° 22' 28" W) between May and September 2006. The site soils are defined as fine-textured formed predominantly on glacio-lacustrine deposits. The mean annual temperature is 13.9° and a mean summer rainfall is 204.25 as averaged from the years 2000 to 2003. The EMEND research project is a large scale, multi-factorial experiment consisting of four stand types that are classified based on cover class and eight different treatment levels. The four cover classes are defined as deciduous dominated (>70% deciduous canopy cover), deciduous dominated with coniferous understory (>70% deciduous canopy cover and coniferous understory at least 50% of the canopy height), mixed (canopy consisting of both deciduous and coniferous cover between 35-65%) and conifer dominated (>70% conifer canopy cover).

For this study four undisturbed stands were chosen; one representing each of the four cover classes. The stands are hereby denoted as: DDom (deciduous aspen (*Populus tremuloides*) dominated), DDom-U (deciduous aspen (*Populus tremuloides*) dominated with coniferous white spruce (*Picea glauca*) understory), Mxwood (mixedwood) and CDom (coniferous white spruce (*Picea glauca*) dominated). These stands represent a chronosequence of boreal forest succession from aspen dominated to spruce dominated. At the time of data collection, the ages of the stands were approximately 107, 110, 142 and 169 years for DDom, DDom-U, Mxwood and CDom, respectively, as determined from increment cores taken from sample trees in the same areas in 1997.

Site locations were carefully chosen using a map to minimize edge effects and ensure that large clearings or roads were not included in the site area. Before the boundaries of the plot were established a physical inspection of the proposed area was conducted to ensure that the selected site was representative of the overall stand. In each of the stands a 100×100 m (1-hectare) plot was established by selecting a point to serve as the south west corner of the plot. The additional plot corner coordinates were referenced from this point.

A Nikon Total Station was used to obtain relative coordinates of each live deciduous tree (>2 cm diameter at breast height), live coniferous tree (>1 cm diameter at breast height) and all snags, stumps and logs within each plot. Each individual tree, snag, log and stump was given a unique tag number and the breast height of live trees was marked as a reference point that was later used for determining the height and diameter at breast height of each individual live tree. The diameter at breast height (DBH, at 1.3 m height) of each tree was measured twice using a caliper and the average of the two measurements was used for dbh. The height of each tree was also measured using a laser hypsometer. The final data contain the location coordinates, dbh, height, and species identity for every live tree, and the coordinates and species identity of all stumps, logs and snags.

2.2.2 DATA ANALYSIS

2.2.2.1 *Preliminary Stand Structure Analysis*

There were six tree species in the four mapped plots: trembling aspen (*Populus tremuloides*) (Aw), white spruce (*Picea glauca*) (Sw), balsam poplar *(Populus balsamifera)* (Bp), balsam fir *(Abies balsamea)* (Bf), lodgepole pine *(Pinus contorta)* (Lp) and paper birch *(Betula papyrifera)* (Pb). The number of stems (*N*) and the relative proportions (%) of both live and dead stems were counted for each species in each stand. Species which made up less than 5% of the overall composition of at least two stands were excluded from the study because a low frequency could result in a statistically unreliable analysis. The mean nearest-neighbour distance (<NN>) as well as the proportion of dead trees (%), and mean DBH (<DBH>) were calculated for each dominant species: aspen, spruce and balsam poplar for each of the four forest types (each representing a different successional phase). Balsam poplar was not analyzed in the mixedwood stand since its overall proportion for both live and deceased stems was below 1%. Intra- and interspecific mortality (%) was calculated as the proportion of dead trees that occurred in conspecific and heterospecific neighbourhoods, respectively. A conspecific neighbourhood was defined as a neighbourhood where at least 4 of a focal tree's 5 nearest-neighbours were of the same species as the focal tree. Alternatively, a heterospecific neighbourhood was defined as a neighbourhood where no more than 1 of a focal tree's 5 nearest-neighbours was of the same species as the focal tree.

High levels of segregation or intermixing could relate to higher occurrences of intra- and interspecific competition, respectively. Thus, Pielou's segregation index *S* (Pielou 1961) was calculated for each dominant species to indicate the level of intermixing that occurred in each stand. Since 3 dominant species were considered in this study, *S* values were calculated by comparing one dominant species against the other two dominant species as well a third group comprised of the remaining species in each stand which were too infrequent to be individually considered. Segregation index values range between 0 and 1, indicating spatial intermixing to spatial separation.

2.2.2.2 *Size-Distance Correlation Analysis*

To investigate the relative importance of density-dependent competition in developing the structure of a forest community I determined a size-distance correlation between the sum of the DBH of the five nearest-neighbours plus the DBH of the focal tree and the sum of the distances from the 5 nearest-neighbours to the same focal tree (Weden and Slauson 1986, Shackleton 2002, Getzin et al. 2006). The coefficient of determination, r^2, has been shown to be a robust index of competition regardless of the additional biotic and abiotic stresses which may also be structuring the forest community (Weden et al. 1988). The overall importance of competition was determined using all focal trees of a given species. The importance of intra- and interspecific competition were determined using only the subset of focal trees for a given species which were in conspecific and heterospecific neighbourhoods, respectively. The importance of overall, intra- and interspecific competition (measured by r^2) was plotted to show how the significance of competition changed over succession.

2.2.2.3 *Spatial Pattern Analysis*

Ripley's *K(t)* function (Ripley 1977) was used to analyze the observed mapped point patterns of trees in each stand. *K(t)* is considered as a standard method for analyzing both univariate and bivariate spatial point patterns in ecology (Kenkel 1988, Duncan 1991, Penittinen et al. 1992, Szwagrzyk and Czerwczak 1993, Gavrikov and Stoyan 1995, He and Duncan 2000). This method is preferred to other point pattern analyses because it can offer a greater understanding of the nature of spatial patterns as it analyzes plant-to-plant distances rather than being restricted to solely examining nearest-neighbour distances (Kenkel 1988).

The unbiased univariate estimator of the *K*-function for detecting intraspecific competition is:

$$\hat{K}(t) = n^{-2}|A|\sum_{i \neq j}\sum w_{ij}{}^{-1} I_t(u_{ij}), \tag{1}$$

where n is the total number of trees in study area A. u_{ij} denotes the distance between the i^{th} (focal) tree and the j^{th} (neighbouring) tree, where the focal tree is located within area A. $I(u_{ij})$ is an indicator function, equaling 1 if $u_{ij} \leq t$ and 0 otherwise. w_{ij} is included to correct edge-effect. It equals the proportion of the circumference of a circle centered at the i^{th} tree with radius u_{ij} which lies within A. w_{ij} equals 1 if the entire circumference of the circle lies within A. To ensure sufficient neighboring pairs for constructing the *K*-function, I computed the function at 0.5 meter intervals with distance $t \leq 25$ meters.

The variance reduction form of the *K*-function (Besag 1977):

$$L(t) = \sqrt{K(t)/\pi} - t \tag{2}$$

was used to compare the observed spatial patterns of each dominant species in each successional phase against a random pattern. If trees are completely spatial random (CSR), then:

$$K(t) = \pi t^2 . \tag{3}$$

$L(t)=0$ for CRS, $L(t)>0$ for aggregated pattern, while $L(t)< 0$ for regular pattern.

The unbiased second order bivariate estimator of the Ripley's *K*-function for detecting interspecific competition is:

$$\widetilde{K}_{12}(t) = (n_1 n_2)^{-1} |A| \sum_{i=1}^{n_1} \sum_{j=1}^{n_2} w_{ij}^{-1} I_t(u_{ij}) . \tag{4}$$

where n_1 and n_2 are the total number of trees of species 1 and 2 that occur in area A. Other terms are of the same interpretation as equation (1).

The variance reduction bivariate transformation of $\widetilde{K}_{12}(t)$ is (Lotwick and Silvermen 1982):

$$L_{12}(t) = \sqrt{K_{12}(t)/\pi} - t . \tag{5}$$

If species 1 and 2 are randomly associated, $L_{12}(t)=0$. If the two species are positively associated, $L_{12}(t)>0$. If they are negatively associated, $L_{12}(t)< 0$.

To assess the significance level of non-CSR, the observed *L* functions for pre-mortality (live+dead) spatial patterns were compared to Monte Carlo intervals generated using independent *random location* selection. This selection method randomly generated relative coordinates for trees within the stand and then evaluated the simulated spatial pattern using the Ripley's *K*-function and *L*-transformation. Alternately observed post-mortality and size class patterns were compared to Monte Carlo intervals generated using *random labeling* selection (Diggle 2003). Unlike random location selection, random labeling selection maintained the original relative coordinates of each tree and randomly assigned variables, such as species identity or living status, to the position and then evaluated the resulting spatial pattern using the same *K*-function and *L*-transformation. Each simulation was repeated 99 times and for every *t*-value and the two minimum and maximum values were removed from the data set. The remaining minimum and maximum values at each *t* were set as the Monte Carlo interval (95% interval) which the observed data was compared against. The observed patterns that fell above, below or within the Monte Carlo intervals indicated aggregated, regular or random patterns, respectively. All Ripley's *K*-functions, *L*-transformations and Monte Carlo simulations were calculated using the spatstat package in the R Statistical Programming Software (Baddeley and Turner 2004).

2.3 RESULTS

2.3.1 *Preliminary Stand Structure Analysis*

Trembling Aspen. The range of mean nearest-neighbour distances for aspen over succession was small (1.33-1.54 m) (Table 2-1), suggesting that despite changes in community structure during succession, there is a specific size of "territory" in which a single aspen tree would prevent other individuals from establishing. The relative frequency and total percentage of aspen stems declined in the later stages of succession, which was expected as the composition of the stand shifts from deciduous to coniferous dominated. The proportion of dead aspen increased over succession from 27.8% in the DDom stand to 49.7% in the CDom stand (Table 2-1). Although the average DBH of aspen was consistently greater than the other dominant species throughout succession, the mean aspen DBH decreased from 26.0 cm in the DDom stand to 21.8 cm in the DDom-U stand. However, the average aspen DBH did increase 39.9% in the final stage of succession (Table 2-1). Excluding the Mxwood stand, aspen had the highest Pielou's segregation index of all the dominant species in each plot. However, the segregation values were low (*S*=0.0859) to moderate (*S*=0.4749) (Table 2-1), indicating aspen was relatively spatially intermixed in each plot.

White Spruce. The proportion of spruce stems was lowest in the DDom stand and approximately doubled over each phase of succession (Table 2-1). In both the DDom and DDom-U stands dead spruce were too infrequent to make conclusion about how competition impacts spruce mortality in these stands. The proportion of spruce mortality is significantly higher in the later stage of succession (Table 2-1); however, these results are likely correlated to the higher frequencies of spruce in both the Mxwood and CDom stands. The mean spruce DBH increases from 3.7 cm in the DDom stand to 14.2 cm in the DDom-U stand and 28.7 cm in the Mxwood stand, but the mean DBH decreases to 19.3 cm in the CDom stand (Table 2-1), suggesting that spruce regeneration is greater in this stand. Similar to aspen, Pielou's segregation values are small in the DDom (*S*=0.1990), DDom-U (*S*=0.1920) and Mxwood (*S*=0.1420) stands and moderate in the CDom stand (*S*=0.4042) (Table 2-1), indicating that spruce was relatively spatially intermixed in each stand.

Balsam Poplar. In the DDom and DDom-U stands the proportion of balsam poplar stems and the proportion of balsam poplar mortality were the second highest of the dominant species. However in the later stages of succession the proportion of Balsam poplar stems is significantly lower than both aspen and spruce (Table 2-1). The four balsam poplar stems observed in the Mxwood stand were all recorded as dead, thus, the proportion of balsam poplar mortality in this stand is 100% and DBH values were not recorded for these trees (Table 2-1). In the CDom stand balsam poplar has a significantly lower relative frequency than both aspen and spruce, but it has a significantly higher proportion of mortality than spruce. Balsam poplar had the lowest segregation index within each plot, with the exception of the DDom-U stand, and thus was more spatially intermixed than the other dominant species.

2.3.2 *Size-Distance Correlation Analysis*

Trembling Aspen. Although the relative importance of overall competition in the aspen population increased from the DDom stand to the Mxwood stand, it decreased in the CDom stand (Figure 2-1A). The relative importance of intraspecific competition in aspen decreased over succession (Figure 2-1B), while the relative importance of interspecific competition increased over succession (Figure 2-1C). Both of these observed patterns are consistent with the hypothesized aspen patterns and these observations are likely related to a decrease in canopy dominance by aspen. An intraspecific correlation was not calculated for aspen in the Mxwood stand since the subset of aspen focal trees in a conspecific neighbourhood was too small for a reliable statistical analysis.

White Spruce. The relative importance of intraspecific competition within the spruce population significantly increased over succession (Figure 2-1A). Moreover, the relative importance of intraspecific competition within the spruce population was higher than the other dominant species in each successional phase (Figure 2-1B). Although intraspecific competition correlation values increased in the DDom-U and decreased in Mxwood stands, these results suggest that the relative importance of intraspecific competition is similar at the beginning and final phase of boreal succession. This is likely related to intense self-thinning (competition) among spruce offspring in both of these stands. Although the relative importance of interspecific competition increased slightly from the DDom stand to the Mxwood stand, it significantly decreased in the CDom stand (Figure 2-1C). The increase in the relative importance of intraspecific competition and the decrease in the relative importance of interspecific competition are likely related to the increase in spruce in the CDom stand.

Balsam Poplar. The intra-and interspecific correlation values were not calculated for balsam poplar in the Mxwood stand because the proportion of balsam poplar in this stand was less than 1% of the overall number of stems. Despite the lack of r^2 values for the Mxwood stands, results suggested that the relative importance of both intraspecific (Figure 2-1B) and overall competition (Figure 2-1A) for Balsam poplar decreased over succession. However, the relative importance of interspecific competition significantly increased over succession (Figure 2-1C). Both the decrease in the relative importance of intraspecific and the increase in the relative importance of interspecific competition within the balsam poplar population are likely related to the decrease in balsam poplar stems from the DDom and DDom-U stands to the CDom stand.

2.3.3 *Spatial Pattern Analysis*

2.3.3.1 Univariate Spatial Patterns (Intraspecific Competition)

Trembling Aspen. The observed $L(t)$ function for pre-mortality aspen fell above the Monte Carlo interval in both the DDom (Figure 2-2A) and CDom (Figure 2-2D) stands, indicating aspen was overall highly aggregated in these stands. However, the observed pre-mortality $L(t)$ function fell within the Monte Carolo interval, indicating a randomly distributed in the Mxwood stand (Figure 2-2C). At scale up to 2 m, pre-mortality aspen was regularly distributed, then became aggregated starting at 5 m in the DDom-U stand (Figure 2-2B). Although post-mortality aspen was regularly spaced between 8.5 and 19.5 m in the Mxwood stand (Figure 2-2G), the random mortality hypothesis could not be rejected for small scale distances due to the fact that pre-mortality aspen is randomly distributed at scales up to 8.5 m. Post-mortality aspen shifted to random distributions in both the DDom and DDom-U stands (Figure 2-2E & 2-2F), and at scales up to 8 m in the CDom stand (Figure 2-2H). Thus, the random mortality hypothesis was rejected for aspen in the DDom, DDom-U and CDom stands. Dead aspen were found to be highly aggregated at scales starting at 1 m in both the DDom and DDom-U stands and randomly distributed in both the Mxwood an CDom stands (Figure 2-6 A-D), which is likely the result of more Aspen present in the earlier successional stands and more intense self-thinning among young stems.

White Spruce. Pre-mortality spruce was aggregated from 2-16 m in the DDom stand (Figure 2-3A), 2.5-25 m in the Mxwood stand (Figure 2-3C), and aggregated at all scale in both the DDom-U and CDom stands (Figure 2-3B & 2-3D), with the strongest aggregation occurring in the CDom stand. The post-mortality pattern cannot be evaluated in the DDom and DDom-U stands because there are 0 and 1 dead Spruce, respectively, in these stands. Post-mortality spruce regularly distributed from 1-13.5 m in the Mxwood stand and at scales starting at 2 m in the CDom stand. Thus, the random mortality hypothesis was rejected for Spruce in both the Mxwood and CDom stands. Dead spruce were found to be highly aggregated in both the Mxwood and CDom stands (Figure 2-6G & 2-6H).

Balsam Poplar. Pre- and post-mortality balsam poplar spatial patterns were not evaluated in the Mxwood stand because there were two few balsam poplar in this stand for the analysis. Pre-mortality balsam poplar was highly aggregated in the DDom, DDom-U and CDom stands (Figure 2-4A, 2-4B & 2-4D). The random mortality hypothesis was rejected for all evaluated stands since post-mortality balsam poplar was randomly distributed in both the DDom and CDom stands (Figure 2-4E & 2-4H), and slightly aggregated from 3-8.5 m in the DDom-U stand (Figure 2-4F). Dead balsam poplar was found to be randomly distributed at small scales throughout succession, but found to be aggregated from 4.5-8 m in the DDom-U stand (Figure 2-6 I-L).

Size Class. Large trees were defined as individuals with DBH >30 cm. Large aspen shifted from aggregated at 1.5 m in the DDom stand to regularly spaced between 4 and 4.5 m in the Mxwood stand (Figure 2-5A & 2-5C), indicating a shift towards regularity over succession. However large aspen were aggregated between 2.5 and 4.5 m in the CDom stand (Figure 2-5D), which suggests that factors other than competition may have affected the spatial distribution of large aspen stems in this stand. A spatial pattern analysis was unable to be conducted for large Spruce in the DDom stand because there were no large spruce stems in this stand. However, the spatial pattern of large spruce shifted from a random distribution in the DDom-U stand to a significantly regular distribution at scales starting at 1 m in the CDom stand (Figure 2-5F-H)., indicating that intraspecific competition between large spruce increased over succession and contributed to the spatial arrangement of these trees. Spatial patterns for balsam poplar in both the DDom-U and Mxwood stands were not determined because there was not enough large balsam poplar in these stands to allow for an analysis. In the DDom and CDom stands large balsam poplar were found to be randomly distributed (Figure not shown).

2.3.3.2 Bivariate Spatial Patterns (Interspecific Competition)

Although interspecific competition is considered to be a vital mechanism in species turnover during succession, the results of the bivariate *K(t)* analysis were not indicative of significant shifts in spatial patterns for heterospecific trees. This suggests that interspecific competition is either not significant in developing stand structure, or that it is probably not strong enough to cause significant tree mortality. All comparisons of the dominant species resulted in random distributions in both pre- and post-mortality, suggesting that the presence of each dominant species considered did not affect the mortality of the other species (Figures not shown).

2.4 DISCUSSION

2.4.1 Competition and Spatial Patterns in Successional Chronosequence

Previous research has shown that it is rare to observe small-scale regularity in nature (Kenkel 1988, Duncan 1991, He et al. 1997, He and Duncan 2000) and that spatial pattern analysis may be successful in providing strong empirical evidence that tree-to-tree competition is affecting the development of stand structure (Getzin et al. 2006). Many studies have shown that competition can be inferred by comparing the pre-mortality and post-mortality patterns in a stand (Kenkel 1988, He et al. 1997, Martens et al. 1997, Getzin et al. 2006) and by comparing spatial patterns of small versus large trees (Antonovics and Levin 1980). If plant-to-plant competition is occurring in the environment, the post-mortality spatial pattern is expected to the more regular than the corresponding pre-mortality pattern. Similarly, the spatial pattern of large trees should be more regular than that of small and large trees together. In this study, I took this approach to detect the importance of competition in the development of stand structure for a chronosequence of boreal forests.

Results showed that with the exception of spruce in the Mxwood (Figure 2-3G) stand, the univariate analyses did not reveal small-scale regularity in post-mortality aspen, balsam poplar or spruce. However, we did see a correlation between size class and spatial distribution. Both the spatial distributions of large aspen (Figure 2-5 A-D) and large spruce (Figure 2-5 E-G) were found to shift towards regularity as succession progressed. This suggests that intraspecific competition does play roles in structuring the dynamics of the two most dominant species over succession.

2.4.2 Intraspecific Competition (Univariate Spatial Pattern Analysis)

Similar to previous studies (Duncan 1991, Szwagrzyk and Czerwczak 1993, He et al. 1997), I have shown that mortality in the 4 stands representing a boreal chronosequence was a non-random process. Results in Figure 2-2 showed the shift from pre-mortality aggregation to a random distribution post-mortality indicating that mortality was not random for aspen in conspecific neighbourhoods in the DDom, CDom and DDom-U stands. Similarly, shifts from pre-mortality aggregation to either post-mortality regular (spruce in the Mxwood stand) or random distributions (spruce in the CDom stand and balsam poplar in all stands), indicated that the mortality of spruce and balsam poplar was not random in their respective conspecific neighbourhoods. These results are the evidence that intraspecific competition is likely playing a role in the development of stand structure for each species respectively.

As an unexpected case, non-random mortality in aspen in the DDom-U stand led to the spatial pattern shifting from small-scale regularity (at scales up to 2 m) (Figure 2-2B) for pre-mortality aspen (live+dead) to a random distribution for surviving trees post-mortality (Figure 2-2F). From the DDom to the DDom-U stand the relative frequency of aspen increased by 40%. Although the proportion of dead aspen is 4% less in the DDom-U than the DDom stand (Table 2-1, DDOM-U), due to the significant increase in the overall number of aspen in the DDom-U stand, there were more dead aspen in the DDom-U stand. In addition, the average aspen DBH decreased from the DDom stand to the DDom-U stand (26.0 to 21.8 cm, Table 2-1) indicating that the majority of aspen in the DDom-U stand were relatively new recruitments. Although I would expect a high frequency of "young" (small DBH) aspen to cause significant aggregation, it is likely that the majority of these stems were adhering to the aspen boundary discussed earlier (aspen preliminary results, Table 2-1), resulting in a regular distribution pre-mortality. Dead aspen were found to be highly aggregated in DDom-U stand (Figure 2-6B), thus when the high number of dead aspen (arranged in clusters) were removed the post-mortality spatial pattern could have been skewed to be random, masking the intraspecific competition occurring within the aspen population. This is supported by the high proportion of intraspecific mortality observed in the DDom-U stand (Table 2-1, DDOM-U). A previous study observed a similar shift from a regular to a random spatial distribution in an aspen population in a Danish deciduous mixedwood forest (Wolf 2005). Thus similar to Wolf (2005), the unexpected shift in the observed spatial distribution could indicate that mechanisms other than competition may have caused the observed mortality in the DDom-U stand.

Although I was able to reject the random mortality hypothesis for each dominant species in almost every successional phase across a boreal chronosequence, I was not able to firmly detect significant small-scale regularity among surviving trees except for the strong trend of the spatial patterns in both aspen and spruce post-mortality populations shifting towards regularity as succession progressed. The results for the two species were further supported by the significantly higher proportions of mortality in conspecific neighbourhoods (Table 2-1).

2.4.3 Interspecific Competition (Bivariate Spatial Pattern Analysis)

Although bivariate $L(t)$ analysis was not able to detect significant shifts between pre- and post-mortality spatial patterns for aspen, spruce and balsam poplar, these results do not rule out the possibility that interspecific competition may be present and affect stand structure over succession. The importance of competition and intensity of competition in a stand are not necessarily correlated, thus failure to detect competition does not exclusively indicate no competition (Weden et al. 1988). My results merely suggest that interspecific competition was not strong enough to cause significant interspecific tree mortality.

The relative importance of interspecific competition strongly increased for both aspen and balsam poplar and decreased for spruce as succession progressed (Figure 2-2C), suggesting that spruce becomes segregated over succession, possibly resulting in spruce having fewer opportunities to competitively interact with aspen and balsam poplar. Although S values were moderate, spatial segregation (Pielou's S Table 2-1) was the highest for all dominant species in the last stage of the boreal chronosequence (Table 2-1, CDOM), indicating that site heterogeneity may have influenced interspecific competition in this stand. Although intra- and interspecific competition are considered to be greater above ground than below ground (Martens et al. 1997, Little 2002), boreal forest soils can be highly variable (Little 2002). It is possible that soil variability in the CDom stand may have caused species segregation, thus minimizing the opportunity for the dominant species to interact.

The clonal growth of aspen was believed to be the cause of interspecific negative spatial associations between itself and white pine (Peterson and Squires 1995b) and jack pine (Little 2002), thus I would expect similar results between aspen and spruce. Yet, my bivariate analysis was not able to detect any spatial association, negative or positive, among aspen and spruce. Stoll and Prati (Stoll and Prati 2001) suggest that the spatial clustering of a species that has a higher likelihood of being out-competed, may improve the performance of that species in competition. Thus the clonal habit of aspen could have masked significant mortality among aspen. Small variation among mean nearest-neighbour distances for aspen over succession could be explained by the clonal habit of aspen; however post-mortality aspen patterns failed to show similar small-scale post-mortality aggregation (Figure 2-2 E-H) that was detected by Peterson and Squires (1995) and Little (2002). Therefore, failing to detect a spatial pattern shift in my bivariate analyses on aspen was probably not related to the clonal growth habit of aspen.

Spatial patterns are only affected when competition is intensive enough to cause significant mortality (Stoll and Bergius 2005). Consequently, failing to detect significant shifts in spatial distribution of stems by point pattern analysis may be due to the fact that competition is not strong enough to cause significant mortality, but rather reduces growth of neighbouring individuals (Getzin et al. 2006). The observation (Figure 2-5) of the spatial patterns of large (DBH>30cm) aspen and spruce moving towards significant regularity as succession progressed suggests that there is a correlation between tree size and spatial distribution. However, further research is needed to examine how density-dependent competition affects tree size (growth) in the absence of significant mortality.

2.5 CONCLUSION

Density-dependent competition can contribute to tree mortality and to shifting spatial point patterns of tree distribution. Thus, by comparing the spatial patterns of pre-mortality and post-mortality of the same species or of different species can provide useful information about the importance of competition in affecting the structure and dynamics of stands. In this study, I rejected the random mortality hypothesis and showed there was intraspecific competition in the two most dominant species, aspen and spruce, in the boreal forest chronosequence I studied. However, I found no significant interspecific competition in the forest stands. More importantly, I was able to show the trend of competition for the dominant species in the forest: aspen, balsam poplar and spruce, over succession. For both aspen and balsam poplar, the relative importance of intraspecific competition decreases over succession while the relative importance of interspecific competition increases. The opposite trend was observed for spruce.

Although spatial point pattern analysis is considered to be a major tool for detecting competitive interaction, it relies on competition being intense enough to cause significant mortality. Further research is needed to determine if additional mechanisms are affecting tree growth or survival when spatial point pattern analysis fails to detect significant shifts between pre- and post-mortality patterns.

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2.7 TABLES

Table 2-1. *Stand structure and composition for dominant species in all successional phases. <NN> = mean nearest-neighbour distance; Pielou's S= Pielou's segregation index (Pielou 1961); Intra mortality = proportion of dead trees located within conspecific neighbourhoods; Inter mortality = proportion of dead trees located within heterospecific neighbourhoods.*

Plot/Species	<NN> (live+dead)	# stems (live+dead)	% total stems in stand	% mortality	<DBH> (cm)	Pielou's S	Intra mortality (%)	Inter mortality (%)
Deciduous Dominated (DDom)								
Aspen	1.45	789	74.4%	27.8%	26.0	0.4081	83.6%	2.3%
White Spruce	1.78	79	7.4%	0%	3.7	0.1990	0%	0%
Balsam Poplar	1.68	189	17.8%	19%	19.2	0.1531	50%	30.6%
Deciduous Dominated with Coniferous Understory (DDom-U)								
Aspen	1.46	1104	76.9%	26.8%	21.8	0.2355	72.3%	3.7%
White Spruce	1.17	203	14.1%	0.5%	14.2	0.1920	0%	0%
Balsam Poplar	1.19	129	9%	19.4%	4.6	0.1935	24%	36%
Mixed wood (Mxwood)								
Aspen	1.33	303	15.3%	48.5%	33.5	0.0859	0%	73.5%
White Spruce	1.26	462	23.3%	33.3%	28.7	0.1420	6.5%	40.9%
Balsam Poplar	1.10	5	0.3%	100%	N/A**	0.1233	0%	100%
Coniferous Dominated (CDom)								
Aspen	1.54	159	20.5%	49.7%	39.9	0.4749	36.7%	25.3%
White Spruce	1.70	518	66.8%	17.2%	19.3	0.4042	75.3%	4.5%
Balsam Poplar	1.45	84	10.8	34.5%	35.1	0.3625	34.5%	24.1%

2.8 FIGURES

Figure 2-1. *Size-distance correlations indicating the relative importance (r^2) of overall competition (A), intraspecific competition (B) and interspecific competition (C) for trembling aspen (—), white spruce (---) and balsam poplar (⋯⋯). Correlation values were calculated for 4 stages of a chronosequence of boreal succession identified as DDom (deciduous dominated), DDom-U (deciduous dominated with coniferous understory), Mxwood (mixedwood) and CDom (coniferous dominated). Changes in the graph indicate either increase or decrease of the relative importance of the corresponding competition in the respective species over succession.*

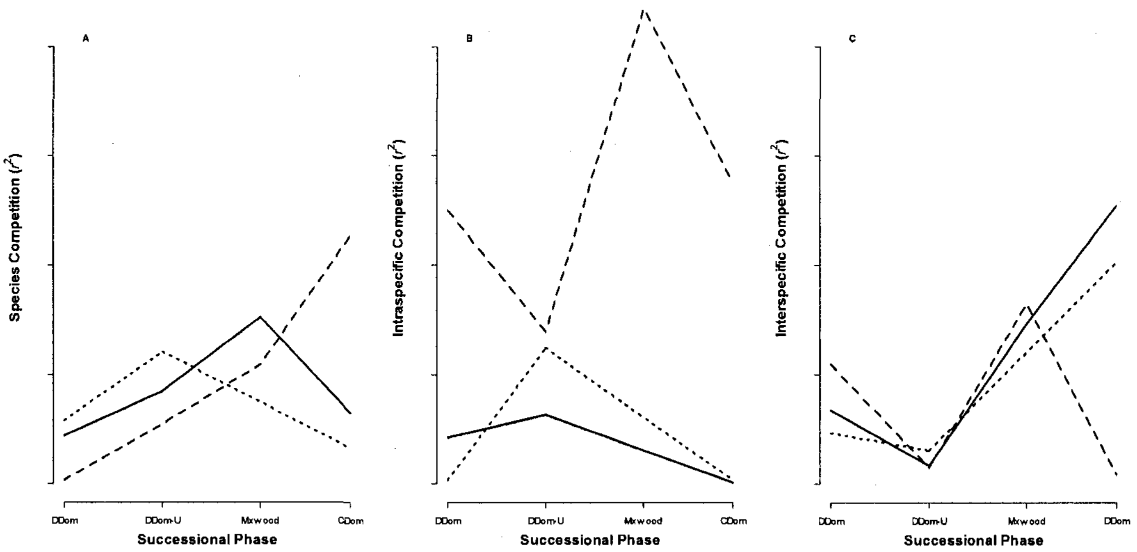


Figure 2-2. *Plots of L(t) for trembling aspen in 4 stages of a chronosequence of boreal succession. Observed patterns (—) that fall above, below and within 95% Monte Carlo intervals (---) indicate an aggregated, regular or random distributed pattern, respectively. Shifts between pre-mortality (live+dead) (top figures: A-D) and post-mortality (live) (bottom figures: E-H) patterns would reject the random mortality hypothesis for the corresponding successional phase.*

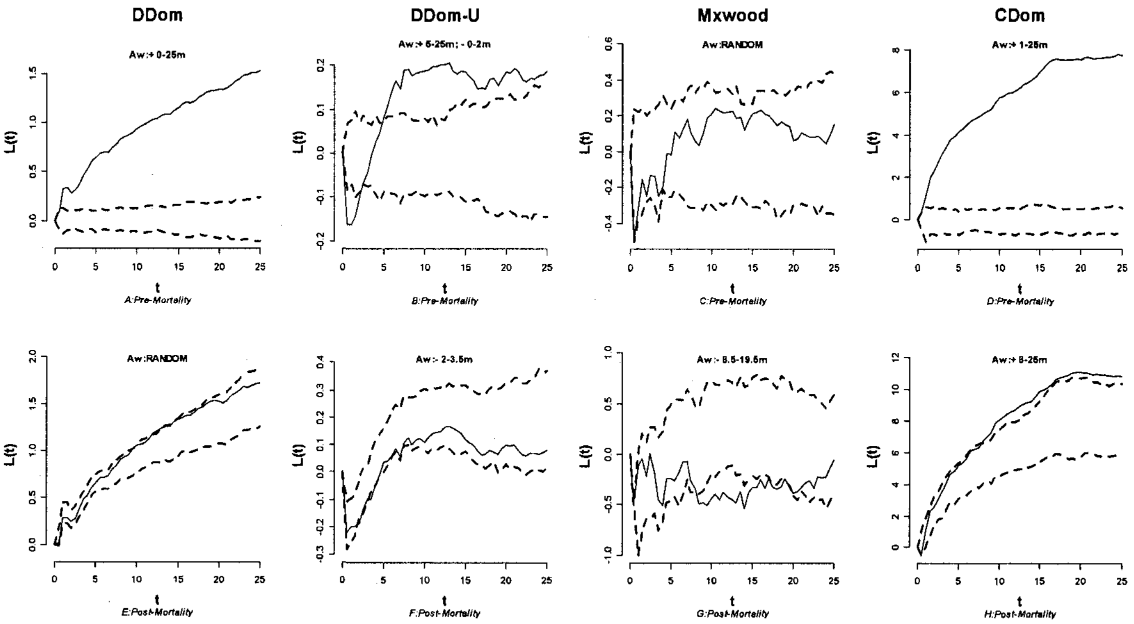


Figure 2-3. *Plots of L(t) for white spruce in 4 stages of a chronosequence of boreal succession. Observed patterns (—) that fall above, below and within 95% Monte Carlo intervals (---) indicate an aggregated, regular or random distributed pattern, respectively. Shifts between pre-mortality (live+dead) (top figures: A-D) and post-mortality (live) (bottom figures: E-H) patterns would reject the random mortality hypothesis for the corresponding successional phase.*

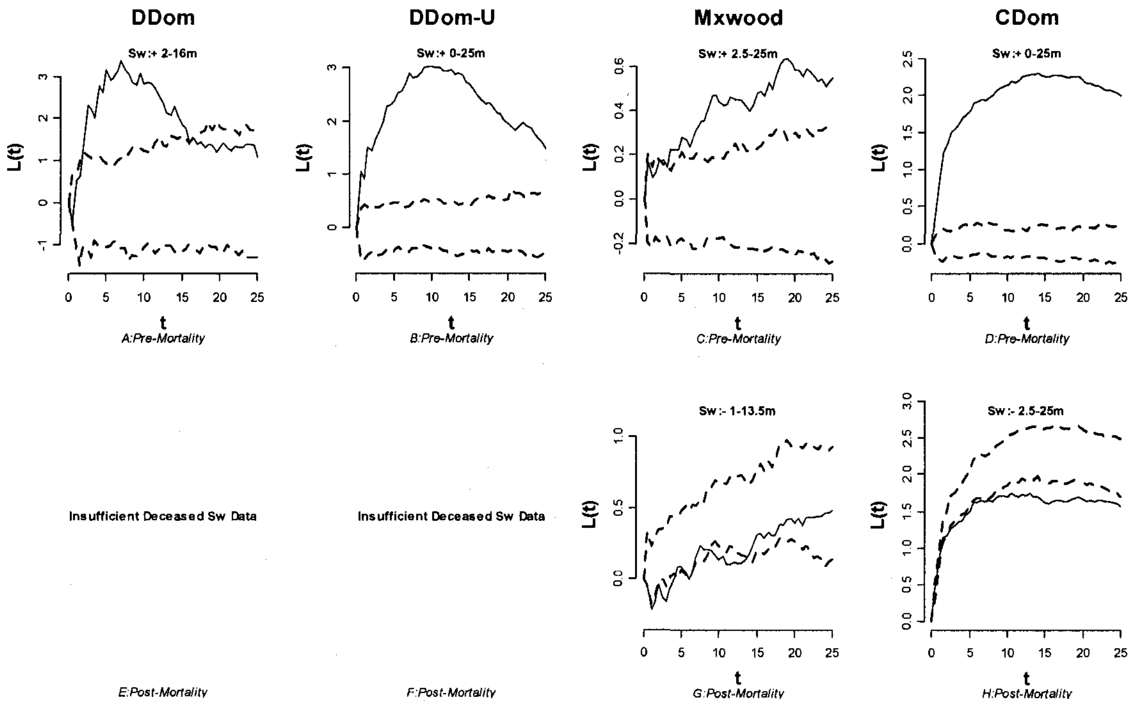


Figure 2-4. *Plots of $L(t)$ for balsam poplar in 4 stages of a chronosequence of boreal succession. Observed patterns (—) that fall above, below and within 95% Monte Carlo intervals (---) indicate an aggregated, regular or random distributed pattern, respectively. Shifts between pre-mortality (live+dead) (top figures: A-D) and post-mortality (live) (bottom figures: E-H) patterns would reject the random mortality hypothesis for the corresponding successional phase.*

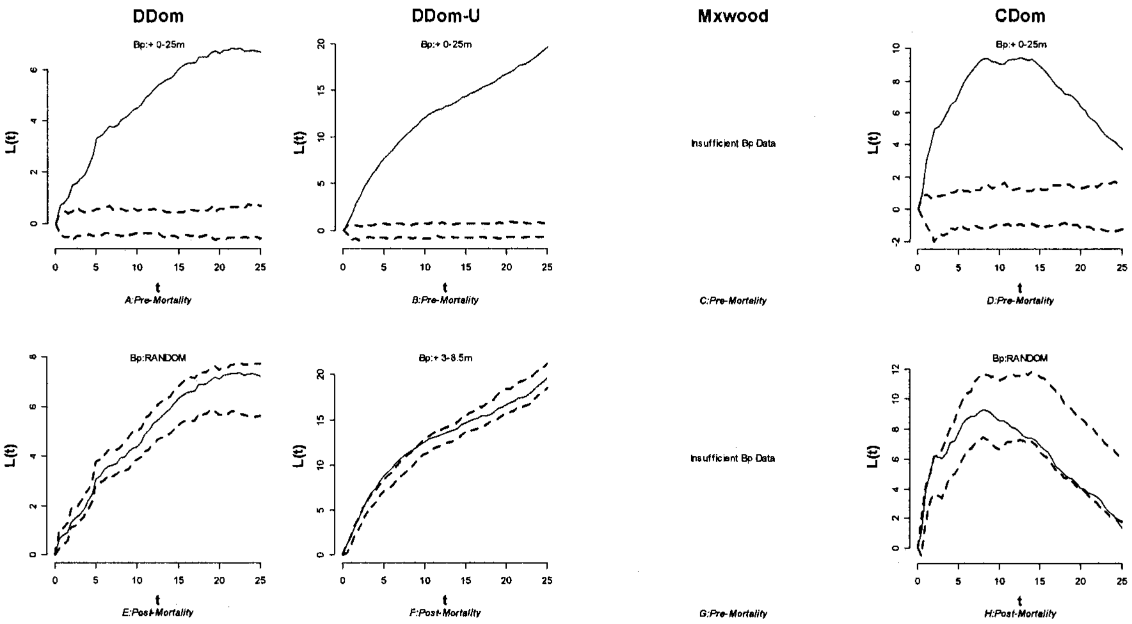


Figure 2-5. *Plots of L(t) analysis for large (DBH>30cm) trembling aspen (top figures: A-D) and white spruce (bottom figures: E-H) in 4 stages of a chronosequence of boreal succession. Observed patterns (—) that fall above, below and within 95% Monte Carlo intervals (---) indicate an aggregated, regular or random distributed pattern, respectively. Detecting a regular pattern provides empirical evidence that density-dependent competition affects the spatial distribution of the respective population.*

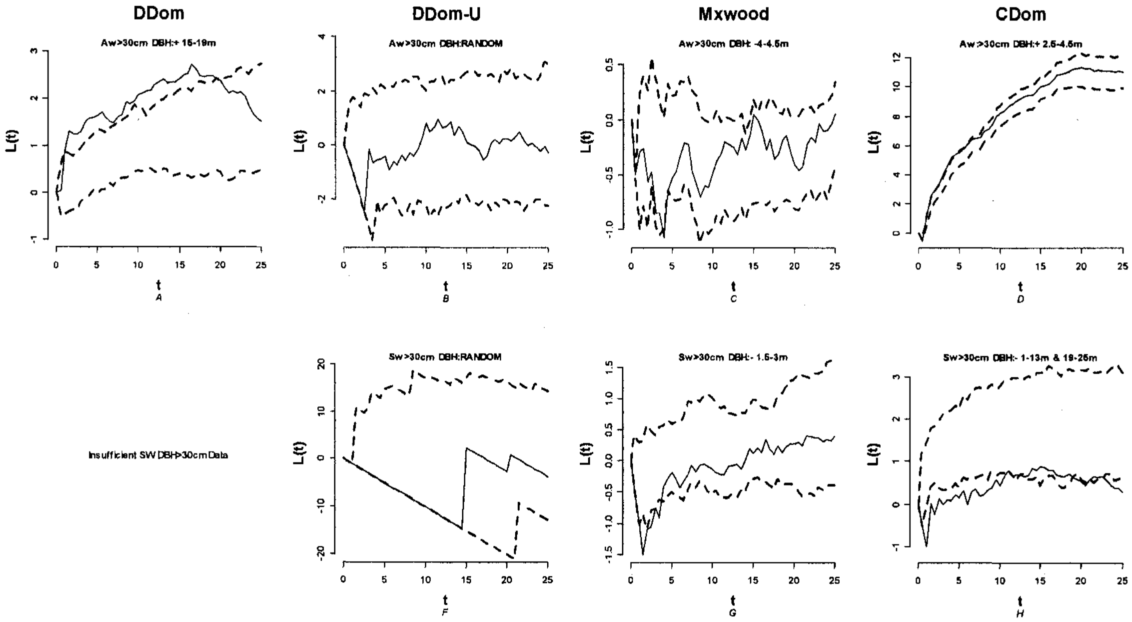
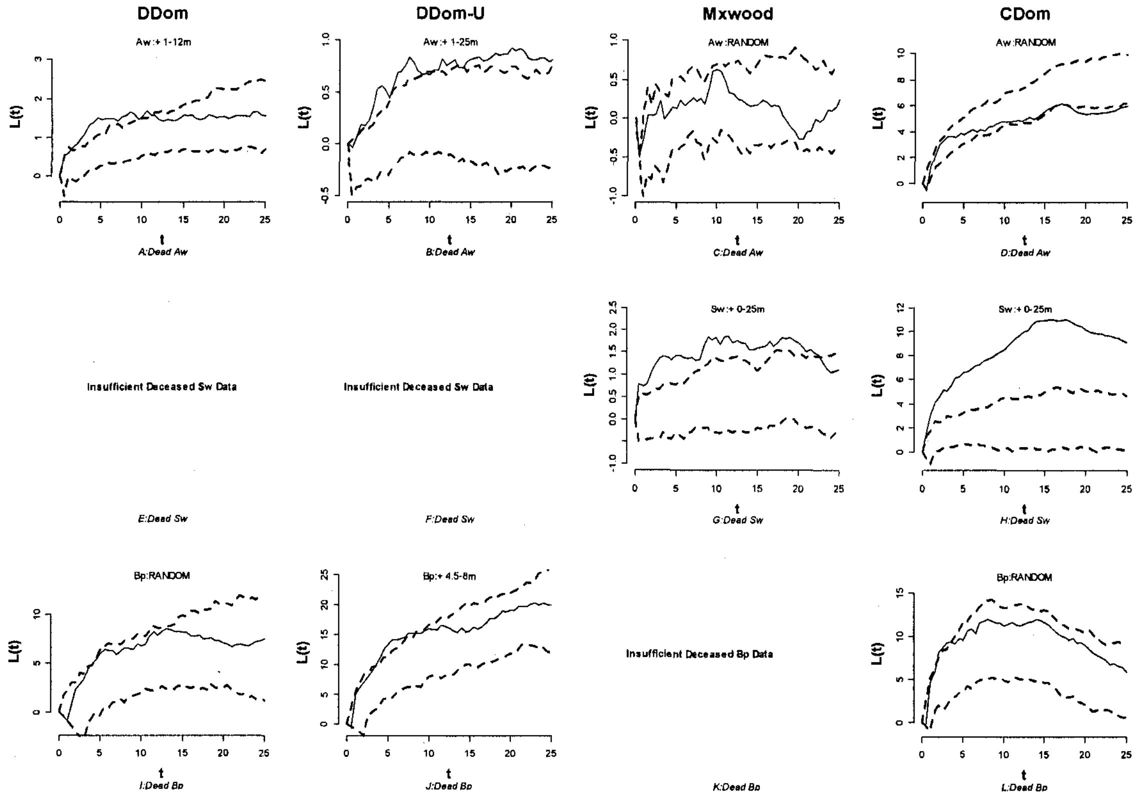


Figure 2-6. *Plots of L(t) analysis for dead trembling aspen (top figures: A-D), white spruce (middle figures: E-H) and balsam poplar (bottom figures: I-L) in 4 stages of a chronosequence of boreal succession. Observed patterns (—) that fall above, below and within 95% Monte Carlo intervals (----) indicate an aggregated, regular or random distributed pattern, respectively. Detecting a regular pattern provides empirical evidence that density-dependent competition affects the spatial distribution of the respective population.*



Chapter 3: Logistic regression models of mortality for inferring the density-dependent effect in a boreal forest of Alberta

3.1 INTRODUCTION

Much research has shown that density-dependent effects can have a significant impact on the spatial structure, biodiversity maintenance and population dynamics in forest stands. For example, density-dependent competition can cause self thinning and thus high mortality among pioneer trees in dense patches of both conspecific and heterospecific neighbourhoods (Antonovics and Levin 1980, Ford and Diggle 1981, Weiner 1984, Peet and Christensen 1987, Kenkel 1988, Duncan 1991, Newton and Joliffe 1998, He and Duncan 2000, Little 2002, Getzin et al. 2006). However, less is understood about how competition would affect individual tree mortality once a tree has successfully established in a stand. Although mortality is considered to be a complex event subject to the effects of multiple factors (Timoney and Lee 2001, Yang et al. 2003), the negative effects of plant-to-plant competition is widely considered to be an underlying cause of tree mortality in high density neighbourhoods (Peet and Christensen 1987, Halpern et al. 1997, Szwagrzyk and Szewczyk 2001). Hence, the occurrence of tree death is expected to be a function of the density of its neighbouring trees.

As I have shown in the previous chapter, spatial point pattern analysis by comparing pre- and post-mortality patterns is a useful approach for studying the effect of competition on stand structure development (Laessle 1965, Phillips and MacMahon 1981, Duncan 1991, Briones et al. 1996, Weiner et al. 1998, Szwagrzyk and Szewczyk 2001, Little 2002, Shackleton 2002, Getzin et al. 2006). However, this method provides limited insight on how the density that each individual tree experiences would affect its survivorship. In addition, this type of analysis is considered unable to fully characterize the dynamic processes of mixed stands (Zhao et al. 2006).

In this study, I was interested in conducting a neighborhood analysis to identify possible density variables that may significantly contribute to mortality. Neighbourhood analysis has been conducted for tropical and temperate forests and have shown a proportion of trees experiencing significant density-dependent mortality (Lambers et al. 2002, Peters 2003, Zhao et al. 2006). The neighborhood analysis for detecting competition can be complicated when analyzing a boreal forest chronosequence because succession in this forest type results in drastic changes in the makeup of the canopy structure and light condition, which could either decease or increase a tree's ability to survive negative density-dependent effects.

The successional pathway of western boreal forest is well documented (Hornberg et al. 1995, Peterson and Squires 1995, Kneeshaw and Bergeron 1998, Cumming et al. 2000). Pioneer stands are dominated by deciduous aspen and poplar and over succession white spruce enters the stand, shifting the canopy composition to mixedwood and spruce which eventually dominates the stand (Kneeshaw and Bergeron 1998). Analyzing the morality in each successional phase along a boreal chronosequence would help identify the effect of neighborhood density on mortality and determine if the effect of neighbourhood density possibly changes over succession. In this study, I used logistic models to quantify the effect of neighbourhood densities on tree mortality.

3.2 METHODS

3.2.1 STUDY SITES and DATA COLLECTION

The study sites are located in the EMEND (Ecosystem Management Emulating Natural Disturbance) research site, approximately 50 km North West of Peace River, Alberta (56° 46' 13" N -118° 22' 28" W). The site soils are defined as fine-textured formed predominantly on glacio-lacustrine deposits. The mean annual temperature is 13.9° and a mean summer rainfall is 204.25 averaged from the years 2000 to 2003. The EMEND research project is a large scale, multi-factorial experiment consisting of four stand types that are classified based on cover class and eight different treatment levels. The four cover classes are defined as deciduous dominated (>70% deciduous canopy cover), deciduous dominated with coniferous understory (>70% deciduous canopy cover and coniferous understory at least 50% of the canopy height), mixedwood (canopy consisting of both deciduous and coniferous cover between 35-65%) and conifer dominated (>70% conifer canopy cover).

For this study four mature, undisturbed stands were chosen; one representing each of the four cover types. The stands are hereby denoted as: DDom (deciduous aspen (*Populus tremuloides*) dominated), DDom-U (deciduous aspen (*Populus tremuloides*) dominated with coniferous white spruce (*Picea glauca*) understory), Mxwood (mixed-wood) and CDom (coniferous white spruce (*Picea glauca*) dominated). These stands represent a chronosequence of boreal forest succession. The age of the stands were estimated, using increment cores, to be approximately 107, 110, 142 and 169 years (DDom, DDom-U, Mxwood, CDom) in 1997 when EMEND was first established.

Site locations were carefully chosen using a map to minimize edge effects and ensure that large clearings or roads were not included in the site area. Before the boundaries of the plot were established a physical inspection of the proposed area was conducted to ensure that the selected site was representative of the overall stand. In each of the stands a 100×100 m (1-hectare) plot was established by selecting a point to serve as the south west corner of the plot. The other plot corner coordinates were referenced from this point.

A Nikon Total Station was used to obtain relative coordinates of each live deciduous tree (>2 cm diameter at breast height) and coniferous (>1 cm diameter at breast height) tree within each plot. Each individual tree, snag and stump was given a unique tag number and the breast height of live trees was marked as a reference point that was later used for determining the height and diameter at breast height of each individual live tree. The diameter at breast height (DBH, at 1.3 m height) of each tree was measured twice using a caliper and the average of the two measurements was used for DBH. The height of each tree was also measured using a laser hypsometer. The final data contain the location coordinates, DBH, height, and species identity for every live tree, and the coordinates and species identity of all stumps, logs and snags.

Although three deciduous: trembling aspen (*Populus tremuloides*) (Aw), balsam poplar *(Populus balsamfera)* (Bp) and paper birch *(Betula papyrifera)* (Pb) and three conifer species: white spruce (*Picea glauca*) (Sw), balsam fir *(Abies balsamea)* (Bf), and lodgepole pine were recorded, trembling aspen, balsam poplar and white spruce were the only species present in all 4 stands. Since this study only focused on analyzing the relationship between deciduous and coniferous trees, I sorted all trees into two groups defined as either deciduous or coniferous.

3.2.2 THE LOGISTIC MODEL and EXPLANATORY VARIABLES

Individual tree mortality is a discrete event where the response variable y is a binary variable represented by y=1 (tree is alive) and y=0 (tree is dead). The logistic regression model for y is:

$$\text{Prob (tree is alive)} = \pi\left(y_i = 1 \middle| x_1, x_2, \ldots, x_n\right) = \frac{e^{\beta_0+\beta_1 x_1+\beta_2 x_2+\ldots+\beta_n x_n}}{1+e^{\beta_0+\beta_1 x_1+\beta_2 x_2+\ldots\beta_n x_n}}, \qquad (1)$$

$$\text{Prob (tree is dead)} = \pi\left(y_i = 0 \middle| x_1, x_2, \ldots, x_n\right) = 1-\pi\left(y_i = 1\right) = 1-\frac{e^{\beta_0+\beta_1 x_1+\beta_2 x_2+\ldots+\beta_n x_n}}{1+e^{\beta_0+\beta_1 x_1+\beta_2 x_2+\ldots\beta_n x_n}}, (2)$$

where $x = (x_1, x_2, \ldots, x_n)$ are explanatory variables and $\beta = (\beta_1, \beta_2, \ldots, \beta_n)$ are unknown parameters for n explanatory variables.

In this study each x_i represents the density of a specific grouping of trees around a specified focal tree. Densities were defined as the numbers of deciduous, coniferous and dead trees occurring into two annuli with width from 0 to 5 m and 5 to 10 m around each tree. Environmental variability, such as soil properties, can significantly affect mortality (Little 2002). Therefore, if the environment is unfavorable there will be a higher probability of mortality in the neighborhood of a focal tree. The inclusion of the density of dead trees within each ring as an explanatory variable provided a measure of the spatial autocorrelation for each of the tree mortality probability models. Alive neighbouring trees were divided into 3 size groupings defined as: small (DBH < 10 cm), medium (10 < DBH < 25 cm), and large (DBH > 25 cm). Since DBH was not recorded for dead trees, all the dead trees within each annulus were grouped together. Deciduous and coniferous mortality were modeled in each stand using the 14 density variables. In a preliminary analysis I also experimented with annulus rings up to 20 meters, but I did not find densities at distances larger than 10 m had any significant effect on tree mortality.

3.2.3 MODEL FITTING

I used the maximum likelihood method to fit model (1), using an iterative weighted least squares procedure (Charnes et al. 1976, Dobson 2002). The log-likelihood function is:

$$\begin{aligned} l(y,\pi(x_i)) &= \sum_{i=1}^{N}\left[y_i \ln(\pi(x_i)) + (1-y_i)\ln(1-\pi(x_i))\right] \\ &= \sum_{i=1}^{N}\begin{bmatrix} y_i\left[(\beta_0+\beta_1x_1+\ldots+\beta_{14}x_{14}) - \ln(1+e^{\beta_0+\beta_1x_1+\ldots+\beta_{14}x_{14}})\right] + \\ (1-y_i)\left[\ln(1) - \ln(1+e^{\beta_0+\beta_1x_1+\ldots+\beta_{14}x_{14}})\right] \end{bmatrix} \\ &= \sum_{i=1}^{N}\left[y_i(\beta_0+\beta_1x_1+\ldots+\beta_{14}x_{14}) - \ln(1+e^{\beta_0+\beta_1x_1+\ldots+\beta_{14}x_{14}})\right] \end{aligned} \tag{3}$$

where each x_i is a vector of the observed explanatory density variables. Maximum likelihood estimates $\hat{\beta}$ for equation (1) were obtained by solving the iterative equation:

$$b^{m} = \left[(X^{T}WX)^{(m-1)}\right]^{-1}\left(X^{T}Wy\right)^{(m-1)} \tag{4}$$

where,

$$b = \begin{bmatrix} \beta_0 \\ \beta_1 \\ \vdots \\ \beta_{15} \end{bmatrix} \qquad X = \begin{bmatrix} x_{1,1} & x_{1,2} & \cdots & x_{1,N} \\ x_{2,1} & x_{2,2} & \cdots & x_{2,N} \\ \vdots & \vdots & \cdots & \vdots \\ x_{15,1} & x_{15,2} & \cdots & x_{15,N} \end{bmatrix} \qquad y = \begin{bmatrix} y_1 \\ y_2 \\ \vdots \\ y_{15} \end{bmatrix}$$

N is the total number of focal trees considered and W is a diagonal 15×15 weight matrix with diagonal entries, $W_{i,i}(b)=\pi(b,x_i)[1-\pi(b,x_i)]$. In equation (4), m is the iterative step. Calculations begin with initial values b=0 and the estimated parameters are obtained once all estimated $\hat{\beta}$ converge (Green 1984, Dobson 2002, Fort and Lambert-Lacroix 2005).

Model fitting and parameter estimations were computed using the "glm" and "glm.fit" functions in the base package of R (R Development Core Team 2005) with the specification family=binomial(link=logit).

3.2.4 VARIABLE SELECTION and GOODNESS-of-FIT TEST

Initial models were derived including all 14 explanatory variables. I then conducted variable selection for each of the model by removing the insignificant variables. The "step" function in the base R package selected explanatory variables which resulted in the lowest Akaike's An Information Criterion (AIC) value. In addition, the Wald test for individual variables obtained from the "glm" of R was used to confirm the results of the step function. Then a new model, including only the significant explanatory variables, was re-fitted to obtain improved parameter estimates $\hat{\beta}$ for both deciduous and coniferous mortality in each stand.

Once the final model was obtained, the Hosmer-Lemeshow goodness-of-fit was used to test the overall model fit (Hosmer and Lemeshow 1989). For this test, observations were sorted by survival probabilities and divided into 10 equal groups. The expected number of live trees under the final model was compared to the observed number of live trees using the Hosmer-Lemeshow statistic and the Person's χ^2 statistic with a significance level of $\alpha = 0.05$. Both statistics were calculated using the "cor" and basic mathematical commands in the base package of R (R Development Core Team 2005).

I also used a locally-weighted polynomial regression to obtain a smooth function to visualize the trend of the mean survival probability values.

Variable selection and the locally-weighted polynomial regression were computed using the "step" and "lowess" functions in the base package of R (R Development Core Team 2005).

3.3 RESULTS

A total of 723, 912, 162 and 135 alive and 225, 321, 169 and 108 dead trembling aspen, balsam poplar and paper birch, respectively, were used to fit each of the 4 deciduous mortality models in the DDom, DDom-U, Mxwood, and CDom stands. In contrast, 1356 and 438 alive and 293 and 95 white spruce, balsam fir and lodgepole pine were used to fit conifer mortality models in the Mxwood and CDom stands, respectively. Mortality models could not be fitted to the coniferous trees in the DDom and DDom-U stands because the number of dead conifers was too low for a reliable analysis. Summary statistics for both the parameter estimates $\hat{\beta}$ and the Hosmer-Lemeshow goodness-of-fit test, for both deciduous and conifer mortality in each stand, are listed in Tables 3-1 to 3-4.

Deviance values for $\hat{\beta}$ indicate the relative importance of the corresponding variable in predicting mortality. Although the step function and corresponding regression p-value can show significance for a variable, a deviance value less then 1 indicates the corresponding value has a low contribution to the overall model. Thus, a variable with a corresponding deviance value ≤ 1 was removed from the final model in the conifer dominated stand. The density of medium sized deciduous trees with a DBH between 10 and 25cm within a 5 m circle (DDensityMed5) significantly in predicted conifer mortality in the CDom stand, but deviance was small (D=1). Thus, this variable was removed from the model. Similarly, the density of coniferous trees with DBH>10 cm between 5 and 10 m annulus (CDensitySm10) was found to be significant in predicting deciduous mortality in the CDom stand, but deviance values indicated it made too small a contribution to the overall model to be included (*D*=0.21).

Final mortality models for both deciduous and conifer trees in each stand are included in the corresponding figures (Figures 3-1 to 3-4), where DDensity, CDensity and DeadDensity represent the number of deciduous, conifer and dead trees in the indicated annulus (5, 10 represent the 0-5 m and 5-10 m annulus, respectively). Variables which include small, medium and large trees are indicated by Sm, Med and Lg, respectively. For example, the variable CDensityMed10 represents the number of medium conifer trees within the 5-10 m annulus.

In each figure (Figures 3-1 to 3-4) the resulting survival probabilities are plotted against the density variable which made the highest contribution to the specific mortality model. Each point on the graph represents an individual tree evaluated in the model. For example in Figure 3-1 the number of dead trees within a 5 meter radius of a focal deciduous tree was plotted against the survival probability of each tree under the resulting deciduous mortality model.

The Hosmer-Lemeshow goodness-of-fit test indicated that the logistic models for deciduous and conifer mortality modeled the observed mortality in the all stands well (at $\alpha = 0.05$, Tables 3-1B, 3-2B, 3-3B and 3-4B). Model smoothers from locally-weighted polynomial regression (Figures. 3-1 to 3-4) further validated the Hosmer-Lemeshow tests by graphically illustrating the trend of the mean residual values which closely fit the observed data in deciduous or conifers dominated stands.

3.4 DISCUSSION

The logistic models of tree mortality for both deciduous and coniferous trees in each successional stage suggested that the density-dependent effect was significant in deciduous and conifers dominated stands as well as in the mixedwood stand. Density-dependent competition is widely considered to be present in dense plant communities, but its effects on communities vary (Keddy 2001). The result from this study is consistent with this finding since the fit of both the deciduous and conifer mortality models varied among stands. However, as pointed out in the previous chapter, failing to detect or detecting a weak effect of competition on mortality may imply that competition is not intense enough to cause significant mortality, but there is still a possibility that competition is responsible for a reduction in tree growth (He and Duncan 2000, Wyckoff and Clark 2002, Getzin et al. 2006). It has been shown that although growth rate increases with stem size, the relationship between growth rate and mortality remains unchanged (Kobe et al. 1995). In addition, stems may exhibit an extended period of growth decline prior to death (Wyckoff and Clark 2002), thus data on tree growth is essential for a complete understanding of the effect of competition on stand structure and dynamics.

It is possible that other factors, such as insect infestation or root diseases (Volney 1988, Brandt et al. 2003), may also contribute to tree mortality in the four study stands. However, the resulting goodness-of-fits for the neighbourhood logistic models in all the stands provide strong empirical evidence that tree density is significant to the observed mortality, thus the important role density-dependent competition plays in tree mortality cannot be ignored in these forests. Moreover, although it is possible that other factors may be contributing to the observed mortality in these forests, there is no recent record of any major insect or disease outbreaks in any of the study stands, further supporting that the observed mortality is likely related to competition for limited resources.

For all models, with the exception of deciduous mortality in the DDom stand and conifer mortality in the Mxwood stand, the most significant factor to mortality was the density of a conspecific variable, indicative of the importance of intraspecific competition. In the DDom stand the density of dead trees was the most important variable factor predicting individual mortality. Following the number of dead trees, the number of medium deciduous trees was the second most important variable. Similarly, following the density of dead trees, the number of large conifer trees was found to be the second highest contributor to conifer mortality in the Mxwood stand. All of these results suggest that intraspecific competition is stronger and more likely to result in individual mortality than interspecific competition.

Over succession, the number of variables which significantly contributed to deciduous mortality increases (Tables 3-1 to 3-4), but the effect of each variable made on mortality varied. This suggests that the density-dependent effect depends on the stand type and the habitat conditions of the stand. The only variable that was shown to be significant for deciduous mortality in all 4 stands was the density of deciduous trees with a DBH between 10 and 25 m in the annulus from 5 to 10 m. However, I did not observe a consistent positive or negative trend for this variable, which makes mortality predictions based on this variable difficult.

Since there are a lack of large deciduous trees in the DDom stand and large coniferous CDom stand, medium trees (10<DBH<25 cm) can be considered to represent the dominant trees of these respective species in each of these stands. As expected, the density of large trees (DBH>25 cm) from both the tree types modeled and the dominant tree types in the canopy within 0-5 or the 5-10 m ranges, emerged as significant factors affecting mortality (Tables 3-1 to 3-4). Large trees suppress smaller trees by shading the stand (Zhao et al. 2006), which explains the highly significant effect of large trees on mortality throughout succession. The negative coefficients in the DDom-U and Mxwood and the positive coefficient in the CDom stand for the density of large deciduous trees suggest that these large deciduous trees are probably more detrimental to their surrounding deciduous neighbours in the earlier successional stages than the later. Moreover, the survival probability of deciduous trees in the DDom-U stand was observed to increase with the density of small deciduous trees (DBH<10 cm) within 5 m. This further supports the hypothesis that in the earlier stages of succession a deciduous tree has a higher survivorship if its nearest neighbours are also small deciduous trees.

In conifer mortality models the positive coefficients for large deciduous trees and the negative coefficients for large conifer trees suggest that deciduous trees are potentially better neighbours to conifer trees because they facilitate rather than hindering survival like the large conifer trees do. Similar to the observations for deciduous trees, I observed a positive association between small conifer trees (DBH<10 cm) within 5 m and conifer survival. In addition, the observed negative coefficient for medium conifer trees (10<DBH<25 cm) further suggests that once conifers reach a certain size they would become superior competitors and have a good chance to outcompete their neighbours.

Mortality models have successfully used the basal area of large trees to model the effect of large trees on tree mortality (Brito et al. 1999, Monserud and Sterba 1999, Bravo et al. 2001, Lessard et al. 2001, Sterba et al. 2002, Wyckoff and Clark 2002, Yang et al. 2003). This confirms that including a measure of the proportion of large trees will improve the accuracy of individual tree mortality models. In addition, this study supports including a measurement of the proportion of small trees (regeneration), in individual tree mortality models to improve their prediction accuracy.

My study found that the density of dead trees within 0-5 and 5-10 m annuli was a significant factor affecting both deciduous and conifer mortality in 3 of the four stands. With one exception in the CDom stand, this variable consistently showed a negative effect, suggesting that a high number of dead neighbours would lower the survival rate of a deciduous or conifer stem. Although the density of dead trees within the 5-10 m annulus was found to be positively correlated with conifer survivorship in the CDom stand, the estimated coefficient is small ($\beta = 0.06778$, Table 3-4A) and the deviance indicates that this variable is less significant to conifer mortality ($D = 4.55$) in the CDom stand than the other variables (Table 3-4A). In addition, the dead tree density variable indicated strong aggregation of dead trees supporting the aggregation of dead aspen and white spruce identified in the previous spatial point pattern analyses. In addition to the density variables previously mentioned, this study including a measurement of the proportion of deceased trees in individual tree mortality models to potentially improve model accuracy.

Although this study was able to identify three density variables that could be used to improve the accuracy of mortality models, there are limitations within the data set used for this analysis which could affect the accuracy of its findings. Knowing the size of a tree at the time of its death is vital to this study since smaller trees are expected to have a lower survival probability in denser neighbourhoods. However, this information was not available, thus the results of this study need to be reexamined with a complete data set to confirm if the density of large, small and dead trees truly affects tree mortality. In addition, stem-mapped data does not provide a measurement of when a tree died, but is rather a snap-shot data set that indicates that a tree died at some point in the past. The size of the surviving neighbours could have changed between the time of a tree's death and data collection, thus skewing the results.

3.5 CONCLUSION

This study highlighted the effect of density-dependence on tree mortality and validated the hypothesis that the negative density-dependent effect of plant-to-plant competition likely caused tree mortality in high density neighbourhoods in all stages of succession. This study also showed that the density-dependent effect is dependent on the size and tree type of the competitors as well as the habitat conditions of the stand. The number of variables and the effect of each identified variable on mortality varied for both deciduous and conifer mortality over succession. However, I also found consistent effects from dead trees and same tree type large trees (DBH>25 cm) and small trees (DBH<10 cm) on mortality. These variables could be potentially incorporated into individual tree mortality models to improve prediction accuracy. The findings of this study further support the importance of density-dependent effects in shaping boreal forest structure and provided insights into stand dynamics of boreal forests over succession.

3.6 LITERATURE CITED

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3.7 TABLES

Table 3-1 (A & B). Results for (A) parameter estimates and (B) Hosmer-Lemeshow goodness-of-fit test for the deciduous mortality model in the deciduous dominated (DDom) stand.

(A) Parameter Estimates

Deciduous Mortality Model

Variables	df	$\hat{\beta}$	SE	*P-Value*	Deviance
(Intercept)		1.44856	0.17368	< 2e-16	
DeadDensity5	1	-0.16467	0.04187	8.39E-05	20.04
DDensityMed10	1	0.03098	0.01358	0.0226	3.95
DeadDensity10	1	-0.04604	0.02183	0.0349	4.42

(B) Hosmer-Lemeshow goodness-of-fit test

Deciduous Mortality Model

		Alive Trees		
Group	**Total # of Trees**	**Observed**	**Expected**	**Difference**
1	98	52	56	-4
2	98	75	65	10
3	98	64	68	-4
4	98	69	71	-2
5	98	77	73	4
6	98	80	75	5
7	98	81	76	5
8	98	73	78	-5
9	97	76	78	-2
10	97	83	82	1
Total	978	730	722	8

Hosmer-Lemeshow statistic = 11.941 with df = 8 (p-value = 0.1539)

Table 3-2 (A & B). Results for (A) parameter estimates and (B) Hosmer-Lemeshow goodness-of-fit test for the deciduous mortality model in the deciduous dominated with conifer understory (DDom-U) stand.

(A) Parameter Estimates

Deciduous Mortality Model

Variables	df	$\hat{\beta}$	SE	*P-Value*	Deviance
(Intercept)		1.72527	0.26156	4.22E-11	
DDensitySm5	1	0.13463	0.03735	0.000313	26.23
CDensityMed5	1	-0.16999	0.04584	0.000209	17.28
CDensityLg5	1	-0.266	0.14878	0.073799	2.09
DDensityMed10	1	-0.02925	0.01287	0.023029	3.81
DDensityLg10	1	-0.04753	0.02919	0.103459	2.64

(B) Hosmer-Lemeshow goodness-of-fit test

Deciduous Mortality Model

		Alive Trees		
Group	**Total # of Trees**	**Observed**	**Expected**	**Difference**
1	123	70	69	1
2	123	81	82	7
3	123	84	87	-3
4	122	93	89	4
5	122	98	91	7
6	122	96	93	3
7	122	99	94	5
8	122	98	97	1
9	122	101	101	0
10	122	111	110	1
Total	1223	931	913	18

Hosmer-Lemeshow statistic = 5.025 with df = 8 (p-value = 0.7549)

Table 3-3 (A & B). Results for (A) parameter estimates and (B) Hosmer-Lemeshow goodness-of-fit test for both the deciduous and conifer mortality models in the mixedwood (Mxwood) stand.

(A) Parameter Estimates

Deciduous Mortality Model

Variables	df	$\hat{\beta}$	SE	*P-Value*	Deviance
(Intercept)		1.17291	0.33695	3.481	
DDensityLg10	1	-0.17018	0.07133	-2.386	5.68
DDensityMed10	1	-0.58438	0.21837	-2.676	5.88
DDensityMed5	1	-0.72009	0.31387	-2.294	4.6
CDensitySm10	1	-0.01874	0.01103	-1.699	2.92

Conifer Mortality Model

Variables	df	$\hat{\beta}$	SE	*P-Value*	Deviance
(Intercept)		1.30531	0.26179	6.16E-07	
DDensityMed5	1	0.39469	0.19415	0.042061	4.35
DDensityLg5	1	0.17772	0.06877	0.009764	6.21
CDensitySm5	1	0.02746	0.01171	0.019044	4.57
DeadDensity5	1	-0.09572	0.02687	0.000367	13.8
CDensityLg10	1	0.0619	0.02403	0.010004	9.04

(B) Hosmer-Lemeshow goodness-of-fit test

Deciduous Mortality Model

		Alive Trees		
Group	**Total # of Trees**	**Observed**	**Expected**	**Difference**
1	34	10	10	0
2	33	12	12	0
3	33	14	13	1
4	33	15	14	1
5	33	13	16	-3
6	33	18	17	1
7	33	16	18	-2
8	33	19	19	0
9	33	24	21	3
10	33	21	23	-2
Total	331	162	162	0

Hosmer-Lemeshow statistic = 3.461 with df = 8 (p-value = 0.9022)

Conifer Mortality Model

		Alive Trees		
Group	**Total # of Trees**	**Observed**	**Expected**	**Difference**
1	165	113	115	-2
2	165	132	125	7
3	165	137	130	7
4	165	123	133	-10
5	165	131	136	-5
6	165	134	139	-5
7	165	137	141	-4

8	165	149	143	6
9	165	147	146	1
10	164	153	148	5
Total	1649	1356	1356	0
Hosmer-Lemeshow statistic = 14.1 with df = 8 (p-value = 0.0792)				

Table 3-4 (A & B). Results for (A) parameter estimates and (B) Hosmer-Lemeshow goodness-of-fit test for both the deciduous and conifer mortality models in the conifer dominated (CDom) stand.

(A) Parameter Estimates

Deciduous Mortality Model

Variables	df	$\hat{\beta}$	SE	*P-Value*	Deviance
(Intercept)		1.01304	0.49588	0.04106	
DDensityMed5	1	-1.26323	0.66189	0.05633	2.52
DDensityLg5	1	0.27229	0.08231	0.00094	8.11
CDensityLg5	1	-0.24179	0.14753	0.10123	1.09
DDensityMed10	1	1.4322	0.58863	0.01497	8.86
CDensityMed10	1	-0.13974	0.06646	0.03551	2.75
CDensityLg10	1	-0.21435	0.09155	0.01921	5.66

Conifer Mortality Model

Variables	df	$\hat{\beta}$	SE	*P-Value*	Deviance
(Intercept)		2.46406	0.29925	< 2e-16	
DDensityLg5	1	0.17594	0.10099	0.081473	8.55
CDensitySm5	1	0.14638	0.05529	0.008112	1.58
CDensityMed5	1	-0.24885	0.09127	0.006401	23.83
CDensityLg5	1	-0.45949	0.13465	0.000644	13.37
DeadDensity5	1	-0.25507	0.0569	7.37E-06	18.51
CDensitySm10	1	-0.07638	0.02936	0.009283	3.26
DeadDensity10	1	0.06778	0.03244	0.036633	4.55

(B) Hosmer-Lemeshow goodness-of-fit test

Deciduous Mortality Model

		Alive Trees		
Group	**Total # of Trees**	**Observed**	**Expected**	**Difference**
1	25	7	7	0
2	25	9	10	7
3	25	8	12	-4
4	24	14	13	1
5	24	15	14	1
6	24	14	15	-1
7	24	17	17	0
8	24	17	18	-1
9	24	16	19	-3
10	24	18	21	-3
Total	243	135	146	-11

Hosmer-Lemeshow statistic = 9.172 with df = 8 (p-value = 0.3280)

Conifer Mortality Model

		Alive Trees		
Group	**Total # of Trees**	**Observed**	**Expected**	**Difference**
1	54	30	24	6
2	54	32	36	7
3	54	39	41	-2

4	53	41	43	-2
5	53	49	45	4
6	53	49	47	2
7	53	46	48	-2
8	53	47	49	-2
9	53	52	50	2
10	53	53	52	1
Total	533	438	435	3
Hosmer-Lemeshow statistic = 12.319 with df = 8 (p-value = 0.1375)				

3.8 FIGURES

Figure 3-1. The estimated survival probabilities of the significant model ($\hat{y}$) for deciduous mortality in the DDom stand, plotted against the explanatory variable that most affected mortality, DeadDensity5. Each point represents an individual deciduous tree that the model was derived from. The smooth curve is the locally-weighted polynomial regression to illustrate the trend of the mean values.

The final model for deciduous mortality in the DDom stand is: $\hat{y} = \frac{e^z}{1+e^z}$, where $z = 1.44856 - 0.16467 * DeadDensity5 + 0.03098 * DDensityMed10 - 0.04604 * DeadDensity10$.

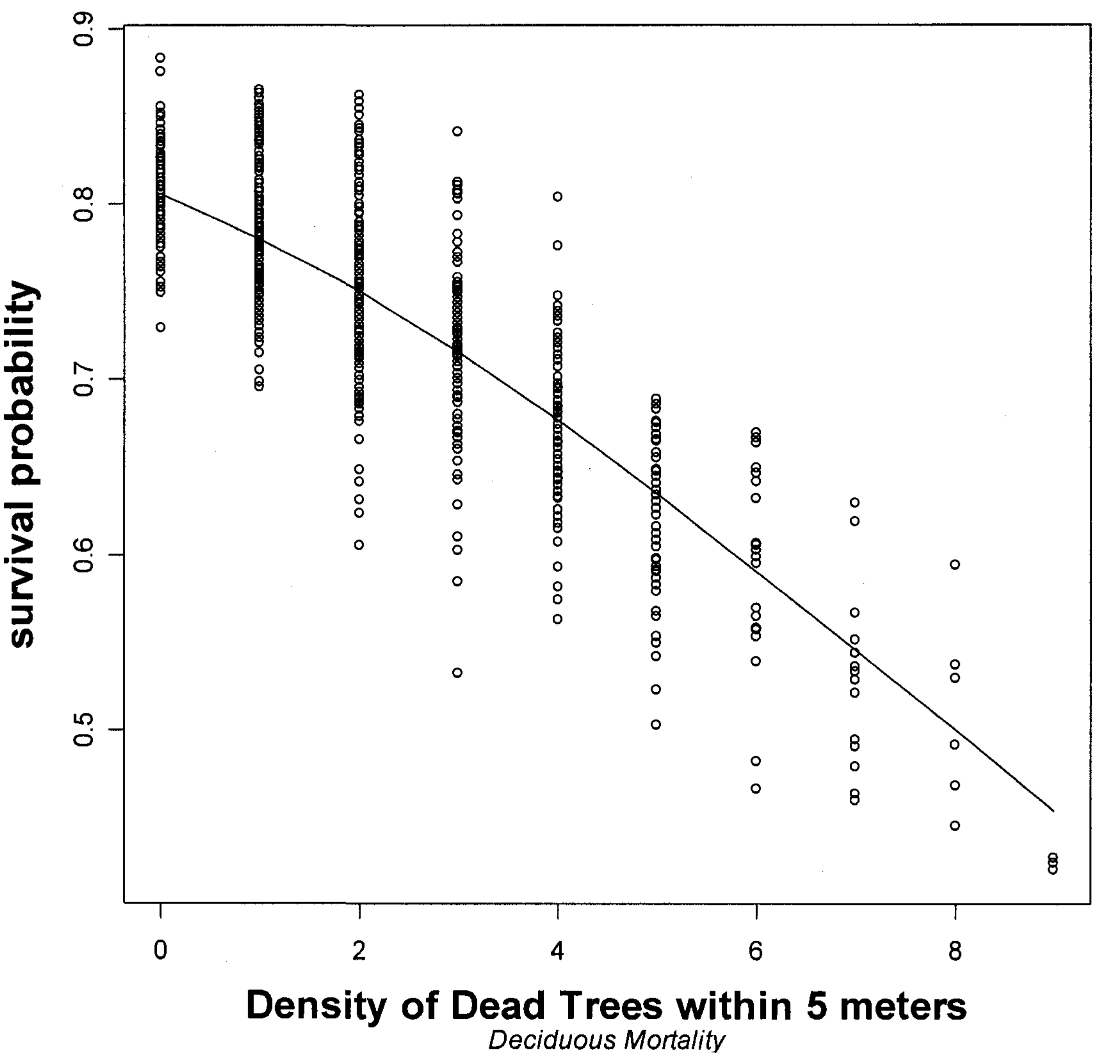


Figure 3-2. The estimated survival probabilities of the significant model ($\hat{y}$) for deciduous mortality in the DDom-U stand, plotted against the explanatory variable that most affected mortality, DDensitySm5. Each point represents an individual deciduous tree that the model was derived from. The smooth curve is the locally-weighted polynomial regression to illustrate the trend of the mean values.

The final model for deciduous mortality in the DDom-U stand is: $\hat{y} = \frac{e^z}{1+e^z}$, where $z = 1.72527 + 0.13463 * DDensitySm5 - 0.16999 * CDensityMed5 - 0.266 * CDensityLg5 - 0.02925 * DDensityMed10 - 0.04753 * DDensityLg10$.

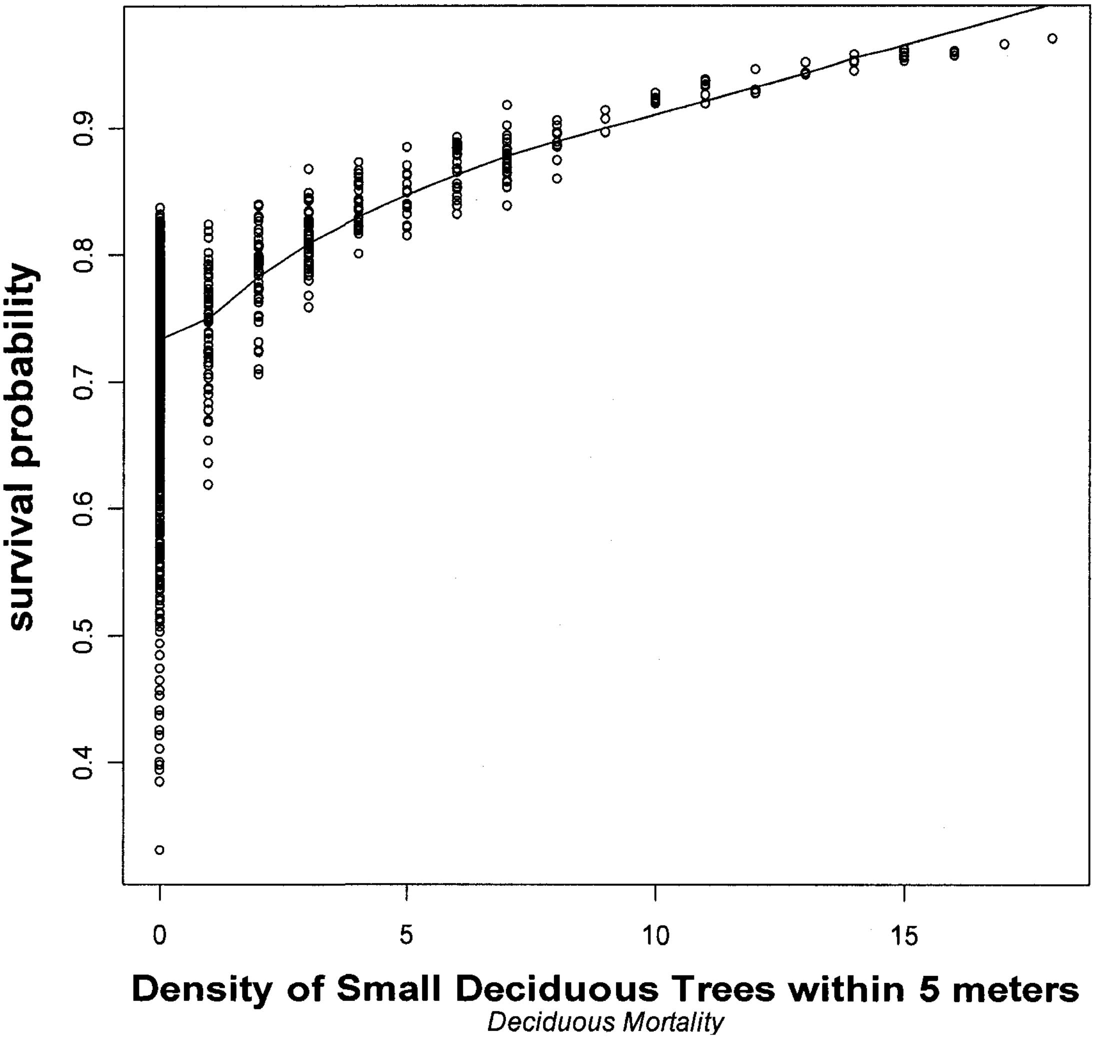


Figure 3-3 (A). The estimated survival probabilities of the significant model ($\hat{y}$) for deciduous mortality in the Mxwood stand, plotted against the explanatory variable that had the second greatest affected mortality, DDensityLg10. Each point represents an individual deciduous tree that the model was derived from. The smooth curve is the locally-weighted polynomial regression to illustrate the trend of the mean values.

The final model for deciduous mortality in the Mxwood stand is: $\hat{y} = \frac{e^z}{1+e^z}$, where $z = 1.17291 - 0.72009 * DDensityMed5 - 0.58438 * DDensityMed10 - 0.017018 * DDensityLg10 - 0.01874 * CDensitySm10$.

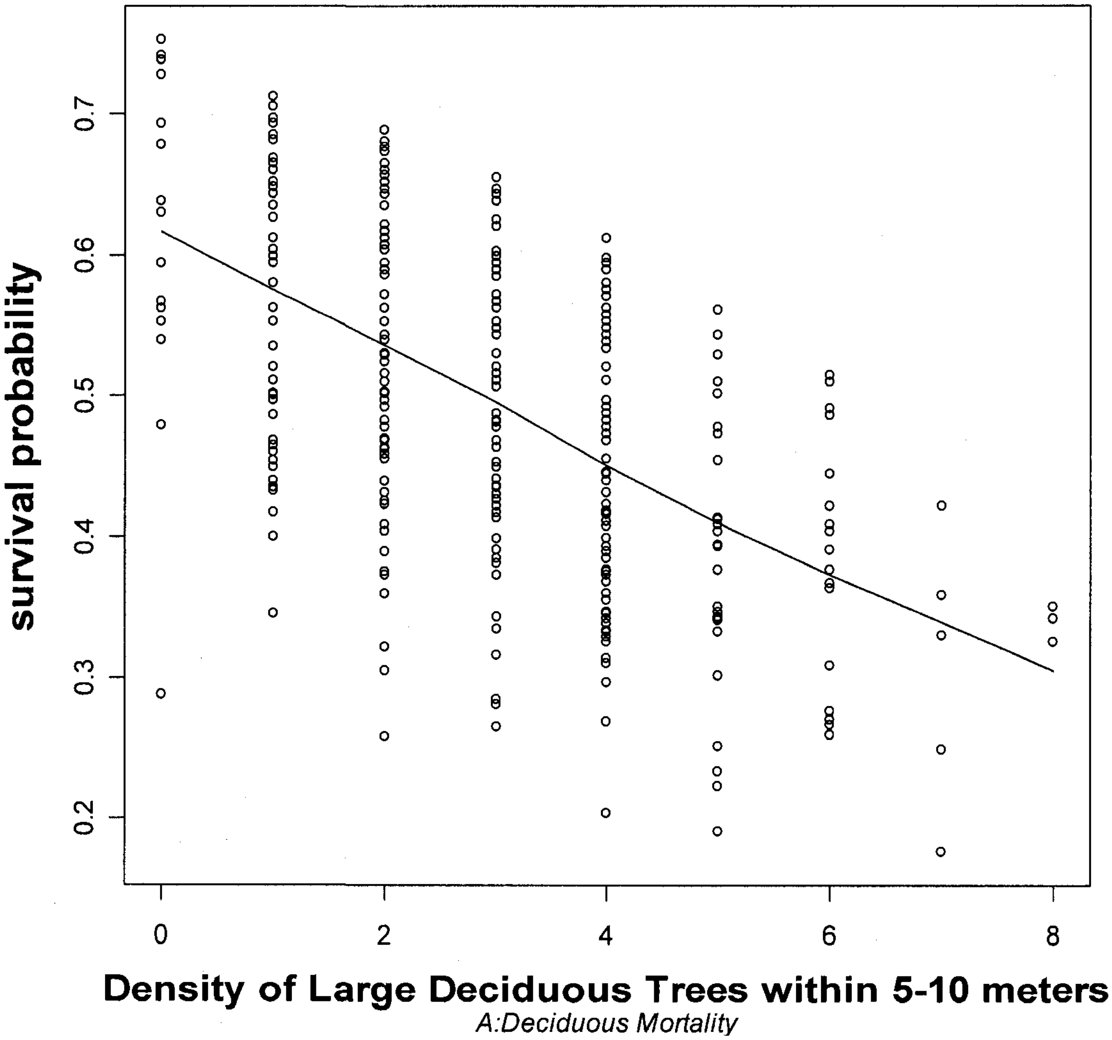


Figure 3-3 **(B)** The estimated survival probabilities of the significant model ($\hat{y}$) for conifer mortality in the Mxwood stand, plotted against the explanatory variable that most affected mortality, DeadDensity5. Each point represents an individual deciduous tree that the model was derived from. The smooth curve is the locally-weighted polynomial regression to illustrate the trend of the mean values.

The final model for conifer mortality in the Mxwood stand is: $\hat{y} = \frac{e^z}{1+e^z}$, where

$z = 1.30531 - 0.09572*DeadDensity5 + 0.0619*CDensityLg10 + 0.17772*DDensityLg5 + 0.39469*DDensityMed5 + 0.02746*CDensitySm5 - 0.02693*DeadDensity10$

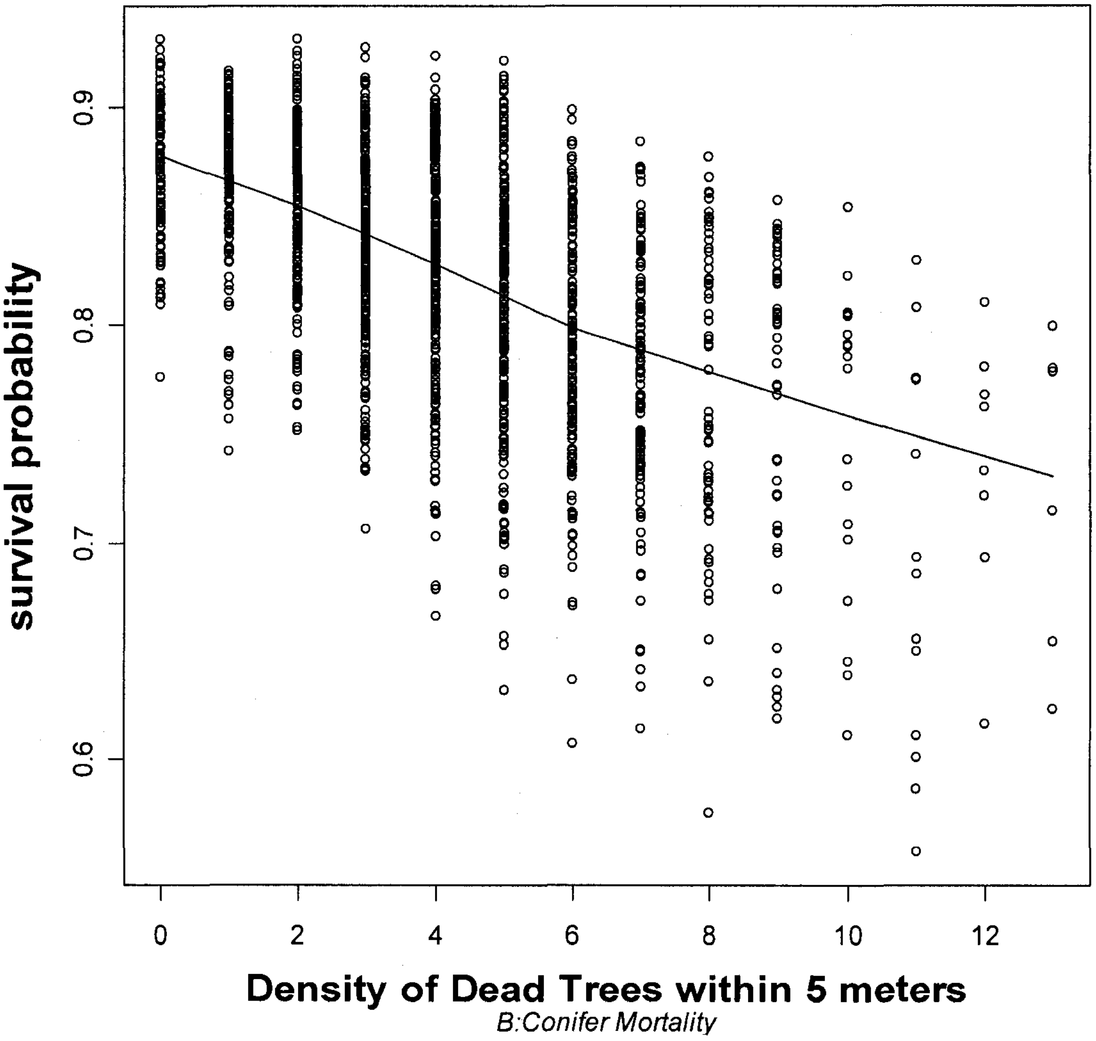


Figure 3-4 (A). The estimated survival probabilities of the significant model ($\hat{y}$) for deciduous mortality in the CDom stand, plotted against the explanatory variable that most affected mortality, DDensityLg5. Each point represents an individual deciduous tree that the model was derived from. The smooth curve is the locally-weighted polynomial regression to illustrate the trend of the mean values.

The final model for deciduous mortality in the CDom stand is: $\hat{y} = \frac{e^z}{1+e^z}$, where

$z = 1.01304 - 1.26326*DDensityMed5 + 0.27229*DDensityLg5 - 0.24179*CDensityLg5 + 1.4322*DDensityMed10 - 0.13974*CDensityMed10 - 0.21435*CDensityLg10.$

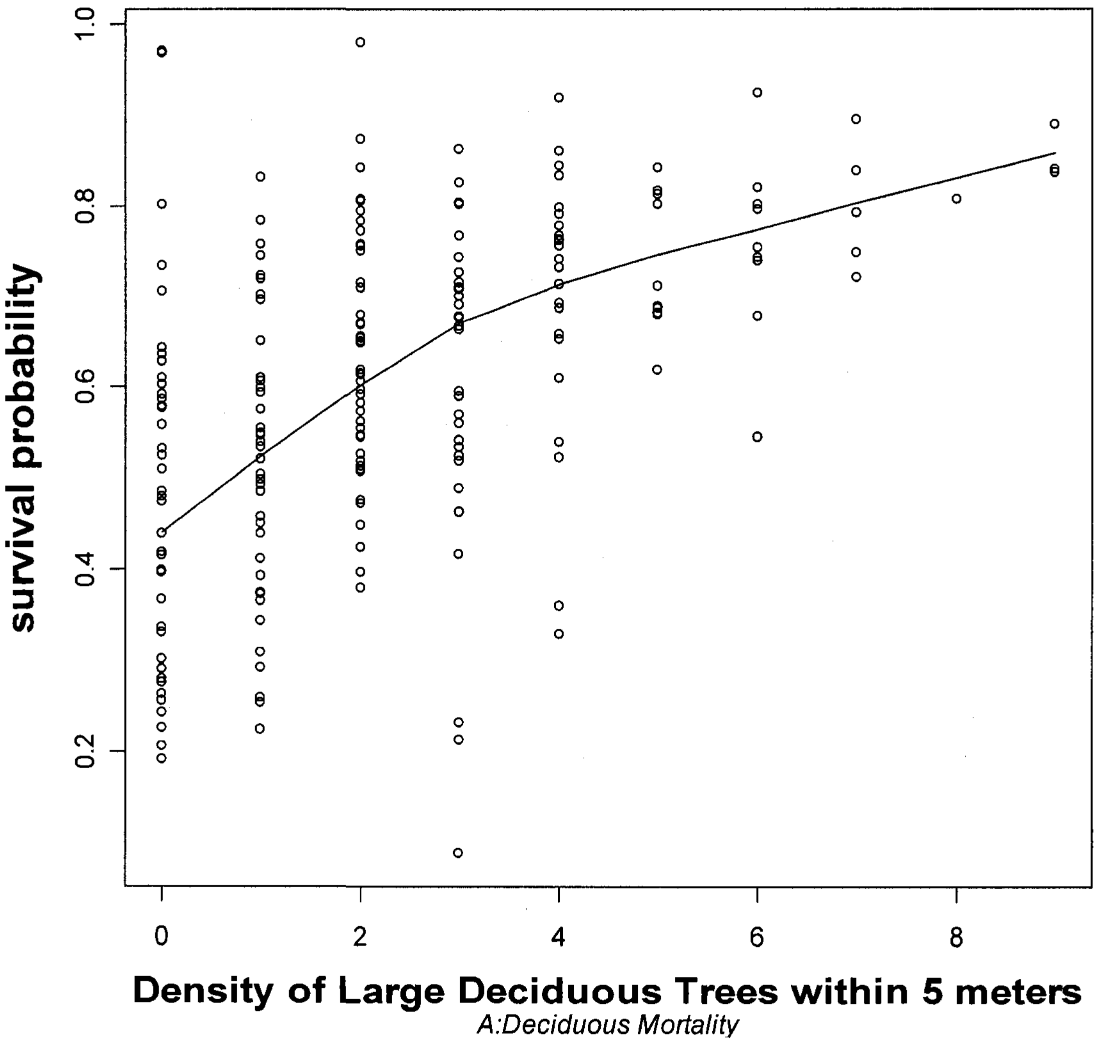
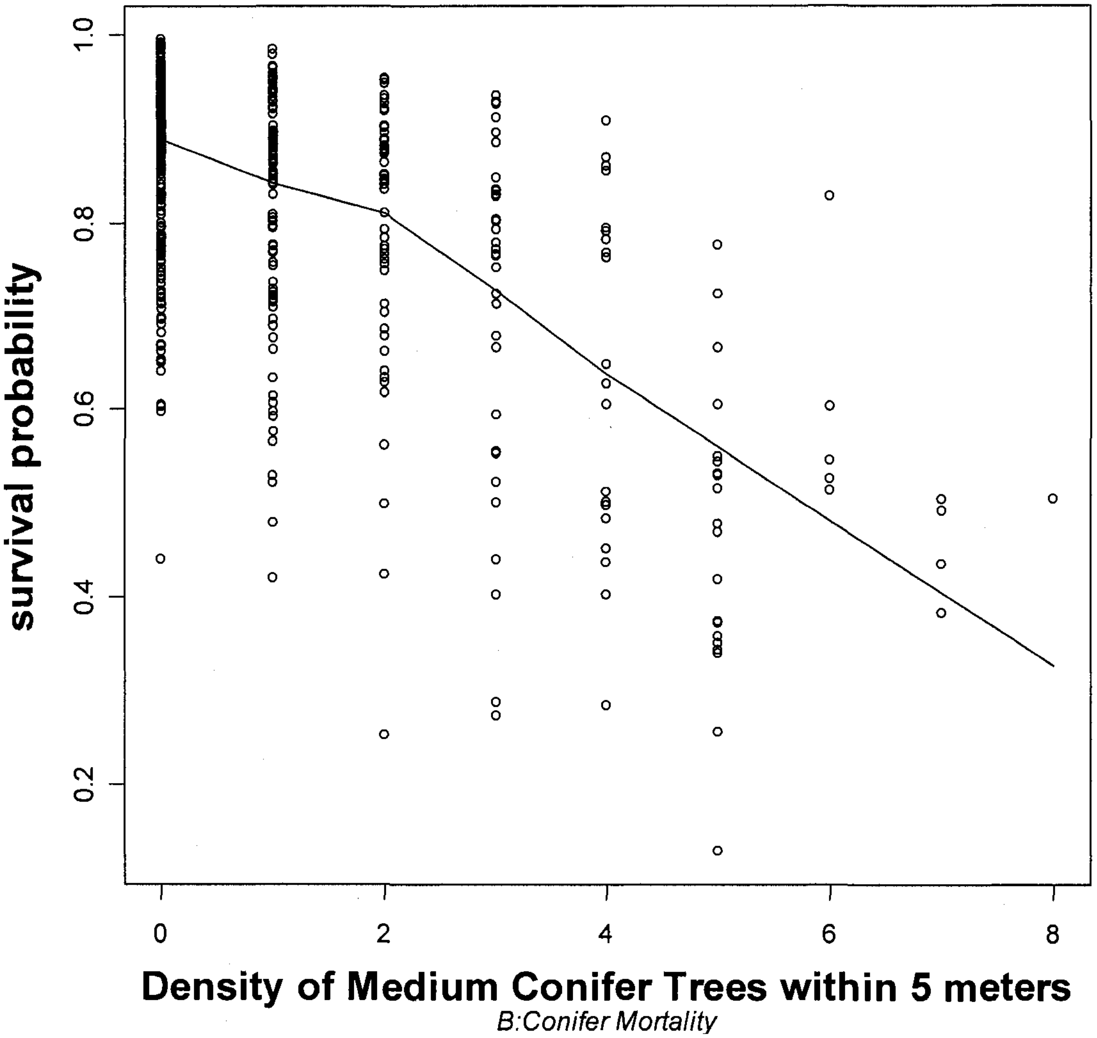


Figure 3-4 (B). The estimated survival probabilities of the significant model ($\hat{y}$) for conifer mortality in the CDom stand, plotted against the explanatory variable that most mortality, CDensityMed5. Each point represents an individual deciduous tree that the model was derived from. The smooth curve is the locally-weighted polynomial regression to illustrate the trend of the mean values.

The final model for conifer mortality in the CDom stand is: $\hat{y} = \frac{e^z}{1+e^z}$, where

$z = 2.46406 + 0.17594*DDensityLg5 + 0.14638*CDensitySm5 - 0.24885*CDensityMed5 - 0.45949*CDensityLg5 - 0.25507*DeadDensity5 - 0.07638*CDensitySm10 + 0.06778*DeadDensity10.$



Chapter 4: Conclusion to thesis

4.1 CONCLUSION and MANAGEMENT APPLICATIONS

In this thesis I investigated the change of spatial point patterns of tree distribution before and after the occurrence of mortality in a chronosequence consisting of four 1-ha stands of a boreal forest in northwest Alberta. I also modeled the probability of tree mortality in these stands in terms of the neighborhood densities of trees. Although there is a possibility that other agents (e.g., disease, pathogens, insects, and wind disturbances) might have also contributed to the observed mortality, the results of my research from both the spatial point pattern analyses and the logistic mortality models I developed indicate that the density-dependent effect is a primary mechanism in tree mortality affecting the development of stand structure in the forest stands studied.

Although competition indices are often included, previous studies have primarily developed individual tree mortality models which are mainly derived from large-scale stand characteristics, such as total basal area (Bravo et al. 2001, Eid and Tuhus 2001, Lessard et al. 2001, Yao et al. 2001, Sterba et al. 2002, Wyckoff and Clark 2002, Yang et al. 2003). However the accuracy of these models could be improved by including small-scale plant-to-plant interactions. This research highlights the contribution of both large and small neighbouring trees of the same species, as well as dead trees, to tree mortality. Similar to previous models, the mortality models I developed included measurements of large trees, which captured asymmetric competition where larger trees suppress smaller trees (Zhao et al. 2006). Although it is important to include this variable, the results suggest that adding the density of small trees and the density of dead trees could also improve model predictability.

Interspecific competition has been considered to be a driving mechanism for species replacement over succession (Keddy 2001). However, the results of the bivariate spatial point pattern analysis of this study showed no significant shifts in spatial pattern of heterospecific trees. This is consistent to the results of logistic mortality models of Chapter 3, which found that the density of alternative species did not have as significant of an effect on mortality than the density of trees of the same species, for respective deciduous and coniferous trees throughout the four chronosequent stands. These results suggest that interspecific competition is probably not strong enough to cause significant tree mortality in the studied stands. However, it is important to note that my analyses do not rule out the possibility that interspecific competition may still be at work suppressing tree growth in these stands, but may just not be strong enough to cause significant death. So, an interesting yet challenging question is: what level of competition is required for controlling species replacement in succession? To convincingly answer this question, stand mapped data of well designed long term observations on growth and mortality are needed. The permanent sampling plots (PSP) of Alberta Sustainable Resources Development (Alberta Sustainable Resources Development 2004) could be of use for addressing this question, although the size of PSP's are small (~1/10 ha) and trees in each plot are not spatially located.

Alternatively, interspecific competition might indeed be trivial in the studied stands. In this case, the traditional paradigm of boreal succession may not apply to the forest in the region I studied. Contrary to the common hypothesis that the succession of boreal forests follows the pathway from deciduous (mainly aspen) dominated forest to mixedwood to conifer (mainly white and black spruces) dominated forest, interspecific competition may play little role in the replacement of aspen by spruce. Instead, the origination and subsequent development of a forest may be dependent on which species is able to first successfully colonize an opening and how long the tree's individual life cycle allows it to hold the space (i.e., the preemption hypothesis). As a conifer species (e.g., white spruce) begins to infiltrate the stand, the probability that it will primarily establish in canopy gaps will increase with the increase of the source of propagules. Once the stand is established, the replacement of species will take a long time to occur, much longer than traditional succession theory can predict. This succession hypothesis is anchored on the preemption hypothesis and is determined almost entirely by the availability of a propagule source. The fact that the four stands I studied are of similar age (107, 110, 142 and 169 years for DDom, DDom-U, Mxwood and CDom stands, respectively), but different stand types may be evidence supporting this hypothesis. This hypothesis challenges the current forest management practices that aim to manage forests following the traditional successional trajectory. The preemption hypothesis suggests that forest stands have little species replacement and therefore stands should be managed individually.

This study has several applied implications. First of all, it shows that neighborhood spatial structure is of great importance for modeling stand dynamics. This will be of use for modeling growth and yield of stands. Spatial data are not usually considered in growth and yield models, but as I have shown, neighborhood structure can explain much of the variation in mortality. Thus, the inclusion of spatial structure will undoubtedly increase the accuracy of growth and yield models and thus improve their predictability. Secondly, the tree mortality models I developed would contribute to the estimation of the future quantity of course woody debris (CWD) that will be added to the forest. This estimate is essential information for management as CWD has been considered to provide vital habitats for many species, regeneration, nutrient cycling and carbon storage (Freedman et al. 1996, Clark et al. 1998, Chen and Popadiouk 2002, Pealar et al. 2002). Thirdly, understanding neighborhood interaction and its effect on mortality would provide insights for improving realism of stand dynamic simulation models. Individual tree based gap dynamics is the fundamental process of many simulation models (Linder et al. 1997, Shugart 2003). The spatial point pattern analysis of Chapter 2 and individual tree mortality model of Chapter 3 have helped further understand how tree mortality occurs and how neighboring trees at the scale of gap would influence the mortality. Thus, this research is useful for formulating gap dynamics in the boreal forest of Alberta. Alternately, the stem-mapped data are also useful for validating the prediction of simulation models.

In summary, the findings of this study indicate that: (1) the relative importance of both intra- and interspecific competition in the shift of spatial patterns of both deciduous and conifer trees over succession; (2) intraspecific competition has a major role in both deciduous and conifer tree mortality and thus significantly affects the development of stand structure throughout succession; (3) in failing to detect significant mortality due to interspecific competition, studies need to investigate if competition suppresses tree growth; (4) the local density of dead trees and the densities of large and small conspecific trees are likely significant factors affecting both deciduous and conifer mortality, and finally (5) understanding the competitive interaction among trees within a single species population or among species can have important forest management applications for predicting mortality, simulating stand dynamics and estimating course woody debris. All of these findings illustrate the importance of density-dependent effects in shaping boreal forest structure in Alberta, as well as provide insights on stand dynamics of boreal forest succession

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