UNIVERSITY OF CALGARY

Understory Vascular Plant Species Diversity in the Mixedwood Boreal Forest of
Western Canada

by

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ABSTRACT

This study examines the implications that arise from the idea of emulating the 'natural' (pre-European) fire regime to maintain plant diversity patterns. In the mixedwood boreal forest, understory species richness, diversity and evenness were sampled in thirty 25 X 25 cm quadrats per stand in 121 upland stands initiated by wildfire and, for comparison, in 22 upland harvested stands. The patterns of species richness, diversity and evenness were primarily controlled by moisture and nutrient gradients and secondarily by a combination of light availability and time-since-fire. Hillslopes and surficial geology, because they control moisture and nutrient gradients, appear to be the fundamental units of species diversity. Compared with stands burned by wildfire, harvested stands have higher species diversity and differ in species composition. These differences appear to be related to forest floor disturbance. This study shows that there is still much to learn before fire can be emulated in forestry management.

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THESIS INTRODUCTION

The boreal forest is often seen as a fire dominated ecosystem since fire is the primary large scale disturbance. As such, one goal of ecosystem based forest management is the preservation of biodiversity (i.e. natural variation found at all levels from molecular to landscapes (Huston 1994)) patterns by emulating the 'natural' (pre-European) fire regime (Weetman 1994). This implies that fire plays the principle role in determining biodiversity. This goal also implies that there is a preferred 'natural' fire frequency and that disturbances by current and past forestry practices exist outside of this natural disturbance variation such that diversity has changed as a consequence. In two self-contained chapters, this study addresses these implications as they apply to understory vascular plant species diversity.

The first chapter addresses the implication that fire is the principle determinant of species diversity. Resource gradients other than fire, primarily moisture and nutrient gradients (e.g. Day Jr. and Monk 1974, Whittaker and Niering 1975, Marks and Harcombe 1981, Roberts and Christensen 1988, Host and Pregitzer 1992) and light availability (Kull and Zobel 1991, Uemura 1994), have been shown to affect vegetation patterns. Therefore, the relative importance of moisture and nutrients, light availability (canopy coverage) and time-since-fire, in controlling understory plant species diversity in the mixedwood boreal forest is determined. Using the relative importances, both local and landscape patterns of diversity are explained, since patterns of species diversity are dictated by species distribution and abundance which are, in turn, determined by the combination of tolerance curves for each species in the community and their overlap along the resource gradients.

The second chapter addresses the implication that diversity has changed as a result of harvesting. Most previous studies have compared diversity in older stands with diversity in recently harvested stands (e.g. Dyrness 1973, Halpern and Spies 1995, Meier et al. 1995, Bråkenhielm and Liu 1998), which requires questionable assumptions about how stands will develop. Here, stands recently burned by wildfire are compared to

recently harvested stands of similar pre-disturbance canopy composition for plant species diversity and composition. The differences in species diversity and composition are then related to differences in the type of forest floor disturbance.

CHAPTER ONE

Hillslopes, light availability and disturbance as determinants of understory vascular plant species diversity in the mixedwood boreal forest

INTRODUCTION

Plant species diversity is influenced by species distribution and abundance. A number of factors have been shown to affect plant species distribution and abundance. These include site conditions (i.e. moisture and nutrient gradients (Day Jr. and Monk 1974, Whittaker and Niering 1975, Marks and Harcombe 1981, Roberts and Christensen 1988, Host and Pregitzer 1992)), canopy coverage (i.e. light availability (Kull and Zobel 1991, Uemura 1994)) and time since the last disturbance (Specht et al. 1958, McConnell and Smith 1970, Auclair and Goff 1971, Dix and Swan 1971, Holland 1971, Shafi and Yarranton 1973, Nicholson and Monk 1974, Mellinger and McNaughton 1975, Roberts and Christensen 1988, Schoonmaker and McKee 1988, De Grandpré et al. 1993, Halpern and Spies 1995).

The boreal forest is considered a fire dominated ecosystem since fire is the primary large scale disturbance. As such, fire is thought to play the principle role in determining plant diversity. Thus, one goal of ecosystem based forest management in the boreal forest is to preserve biodiversity patterns by emulating the 'natural' (pre-European) fire regime (Hunter 1993, Attiwill 1994, Bender 1994, Weetman 1994). While there is no doubt that disturbance influences diversity, it is unknown how important disturbance is *relative* to site conditions (moisture and nutrient gradients) and canopy coverage (light availability).

Plant species diversity, influenced by species distribution and abundance, is a reflection of community organization. The abundance and distribution of a species can be described by its tolerance curve. A tolerance curve reflects the ability of a species to

survive and reproduce along one or more resource gradients (McNaughton and Wolf 1973). Each resource gradient explains a different amount of the variation in a species' distribution and abundance. Diversity patterns are determined by the combination of tolerance curves for each species in the community and the overlap of those tolerances along the resource gradients. Thus, the objectives of this study were to 1) determine the relative importance of moisture and nutrients, canopy coverage (light availability) and time (since fire) in controlling understory vascular plant species diversity in the mixedwood boreal forest, 2) explain the local diversity patterns by determining how species' tolerances and the overlap of species are organized along the most important gradient and 3) predict the landscape diversity patterns.

METHODS

Study Area

The study area is located in central Saskatchewan (Figure 1.1) and covers approximately 8000 km² (53°34' N to 54°24' N and from 105°25' W to 107°52' W). It is characterized by long, cold winters and short, cool summers. The frost free period is generally less than 80 days and freezing can occur in any month. July and August are the warmest months with the average maximum temperature exceeding 20°C three days out of four. The average annual precipitation ranges from 400 to 500 mm, 70% of which occurs as rain.

The primary large scale disturbance is lightning-caused crown fires. These crown fires produce even-aged stands with all tree species (except *Abies balsamea*) recruiting primarily within the first five years following fire (Gutsell, pers. comm.). The fire cycle has changed twice in the last 200 years, and has varied from 15-75 years (Weir et al. 2000). Only 5% of the area is older than 200 years (Johnson et al. 1995). Therefore, most trees are killed before replacement by understory trees of a different species can occur (Dix and Swan 1971, Bridge and Johnson 2000). Insect outbreaks do not seem to

Figure 1.1 **Location of the study area: Prince Albert National Park and Weyerhaeuser's Forest Management License Agreement. The light grey area represents the extent of the boreal forest in Canada and the hatched area is the southern mixedwood boreal forest.**

have been a major source of large scale disturbance in the last hundred years.

The area has a gentle relief with elevation ranging from 450 m to 900 m a.s.l.. The surficial geology is undifferentiated glacial till, glaciofluvial and glaciolacustrine surfaces with only a small proportion of the study area covered by glaciolacustrine substrates. Surficial geology determines the shape of the hillslope (Hack and Goodlet 1960, Bull 1975, Bridge and Johnson 2000) and thus the rates of change of moisture and nutrients down the hillslope (O'Loughlin 1981, Wood et al. 1988, Bridge and Johnson 2000). This is due to the consistent way in which the geomorphic processes of erosion and resistance form hillslopes (Hack and Goodlet 1960, Bull 1975). Glaciofluvial substrates consist of small, clay-like particles sorted by rapidly moving glacial meltwater while glacial till substrates consist of an undifferentiated mixture of stones, gravel, sand, silt and clay. Therefore, glacial till slopes are steeper for any given distance from the ridgeline than glaciofluvial slopes (Bridge and Johnson 2000). Consequently, hillslope shape can be quantitatively described by allometric equations (Bridge and Johnson 2000).

Moisture and nutrient gradients are prevalent across the landscape due to the repeatability of hillslopes (Bridge and Johnson 2000). As soil water diverges on top slopes and converges on toe slopes (Anderson and Burt 1977, Harr 1977, Sinai et al. 1981, O'Loughlin 1981, 1986, Wood et al. 1988), it carries with it nutrients that are leached from top slopes to accumulate in toe slopes (Trudgill 1988, Litaor 1992, Tsuboyama et al. 1994). Therefore, top slopes of similar surficial material are generally dry and nutrient poor while toe slopes are wet and nutrient rich (Malo et al. 1974, Harr 1977, Anderson and Burt 1977, Johnson 1981, O'Loughlin 1981, Sinai et al. 1981, Ciha 1994, Bridge and Johnson 2000). Therefore, moisture and nutrients can be quantitatively linked to the allometric equations and qualitatively linked to position on the hillslope where top slopes have lower moisture and nutrient status and toe slopes are characterized by higher moisture and nutrients (Bridge and Johnson 2000). However, the magnitudes of moisture and nutrients depend on surficial geology where glaciofluvial top slopes have intermediate moisture status and low nutrients while downslope stands are characterized by high moisture and nutrients. On glacial till, moisture is low and nutrients are

intermediate on top slopes while further downslope moisture is intermediate and nutrients are high (Bridge and Johnson 2000).

The study area is part of the southern mixedwood boreal forest (Rowe 1972). It is characterized by white spruce (*Picea glauca* (Moench) Voss.), black spruce (*Picea mariana* (Mill) B.S.P.), jack pine (*Pinus banksiana* Lamb.), balsam fir (*Abies balsamea* (L.) Mill.), tamarack (*Larix laricina* (Du Roi) K. Koch), trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.) and white birch (*Betula papyrifera* Marsh.). Bridge and Johnson (2000) used slope position and surficial geology to depict the general landscape patterns of upland vegetation composition. On glaciofluvial hillslopes, jack pine are found in higher abundance near top slopes while black spruce are found in higher abundance further downslope. On glacial till hillslopes, trembling aspen are found in higher abundance near top slopes while mixedwood stands are found further downslope. The mixedwood stands are comprised of trembling aspen, white spruce and balsam fir.

Sampling Regime

One hundred and twenty-one upland stands were sampled for understory vascular plant species diversity. One hundred and one of these stands were from Bridge and Johnson (2000) and ranged in age from 5 to 234 years old. However, only 3 of their stands were younger than 30 years. Thus, the other 20 stands were younger than 15 years since the last fire. Each stand was greater than 4 hectares in size, had vegetation rooted in the mineral soil with no evidence of standing water in the top 30 cm of the mineral soil, was visually homogeneous with respect to stand age, structure and species composition, and had no evidence of significant anthropogenic disturbance. In each stand, presence or absence of vascular understory species was recorded in each of thirty 25 cm x 25 cm quadrats. The frequency of a species (f_i) was calculated as the number of quadrats that contained species i divided by the number of quadrats sampled (i.e. 30). Therefore, the relative frequency of species i (x_i) is simply the frequency of species i (f_i) divided by the sum of the frequencies of each species in the stand multiplied by 100. Note that tree and

shrub species were only included in the understory plants if they were <1 m in height.

In this study, the moisture and nutrient gradient was measured using slope position and surficial geology based on a previous study by Bridge and Johnson (2000). Together, slope position and surficial geology determine moisture and nutrient gradients. There are 4 slope position/surficial geology categories: glaciofluvial top slope and toe slope and glacial till top slope and toe slope. Slope position was determined by measuring the distance from the ridgeline using the image analysis software PCITM version 5.2, a Digital Elevation Model (DEM) and an algorithm developed by Warren (1999) that located the closest ridge based on a path of water flow calculated from local aspect. Distance from the ridgeline was related to the general change in dominant canopy species down the hillslope which is based on the relationship between stand positions on the abstract moisture and nutrient gradients (Bridge and Johnson 2000). Moisture and nutrients increase with distance from the ridgeline but the magnitudes of those increases and thus, the changes in the dominant canopy species, also depend on surficial geology (Bridge and Johnson 2000). Therefore, in general, stands within 600 m of the ridgeline on glaciofluvial substrates are characterized by high abundances of jack pine while further downslope, black spruce are found in higher abundance (Bridge and Johnson 2000). On glacial till substrates, trembling aspen are generally found in higher abundance within 500 m of the ridgeline while mixedwood stands are found further downslope (Bridge and Johnson 2000). Surficial geology was determined using a combination of land form, soil texture and colour, presence of stones and a surficial geology map. Therefore, stands within 600 m of the ridgeline on glaciofluvial substrate were considered glaciofluvial top slope while stands further downslope were glaciofluvial toe slopes. Stands within 500 m of the ridgeline on glacial till material were considered glacial till top slopes and stands further downslope were called glacial till toe slopes.

Light availability was measured as canopy basal area. It would have been preferable to measure light availability directly; however, this was unrealistic due to the number of stands. On clear days, because of the rapid change in solar angle in the morning and late afternoon, sampling would have been restricted to 3 hours in the middle

of the day. Also, the large contribution of direct sunlight due to sunflecks meant that the data would have had to have been temporally or spatially averaged. Light readings on overcast days would not have been more reliable due to the rapid change in cloud density. Therefore, although not ideal, canopy basal area was used as a surrogate measure of light availability, with light availability decreasing as canopy basal area increases (Cutini et al. 1998). Canopy basal area (m^2/ha) was calculated by multiplying diameter at base height (dbh) with canopy stem density. Canopy stem density was sampled using the point centred quarter method at 15 points per stand (Cottam and Curtis 1956).

Disturbance was measured as time since the last fire and was determined from a map created for a fire frequency study in Prince Albert National Park (Weir et al. 2000). Other aspects of fire including fire line intensity, duff (F and H organic layers) consumption by smoldering combustion, burn shape and size and the spatial distribution of unburned patches within it (Johnson et al. 1992) are difficult, if not impossible to measure if they are not measured during or soon after fire.

Analysis

Understory vascular plant species diversity (H) was partitioned into species richness (S) and evenness (E) by $H = \ln(S) + \ln(E)$ (Buzas and Hayek 1996). Species richness was defined as the number of species summed over all 30 quadrats in each stand. Evenness was estimated as $\exp(H)/S$ and diversity was defined as

$$H = - \sum_i^S (x_i \cdot \ln x_i) \quad (1.1)$$

where x_i is relative frequency of species i (Shannon 1948).

Standard partial regression coefficients from a standard least squares multiple regression were used to determine the relative importance of stand characteristics (slope position/surficial geology, canopy basal area and time-since-fire) on species richness, diversity and evenness (Snedecor and Cochran 1971, Zar 1984). Standard partial

regression coefficients estimate the fraction of the variance in the dependent variable (i.e. species richness, diversity or evenness) attributable to its linear regression on the stand characteristic, corrected for scale. Scale correction is achieved by estimating the change in the dependent variable as a fraction of the standard deviation in the dependent variable produced by one standard deviation change in the stand characteristic (Snedecor and Cochran 1971).

The patterns of species richness, diversity and evenness at the hillslope scale were determined using the Tukey-Kramer Honestly Significant Difference (HSD) test ($p < 0.05$) by making multiple comparisons of mean species richness, diversity or evenness between all slope positions regardless of surficial geology.

Species tolerance along slope positions, overlap of species relative frequencies in adjacent slope positions, percent similarity of species relative frequencies in adjacent slope positions and the percent of rare species per slope position were used to determine how species richness was related to community organization. To calculate both tolerance and overlap, slope position was given a numeric value by dividing the slope into distances from the ridgeline. This was done using the image analysis software PCITM version 5.2, a Digital Elevation Model (DEM) and an algorithm developed by Warren (1999) that located the closest ridge based on a path of water flow calculated from local aspect. Intervals were divided based on two criteria: 1) that there be more than one stand in an interval and 2) that intervals be continuous and equal along the gradient. The glacial till hillslope is longer than the glaciofluvial slope (Bridge and Johnson 2000). Unfortunately, there were few stands sampled further downslope on glacial till hillslopes and thus those intervals did not meet the first criterion. As a result, both the glaciofluvial and glacial till substrates were divided into 5 distances from the ridgeline.

The relationship between species richness and mean species tolerance per stand will explain mechanistically why species richness is high or low. Species tolerance (T) was measured as the variance in the relative frequency of a species on the hillslope (cf. McNaughton and Wolf 1970):

$$T_i = \left[\frac{\sum_{j=1}^5 (x_{ij})^2 - \left[\left(\sum_{j=1}^5 x_{ij} \right)^2 / \sum_{j=1}^5 x_j \right]}{\sum_{j=1}^5 x_j} \right]^{1/2} \quad (1.2)$$

where T_i is the tolerance width for species i , x_j is the relative frequency of species i in slope position j and j is the interval of slope position weighted from 1 to 5 (1 being the top slope and 5 the toe slope). Therefore, the mean of the species tolerances per stand ($\bar{T}$) is:

$$\bar{T} = \frac{\sum_{i=1}^S T_i}{S} \quad (1.3)$$

The relationship between the overlap of species' relative frequencies and distance from the ridgeline will determine how similar stands in adjacent slope positions are to one another with respect to relative species frequencies. Overlap is measured as the overlap of all species' relative frequencies in adjacent slope positions and was calculated following Horn (1966):

$$R_o = \frac{\sum_{i=1}^{n_j} [(x_{ij} + x_{i,j+1}) \log(x_{ij} + x_{i,j+1})] - \sum_{i=1}^{n_j} [x_{ij} \log x_{ij}] - \sum_{i=1}^{n_j} [x_{i,j+1} \log x_{i,j+1}]}{(X_j + X_{j+1}) \log(X_j + X_{j+1}) - X_j \log X_j - X_{j+1} \log X_{j+1}} \quad (1.4)$$

where x_{ij} is the relative frequency of species i in slope position j , $x_{i,j+1}$ is the relative frequency of species i in the adjacent slope position $j+1$, n_j is the number of species found at slope position j and X_j is the sum of the relative frequencies of all species in slope position j :

$$X_j = \sum_{i=1}^n x_i \quad (1.5)$$

and is equal to 1. Therefore the denominator of R_o (equation 1.4) reduces to 0.602 which is the highest value the numerator could be if the adjacent slope positions were identical with respect to relative species frequencies. Therefore, R_o varies between 0 where none of the species in the adjacent slope positions overlap and 1 where all of the species frequencies in adjacent slope positions are identical.

In addition, multiple comparisons were made of the percent similarity of species relative frequencies between each pair of slope positions. The percent similarity was calculated using the relative frequencies of each species averaged across the stands within each slope position (Renkonen 1938):

$$\%similarity = \sum_{i=1}^n [minimum(x_{ij}, x_{ij+1})] \quad (1.6)$$

Percent similarity is one of the best quantitative measures of similarity available since it is not greatly affected by sample size or by species diversity (Wolda 1981). Analysis for significance could not be performed since percent similarity calculations were not independent.

Finally, multiple comparisons were made of the number of species with a relative abundance of less than 5% (rare species) between each pair of slope positions ($p < 0.05$) to determine which slope positions supported more rare species.

A LANDSAT TM image (for cover type and percent coverage), a Digital Elevation Model (DEM) for hillslope position (i.e. moisture and nutrients) and a digitized time-since-fire map were used to predict the patterns of understory vascular plant species richness on the landscape using the image analysis software PCI™ version 5.2. The LANDSAT TM image was taken on July 12, 1990 under cloud free conditions. Stands were located on the image with coordinates obtained from a differential global positioning system. The pixels were randomized and half of the pixels in each stand were used as training sites in a supervised classification while the other half were retained as test sites to calculate accuracy. The supervised classification required the user to delineate classes. Based on vascular species richness from our field sampling, stands were grouped into one

of four classes; species rich or species poor on each of the two substrates. Non-forested areas were divided into seven classes, including three classes of water; deep, shallow and intermittent, tree and shrub marsh, grassland and low density aspen (less than 20% canopy cover) using a combination of aerial photographs and forestry cover maps. A maximum likelihood classifier (PCI Inc. 1994) was then used to classify each pixel into one of the eleven classes. The maximum likelihood classifier is preferred because it evaluates both the variance and correlation of the category's spectral response patterns when classifying unknown pixels (PCI Inc. 1994). However, it assumes that the distribution of points in the category training data is Gaussian. The overall accuracy of the classified richness map was assessed using the kappa coefficient of agreement (Hudson and Ramm 1987, Congalton 1991) which compared the similarity of the two raster maps after the similarity due to chance had been removed. Since diversity was not greatly affected by evenness, only a map of species richness was constructed.

RESULTS

Relative Importance of Moisture and Nutrient Gradients, Light Availability and Time Since Disturbance in Explaining Species Richness, Diversity and Evenness

The standardized multiple regression using slope position/surficial geology, canopy basal area and time-since-fire was significant ($p < 0.0001$) and accounted for 52% of the variation in species richness (Table 1.1). Slope position/surficial geology showed a significant relationship with species richness and when the relative importances of the slope position/surficial geology categories were combined, they showed the highest relative importance. Canopy basal area and time-since-fire were not individually significant because canopy basal area and time-since-fire interact and their interaction showed a significant relationship with species richness. The interaction indicates that the relationship between canopy basal area and time-since-fire is not linear. Instead, the relationship is described by a parabola and was plotted using the intercept and parameter

Table 1.1 **Standard least squares multiple regression of the effect of stand characteristics (slope position/surficial geology, canopy basal area and time-since-fire) on understory vascular plant species richness. Relative importance was assessed using standardized partial regression (beta) coefficients.**

A) Analysis of variance

Source	df	F	Prob>F	R2
Model	6	20.105	<0.0001	0.52
Error	111			
Total	117			

B) Parameter estimates

Variable	df	Parameter		Relative Importance	
		Estimate	t	Prob<F	(Beta Coefficient)
Intercept		16.86	16.09	<0.000	0
Slope position / Surficial geology:	3				Total = 1.44
Glaciofluvial top slope vs glacial till toe slope		0.388	0.43	0.6662	0.04
Glaciofluvial toe slope vs glacial till toe slope		-6.546	-6.26	<0.000	0.59
Glacial till top slope vs glacial till toe slope		6.719	9.69	<0.000	0.81
Canopy basal area	1	0.0005	1.59	0.115	
Time-since-fire	1	0.022	1.41	0.162	
Interaction of Canopy basal area and Time-since-fire	1	-1E-05	-3.3	0.0013	0.53

estimates from Table 1.1 (Figure 1.2). At a constant richness there is a trade off between canopy basal area and time-since-fire (i.e. as time-since-fire increases basal area decreases) that is not simply a linear relationship. For example, at certain time-since-fires there are a range of canopy basal areas that will produce a constant richness and at certain canopy basal areas there are a range of time-since-fires that will produce a particular species richness value. Overall, as stands age and increase in canopy basal area, species richness decreases. Note that the parameter estimates (Table 1.1) for canopy basal area and time-since-fire simply give the intercepts for the interaction and not relative importance since the relative importance of the interaction contains the same information.

The standardized multiple regression for diversity (Table 1.2) and evenness (Table 1.3) showed the same trend in relative importance as species richness (i.e. slope position/surficial geology had the highest relative importance and the interaction between canopy basal area and time-since-fire had the next highest relative importance). However, slope position/surficial geology, canopy basal area and time-since-fire only accounted for 47% of the variation in diversity and only 16% in evenness.

A potential problem of multiple regressions is the correlation of stand characteristics. The only correlation of potential concern (because of a correlation of 0.64) was between canopy basal area and time-since-fire. However, canopy stem density is only slightly correlated with time-since-fire (correlation = 0.32) and when used in place of canopy basal area in the standardized multiple regression, the same trend in relative importance with species richness, diversity and evenness was evident (i.e. slope position/surficial geology had the highest relative importance and the interaction between canopy stem density and time-since-fire had the next highest relative importance). The magnitudes of the relative importances were different so that the differences between the relative importance of slope position/surficial geology and that of the interaction were greater. Therefore, the correlation did not affect the trend in relative importance nor did it affect the trend in the interaction between canopy basal area and time-since-fire (Figure 1.2).

Figure 1.2 A contour plot showing how understory vascular species richness (# on the contours) is related to the interaction between canopy basal area (m^2/ha) and time-since-fire (years) as predicted from the standard least squares multiple regression (Table 1.1). The parabolic relationship indicates that there is a trade-off between canopy basal area and time-since-fire that is not simply linear. Overall, species richness decreases as stands age and as canopies increase in basal area.

Table 1.2 Standard least squares multiple regression of the effect of stand characteristics (slope position/surficial geology, canopy basal area and time-since-fire) on understory vascular plant species **diversity**. Relative importance was assessed using standardized partial regression (beta) coefficients.

A) Analysis of variance

Source	df	F	Prob>F	R2
Model	6	16.26	<0.0001	0.47
Error	111			
Total	117			

B) Parameter estimates

Variable	df	Parameter Estimate	t	Prob<F	Relative Importance (Beta Coefficient)
Intercept		2.33	30.83	<0.000	0
Slope position / Surficial geology:	3				Total = 1.49
Glaciofluvial top slope vs glacial till toe slope		0.0346	0.53	0.5944	0.05
Glaciofluvial toe slope vs glacial till toe slope		-0.519	-6.87	<0.000	0.68
Glacial till top slope vs glacial till toe slope		0.434	8.66	<0.000	0.76
Canopy basal area	1	3E-05	1.25	0.2144	
Time-since-fire	1	0.0012	1.07	0.2877	
Interaction of Canopy basal area and Time-since-fire	1	-5.9E-07	-2.52	0.0131	0.43

Table 1.3 **Standard least squares multiple regression of the effect of stand characteristics (slope position/surficial geology, canopy basal area and time-since-fire) on understory vascular plant species evenness. Relative importance was assessed using standardized partial regression (beta) coefficients.**

A) Analysis of variance

Source	df	F	Prob>F	R2
Model	6	3.37	0.0043	0.16
Error	111			
Total	117			

B) Parameter estimates

Variable	df	Parameter		Prob<F	Relative Importance
		Estimate	t		(Beta Coefficient)
Intercept		0.688	36	<0.000	0
Slope position / Surficial geology:	3				Total = 0.82
Glaciofluvial top slope vs glacial till toe slope		-0.0387	-2.36	0.02	0.29
Glaciofluvial toe slope vs glacial till toe slope		0.0511	2.59	0.011	0.33
Glacial till top slope vs glacial till toe slope		-0.022	-1.75	0.083	0.2
Canopy basal area	1	-5E-06	-0.76	0.045	
Time-since-fire	1	0.00017	0.62	0.539	
Interaction of Canopy basal area and Time-since-fire	1	6.3E-08	1.08	0.285	0.23

Local (Hillslope) Patterns of Species Richness, Diversity and Evenness

Species richness and diversity (Figure 1.3) were significantly different between all combinations of slope positions/surficial geologies ($p < 0.05$) with the exception of glaciofluvial top slopes and glacial till toe slopes ($p > 0.05$). Within substrates, species richness and diversity decreased from top slopes to toe slopes. Evenness (Figure 1.3) was generally similar across slope positions/surficial geologies and was only significantly different between glaciofluvial top and toe slopes and between glacial till toe slopes and glaciofluvial top slopes ($p < 0.05$). Therefore, from the relationship $H = \ln(S) + \ln(E)$ (Buzas and Hayek 1996), diversity is largely determined by species richness. The results from the standardized multiple regression (Tables 1.1 - 1.3) and the multiple comparisons for slope position/surficial geology (Figure 1.3) were consistent. For example, the low relative importance of glaciofluvial top slope versus glacial till toe slope indicates that species richness is similar on both slope positions (Table 1.1). The high relative importance of the remaining two slope position/surficial geology categories indicates that species richness is very different between these slope positions/surficial geologies (Table 1.1).

These comparisons can be summarized with respect to canopy species (Figure 1.4) since canopy species are organized according to slope position/surficial geology (Bridge and Johnson 2000). On glaciofluvial top slopes, jack pine stands are relatively species rich and diverse while toe slope black spruce stands have fewer species and are less diverse. On glacial till top slopes, aspen stands are species rich and diverse and toe slope mixedwood stands of aspen, white spruce and balsam fir are species poor and less diverse. However, jack pine stands and mixedwood stands have similar species richness and diversity even though jack pine stands are found on the top slopes of glaciofluvial substrates and mixedwood stands are found on toe slopes of glacial till. Evenness is only significantly different between jack pine and black spruce stands and between jack pine and mixedwood stands.

In short, the *highest* species richness is found in young trembling aspen stands, where moisture and nutrients are low (top slopes) and light availability is high (low

Figure 1.3 **Mean understory vascular plant species richness, diversity and evenness (with standard errors). Bars within a grey scale with the same letter are not significantly different ($p>0.05$) based on multiple comparisons and the Tukey-Kramer HSD test.**

Figure 1.4 **General landscape patterns of vegetation composition** where the shapes of the hillslopes depict the actual profile of most hillslopes in the southern mixedwood boreal forest (cf. Bridge and Johnson 2000). The tree symbols depict the general change in dominant canopy species down the hillslope, and are based on the relationship between stand positions on the abstract moisture and nutrient gradients and on the distances of the stand from the ridgeline. Mean understory vascular plant species richness is represented on the hillslopes using grey scales, where dark grey represents high species richness and light grey represents low species richness. Mean species richness values with the same letter are not significantly different ($p > 0.05$) based on multiple comparisons and the Tukey-Kramer HSD test.

Mean Understory Vascular Species Richness	
a	25.08 +/- 0.62
b	22.68 +/- 1.22
b	19.78 +/- 0.92
c	14.07 +/- 1.85

canopy basal area). The *lowest* species richness is found in old black spruce stands, where moisture and nutrients are high (toe slopes) but light availability is low (high canopy basal area). Other combinations of canopy species (slope positions/surficial geologies), light availability (canopy basal area) and age produce the intermediate values of species richness.

Species Richness In Relation to Community Organization

In our study area, the community was organized such that species richness was negatively correlated to species tolerances (Figure 1.5). Therefore, species richness was high where species tolerances were narrow.

Overlap generally decreased from top slopes to toe slopes but was not significant (Figure 1.6). Since species richness decreases from top slopes to toe slopes (Table 1.1), overlap was higher where species richness was high and lower where species richness was poor.

The number of rare species increased with increasing species richness (Figure 1.7). Therefore, species richness was high where the number of rare species was high.

The similarity in composition between different slope positions, ranged from 48% to 71% (Table 1.4). Glacial till top slopes and toe slopes had the highest percent similarity values.

In summary, the highest species richness is found where species tolerances are narrow and where both the overlap of species relative frequencies and the number of rare species is high. In addition, percent similarity of species relative frequencies is high (averaging 57%) across slope positions.

The Landscape Pattern of Species Richness

The supervised classification (Figure 1.8) using the LANDSAT TM image for canopy species, the DEM for hillslope position and the digitized time-since-fire map had an accuracy of 76% and a kappa coefficient of 0.7221. The majority of pixels were correctly classified (Table 1.5) with accuracies (reading diagonal in the table) ranging

Figure 1.5 The relationship between mean tolerance width and understory vascular plant species richness of stands on glaciofluvial and glacial till substrate.

Figure 1.6 The relationship between the overlap of species relative frequencies along the glaciofluvial and glacial till hillslope and slope position where slope position was divided into intervals of distance from the ridgeline (see methods).

Figure 1.7 The relationship between the number of rare species and understory vascular plant species richness of stands on glaciofluvial and glacial till substrate.

Table 1.4 Percent similarity of the relative frequencies of understory vascular plant species between each pair of slope positions.

Slope position / Surficial Geology	Glaciofluvial top slope	Glaciofluvial toe slope	Glacial till top slope	Glacial till toe slope
Glaciofluvial top slope	1.00			
Glaciofluvial toe slope	0.59	1.00		
Glacial till top slope	0.54	0.48	1.00	
Glacial till toe slope	0.56	0.55	0.71	1.00

Figure 1.8 The upland understory vascular plant species richness based on a supervised classification using a LANDSAT TM image for canopy species, a Digital Elevation Model for hillslope position and a digitized time-since-fire map. The mean species richness and standard deviation for each slope position/surficial geology category on the map are:

- Glaciofluvial species rich 23.63 ± 5.25 ;
- Glaciofluvial species poor 14.50 ± 6.76 ;
- Glacial till species rich 24.61 ± 3.94 ; and
- Glacial till species poor 19.48 ± 5.22 .

Glaciofluvial Species Rich	Treed Marsh	Rivers
Glaciofluvial Species Poor	Shrub Marsh	Lakes
Glacial Till Species Rich	Low Density Aspen	Unclassified
Glacial Till Species Poor	Grassland	

Table 1.5 Error matrix: the percentage of pixels assigned to a category (using a maximum likelihood classifier (PCI Inc.)) relative to the actual category, according to the field data. The columns represent the field data while the rows represent the classification generated from the LANDSAT TM image. Reading diagonally across the table gives the percentage of pixels correctly assigned to a category.

Category	Percent Pixels Classified by Category													
	Glaciofluvial		Glaciofluvial		Glacial Till		Glacial Till		Treed		Shrub		Deep	
	Null	Species Rich	Species Poor	Species Rich	Species Poor	Species Rich	Species Poor	Marsh	Marsh	Marsh	Lakes	Lakes	Shallow	Intermittent
Glaciofluvial Species Rich	1.6	60.4	15.2	5.1	7	3.5	4.7	0	0	0	0	0	0	2.5
Glaciofluvial Species Poor	2.7	3.4	82.4	3.4	7.4	0	0.7	0	0	0	0	0	0	0
Glacial Till Species Rich	8.5	5.4	7.1	63.5	11.5	1.1	1.1	0	0	0	0	0	0	1.8
Glacial Till Species Poor	7.7	4.3	9.6	13.6	63.3	1.3	0.2	0	0	0	0	0	0	0
Treed Marsh	5.4	4.4	4.9	1.5	1.7	77.5	4	0	0	0	0	0	0	0.6
Shrub Marsh	10.4	5.3	0.1	0.4	0	8.6	67.3	0	0	0	0	0	0.4	6.7
Deep Lakes	11.8	0	0	0	0	0	0	84.5	1.7	0	0	0	2.1	0
Shallow Lakes	4.7	0	0	0	0	0	0.1	26.7	66.1	0	0	0	2.4	0
Intermittent Lakes	13.6	0	0	0	0	0	0.1	1.8	0	84.5	0	0	0	0
Grassland	13.5	0	0	0	0	0	4.3	0	0	0	0	0	82.2	0
Low Density Aspen	1.6	0.8	0	0	0	0.6	4.8	0	0	0	0	0	0.1	92.1

from 60.4% for glaciofluvial species rich to 92.1% for low density aspen. The greatest misclassifications occurred between classes on adjacent slope positions, e.g. glaciofluvial species rich and poor classes and glacial till species rich and poor classes (Table 1.5). This likely occurred as an artifact of continuous variables having been divided into discrete classes.

DISCUSSION

The mixedwood boreal forest (cf. Rowe 1972) of western Canada is relatively poor in understory vascular plant species richness. In the 121 stands sampled, 122 vascular species were recorded, only 6 of which were trees. Further, the similarity between stands is high where all pairs of stands share at least 48% of their vascular species. Evenness is relatively constant; consequently, richness is the primary determinant of diversity.

The environmental variables of moisture and nutrients (i.e. slope position/surficial geology) are relatively more important in predicting understory plant species richness, diversity and evenness than light availability and time-since-fire. This is consistent with other studies in a range of forest types that have indicated the importance of moisture and nutrient gradients in explaining vegetation composition (e.g. Day Jr. and Monk 1974, Whittaker and Niering 1975, Marks and Harcombe 1981, Roberts and Christensen 1988, Host and Pregitzer 1992). Moisture and nutrient gradients are related to position on the hillslope and surficial geology (Bridge and Johnson 2000). Therefore, the hillslope is the fundamental unit of species richness and diversity.

Communities were organized along the moisture and nutrient (hillslope) gradient such that species rich communities had high percent similarity of species relative frequencies and narrow species tolerances. The narrow tolerances result in a greater subdivision of the gradient and this allows for not only more species (high species richness) but also more species with lower abundances (more rare species). Species with

narrow tolerances also have lower relative abundances (McNaughton and Wolf 1970, Johnson 1977) and lower biomass (Parrish and Bazzaz 1976). A possible evolutionary reason for this is that individuals with wide tolerances and high abundance interact with individuals of the same species so that divergence of the individual's tolerance occurs and thus the species tolerances increase (Johnson 1977). Narrow tolerance species interact with more individuals of different species which does not cause the individual's tolerance to widen to the same extent. Consequently, tolerances remain narrow and species diversity remains high.

The overlap of species relative frequencies in communities exhibited a decreasing trend from top slopes to toe slopes. Since species richness also decreases from top slopes to toe slopes, overlap is higher where species richness is high and lower where species richness is low. Compared to glacial till stands, glaciofluvial stands have lower overlap and lower percent similarity.

It is not too surprising that the interaction between light availability (canopy basal area) and time-since-fire is more important in determining species richness, diversity and evenness than either of these variables separately. Several studies have suggested that light availability and time interact to produce understory vegetation patterns (De Grandpré et al. 1993, Lieffers 1994, De Grandpré and Bergeron 1997). The interaction between canopy basal area and time-since-fire indicates that their relationship is not simply linear but is described by a parabola. For richness (Figure 1.2) to remain constant, there is a trade-off between high basal area (low light availability) and a short time-since-fire, or low basal area and a long time-since-fire. Thus, there are two means of maintaining the same level of richness. Alternatively, as stands age and increase in canopy basal area, species richness decreases.

The pattern of understory plant species richness is related to the pattern of canopy trees, where trembling aspen stands have high species richness and high diversity, jack pine and mixedwood stands have intermediate species richness and diversity and black spruce stands have low species richness and diversity. Both the canopy trees (Bridge and Johnson 2000) and the understory vascular plant species richness are organized primarily

by moisture and nutrient gradients which are determined at the hillslope scale by both slope position and surficial geology. The similarity in richness and diversity between jack pine and mixedwood stands is likely due to a combination of both moisture gradients and light availability. Both moisture and nutrients increase downslope, however, due to surficial geology, the magnitudes of moisture and nutrients differ. On glaciofluvial substrate under jack pine stands, moisture is intermediate and nutrients are low while downslope black spruce stands are characterized by high moisture and nutrients. On glacial till under aspen stands, moisture is low and nutrients are intermediate while further downslope in mixedwood stands moisture is intermediate and nutrients are high (Bridge and Johnson 2000). Therefore, both jack pine and mixedwood stands dominate the intermediate portion of the moisture gradient (Bridge and Johnson 2000). In addition, it is likely that light availability in mixedwood and jack pine stands is similar since light availability is greatest in aspen stands, lowest in white spruce stands (Lieffers and Stadt 1994) and intermediate in pine stands. In a mixedwood stand of aspen and white spruce, light availability should also be intermediate.

Perhaps one of the most interesting results of this study is the ability to map species richness at the landscape scale. A LANDSAT TM image for cover type and amount, a DEM for hillslope position (i.e. moisture and nutrients) and a time-since-fire map were used to produce a supervised classification of richness (the most important determinant of diversity). Misclassification occurred between slope positions of similar surficial geology. That is, glaciofluvial species rich and poor were confused as well as glacial till species rich and poor. Remember that glaciofluvial species rich and poor are associated with jack pine and black spruce canopies, respectively, and glacial till species rich and poor are associated with trembling aspen and mixedwood canopies, respectively. Jack pine and trembling aspen are found in high abundance on top slopes. This does not preclude their occurrence further downslope, only that they are found in lower abundance. Similarly, black spruce and mixedwood stands are found in higher abundance on toe slopes but are still found further up the slope in low abundance. Therefore, in the mid slope region, it is difficult to distinguish between canopy species because a continuous

variable (abundance of canopy species) has been divided into two discrete classes (species rich and poor on the two surficial geologies). Thus, species rich and poor classes on the same surficial material are confused. This may indicate that surficial geology is more important than slope position in determining species richness.

Comparison of the species richness map to the time-since-fire map (Figure 1.9) shows that the pattern of species richness varies greatly at a smaller scale relative to the larger scale pattern of forest ages resulting from the current fire frequency regime. Hillslopes are structured according to ridgelines and stream channels and it appears that the smaller scale pattern of species richness follows that of the stream channels and ridgelines (Figure 1.8). This is consistent with our results showing the higher relative importance of slope position/surficial geology in determining species richness. In short, the hillslope appears to be a more fundamental unit of species richness than fire.

Satellite data has been used with varying degrees of success to predict vegetation patterns since collecting field data can be time consuming and costly. For mapping broad forest types at the stand level, the low resolution of satellite data (e.g. 30m x 30 m) is often better than higher resolutions (e.g. 2m x 2m), since homogenous stands often appear heterogeneous due to species mixtures (Leckie 1990). Ideally, the resolution (or pixel size) would correspond to stand sizes. However, stand sizes vary greatly due to a variety of factors including substrate, land form and disturbance. Warren (1999) attempted to use remote sensing and GIS techniques to predict species diversity at the landscape scale using variables related to species diversity which included: distance from the ridgeline (for moisture and nutrient gradients), canopy species, canopy stem density (for light availability) and time-since-fire. As an innovative approach, Warren (1999) also propagated the error associated with estimating the spatial variables in an attempt to predict diversity under the worst case scenario. The result was a correlation of 0.18 - 0.28 between field measured species diversity and the species diversity predicted from the remote sensing and GIS techniques. Remember that this is the worst case scenario. It does indicate that the techniques for estimating the variables primarily responsible for diversity have not been perfected. For example, Warren's (1999) prediction of canopy

Figure 1.9 A digitized map of time since the last fire in Prince Albert National Park (Weir et al. 2000). The map colours range from light grey for the youngest stands (5 years) through to dark grey for the oldest stands (234 years). The hatched areas are lakes.

stem density was poor. However, his prediction of distance from the ridgeline was quite successful. Warren's (1999) study shows the potential for using GIS and remote sensing techniques to predict diversity. The results from this study indicate the effectiveness of using satellite data, a DEM and a time-since-fire map to predict species richness.

In summary, hillslope position/surficial geology (moisture and nutrient gradients) appears to be the fundamental unit of species richness at the landscape scale while canopy basal area (light availability) and time-since-fire (age) play a secondary role in determining species richness.

APPLICATIONS

The forest management goal of simply regenerating target tree species has changed over the last 25 years to a sustainable ecosystem-based forest management (Perry 1998). Concern has centred on the conservation of biodiversity (Walton 1997, Boyle 1991). Conservationists suggest that managers should maximize the number of species preserved (Walton 1997), often with little understanding of the ecological processes involved (Pickett et al. 1992). In fact, one goal of ecosystem-based forest management is to preserve biodiversity by emulating the 'natural' (pre-European) disturbance regime (Hunter 1993, Attiwill 1994, Bender 1994, Weetman 1994). This goal implies that natural disturbance plays a significant, if not principal, role in determining diversity and that the variation in disturbance in the past (natural) is preferable to the current (European) disturbance variation. Emulation, usually through forestry practices, is intended to remain within this preferred natural disturbance variation. Further, ecosystem management implies that current and past forestry practices are outside of this natural disturbance variation and that diversity has changed as a consequence.

The boreal forest is considered a fire dominated ecosystem because fire is the primary large scale disturbance. This implies that fire is the principal determinant of diversity. However, as has been demonstrated in this study, the understory vascular plant

diversity in the mixedwood boreal forest is primarily determined by the moisture and nutrient gradient. This gradient is determined by the hillslope hydrology and surficial geology. Thus the primary pattern of vascular plant diversity is determined by both the hillslope shape and the hillslope assembly between ridgelines and streams. The hillslope-basin structure ensures that species occupy a constant proportion of the basin regardless of basin size (Bridge 1996). This characteristic is due to the allometric relationship between drainage basin area and length. Large basins are disproportionately longer and narrower than smaller basins and therefore hillslope length tends to remain constant (Hack 1957, Gray 1961, Shreve 1975, Newsson 1978). Thus, hillslope and surficial geology are the principle determinants of the variation in vascular plant diversity across the landscape.

Time-since-fire does affect diversity through its interaction with canopy coverage. Figure 1.2 shows clearly how these two variables organize vascular plant diversity. However, fire is not only characterized by time-since-fire (fire frequency) but also by fire line intensity (flaming heat output at the fire front), duff (F and H organic layers) consumption by smoldering combustion and the burn shape and spatial distribution of unburned patches within it (Johnson 1992). The results of this study, however, are restricted to fire frequency.

In the mixedwood boreal forest, the fire cycle has changed at least twice in the last 200 years (Weir et al. 2000). These changes have been attributed to large scale climatic changes because of their synchronous timing over large parts of the boreal forest (Johnson 1992, Bergeron and Archambault 1993, Johnson et al. 1998). Changes in the fire cycle were found to be unrelated to vegetation type, slope or terrain. The variation in the fire cycle has been between 15 years to 75 years. Studies in other parts of the boreal forest have found variation in the fire cycle of the same magnitude but not necessarily the same values (the fire cycle tends to be longer further north and in the wetter (eastern) parts of the boreal forest (Johnson 1992)). In fact, the data on the fire cycle suggests that the 'natural' situation is frequent changes in the fire cycle within a range between approximately 15 and 150 years. Thus, there is no one preferred historic fire cycle that should necessarily be emulated (Johnson et al. 1998).

What does the variation in the fire cycle in the past tell us about variation in diversity in the mixedwood boreal forest? Our results indicate that a short fire cycle will increase diversity and longer fire cycles will decrease diversity. However, the variation was never large enough to significantly change the diversity. This assumes that the climatic changes which altered the fire cycle were not large enough (nor perhaps long enough) to cause major changes in the moisture and nutrient gradient. This assumption, however, should be accepted with considerable care given our level of understanding.

Forestry in the study area has occurred since 1890 (Weir and Johnson 1998). It began with selective cutting for white spruce sawlogs and currently involves mostly clearcutting. Current forestry practices follow a rotation schedule of 70 years (Weyerhaeuser Canada 1999) in keeping with the current approximate 75 year fire cycle. Harvesting may change moisture and nutrients compared with unharvested sties (e.g. Schmidt et al. 1996), however, these changes do not appear to translate into changes in foliar nutrient status (e.g. Macdonald et al. 1998).

Our results suggest that fire frequency is not the principle determinant of diversity. Instead, the hillslope coupled with surficial geology is the more fundamental unit of diversity while the interaction with light and fire plays a secondary role (Figure 1.2). Further, there is no one preferred historic fire frequency that should necessarily be emulated since the 'natural' ecosystem has seen frequent changes in the disturbance (fire) frequency. It is clear that site preparation techniques such as disk trenching and anchor chain scarification after harvesting could lead to changes in vascular plant composition and diversity (Chapter Two). This seems to be a consequence of these site preparation techniques affecting the seed bank, residual vegetation and the availability of suitable seedbeds. We still have a great deal to learn about fire behaviour and its effects before we are able to emulate fire in our forestry management (Johnson and Miyanishi in press).

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CHAPTER TWO

A Comparison of Understory Vascular Plant Species Diversity in Recently Harvested Stands and Stands Recently Burned by Wildfire in the Mixedwood Boreal Forest

INTRODUCTION

The forest management goal of simply regenerating target tree species has expanded over the last 25 years to a sustainable ecosystem-based forest management where much of the concern centers on ecosystem attributes such as biodiversity (Boyle 1991, Weetman 1994, Walton 1997, Perry 1998). One goal of ecosystem-based forest management is to emulate the 'natural' (pre-European) disturbance regime (Weetman 1994), which, in the boreal forest, is large scale, crown-replacing wildfire. This goal implies that natural disturbance (wildfire) plays a significant role in determining biodiversity. Chapter one addressed this implication by comparing the relative importance of moisture and nutrient gradients, light availability and time since the last fire in determining plant species diversity. The results indicated that moisture and nutrient gradients, which are determined by a stand's position on the hillslope and the hillslope's surficial geology, were of primary importance while the interaction between light availability and time (since fire) played only a secondary role.

The goal of emulating the 'natural' disturbance regime has two other important implications. The first is that the variation in disturbance frequency in the past is preferable to the current variation in disturbance frequency. The second is that current and past forestry practices are outside of this 'natural' variation in disturbance frequency and have changed species diversity as a consequence. This chapter will address the implication that plant species diversity has changed as a result of harvesting. I will compare harvested stands and stands burned by wildfire of similar ages to avoid

questionable assumptions about how stands develop that are evident in studies that compare diversity in old stands with diversity in recently harvested stands (e.g. Dyrness 1973, Halpern and Spies 1995, Meier et al. 1995, Bråkenhielm and Liu 1998).

Many of the differences between stands burned by wildfire and stands that have been harvested reside in the disruption of the forest floor. Other differences may not affect vascular plant diversity. For example, while harvesting removes most of the canopy trees in a stand, wildfire kills the trees without removing them. Since all fire-killed trees remain in the stand, nutrient inputs to the forest floor may differ between harvested and burned stands. Schmidt et al. (1996) found differences in some soil chemical properties between harvested and unharvested sites, however, these differences had little impact on foliar nutrient status in white spruce seedlings (Macdonald et al. 1998). Further, the amount of logging debris left on a site seems to have little effect on vascular plant species composition (Olsson and Staaf 1995).

Disruption of the forest floor differs between harvested and burned stands, primarily as a result of species specific site preparation. Site preparation techniques differ depending on which species is to be regenerated. In this study, trembling aspen stands were left to naturally regenerate, jack pine and black spruce stands were either left to naturally regenerate or were anchor chain scarified and left to naturally regenerate, and white spruce stands were disk trenched to expose rows of mineral soil and planted with white spruce seedlings since natural regeneration does not produce the desired stocking density of white spruce (Weyerhaeuser Canada, pers. comm.). These techniques disrupt the forest floor much differently than wildfires. For example, the availability of suitable seedbeds (thin humus or mineral soil) is increased in burned stands due to the spatial pattern of duff consumption (Charron 1998) while in harvested stands, mineral soil is only exposed by disk trenching or anchor chain scarification. Therefore, it was hypothesized that the type of forest floor disturbance (i.e. by harvesting or burning) will affect the seed bank, residual vegetation and the availability of seedbeds which, in turn, may affect plant species diversity and composition. To examine this, stands recently burned by wildfire and recently harvested stands were compared for understory vascular plant species

diversity and composition. The objectives were to determine: 1) whether harvesting changes species diversity or species composition, and 2) whether the differences or similarities in species diversity or composition could be attributed to differences in the type of forest floor disturbance.

METHODS

Study Area

The study area is located in central Saskatchewan and covers approximately 8000 km² (53°34' N to 54°24' N and from 105°25' W to 107°52' W) (Figure 2.1). It is characterized by long, cold winters and short, cool summers. The frost free period is generally less than 80 days and freezing can occur in any month. July and August are the warmest months with the average maximum temperature exceeding 20°C three days out of four. The average annual precipitation ranges from 400 to 500 mm, 70% of which occurs as rain.

The primary large scale disturbance is lightning-caused crown fires. These crown fires produce even-aged stands with all tree species (except *Abies balsamea*) recruiting primarily within the first five years following fire (Gutsell, pers. comm.). The fire cycle has changed twice in the last 200 years, and has varied from 15-75 years (Weir et al. 2000). Only 5% of the area is older than 200 years (Johnson et al. 1995) and therefore older trees are not replaced by younger trees of a different species (Dix and Swan 1971, Bridge and Johnson 2000). Insect outbreaks do not seem to have been a major source of large scale disturbance in the last hundred years.

The area has a gentle relief with elevation ranging from 450 m to 900 m a.s.l.. The surficial geology is undifferentiated glacial till, glaciofluvial and glaciolacustrine surfaces with only a small proportion of the study area covered by glaciolacustrine substrates. Surficial geology determines the shape of the hillslope (Hack and Goodlet 1960, Bull 1975, Bridge and Johnson 2000) and thus the rates of change of moisture and

Figure 2.1 **Location of the study area: Prince Albert National Park and Weyerhaeuser's Forest Management License Agreement. The light grey area represents the extent of the boreal forest in Canada and the hatched area is the southern mixedwood boreal forest.**

nutrients down the hillslope (O'Loughlin 1981, Wood et al. 1988, Bridge and Johnson 2000). This is due to the consistent way in which the geomorphic processes of erosion and resistance form hillslopes (Hack and Goodlet 1960, Bull 1975). Glaciofluvial substrates consist of small, clay-like particles sorted by rapidly moving glacial meltwater while glacial till substrates consist of an undifferentiated mixture of stones, gravel, sand, silt and clay. Therefore, glacial till slopes are steeper for any given distance from the ridgeline than glaciofluvial slopes (Bridge and Johnson 2000). Consequently, hillslope shape can be quantitatively described by allometric equations (Bridge and Johnson 2000).

Moisture and nutrient gradients are prevalent across the landscape due to the repeatability of hillslopes (Bridge and Johnson 2000). As soil water diverges on top slopes and converges on toe slopes (Anderson and Burt 1977, Harr 1977, Sinai et al. 1981, O'Loughlin 1981, 1986, Wood et al. 1988), it carries with it nutrients that are leached from top slopes to accumulate in toe slopes (Trudgill 1988, Litaor 1992, Tsuboyama et al. 1994). Therefore, top slopes of similar surficial material are generally dry and nutrient poor while toe slopes are wet and nutrient rich (Malo et al. 1974, Harr 1977, Anderson and Burt 1977, Johnson 1981, O'Loughlin 1981, Sinai et al. 1981, Ciha 1994, Bridge and Johnson 2000). Therefore, moisture and nutrients can be quantitatively linked to the allometric equations and qualitatively linked to position on the hillslope where top slopes have lower moisture and nutrient status and toe slopes are characterized by higher moisture and nutrients (Bridge and Johnson 2000). However, the magnitudes of moisture and nutrients depend on surficial geology where glaciofluvial top slopes have intermediate moisture status and low nutrients while downslope stands are characterized by high moisture and nutrients. On glacial till, moisture is low and nutrients are intermediate on top slopes while further downslope moisture is intermediate and nutrients are high (Bridge and Johnson 2000).

The study area is part of the southern mixedwood boreal forest (Rowe 1972). It is characterized by white spruce (*Picea glauca* (Moench) Voss.), black spruce (*Picea mariana* (Mill) B.S.P.), jack pine (*Pinus banksiana* Lamb.), balsam fir (*Abies balsamea* (L.) Mill.), tamarack (*Larix laricina* (Du Roi) K. Koch), trembling aspen (*Populus*

tremuloides Michx.), balsam poplar (*Populus balsamifera* L.) and white birch (*Betula papyrifera* Marsh.). Bridge and Johnson (2000) used slope position and surficial geology to depict the general landscape patterns of upland vegetation composition. On glaciofluvial hillslopes, jack pine are found in higher abundance near top slopes while black spruce are found in higher abundance further downslope. On glacial till hillslopes, trembling aspen are found in higher abundance near top slopes while mixedwood stands are found further downslope. The mixedwood stands are comprised of trembling aspen, white spruce and balsam fir.

Sampling Regime

Thirty-nine upland stands were sampled for understory vascular plant species richness and composition. Each stand was greater than 4 hectares in size, had vegetation rooted in the mineral soil with no evidence of standing water in the top 30 cm of the mineral soil and was visually homogeneous with respect to stand age, structure and species composition. In each stand, understory vascular species frequency was recorded in thirty 25 X 25 cm quadrats. The frequency of a species (f_i) was calculated as the number of quadrats that contained species i divided by the number of quadrats sampled (i.e. 30). Therefore, the relative frequency of species i (x_i) is simply the frequency of species i (f_i) divided by the sum of the frequencies of each species in the stand multiplied by 100. Note that tree and shrub species were only included in the understory plants if they were <1 m in height. Only understory vascular plant species richness (S) was sampled because diversity (H) is largely determined by species richness (Chapter One) according to $H = \ln(S) + \ln(E)$ (where E is evenness) (cf. Buzas and Hayek 1996) and because species richness is easily understood. Species richness (S) was simply the number of species summed over the thirty quadrats per stand.

Stands were categorized according to the pre-disturbance canopy composition. Bridge and Johnson (2000) depicted landscape patterns of plant species composition using hillslope position and surficial geology (see above) due to their influence on moisture and nutrient gradients. Jack pine are found in higher abundance on glaciofluvial

top slopes while black spruce are found in higher abundance further downslope. Trembling aspen are found in higher abundance on glacial till top slopes and mixedwood stands of trembling aspen, balsam fir and white spruce are found further downslope. A stand categorized as jack pine, may still contain black spruce as long as the jack pine are found in higher abundance (generally >50%).

Seventeen of the 39 stands were recently burned by wildfire and ranged in age from 1 year to 8 years. The remaining 22 stands were harvested by Weyerhaeuser Canada Ltd. and ranged in age from 0 to 11 years since Weyerhaeuser only began clearcutting in Saskatchewan in 1986. In this study, only stands similar in canopy composition that underwent the same harvesting and site preparation techniques were sampled (Table 2.1). Therefore, all white spruce stands were disk trenched to expose mineral soil and planted with white spruce since natural regeneration does not produce the desired stocking density of white spruce (Weyerhaeuser Canada, pers. comm.). The white spruce are planted in mineral soil which has a higher moisture holding capacity than organic matter and thus does not dry out as quickly (Weyerhaeuser Canada, pers. comm.). Further, all trembling aspen, jack pine and black spruce stands were naturally regenerated or anchor chain scarified and then left to naturally regenerate. As a result, the pre-harvest canopy species were similar to post-harvest seedling species.

Analysis

Mean understory vascular species richness was compared between harvested and burned sites, controlling for pre-disturbance canopy composition using a two-factor ANOVA ($\alpha < 0.05$) to determine whether harvesting had changed species richness. The two factors were disturbance type (i.e. harvested or burned) and pre-disturbance canopy species (i.e. jack pine, black spruce, trembling aspen and white spruce).

Percent similarity was calculated for each pair of stands similar in pre-disturbance canopy composition, regardless of disturbance type. Therefore, percent similarity was calculated for each stand with every other stand of the same pre-disturbance canopy composition. The percent similarities were then grouped and averaged according to

**Table 2.1 Site preparation techniques used in Weyerhaeuser
Canada's harvested stands.**

Canopy Species	Site Preparation
Jack pine	Anchor chain scarified Naturally regenerated
Black spruce	Anchor chain scarified Naturally regenerated
Trembling aspen	Naturally regenerated
Mixedwood: Trembling aspen White spruce Balsam fir	Disc trenched and planted with white spruce

disturbance type. The result was 3 average percent similarities for each pre-disturbance canopy composition (i.e. one percent similarity for all pairs of harvested stands, one for all pairs of burned stands and one for all pairs of harvested versus burned stands, within a pre-disturbance canopy composition). This determined both the natural variation in species composition as well as whether stands were more similar within a disturbance type (i.e. harvested vs harvested, burned vs burned) than between disturbance types (i.e. harvested versus burned). Analysis for significance could not be performed since percent similarity calculations were not independent. Percent similarity was calculated according to Renkonen (1938):

$$\%similarity = \sum_{i=1}^n [minimum(x_{ij}, x_{ij+1})] \quad (2.1)$$

Percent similarity is one of the best quantitative measures of similarity available since it is not greatly affected by sample size or by species diversity (Wolda 1981).

Linear Discriminant Analysis (LDA) was used to detect differences in species composition between harvested and burned stands (Wilks' Lambda, $p < 0.05$) (Legendre and Legendre 1983). Using species frequencies, stands were classified as harvested or burned. LDA is used when the categories are known a priori (i.e. in this case, harvested and burned categories). LDA indicates which species are different and uses those species to differentiate between the categories (Legendre and Legendre 1983). The species frequencies were logistically transformed for multinormality.

Tolerance curves were constructed for each species from the LDA to determine how the frequency of species changes along a gradient of harvested to burned stands. The gradient of harvested to burned stands was constructed using stand loadings (SL) calculated as:

$$SL = \sum_1^i d_i(f_i) \quad (2.2)$$

where d is the discriminant function for species i from the LDA and f is the frequency of

species *i* in the stand. The frequency of each species from the LDA was plotted along this gradient. The tolerance curves of the species presented represent the shapes of the majority of tolerance curves.

The mean relative frequency of non-native species was compared between harvested and burned stands, controlling for pre-disturbance canopy composition using a two-factor ANOVA ($\alpha < 0.05$) to determine whether harvested stands supported more non-native species than burned stands. The two factors were disturbance type (i.e. harvested or burned) and pre-disturbance canopy species (i.e. jack pine, black spruce, trembling aspen and white spruce). The ANOVA was performed on the log transformed relative frequencies because of the non-homogeneity of variances. The non-transformed data is presented in the results. Species were classified as non-native if they were not native to North America (Frankton and Mulligan 1993, Whitson et al. 1996).

The number of rare species in a stand was compared between harvested and burned sites, controlling for pre-disturbance canopy composition using a two-factor ANOVA ($\alpha < 0.05$) to determine whether harvested stands supported more rare species than burned stands. Again, the two factors were disturbance type (i.e. harvested or burned) and pre-disturbance canopy species (i.e. jack pine, black spruce, trembling aspen and white spruce). Rare species were defined as having a frequency of 1/30 quadrats (3.3%) which is the lowest frequency a species can have and still be present in the stand.

RESULTS

The mean species richness of stands burned by wildfire was significantly lower than species richness of harvested stands (Figure 2.2). The interaction between disturbance type (i.e. harvested and burned) and pre-disturbance canopy composition was not significant ($p = 0.86$) indicating that the patterns of changes in species richness with pre-disturbance canopy type are not affected by disturbance type. Therefore, species richness is highest in trembling aspen stands, intermediate in white spruce and jack pine

Figure 2.2 Mean understory vascular plant species richness and standard error compared between harvested and burned stands. The results of the two-factor ANOVA are presented.

stands and lowest in black spruce stands ($p=0.0439$).

Percent similarities were highest in trembling aspen stands, intermediate in mixedwood and jack pine stands and lowest in black spruce stands (Figure 2.3). Burned stands were more similar to other burned stands than to harvested stands. As well, harvested stands were more similar to other harvested stands than to burned stands. Therefore, species compositions were more dissimilar between disturbance types than within disturbance types. Remember that significance could not be performed since the percent similarity calculations were not independent.

Linear discriminant analysis, based on species frequencies, detected differences in species composition between harvested and burned stands of similar pre-disturbance canopy composition (Wilks' Lambda, $p<0.05$) (Table 2.2). The discriminating species differed depending on the pre-disturbance canopy species. Using those frequencies, stands were correctly classified as harvested or burned with 100 % accuracy.

The tolerance curves show how the frequency of species change along a gradient of harvested to burned stands (Figure 2.4). The shape and position of the tolerance curve differs depending on the species and the pre-disturbance canopy composition. The species on the left represent those species with higher frequencies in harvested stands while the species on the right represent those species with higher frequencies in burned stands. Therefore, the type of disturbance selects for different species due to differences in species tolerances.

Non-native species in harvested stands did not have a higher frequency than non-native species in wildfire burned stands (Figure 2.5). The interaction between disturbance type (i.e. harvested and burned) and pre-disturbance canopy composition was not significant ($p=0.705$). The effect of pre-disturbance canopy composition was not significant either ($p=0.324$). Overall, few non-native species were detected.

Harvested stands had significantly more rare species than did burned stands (Figure 2.6). The interaction between disturbance type (i.e. harvested and burned) and pre-disturbance canopy composition was not significant ($p = 0.762$) indicating that the patterns of changes in the number of rare species with pre-disturbance canopy type are

Figure 2.3 The percent similarity of understory vascular plant species' frequencies within stands of similar pre-disturbance canopy composition calculated within a disturbance type (i.e. harvested vs harvested or burned vs burned) and between disturbance types (i.e. harvested vs burned).

Table 2.2 Understory vascular plant species that discriminate between harvested and burned stands of the same pre-disturbance canopy species. Using the discriminating species, stands can be classified as burned or harvested with a percent accuracy. Wilks' Lambda tests the significance of the discriminating function and has an associated probability.

Dominant Pre-Disturbance Canopy Species				
	Jack pine	Black spruce	Trembling Aspen	Mixedwood
Harvested Stands	<i>Carex siccata</i> Dewey <i>Elymus innovatus</i> Beal <i>Rubus idaeus</i> L.	<i>Carex siccata</i> <i>Oryzopsis pungens</i> (Torr.) A.S. Hitche.	<i>Galium boreale</i> L. <i>Rubus idaeus</i>	<i>Aster</i> sp. <i>Calamagrostis canadensis</i> (Michx.) Beauv. <i>Elymus innovatus</i> <i>Fragaria virginiana</i>
Burned Stands	<i>Campanula rotundifolia</i> L. <i>Carex aenea</i> Fern. <i>Geranium bicknellii</i> Britt. <i>Linnaea borealis</i> L. <i>Pinus banksiana</i>	<i>Dracocephalum parviflorum</i> Nutt. <i>Epilobium angustifolium</i> L.	<i>Equisetum sylvaticum</i> L.	<i>Cornus canadensis</i> L. <i>Maianthemum canadense</i> Desf.
Percent Accuracy	100	100	100	100
Wilks' Lambda	0.044	0.0016	0.014	0.093
Probability	0.0174	0.002	0.0206	0.0454
n	13	8	6	11

Figure 2.4 Tolerance curves for the majority of understory vascular plant species from the Linear Discriminant Analysis (LDA). The gradient of harvested to burned stands was constructed from the stand loadings (see methods for the calculation of the stand loadings) and the frequency of each discriminating species was plotted along this gradient. The stands along the x-axis change from harvested stands on the left to burned stands on the right with the dashed line representing the division between the two. The species presented represent the majority of the discriminating species from the LDA.

Jack Pine

Black Spruce

Trembling Aspen

White Spruce

Figure 2.5 The mean relative frequency and standard error of non-native species compared between harvested and burned stands. The two-factor ANOVA was performed on the log transformed data to satisfy the non-homogeneity of variances but the data presented is the non-transformed data.

Figure 2.6 The number and standard error of rare understory vascular plant species (frequency of 3.3% or 1/30 quadrats) in harvested and burned stands. The results of the two-factor ANOVA are also presented.

not affected by disturbance type. The effect of pre-disturbance canopy composition was not significant either ($p=0.126$). No species was consistently rare, either within a canopy type or between disturbance types.

In short, harvested stands have higher species richness, more rare species and different species composition compared with stands burned by wildfire.

DISCUSSION

The forest management goal of emulating the 'natural' (pre-European) fire regime to maintain plant species diversity implies that natural disturbance plays a significant role in determining diversity and also that forest harvesting has changed diversity because the harvesting regime is different from the pre-European fire regime. Our data indicate that following the first 11 years after harvesting, there is an increase in species richness (i.e. diversity) compared to stands burned by wildfire. Species composition also differs between harvested and burned stands.

Species richness in harvested stands is significantly higher than species richness in burned stands. This may be due to how the forest floor is disturbed. Site preparation in harvested stands such as disk trenching and anchor chain scarification expose mineral soil, thereby increasing the availability of suitable seedbeds. Regeneration and survivorship of tree (Fleming and Mossa 1995, Charron 1998) and shrub seedlings (Roberts and Dong 1993) is higher on thin duff (<5cm) or mineral soil primarily because of the reduced susceptibility to drought compared to organic matter. In addition, some of the forest floor is left relatively undisturbed, allowing species already present to continue to proliferate. In burned stands, all of the organic matter (especially litter and fermentation layers) is burned in patches by smouldering combustion (Johnson and Miyanishi in press) which kills all of the vegetation as well as a proportion of the seed bank. Therefore, it appears that species richness is higher in harvested stands because site preparation increases the availability of suitable seedbeds and yet preserves large areas of

undisturbed forest floor. Therefore, species richness in harvested stands is a product of the species that remain after disturbance and the species that regenerate in mineral soil while species richness in burned stands is only a result of the species that regenerate in the patches of mineral soil. It may be interesting to examine in more detail how the different types of site preparation techniques affect species richness. For example, since harvested trembling aspen stands are left to naturally regenerate, they may not have significantly different species richness from burned stands. However, the interaction between disturbance type and pre-disturbance canopy composition was not significant for determining species richness, suggesting that such an effect may be very small, if at all. Unfortunately, we did not have enough stands in each site preparation technique to examine this.

Species composition of the understory vascular plants also differs. This could also be a consequence of the different ways that harvesting and burning disturb the forest floor where the type of disturbance selects for different species through its effects on the seed bank, residual vegetation and the availability of suitable seedbeds. Harvesting has been shown to alter the distribution of seeds in the soil profile but not change the species richness of post-harvested seed banks (Qi and Scarratt 1998). However, depending on fire intensity, fire kills some proportion of the seed bank, the majority of which occupies the upper 2 cm of soil (Moore and Wein 1977). The abundance of *Calamagrostis canadensis* is higher in harvested stands compared with burned stands (Figure 2.4) partly because *Calamagrostis canadensis* seeds recruit poorly on burned substrates (Lieffers et al. 1993). However, it is not clear if this is due to poor germination of *Calamagrostis canadensis* seeds on ash seedbeds or because the seeds are destroyed by fire (Dyrness and Norum 1983).

Species composition in harvested and burned sites also depends on the type of residual vegetation and their life histories. For example, both *Cornus canadensis* and *Calamagrostis canadensis* have rhizomes. At the nodes of each rhizome segment, there are buds that are capable of sprouting. In *Cornus canadensis*, the buds on the rhizomes are usually dormant. However, when the main shoot is killed (e.g. by wildfire), each bud

will begin to grow (Bush 1990). Consequently, *Cornus canadensis* is more abundant in burned stands (Figure 2.4). The rhizomes of *Calamagrostis canadensis* grow into new plants when they are cut (Powelson and Lieffers 1992). The process of disk trenching is capable of severing the rhizomes. Thus, *Calamagrostis canadensis* is able to regenerate rapidly and is more abundant in harvested stands (Lieffers et al. 1993) (Figure 2.4). Stands burned by wildfire often do not see this prolific regeneration of *Calamagrostis canadensis* because *Calamagrostis canadensis* rhizomes are killed by deep burns (Ahlgren 1960, Dyrness and Norum 1983, Lieffers et al. 1993).

The type of forest floor disturbance also affects the availability of suitable seedbeds and thus the survivorship of regenerating vegetation. Wildfire results in a pattern of duff consumption similar to the spatial pattern of pre-fire canopy trees as a result of smoldering combustion around tree boles (Miyaniishi et al. 1999). Tree seedling survivorship is higher in these patches where the duff has been consumed down to thin duff (>5cm) or to mineral soil (Charron 1998). Further, a greater establishment of herbs has been observed to occur in these burned patches. Species with light seeds such as *Geranium bicknellii* and *Dracocephalum parviflorum* (Figure 2.4) are favoured by forest floor removal (such as burning) due to increased seedbed availability (Roberts and Dong 1993). Treatments such as anchor chain scarification and disk trenching increase the availability of suitable seedbeds, promoting the regeneration of species with stored viable seed such as *Rubus idaeus* (Roberts and Dong 1993) (see Figure 2.4) and *Carex* sp. (Archibold 1979). Despite these relationships, there have been few, if any, studies comparing the seed banks, residual vegetation or availability of suitable seedbeds in burned and harvested stands.

Finally, it is interesting to note that there was no significant difference in the frequency of non-native species in harvested and burned stands. The frequency of non-natives was always low. However, this is consistent with Halpern and Spies (1995) who also report that in the Pacific Northwest, exotic species contributed minimally in cover and number to post-harvest vegetation.

CONCLUSIONS

Given that this study only looked at stands younger than 11 years, it is not clear how species composition or diversity in older harvested stands would compare to species composition or diversity in older stands initiated by wildfire. Results from studies in the western Cascades and the Pacific Northwest, suggest that over time, species composition in harvested stands will become similar to species composition in stands burned by wildfire (Dymess 1973, Halpern and Spies 1995). Species richness is higher in harvested stands compared to burned stands. It appears that this is because site preparation increases the availability of suitable seedbeds and yet preserves large areas of undisturbed forest floor. This allows species already present to remain and species that use mineral soil as seedbeds to establish. In burned stands, however, smoldering combustion kills all the vegetation and a proportion of the seedbank, thereby restricting species richness. Differences in species composition may also be due to the differences in how harvesting and burning affect the forest floor (i.e., the seed bank, residual vegetation as well as the availability of suitable seedbeds).

White spruce stands have always been a problem for forest managers because of the difficulty in regenerating white spruce. This research suggests that the method of forest floor disturbance, which has largely been ignored by forest managers and conservationists, particularly in regards to understory vegetation, plays an important role in regeneration due to its effect on the seed bank, residual vegetation and the availability of suitable seedbeds. Problems with successful regeneration of white spruce due to competition from understory plants such as *Calamagrostis canadensis* (Lieffers et al. 1993, Lieffers and Stadt 1994) indicate the importance of understanding the processes that determine species composition. Stands other than white spruce also support *Calamagrostis canadensis* in the understory but are not dominated by it when the stands are harvested. Therefore, it appears that mechanical site preparation, which is needed to regenerate white spruce, is at least partly responsible for the prolific regeneration of *Calamagrostis canadensis* because of its effect on the forest floor and thus the

regeneration of rhizomes. The results of this study suggest that if the goal is to more efficiently emulate the 'natural' disturbance patterns of species diversity and composition, we still have a great deal to learn about the processes that determine plant species diversity and composition, particularly the effects of forest floor disturbance.

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THESIS CONCLUSION

The goal of emulating the 'natural' (pre-European) fire regime to preserve biodiversity implies that: 1) fire is the principle determinant of species diversity, 2) the variation in the forest harvesting regime is different from the variation in the 'natural' disturbance (fire) cycle and therefore 3) harvesting has changed species diversity. This study has resolved these common misconceptions with respect to understory vascular plant biodiversity in the boreal forest. First, the moisture and nutrient gradient is the primary determinant of species diversity (richness) and not time-since-fire. This is not surprising. Forest managers have always been aware of the importance of moisture and nutrient gradients because of their relationship with site productivity. In addition, there is an array of literature relating vegetation composition to moisture and nutrient gradients (e.g. Day Jr. and Monk 1974, Whittaker and Niering 1975, Marks and Harcombe 1981, Roberts and Christensen 1988, Host and Pregitzer 1992).

Second, harvesting has changed species diversity compared to burned stands. The fire cycle is variable and therefore, it is unlikely that the harvesting regime exists outside the variation in the 'natural' disturbance regime. However, fire frequency is only one aspect of the 'natural' (pre-European) disturbance regime. This research suggests that the type of forest floor disturbance plays an important role in regenerating understory vascular plant species diversity and composition due to its effect on the seed bank, residual vegetation and the availability of suitable seedbeds. For example, competition from understory plants such as *Calamagrostis canadensis* may interfere with the successful regeneration of white spruce. This indicates the importance of understanding the processes that determine species composition.

Finally, the results of this study suggest that if the goal is to emulate the 'natural' (pre-European) fire regime to preserve the 'natural' patterns of species diversity and vegetation composition, we still have a great deal to learn about the processes that determine plant species diversity and composition, particularly the effects of forest floor disturbance.