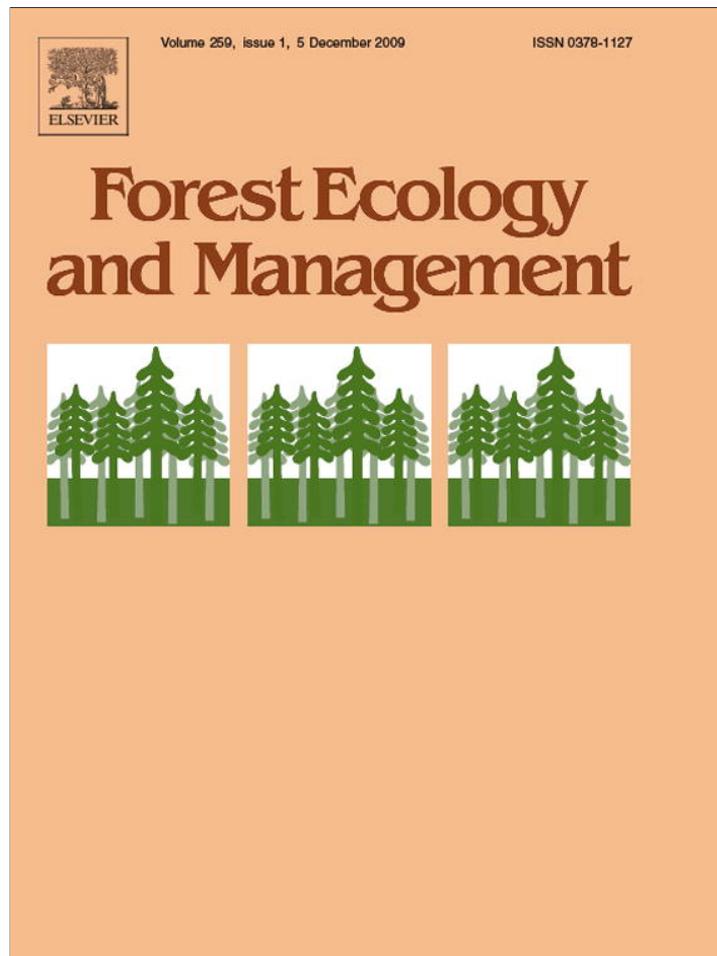


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Spatial point-pattern analysis for detecting density-dependent competition in a boreal chronosequence of Alberta

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ABSTRACT

In the boreal forest of Alberta, fire and wind often open gaps in the canopy where late-successional species can establish and over time cause a shift in the species distribution from deciduous (e.g., trembling aspen) dominated to mixedwood, to shade-tolerant conifer (e.g., white spruce) dominated stands. This study attempted to understand the change of density-dependent competition in a boreal chronosequence and the role of tree competition in affecting stand structure and mortality. Four 1-ha stem-mapped plots were established to represent a chronosequence comprised of aspen dominated, mixedwood, and spruce dominated stands in Alberta. Second order spatial point-pattern analysis using Ripley's $K(t)$ function showed that intraspecific competition is a prevailing force causing conspecific tree mortality and thus shaping the stand structure. The results of bivariate $K(t)$ function analysis did not reveal sufficient evidence of interspecific competition. This suggested that competitive interaction among heterospecific trees was not strong enough to cause significant tree mortality, but the analysis of marked correlation function revealed that interspecific competition could have a negative impact on tree growth. This study highlights the importance of density-dependent competition in understanding stand dynamics of boreal forests over succession.

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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 both species turnover and succession and it is responsible for shaping stand-level structure (Kneeshaw and Bergeron, 1998). Therefore, understanding competition is critical for predicting succession and its effects 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 utilization 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 neighbouring trees, the spatial locations of trees provide signatory information for inferring competition in field conditions. Growth reduction is expected if there is neighbourhood competition, and the intensity of competition is often assessed by using competition coefficients derived from basal area increments or a ratio of height growth and distance between neighbouring 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 neighbours would suffer higher mortality rates. This is strong evidence of competition because competition must be more severe to cause mortality than just to reduce growth.

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

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history traits, are known to strongly impact survivorship of competing trees (Huston and Smith, 1987), but competition for resources (primarily light) is responsible for tree mortality (Halpern et al., 1997), thus leading to a 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 small-scale 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 common 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; Kneeshaw 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 (Kneeshaw and Bergeron, 1998). The species composition then shifts to a mixedwood forest and, finally emerges as a conifer dominated forest.

Comparing the pre- (live and dead trees together) and post-mortality (live trees only), spatial patterns of trees in each chronosequence stage provide 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 significant change between pre- and post-mortality spatial patterns. In contrast, a post-mortality shift in the spatial distribution of trees would indicate that plant-to-plant competition contributes to selective tree mortality within the stand (Sternier et al., 1986; Getzin et al., 2006). Trees in high-density stands often suffered elevated mortality as a result of higher level of competition within dense neighbourhoods. As a result, the post-mortality spatial pattern of surviving trees shifts towards a more regularly (evenly) spaced pattern, providing 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 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, spatial 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 denounce 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 as a primary force driving the species turnover and succession of boreal forests (Kneeshaw and Bergeron, 1998), it is not yet clear how the importance of intra- and interspecific competition changes over boreal succession, as deciduous trees are replaced by coniferous trees, or how competition would induce mortality and contribute to the development of stand structure of boreal forests. In this study we analyzed fine-scale spatial distributions of

two dominant deciduous species, trembling aspen (*P. tremuloides*) and balsam poplar (*P. balsamifera*), and a dominant coniferous species, white spruce (*P. glauca*), in a successional chronosequence of boreal mixedwood of Alberta, Canada to address these questions. We hypothesized that (1) intraspecific competition would cause the spatial pattern of all species to become more regular over succession, (2) interspecific competition would result in significant spatial repulsion between dominant deciduous and coniferous species, and (3) a significant negative spatial association between trees of different sizes, i.e., small trees are expected to be associated with large neighbouring trees if competition would suppress growth.

2. Methods

2.1. Study sites and data collection

The study was conducted at the EMEND (Ecosystem Management Emulating Natural Disturbance) (Volney et al., 1999) 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 °C and a mean summer rainfall is 204.25 mm (from data of 2000–2003). The EMEND research 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 and 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 dominated), DDom-U (deciduous aspen dominated with coniferous white spruce understory), Mxwood (mixedwood) and CDom (coniferous white spruce 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. These ages were determined from dendrochronological analysis conducted in each stand in the establishment of the EMEND research site.

In each of the four stands a 100 m × 100 m (1-ha) plot was established. In each plot, the coordinates of live deciduous trees (>2 cm diameter at breast height, dbh, at 1.3 height), live coniferous trees (>1 cm dbh), all snags, stumps and logs were mapped. Each individual was uniquely tagged and the diameter at breast height of the live trees was measured twice 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 coordinates, dbh, height, species identity, and status (live, stump, snag, log) of each tree.

2.2. Data analysis

2.2.1. Stand structure analysis

There were six tree species in the four mapped plots: trembling aspen (*P. tremuloides*, Aw for short), white spruce (*P. glauca*, Sw), balsam poplar (*P. balsamifera*, Bp), balsam fir (*Abies balsamea*, Bf), lodgepole pine (*Pinus contorta*, Lp) and paper birch (*Betula papyrifera*, Pb). Lodgepole pine and paper birch did not make up more than 5% of the overall composition in any of the plots and thus these species were excluded from the analyses in this study.

Although balsam fir was highly present in the mixedwood stand it was almost non-existent in the remaining stands, thus it was also excluded. Balsam poplar was not analyzed in the mixedwood stand since its overall proportion for both live and dead stems was below 1%.

The number of stems (N) and the relative proportions (%) of both live and dead stems were counted for each species in each stand. The mean nearest-neighbour distance ($\langle NN \rangle$) as well as the proportion of dead trees (%), and mean dbh ($\langle dbh \rangle$) were calculated for each dominant species: aspen, spruce and balsam poplar for each of the four plots. 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. Those neighbourhoods where only had 2 or 3 of a tree's 5 nearest-neighbours were of the same species were excluded to ensure a strong neighbourhood relationship.

2.2.2. Size–distance correlation analysis

To investigate the relative importance of density-dependent competition in developing the structure of a stand, we 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. The coefficient of determination, r^2 , has been shown to be a robust index of competition even if other biotic and abiotic stresses may also affect tree size (Welden 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 was determined using only the subset of focal trees for a given species that 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 intensity of competition changed over succession.

2.2.3. Spatial pattern analysis

Ripley's $K(t)$ function was used to analyze the observed mapped point patterns of trees in each stand (Diggle, 2003). The unbiased univariate estimator of the K -function for detecting intraspecific competition is

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

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 neighbouring pairs for constructing the K -function, we computed the function at 0.5-m intervals with distance $t \leq 25$ m.

The variance reduction form of the K -function:

$$L(t) = \frac{\sqrt{\hat{K}(t)}}{\pi} - t \quad (2)$$

was used to compare the observed spatial patterns of each dominant species in each successional phase against a random pattern. $L(t) = 0$ for completely spatial randomness (CSR), $L(t) > 0$ for aggregated pattern, while $L(t) < 0$ for regular pattern.

Similarly, we defined the second order bivariate estimator of the Ripley's K -function for detecting interspecific competition as

$$\tilde{K}_{12}(t) = (n_1 n_2)^{-1}|A|\sum_{i=1}^{n_1} \sum_{j=1}^{n_2} w_{ij}^{-1} I_t(u_{ij}), \quad (3)$$

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 Eq. (1).

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

$$L_{12}(t) = \frac{\sqrt{\tilde{K}_{12}(t)}}{\pi} - t. \quad (4)$$

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 the intervals generated by Monte Carlo simulation of random location selection, where the relative coordinates for the same number of trees were randomly generated. Alternatively the observed L -functions for post-mortality (live) spatial patterns were compared to the intervals generated by Monte Carlo simulation of random labeling (Diggle, 2003). The random labeling procedure maintained the original coordinates of each tree and randomly removed ("killed") the same number of dead trees from the live and dead pool. The remaining trees were those alive after random mortality. In a separate analysis for evaluating spatial patterns of large trees versus small trees, random labeling was used to randomly assign a finite number of live individuals, equal to the number of observed large trees in the stand (defined as $dbh > 30$ cm), as large trees. The remaining trees were considered to be smaller size. The Monte Carlo was repeated 99 times and each time a $L(t)$ function was calculated. The second to the minimum and second to the maximum of $L(t)$ at each t distance were used as the 95% Monte Carlo interval for each given t . The observed patterns that fell above, below or within the Monte Carlo intervals indicated aggregated, regular or random pattern, respectively. All the L -functions and Monte Carlo simulations were calculated using the "spatstat" package in the R Statistical Programming Software (Baddeley and Turner, 2005).

2.2.4. Growth impact analysis

A mark correlation function (MCF) $\kappa_{mm}(t)$ (Stoyan and Stoyan, 1994; Getzin et al., 2008) using dbh as marks was used to analyze the distance-dependent size correlation of trees for distances up to 25 m. This MCF is to detect whether interspecific competition affects tree growth. The similarity or dissimilarity between the dbh marks of two trees at a distance t apart is quantified by the equation $f(m_1, m_2) = m_1 \times m_2$, where m_1 and m_2 are dbh values of two neighbouring trees. $\kappa_{mm}(t)$ is defined as the normalized mean value of $f(m_1, m_2)$ for all marks at distance t . Marks are considered independent, positively or negatively correlated at distance t if $\kappa_{mm}(t) = 1$, $\kappa_{mm}(t) > 1$ or $\kappa_{mm}(t) < 1$, respectively. The significance of the departure from an independent dbh distribution was quantified by a 95% confidence interval derived from 99 Monte Carlo simulations where random labeling was used to randomly shuffle the observed dbh's among all the stems. The $\kappa_{mm}(t)$ and Monte Carlo simulations were calculated using the *markcorr* function in the "spatstat" package of R (Baddeley and Turner, 2005).

Table 1

Summary on density, mortality and spatial distribution for three dominant species across the four forests. <dbh>, mean diameter at breast height; <NN>, mean nearest-neighbour distance; intra-mortality, proportion of dead trees located within conspecific neighbourhoods; inter-mortality, proportion of dead trees located within heterospecific neighbourhoods. N/A: no live balsam poplar in the mixedwood site.

Plot/species	<NN> (live + dead)	# stems (live + dead)	% total stems in stand	% mortality	<DBH> (cm)	Intra-mortality (%)	Inter-mortality (%)
Deciduous dominated (DDom)							
Aspen	1.45	789	74.4%	27.8%	26.0	83.6%	2.3%
White spruce	1.78	79	7.4%	0%	3.7	0%	0%
Balsam poplar	1.68	189	17.8%	19%	19.2	50%	30.6%
Deciduous dominated with coniferous understory (DDom-U)							
Aspen	1.46	1104	76.9%	26.8%	21.8	72.3%	3.7%
White spruce	1.17	203	14.1%	0.5%	14.2	0%	0%
Balsam poplar	1.19	129	9%	19.4%	4.6	24%	36%
Mixedwood (Mxwood)							
Aspen	1.33	303	15.3%	48.5%	33.5	0%	73.5%
White spruce	1.26	462	23.3%	33.3%	28.7	6.5%	40.9%
Balsam poplar	1.10	5	0.3%	100%	N/A	0%	100%
Coniferous dominated (CDom)							
Aspen	1.54	159	20.5%	49.7%	39.9	36.7%	25.3%
White spruce	1.70	518	66.8%	17.2%	19.3	75.3%	4.5%
Balsam poplar	1.45	84	10.8%	34.5%	35.1	34.5%	24.1%

3. Results

3.1. Stand structure

Density, tree size, mortality and spatial patterns of the three dominant species across the four forests studied are compared in Table 1. The comparisons of these basic variables and structures across these four distinct successional stands allow us to make observations of general dynamic trends underlying the chronosequence in this boreal forest.

3.1.1. Trembling aspen

The range of mean nearest-neighbour distances for aspen over succession was small (1.33–1.54 m), with little variation across plots despite of the huge variation in aspen density (Table 1). The abundance and total percentage of aspen stems declined dramatically in the later stages of succession 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 1). The average dbh of aspen was consistently greater than the other dominant species throughout succession. The average dbh overall increased with succession except in the DDom-U plot (Table 1).

3.1.2. White spruce

The proportion of spruce stems was lowest in the DDom plot and approximately doubled over each phase of succession (Table 1). Spruce mortality is very low in both the DDom and DDom-U stands, but the mortality significantly increased in the later successional stages (Table 1). The mean spruce dbh consistently increased from 3.7 cm in the DDom stand to 28.7 cm in the Mxwood stand until the CDom plot. The decrease in dbh to 19.3 cm in the CDom stand was due to the increased spruce regeneration at this later stage.

3.1.3. Balsam poplar

Except in the DDom, the proportion of balsam poplar stems was the lowest of the three species (Table 1). In the Mxwood stand, balsam poplar was completely wiped out; there were only five balsam poplars found in the Mxwood stand and all were dead.

3.2. Size–distance correlation

3.2.1. 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 (Fig. 1A). The relative importance of intraspecific competition in aspen decreased over succession (Fig. 1B), while the importance of interspecific competition increased (Fig. 1C). These results are consistent with the fact that aspen is a pioneer species whose canopy dominance decreased over time. The intraspecific correlation was not calculated for aspen in the Mxwood stand because the subset of aspen focal trees in a conspecific neighbourhood was too small for a reliable statistical analysis.

3.2.2. White spruce

The relative importance of overall competition within the spruce population significantly increased over succession (Fig. 1A). Intraspecific competition within the spruce population was higher than the other species in each successional phase (Fig. 1B). Intraspecific competition decreased in the DDom-U but increased in Mxwood stands. The importance of interspecific competition had a similar changing pattern as the intraspecific competition across the four stands (Fig. 1C), although the overall intraspecific competition from DDom to CDom increased (Fig. 1B) and the interspecific competition decreased (Fig. 1C).

3.2.3. Balsam poplar

The overall, intra- and interspecific correlations were not calculated for balsam poplar in the Mxwood stand because there were too few balsam poplars (<1%) in this stand. Despite the lack of r^2 values for the Mxwood stands, results suggested that the strength of overall competition (Fig. 1A) for balsam poplar slightly decreased over succession. Although intraspecific competition fluctuated over succession, correlation values were similar at the beginning and end phases (Fig. 1B). However, interspecific competition significantly increased over succession (Fig. 1C). The little change in intraspecific and the increase in interspecific competition within the balsam poplar population are possibly due to the decrease in the density of balsam poplar from the DDom and DDom-U stands to the CDom stand.

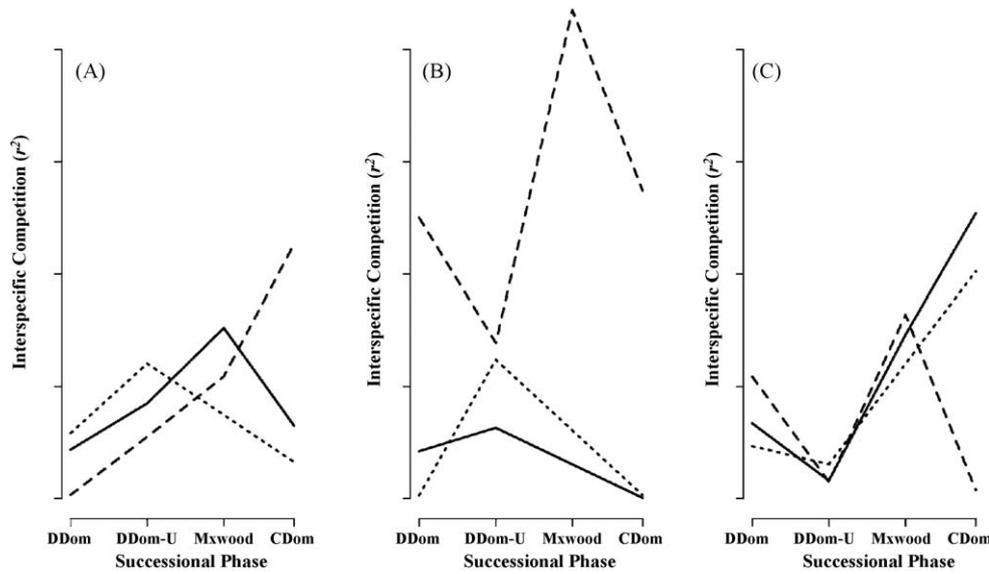


Fig. 1. The correlation between tree size and distance, indicating the relative importance of overall competition (A), intraspecific competition (B) and interspecific competition (C) for trembling aspen (—), white spruce (---) and balsam poplar (···). Correlation values were calculated in each stage of a chronosequence identified as DDom (deciduous dominated), DDom-U (deciduous dominated with coniferous understorey), Mxwood (mixedwood) and CDom (coniferous dominated). Changes in the correlation indicate either increase or decrease of the relative importance of the corresponding competition in the respective species over succession.

3.3. Spatial patterns

3.3.1. Univariate spatial patterns for inferring mortality from intraspecific competition

3.3.1.1. Trembling aspen. The observed $L(t)$ function for pre-mortality aspen fell above the Monte Carlo interval in the DDom (Fig. 2A) and CDom (Fig. 2D) stands, indicating pre-mortality aspen

was highly aggregated in these two stands. The observed pre-mortality $L(t)$ of aspen in the Mxwood stand fell within the Monte Carlo interval, indicating a random distribution (Fig. 2C). At scale up to 2 m, pre-mortality aspen was regularly distributed, but became aggregated starting at 5 m in the DDom-U stand (Fig. 2B). Although post-mortality aspen was regularly spaced between 8.5 and 19.5 m in the Mxwood stand (Fig. 2G), the random mortality hypothesis could not be rejected for small scale distances due to

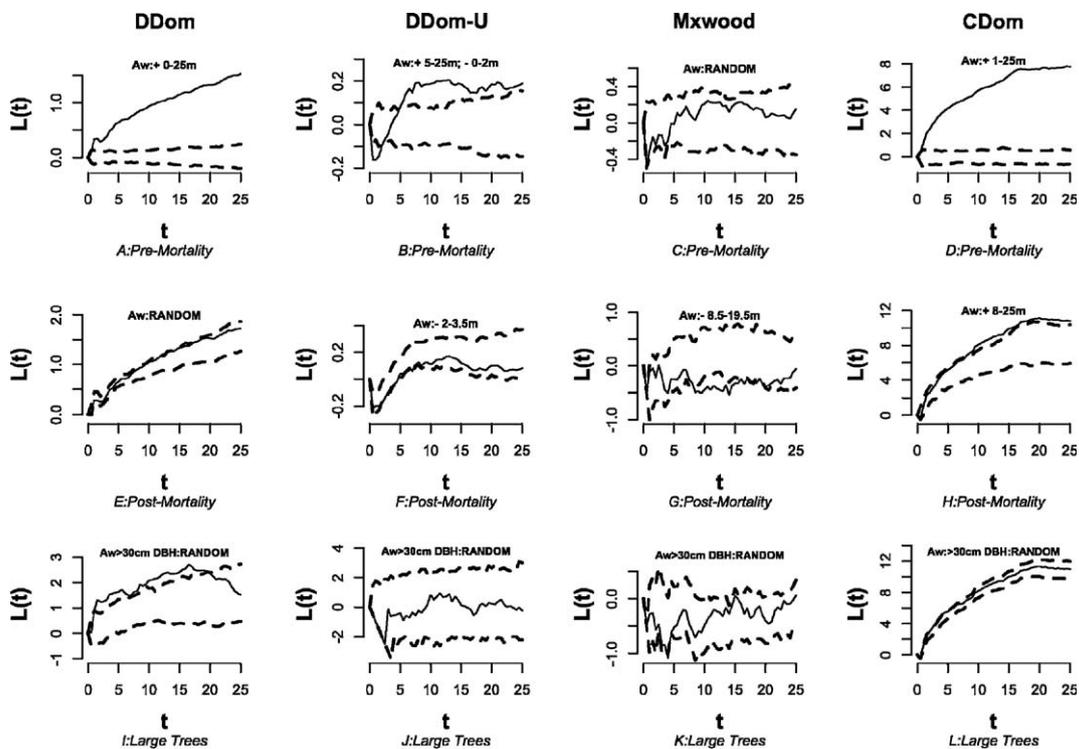


Fig. 2. Graphs showing both the univariate $L(t)$ functions and Monte Carlo intervals for trembling aspen in 4 stages of a chronosequence of boreal succession. Observed patterns (—) that fall above, below and within 95% Monte Carlo intervals (---) indicate an aggregated, regular or random pattern, respectively. Shifts between pre-mortality (live + dead) (top figures: A–D), post-mortality (live) (middle figures: E–H) and large trees (DBH > 30 cm) (bottom figures: I–L) patterns reject the random mortality hypothesis for the corresponding successional phase.

the fact that post-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 (Fig. 2E and F), and at scales up to 8 m in the CDom stand (Fig. 2H). Thus, the random mortality hypothesis was rejected for aspen in the DDom, DDom-U and CDom stands. Dead aspen was highly aggregated at scales starting at 1 m in both the DDom and DDom-U stands and randomly distributed in both the Mxwood and CDom stands.

Large aspen (dbh > 30 cm) shifted from aggregation at 1.5 m in the DDom stand to slight regularity between 4 and 4.5 m in the Mxwood stand (Fig. 2I and K), suggesting competition may drive the shift over succession for this stand. However, in the CDom stand large aspen was slightly aggregated between 2.5 and 4.5 m (Fig. 2L). This may suggest that factors other than competition affect the spatial distribution of large aspen stems in this stand.

3.3.1.2. White spruce. Pre-mortality spruce was aggregated from 2 to 16 m in the DDom stand (Fig. 3A), 2.5–25 m in the Mxwood stand (Fig. 3C), and aggregated at all scale in both the DDom-U and CDom stands (Fig. 3B and D), 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 were 0 and only 1 dead spruce, respectively. Post-mortality spruce was regularly distributed at 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 was found to be highly aggregated in these two stands.

Spatial pattern analysis cannot be conducted for large spruce in the DDom stand because there were no large spruce stems in this stand. Nevertheless, the spatial pattern of large spruce shifted from a random distribution in the DDom-U stand to regular distributions at scales starting at 1 m in both the Mxwood and CDom

stands (Fig. 3J–L). This result indicates that intraspecific competition between large spruce increased over succession and contributed to the spatial regularity of this species.

3.3.1.3. Balsam poplar. Pre- and post-mortality balsam poplar spatial patterns were not evaluated in the Mxwood stand because there were too few stems in this stand. Pre-mortality balsam poplar was highly aggregated in the DDom, DDom-U and CDom stands (Fig. 4A, B and D). The random mortality hypothesis was rejected for all the evaluated stands since post-mortality balsam poplar was randomly distributed in both the DDom and CDom stands (Fig. 4E and H), and only slightly aggregated at 3–8.5 m in the DDom-U stand (Fig. 4F). Dead balsam poplars were found to be randomly distributed at small scales throughout succession.

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. In the DDom and CDom stands large balsam poplar were randomly distributed (figure not shown).

3.3.2. Bivariate spatial patterns for inferring mortality from 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 the development of 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).

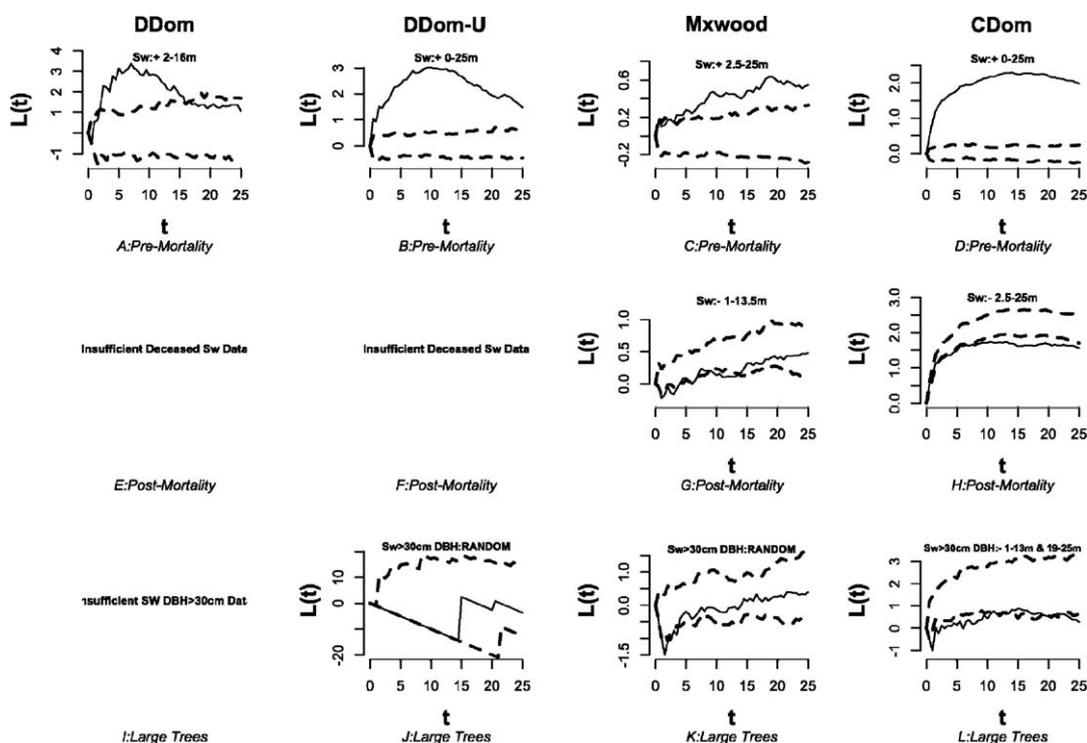


Fig. 3. Graphs showing both the univariate $L(t)$ functions and Monte Carlo intervals for white spruce in 4 stages of a chronosequence of boreal succession. Observed patterns (—) that fall above, below and within 95% Monte Carlo intervals (---) indicate an aggregated, regular or random pattern, respectively. Shifts between pre-mortality (live + dead) (top figures: A–D), post-mortality (live) (middle figures: E–H) and large trees (DBH > 30 cm) (bottom figures: I–L) patterns reject the random mortality hypothesis for the corresponding successional phase.

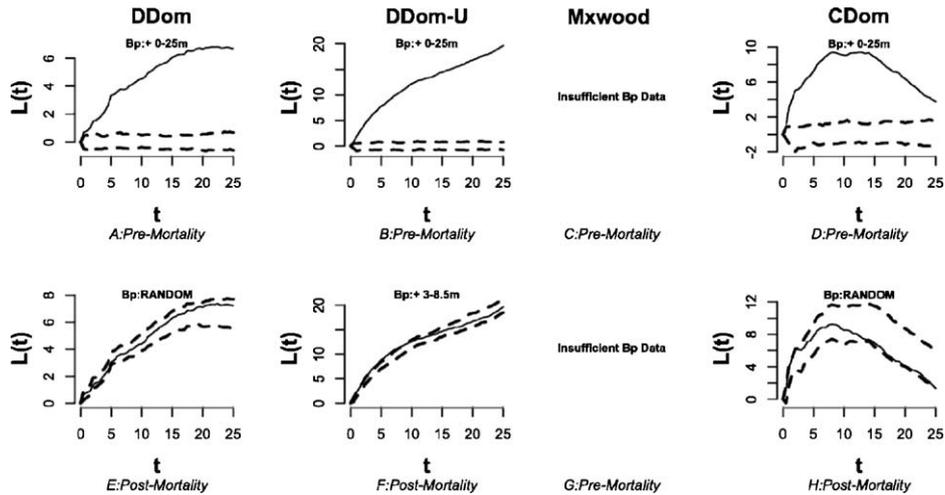


Fig. 4. Graphs showing both the univariate $L(t)$ functions and Monte Carlo intervals for balsam poplar in 4 stages of a chronosequence of boreal succession. Observed patterns (—) that fall above, below and within 95% Monte Carlo intervals (---) indicate an aggregated, regular or random pattern, respectively.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

3.4. Growth impact

Despite the bivariate $K(t)$ results suggesting that interspecific competition does not affect tree mortality, the results from the marked correlation function $\kappa_{mm}(t)$ indicate there is a significant negative correlation between dbh marks (small trees are associated with large neighbouring trees) in the DDom-U, Mxwood and CDom stands between 0 and 25 m (Fig. 5B–D). This suggests that competition (whether it is intraspecific or interspecific) is a significant mechanism that negatively affects tree growth in these stands.

4. Discussion

Many previous studies have shown that competition can be inferred by comparing the pre-mortality and post-mortality patterns of trees within 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 a stand, the post-mortality pattern is expected to be more regular than the 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, we took this approach to detect the importance of competition in the development of stand structure for a chronosequence of boreal forests.

4.1. Intraspecific competition as evaluated by univariate spatial pattern analysis

Our results showed that, with a few exceptions (e.g., aspen at the scale of 0–5 m in the Mxwood stand; see Fig. 2C and G), there is evident shift in spatial distribution from aggregation to randomness (and even to regularity) for the three dominant species analyzed in this study (Figs. 2–4). This provides prevailing evidence suggesting the importance of intraspecific competition in governing the spatial distribution and population dynamics of the tree populations in these forests. Both the spatial distributions of large aspen (Fig. 2I–L) and large spruce (Fig. 3I–L) were found to shift towards regularity as succession progressed, providing further evidence of competition in the development of boreal forest structure.

The non-random mortality of the four stands driven by intraspecific competition is also observed in other forests (Duncan, 1991; Szwagrzyk and Czerwczak, 1993; He et al., 1997), suggesting that density-dependent mortality is a prevailing mechanism in forest communities. Similar to a previous study conducted on an aspen population in a Danish deciduous mixedwood forest (Wolf, 2005), 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) (Fig. 2B) for pre-mortality aspen (live + dead) to a random distribution for surviving trees post-mortality (Fig. 2F), indicating that intraspecific competition is

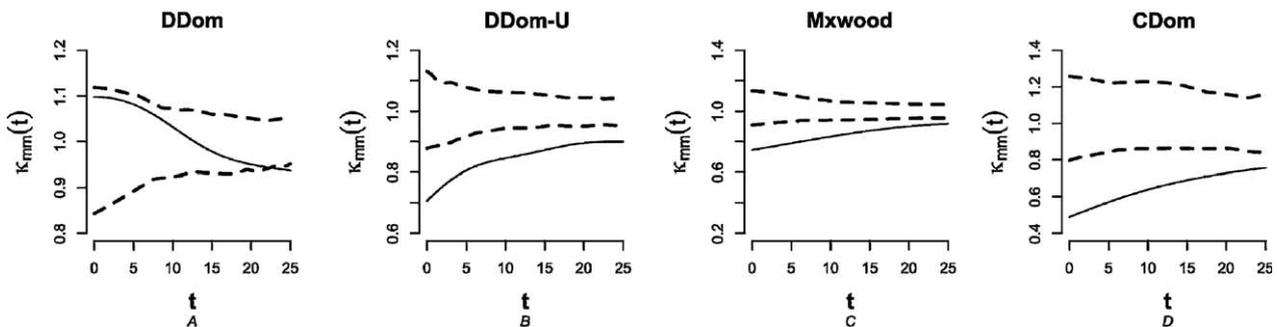


Fig. 5. Marked correlation function $\kappa_{mm}(t)$ for diameter at breast height and the Monte Carlo intervals for the trees of the three dominant species (trembling aspen, white spruce and balsam poplar) in four seral stages of the chronosequence of the studied boreal mixedwood forest. Observed patterns (—) that fall below the 95% Monte Carlo intervals (---) indicate a negative correlation between trees of different marks (i.e., dbh) at distance t .

of lesser importance. However, like Wolf, we found that dead trees were aggregated or randomly associated around live trees suggesting that, in this stand, competition may be more important in the change of spatial pattern than mortality.

Although the random mortality hypothesis was rejected for the three dominant species in almost every successional phase across the boreal chronosequence studied, not every post-mortality pattern showed significant small-scale regularity among surviving trees except for the strong trend of regularity in aspen and spruce post-mortality populations as succession progressed. The significantly higher proportions of mortality in conspecific neighbourhoods (Table 1) supports these results for aspen and spruce.

4.2. Interspecific competition as evaluated by bivariate spatial pattern analysis and marked correlation function

Although the bivariate $L(t)$ analysis was not able to detect significant shifts between pre- and post-mortality spatial patterns for the species pairs of 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. Failure to detect competition does not exclusively indicate absence of competition (Welden et al., 1988), it may be simply because interspecific competition is just not strong enough to cause significant mortality of heterospecific trees. In some situations, spatial “repulsion” between deciduous and conifer species may be undetectable because these species can avoid competition for light since white spruce is a species that can tolerate some degree of shading from light-demanding deciduous neighbours.

In previous studies, 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 we would expect similar results between aspen and spruce. Yet, the bivariate analysis was not able to detect any spatial association, negative or positive, among aspen and spruce. 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 growth of aspen could have masked significant mortality among aspen, thus obscuring the spatial bivariate analysis, as also found by Peterson and Squires (1995b) and Little (2002).

Spatial patterns only become detectable when competition is intensive enough to cause significant mortality (Stoll and Bergius, 2005). Consequently, failing to detect significant shifts in spatial distribution of stems 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 of the spatial patterns of large (dbh > 30 cm) aspen (Fig. 2I–L) and spruce (Fig. 3I–L) moving towards significant regularity as succession progressed suggests that there is a correlation between tree size and spatial distribution. This result is further supported by the marked correlation analysis (Fig. 5). The significant negative correlation among dbh marks shown by the $\kappa_{mm}(t)$ for the dominant species in the DDom, Mxwood and CDom stands indicates that large trees tend to have smaller neighbours (less intense competitors) and similar sized tree tend to “repel” one another as a result of neighbourhood competition. These results also suggest that interspecific competition likely reduces tree growth in these stands. No negative correlation in the DDom stand as indicated by $\kappa_{mm}(t)$ is likely due to that this stand is young and light was not a limiting factor.

Sustainable forest management in Alberta has long been interested in managing mixedwoods dominated by both deciduous and conifer species rather than single species plantations. The results of our spatial analyses suggest that minimizing the intraspecific competition between conspecific trees will likely

increase the survivorship of trees. Although failing to detect the effect of interspecific competition on tree mortality suggests that trees with heterospecific neighbours have a higher likelihood of survival, the analysis of the mark correlation function showed that neighbourhood competition had negative effect on tree size in the stands of this chronosequence. The maintenance of mixedwood forests will not only increase the diversity in stand composition but also will reduce the intensity of intraspecific competition and consequent mortality. However, the stand density and dbh distribution must be optimized to maintain a tree growth that compensates the loss due to competition.

5. Conclusion

In this study, we showed that intraspecific competition was an important process in three dominant species (aspen, balsam poplar and spruce) in a boreal forest chronosequence in Alberta. Our analysis further showed that interspecific competition in these forests was not strong enough to cause significant mortality (and shift in spatial patterns of tree distribution) but it significantly reduced tree growth. More importantly, this study provided strong evidence that competition played a central role in species displacement over succession of the mixedwood boreal forest. For aspen and balsam poplar, the relative importance of intraspecific competition decreases over succession. The opposite trend was observed for spruce. As a final caveat some caution is needed to interpret the results obtained from this study because of the inherent limitations of chronosequence approach, not the spatial pattern analysis itself, for inferring succession. Chronosequence is a space-for-time approach which is approximation but not a true representation of the dynamics of succession.

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