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forest ecology

Regeneration Dynamics of White Spruce, Trembling Aspen, and Balsam Poplar in Response to Disturbance, Climatic, and Edaphic Factors in the Cold, Dry Boreal Forests of the Southwest Yukon, Canada

Shyam K. Paudel, Craig R. Nitschke, Suzanne W. Simard, and John L. Innes

The southwestern region of the Yukon Territory of Canada has experienced an unprecedented spruce bark beetle outbreak (*Dendroctonus rufipennis*) and an increase in the frequency of forest fires that extend beyond historical trends and that have caused significant impacts on forest structure and composition. A Strategic Forest Management Plan (SFMP) for the Champagne and Aishihik Traditional Territory located in the southwest Yukon was implemented in 2004 in response to the spruce bark beetle (*D. rufipennis*) infestation and increased fire risk. The plan has recommended salvage harvesting of beetle-killed stands as a strategy to facilitate the development of a timber industry in the region and reduce the fire risk around communities. One of the objectives of the SFMP is to maintain, restore, or enhance forest regeneration, which requires an understanding of regeneration dynamics in the region. In this study, we investigated the regeneration of white spruce (*Picea glauca*), trembling aspen (*Populus tremuloides*), and balsam poplar (*Populus balsamifera*) and the relationship with climatic, disturbance, and edaphic factors within the region. Multivariate canonical correlation analysis was used to assess the weighted relationship between regeneration presence/absence and environmental factors, and negative binomial regression analysis was used to model regeneration abundance of white spruce, trembling aspen, and balsam poplar. We found that although regeneration of all three species responded positively to disturbance, the broadleaved species occupied disturbed plots at higher ratios than white spruce. Regeneration of broadleaved species was higher in open sites with exposed aspects, indicating a preference for warmer sites with higher solar radiation inputs. These findings support the hypothesis that if fire increased in the region with the warmer climate predicted by the Intergovernmental Panel on Climate Change, then the region will probably experience an increase in broadleaved species, leading to a more heterogeneous landscape.

Keywords: regeneration, boreal forest, disturbances, climate variability

Climate in the Canadian north is changing significantly, with increased temperature and precipitation being reported over the last 50 years (Frugal and Prowse 2008). These changes in regional climate, exacerbated by the presence of large areas of unmanaged and mature white spruce (*Picea glauca*) stands, have facilitated an unprecedented 380,000-ha outbreak by the spruce bark beetle (*Dendroctonus rufipennis*) in the region (Berg et al. 2006, Government of Yukon 2010). Within the Champagne and Aishihik Traditional Territory (CATT) of the southwest Yukon, the outbreak covered more than 270,000 ha; between 1993 and 2006, about 85% of the forests were affected (Arctic Climate Impact Assessment [ACIA] 2004, Government of Yukon 2009). This has resulted in a dramatic increase in dead fuel that has increased the risk of forest fires occurring within the

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This article uses metric units; the applicable conversion factors are: centimeters (cm): 1 cm = 0.39 in.; meters (m): 1 m = 3.3 ft; square meters (m²): 1 m² = 10.8 ft²; millimeters (mm): 1 mm = 0.039 in.; hectares (ha): 1 ha = 2.47 ac.

region (Garbutt et al. 2006). Concurrent with the bark beetle outbreak, the Yukon has also been experiencing increases in wildfire severity and frequency (Hogg and Wein 2005, Rosenzweig et al. 2007). In the absence of active fire management, the average annual fire frequency and total area burned in the Yukon Territory is projected to double by the 2070s (McCoy and Burn 2005). The impacts of recent climate change, expressed through increases in disturbance, not only are affecting the CATT region but also are becoming increasingly important issues across the boreal forest (Johnson et al. 2003). Climate can have significant effects on the growth and recruitment dynamics in the boreal forest (Barber et al. 2000, Johnstone et al. 2010). Disturbances also affect boreal ecosystems by shaping community structure and composition (Johnstone and Chapin 2006a), which in turn can influence the regeneration of boreal tree species as well as their abundance and distribution (Johnson et al. 2003). Postdisturbance recruitment plays an important role in shaping landscape patterns of boreal forest vegetation (Johnstone et al. 2004). For example, moisture availability is a key factor driving the successful establishment of white spruce on mineral substrates (Johnstone and Chapin 2006b) with reductions in soil moisture capable of preventing or delaying regeneration of white spruce, particularly after fire (Oswald and Brown 1990). Fire is considered to be a very important disturbance factor for white spruce regeneration, as the interaction between masting years and fire can result periodically in abundant regeneration (Peters et al. 2005). Fire also plays an important role by removing organic layers and causing the degradation of permafrost, which increases soil temperature (Yoshikawa et al. 2003). Intense and severe fire may also kill seeds and reduce the probability of germination due to loss of nutrients by vaporization and combustion of organic matter (Neary et al. 2005).

Climate change may have significant effects on the regeneration of white spruce, trembling aspen (*Populus tremuloides*), and balsam poplar (*Populus balsamifera*) (Oswald and Brown 1990, Perala 1990, Barber et al. 2000, Hogg and Wein 2005). Annual variation in precipitation is an important factor for the regeneration of both trembling aspen and balsam poplar as these species are sensitive to dry climatic conditions and moisture stress, which can limit their regeneration (Perala 1990, Hogg and Wein

2005). Aspen regeneration responds positively to increasing fire severity (Johnstone and Chapin 2006b) with postfire regeneration being prolific and rapid where moisture is not limiting (Johnstone et al. 2004). Where soil moisture, temperature, and substrate are unfavorable, regeneration by seed is sporadic or negligible and regeneration by resprouting can be scattered. Regeneration success thus requires disturbance followed by suitable climate conditions (Hogg et al. 2002, Hogg and Wein 2005).

In response to the recent spruce bark beetle outbreak in the CATT, salvage harvesting has been proposed to generate economic growth opportunities for local communities in the region. Forest reestablishment using natural regeneration is planned (Government of Yukon 2004). However, factors that have influenced past recruitment success of forests in the region have not been assessed. The main objective of this study is to assess the factors affecting the density and composition of natural regeneration in the southwest Yukon Territory (SWY). Specifically, the article deals with three major research questions: How do climate variability and environmental factors affect the density and distribution of regeneration in the SWY? What is the role of disturbance on regeneration of three species in the region? and What factors determine the regeneration potential of white spruce, trembling aspen, and balsam poplar in the SWY?

Methods

Study Area

This study was carried out in the CATT in the SWY of western Canada. The CATT

covers about 1.9 million ha and extends across four ecoregions of the SWY: the St. Elias Mountains, the Ruby Range, the Yukon Southern Lakes, and the Yukon Stikine Plateau, representing a landscape of great diversity and variability. The study area lies between 60.63 and 61.20°N and between -137.35 and -136.97°W (Figure 1). The elevation ranges from 651 to 1,158 m above mean sea level. The climate of the study area is characterized by cold winters and warm and dry summers with the mean annual temperature being -1.65° C and precipitation being 319.5 mm. The variability in mean annual temperature across the study area is 1.3° C. As the projected increase in temperature in the region will be from 2° C by 2040 to 7° C by 2100 (ACIA 2004), any variation in abundance and distribution of natural regeneration within 1.3° C would suggest that there may be significant impacts under predicted climate change. Soil texture varies from mixtures of sandy and silty fluvial deposits by rivers and lakes in lowland areas to mixtures of sandy and silty clays in the rest of the area. Permafrost is also common but discontinuous in the study area.

The study area is dominated by white spruce (86%), followed by trembling aspen (13%) and balsam poplar (<1%). The majority of the stands are between 80 and 120 years old, with about 20% of the stands being younger than 70 years old (Government of Yukon 2004). The average stand density is 813 stems/ha, with the highest and lowest densities in spruce bark beetle-affected and burned plots, respectively. Subalpine and alpine plant communities are abundant in the mountainous areas higher than 1,100 m.

Management and Policy Implications

Maximizing regeneration success plays an influential role in the selection of an appropriate silvicultural system to apply to a forest. Trees, like all plants, are most sensitive to environmental cues in the regeneration phase, making it the most critical stage for survival. Understanding the role of environmental variability on the regeneration dynamics of tree species is therefore critical for selecting the appropriate sites and silvicultural systems that can facilitate successful regeneration. This is of particular importance when natural regeneration is being relied on. Emulating natural disturbance patterns is one approach advocated in the selection of silvicultural systems, so an understanding of regeneration dynamics after perturbation can provide important insights into the selection of appropriate practices. We found that abundance of regeneration for all species exhibited a multivariate response to climate and site factors in interaction with disturbance. Local forest managers concerned about the future risks of climate change, wildfire, and bark beetle infestations could use this understanding to develop a mixture of spruce, broadleaved, and mixed spruce-broadleaved stands, on ecologically suitable sites, to increase landscape heterogeneity and maintain, restore, or enhance regeneration through the application of appropriate silvicultural practices that emulate natural disturbance patterns in the region.

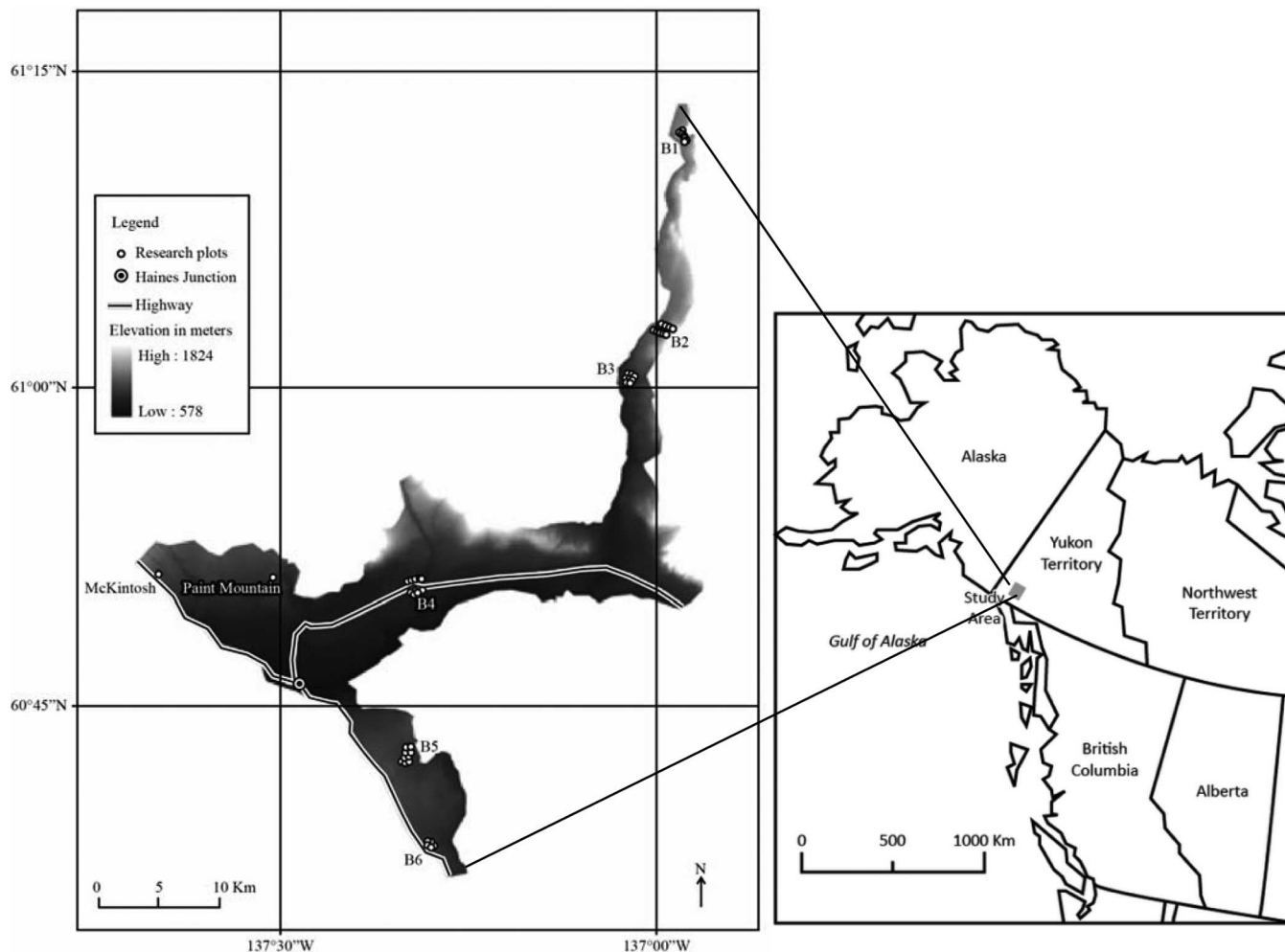


Figure 1. Map of the study area showing blocks and plots where the data were collected. B1 (number of plots = 13) is mostly undisturbed forest and predominantly consists of white spruce with small patches of aspen and willow; B2 (number of plots = 20) has traces of old fires in 50% of its plots and consists of white spruce dominance with scattered patches of willow bushes; B3 (number of plots = 10) has old burned logs in the most of the plots and consists of white spruce and aspen; B4 (number of plots = 25) has been affected by spruce bark beetle, has gone through recent fire, and has white spruce with scattered patches of willow; B5 (number of plots = 13) has beetle and harvesting and consists of mainly white spruce trees; B6 (number of plots = 9) is a harvesting plot and has mixed white spruce and aspen trees.

Data Collection

Data were collected using a stratified systematic sampling design (Kendt and Coe 2005). Stratified sampling has been suggested for landscape-level vegetation assessment when the vegetation has heterogeneous characteristics (Kendt and Coe 2005, Cooper et al. 2006, Rolecek et al. 2007). Stratified sampling techniques are able to capture the heterogeneity of the landscape in a representative way (Cooper et al. 2006). They capture the major sources of variability and generate data that are useful for gradient analysis (Kendt and Coe 2005).

Data were collected from 90 randomly sampled plots located in 6 research blocks within the forested landscape of the CATT (Figure 1) in the summer of 2008 by a team of researchers from the Faculty of Forestry,

University of British Columbia. The plots were classified into 5 strata based on disturbance type: (1) undisturbed forest (number of plots = 31); (2) an old fire forest (more than 50 years old and had no traces of beetle damage; number of plots = 14); (3) a recent fire forest (less than 15 years old and previously affected by beetle; number of plots = 11), (4) a beetle-affected forest (number of plots = 14); and (5) a salvage harvested area (previously affected by beetle; number of plots = 20). Based on the types and intensity of disturbances, the five types of disturbed plots could broadly be classified into three severity classes: (1) high severity: plots that were disturbed by a combination of either spruce bark beetle and fire (plots with recent fires) or spruce bark beetle and salvage harvested; (2) medium severity: plots disturbed

by more than 50% by spruce bark beetle infestation without fire and salvage harvested (bark beetle-affected plots); and (3) low severity: plots that had signs of old fires and were not affected by spruce bark beetle (old fire plots; 1948 constitutes the earliest available data for this region; hence, older fires are grouped here). The disturbed plots were identified and delineated using the local knowledge of the Yukon Government's Ministry of Energy, Mines and Resources and the Champagne and Aishihik First Nations government.

In each block, a point of commencement was chosen, which was generally a visible landmark located within the block. The first plot was selected 100 m from the point of commencement along a random bearing. The subsequent plots were systematically lo-

Table 1. Mean variations in soil moisture, organic depth, crown coverage, stand density, and shrub coverage by disturbance types.

Disturbance type	Soil moisture (%), <i>P</i> < 0.05	Crown coverage (%), <i>P</i> < 0.001	Stand density (tree/ha), <i>P</i> < 0.001	Organic depth (cm), <i>P</i> = 0.05	Shrub coverage, <i>P</i> < 0.001
Beetle-affected plots	26	63.9	1,400	11.3	40.7
Plots with recent fire	20	12	247	2.8	36.2
Harvested plots	18.6	29	591	5.2	40.1
Undisturbed	19.4	44.5	789	9	61.1
Old fire plots	25.1	48.2	1,039	8.2	55.6
Average of all plots	21.8	39.5	813.2	7.2	46.7

The variations were significant at *P* < 0.05. The table values indicate the disturbance severity for each type of disturbance. Fire and harvested plots have the thinnest organic depth, the lowest soil moisture, and lowest crown coverage indicating high-severity plots.

cated 100 m from the previous plot following the dominant topographic gradient. At each plot location, a 20 × 20 m (400-m²) plot was established to collect data on elevation, slope, aspect, latitude, longitude, tree density, and crown cover. Within each 400-m² plot, three 5 × 5 m nested subplots were randomly selected to collect shrub and sapling data. Regeneration density and shrub data were collected separately from three additional randomly selected 1 × 1 m microplots located within the 25-m² subplots. One soil pit was located in a randomly selected microplot for soil sampling and characterization.

Variables

The data were classified broadly into topographical, edaphic, disturbance, stand structure, and climatic variables.

Topographical Variables. Topographical variables represent macro-scale factors and consisted of latitude, longitude, elevation, slope, and aspect. Aspect was transformed into cosine of aspect ($\text{COS}\alpha = \text{northness}$) and sine of aspect ($\text{SIN}\alpha = \text{eastness}$). The northness value ranged from 1 to -1 (1 = northward, -1 = southward, and 0 = either eastward or westward). Similarly, a SIN value close to 1 represented east-facing slopes (1 = eastward, -1 = westward, and 0 = either northward or southward) (Robert 1986).

Stand Structure Variables. At each plot, tree density, dbh, crown cover, seedling density (trees < 1.3 m tall and < 7 cm diameter), and sapling density (trees > 1.3 m tall but < 7 cm dbh) represented meso-scale factors. Total and species-specific basal area (BA) per ha were calculated. Tree and regeneration (seedling/sapling) density were converted into a per ha basis to standardize the data from the plots and subplots.

Edaphic Variables. Soil depth, soil moisture, and soil texture were used as micro-scale variables. The Canadian soil classification system (Soil Classification Working

Group 1998) was applied to assess soil texture. A soil pit up to bedrock was dug in each plot, and soil moisture was collected from different layers of the soil using a Vernier soil moisture sensor (accuracy ± 4%), which measures the dielectric permittivity of soil to determine the volumetric water content. At least three soil moisture readings were taken from each mineral soil horizon in each soil pit. The values from each pit were then averaged for the statistical analysis. Soil texture was segregated into percentages of sand and clay based on the classification of each sampled soil layer using a standard soil texture diagram of the Canadian Soil Classification System.

Climatic Variables. Climatic variables were used to represent large-scale factors. The ClimateBC model was used (Wang et al. 2006) to project mean annual temperature, mean annual precipitation, mean annual maximum temperature, mean annual minimum temperature, number of frost-free days, and number of growing days above 5° C for each plot. Climate normals were based on the 1970–2000 time period. The ClimateBC model uses longitude, latitude, and elevation to project climate variables. The standard errors of predictions for British Columbia climate monthly temperatures and precipitation vary from 0.8 to 1.3° C for temperature and from 8 to 24 mm for precipitation (Wang et al. 2006).

Disturbance Variables. Disturbance was considered an explanatory variable and represented large-scale variation. Disturbance was included as a dummy variable in the form of presence and absence for the data analysis.

Data Analysis

Multivariate canonical correlation analysis (MCA) (McGarigal et al. 2000) was used to investigate the multivariate correlation among variables. Scatter plots with a

fitted regression line were plotted for quantitative independent variables, and the means of plots were drawn for independent categorized variables against seedling and sapling density of each tree species. The plots were tested for their significance at the 95% confidence level.

Mean soil moisture, crown cover, stand density, and organic soil depths were also calculated by disturbance types (Table 1) to explain the physical characteristics of each disturbance type. Similarly, analysis of variance (ANOVA) was used to calculate variation of mean regeneration by disturbance types. A negative binomial model (PROC Genmod), which uses the maximum likelihood parameter estimate method, was used to model the regeneration abundance of white spruce, trembling aspen, and balsam poplar (McCullagh and Nelder 1989, SAS Institute, Inc. 2008). Poisson and negative binomial probability distributions are generally used for count data modeling. A negative binomial distribution is generally preferred to Poisson when the variance is higher than the mean value; this was the case in this study, so the former was used. Negative binomial distributions have been used frequently for modeling forest regeneration (Venables and Ripley 2002, Fyllas et al. 2008). The overall model to estimate regeneration density is

$$R_D = f(\text{topographical variables} + \text{ecological variables} + \text{climatic variables} + \text{disturbance regime} + \text{residual error}) \quad (1)$$

$$R_D = \exp^{(b_0 + b_1 \cdot X_1 + b_2 \cdot X_2 + \dots + b_n \cdot X_n)} \quad (2)$$

where R_D is the regeneration count for each plot, b_0 is the intercept of the slope of the model, and X_1 to X_n are explanatory variables that represent topographical, environmental, and climatic variables as well as the

Table 2. Ratios of density of regeneration to density of their parent trees.

Disturbance type	White spruce			Trembling aspen			Balsam poplar		
	Regeneration density	Tree density	Tree/regeneration ratio	Regeneration density	Tree density	Tree/regeneration ratio	Regeneration density	Tree density	Tree/regeneration ratio
 (number/ha) (number/ha) (number/ha)		
Beetle plots	142,295	1,373	1:104	7,629	27	1:283	238	0	0:238
Fire plots	163,394	230	1:710	106,812	18	1:5,934	13,042	1	1:13,042
Harvested plots	66,337	511	1:130	43,600	75	1:581	7,253	5	1:1,451
Undisturbed	63,273	656	1:96	28,331	131	1:216	860	2	1:430
Old fire plots	61,743	861	1:72	41,924	177	1:237	0	2	0
Total	497,042	3,631	1:137	228,296	428	1:533	21,393	10	1:2,139

The mean variations of tree and seedling densities by disturbance type were significant at $P < 0.05$. Overall, trembling aspen (1:533) and balsam poplar (1:2,139) had much higher ratios than white spruce (1:137). The broadleaved species in particular had much higher ratios in disturbed plots.

Table 3. Correlation between sites and their associated factors.

Site 1	Site 2	Site 3	Site 4
Balsam poplar density (0.9156)	White spruce density (-0.4883)	Elevation (-0.4580)	Elevation (-0.3133)
Balsam poplar BA (0.9923)	Fire (0.4852)	Slope (-0.3031)	Slope (0.3895)
Latitude (-0.1514)	Average soil moisture (-0.4142)	TMXsm (0.4073)	DD5 (0.3213)
Salvage harvesting (0.231)	Total crown cover (-0.3114)	DD5 (0.4812)	TMXsm (0.2968)
% sand (0.134)	Organic depth (-0.3870)	Fire (0.5213)	Beetle (0.2810)

The table was generated by MCA. MCA has classified landscape into four sites based on disturbance, edaphic, and climatic factors. The coefficient values were significant at $P < 0.05$. BA, basal area; TMXsm, mean summer maximum temperature; DD5, number of days $>5^{\circ}\text{C}$.

disturbance regime. The models were run using a stepwise method that resulted in many variables that were not significant at $P > 0.05$ being dropped.

A goodness-of-fit test for the model was conducted by comparing the Akaike information criterion (AIC) values of full models to those of the final reduced model. The smaller the AIC value, the better the model was judged to be. Similarly, the model's significance was tested using a χ^2 test

$$F \text{ calculated} = 2 \cdot (\log \text{ likelihood of full model} - \log \text{ likelihood of reduced model})$$

If F calculated was larger than F critical at $\alpha = 0.05$, then the model was regarded as significant. SAS software was used to develop the models (SAS Institute, Inc. 2008).

Results

Physical Characteristics of Sites

Most of the beetle-affected forests that were not harvested or affected by fire had higher stand density (1,400 stems/ha) and average crown cover (64%) (Table 1). The bark beetle disturbance had little impact on soil and understory vegetation. The old fire plots that were burned during the 1950s mostly had mixed stands of white spruce and

trembling aspen, with an average of 48% crown cover and 8-cm soil organic depth (Table 1) and did not have any trace of spruce bark beetle. The most recent large fire occurred in 1998 in a portion of our research area (Figure 1), severely affecting both forest crown cover and soil humus layers. Some of these plots were affected by spruce bark beetle before the occurrence of fire. These recent fire plots had a low average crown cover (12%) and organic depth (3 cm), indicating higher fire severity (Table 1). In response to these disturbances, the salvage harvesting of beetle-affected stands commenced in 2006, targeting dead trees. This has had noticeable impacts on both soil and understory vegetation due to the operation of heavy equipment (mechanical impacts). The harvested plots had lower average organic depth (5 cm).

Regeneration in Response to Disturbance and Environmental Factors

The results suggest that increased disturbance severity promotes tree recruitment in our study area, as the regeneration of white spruce, trembling aspen, and balsam poplar varied significantly ($P < 0.05$) by disturbance type (Table 2). Seedling and sapling density of all three species was highest in the recent fire plots. Interestingly, the den-

sity of broadleaved species regenerating had a higher ratio of seedlings and saplings to trees in the recent fire plots than white spruce (Table 2). The fire plots were characterized by a thin organic humus layer (3 cm), the lowest crown cover (12%), the lowest soil moisture (20%), and the least shrub cover (36%) compared with those of other disturbance types (Table 1). Both undisturbed and old fire plots had the lowest seedling and sapling density of all the species. These plots were characterized by about 50% crown cover, more than 8 cm of organic humus, and higher shrub cover (more than 50%) (Table 1).

MCA showed that the seedling and sapling densities of the two broadleaved species were mainly affected by edaphic factors, whereas the regeneration of white spruce was affected by both edaphic and climatic factors. MCA classified the total landscape into four site types (Table 3), which included other variables besides disturbance types. Site type 1 was defined by the variables balsam poplar basal area and balsam poplar tree density and matched the occurrence of balsam poplar regeneration (Table 4). Site type 2 correlated positively with fire and negatively with total crown cover and soil moisture. This site type was characterized by trembling aspen regeneration. Site type 3 was characterized by sites at lower elevation (650–750 m) and of lower slope (less than 15%) with higher mean annual temperatures, higher growing degree-days, and the occurrence of fire, which favored white spruce regeneration. Site type 4 was influenced by lower elevation, slope, and summer maximum temperature and the occurrence of spruce bark beetle, which also favored the occurrence of white spruce regeneration.

The regression plots between regeneration (seedling and sapling) densities and en-

Table 4. Synthesis of canonical correlation analysis.

	Site 1	Site 2	Site 3	Site 4
White spruce seedling	0.0418	0.1954	0.3562	0.3734
Trembling aspen seedling	-0.0362	0.7464	0.1697	-0.0184
Balsam poplar seedling	0.8748	0.0504	0.2375	-0.1172
Trembling aspen sapling	-0.0291	0.2757	0.1991	-0.3689
White spruce sapling	-0.0208	-0.4111	0.3798	0.3600
Balsam poplar sapling	0.9975	-0.0001	-0.0124	-0.0008

The table shows the correlations between the tree regeneration and the habitat factors. It indicates that habitats 1 and 2 are related to balsam poplar and trembling aspen, respectively, and habitats 3 and 4 are related to white spruce regeneration.

environmental factors (Figures 2–4) are consistent with the MCA results. White spruce exhibited a positive relationship with well-drained sites that were recently subjected to disturbance and that occurred at lower elevations and on lower slope positions. These sites were characterized by having a higher number of growing degree-days, higher mean summer temperatures, and soils with soil moisture (Figure 2). Regeneration densities for trembling aspen and balsam poplar were found to be higher in sites affected by

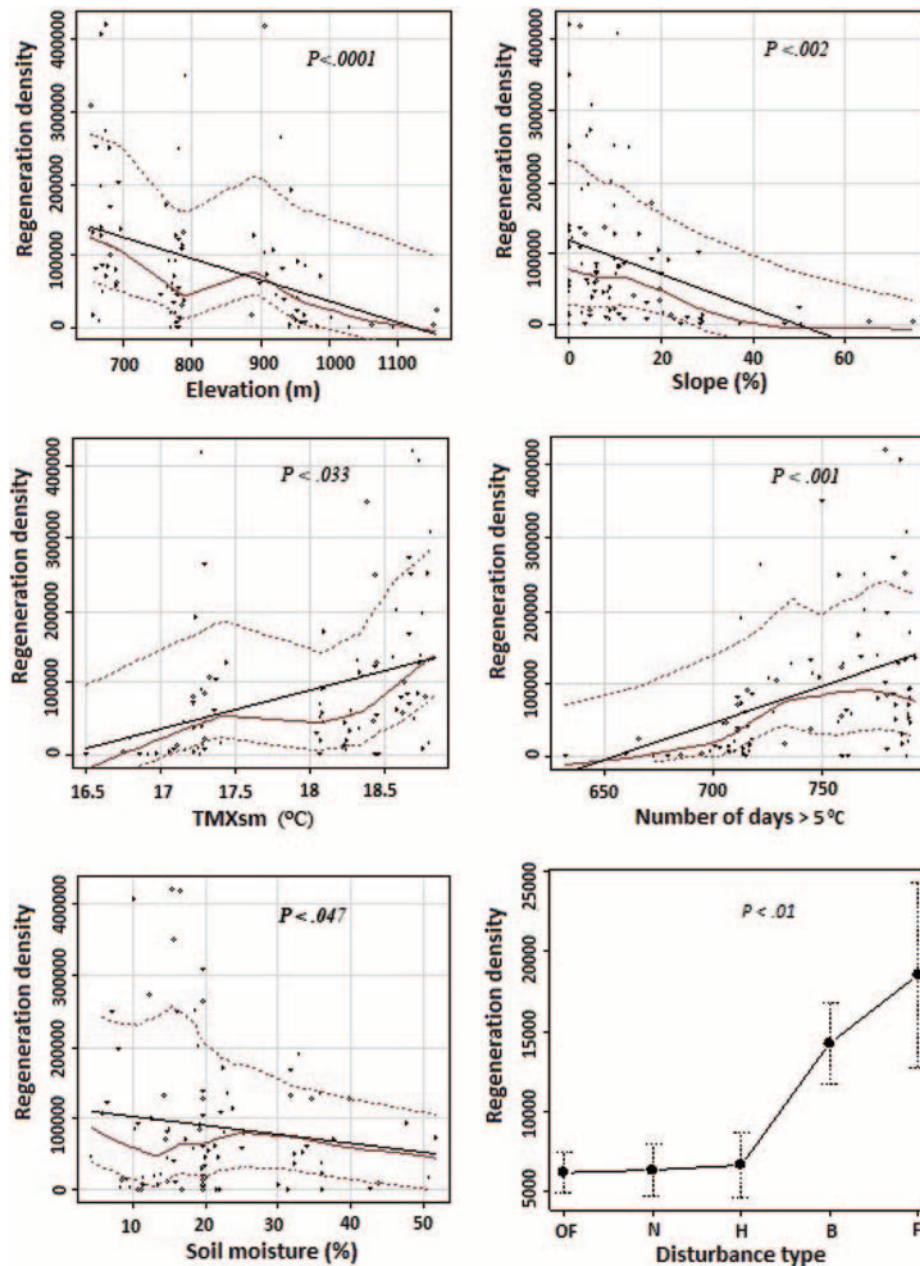


Figure 2. Responses of white spruce regeneration (number/ha) to environmental factors. Scattered plots indicated that white spruce responded negatively to increasing slopes, elevation, and soil moisture and positively to increasing summer temperature (TMXsm) and number of growing days at significance level $P < 0.05$. Means of plots (ANOVA; $P < 0.05$) indicated that it varies significantly by disturbance regime with higher abundance in fire and beetle plots. OF, old fire; N, undisturbed; H, salvage harvested; B, beetle-affected forests; F, plots with recent fire.

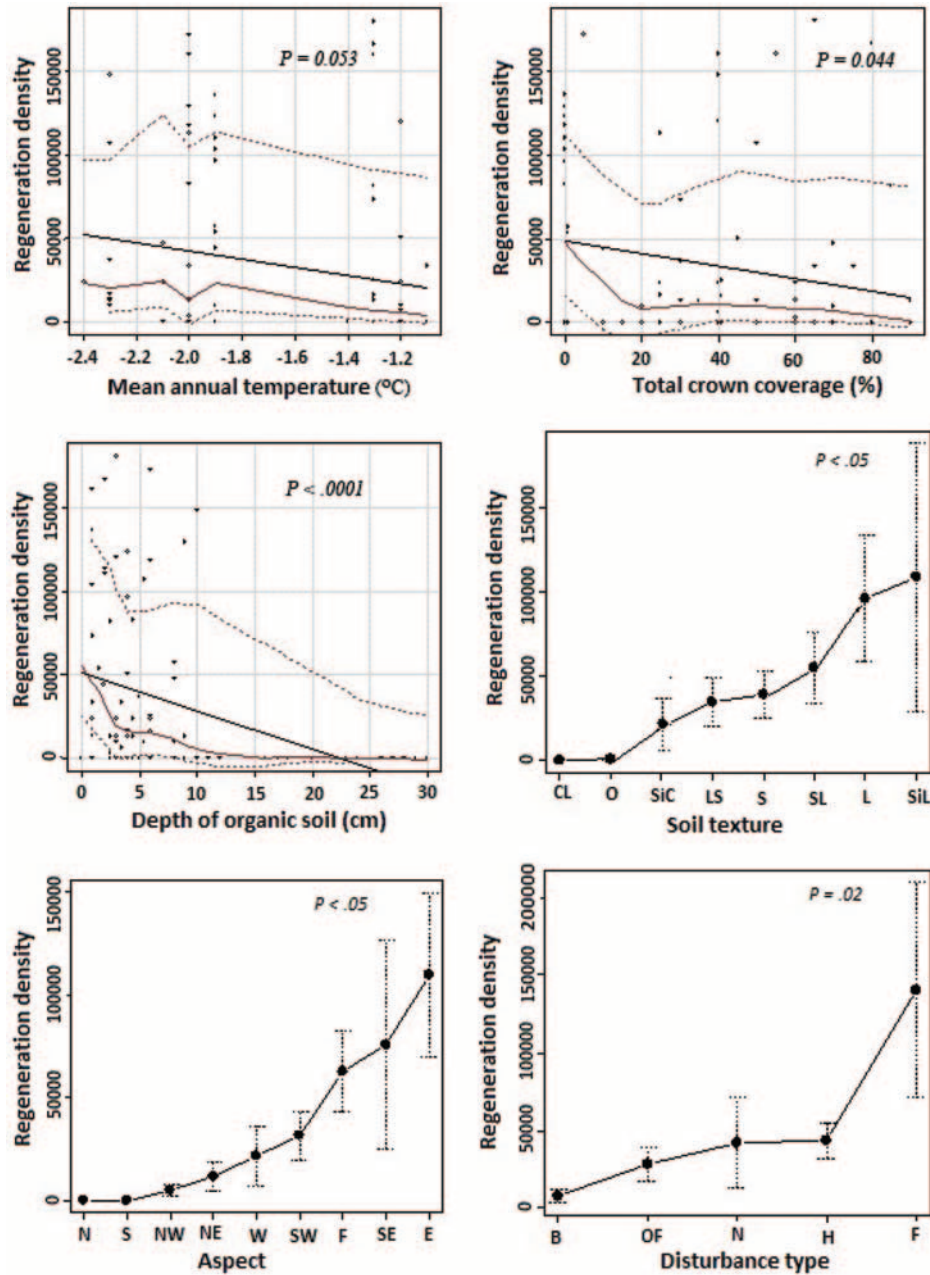


Figure 3. Responses of trembling aspen regeneration (number/ha) with environmental factors. Scattered plots indicated that trembling aspen responded negatively to increasing mean annual temperature, total crown coverage, and organic depth layer at significance level $P < 0.05$. Means of plots (ANOVA; $P < 0.05$) indicated its higher abundance in loamy to silty loam soil in eastern aspect and fire. Abbreviations: CL, clay; O, organic; SiC, silty clay; LS, loamy sand; S, sandy; SL, silty loam; L, loamy; SiL, silty loam (middle right); N, north; S, south. NW, northwest; NE, northeast; W, west; SW, southwest; F, flat; SE, southeast; E, east (bottom left); B, beetle-affected forests; OF, old fire; N, no disturbances; H, salvage harvested; F, recent fire (bottom right).

fire and harvesting, indicating their preference for stand-initiating disturbances. Their regeneration also responded positively to sites with exposed aspects (flat, east to south to west), indicating a preference for sites with higher solar radiation inputs for successful regeneration. Trembling aspen responded negatively to increasing mean annual temperature, crown cover, and organic depth but responded positively to sites with well-drained soils with loamy to silty loam

soil textures. Regeneration of balsam poplar was higher on sites with sandy or silty clay soils.

Negative Binomial Model

A total of 32 explanatory variables were used to predict the seedling and sapling abundance of white spruce, trembling aspen, and balsam poplar. Following a stepwise process, 8, 14, and 9 variables were retained for white spruce, trembling aspen,

and balsam poplar, respectively. The algorithms of all three models were combined, and the final results are provided for white spruce (Table 5), trembling aspen (Table 6), and balsam poplar (Table 7). The dispersion values were higher than zero in all the models, justifying the application of a negative binomial model. At least four climate variables were significant for all three species. The AIC values of the full models for white spruce, trembling aspen, and balsam poplar

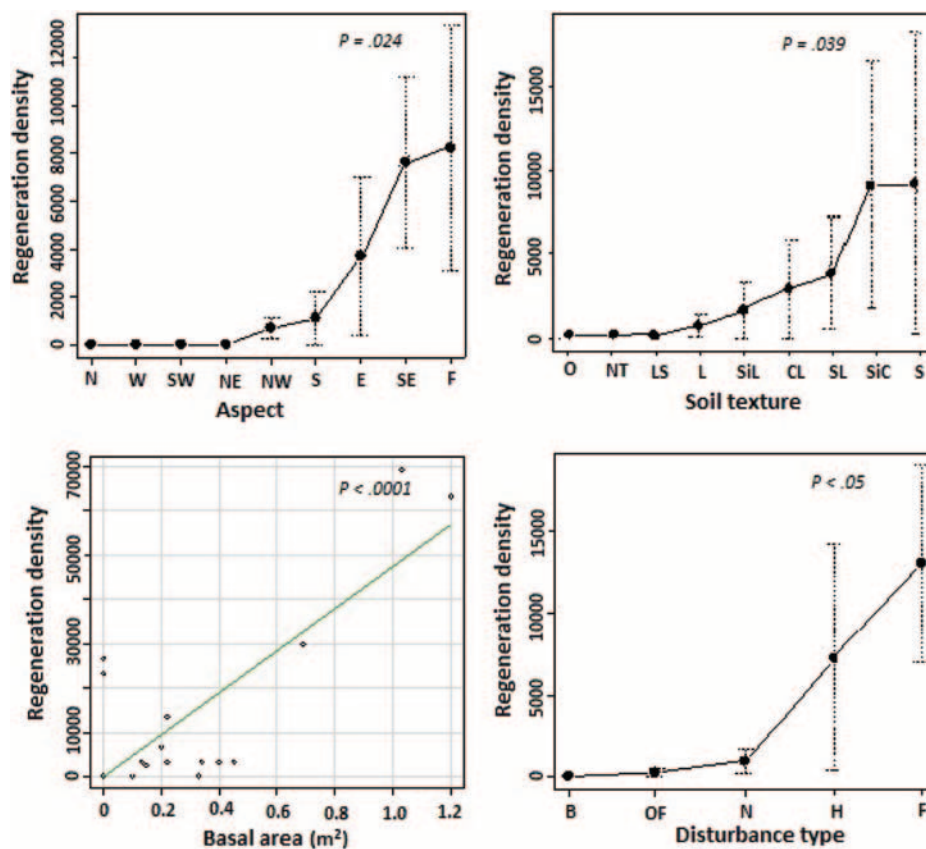


Figure 4. Response of balsam poplar regeneration (number/ha) to environmental factors. Scattered plots indicated that white spruce responded positively to increasing basal area at significance level $P < 0.05$. Means of plots (ANOVA; $P < 0.05$) indicated its higher abundance in level or southeastern facing sites, in sandy to silty clay soil, and in fire plots. Abbreviations: N, north; W, west; SW, southwest; NE, northeast; NW, northwest; S, south; E, east; SE, southeast; F, flat (top left); O, organic; NT, no texture; LS, loamy sand; SL, silty loam; L, loamy; SiL, silty loam; CL, clay; SiC, silty clay; S, sandy (top right); B, beetle-affected forests; OF, old fire; N, no disturbances; H, salvage harvested; F, recent fire (bottom right).

Table 5. Analysis of maximum likelihood parameter estimates of white spruce.

Parameter	df	Estimate	SE	Wald χ^2	Pr > χ^2
Intercept	1	-35.8779	21.5492	2.77	0.0959
Elevation	1	0.0168	0.0051	10.93	0.0009
Slope	1	-0.0705	0.0127	30.83	<0.0001
Mean annual temperature	1	9.5482	0.5310	14.23	0.0002
Mean annual precipitation	1	-0.0222	0.0100	4.96	0.0260
Mean summer maximum temperature	1	5.0724	1.0646	22.70	<0.0001
Mean summer minimum temperature	1	-6.8105	2.3985	8.06	0.0045
Average white spruce diameter	1	0.0629	0.0294	4.58	0.0323
Total basal area	1	-0.0421	0.0140	9.02	0.0027
Dispersion	1	1.4336	0.1907		

Algorithm converged. The stepwise modeling process retained only eight variables that were significant at $P < 0.05$.

were 2,207.3, 1,302.4, and 346.7, respectively, which were reduced to 2,165, 1,273.9, and 340.7, respectively (Table 8). The reduced AIC signifies the robustness of the models. The F -tests demonstrated that all three models were statistically significant (Table 9). The results indicate that the models are significant and robust for predicting regeneration potential for white spruce,

trembling aspen, and balsam poplar in the SWY.

Discussion

The results from the MCA, univariate plots, and negative binomial models indicated that the regeneration of white spruce, trembling aspen, and balsam poplar in the SWY is significantly related to a combina-

tion of disturbance, climatic, and edaphic factors. All three species showed positive responses to the occurrence of disturbance, open sites with higher solar radiation, mesic to hygric edaphic conditions, and warmer temperatures. The broadleaved species preferred sites with lower crown cover, particularly sites with sandy to loamy soils. Based on the results of the study, the regeneration niches of each species in the SWY are described below.

Disturbance versus Regeneration

Not surprisingly we found that disturbance is very important for the regeneration of all three species. There were two interesting findings worth discussing regarding the relationship between disturbance and regeneration in this study. First, after disturbance, higher seedling and sapling densities occur for the broadleaved species than for white spruce. Second, regeneration of all three species was significantly higher in recent fire plots than for other disturbance types. The recent fire plots had a thin organic matter

Table 6. Analysis of maximum likelihood parameter estimates of trembling aspen.

Parameter	df	Estimate	SE	Wald χ^2	Pr > χ^2
Intercept	1	1,615.747	350.2974	21.28	<0.0001
Mean annual precipitation	1	-7.2888	1.4988	23.65	<0.0001
Number of degree-days <0° C	1	-0.9802	0.2149	20.81	<0.0001
Number of growing days >5° C	1	-0.6309	0.1324	22.72	<0.0001
Mean maximum temperature in winter	1	-108.069	23.3856	21.36	<0.0001
Mean winter precipitation	1	15.5011	3.1567	24.11	<0.0001
Mean summer precipitation	1	9.7162	2.0579	22.29	<0.0001
Beetle	1	4.1393	2.0639	4.02	0.0449
Fire	1	5.8653	2.4133	5.91	0.0151
Total soil depth	1	0.1200	0.0306	15.38	<0.0001
Soil organic layer depth	1	-0.5828	0.1518	14.75	0.0001
% clay	1	-0.1613	0.0587	7.55	0.0060
% sand	1	-0.0572	0.0275	4.33	0.0375
Trembling aspen density/ha	1	0.0056	0.0018	09.43	0.0021
Total basal area/ha	1	-0.1451	0.0478	9.21	0.0024
Dispersion	1	6.5292	1.0832		

Algorithm converged. The stepwise modeling process retained only 14 variables that were significant at $P < 0.05$.

Table 7. Analysis of maximum likelihood parameter estimates of balsam poplar.

Parameter	df	Estimate	SE	Wald χ^2	Pr > χ^2
Intercept	1	2,320.864	634.8263	13.37	0.0003
Mean annual temperature	1	-104.543	23.3149	20.11	<0.0001
Mean summer maximum temperature	1	-182.000	42.4992	18.34	<0.0001
Number of growing days >5° C	1	2.1080	0.5003	17.75	<0.0001
Number of frost-free days	1	-6.8581	2.5049	7.50	0.0062
Spruce bark beetle	1	17.1877	4.6270	13.80	0.0002
Fire	1	22.0183	4.8637	20.49	<0.0001
Average soil moisture	1	0.5281	0.1254	17.74	<0.0001
Balsam poplar basal area	1	5.4432	1.9198	8.04	0.0046
Total basal area	1	-0.4374	0.1172	13.92	0.0002
Dispersion	1	11.0603	2.8743		

Algorithm converged. The stepwise modeling process retained only nine variables that were significant at $P < 0.05$.

Table 8. Criteria for assessing goodness of fit.

Criterion	Balsam poplar		Trembling aspen		White spruce	
	df	Value	df	Value	df	Value
Deviance	80	30.07	75	75.48	81	109.64
Pearson χ^2	80	27.43	75	27.02	81	43.12
Log likelihood (full model)		-159.3446		-620.97		-1,072.49
Log likelihood (null model)		-185.0490		-656.6811		-1,095.7875
AIC full model		346.74		1,302.41		2,207.32
AIC reduced model		340.69		1,273.94		2,164.98

Log likelihood and AIC values are higher in full models than reduced models, which indicates the goodness of fit of the models.

Table 9. χ^2 tests of the models.

Species	Log likelihood of final model (l)	Log likelihood of null model (l_0)	χ^2 value $2 \cdot (l - l_0)$	F table value, $P < 0.05$
White spruce	-1,072.4911	-1,095.7875	46.59	15.51 ($df = 8$)
Trembling aspen	-620.9703	-656.3446	71.74	23.69 ($df = 14$)
Balsam poplar	-159.3446	-185.0490	51.04	16.92 ($df = 9$)

Tests showed that calculated F values are higher than tabulated values for all the species, indicating that models are statistically significant at $P < 0.05$.

layer and lower moisture contents. Fire generally facilitates regeneration by removing cold wet organic soils and degrading perma-

frost, thereby creating an excellent seedbed through the exposure of mineral soil (Purdy et al. 2002, Yoshikawa et al. 2003, Peters et

al. 2005). Time since the last fire was also an important factor for white spruce regeneration in our study as lower seedling and sapling densities were found in plots that had not been subjected to wildfire in the last 50 years. In other studies, white spruce regeneration was found to be highest in the 7 years after a fire, before declining, with the decline becoming significant after 10–14 years (Macdonald et al. 2001, Purdy et al. 2002, Johnstone et al. 2004). The changes in micro-habitat conditions in the old fire plots are probably the main reason for lower seedling and sapling densities as these plots were characterized by soils with thick organic horizons, higher crown cover, and the presence of a dense cover of shrubs. Recruitment success after fire in white spruce can also depend on the co-occurrence of masting events (every 4–7 years) with fire events (Peters et al. 2005). We were unable to test for the occurrence of masting years in interaction with fire in this study. We did find a high abundance of white spruce regeneration in beetle-affected plots, although the micro-sites of these plots were quite different from recent fire plots, with thicker organic matter layers (11.3 cm), higher crown cover (64%), higher average moisture (26%), lower shrub coverage (40%), and the presence of abundant decayed logs, which indicated that the recent spruce bark beetle disturbance had had little effect on the understory vegetation and forest soils. The presence of abundant decayed logs may be the reason for the higher regeneration in these plots as they provide favorable seedbeds for white spruce regeneration (Purdy et al. 2002, Peters et al. 2006). The lower recruitment of white spruce in “undisturbed” forest or old fire forests was generally lower, probably due to the deterioration of the mineral seedbed with time since disturbance (Nienstadt and Zasada 1990, Simard et al. 1998). Because the majority of the study area is composed of stands of white spruce between 80 and 120 years old (Government of Yukon 2004), this pattern of regeneration is probably very typical. Regeneration in these stands is or may become progressively restricted to decayed logs where sufficient moisture availability occurs (Coates et al. 1994).

Open canopy conditions created by disturbances had a positive impact on trembling aspen and balsam poplar regeneration. Both species are shade intolerant and are unable to regenerate in the understory of mature stands (Landhäusser and Lieffers 2001). In the SWY, Johnstone et al. (2004) also

found that seedling establishment of trembling aspen was highest after fire. Because of its ability to sucker, trembling aspen has a high tolerance to fire, making it better at recolonizing fire-disturbed areas than white spruce (Purdon et al. 2002). Similarly, fire can benefit regeneration of balsam poplar by promoting vegetative reproduction (Rood et al. 2007). The higher ratios of seedlings and saplings to mature trees for these species than for white spruce highlight the preference of stands recently disturbed by wildfire for the regeneration of these broadleaved species. Regeneration of both broadleaved species was also higher in salvage-harvested plots. Harvested plots had micro-site conditions similar to those of recent fire sites, with thinner organic matter layers, lower moisture contents, and lower crown and shrub cover. Similar results were found by Kurulok and Macdonald (2007), although they concluded that salvage logging may negatively affect aspen regeneration because the salvaged stands tended to have higher abundance of shrubs and grasses.

Climate versus Regeneration

Although the variations in mean temperature and precipitation in the study area are only 1.3° C and 80 mm, respectively (Paudel 2014), the density and distribution of seedlings and saplings of white spruce and trembling aspen varied significantly within this low climatic variability, indicating a high sensitivity to climate, in particular, temperature. White spruce regeneration was more abundant on sites with higher summer temperatures and a higher number of growing degree-days. This finding is supported by Andalo et al. (2005), who reported that temperature was the key factor for the germination of white spruce. According to Archibald et al. (2000), the base germination temperature of white spruce correlated well with average June precipitation. The optimal temperature for germination of white spruce is 20° C, which can occur in June. Drought and moisture limitations can be induced, however, by higher temperatures and evapotranspiration, which can significantly affect white spruce regeneration and growth (Barber et al. 2000, Hogg and Wein 2005).

In our analysis, both the regeneration model and the MCA indicated that temperature was negatively and precipitation positively correlated with aspen regeneration, suggesting that moisture is an important factor for regeneration and that the species is sensitive to the drought stress caused by

higher temperatures (Frey et al. 2003). These findings are consistent with those of Hogg et al. (2005), who found that aspen is sensitive to drought conditions mediated by increasing atmospheric vapor pressure deficits. The model coefficients also suggested that balsam poplar is sensitive to high temperatures and soil moisture. The species was found to be significantly affected by changes in soil moisture. According to Tyree et al. (1994), this species is very sensitive to drought, which can be induced by high temperatures and low soil moisture regimes. We found that the number of growing degree-days above 5° C had a positive influence in the model, indicating that the species prefers a warm growing season with sufficient soil moisture for regeneration, which is supported by Kalischuk et al. (2001), who found that seedling growth was positively correlated with the accumulation of growing degree-days.

Edaphic Factors versus Regeneration

Our study showed that each species responded uniquely to different edaphic variables. Trembling aspen regeneration was higher on loamy to silty loam soils, which is supported by Perala (1990) and Hogg et al. (2008), who state that aspen prefers well-drained loamy soils. Balsam poplar regeneration was greater on sandy or silty clay soils, the major soil types found on alluvial and flooded sites where this species is commonly observed (Viereck et al. 1993). White spruce regeneration was not significantly influenced by soil texture, although it has been reported to grow well on loamy to clay loam soils (Kabzems 1971). Regeneration abundance of white spruce decreased with increasing moisture content, with higher abundances found on sites with soil moisture contents between 10 and 20%. Excessive soil moisture can limit white spruce regeneration (Purdy et al. 2002). Similarly, trembling aspen regeneration decreased with increasing depth of the organic matter layer. These findings are consistent with their higher abundance in fire plots that had thinner organic layer depths, resulting in the lower soil moisture contents and exposed mineral soil (Purdy et al. 2002, Johnstone and Chapin 2006b).

White spruce regeneration was found to be poorer on north-facing slopes. Supportive findings were reported by Danby and Hik (2007), who found that growth of seedlings on north-facing slopes was limited by low soil temperature and the presence of

permafrost. Similarly, both broadleaved species and white spruce occupied sites at medium to lower elevations with gentle slopes and east to southeast aspects or level ground in our study area, confirming that they are light- and temperature-demanding species that grow best in open spaces (Frey et al. 2003). Balsam poplar is typically found in riparian areas and thus prefers moist sites close to permanent water sources and floodplain areas (Viereck et al. 1993, Bockheim et al. 2003). Floods can promote balsam poplar regeneration by scarifying shallow roots, thereby promoting suckering (Rood et al. 2007). In this study, the presence of mature trees in disturbed plots was an important factor for balsam poplar regeneration, suggesting that dispersal may be limited and/or vegetative reproduction may be the dominant mechanism for regeneration within the study region.

Conclusion

The southwestern part of the Yukon Territory of Canada has experienced an unprecedented spruce bark beetle outbreak, and the frequency of forest fires is increasing beyond historical trends. These disturbances have affected the forest structure and composition and raised significant concerns for local forest managers and policymakers. Our results shed some light on the responses of natural regeneration of the three main tree species to disturbances and environmental factors that may have important implications for forest management and policy in the southwest Yukon. Because regeneration of broadleaved trees was proportionately higher in disturbed sites, broadleaved species may increase in abundance on the landscape if the frequency of disturbances continues to increase. This is particularly important if the region's summers become drier, as predicted by the Intergovernmental Panel on Climate Change (IPCC) (Christensen et al. 2007), which might lead to an increase in fire frequency (Johnstone et al. 2010). Regeneration of both white spruce and trembling aspen also varied significantly with mean annual temperature, indicating a high sensitivity of these species to temperature, which may have important implications if the mean temperature in the region rises as predicted under climate change. Model projections from the IPCC suggested that temperature in the region may increase by more than 2° C by the 2040s and 7° C by the 2080s (ACIA 2004). These findings suggest that if fires increase in the region along with

predicted changes in temperature and precipitation than the stand-level regeneration dynamics will probably be altered, which could lead to changes in species abundance and composition at the landscape scale. The landscape is currently dominated by white spruce (>80% of stands). A likely scenario of the warmer, wetter future predicted for the region is a decrease in conifer-dominated stands and an increase in mixed wood stands; however, this may benefit future fire risk (see Bergeron et al. 2004, Johnstone et al. 2010) and reduce the risk of another unprecedented spruce bark beetle outbreak.

Applying forest management practices under the uncertainty of future climate and disturbance events is a challenging task for boreal mixed wood forests, which are characterized by a remarkable diversity of stand composition and structure (MacDonald 1995). However, the information and knowledge generated by this study should help forest managers and policymakers understand the recruitment dynamics in the region and select appropriate management activities. The following three management practices are recommended to enhance natural regeneration in the study region: apply a variable retention strategy in areas affected by spruce bark beetle to provide sheltered conditions that will promote white spruce regeneration (Goodman and Hungate 2006) and also increase the number of mature trees to increase seedling densities; apply prescribed burning after harvesting to promote natural regeneration of both white spruce and broadleaved species through the reduction of shrub cover and exposure of mineral substrates; and apply seed tree systems along with prescribed burning to promote recruitment of balsam poplar and trembling aspen. The recommended set of forest management practices should enhance natural regeneration in stands selected for forest harvesting if they fall within the regeneration niche of the targeted species; however, additional silvicultural practices may be required to shape the inherent stand dynamics that will occur as species regenerate and grow after perturbation.

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