Original article

Structure, spatial distribution and competition in mixed jack pine (*Pinus banksiana*) stands on clay soils of eastern Canada

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Abstract – The dynamics of pure jack pine (*Pinus banksiana*) stands and of those also comprising a component of white birch (*Betula papyrifera*) and trembling aspen (*Populus tremuloides*) was assessed in natural post-fire stands on clay soils of eastern Canada boreal mixed woods in order to shed some light on mechanisms controlling composition. Age structures indicated that the presence of birch or aspen merely shortened the establishment of jack pine. Basal area structures of jack pine showed lower skewness coefficients in mixtures with birch than in pure jack pine stands or when mixed with aspen indicating that birch is probably a weaker competitor. Its effect on mean pine diameter probably reflects the lower pine stem density when mixed with birch. Inter-specific competition however had no effect on pine diameter at the tree level. Competition between birch, aspen and pine is avoided by species spatial exclusion measured by Ripley's statistic and reflects the reproductive strategies of the species and history of the site.

Ripley's K / asymmetric competition / interspecific competition / composition / stand structure

Résumé – Structure, distribution spatiale et compétition dans les peuplements mélangés et purs de pin gris (*Pinus banksiana*) sur argile dans l'est canadien. Nous avons étudié la dynamique des peuplements de pin gris purs (*Pinus banksiana*) et mélangés au bouleau à papier (*Betula papyrifera*) et au peuplier faux-tremble (*Populus tremuloides*), établis naturellement après un incendie sur sol argileux en forêt boréale mixte de l'est canadien dans le but de mieux comprendre ce qui contrôle leur composition. Les structures d'âge indiquent peu de différence dans le délai d'établissement du pin gris selon la composition. Les surfaces terrières des pins gris montrent de plus faibles coefficients d'asymétrie en mélange avec le bouleau qu'avec le peuplier, ce qui laisse à penser que le bouleau est un plus faible compétiteur. L'effet du bouleau sur le diamètre moyen du pin reflète la plus faible densité du pin en peuplements mélangés à du bouleau. La compétition interspécifique n'a cependant pas affecté le diamètre du pin à l'échelle de l'arbre. La compétition interspécifique est évitée par l'exclusion spatiale des espèces mise en évidence par la statistique de Ripley, ce qui reflète leur stratégies reproductives et l'historique du site.

statistique *K* de Ripley / compétition asymétrique / compétition interspécifique / composition / structure des peuplements

1. INTRODUCTION

The dynamics of jack pine stands on sandy or coarse-textured soils have been described in detail [10, 12, 16, 24, 25, 35, 45]. Jack pine (*Pinus banksiana* Lamb.), white birch (*Betula papyrifera* Marsh.) and trembling aspen (*Populus tremuloides* Michx.) stands occur extensively and in various mixtures in the post-fire landscapes of the clay belt of Ontario and Quebec [28]. However, information about these stands is more limited [1, 3].

Longpré et al. [28] have compared the growth of jack pine in pure jack pine stands and stands mixed with aspen or birch.

They found no difference in the effect of intraspecific competition from jack pine and interspecific competition from aspen. Their results also led them to believe that birch was not as good a competitor as jack pine because of its slower height growth rate [6].

The aim of this paper, is to investigate in more detail the dynamics of post-fire pure and mixed jack pine stands on clay soils in order to clarify the mechanisms controlling their composition. Specifically, we use a set of complementary tools to (i) compare the age structures in order to see if the establishment period of jack pine after fire differs in various species mixtures; (ii) compare the size structures of each species to

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explore the types of competition (symetric competition for soil resources or assymetric competition for light) occurring between trees of the same species and of different species [30, 43]; (iii) relate jack pine diameter to intra- and inter-specific competition at the tree level and (iv) compare the spatial distribution of trees of each species in order to evaluate the proportion of the stand experiencing interspecific or intraspecific competition.

We hypothesize that jack pine establishment period in jack pine mixed with aspen or birch is not different from that of pure stands. Because of the high productivity of clay soils in the study area [3], we suppose that competition for light is the major limiting growth factor in jack pine stands. Additionally, because of the difference in relative growth rates of the three species [6, 32], we suppose there is a gradient of increasing intensity of competition exerted upon jack pine trees by birch, jack pine to aspen. This gradient should be noticeable by increased skewness of size distribution of jack pine. Accordingly, accompanying species are expected to have higher skewness of size distribution when they are supressed and lower skewness of size distribution when they are dominant over jack pine. The gradient just described should also be noticeable by an effect of species-specific competition index on the DBH of jack pine.

The spatial distribution of trees in mixed and pure jack pine stands are expected to reflect the species dominant reproductive strategies. White birch stem patterns is expected to be clumpy due to its stump sprout origin and that of aspen is expected to be more random since it can root sprout as individual stems at a long distance from the other trees of its parent clone [27]. Consequently, aspen stems will be competing with a greater number of jack pine than birch stems. Some authors have hypothesized that competition between tree species have a large impact on spatial patterns of trees (association or repulsion) [37]. But spatial patterns of mixed species stands could also be related to site history. The study of spatial patterns of trees can be useful in explaining the intensity of competition measured with competition indices.

2. METHODS

2.1. Study area

The study area is located in the southern portion of Hébécourt township, Québec (48° 30' N, 79° 30' W), where the forest originated from a large fire in 1923 [11]. The stands are even aged. The area is located at the southern tip of the Clay Belt of northwestern Quebec and is included in the ecological region of the Amos Lowlands, which is characterized by glaciolacustrine clay deposits originating from the presence of the proglacial Lakes Barlow and Ojibway [42]. It is also at the southern limit of the Boreal Forest [36], within the balsam fir (*Abies balsamea* (L.) Mill.) – paper birch domain [39]. The regional climate is cold and continental with a mean annual temperature of 0.4 °C and annual precipitation of 800–900 mm, falling mostly during the growing season [15]. Although the average frost-free period is 147 days per year, the risk of frost persists throughout the year [44].

The sites where jack pine is found vary between two extremes: thin organic soil on rock and moderately to well-drained lacustrine clay deposits with a high base content [5].

2.2. Data

To minimize the effect of abiotic factors, the study sites were all selected on a similar site type: moderately well-drained glacio-lacustrine clay. The ecological mapping of the area [4] was used for site selection. Three stand types were selected: (i) pure jack pine stands, (ii) mixture of jack pine and trembling aspen, and (iii) mixture of jack pine and paper birch. Five 400-m^2 square plots were selected per stand type, and the 15 plots were well distributed over the 5-km^2 study area. In the mixed stands, the proportion of stems (greater than 10 cm DBH) of each species was approximately 50%.

In each plot, a soil profile was described to verify that they all were on moderately drained clays. All trees (an average of 44 trees per plot, range 26–52) were mapped and had their DBH measured. Between 16 and 19 jack pine trees per plot were cored with an increment borer for age determination.

2.3. Analysis

2.3.1. Age structure

The quartiles of age (1st quartile, median and 3rd quartile) of the jack pine population of each stand were used in order to compare the age structure of the three stand types. We chose this parameter because we were not so much interested in the form of the age structure as in the possible delay in stand establishment, i.e. time for establishment of 25%, 50% and 75% of the stems. Moreover, we think that mean age would have been misleading because distributions were skewed towards younger ages. A one-way analysis of variance (ANOVA) was performed to compare mean values between stand types. Levene's test of homogeneity of variance confirmed validity of the ANOVA.

2.3.2. Size structure

The theories of Weiner [43] about competition have the potential to be applied to mixed stands. These theories explore the frequency distribution in size of individuals in a population rather than the mean. An initially normal distributed population will first become positively skewed as a result of variance in initial exponential growth even without competitive interaction between individuals [30]. When competition is introduced, size structures become positively skewed as a result of differences in relative growth rate of small and large trees [31]. When competition is assymetric, as in competition for light, large individuals suppress growth of smaller ones more than would be expected from their relative sizes [14, 33, 46]. A population with a more asymmetric size structure is assumed to experience more asymmetric competition for light whereas a population with a more symmetric size structure would compete for other resources. Problems usually encountered in the application of this approach to tree populations are various: trees grow slowly and experience mortality, sites are seldom comparable, age is not the same and real size data are not always reliable. In addition, such applications usually deal with intraspecific competition [8, 18, 25, 26, 30, 31].

The data gathered by Longpré et al. [28] is well suited for this type of application. Among the size variables available, we chose tree basal area because it was available for every species and because it was assumed to be more closely related to tree volume than DBH. Inequality in the basal area distribution was evaluated by the skewness coefficient. One-way analysis of variance (ANOVA) was performed to compare skewness between stand types. Multiple comparisons were performed using the Tukey procedure at the 0.05 significance level.

2.3.3. Competition index

For all jack pine trees in each of the 15 stands, except those whose competitors were located outside the plot, a competition index was computed that differentiates the contribution of each competing species. The chosen index is modified from Hegyi's competition index [21]:

$$Hegyi_i = \sum_{j=1}^{n} \left[\frac{DBH_j/DBH_i}{R_{ij}^2} \right]$$

where DBH_j is DBH of jth competitor, DBH_i is DBH of subject tree i, R_{ij} is the linear distance between ith subject tree and the jth competitor. Competitor trees included in the calculation of the index were limited to those closer than a certain radius from the target tree [21]. We tested radii from 3 to 9 m. We chose this index because it was simple to use and, according to Holmes and Reed [22], performs as well as more complex indices. This index was modified to differentiate the relative influence of competitor species:

$$Hegyi_i = [Hegyi_{i,\,Pinus}] + [Hegyi_{i,\,other\;species}].$$

Multiple linear regressions were performed with jack pine DBH as dependent variable and the various components of competition as measured by the competition indices and the total index as independent variables. Selection of the variables was performed with the stepwise procedure. The procedure was repeated for each radius. A normality test performed on regression residuals confirmed the validity of the regressions.

2.3.4. Spatial distribution

Analysis of the spatial distribution of trees in each stand was performed using Ripley's K(d) function [34]. This method tests randomness of the distribution at multiple scales, based on the Poisson distribution, by examining the proportion of total possible pairs of points whose pair members are within a specified distance (d) of each other. We applied a square root transformation

$$L(d) = \sqrt{\frac{K(d)}{\pi}} - d$$

that linearize K(d), stabilizes its variance and has an expected value of zero under the Poisson assumption [7]. The test of departure from a random distribution is evaluated by determining a 95% Monte Carlo envelope. The approximate interpretation of the results leads to consider that, for a clustering pattern, L(d) is greater than this envelope, for a random pattern, it is within the envelope, and for a regular pattern, L(d) is below the envelope [13]. The univariate L(d) statistic was computed for each species separately. The bivariate $L_{12}(d)$ sta-

tistic was computed to assess the spatial relationship between competing species [29]. For this $L_{12}(d)$ statistic, 2 null hypothesis are commonly used: random labelling and population independence. Since 2 different species are concerned, the latter was tested by comparing $L_{12}(d)$ against a 95% Monte Carlo envelope defining independence of the two species [19]. $L_{12}(d)$ values above the envelope indicate spatial attraction and values below indicate spatial repulsion between the two species [29]. Univariate L(d), bivariate $L_{12}(d)$ and Monte Carlo envelopes were computed using Potemkin software developed by John Brzustowski from University of Alberta. Potemkin uses Ripley's [34] method of edge correction in which the sum calculated for each tree is weighed by the fraction of the circumference of a circle defining the neighbourhood assessed that lies within the sampled region.

3. RESULTS

3.1. Age structures

Overall, the age of sampled jack pine trees varied between 69 and 45 years with peaks between 65 and 60 years. These ages correspond to a period of establishment extending from the 1923 fire up to 22 years after fire but 75% of trees were established within 10 years after fire. The first quartile of establishment time since fire is significantly higher in pure stands than in stands mixed with either aspen or birch; the first 25% of pine trees in pure stands establishes approximately 1.5 years later than in mixed stands (Tab. I). Median and 3rd quartile are not significantly different between stand types indicating that later establishment is not delayed by companion species.

3.2. Size structures

Skewness of basal area distribution was positive no matter the stand type and was much higher for jack pine in pure stands and in mixture with aspen than in mixture with birch. Moreover, skewness for aspen was very small compared with that for birch (Fig. 1). There is a trend toward higher values of skewness for jack pine in mixture with aspen than in pure stands, but the difference is very small and not significant (Tab. II). However, aspen shows very low values of skewness compared to its pine competitor.

Table I. Effect of stand type on 1st quartile, median and 3rd quartile of time after the stand initiating fire of jack pine trees.

Variable	Source	Sum of squares	df	Mean square	F	P
1st quartile	Stand type	6.749	2	3.374	7.540	0.008
	Error	5.370	12	0.448		
Median	Stand type	1.665	2	0.832	0.748	0.494
	Error	13.362	12	1.114		
3rd quartile	Stand type	4.003	2	2.002	1.833	0.202
	Error	13.105	12	1.092		

Tukey comparison of means			
Stand type	Pure jack pine	Jack pine + white birch	Jack pine + trembling aspen
1st quartile	4.98a	3.50b	3.60b

Means with the same letter are not significantly different between stand types.
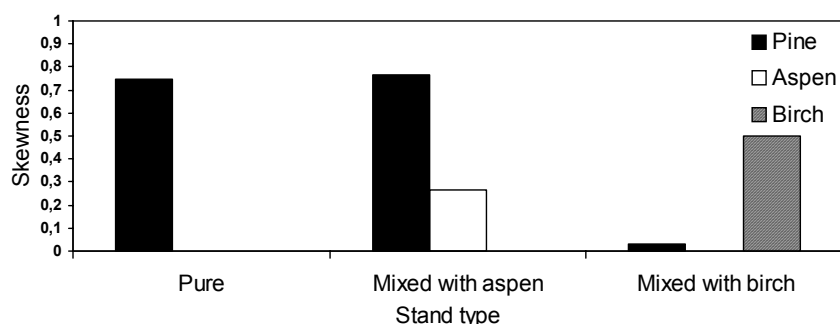
Figure 1. Skewness of basal area distribution of the three main tree species in 68-years old pure jack pine stands, stands mixed with aspen and stands mixed with white birch.

3.3. Effect of competition on dbh

Multiple linear regressions measuring the effect of various sources of competition on DBH of jack pine trees indicated that the index combining all species was the only component retained by the stepwise procedure except for stands mixed with birch where the contribution of black spruce (a minor component of some of the stands) was also significant. The radius chosen for the calculation of the competition indices was 6 m (lower radii had smaller R^2 and higher had to few subject trees). Competition from aspen or birch had little effect on the DBH of jack pine on the three stand types. Adjusted R^2 for the regressions varied between 0.58 and 0.768 (Tab. III).

3.4. Spatial distributions

L statistic for the spatial distribution of trees in one of the 5 pure jack pine stands is presented in Figure 2a superimposed on the complete spatial randomness 95% Monte Carlo envelope. For concision, we combined the five stands on the same graph but showed only the L statistic for the range of values that are over their envelope (significantly clumped) and below their envelope (significantly regular) for the five stands (Fig. 2b). This graph indicates that stems are usually randomly distributed at all scales except for a tendency to have a uniform distribution at a scale between 1–1.5 m for all five stands (Fig. 2). Some uniformity is still to be found at distance 6 m.

The spatial distribution of trees in jack pine stands mixed with birch shows that jack pine trees are randomly distributed at all scales for three of the five stands and have a clumped distribution at scales higher than 3.6 m for the two remaining stands (Fig. 3a). One exception to that is a trend toward uniformity between 1–3 m (Fig. 3a). Birch trees are clumped at small scales with a trend towards uniform distribution at larger scales (Fig. 3b). The bivariate statistic shows the two species are independant except for repulsion at 3 m and 6 m (Fig. 3c). Individual stand graphs (not shown) indicate that this repulsion is present only on one stand.

Table II. Effect of stand type on skewness of basal area distribution of the three main tree species in pure jack pine stands and stands composed of a mixture of jack pine and white birch and jack pine and trembling aspen.

Source	DF	Mean square	$P > F$
Stand type	4	0.498	0.711
Error	19	0.929	

The spatial distribution of trees in jack pine stands mixed with aspen shows that jack pine trees are usually clumped at scales between 6 and 10 m otherwise, they are randomly distributed (Fig. 4a). Aspen trees are clumped through a large range of scales for most stands (Fig. 4b). The bivariate statistic shows repulsion between the two species for a wide range of scales (Fig. 4c).

4. DISCUSSION

The results of this study shed some light on some of the processes controlling stand composition, structure and spatial distribution in mixed pine stands on clay soils.

Table III. Multiple linear regression of jack pine DBH as a function of various sources of competition from trees inside a 6 m radius for the three stand types.

| Stand type	Model	Unstandardized coefficients	Standardized coefficients	P
Pure pine	Constant	24.742		0.000
Adj R^2 = 0.580,	All species	–1.267	–0.763	0.000
N = 38	Pin cherry	–6.49	–0.259	0.021
Excluded	Pine		0.766	0.466
variables:	Black spruce		–0.040	0.712
	White birch		–0.088	0.423
	White spruce		0.175	0.105
Pine with birch	Constant	31.122		0.000
Adj R^2 = 0.724,	All species	–2.283	–0.724	0.002
N = 11	Black spruce	–12.831	–0.547	0.011
Excluded	Pine		–0.283	0.676
variables:	White birch		0.044	0.825
	White spruce		0.107	0.579
	Trembling aspen		–0.169	0.397
	Salix		0.460	0.646
Pine with aspen	Constant	28.116		0.000
Adj R^2 = 0.768,	All species	– 2.979	–0.886	0.000
N = 15				
Excluded	Pine		–0.193	0.451
variables:	White birch		0.007	0.963
	Trembling aspen		0.099	0.465

a

b
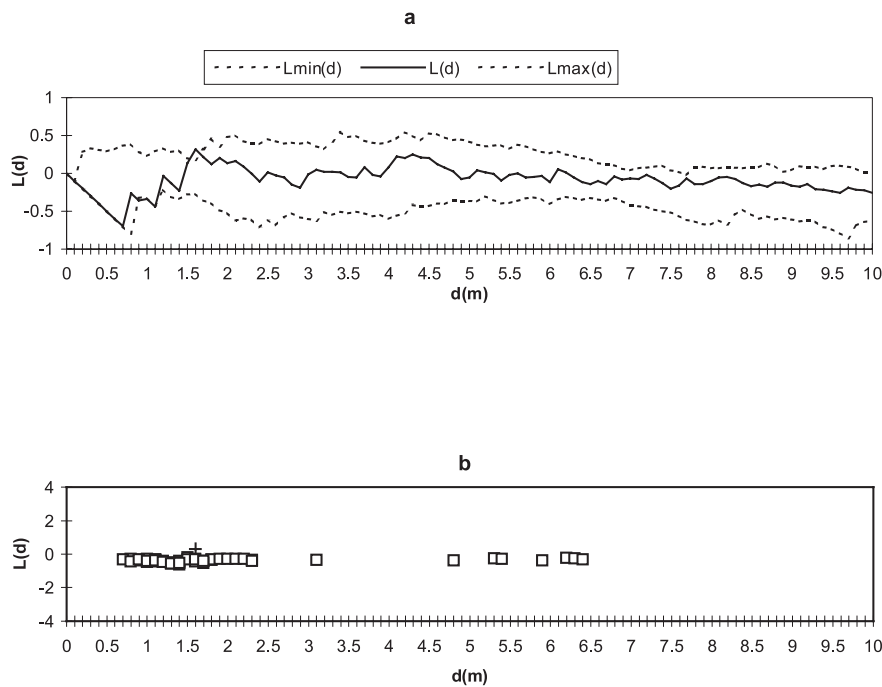
Figure 2. Ripley's univariate L statistic showing the spatial patterns of trees in 68-years old pure jack pine stands. (a) L statistic for one of the 5 stands superimposed on the complete spatial randomness 95% Monte Carlo envelope, (b) L statistic for the range of values that are over their envelope (significantly clumped "+") and below their envelope (significantly regular "□") for the five stands.

Establishment of most of jack pine trees within about 10 years is consistent with Gauthier et al. [17] who reported age structures indicative of establishment within 10 to 20 years after fire on mesic mainland jack pine populations of the same area. The small initial delay in tree establishment in pure stands relative to mixed stands, is small enough to allow us to use DBH as a surrogate for diameter growth for further analysis. It also excludes the possibility that the outcome of competition between species be influenced by such a delay at least for this particular fire year. It would have been interesting to also core aspen and birch trees to see if they experience the same delay.

As of the size structures, in theory, high values of skewness of size structure ought to be associated with a population experiencing more assymetric competition for light whereas low values are expected for symmetric competition for soil resources. This could explain why jack pine shows low skewness when mixed with birch and seems to confirm the hypothesis of Longpré et al. [28] about lower competition for light from birch than from pine or aspen. The very high values of skewness for birch trees in mixtures with pine is consistent with the fact that birch trees are overtopped by pine trees. Although comparisons of size inequalities to characterize competition between species are not common in the literature and should be made with caution, low values of skewness of aspen compared with pine in mixtures could indicate that aspen is a stronger competitor than jack pine.

The influence of mortality might have had an important influence on our results. According to Mohler et al. [30], skewness is supposed to be maximal just prior to the beginning of self thinning. Skewness is expected to be reduced afterwards as the smaller trees in the understory die but still be positive. Some mortality was recorded in the studied stands. However,

if the mortality was due to old tree senescence rather than to self-thinning, then any inference concerning the influence of spatial patterns and competition on diameter growth would be biased because of the loss of large trees that had an important competitive effect. However, field observation of the relative diameter of dead trees and their coordinates indicates that they are predominantly small trees from the understory that died from self-thinning.

In order to see if results from the analysis of size structures can be extrapolated to other stands, 1719 stands of various species composition and soil type were selected in the database of the Quebec Ministry of Natural Resources temporary sample plots for the Abitibi-Témiscamingue region. These plots indicate that skewness of basal area distribution do not follow exactly the same trends as in study plots (unpublished). Conversely, there was no difference in skewness in basal area distribution of jack pine between pure jack pine stands and stands composed of a mixture of jack pine and either of white birch or aspen. Trembling aspen basal area distribution did not show a lower skewness than that of jack pine when mixed together but did show a significantly higher skewness in pure stands. Birch skewness was not significantly different between pure stands or mixtures with pine. However, skewness of birch in pure stands was higher than that of jack pine and was not significantly different from that of birch in mixture with jack pine. The trend in aspen skewness seems to confirm that intraspecific competition is of higher intensity than inter-specific competition [38]. The trend in birch is in contradiction with our hypothesis of higher intensity of competition exerted on birch when overtopped by pine. One possible explanation of these results is that pure stands would be more regular and thus have fewer gaps which is confirmed in the study plots for pine stands but would have to be confirmed for pure birch and pure aspen stands since no stem mapping was done on those plots.
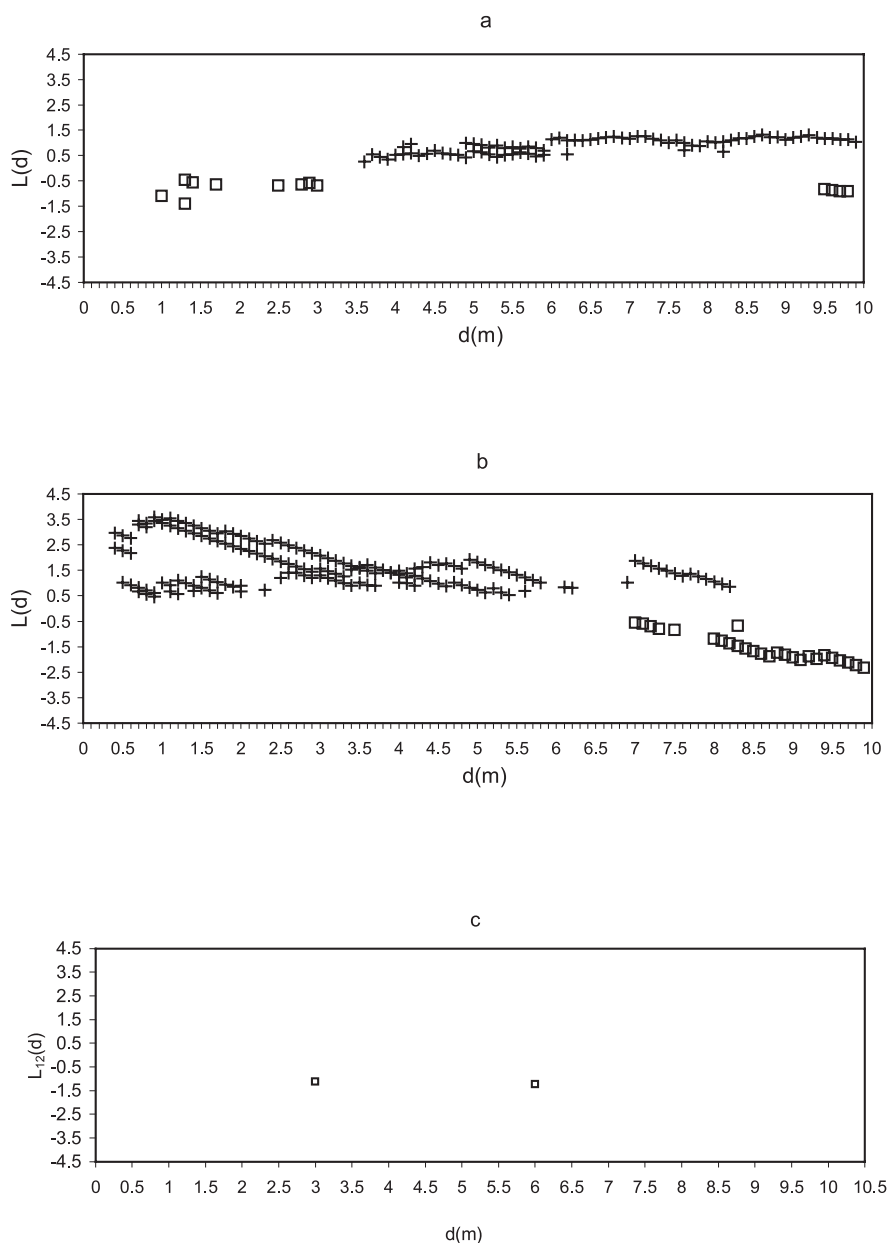
a

b

c

Figure 3. Ripley's L statistic showing the spatial patterns of trees in five 68-years old stands composed of a mixture of jack pine and white birch. (a) univariate L statistic for the range of values that are over their complete spatial randomness 95% Monte Carlo envelope (significantly clumped "+") and below their envelope (significantly regular "□") computed for jack pine alone, (b) univariate statistic computed for birch alone and c. Bivariate L_{12} statistic computed to test the the relationship between jack pine and white birch (values above their envelope indicate attraction between species "+" and values below their envelope indicate spatial repulsion between species "□").

The little effect of the presence of nearby aspen or birch on the DBH of jack pine trees on the three stand types support Szwagrzyk's [38] hypothesis that intra-specific competition is more intense than inter-specific competition.

The uniform distribution of jack pine stems at a scale of 1–1.5 m is probably indicative of the scale at which competition between jack pine trees influence stem distribution, i.e. two jack pine stems tend to exclude themselves when closer than 1.5 m apart. Uniformity found at distance 6 m is consistent with the fact that radius 6 m is the best radius for the competition index. The random distribution of jack pine is consistent with its reproduction by seed. Kenkel et al. [25, 26] and Yarranton and Yarranton [45] have shown that the distribution of jack

pine trees evolved with stand development from random at a young age toward uniform as a consequence of self-thinning. The trend toward uniformity of jack pine tree distribution in mixture with birch may be explained in the same way as for pure stands.

The spatial independance of jack pine and birch is explained by birch reproducing itself by seed and by stump sprouts and by its lower position in the canopy. Seed-origin birch trees are probably randomly distributed and intricately mixed among pines and influence little the spatial structure of pines, whereas stump sprouts produce clumps of stems that are variable in size. Larger clumps exclude pine trees over a larger area which explains the occurence of spatial repulsion in one of the stands,
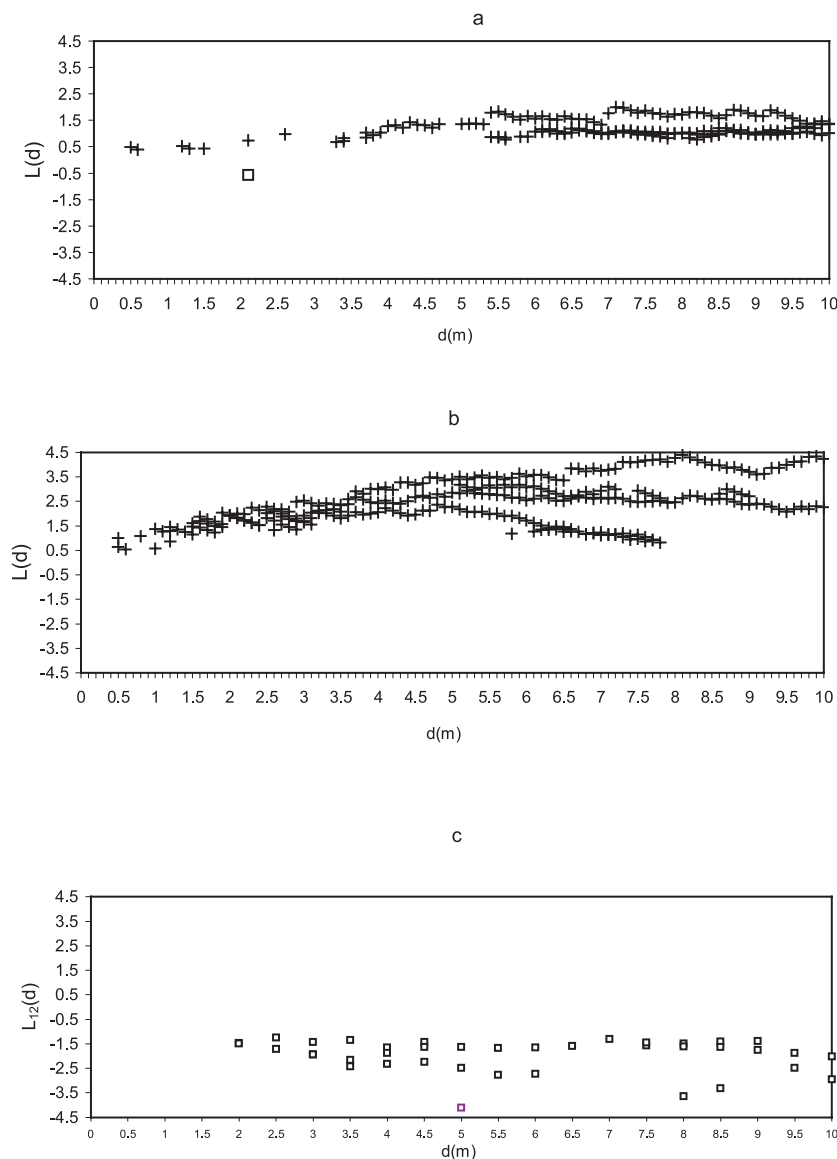
a

b

c

Figure 4. Ripley's L statistic showing the spatial patterns of trees in five 68-years old stands composed of a mixture of jack pine and trembling aspen. (a) univariate L statistic for the range of values that are over their complete spatial randomness 95% Monte Carlo envelope (significantly clumped "+") and below their envelope (significantly regular "□") computed for jack pine alone, (b) univariate statistic computed for aspen alone and (c) Bivariate L_{12} statistic computed to test the the relationship between jack pine and trembling aspen (values above their envelope indicate attraction between species "+" and values below their envelope indicate spatial repulsion between species "□").

whereas small clumps probably have no effect. Birch clumps are probably uniformly distributed. These results and the trends in skewness of basal area of pine in mixtures with birch (described above) leads us to think that birch influence on pine could be limited to symmetric competition for soil resources. This effect was apparent at the stand level in Longpré et al. [28] because the two species are more intricately mixed as a result of smaller stump sprout clumps than aspen root sucker clumps.

Spatial repulsion between pine and aspen might be explained by the strong dominance of vegetative reproduction by root suckers for the regeneration of trembling aspen [27]. Aspen trees form large clumps that exclude pine trees. Between clumps of aspen, pine trees are randomly distributed.

These results added to the fact that competition from aspen in mature stands did not significantly reduce the diameter growth of individual stems of jack pine and did not impact jack pine basal area structure are consistent with the lack of

difference in mean jack pine diameter observed by Longpré et al. [28] and are explained by the fact that the two species are not intricately mixed but rather form clumps. Competition between pine and aspen is thus limited to a relatively small proportion of trees in mixed stand.

Overall, since competition from companion species seems not to have had a large influence on the establishment delay, size structure and growth of jack pine in mature stands, we are forced to conclude that actual spatial structure and composition of the stands is either dependent on pre-fire stand composition, reproductive strategies of the species involved (as mentioned earlier) or on competition induced mortality that may have occured earlier in stand development. According to Greene and Johnson [20], post-fire composition in aspen, jack pine and black spruce stands is largely dependant on composition before fire. This stability in forest composition could be caused by the effect of forest composition on fire intensity; jack pine fuels

would favor more intense fires that kill most of the aspen roots and aspen fuels would lower fire intensity favoring more aspen root suckering. Another hypothesis involves the influence of aspen wood ash which Thomas and Wein [41] showed to be detrimental to jack pine germination before its alcaline content is drained away by rain. The main weaknesses of these conclusions is in the lack of data on stands at an earlier developmental stage and for different fire years.

Based on that process, our study may have implications for forest management since it is possible that cutting could favor forest compositions dominated by aspen more so than fire would [2, 9] even when large seedling stock are used [23, 40]. Greene and Johnson [20] argued that initial high aspen densities found after cutting are likely to diminish due to rapid self-thinning among root suckers. However, that may not be enough to change the relative dominance of species.

Our study could also have implications for the development of growth and stand dynamics models of the boreal mixed woods of Canada. Among other things, they stress the importance of explicitly taking into account the spatial distribution of trees. A model like SORTIE, in the process of being calibrated in the study area would respond to this concern.

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