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**Spatial and Temporal Patterns of White
Spruce Recruitment in Two Boreal
Mixedwood Stands, Duck Mountains,
Manitoba**

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EXECUTIVE SUMMARY

The effects of distance to seed source, biotic variables, and environmental variables on spatial and temporal recruitment patterns of white spruce were examined in two naturally regenerating stands in the Duck Mountains, Manitoba that burned in 1961. A total of 2 042 white spruce trees were aged at the base, 938 of which were also aged at a height of 1.25 m. Establishment density of the first cohort (ages 25-39) was unaffected by seed source proximity. At one of the two stands, higher cover of beaked hazelnut and aspen reduced recruitment of the first cohort. Density of the second cohort (ages 5-24) was greater in areas more proximate to the seed source. In addition, both biotic and environmental variables predicted abundance of the second cohort of white spruce: recruitment was higher in moister, more nutrient-rich sites with low beaked hazelnut cover. It is concluded that beaked hazelnut, and other deciduous vegetation, limits white spruce recruitment by reducing ground-level light availability and producing smothering broadleaf litter. A growth model based on empirical age-height relationships was developed to study growth suppression. In both stands, few of the initially-establishing trees were suppressed, but the proportion of suppression increased for later-establishing trees. The proportion of suppressed trees was also greater in the stand with higher cover of beaked hazelnut. Based on these findings, the following management recommendations are made: (1) Harvesting methods that promote the retention of mature white spruce as seed sources should be utilized; (2) Management alternatives should be developed to promote natural white spruce regeneration following harvesting of mixedwood stands; (3) Forest management should implement strategic planning strategies at the landscape scale, in order to maintain the historical diversity in stand composition, structure and successional stage characteristic of boreal mixedwood forest. Practical strategies for the implementation of these recommendations are discussed.

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INTRODUCTION

Boreal silviculture increasingly emphasizes mixedwood management strategies and natural regeneration, necessitating the need for greater knowledge of white spruce regeneration dynamics (Wang et al. 1995). Such knowledge will ensure sustainable yields of economically important species, while also conserving forest biodiversity and ecological integrity (Messier et al. 1999).

Natural regeneration of white spruce is often problematic: competition from aspen, shrubs, herbs and grasses, or mechanical injury during harvesting, may limit recruitment (Harvey and Bergeron 1989; Lieffers and Beck 1994). Adequate seed availability and appropriate seedbed conditions are also critical to promoting recruitment (Youngblood 1995; Kneeshaw and Bergeron 1996; Lieffers et al. 1996a; MacDonald et al. 2001). Numerous studies have demonstrated that white spruce regeneration may be improved by managing seed sources, by improving seedbeds conditions, and by optimizing stand densities (Lieffers and Beck 1994; Wang et al. 1995; Man and Lieffers 1999; MacPherson et al. 2001). Seedbed preparation by burning increases natural regeneration of white spruce in post-harvest stands (Densmore et al. 1999).

Regeneration of white spruce may also be promoted using appropriate mixedwood management strategies (Wang et al. 1995; Man and Lieffers 1999; MacPherson et al. 2001). An understanding of white spruce regeneration is critical in areas where fire remains a common stand-initiating disturbance, and where logging practices protect and promote natural advanced regeneration. Conifer recruitment into early post-disturbance stands is particularly difficult to model. Differential recruitment is typical, producing strong “patchiness” in the relative dominance of hardwoods versus softwoods in mixedwood stands. The rate of conversion from hardwood to softwood dominance is largely a reflection of changes in seed source availability and seedbed conditions (Lieffers et al. 1996a; Galipeau et al. 1997; Simard et al. 1998; Stewart et al. 1998; Hamel and Kenkel 2001). Recruitment of conifers into hardwood-dominated stands is often limited by competition from shrubs (Kneeshaw and Bergeron 1996; Messier et al. 1999).

The factors affecting natural white spruce regeneration in mixedwood stands, and changes in the relative importance of these factors over time, are best elucidated by studying spatial and temporal patterns of spruce recruitment in early post-fire stands. Baskerville (1986) notes that natural regeneration is one of the most challenging problems facing forest managers. This study complements others that have investigated white spruce regeneration in post-disturbance stand, and will further our understanding of the conditions required for successful

natural regeneration of white spruce in the boreal mixedwoods of the Duck Mountains, Manitoba.

Objectives

This study examines various factors that can potentially affect the regeneration dynamics of white spruce in two 39-year-old boreal mixedwood stands (Foster 2002). Seed source availability, seedbed suitability, and growing conditions are evaluated in relation to cohorts established at different times since fire. The specific goals of this study are:

- To determine temporal patterns of white spruce recruitment: age distributions are produced to determine the timing of white spruce dispersal and establishment.
- To determine spatial patterns of white spruce recruitment: the effects of distance from seed source, and various biotic and environmental factors, on white spruce recruitment are determined.
- To examine growth and mortality of regenerating white spruce: age-size relationships, growth rates, mortality, and degree of suppression are determined.

STUDY AREA

The study area is the Duck Mountain Provincial Park and Forest Reserve, an area of approximately 3770 km². The Duck Mountains are part of the Manitoba Escarpment, which includes Riding Mountain to the south and the Porcupine Hills to the north. Mean annual air temperature of the Duck Mountain uplands is approximately -1 C. Summers are short and warm, and the frost-free period is less than 100 days. The landscape is an undulating to hummocky till-plain underlain by loamy, moderately calcareous glacial till. Soils are highly variable, reflecting heterogeneity in parent material and the undulating topography. The complex physiography of the region gives rise to many different types of forest communities, interspersed with lakes and wetlands (Hamel and Kenkel 2001). Mixedwood stands composed of trembling aspen, balsam poplar, jack pine, white birch, white spruce and/or balsam fir dominate the uplands of the Duck Mountains. Trembling aspen stands occur in well-drained sites at lower elevation, often mixed with balsam poplar in richer, moister sites. Black spruce is common in poorly-drained, nutrient-deficient areas, often in association with tamarack. White spruce often occurs in the understory of aspen stands, and may remain in a suppressed state for extended periods. However,

recruitment of white spruce advanced regeneration into the upper canopy is also common (Hamel and Kenkel 2001).

Disturbance History

As in much of the boreal forest, large stand-destroying crown fires were historically characteristic of the Duck Mountains region. In 1885 a huge wildfire burned much of the Duck Mountains, and in 1961 a smaller fire burned the central portion of Duck Mountain Provincial Park.

Logging in the Duck Mountains began in the late 1880's, following agricultural settlement of the Swan River valley. The Duck Mt. Forest Reserve was created in 1906 to regulate timber supplies. Early logging operations selectively harvested large white spruce, and this continues to this day. Clear-cutting of both softwood and hardwood stands occurs in the Forest Reserve.

Study Sites

Research was carried out at two stands (named MAINLAND and PENINSULA) located near the north-west shore of Childs Lake (**Figure 1**). Both stands occur within the area burned in 1961. This fire, which was detected on August 16, 1961 on grass and scrub about a half mile northwest of Childs Lake, is thought to have originated from an unextinguished campfire. The fire spread rapidly on west and southwest winds gusting to 35 mph. Conditions at the time of the fire were extremely dry: from June 1960 to September 1961 little precipitation was recorded. The fire burned a total 21 000 ha and was not brought under control until early September 1961. The study area is quite variable topographically, with ridges, hills and depressions forming an irregular, hummocky terrain. Both study sites are adjacent to "old-growth" forest to the south. A few mature white spruce with fire scars on their lower trunks and burned lower branches were observed in the area between the two study sites.

Sampling Design

Eighty plots were established at each of the two study sites (**Figure 1**). At both sites, plots were arranged in a 10 x 8 grid oriented lengthwise away from the old-growth forest edge. Plot centroids were spaced 30 m apart. At the MAINLAND site the plots were 10 x 10 m in size, while those at the PENINSULA site were 5 x 5 m. The difference in plot size reflects the much higher density of white spruce regeneration at the PENINSULA site.

Within each plot all live and dead trees were identified and mapped, and their heights and trunk diameters (at 1.25 m) were measured. Fallen logs were also mapped, and their decay classes recorded. Percent cover was estimated for tree and tall shrub species. Randomly placed 1 x 1 m quadrats (four in each plot at the MAINLAND site, two at the PENINSULA site) were used to estimate percent cover of herbaceous species, low shrub species and moss species, and to record seedbed characteristics (relative cover of moss, exposed mineral soil, broadleaf litter and needle litter, decayed and undecayed logs). A soil pit was dug in each plot to describe the soil. Depth of the organic layer was recorded, and mineral soil from the upper 30 cm was taken for later determination of soil moisture, texture, pH, and conductivity.

All white spruce trees occurring in the plots were aged by taking full stem cross-sections at the tree base. For trees > 1.4 m in height, stem cross-sections were also taken at 1.25 m above the base. A total of 1 742 live trees were aged, of which 900 were aged at both the base and at 1.25 m. The total number of rings were counted using a dissecting microscope, after finely sanding the stem cross-sections. Four counts were made on each face of each cross section, and the highest count was used to estimate age.

A topographic survey of each site was undertaken using a Sokkia Set 4110 Series digital laser total station (angle accuracy 2 seconds, distance accuracy 2 mm to 1 km). Elevations were recorded at 10 m intervals at each site, including a 10 m buffer zone. Elevations were corrected to absolute elevation using the water level of Childs Lake as a reference point.

Characterization of Study Sites

Aerial photos taken prior to (1947) and immediately following (1963) the 1961 burn reveal higher conifer cover at the PENINSULA site compared to the MAINLAND site (Figure 1a). However, prior to the fire both sites were predominately mixedwood stands with an appreciable deciduous component. Following the fire, white spruce seed source occurred mainly to the south-east of the sites, with seed source being both more dense and proximate to the PENINSULA site (Figure 1b, Table 1). The sites have similar soils and are of similar elevational range, although the MAINLAND site is more sloping (13.3 vs. 6.9% mean slope). Trembling aspen density is virtually the same at both sites, but white spruce density is almost five times higher at the PENINSULA site. At both sites, aspen trees averaged 15-16 m in height. Tall shrubs (mainly beaked hazelnut) are common at the MAINLAND site, but are virtually non-existent at the PENINSULA site. The MAINLAND site has a higher proportion of broadleaf litter cover, and a lower proportion of moss and downed wood cover.

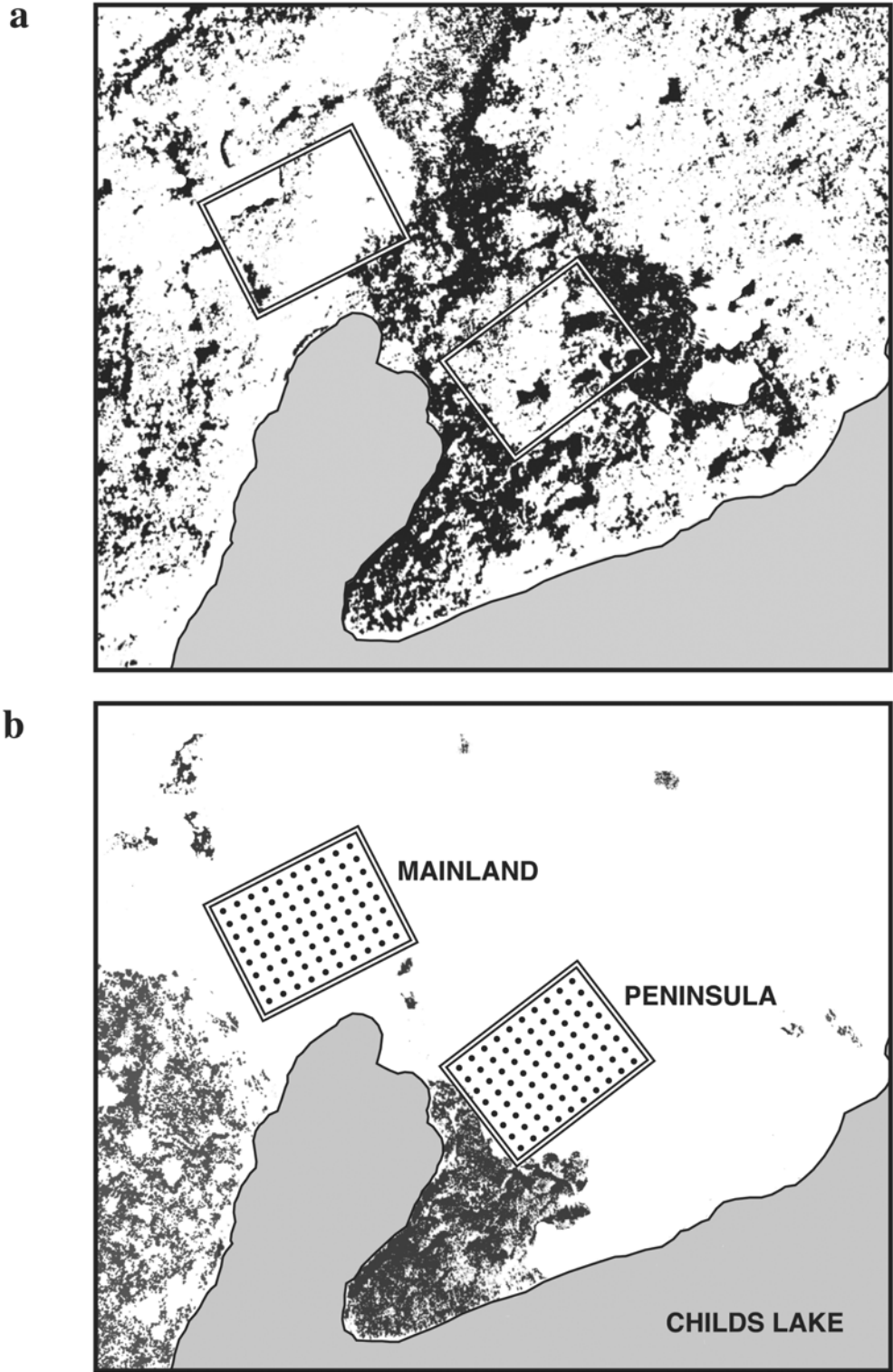


Figure 1. Comparison of the two study sites before and after the 1961 burn. (a) 1947; (b) 1963. Conifer dominated areas are indicated in black. Dots indicate locations of study plots.

Table 1. Characterization of the two study sites.

	MAINLAND	PENINSULA
UTM Coordinates (site centre):		
Easting	356859	357318
Northing	5722205	5721941
Elevation and Topography		
Mean (a.s.l., m)	678.93	675.24
Range (m)	669.9-688.7	670.5-679.9
Mean Slope (%)	13.33	6.86
Soils		
Sand (%)	64.3	57.9
Clay (%)	17.6	21.5
Organic Matter Depth (cm)	4.2	4.0
pH	6.7	6.4
Conductivity (uS/cm)	59.6	60.9
White Spruce Seed Source		
Distance from Plot Edge (m)	40	5
Density (trees/ha)	95	372.5
Basal Area (m ² /ha)	12.17	36.55
Tree Density (live trees/ha)		
White Spruce	954	4895
Trembling Aspen	3019	3080
White Birch	875	370
White Spruce Sampled (no. trees)		
Total Area Sampled (ha)	0.8	0.2
Live	763	979
Cohort 1 (ages 25-39)	407	638
Cohort 2 (ages 5-24)	266	264
Cohort 3 (ages 3-4)	90	77
Dead	28	262
Mean Cover (%)		
White Spruce	6.34	23.81
Deciduous Trees	53.65	37.05
Tall Shrubs	27.83	0.52
Herbaceous Species	44.61	40.57
Broadleaf Litter	89.17	42.19
Decayed Wood	8.66	9.60
Undecayed Wood	1.65	3.45
Mosses	5.43	10.21

DATA ANALYSIS

Temporal Patterns of White Spruce Recruitment

Tree ring counts taken from the base of each tree were used to construct age distributions for live white spruce trees. For synoptic purposes three cohort classes were recognized: cohort 1 = initial cohort (ages 25-39); cohort 2 = intermediate cohort (ages 5-24); cohort 3 = recently established (ages 3 and 4). No seedlings < 3 years old were found.

Spatial Patterns of White Spruce Recruitment

Three sets of variables are of interest in predicting white spruce recruitment into the plots: (1) distance to, and density of, seed source; (2) biotic variables, including deciduous tree, shrub, herb, and moss cover/abundance; (3) environmental variables, including elevation, slope, soil factors, and seedbed characteristics. Exploratory analyses indicated strong intercorrelations among variables in both the biotic and environmental data sets, at both sites. Principal component analysis (PCA, correlations on log-transformed data) was therefore employed to create single-variable (principal component) “gradients” of biotic and environmental variation for the two sites. For both sites, the principal environmental gradient was one of increasing soil moisture and nutrient availability. At the MAINLAND site, the principal biotic gradient was one of increasing cover/abundance of beaked hazelnut and trembling aspen. At the PENINSULA site (which lacked beaked hazelnut), the biotic gradient reflected increasing trembling aspen cover/abundance.

Distance to seed source is clearly a spatial variable. Spatial dependence may also characterize the biotic and environmental data, since both study sites were sampled using a regular grid of plots (Legendre and Legendre 1998). Prior to determining which variables best predict white spruce recruitment, the degree of spatial autocorrelation of the variables must be determined. Mantel tests (Manly 1991) were performed to determine the degree of spatial autocorrelation in white spruce abundance in each cohort (log-transformed), the biotic gradient, and the environmental gradient. The Mantel test determines the correlation between two association matrices: the “ecological” matrix (e.g. white spruce abundance in plots), and a matrix containing reciprocals of interplot distances. A negative correlation between the ecological matrix and the reciprocal distance matrix indicates that adjacent plots have similar values and are therefore positively spatially autocorrelated. Significance of the Mantel test was determined using a randomization test (999 randomizations were performed).

Because most of the variables proved to be significantly spatially autocorrelated, partial Mantel tests were performed to determine correlations between spruce abundance and various predictor variables, after removing spatial effects. A positive correlation between the variation of two variables, after accounting for geographic location, suggests that the two variables are associated over and above the confounding spatial effects (Legendre and Legendre 1998).

Regression analysis is commonly employed to predict a dependent variable (white spruce abundance) using one or more predictor variables (distance from seed source, biotic and environmental gradients). However, standard regression modelling is inappropriate when data are spatially autocorrelated. To overcome this problem, we used spatial location as a predictor variable in multiple regression analysis (Preisler et al. 1997). Partial regression analyses were also performed to partition the variation in white spruce abundance attributable the spatial, biotic and environmental variables (Legendre and Legendre 1998).

Growth and Suppression of White Spruce

For trees > 1.4 m in height, the difference in the number of tree rings at the base and at 1.25 m height was used to determine height growth rates (i.e. the number of years to achieve a height of 1.25 m). The heights (log-transformed) of all trees from both sites were regressed against their ages (log-transformed) to model height growth rates of white spruce. The regression was forced through the origin (corresponding to a height of 1 cm in the first year). The resulting power-law relationship:

$$\log [\text{height, cm}] = 1.609 \log [\text{age, yrs}]$$

was used to determine the proportion of suppressed white spruce as a function of age. Specifically, an aged tree that has not reach its predicted height (based on the power-law relationship) was considered suppressed.

RESULTS

Temporal Pattern of White Spruce Recruitment

The two study sites are approximately 260 m from one another, were burned by the same fire, are both close to the lakeshore, and shared other similarities (**Table 1**). However, white spruce recruitment was approximately five-fold higher at the PENINSULA site (4895 live

trees/ha, vs. 954 live trees/ha at the MAINLAND site). This is presumably attributable to the much higher density of white spruce seed source immediately adjacent to the PENINSULA site. However, the proportion of live spruce was higher at the MAINLAND site (96%) than the PENINSULA site (79%), indicating that higher density of white spruce recruitment results in increased density-dependent mortality (Lieffers et al. 1999; Messier et al. 1999). This is confirmed by examining mortality (the percentage of dead trees) as a function of total plot density of white spruce. Plots with < 12 trees per 10 x 10 m had < 5% mortality, while plots with > 80 trees per 10 x 10 m had approximately 30% mortality. It should be noted that mortality of seedlings went undetected, and fallen dead trees that had begun to decay were not enumerated. It is therefore likely that mortality is underestimated, particularly in dense plots.

Although total recruitment was higher on the PENINSULA site, the two sites show similar overall patterns of temporal recruitment (**Figure 2**). Both sites had a large cohort of four year old seedlings (cohort 3), possibly resulting from a recent mast year. At both sites, the majority of white spruce established between 5 and 14 years post-fire (cohort 1). However, recruitment was greater at the PENINSULA site during this period (coefficient of variation CV = 27.41%), while at the MAINLAND site recruitment was more continuous (CV = 35.97%, cohort 3 excluded). The cumulative frequency distribution (cohort 3 excluded) confirms these trends (**Figure 3**). At the MAINLAND site, 53% of trees belonged to the first cohort, 35% to the second cohort, and 12% to the third cohort. By contrast, at the PENINSULA site 65% belong to the first cohort, 27% to the second cohort, and 8% to the third cohort.

Spatial Pattern of White Spruce Recruitment

Distance to Seed Source

Distance from seed source is not important in determining recruitment of the first cohort, but has a greater effect on the second cohort (**Figure 4a**). The absence of a significant distance effect immediately post-fire suggests that fire severity may have been low, such that some seed source trees did not immediately succumb to the fire and were able to reseed these areas. Overall, seed source distance had less of an effect on recruitment at the PENINSULA site, which may be attributable to it having a denser and more proximate seed source stand.

Biotic Gradient

At the MAINLAND site, white spruce recruitment was significantly greater in areas with higher white birch and moss cover, and lesser amounts of trembling aspen and beaked hazelnut (**Figure 4b**). By contrast, at the PENINSULA site white spruce recruitment is not correlated with the biotic gradient. This may reflect greater vegetation uniformity at the PENINSULA site, and

the absence of beaked hazelnut. The MAINLAND site, by contrast, was characterized by alternating low and high-density areas of beaked hazelnut and aspen. The results indicate that white spruce recruitment is much lower in areas of high cover of beaked hazelnut and/or aspen.

Environmental Gradient

Recruitment of white spruce cohort 2 is greater in moister, nutrient-richer areas, particularly at the MAINLAND site (**Figure 4c**). This trend is less apparent for cohort 1 at either site, however, suggesting that immediate post-fire establishment of white spruce is less affected by edaphic conditions.

Spatial Autocorrelation

All variables at the MAINLAND site were significantly and positively autocorrelated (**Table 2**). By contrast, at the PENINSULA site only the environment and cohort 2 abundance were significantly positively autocorrelated. The absence of spatial autocorrelation for the biotic data at the PENINSULA site is not surprising, since there was limited floristic variation among plots at this site. The lack of significant autocorrelation of cohort 1 at the PENINSULA site confirms that limited role that seed source distance played at this site.

Correlations Among Variables After Removing Spatial Effects

At the MAINLAND site, significant positive correlations were found between white spruce recruitment (cohorts 1 and 2) and both the biotic and environmental gradients, after removing spatial effects (**Table 2**). These results indicate that over and above spatial effects (i.e. distance to seed source), white spruce recruitment of cohorts 1 and 2 is dependent on both biotic and environmental variation among plots.

At the PENINSULA site, recruitment of cohort 1 is not significantly correlated with either biotic or environment gradients, after removing spatial effects (**Table 2**). There is, however, a tendency towards positive correlation between biotic variation and cohort 1 abundance ($P = 0.074$). By contrast, variation in cohort 2 abundance is positively correlated with both the biotic and environmental variation, again after removing spatial effects.

When the same variables used in these partial Mantel tests were examined using simple Mantel tests (i.e. without removing spatial effects), similar results were obtained (not presented). Thus spatial effects do not have a strong influence on the correlations between white spruce abundance and biotic/environmental variation.

Multiple and Partial Regression Analysis

Overall, the multiple regression analysis results are similar to those obtained using Mantel and partial Mantel tests (not shown). However, regression analysis considers all variables simultaneously rather than in pairs. At the MAINLAND site, white spruce abundance (both cohorts 1 and 2) is significantly predicted by biotic variation; in addition, cohort 2 abundance is also significantly predicted by distance to seed source. For the PENINSULA site, cohort 1 abundance cannot be predicted to any significant degree by any of the variables. By contrast, cohort 2 abundance is significantly predicted by both environmental variation and distance to seed source.

The partial regression results summarize the proportion of variation in white spruce abundance accounted for by each set of variables: spatial, biotic/environment, and their interaction (shared variation). At the MAINLAND site, biotic/environmental variables account for 15% of the variation in cohort 1 abundance, with spatial variables accounting for an additional 7.9% (total $R^2 = 24.9\%$). Prediction is greater for cohort 2 (total $R^2 = 39.4\%$), and spatial variables become more important than biotic/environmental variables (18.4% vs. 10.3%, with an additional 10.7% determined by the variation shared by the spatial and environmental variables). For the PENINSULA site, cohort 1 abundance cannot be predicted by any of the variables (total $R^2 = 2.6\%$), whereas cohort 2 abundance is predicted by both biotic/environment (13.3%) and spatial (10.2%) variables (total $R^2 = 25.5\%$).

The highest amount of variation in white spruce abundance explained by spatial and biotic/environmental variables was 39.4%, leaving > 60% unexplained. Asselin et al. (2001) obtained similar results, and suggested that the high proportion of unexplained variation may reflect unmeasured variables (e.g. seedbed conditions at time of germination, light levels, humidity, soil temperatures, depth of the organic layer, nutrient availability, interspecific competition) as well as stochastic variation (see also Greene and Johnson 2000).

Summary of Results

A synopsis of results from the Mantel test, multiple regression, and partial regression analyses is presented in **Table 3**. Spatial effects (distance from seed source) are unimportant in explaining cohort 1 recruitment at both sites, but are important in predicting cohort 2 recruitment. Biotic variables are important in predicting recruitment of both cohorts at the MAINLAND site, with little recruitment occurring in plots with high cover/abundance of beaked hazelnut and trembling aspen. Environmental variables are less important, but there is a tendency for recruitment to be greater on moister, more nutrient-rich substrates. At the PENINSULA site, no variables are able to predict cohort 1 recruitment. For cohort 2, the most important predictor

of recruitment is the environment, with greater recruitment occurring on moist, nutrient-rich substrates.

Growth and Suppression of White Spruce

There is a great deal of variability in white spruce heights for trees of similar age (**Figure 5**), suggesting that the past and present growing environment has a strong effect on tree height. Variability in height increases as trees grow older as a result of the divergence of individual trees towards either a “suppressed” or a “free to grow” state, depending on light availability and other environmental conditions. On average, white spruce individuals > 1.4 m in height took approximately 12 to 13 years to grow to 1.25 m in height at both the PENINSULA and MAINLAND sites.

Power-law (log-log) regressions of height as a function of age fit the data well ($R^2 = 87\%$ for the MAINLAND, and 89% for the PENINSULA). The power-law growth model derived by regressing height against age for all trees (i.e. pooled data from the MAINLAND and PENINSULA sites) is shown in **Figure 6**, together with mean heights from the empirical data. In the model, one year old trees are assumed to be 1 cm in height. This model predicts that, in an unsuppressed state, white spruce reaches a height of 1.25 m by age 20. This is confirmed by both Eis (1967) and our empirical data, which indicates that over 97% of the tallest trees aged in this study (those > 1.4 m in height, 51% of the total number aged) reached a height of 1.25 m by age 20. Thus the model is rather conservative, and we are confident that any tree occurring below the modelled regression line is almost certainly suppressed.

At both sites, the proportion of suppressed trees is low for early-establishing trees (cohort 1, ages 25-39), but increases considerably for later-recruiting (cohort 2) trees (**Figure 7**). Thus trees that established soon after the fire have experienced much better growing conditions. Over time, competition from shrubs and an established tree canopy increases, and seedbed conditions become less favourable, resulting in a higher proportion of suppressed trees. The proportion of suppressed cohort 2 trees is greater at the MAINLAND site, perhaps reflecting strong competition from beaked hazelnut (which is absent from the PENINSULA site).

Table 2. Mantel and partial Mantel correlations (r) and associated probability values (P). Mantel tests are correlations between variables and spatial position (negative values indicate a positive autocorrelation). Partial Mantel tests are correlations between variables after removing spatial effects.

	MAINLAND		PENINSULA	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Mantel Tests				
Biotic Gradient	-0.052	0.028	-0.036	0.120
Environmental Gradient	-0.111	0.001	-0.073	0.007
White Spruce Abundance, Cohort 1	-0.102	0.002	-0.042	0.071
White Spruce Abundance, Cohort 2	-0.113	0.001	-0.084	0.001
Partial Mantel Tests				
Cohort 1 x Biotic Gradient	0.104	0.012	0.111	0.074
Cohort 1 x Environmental Gradient	0.094	0.023	0.004	0.465
Cohort 2 x Biotic Gradient	0.092	0.072	0.181	0.017
Cohort 2 x Environmental Gradient	0.133	0.019	0.094	0.054
Environment x Biotic Gradients	0.034	0.285	0.052	0.187

Table 3. Synopsis of the relative importance of spatial, biotic and environmental variables in predicting white spruce abundance (cohorts 1 and 2) at the two study sites. Codes: - = unimportant; 1 = minor importance; 2 = intermediate importance; 3 = most important. Values are based on results of the Mantel, partial Mantel, multiple regression, and partial regression results.

Variable	MAINLAND		PENINSULA	
	Cohort 1	Cohort 2	Cohort 1	Cohort 2
Spatial	*	***	-	**
Biotic	***	***	-	*
Environmental	**	**	-	***

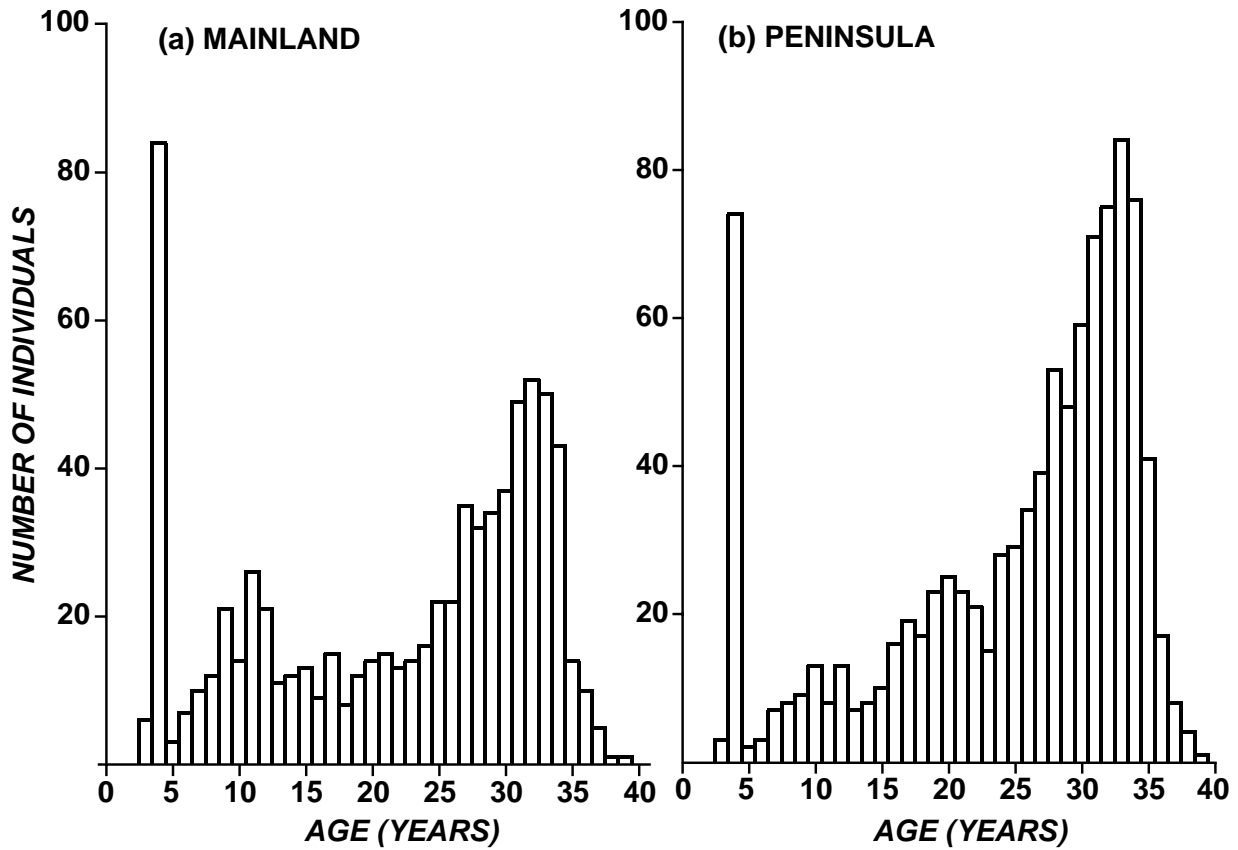


Figure 2. Age histograms for (a) MAINLAND site, $n = 673$; (b) PENINSULA site, $n = 979$.

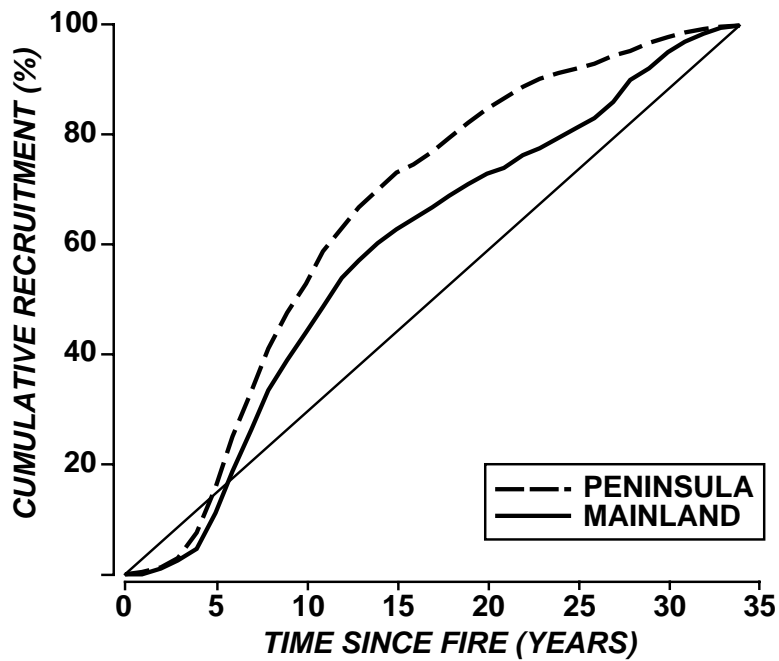


Figure 3. Cumulative age distributions (time since fire, years) for the MAINLAND and PENINSULA sites (excluding individuals < 5 years old).

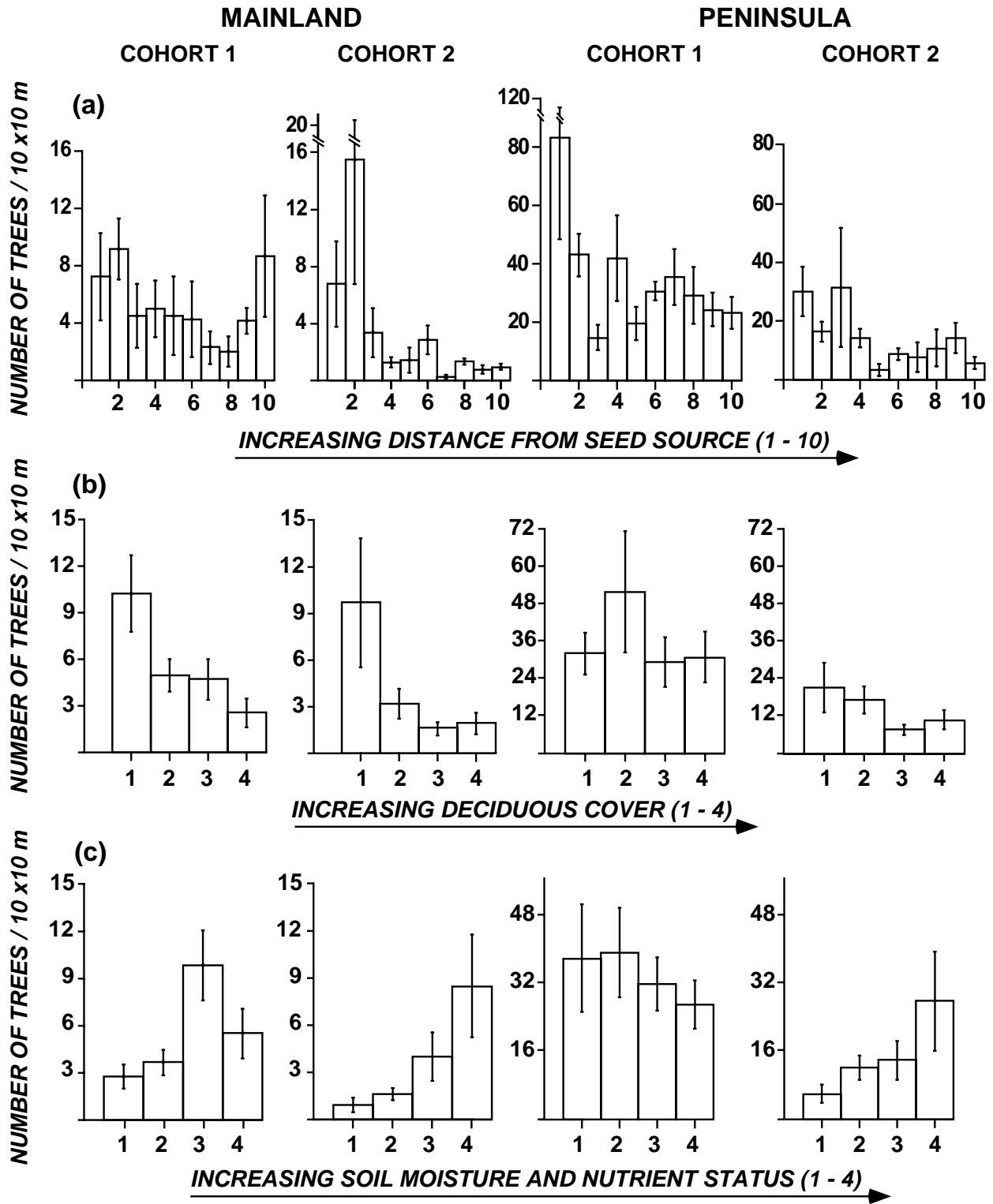


Figure 4. White spruce density (no. trees per 10 x 10 m, mean \pm s.e.) at the MAINLAND and PENINSULA sites, for two cohort classes (1 = ages 25-39, 2 = ages 5-24) as a function of: (a) seed source distance, ten 30 m intervals; (b) increasing deciduous cover (4 PCA axis score classes); (c) increasing soil moisture and nutrient status (4 PCA axis score classes).

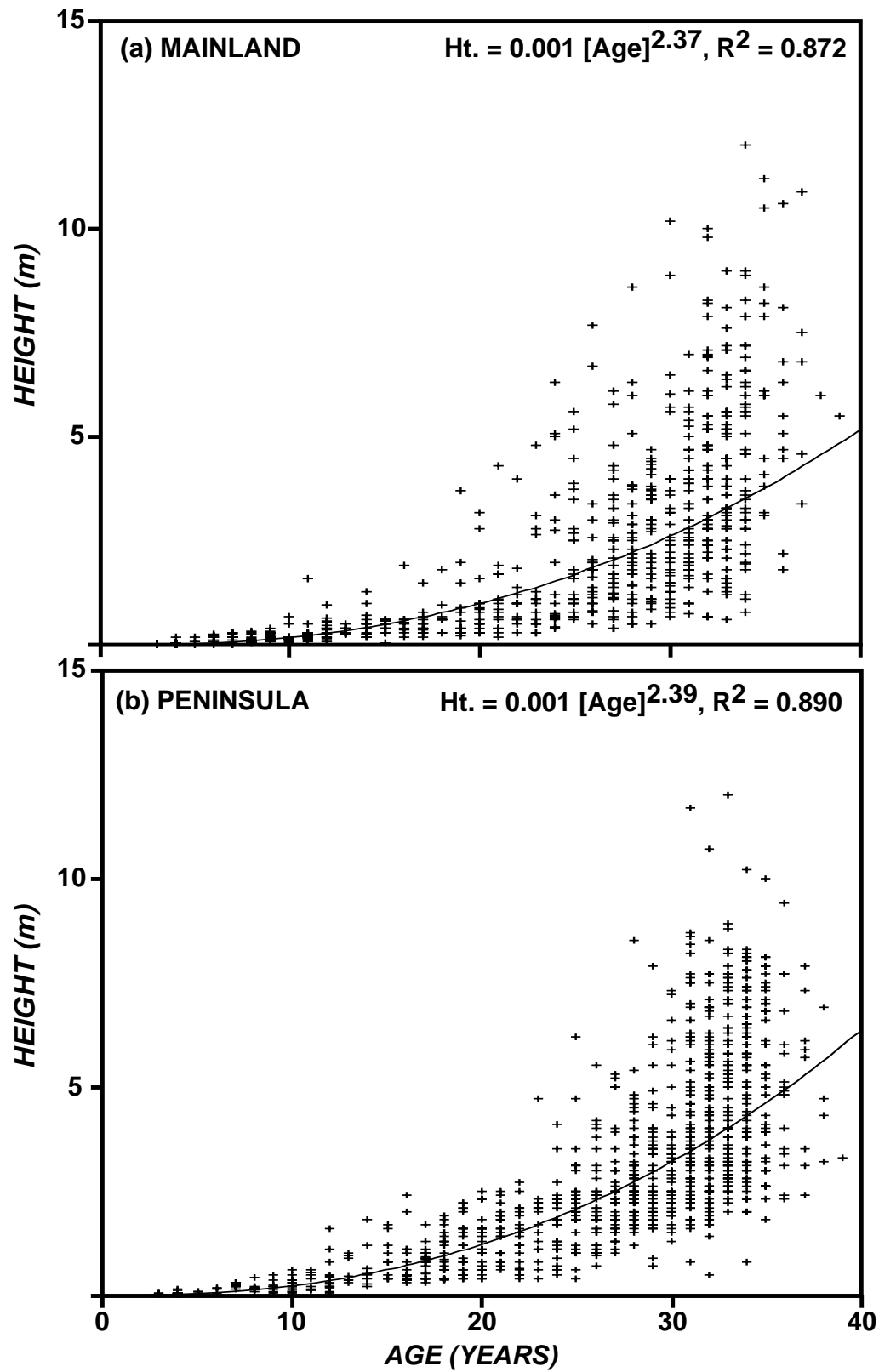


Figure 5. Height (m) as a function of age (years) for: (a) MAINLAND site, $n = 763$; (b) PENINSULA site, $n = 797$. Data are fit to a power-law model.



Figure 6. Suppression model for white spruce. The solid line is power-law regression. Circles denote observed mean heights for each age class.

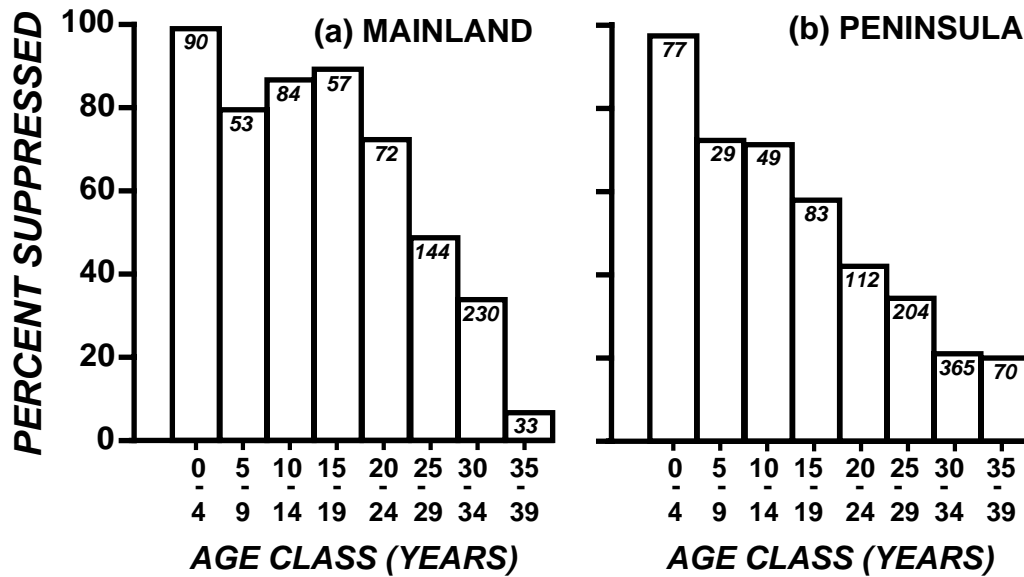


Figure 7. Percentage of suppressed trees as a function of age class, for (a) MAINLAND site; (b) PENINSULA site. Suppression is defined using the model given in Figure 6. Values in italics are the number of trees in each age class.

DISCUSSION

Temporal Patterns of White Spruce Recruitment

Our results indicate a 4-5 year delay in post-fire white spruce recruitment, which is in agreement with a number of other studies (Bergeron and Charron 1994; Youngblood 1995; Lieffers et al. 1996a; Galipeau et al. 1997). Using cross-dating techniques, Bergeron and Charron (1994) found a five-year delay in post-fire white spruce recruitment. In another Quebec study, initial recruitment was found to occur 10 to 25 years post-fire, with a second wave of recruitment occurring 40-50 years post-fire and sporadic recruitment thereafter (Galipeau et al. 1997). Mixedwood stands in Alberta show highly variable patterns of white spruce recruitment, with some stands displaying a “flush” of recruitment (lasting 15 to 20 years), and others more continuous recruitment lasting up to 80 years (Lieffers et al. 1996a).

Peters et al. (2002) provide evidence that static white spruce age structures must be interpreted with caution. They note that white spruce may grow slowly in the first few years, making it difficult to view early rings in older trees. In addition, they found that slowly-growing (suppressed) trees may be missing rings. While acknowledging that these problems may be relevant to our study, we note the following:

1. Trees in our study are much faster-growing (unsuppressed), thus minimizing the problem of missing rings and the detection of early rings (Peters et al. 2002). In their northern Alberta sites, Peters et al. (2002) found that “only trees aged 34 years old and older had mean heights exceeding 1.3 m” which suggests that their trees were strongly suppressed. By comparison, trees in our cohort class 1 (estimated ages 25-39) were much taller: mean height is 3.81 m, and 93.4% are at least 1.3 m in height ($n = 1045$, data pooled over the two sites).
2. Even after correcting for age discrepancies, Peters et al. (2002) found continuous recruitment in their 38 year-old stands: indeed, only 16% of their aged trees established in the first year. Thus correcting for potential age “bias” does not substantially alter the overall interpretation of temporal recruitment patterns, even for very slow-growing trees.

Thus, while acknowledging that our estimates of tree age may be slightly biased (on the order of a few years), we are confident that our results give a clear and accurate picture of temporal recruitment patterns in our sites.

Delays in post-fire recruitment may be attributable to poor seed production (non-masting years) immediately post-fire, with substantial recruitment occurring only in the first mast year

following fire. White spruce masting records are not available for the Duck Mountains, but data from Riding Mountain National Park (south of Duck Mountain) indicate a moderate white spruce seed crop in 1962, but no seed crop in 1963 (Waldron 1965). Unusually cool summer weather in 1962 delayed seed dissemination until mid-September. These factors may account for the recruitment delay seen in our study sites.

Our results indicate that white spruce recruitment at both sites began to decline after approximately 15 years post-fire (see also Peters et al. 2002). Seed source proximity is often cited as the factor most limiting to conifer recruitment, especially when dispersal is into full-canopy stands (Kneeshaw and Bergeron 1996; Galipeau et al. 1997; Greene and Johnson 2000; Asselin et al. 2001). Forest canopies act as physical barriers, and alter air currents. It seems likely that the number of seeds dispersing into the study sites declined over time as the aspen canopy developed (Stewart et al. 1998).

Lieffers et al. (1996a) related periods of lower white spruce recruitment to decreased light availability under already-established white spruce. They observed shorter periods of recruitment in stands with higher spruce basal areas. Galipeau et al. (1997) found that white spruce recruitment declined 25 years post-fire, a result they attributed to increased competition from tall shrub and herbaceous species. Tall shrubs and herbs attenuate light, and produce broadleaf litter that inhibits seed germination and smothers established seedlings. Youngblood (1995) notes that white spruce seed will germinate in older stands, but poor seedbed conditions result in low survival rates and thus low perceived recruitment.

Temporal recruitment patterns of white spruce at the two sites differ somewhat. The PENINSULA site has much higher recruitment (4510 trees/ha, vs. 841 trees/ha at MAINLAND), and a higher proportion of individuals established as the first cohort (within 14 years post-fire): 71% at the PENINSULA site, versus 60% at the MAINLAND site (these values exclude seedlings < 5 years old). The low cover of tall shrubs (mostly beaked hazelnut), combined with a more proximate seed source, may have been more conducive to rapid and dense white spruce recruitment at the PENINSULA site (Youngblood 1995; Lieffers et al. 1996a).

Spatial Patterns of White Spruce Recruitment

Distance to Seed Source

A number of studies have demonstrated the importance of seed source proximity to post-disturbance recruitment of white spruce (e.g. Galipeau et al. 1997; Asselin et al. 2001). The majority of white spruce seed falls within a few tens of meters of the parent tree, although adequate dispersal for natural regeneration may occur up to 300 m (Dobbs 1976) and some regeneration occurs as far as 2000 m from a seed source (Galipeau et al. 1997). Our results indicate that density of the initial post-fire cohort is unaffected by distance to seed source (over a distance of 300 m), but that second cohort establishment occurs in areas nearer a seed source. This result may reflect the ability of seed to readily disperse into newly-burned sites, with dispersal becoming more limited once the aspen canopy develops (Stewart et al. 1998). It is possible that a few white spruce trees were only scorched by the fire, and survived long enough to disperse their seed into the sites immediately post-fire (Greene et al. 1999; Bergeron 2000). Indeed, a few mature white spruce with fire scars and burned lower branches were observed in the area between the two study sites.

Environmental Factors Affecting Recruitment

At both study sites, greater white spruce recruitment occurred in plots of higher soil moisture availability and nutrient status. White spruce regeneration occurs on various substrates, from sandy loams (Galipeau et al. 1997) to fine-textured clays (Kneeshaw and Bergeron 1996). The soils of our study sites are well-drained sandy loams that are subject to drying. This, coupled with a variable topography, supports the notion that soil moisture availability is an important factor at our sites.

Biotic Factors Affecting Recruitment

Compared to the PENINSULA site, the MAINLAND site had much higher cover of beaked hazelnut (mean = 27.83% vs. 0.52%) and more broadleaf litter (mean = 89.17% vs. 42.19%). The density of white spruce recruitment was strongly predicted by biotic variables only at the MAINLAND site, being much greater in plots with low cover of beaked hazelnut and broadleaf litter. This result, coupled with the unimportance of biotic variables in predicting recruitment at the PENINSULA site (where beaked hazelnut is rare), suggests that white spruce has difficulty establishing in areas where beaked hazelnut is abundant. Beaked hazelnut and other tall shrubs limit white spruce establishment and growth by attenuating light (Buckman 1964; Lieffers and Stadt 1994; Kneeshaw and Bergeron 1996; Messier et al. 1998), and by increasing the amount of smothering deciduous leaf litter (Kneeshaw and Bergeron 1996; Lieffers et al. 1996a; Delong et al. 1997; Galipeau et al. 1997). Furthermore, broadleaf litter

inhibits white spruce germination and establishment by forming a mechanical barrier of low moisture holding capacity.

Growth and Suppression of White Spruce

There is much variability in white spruce heights for trees of a given age, at both study sites. Light availability strongly affects the growth rates of understory conifers occurring beneath an established forest canopy (Lieffers et al. 1996a; Aubin et al. 2000), but the spatial and temporal dynamics of light availability are complex and very difficult to quantify in developing forest stands. Indeed, the effects of competition (for light, nutrients and water) are cumulative, and therefore have strong long-term impacts on tree growth (Jobidon 2000).

While few of the early-establishing trees are growing in a suppressed state, the proportion of suppressed trees increases considerably for later-establishing individuals. Early-establishing white spruce are able to overtop the developing understory vegetation, and therefore are able to grow under light conditions adequate to maintain healthy growth. Above the shrub layer aspen canopies transmit 15 – 40% of ambient light, which is considered adequate for acceptable growth of white spruce saplings (Constabel and Lieffers 1996). Indeed, growth of white spruce under 40% light may be better than under full light conditions (Lieffers and Stadt 1994). By contrast, later-establishing individuals are subject to strong competition from both understory vegetation (tall shrubs and herbaceous plants) and a well-developed forest canopy (aspen and earlier-establishing individuals). Under these low light conditions, white spruce is able to survive in a low-growth “suppressed” condition for several decades (Wright et al. 2000). The proportion of suppressed trees in the second cohort (ages 5-24) was much greater at the MAINLAND site (80%, vs. 55% for the PENINSULA site), suggesting the importance of beaked hazelnut cover in suppressing regenerating white spruce (DeGrandpre et al. 1993; Lieffers et al. 1996a). White spruce density is much higher at the PENINSULA site, however, and it is possible that later-establishing individuals have simply acquired a taller, more slender growth form to compete for light with their intraspecific neighbours.

MANAGEMENT APPLICATIONS

In the past few decades, boreal forest managers have increasingly emphasized principles of sustainable forest management (Baskerville 1986; Bergeron et al. 1999). These principles include emulating natural processes and disturbances, operating within the natural limits of interstand variation, and considering ecological processes at all spatial scales (Burton et al. 1992; Lieffers et al. 1996b; Andison and Kimmins 1999; Oliver 1999; Harvey et al. 2002). Implicit in

this approach is the need to achieve multiple management objectives, and to consider management effects on long-term forest health, biodiversity maintenance, public scrutiny, and stewardship of the land (Spies 1997). The development of sustainable management practices is particularly challenging for boreal mixedwood forests, which are characterized by a remarkable diversity of stand composition and structure (MacDonald 1995). This diversity reflects variations in factors such as historical disturbance regimes, disturbance type, climate, edaphic factors, and successional stage, all of which operate over a multitude of spatial scales (Bergeron 2000; Frelich 2002).

Conifer regeneration is one of the most difficult and challenging issues facing boreal mixedwood forest managers (Greene et al. 1999). Recruitment of white spruce in both managed and natural mixedwood stands is complex and difficult to predict (Kneeshaw and Bergeron 1996; Macdonald et al. 2001). A number of synergistically-interacting factors are thought to affect spatial and temporal patterns of recruitment, including seed availability, seedbed conditions, competition from understory vegetation, light availability, soil moisture and nutrients, site drainage, and mechanical injury during harvesting. The relative importance of these factors in affecting white spruce regeneration, and changes in their importance over time, are best elucidated by studying recruitment patterns in early post-disturbance stands (Lieffers et al. 1996a; Cornett et al. 1998).

The present study was undertaken to investigate post-disturbance recruitment patterns of white spruce in the boreal mixedwood of Duck Mountain, Manitoba. A number of our findings are of direct relevance to the development and promotion of sound management principles for mixed aspen-white spruce stands in the region:

1. Seed availability is of critical importance in determining the rate and density of post-disturbance white spruce recruitment.
2. The majority of trees recruiting in the first 10 years post-disturbance grow rapidly, and are destined to reach merchantable size. By contrast, later-establishing individuals are subject to strong competition for light (from understory plants, tall shrubs, and the developing stand canopy). These individuals remain in a highly suppressed state and may eventually die.
3. Lower recruitment of white spruce occurs on drier, nutrient-impooverished substrates. This, in combination with limited seed availability and interspecific competition, results in a strongly “clumped” pattern of white spruce abundance at all spatial scales (plot, stand, and landscape).

These findings naturally lead to the following specific management recommendations:

1. Harvesting alternatives should be implemented to promote the retention of mature white spruce as seed sources.

Clear-cutting is the most common harvesting method in the boreal mixedwoods of Manitoba (including the Duck Mountains), although selective harvesting of mature white spruce trees is also practiced. Full-tree harvest clear-cutting removes white spruce seed sources, resulting in post-harvest stands that are almost completely dominated by aspen and other hardwoods (Lieffers et al. 1996a; Qi and Scarratt 1998). Under such circumstances, artificial regeneration may be required to maintain a softwood-hardwood mixture. A more desirable approach is to implement “careful logging” practices, retaining the advance growth of white spruce during harvesting (Bergeron and Harvey 1997; Bergeron et al. 1999). Modified approaches to large-scale simple clear-cutting, such as decreasing the size of cut-blocks (increasing the perimeter:area ratio), the retaining strips or patches within cut-blocks, and implementing shelterwood harvesting systems, are effective both in maintaining a white spruce component and in emulating the historical “patchiness” of boreal mixedwood stands (Lieffers et al. 1996a,b; Wurtz and Zasada 2001; Bergeron et al. 2001). Many of these approaches have been implemented by Sustainable Forest Management Network partners, including Louisiana-Pacific operations in Manitoba.

2. Management alternatives should be developed to promote natural white spruce regeneration following harvesting of mixedwood stands.

In addition to implementing methods to protect white spruce advanced regeneration at harvest (discussed above), management strategies that promote post-harvest white spruce establishment should be implemented. White spruce recruitment is promoted when mixedwood harvesting is timed to a white spruce mast year (Wurtz and Zasada 2001). In non-mast years, white spruce recruitment is delayed and established seedlings are subject to increased interspecific competition from understory vegetation and regenerating aspen suckers. Proper site preparation, such as the creation of appropriate seedbeds and reduction in the cover/abundance of competing understory vegetation, promotes post-disturbance establishment and growth of white spruce (Ball and Walker 1995; Cole et al. 1999; Groot 1999). Competition from beaked hazelnut, a tall shrub, has long been recognized as a major factor compromising white spruce recruitment in western Manitoba mixedwoods (Rowe 1955; Waldron 1959, 1966; Caners and Kenkel 1998) and elsewhere (Buckman 1964; Ross et al. 1986; Messier et al. 1998). Tall shrub cover is greatly reduced following clear-cutting in the Duck Mountains (Murray and Kenkel 2001), offering a “window of opportunity” for post-disturbance recruitment of white spruce. Consideration should

be given to developing harvesting and management strategies that reduce the cover/abundance of beaked hazelnut.

3. Forest management should implement strategic planning strategies at the landscape scale, in order to maintain the historical diversity in stand composition, structure and successional stage characteristic of boreal mixedwood forest.

Forest management strategies should be “scaled up” to consider how decisions made at the stand level affect the entire landscape (Andison and Kimmins 1999). Planning decisions must consider the timing, location, shape and spatial extent of clearcuts so as to maintain the structural, compositional and successional properties of the landscape and thus promote habitat heterogeneity (Burton et al. 1992; Frelich 2002). Gauthier et al. (1996) and Harvey et al. (2002) discuss methods for integrating stand-level and landscape-level decisions in the context of disturbance-based management. In the Duck Mountains, Louisiana-Pacific takes into consideration natural compositional variation of forest stands in their harvesting strategies and management decisions. Aspen-dominated stands (with little or no conifer component) should be managed for hardwood production, while efforts are made to maintain the conifer component of harvested mixedwood stands.

CONCLUSIONS

This study demonstrates that recruitment density of white spruce trees establishing within 15 years post-fire is unaffected by seed source proximity over a distance of 300 m. However, the density of the later-establishing trees is greater in areas more proximate to the seed source. Both biotic and environmental variables predict white spruce abundance, particularly later-establishing trees. Recruitment is highest in moist, more nutrient-rich sites with low beaked hazelnut cover. In the study area, beaked hazelnut and other deciduous vegetation limits white spruce recruitment by reducing ground-level light availability and producing smothering broadleaf litter. Time of establishment is a strong predictor of suppression: later-establishing trees are much more likely to remain in a suppressed state. These findings naturally lead to specific forest management recommendations for maintaining the structural, compositional and successional properties of mixedwood stands and landscapes. Harvesting methods that promote the retention of some mature white spruce seed sources should be practiced. In addition, post-harvest management strategies such as tall shrub control should be developed to promote natural white spruce regeneration. Finally, strategic planning strategies for forest management should be

developed at the landscape scale so as to maintain the historical diversity in stand composition, structure and successional stage characteristic of boreal mixedwood forest.

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