

**Landscape-Level Vegetation Dynamics in Riding Mountain National Park,  
Manitoba, Canada**

by  
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A thesis presented to the University of Manitoba in partial fulfillment of the requirements  
for the degree of Master of Science in the Faculty of Graduate Studies

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**LANDSCAPE-LEVEL VEGETATION DYNAMICS IN RIDING MOUNTAIN NATIONAL  
PARK, MANITOBA, CANADA**

**BY**

**RICHARD CANERS**

**A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University of**

**Manitoba in partial fulfillment of the requirement of the degree**

**of**

**MASTER OF SCIENCE**

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## ABSTRACT

The complex physiography and disturbance history of Riding Mountain National Park have resulted in a complex assemblage of aspen parkland, eastern deciduous and boreal forest communities on the landscape. Few studies have examined forest composition, structure and dynamics in the eastern extension of the mixedwood forest region.

This study uses detailed vegetation, edaphic and environmental data collected from 202-100 m<sup>2</sup> forest plots distributed throughout the Park to elucidate landscape-level trends in forest structure and dynamics. Stands were first classified into 8 dominant stand types, and described in terms of their biotic and abiotic characteristics. Factors affecting patterns of understory tree regeneration and the timing of their recruitment were examined on the landscape, and growth of understory green ash (*Fraxinus pennsylvanica* Marsh.) and white spruce (*Picea glauca* (Moench) Voss) were analyzed in different habitats to infer future changes in stand composition. Successional trajectories were created for each of the 8 stand types using a static size-class analysis of tree species, and a comprehensive conceptual model of stand dynamics was created. Sections of this thesis have previously been published in Caners & Kenkel (1998).

Results indicate that successional trajectories for stand types in the Park do not converge towards a single self-perpetuating 'climax' community. Instead, vectors diverge, converge and remain cyclical, with multiple potential pathways recognized for each stand type. This study demonstrates that species assemblages, and the propensity for change, are governed by the cumulative and synergistic effects of climate, topography, disturbance frequency, size and intensity, edaphic conditions and the proximity of parental seed sources. These factors have resulted in a patchwork mosaic of forest stands on the landscape of varying structure, composition and seral stage.

Overall, results are in general agreement with studies from central and eastern regions of the boreal forest. Post-fire stands are dominated by pioneering hardwoods such as aspen, balsam poplar and paper birch. Mid-succession stands show an increasingly greater proportion of white spruce in the canopy, whereas late-succession stands are dominated by white spruce and balsam fir and are driven by gap dynamic processes. The oldest stands are commonly open and shrub-dominated, especially by beaked hazelnut and mountain maple. In areas of dense shrub cover and/or areas without a proximate seed source, regeneration of tree species is dramatically reduced. Ungulate herbivores selectively browse trees and shrubs, impacting the long-term dynamics of forest systems.



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## LIST OF FIGURES

<b>Fig 2.1.</b> The location of Riding Mountain National Park in relation to surrounding vegetation regions. ....	66
<b>Fig 2.2.</b> Total precipitation (June – Sept.; mm) and maximum July temperature (°C) in relation to elevational changes along the Manitoba Escarpment. ....	67
<b>Fig 3.1.</b> Location of plots sampled within Riding Mountain National Park between 1996-1997 for stand types I-VIII. ....	102
<b>Fig 3.2.</b> Height ranges for each tree canopy, and quadrat design. ....	104
<b>Fig 3.3 a-d.</b> Residual correspondence analysis ordinations of $n=196$ (a), $n=164$ (b), $n=133$ (c), and $n=115$ (d) sampled stands. ....	105
<b>Fig 3.4.</b> Minimum stand age frequency histograms for each of the eight stand types I-VIII. ....	107
<b>Fig 3.5 a-h.</b> Canonical correspondence analysis biplots of environmental variables (a), trees (b), shrubs (c), herbs (d), graminoids (e), ferns and fern allies (f), bryophytes (g), and plots (h) for $n=179$ stands and 6 environmental variables, utilizing $n=171$ species. ....	108
<b>Fig 4.1.</b> Measurement of ring widths for green ash ( <i>Fraxinus pennsylvanica</i> Marsh.). ....	160
<b>Fig 4.2.</b> Calculation of mean annual incremental radial growth ( $\text{mm} \cdot \text{yr}^{-1}$ ) for green ash. ....	160
<b>Fig 4.3.</b> Multiple discriminant analysis of 3 groups using $n=75$ stands and $p=14$ variables. ....	161
<b>Fig 4.4.</b> Mean density and height class of tree species for $n=7$ aspen-dominated boreal forest and $n=3$ mixed eastern deciduous forest stands from which understory green ash were sampled. ....	162
<b>Fig 4.5.</b> Age (years), basal diameter (cm) and height (m) relationships for $n=44$ understory (<10 m in height) green ash sampled from $n=7$ aspen-dominated boreal forest stands and $n=3$ mixed eastern deciduous stands. ....	163
<b>Fig 4.6.</b> Age of $n=44$ understory (<10 m in height) green ash in relation to the minimum age of the stand (years) from which they were sampled. ....	164
<b>Fig 4.7.</b> Comparison of incremental radial growth ( $\text{mm} \cdot \text{yr}^{-1}$ ) for $n=21$ harvested understory green ash from $n=7$ aspen-dominated boreal stands, as well as $n=8$ canopy green ash from $n=3$ mixed eastern deciduous stands and $n=14$ understory green ash from the same $n=3$ mixed eastern deciduous stands. ....	165

<b>Fig 4.8.</b> Mean incremental radial growth ( $\text{mm} \cdot \text{yr}^{-1}$ ) for understory and canopy green ash sampled from $n=7$ aspen-dominated boreal and $n=3$ mixed eastern deciduous stands. ....	166
<b>Fig 4.9.</b> The effects of Dutch elm disease on two mixed eastern deciduous forest canopies. ....	167
<b>Fig 5.1.</b> Measurement of ring widths for white spruce ( <i>Picea glauca</i> (Moench) Voss). ....	185
<b>Fig 5.2.</b> Calculation of mean annual incremental radial growth ( $\text{mm} \cdot \text{yr}^{-1}$ ) for white spruce. ....	185
<b>Fig 5.3.</b> Specimen age (years) against square root of height for $n=67$ harvested understory (<10 m in height) white spruce. ....	186
<b>Fig 5.4.</b> Multiple discriminant analysis of 4 groups using $n=119$ stands and $p=14$ variables. ....	187
<b>Fig 5.5.</b> Age of $n=92$ understory (<10 m in height) white spruce in relation to the minimum age of the stand (years) from which they were sampled. ....	188
<b>Fig 5.6.</b> Principal components analysis of $n=67$ understory white spruce using 5 variables. Individuals in the ordination space are highlighted according to the type of canopy beneath which they were sampled (coniferous, $n=24$ ; mixed-coniferous, $n=20$ ; and deciduous, $n=23$ ). ....	189
<b>Fig 5.7.</b> Principal components axis 1 scores against incremental radial growth ( $\text{mm} \cdot \text{yr}^{-1}$ ) and residual height for the $n=67$ sampled white spruce. ....	190
<b>Fig 5.8.</b> Mean incremental radius (mm) for the last 5 years of growth for white spruce belonging to coniferous, mixed-coniferous and deciduous forest stands. Coniferous stands have been divided into open canopy (gap present) and closed canopy (no gap present). ....	191
<b>Fig 5.9.</b> Incremental radius (mm) for understory white spruce sampled from coniferous, mixed-coniferous and deciduous forest stands. Coniferous stands have been divided into open canopy (gap present) or closed canopy (no gap present). ....	192
<b>Fig 5.10.</b> Boxplots of incremental radial growth ( $\text{mm} \cdot \text{yr}^{-1}$ ) for white spruce belonging to closed-coniferous ( $n=16$ ), coniferous-gap ( $n=8$ ), mixed-coniferous ( $n=20$ ) and deciduous ( $n=23$ ) stand types. ....	193
<b>Fig 5.11.</b> Boxplots of residual height for white spruce belonging to closed-coniferous ( $n=16$ ), coniferous-gap ( $n=8$ ), mixed-coniferous ( $n=20$ ) and deciduous ( $n=23$ ) stand types. ....	193
<b>Fig 5.12.</b> A model of mean incremental radial growth ( $\text{mm} \cdot \text{yr}^{-1}$ ) and residual height along a continuum of canopy types. ....	194

<b>Fig 6.1 a,b.</b> Timing of recruitment for 9 dominant boreal (a) and eastern deciduous (b) tree species sampled throughout the Park. ....	228
<b>Fig 6.2.</b> Canonical correspondence analyses of understory regeneration abundance for 9 dominant tree species using $n=154$ stands and 3 variable sets. ....	230
<b>Fig 6.3 a,b.</b> Correspondence analysis ordination of stand types I-VIII (a) and IV-VIII (b) by three tree strata for 12 boreal and eastern deciduous tree species. ....	231
<b>Fig 6.4.</b> A synoptic forest succession model for Riding Mountain National Park. ....	233

## LIST OF TABLES

<b>Table 3.1.</b> Mean, range and standard deviation of edaphic and environmental variables measured for each of the eight stand types I-VIII. ....	114
<b>Table 3.2.</b> Frequency of soil types for stands sampled during the second field season. ....	115
<b>Table 3.3.</b> Minimum stand ages (mean, range and standard deviation) by stand type, for all stands. ....	116
<b>Table 3.4.</b> Effective species richness (calculated using Simpson's Index) and standard deviation for various plant canopies for stand types I-VIII. ....	117
<b>Table 3.5.</b> Stand type I (Black Spruce Organic $n=15$ ) - Relative frequency, mean density per plot and mean basal area ( $m^2$ ) per plot. ....	118
<b>Table 3.6.</b> Stand type I (Black Spruce Organic $n=15$ ) - Frequency, mean cover and variance of tree species. ....	119
<b>Table 3.7.</b> Stand type I (Black Spruce Organic $n=15$ ) - Frequency, mean cover and variance of common shrubs ( $f>0.1$ ). ....	119
<b>Table 3.8.</b> Stand type I (Black Spruce Organic $n=15$ ) - Frequency, mean cover and variance of common herb, fern and fern-ally taxa ( $f>0.1$ ). ....	120
<b>Table 3.9.</b> Stand type I (Black Spruce Organic $n=15$ ) - Frequency, mean cover and variance of common bryophyte and lichen taxa ( $f>0.1$ ). ....	121
<b>Table 3.10.</b> Stand type II (Jack Pine - Black Spruce $n=17$ ) - Relative frequency, mean density per plot and mean basal area ( $m^2$ ) per plot. ....	122
<b>Table 3.11.</b> Stand type II (Jack Pine - Black Spruce $n=17$ ) - Frequency, mean cover and variance of tree species. ....	123
<b>Table 3.12.</b> Stand type II (Jack Pine - Black Spruce $n=17$ ) - Frequency, mean cover and variance of common shrubs ( $f>0.1$ ). ....	123
<b>Table 3.13.</b> Stand type II (Jack Pine - Black Spruce $n=17$ ) - Frequency, mean cover and variance of common herb, fern and fern-ally taxa ( $f>0.1$ ). ....	124
<b>Table 3.14.</b> Stand type II (Jack Pine - Black Spruce $n=17$ ) - Frequency, mean cover and variance of common bryophyte and lichen taxa ( $f>0.1$ ). ....	125
<b>Table 3.15.</b> Stand type III (Bur Oak $n=15$ ) - Relative frequency, mean density per plot and mean basal area ( $m^2$ ) per plot. ....	126
<b>Table 3.16.</b> Stand type III (Bur Oak $n=15$ ) - Frequency, mean cover and variance of tree species. ....	127

<b>Table 3.17.</b> Stand type III (Bur Oak $n=15$ ) - Frequency, mean cover and variance of common shrubs ( $f>0.1$ ). .....	127
<b>Table 3.18.</b> Stand type III (Bur Oak $n=15$ ) - Frequency, mean cover and variance of common herb, fern and fern-ally taxa ( $f>0.1$ ). .....	128
<b>Table 3.19.</b> Stand type III (Bur Oak $n=15$ ) - Frequency, mean cover and variance of common bryophyte and lichen taxa ( $f>0.1$ ). .....	128
<b>Table 3.20.</b> Stand type IV (Eastern Deciduous $n=16$ ) - Relative frequency, mean density per plot and mean basal area ( $m^2$ ) per plot. ....	129
<b>Table 3.21.</b> Stand type IV (Eastern Deciduous $n=16$ ) - Frequency, mean cover and variance of tree species. ....	130
<b>Table 3.22.</b> Stand type IV (Eastern Deciduous $n=16$ ) - Frequency, mean cover and variance of common shrubs ( $f>0.1$ ). ....	130
<b>Table 3.23.</b> Stand type IV (Eastern Deciduous $n=16$ ) - Frequency, mean cover and variance of common herb, fern and fern-ally taxa ( $f>0.1$ ). ....	131
<b>Table 3.24.</b> Stand type IV (Eastern Deciduous $n=16$ ) - Frequency, mean cover and variance of common bryophyte and lichen taxa. ....	132
<b>Table 3.25.</b> Stand type V (Balsam Fir $n=18$ ) - Relative frequency, mean density per plot and mean basal area ( $m^2$ ) per plot. ....	133
<b>Table 3.26.</b> Stand type V (Balsam Fir $n=18$ ) - Frequency, mean cover and variance of tree species. ....	134
<b>Table 3.27.</b> Stand type V (Balsam Fir $n=18$ ) - Frequency, mean cover and variance of common shrubs ( $f>0.1$ ). ....	134
<b>Table 3.28.</b> Stand type V (Balsam Fir $n=18$ ) - Frequency, mean cover and variance of common herb, fern and fern-ally taxa ( $f>0.1$ ). ....	135
<b>Table 3.29.</b> Stand type V (Balsam Fir $n=18$ ) - Frequency, mean cover and variance of common bryophyte and lichen taxa ( $f>0.1$ ). ....	136
<b>Table 3.30.</b> Stand type VI (Trembling Aspen - Birch - Mountain Maple $n=22$ ) - Relative frequency, mean density per plot and mean basal area ( $m^2$ ) per plot. ....	137
<b>Table 3.31.</b> Stand type VI (Trembling Aspen - Birch - Mountain Maple $n=22$ ) - Frequency, mean cover and variance of tree species. ....	138
<b>Table 3.32.</b> Stand type VI (Trembling Aspen - Birch - Mountain Maple $n=22$ ) - Frequency, mean cover and variance of common shrubs ( $f>0.1$ ). ....	138

<b>Table 3.33.</b> Stand type VI (Trembling Aspen - Birch - Mountain Maple $n=22$ ) - Frequency, mean cover and variance of common herb, fern and fern-ally taxa ( $f>0.1$ ). .....	139
<b>Table 3.34.</b> Stand type VI (Trembling Aspen - Birch - Mountain Maple $n=22$ ) - Frequency, mean cover and variance of common bryophyte and lichen taxa. ....	140
<b>Table 3.35.</b> Stand type VII (Trembling Aspen - Balsam Poplar $n=46$ ) - Relative frequency, mean density per plot and mean basal area ( $m^2$ ) per plot. ....	141
<b>Table 3.36.</b> Stand type VII (Trembling Aspen - Balsam Poplar $n=46$ ) - Frequency, mean cover and variance of tree species. ....	142
<b>Table 3.37.</b> Stand type VII (Trembling Aspen - Balsam Poplar $n=46$ ) - Frequency, mean cover and variance of common shrubs ( $f>0.1$ ). ....	142
<b>Table 3.38.</b> Stand type VII (Trembling Aspen - Balsam Poplar $n=46$ ) - Frequency, mean cover and variance of common herb, fern and fern-ally taxa ( $f>0.1$ ). ....	143
<b>Table 3.39.</b> Stand type VII (Trembling Aspen - Balsam Poplar $n=46$ ) - Frequency, mean cover and variance of common bryophyte and lichen taxa. ....	144
<b>Table 3.40.</b> Stand type VIII (White Spruce $n=47$ ) - Relative frequency, mean density per plot and mean basal area ( $m^2$ ) per plot. ....	145
<b>Table 3.41.</b> Stand type VIII (White Spruce $n=47$ ) - Frequency, mean cover and variance of tree species. ....	146
<b>Table 3.42.</b> Stand type VIII (White Spruce $n=47$ ) - Frequency, mean cover and variance of common shrubs ( $f>0.1$ ). ....	146
<b>Table 3.43.</b> Stand type VIII (White Spruce $n=47$ ) - Frequency, mean cover and variance of common herb, fern and fern-ally taxa ( $f>0.1$ ). ....	147
<b>Table 3.44.</b> Stand type VIII (White Spruce $n=47$ ) - Frequency, mean cover and variance of common bryophyte and lichen taxa ( $f>0.1$ ). ....	148
<b>Table 4.1.</b> Means and standard deviations for $n=14$ variables used to discriminate between 3 groups of forest stands. ....	168
<b>Table 5.1.</b> Means and standard deviations for $n=14$ variables used to discriminate between 4 groups of forest stands. ....	195
<b>Table 6.1.</b> The relative propensity for 9 boreal and eastern deciduous tree species to a) establish in sites without conspecific adult canopy trees and to b) establish in sites with conspecific adult canopy trees. ....	234

**LIST OF APPENDICES**

**APPENDIX 1.** A list of all vascular and non-vascular plant species enumerated in Riding Mountain National Park. ....256

**APPENDIX 2.** Selected photographs of field observations. ....262



## TABLE OF CONTENTS

<b>ABSTRACT</b> .....	i
<b>ACKNOWLEDGEMENTS</b> .....	ii
<b>LIST OF FIGURES</b> .....	iii
<b>LIST OF TABLES</b> .....	vi
<b>LIST OF APPENDICES</b> .....	ix
<b>TABLE OF CONTENTS</b> .....	x
<b>CHAPTER 1 - Literature Review</b> .....	1
<b>1.1 The North American Boreal Forest</b>	1
1.1.1 Introduction	1
1.1.2 Climate	2
1.1.3 Quaternary Ecology	3
1.1.4 Landscape and Landform	6
1.1.5 Edaphic Factors	8
1.1.6 Studies of the Boreal Forest Ecosystem	8
<b>1.2 Disturbance</b>	9
1.2.1 Introduction	9
1.2.2 Fire	9
1.2.3 Herbivory	18
1.2.4 Gap Dynamics	21
1.2.5 Human Activity	22
<b>1.3 Succession And Vegetation Dynamics</b>	24
1.3.1 Introduction	24
1.3.2 A Chronological Review of Forest Succession Theory	24
1.3.3 Studies on Boreal Forest Succession	28
1.3.4 Methods for Studying Boreal Forest Succession	35
<b>CHAPTER 2 - Riding Mountain National Park</b> .....	39
<b>2.1 Introduction</b>	39
<b>2.2 Climate</b>	39
<b>2.3 Quaternary Ecology: Post-Glacial Development of the Flora</b>	40
<b>2.4 Landscape and Landform</b>	41
<b>2.5 Disturbance</b>	42
<b>2.6 Ecology of Major Tree Species in Riding Mountain National Park</b>	47

<b>CHAPTER 3 - Classification and Description of Forest Stands</b> .....	68
<b>3.1 Introduction</b>	68
<b>3.2 Methods</b>	69
3.2.1 Data Collection	69
3.2.2 Data Analysis: Methods	71
<b>3.3 Results and Discussion</b>	75
3.3.1 Classification of Stand Types	75
3.3.2 Stand Type Characteristics	76
3.3.3 Vegetation-Environment Relationships	77
3.3.4 Description of Stand Types	79
<b>3.4 Conclusion</b>	100
<b>CHAPTER 4 - Growth Response of Green Ash (<i>Fraxinus pennsylvanica</i> Marsh.) in Boreal and Mixed Eastern Deciduous Forest Communities</b> .....	149
<b>4.1 Introduction</b>	149
<b>4.2 Methods</b>	151
4.2.1 Data Collection	151
4.2.2 Data Analysis	152
<b>4.3 Results</b>	153
4.3.1 Landscape-Level Patterns of Green Ash Regeneration	153
4.3.2 Growth of Green Ash in Two Communities	154
<b>4.4 Discussion</b>	155
<b>CHAPTER 5 - Growth Response of White Spruce (<i>Picea glauca</i> (Moench) Voss) Across a Broad Range of Habitat Conditions</b> .....	169
<b>5.1 Introduction</b>	169
<b>5.2 Methods</b>	171
5.2.1 Data Collection	171
5.2.2 Data Analysis	173
<b>5.3 Results</b>	175
5.3.1 Landscape-Level Patterns of White Spruce Regeneration	175
5.3.2 Growth of White Spruce Under Various Habitat Conditions	176
<b>5.4 Discussion</b>	178
5.4.1 Patterns of White Spruce Regeneration on the Landscape	178
5.4.2 Growth of White Spruce Under Various Habitat Conditions	180
5.4.3 Implications on Stand Dynamics	183

<b>CHAPTER 6 - Stand Dynamics</b> .....	196
<b>6.1 Introduction</b>	196
6.1.1 Background	196
6.1.2 Patterns of Natural Regeneration on the Landscape	198
<b>6.2 Methods</b>	200
6.2.1 Data Collection	200
6.2.2 Data Analysis	201
<b>6.3 Results</b>	204
6.3.1 Patterns of Natural Regeneration on the Landscape	204
6.3.2 Ranking the Dispersal and Regeneration of Tree Species	205
6.3.3 Succession Trajectories	206
6.3.4 Landscape Model of Stand Dynamics	213
<b>6.4 Discussion</b>	214
6.4.1 Patterns of Natural Regeneration on the Landscape	214
6.4.2 Ranking the Dispersal and Regeneration of Tree Species	217
6.4.3 Succession Trajectories	220
6.4.4 Landscape Model of Stand Dynamics	222
<b>6.5 A Summary of Disturbance and Stand Dynamics</b>	224
<b>6.6 Management Considerations and Implications</b>	226
<b>LITERATURE CITED</b> .....	235
<b>APPENDICES</b> .....	256

## CHAPTER 1 LITERATURE REVIEW

### 1.1 The North American Boreal Forest

#### 1.1.1 Introduction

The boreal forest is circumpolar in extent, covering approximately  $12 \times 10^6$  km<sup>2</sup> of northern North America and Eurasia (Payette 1992). The North American segment, which constitutes a well-delineated biome both geographically and ecologically, stretches in a broad transcontinental belt from Newfoundland across central and northern Canada to Alaska (Rowe & Scotter 1973). In Canada, the boreal forest spans over 10° of latitude in the east and west (Payette 1992). It is approximately 800 km wide in the eastern and central portions of Canada, being somewhat more contracted south of Hudson Bay and in Alaska (Payette 1992). The constriction is about 240 km wide south of Hudson Bay, and is likely the result of summer cooling from Hudson Bay and amelioration of winter temperatures from the Great Lakes (Carleton & Maycock 1980). The boreal forests of central Canada are geologically young, having developed over the past ca. 10,000 years (Ritchie & Yarranton 1978a).

At the continental scale, the boreal forest has been described as “floristically depauperate” (Oechel & Lawrence 1985), with only nine tree species dominating regionally or throughout the range (Payette 1992). It is primarily a “coniferous forest, mossy-floored or with low herbs and shrubs, interspersed with extensive lakes and organic terrain” (Rowe & Scotter 1973). The southern limit of the boreal forest is not as sharply defined as the forest-tundra ecotone in the north (Larsen 1980). East of Manitoba, the southern limit of the forest forms a broad tension zone with deciduous forest, while in the Prairie Provinces the southern edge borders the aspen parkland region which separates it from grassland (Swan & Dix 1966). Canadian boreal forests are a valuable economic and sociologic resource (Hall 1995).

There are three commonly recognized vegetation zones in the Canadian boreal forest. From south to north these are the closed-crown forest, open-crown forest or lichen woodland, and forest-tundra (Rowe 1972; Rowe & Scotter 1973; Payette 1992). Several dominant tree species comprise these zones. Balsam fir (*Abies balsamea* (L.) Mill) is dominant on well-drained sites in eastern Canada, and diminishes in abundance in the central and western regions (Rowe & Scotter 1973). White spruce (*Picea glauca* (Moench) Voss) becomes more abundant in central and western Canada (Rowe & Scotter 1973), although it has a transcontinental range (Nienstaedt & Zasada 1990; Payette 1992). Black spruce (*Picea mariana* (Mill.) B.S.P.) ranges in a broad,

transcontinental band from northern Massachusetts to northern Labrador on the Atlantic coast, to the west coast of Alaska (Viereck & Johnston 1990). Northward the boreal forest is increasingly dominated by black spruce, as fire frequency and the occurrence of peaty or shallow, cold substrates increase (Rowe & Scotter 1973). Eastern larch (*Larix laricina* (Du Roi) K. Koch) has the widest range of North American conifers (Johnston 1990), extending from the Atlantic coast to the northern Yukon Territory and across the Continental Divide, in a fairly broad band across Canada and northeastern United States (Johnston 1990). Eastern larch has a predominantly central and eastern distribution (Payette 1992). Jack pine (*Pinus banksiana* Lamb.) is most abundant in Ontario and is typically present on dry, sandy sites (Rudolph & Laidly 1990). The species is widely but not continuously distributed within its range. In the northwestern Cordilleran region (Alberta foothills, northern British Columbia and the Yukon territory) lodgepole pine (*Pinus contorta* Dougl. var *latifolia* Engelm.) and alpine fir (*Abies lasiocarpa* (Hook.) Endl.) replace jack pine and balsam fir, respectively. The most abundant deciduous tree species in the boreal forest are trembling aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marsh.), and balsam poplar (*Populus balsamifera* L.), which are all distributed throughout the biome (Payette 1992). This literature review places emphasis on the Interior Plains Region of the boreal forest.

### 1.1.2 Climate

Considerable variation in climatic conditions is encountered across the continental range of boreal forest in Canada (Payette 1992). Canada has cold temperatures due to the influence of its physiography on air movements, specifically the north-south alignment of the Cordillera in the west combined with the vast plains of modest relief to the east (Smith 1989). East of the Cordillera, the annual temperature cycle is not tempered by air mass exchanges with the ocean, which subjects the region to extreme continental conditions (Smith 1989). The Canadian Interior Plains are under the influence of Polar continental air for most of the year, with the exceptions of warm, down-slope-flowing Pacific air in southern Alberta and southwest Saskatchewan, precipitation from Pacific air in northern Alberta, and random incursions of warm and moist tropical air from the Gulf of Mexico in southeastern Manitoba (Klassen 1989). Such air masses contribute to the distinct seasonality, as well as storminess and changeability of the region (Smith 1989).

The Interior Plains receive less precipitation than the Pacific coast as a result of the rainshadow effects of the Cordillera, and the northern regions of the boreal forest receive less precipitation than the southern regions as a result of colder air and the infrequency of atmospheric disturbances (Smith 1989). Mean annual temperatures decrease as one moves inward from the Pacific and Atlantic coasts, and from south to north. From the Pacific coast to central Canada winter severity and seasonality increase. The frost-free period is typically >200 days on the west coast, but is only about 120 days in interior continental regions (Smith 1989). Forest fire intensity and frequency are largely controlled by climatic factors, especially air temperature and precipitation (Johnson 1992).

The influence of climate on the boreal forest is “all-pervasive” (Larsen 1980). The southern limit of the boreal forest occurs along the July 18°C isotherm which is the mean winter location of the arctic front (Oechel & Lawrence 1985). Lenihan (1993) suggests that the dominance and distribution of major boreal tree species can be determined using predictor variables related to precipitation and air temperature. The geographic distribution of boreal forest types in relation to seasonal airmass dynamics suggests that species assemblages are also primarily controlled by climate (Lenihan 1993; Hogg 1994). However, a shift in the relative dominance of trembling aspen and jack pine across a distinct boundary of substrate types in Canada's central interior may be an exception to the general principle of broad-scale climatic control (Lenihan 1993). Increasingly harsh environments are encountered in central Canada from prairie to tundra edge, resulting in a decline in broad-leaved deciduous trees and a corresponding increase in conifers, a more open canopy and decreased tree heights (Rowe & Scotter 1973).

### 1.1.3 Quaternary Ecology

#### *Late Stages of the Wisconsin Glaciation*

The boreal forests of Canada are geologically young and constitute an ever-changing biome (Payette 1992). Over 95% of Canada's land mass was covered by ice during the Late Wisconsin (ca. 23,000-10,000 yr BP), the last major glacial advance of the Pleistocene epoch (ca. 1.5M-10,000 yr BP). The entire glacier complex consisted of a large Laurentide Sheet that covered the interior mainland of Canada and extended into the United States, an Appalachian glacier complex that included several coalescent ice caps in the Maritime Provinces, a Cordilleran glacier complex that covered the mountains from the Coastal Range to the Rocky Mountains, and a Queen

Elizabeth Islands glacier complex that covered parts of the Arctic. The Laurentide Sheet has been subdivided into the Keewatin and Labradorean sectors (Ritchie 1985).

The Cypress Hills and adjacent areas of southern Saskatchewan and southern Alberta and large areas of the northern Yukon and adjacent Northwest Territories were ice-free at the maximum extent of the Late Wisconsin glaciation (ca. 18,000 yr BP) (Ritchie 1987). In addition, all of lowland Alaska and a large part of the central United States remained free of glaciers. The maximum extent of the Laurentide Ice Sheet reached their termini at various times between 19,000-21,500 yr BP (Ritchie 1987).

A warmer climate near the start of the Holocene epoch (ca. 12,000 yr BP to present) resulted in the initiation of glacial retreat. Ice retreat was not uniform, having local asynchronous advances and recessions at the ice front position (Ritchie 1987). The boreal forests of Alaska and western Canada developed during the early Holocene, whereas eastern forests are much younger (4,000-8,000 years old) as a result of later glacial retreat (Payette 1992). Parts of southern Newfoundland, southern Ontario, southern Alberta, and the far northwest of Northwest Territories and the Yukon were already ice-free between 12,000 and 13,000 yr BP (Ritchie 1987). By 10,000 yr BP the ice margin was approximately coincident with the southern limit of the Canadian Shield, and several large proglacial lakes were forming in the Interior Lowlands all along the margin of the Laurentide Ice Sheet, near Great Bear Lake, Great Slave Lake, the Peace and Athabasca rivers in central Manitoba and Saskatchewan, and in Ontario and Québec. Thick beds of sediment were deposited in these proglacial lakes to form flat or gently undulating surfaces (Ritchie 1987).

Lake Agassiz was the largest of all the glacial lakes in North America, covering an area of approximately 950,000 km<sup>2</sup> in North Dakota, Minnesota, Saskatchewan, Manitoba and Ontario (although not all regions at the same time) (Trenhaile 1990). Lake Agassiz began to form ca. 11,700 years BP, as meltwater from the retreating Keewatin and Labradorean Sectors of the Laurentide Ice Sheet was impounded between the ice margins and the Manitoba Escarpment. The lake disappeared between ca. 7,800 and 8,000 years BP, when the disintegration of the ice sheet allowed it to drain into Hudson Bay, leaving behind Lakes Manitoba, Winnipeg, Dauphin and Winnipegosis as remnants (Trenhaile 1990).

## *Post-Glacial Development of the Boreal Flora*

Several authors have examined changes in the distribution and abundance of plant species during the climatic and landscape alterations of the Holocene in central and western Canada (Ritchie & Yarranton 1978a,b; Ritchie 1985, 1987, 1989; Anderson et al. 1989; Matthews & Anderson 1989). Several factors are responsible for the variability in the long-term patterns and processes of western Canada's boreal forests (Ritchie 1987). These include time since deglaciation, regional landscape variability, availability and dispersal capability of boreal tree populations, and the proximity of sites to ecotones (e.g. tundra-woodland; forest-grassland). However, climatic change alone cannot explain the migration of the boreal forest over time, since the composition and abundance of plant species vary along environmental gradients (Ritchie 1987).

The sequence and chronology of glacial recession are of interest because they set out the spatial and temporal framework for revegetation processes (Ritchie 1987). The waning and eventual disappearance of glaciers that covered continental Canada and the adjacent US during the latest glacial epoch exposed a vast landscape for plant re-occupancy (Ritchie & MacDonald 1986). Plant recolonization during glacial retreat was dependent upon the physiological tolerances and reproductive capabilities of the vegetation (Oechel & Lawrence 1985). Pollen-stratigraphic and macrofossil evidence suggest that a spruce-dominated boreal forest lacking pine and birch existed in the Western Interior of Canada ca. 10,000-12,000 years ago (Ritchie & Yarranton 1978b). Although there were remains of stagnant ice in the area, this forest occupied a large portion of the land surface exposed by the receding glaciers and glacial lakes. The present boreal forests of the Western Interior are the result of different "post-glacial modifications and adjustments of this primeval, late-glacial spruce forest" (Ritchie & Yarranton 1978a).

The southern fringe of the boreal forest in western Canada provides evidence that the prairie zone once extended farther north in the mid-Holocene, and that the modern boreal forest at particular sites (e.g. Riding Mountain National Park, Manitoba) has a comparatively short history (Ritchie 1987). The early spruce forests of Alberta, Saskatchewan, Manitoba and Ontario west of Lake Superior were replaced by prairie grassland and parkland ca. 10,000 years ago and slightly later to the north (Anderson et al. 1989). This replacement was the result of warmer, drier climatic conditions that existed between ca. 8,000-6,000 years ago, increasing fire frequency (Anderson et al. 1989). These conditions also favoured the incursion of jack pine into northern Manitoba and influenced the distribution of flora and fauna in Alberta (Anderson et al. 1989).



These events correspond with the beginning of the warmer and drier Hypsithermal, which lasted from ca. 10,000-4,500 yr BP (Ritchie 1987).

Cooler and moister climatic conditions between ca. 4,500-2,000 years before present resulted in a southern shift of the boreal forest, and a replacement of prairie grassland by *Picea*, *Pinus*, *Betula*, *Quercus* and *Alnus* stands. Most boreal tree species ceased their northward migration a few thousand years ago in response to cooler climatic conditions (Payette 1992). Ritchie (1985) indicates that there is no evidence to suggest a southward expansion of the boreal forest over the past 2000 years.

Ritchie & MacDonald (1986) suggest that modern populations of white spruce were derived from a full-glacial refugial population which occurred in a wide belt of the US between 45 and 35°N latitude. According to pollen and macrofossil records, the post-glacial spread of white spruce was a more or less continuous, time-transgressive process in eastern and central Canada. However, the spread of white spruce populations along the length of the Western Interior 'corridor' (ca. 9 000 years ago) was exceptionally rapid. Ritchie & MacDonald (1986) suggest that at this time the glacial ice mass generated frequent adiabatic winds in winter, causing a strong down-ice flow and producing southeasterly winds along the ice front margin. These winds, together with water transport and a flat, open landscape, facilitated the rapid northwestern dispersal of white spruce seed.

Until they were nearly exterminated in the 1870s, bison (*Bison bison* L.) may have contributed to the suppression of trembling aspen in the aspen parkland region of the prairies (Campbell 1994). The Canadian prairies supported a population of roughly 75 million bison, which browsed trembling aspen saplings, wallowed, and trampled grassland, and toppled mature aspen by rubbing against them. Pollen records from Saskatchewan and Alberta indicate that expansion of trembling aspen occurred following bison extirpation, but prior to widespread European settlement.

#### 1.1.4 Landscape and Landform

##### *Landform*

Landform (defined as parent materials and surficial topography) controls local patterns of insolation and drainage, and strongly influences the direction of soil development and species establishment and growth (Host et al. 1987). Landform is an important factor in the distribution,

abundance, and regeneration dynamics of boreal forest species (Kenkel & Watson 1996). Physiography and microrelief influence water movement and soil leaching potential (Fuller & Anderson 1993). Host et al. (1987) found that patterns of vegetation change in the forests of northwestern Lower Michigan were related to topographic and edaphic differences of various glacial landforms. Physiography dramatically influences fire by controlling surface moisture (Rowe & Scotter 1973). Convex surfaces shed water and dry swiftly and are therefore more prone to burning. Dry, south-facing forest stands are more susceptible to burning than are moister, north-facing stands (Rowe & Scotter 1973).

### *Bedrock and Glacial Deposits*

Bedrock and the composition of glacial deposits have greatly influenced topographic and soil development in the boreal forest ecoregion (Klassen 1989). Cretaceous rocks occur throughout the southern regions of the Interior Plains of Canada, except for incursions of Paleozoic rock (mostly limestone, as well as dolomite, sandstone and shale) along the edge of the Precambrian Shield. Cretaceous rocks typically consist of shales and siltstones deposited by shallow seas, which combine with deltaic and fluvial siltstone and sandstone as one moves westward. Lower Tertiary deposits are found in the southern and western parts of the Interior Plains (e.g. Porcupine Hills and Cypress Hills) and consist mainly of coarse, resistant siltstones and sandstones. Younger Tertiary deposits consisting of coarse to fine sand and quartzite pebble gravel are found locally in the southern Interior Plains (e.g. Swan Hills).

The Interior Plains are composed of thick glacial deposits (Ritchie 1985), and change in elevation from approximately 250 m a.s.l. near the edge of the Precambrian Shield in Manitoba to approximately 1,200 m a.s.l. near the Rocky Mountain Front (Klassen 1989). The Manitoba Escarpment and the Missouri Coteau are two sharp rises in elevation as one moves east to west. Both were formed by differential preglacial erosion of soft and resistant bedrocks. Along the Manitoba Escarpment, the Riding and Duck Mountains and the Porcupine Hills are separated by broad preglacial river valleys (Klassen 1989). The glacial tills of the region are quite uniform, as they were created from the underlying shale, siltstone and sandstone. They contain approximately equal amounts of sand, silt and clay, with minor amounts of coarse material. Fine-textured (silt, clay) glacial lake deposits are widespread throughout the region, and sand in the western and hummocky portions of the region. More coarse-textured (sand, gravel) glaciofluvial deposits (kames, eskers, deltas, fans, outwash trains, and kame and kettle complexes) are also widespread.

### 1.1.5 Edaphic Factors

Substrate type is an important factor in the distribution of boreal forest species and in forest dynamics (Carleton & Maycock 1978). Most of the soil parent material has been moved, sorted and redeposited by ice, water and/or wind (Acton 1989b). The relatively young soils of the boreal forest have developed under the influence of glacial and post-glacial sediments (Valentine 1989). Disturbances such as organic matter addition, decomposition and transformation, mineral weathering, and the precipitation of secondary products may alter soil processes in the region (Fuller & Anderson 1993).

Moving north and east across the boreal forests of the Interior Plains, there is a transition from Black and Dark Gray Chernozemic soils associated with a moderately cold, subhumid climate, to Gray Luvisolic, Brunisolic, peaty Gleysolic, and Organic soils associated with a cold, subhumid to humid climate (Acton 1989a). Gray Luvisolic, Brunisolic, and Organic Cryosols predominate throughout the northern part of the Interior Plains. The soils of the Canadian Shield are mostly Luvisols, Brunisols, and Podzols, with organic soils in the poorly drained southwestern portion, and organic Cryosols in northern portions.

### 1.1.6 Studies of the Boreal Forest Ecosystem

Early studies of the boreal forest were largely descriptive, examining phytosociological associations and speculating on vegetation dynamics (e.g. Ritchie 1956; Rowe 1956, 1961; Swan & Dix 1966; La Roi 1967; Newsome & Dix 1968; Achuff & La Roi 1977; Rowe 1983). These studies facilitated later studies of vegetation-environment relationships (Bergeron & Bouchard 1983; Kenkel 1986, 1987) and vegetation dynamics (Dix & Swan 1971; Shafi & Yarranton 1973; Carleton & Maycock 1978, 1980; Bergeron & Dubuc 1989; Zoladeski & Maycock 1990; Bergeron & Charron 1994; Bergeron & Dansereau 1993; Gutsell & Johnson 1999; Bergeron 2000).

Distinct community composition in different regions of the boreal forest may imply dissimilarities in interregional vegetation dynamics. The high floristic diversity of the Great Lakes region is attributable to a combination of boreal and deciduous elements. However, as one moves north and west the number of species markedly declines, as many species reach their range limits at Minnesota, western Ontario and eastern Manitoba (Swan & Dix 1966). Rowe (1956) comments on the “remarkable floristic similarity” that exists in Manitoba, Saskatchewan and Alberta.

## **1.2 Disturbance**

### 1.2.1 Introduction

Understanding disturbance regimes is necessary for the modelling of Canadian boreal forest dynamics (Li & Apps 1995). The nature of disturbance, in terms of type, intensity, frequency and area, has direct implications for population structures and the course of succession (DeGrandpré et al. 1993). Large-scale disturbances are particularly dramatic and influential in boreal ecosystems (Engelmark et al. 1993; DeGrandpré et al. 1993; Rowe 1961; Bergeron & Dansereau 1993). However, the intervals between disturbances are typically too short for forest species assemblages to achieve a climax (Li & Apps 1995).

Disturbance has created a patchwork mosaic of boreal forest stands at the landscape level (Dix & Swan 1971; Carleton & Maycock 1978; DeGrandpré et al. 1993) and has influenced forest structure and dynamics at many spatial and temporal scales. Modelling boreal forest dynamics can be problematic since disturbance exhibits many quantitative and qualitative origins and consequences, and the temporal nature of disturbance is highly unpredictable (Engelmark et al. 1993).

### 1.2.2 Fire

#### *Introduction*

Fire is the dominant disturbance in the boreal forest at the landscape level (Wein & MacLean 1983; Johnson 1992), although windthrow, hail storms, ice storms, and insect and fungal attack markedly influence boreal forest structure at smaller spatial scales (Kneeshaw & Bergeron 1998). In the boreal forest, crown fires commonly initiate secondary (regeneration) succession processes (Bergeron & Dansereau 1993). Fire cycles are typically <50 years in northern areas of the prairie provinces, limiting arboreal succession in most parts of the boreal forest (Heinselman 1978; Bergeron & Charron 1994). However, the southern and eastern boreal forest has longer fire cycles which allow for directional succession involving changes in species dominance (Bergeron & Charron 1994). The fire rotation period in the southern boreal forest is approximately 130 years (Payette 1992). From the southern boreal forest to the northern limits of the lichen-spruce woodland zone, the oldest forest stands growing on mesic substrata are typically <250 years (Payette 1992). Fire cycles may vary both spatially and temporally, influencing the composition of the forest in complex ways (Bergeron & Dansereau 1993). Fire results in a patchwork mosaic

of forest stands that are sharply delimited by abrupt changes in tree composition and/or crown height (Carleton & Maycock 1978). Within each forest patch, stands are relatively uniform in stature and composition (Dix & Swan 1978). Payette (1992) suggests that fire cycles of <150 years tend to preserve the pre-fire vegetation composition and structure of a site.

### *The Initiation of Fire on the Landscape*

The occurrence and spread of fire on the landscape is controlled by climate (Johnson 1992). Airstream movements and boundaries limit the length of the fire season and determine the seasonal geographic progression of fires (Johnson 1992). Lightning is the most significant cause of forest fires in the boreal and subalpine forests of western Canada, providing the ignition source for 60% of all fires, and 90% of the area burned (Nash & Johnson 1996). The incidence of lightning-caused fires declines as one travels northward, as the frequency of thunderstorm days declines (Johnson 1992). The seasonal variation in climate of the boreal forest is controlled by the interaction of the Arctic, cool Pacific, mild Pacific and North Atlantic airstreams. The 'fire season' is determined by the alteration of atmospheric circulation, and is initiated when there is a switch from a colder stable Arctic airstream to warmer unstable Pacific and Tropical airstreams (Johnson 1992). The readvancement of the Arctic airstream in the autumn ends the conditions suitable for fire ignition and spread.

Large and widespread fires occur when dry fuels, ignition and high winds occur in sequence (Johnson 1992). Through most of the boreal forest 'critical' fire weather is associated with a characteristic persistent 50 kPa high pressure system (Johnson 1992). The high temperatures, low humidity and usually light winds associated with these systems leads to the rapid drying of fuels (Johnson 1992). Convective (thunder) storms result from atmospheric instability in the lower troposphere caused by the interaction of low and high pressure systems, and the diurnal cycle of surface heating (Nash & Johnson 1996). Convective storms produce localized precipitation and a high density of lightning strikes (Nash & Johnson 1996). In comparison, low pressure (or 'frontal') systems also produce lightning but have widespread precipitation (Nash & Johnson 1996). Whereas convective storms last from 30 minutes to several hours, frontal systems may last from hours to days (Nash & Johnson 1996).

Lightning fires require the occurrence of lightning and certain fuel characteristics, of which fuel architecture (fuel size, load, arrangement, continuity and species) and fuel moisture are the most important (Nash & Johnson 1996). Fine fuels (<2 mm in diameter) dry very quickly, taking about

2/3 of a day to lose 2/3 of their free moisture when the air is 20°C and 40% relative humidity. Fine fuels have a very low water holding capacity which, in combination with their high surface area/volume ratio, results in rapid drying (Johnson 1992). The ground litter layer, as a result of its compact geometry, typically takes 12 days to dry to 2/3 of its free moisture (Johnson 1992). The deepest and most compact ground litter layers and large, downed boles on the forest floor require 52 days to dry to 2/3 its free moisture (Johnson 1992). Large boles, which largely contribute towards biomass, play a small role in flaming combustion and the spreading of fire (Johnson et al. 1998). Generally, Nash and Johnson (1996) conclude the following: (i) the probability of lightning-caused fire occurrence is correlated primarily with the dryness of fine and medium size fuels; (ii) there are more fires, more strikes and a higher probability of fire during persistent high pressure weather systems; and (iii) the occurrence of lightning during high pressure systems is correlated with atmospheric instability.

### *The Behaviour and Effects of Fire*

Fires are characterized by both the 'behaviour' they exhibit and the 'effects' they elicit on the landscape. Fire behaviour is influenced by weather conditions, fuel moisture and connectivity, and topographic variability. These factors determine the rate of spread and intensity of the fire, and the extent of area burned. The two dominant types of fire behaviour are wind driven and convectively driven fires, with wind driven fires being more common (Johnson 1992). Wind driven fires are spread by tilting the flame and convectively heating the fuel in front. Increasing slope steepness has the same effects as increasing windspeed. Convectively driven fires, in contrast, have a low horizontal spread but high vertical turbulence, with heat transfer through radiation. Wind driven fires have high spread rates and low fuel consumption, whereas convective fires have low rates of spread and high fuel consumption (Johnson 1992). Fire effects, are the direct and indirect effects of fire on the biotic and abiotic components of plant communities. Effects of fire include plant damage, mortality and consumption, the extent to which the litter layer is consumed and mineral soil is exposed, changes in watershed dynamics and nutrient turnover.

Fires can be divided into flaming combustion and glowing combustion. Flaming combustion is caused by the ignition of gases released as fuels are thermally broken down or 'pyrolyzed', which is controlled by fuel chemistry, structure and moisture content (Johnson & Miyanishi 1995). Glowing combustion is the burning of the remaining carbon through surface oxidation. Both forms of combustion have different ecological effects. Whereas flaming combustion is primarily

responsible for plant mortality, glowing combustion is responsible for the consumption of organic matter and seedbed preparation (Johnson 1992).

Fires in the boreal forest are typically high intensity wind driven crown fires, with flames extending into tree crowns. Fire 'intensity' is the output of heat ( $\text{kW} \cdot \text{m}^{-1}$ ) at the flaming front, and directly related to the heat of combustion, fuel consumed and rate of spread (Johnson & Miyanishi 1995). Three types of crown fires are recognized: passive, active and independent (Johnson 1992). Passive crown fires do not burn continuously in the canopy, dropping back to the surface fuels. Active crown fires form a wall of flames from the ground into and about the tree canopy, requiring high surface intensities as well as continuous and moderate canopy bulk densities. Independent crown fires burn independently of the surface fuels. Independent crown fires are rare, existing only for short periods under unusual heat transfer conditions.

Plant death and injury are dependant on the heat transferred to them, and how much heat they absorb. Different fire intensities kill or damage trees by girdling the stem or by scorching or consuming leaves, needles and buds (Johnson 1992). Bark thickness, which is related to tree size, protects the tree by increasing the time it takes to heat the vascular cambium to the lethal temperature of  $60^{\circ}\text{C}$ .

Crown fires rarely consume an entire forest due to changing windspeeds, topographic and physiographic variability, vegetation patchiness and changes in species composition, fuel connectivity, and the time of day that fires burn (Rowe & Scotter 1973; Turner & Romme 1994; Turner et al. 1994; Lertzman 1998). These factors result in areas of low and high fire intensity, which result in a heterogeneous pattern of burn severities and islands of unburned vegetation (Turner et al. 1994; Kneeshaw & Burton 1997). Fire 'severity' is a term that is often used in conjunction with (and is often confused with) fire intensity, and has been defined as the "effects of fire on the ecosystem" (Turner et al. 1994). For the purposes of this thesis, fire severity and fire effects are used synonymously.

The spatial heterogeneity of fire influences species regeneration on the landscape. The reestablishment of plants that rely on seed dispersal (e.g. white spruce, balsam fir) will be influenced by the size of the burned patch, the distance to the nearest unburned forest patch, and the spatial distribution of burn severities (Turner & Romme 1994; Turner et al. 1994). In comparison, species which reestablish by sprouting (e.g. beaked hazelnut, trembling aspen) are primarily controlled by burn severity regardless of the size of the burned patch or distance to

unburned forest patches (Turner et al. 1994). The spatial heterogeneity of burns also influences a host of other ecosystem processes, including the amount of edge between late- and early-successional forests, the amount of browse available for ungulate populations and watershed dynamics. Watershed dynamics are altered as a result of vegetation removal by fire, which affects the amounts of water lost through evapotranspiration, as well as surface flow and substrate flow (Turner et al. 1994).

Landscape heterogeneity has profound implications for biological diversity, enhancing the long-term coexistence of a diverse assemblage of ecosystems (Lertzman et al. 1998). This effect is greater when landscape features are stable in ecological time (e.g. large water bodies, topographic divides) (Lertzman et al. 1998). Under conditions of extreme drought and high winds, all fuels across the landscape become highly susceptible to burning, resulting in large stand-replacing fires. Under these conditions landscape patterns may have little influence on fire behaviour (Turner & Romme 1994; Bessie & Johnson 1995).

Previous studies have indicated that as forests age, fuel buildup increases the flammability of the forest (Johnson et al. 1998). Although fuel variables influence fire intensity (fuel loadings, fuel depth, mass density, heat of combustion and surface-to-volume ratio), climate is the overriding factor (fuel moisture content and wind speed) (Johnson et al. 1998). During extremely dry and windy weather conditions the relative importance of fuel loads decreases and all stands, regardless of their fuel load or composition, achieve the threshold required for crown fires to develop (Johnson et al. 1998).

### *Regional Fire Regimes*

The fire 'regime' of an area is defined as a set of fire activities that characterize a particular region (Heinselman 1973). Fire regimes are defined with reference to a particular period of time (Lertzman et al. 1998). Variability at time scales shorter than this reference scale is interpreted as noise inherent to the fire regime, whereas variation on longer time scales is interpreted as change in the fire regime (Lertzmen et al. 1998).

The fire regime of a region can be characterized by different parameters including fire 'frequency' or its inverse, the fire 'cycle'. Fire frequency is an estimate of the probability distribution of survival or mortality from fire for a given landscape unit, whereas a fire cycle is the time required to burn an area equal in size to the study area (Johnson & Gutsell 1994). Fire frequency is estimated from the time-since-fire distribution (a cumulative distribution) for



different forest age-classes, and is derived from stand-origin maps. In the boreal forest the fire frequency distribution can usually be described using a negative exponential distribution, which hypothesizes that the hazard of burning is constant and that no change in flammability occurs with stand age (Johnson 1992). Changes in the fire cycle over time are indicated as abrupt changes in the slope of the time-since-fire distribution.

### *Fire and the Landscape Mosaic*

The boreal forest is a complex mosaic of forest stands with differing stand origin dates. Forests burn frequently enough so that virtually all areas will have burned within 300 to 400 years (Johnson et al. 1998). As a result, old-growth stands will be limited on the landscape, with rarely more than 5-10% of the landscape exceeding 200 years of age (Johnson et al. 1998).

Small fires play a relatively unimportant role in determining the age mosaic of the landscape since they constitute a very small proportion of the landscape and are spatially rare occurrences (Johnson et al. 1998). The distribution of fire sizes and numbers is skewed, with 98% of fires accounting for <1% of the area burned (Nash & Johnson 1996; Johnson et al. 1998). Landscapes created by wildfire are determined by the few large fires that have occurred in the past. Since older burns are subsequently overburned, the mosaic of forest patches on the landscape consists of large areas of young forest interspersed with small patches of older forest which are remnants from past large fires (Johnson et al. 1998). This indicates that old-growth forests did not dominate most of the western boreal landscape prior to European settlement (Johnson 1998).

Old-growth forests have structural attributes which include large trees, wide variation in tree sizes and spacing, accumulation of large, dead standing and fallen trees, broken and deformed tops, bole and root rot, multiple canopy layers, canopy gaps and understory patchiness. In addition, functional characteristics of these stands include cessation of height growth of the oldest trees, low net productivity, and production of metabolites which provide resistance to insects and disease (Johnson et al. 1995). Kneeshaw & Burton (1997) indicate that old-growth stands in the sub-boreal spruce zone of British Columbia are characterized by a range of tree ages and sizes, having diverse origins in response to within-stand disturbance events. The recruitment and subsequent development of understory regeneration in the boreal forest is not commonly studied, under the assumption that fires events are frequent enough to preclude canopy replacement.

### *Fire Suppression and Climate Change*

Global temperatures have clearly been increasing since the end of the 'Little Ice Age' (ca. 1,550-1,850 AD). Since 1890, temperatures in Canada have increased by 1.7°C (Flannigan et al. 1998), peaking in the 1940s, followed by a cooling in the mid-1960s, and a warming trend since 1970 (Bergeron & Archambault 1993). General circulation models predict a rise in global temperature of 1.5-4.5°C within the next 100 years, with increased temperatures at higher latitudes and decreased summer precipitation and soil moisture at mid-latitudes of the northern hemisphere (Turner & Romme 1994). Changes in fire frequency in response to climatic warming will have a major impact on circumpolar boreal forests.

Fire frequencies throughout the North American boreal forest have either showed no change or more commonly have decreased over the past 100 years (Flannigan et al. 1998). These empirical results are not in agreement with models that predict an increase in fire frequency with climatic warming. Active fire suppression was considered (and is commonly still considered) to be the major reason for this change (Heinselman 1973). However, the fact that corresponding changes in fire frequency were seen in areas with and without fire suppression, makes the argument unconvincing (Johnson 1992; Johnson et al. 1998). The decreased number and extent of fires has been attributed to a moister climate since the end of the Little Ice Age (Clark 1990a,b; Johnson & Larsen 1991; Johnson 1992; Bergeron & Archambault 1993; Turner & Romme 1994), although fire suppression may have had a minor contribution to the decrease (Flannigan et al. 1998). An individual fire is the result of a complex set of interactions between ignition, fuel conditions, topography and weather including temperature, relative humidity, wind velocity and precipitation. Increasing temperature alone does not necessarily mean that fire frequencies will increase, since changes in precipitation are not synchronous with temperature changes (Flannigan et al. 1998; Bergeron & Archambault 1993). Consequences of climate change on fire disturbance must be viewed in a spatially dependent context (Flannigan et al. 1998). Whereas some regions of Canada will experience decreased precipitation with increasing global temperatures, other regions will experience higher precipitation and a corresponding decrease in fire frequency. Flannigan et al. (1998) used the Canadian General Circulation Model to predict changes in fire regimes for different regions of North America using the 'fire weather index' (FWI). FWI uses temperature, relative humidity, wind speed and precipitation to represent the intensity of a spreading fire. The model predicts increases in FWI with global warming over central North America, in particular the lower Great Lakes, the Dakotas, Montana and Wyoming. The western and northwestern

sections of Canada, which historically have experienced large burns, are expected to have major reductions in FWI (Flannigan et al. 1998).

#### *Fire and Nutrient Dynamics*

Fire influences the allocation of soil nutrients in forest ecosystems both directly and indirectly. In northern climates, humus accumulates since colder temperatures limit microbial activity and decomposition rates (MacLean et al. 1983). This induces 'nutrient lock-up' (Rowe & Scotter 1973) or paludification ('swamping'), defined as "the growth of peat over forest soils" (Glaser 1987). When paludification occurs, nutrients are removed from circulation and nutrient supply may become more limiting to plant growth (MacLean et al. 1983). Paludification is a "hydrological problem" initiated when transpiring vegetation cover is removed and water tables rise (Wein 1983). If the soil is too wet to allow the establishment of trees and shrubs, mosses may dominate (Wein 1983). MacLean et al. (1983) indicate that paludification results in the immobilization of nutrients in soil organic matter and so limits plant productivity. The process results in successional processes leading from coniferous forest to a *Sphagnum* bog. Most nitrogen is located deep within the *Sphagnum* soil "because of the low density and nutrient concentration of the upper part of the profile", and because the accumulation of insulating *Sphagnum* mosses often raises the permafrost level. The 'paludification-fire-nutrient release hypothesis' of Wein (1983) suggests that aging ecosystems can be "revitalized through improved nutrient cycling conditions brought about by fire". Fire may reverse the trend towards paludification and extreme nutrient lock-up, and act as a mineralizing agent to restore plant nutrients to circulation (MacLean et al. 1983).

#### *Fire Effects on Vegetation Regeneration*

Groups of species differing in life-history traits have different patterns of recovery after disturbance (Rydgren et al. 1998). Heterogeneity in post-fire vegetation composition is the result of two processes: spatial variation in fire intensity (particularly when unburned patches or different depths of peat remain) and heterogeneity in pre-fire vegetation if large unburnt patches exist or if underground rhizomes survive (Shafi & Yarranton 1973). Rapidly-spreading fires are more elliptical in shape, increasing the rate of vegetation reestablishment from windblown seed (Johnson 1992). All North America boreal tree species have wind-dispersed seeds. The distance of seed dispersal and the quantity of seed reaching various distances from the seed source depends upon the height of the release point, stand characteristics, size of the seed crop, air

temperature and moisture content, and wind and atmospheric stability at the time of seed release (Zasada et al. 1992). Secondary seed dispersal has the potential to disperse seed over longer distances (e.g. along watercourses or over snow). The seed bank (defined as the viable seed present in the soil) increases by annual seed rain but is reduced by seed mortality, predation and germination. Semi-serotinous black spruce and serotinous jack pine cones have an advantage over non-serotinous species in the recolonization of large burns if they were present before the burn. Non-serotinous species, in comparison, may have difficulty colonizing large burn areas from seed. However, trembling aspen, balsam poplar, paper birch, and many understory herbs and shrubs successfully resprout from an established rootstock after a fire (Oechel & Lawrence 1985). Dominant tall shrubs such as beaked hazelnut (*Corylus cornuta* Marsh.) and mountain maple (*Acer spicatum* Lam.) resprout vigorously following fire (Heinselman 1973).

Partial or full mortality of all beaked hazelnut aboveground stems has been shown to occur after fire (Johnston & Woodard 1983). Lethal temperatures are achieved through convective and radiative heat transfer from adjacent fuel loads; direct contact with flames is not necessary to produce mortality. In contrast, mortality of belowground tissue is very uncommon (Johnston & Woodard 1983). Although beaked hazelnut vigorously resprouts after low intensity fires, repeated low intensity fires destroy the ability of the species to propagate by exposing and destroying underground stem systems and exhausting stored food reserves (Buckman 1964; Johnston & Woodard 1983). Single high intensity fires may eliminate beaked hazelnut from an area if the soil LFH horizon (developed primarily from an accumulation of leaves, twigs and woody materials) is completely consumed by fire (Buckman 1964).

Many bryophytes strongly influence soil moisture, temperature, erosion and seedbed conditions, and therefore constitute an important component of boreal forest vegetation. Species distributions are controlled by microclimate, substrate type and time (i.e. time for logs to decompose, and for successful species growth, dispersal and colonization) (Crites & Dale 1998). Since many bryophytes have relatively slow rates of growth and dispersal, it may take several decades for a high cover and species richness to develop. Several studies have indicated that rare nonvascular species become established in forests that are old enough to have acquired numerous microhabitats (e.g. substrates in various stages of decay) (Crites & Dale 1998; Rydgren et al. 1998). Size, decay stages and distributions of downed woody material have been shown to change with stand age and composition (Sturtevant et al. 1997).

The diaspore bank of the mineral soil and humus layer contain both sexually and asexually produced propagules (spores, gemmae, gametophyte fragments) (Jonsson 1993). This diaspore bank is dominated by early successional bryophytes, and is therefore an important resource for the colonization of mineral soil after disturbance events (e.g. windthrow; Jonsson & Dynesius 1993). The acrocarps *Pohlia nutans* (Hedw.) Lindb. and *Polytrichum* spp. rapidly colonize exposed mineral soil after the uprooting of trees or fire (Jonsson 1993; Rydgren et al. 1998). Other species do not appear until later stages of succession. Species such as *Orthotrichum obtusifolium* Brid. are associated with logs in early stages of decay, likely colonizing the wood when it was in tree form but before it fell to the ground (Crites & Dale 1998). As decay proceeds, logs are colonized by a host of epixylic species such as *Platygyrium repens* (Brid.) Schimp. and *Haplocladium microphyllum* (Hedw.) Broth. once the bark is gone. Many liverworts are associated with logs in intermediate stages of decomposition. Terricolous species such as *Hylocomium splendens* (Hedw.) BSG, *Pleurozium schreberi* (Brid.) Mitt. and *Ptilium crista-castrensis* (Hedw.) De Not. colonize the ground and logs covered in litter and other species at the most advanced stage of decay (Crites and Dale 1998). The specific habitat requirements of many bryophytes makes them excellent indicators of habitat conditions.

### 1.2.3 Herbivory

#### *Introduction*

The effects of herbivory in the boreal forest are potentially large and long-lasting (Pastor et al. 1993), and may be more important than competition in the development of terrestrial plant communities (Hulme 1996). Herbivores change the structure, biomass, production and species composition of vegetation in heavily browsed areas (McInnes et al. 1992). Selective herbivory and physical disturbance by large vertebrates can alter important ecosystem properties, resulting in long-term community changes. Herbivores are known to demonstrate preferences for different plant species and individual plants within a species (Belovsky 1981).

#### *Influence of Moose on Boreal Forest Structure and Dynamics*

The moose (*Alces alces* L.) is a generalist herbivore that can strongly influence boreal forest structure and dynamics. A moose consumes between 3,000-6,000 kg of dry matter per year (Pastor et al. 1988, 1993). They browse heavily on trembling aspen, paper birch, red-osier dogwood (*Cornus stolonifera* Michx.) and other hardwoods, as well as balsam fir (McInnes et al. 1992), willow (*Salix* spp.), beaked hazelnut (Trottier 1983; Pastor et al. 1993) and mountain

maple (McInnes et al. 1992). However, they rarely browse on white spruce (McInnes et al. 1992; Pastor et al. 1993; Sutton 1969) or black spruce (Pastor et al. 1993). Plant nutrient content, the size of food items, and relative species abundances are useful in predicting moose feeding preferences (Belovsky 1981). Preferential browsing by moose can potentially alter forest production, litterfall quality and nutrient cycling (McInnes et al. 1992).

Herbivores directly influence plant species coexistence through selective browsing (Hulme 1996). On Isle Royale in Michigan, moose browsing hindered the growth of saplings of preferred species, maintaining them in the shrub layer (McInnes et al. 1992). Browsing causes shrubs to become more branched, since lateral stems are released from the apical dominance of the terminal bud (McInnes et al. 1992). Suckering and stem density of beaked hazelnut increase in plants subject to heavy clipping, resulting in a dense canopy that outcompetes tree seedlings and suckers by suppressing light and soil temperatures (Trottier 1983). Poor regeneration of trembling aspen (Zoladeski & Maycock 1990) and white spruce (Rowe 1956) have been attributed to the effects of shading and nutrient shortages caused by a dense shrub canopy. This suppression of tree establishment by heavily browsed shrubs may prevent the development of a complete tree canopy (McInnes et al. 1992).

#### *Herbivory and Nutrient Dynamics*

Because nutrient availability is low in most boreal forest stands, changes in nutrient availability are a major driving force in vegetation dynamics (Pastor & Naiman 1992). Selective herbivore browsing can indirectly control the nitrogen cycle and the long-term productivity of boreal forest stands (Pastor et al. 1993). In turn, soil processes affect herbivores by controlling the supply of browse and the rate at which plants recover from browsing (Pastor et al. 1988).

Moose prefer the high nitrogen and low lignin content of trembling aspen leaves and twigs, stripping leaves in summer and eating young twigs in the winter (Pastor & Naiman 1992). Consequently, trembling aspen suckers and saplings are often killed by continuous, heavy browsing. Selective foraging of hardwood species by moose depresses nitrogen mineralization and productivity by changing plant community composition and litter quality and quantity (Pastor et al. 1993). However, excretion of fecal pellets and urine may compensate for decreases in soil nutrient availability to a limited extent (Pastor et al. 1988; Pastor & Naiman 1992; Pastor et al. 1993). Once a pathway is initiated by a particular foraging behaviour, feedbacks between plant species and resource availability are amplified (Pastor & Naiman 1992).

Under certain conditions, selective foraging can drive boreal forest succession toward a coniferous-dominated system (Naiman 1988; Pastor et al. 1993). Coniferous species such as white spruce, black spruce and balsam fir may invade heavily browsed areas in a two-step process: a few individuals first become established, and subsequently serve as seed source for further establishment (Pastor et al. 1988). Conifer litter decomposes slowly and is nitrogen-poor, thus depressing soil nitrogen availability (Pastor & Naiman 1992). Conifers can tolerate low soil nitrogen levels since they grow relatively slowly and retain nitrogen for several years in their needles (Pastor & Naiman 1992). Moreover, white spruce and black spruce produce phenolic polymers (lignin and other secondary compounds) that are difficult for herbivores to digest (Pastor & Naiman 1992). Ultimately, the relationship between herbivore feeding preferences and litter quality results in a shift in plant community composition (Pastor et al. 1988).

The effects of herbivory on boreal forest vegetation dynamics are mediated by factors that inhibit spruce dominance, such as fire, windthrow, disease and insect herbivory (Pastor et al. 1993). Such forces may revert the forest to an earlier successional stage dominated by hardwoods.

#### *Influence of Other Animals on Boreal Forest Structure and Dynamics*

A number of other herbivore species influence ecosystem processes in the boreal forest, including elk (*Cervus elaphus* L.) (Trottier et al. 1983; Pastor et al. 1988) white-tailed deer (*Odocoileus virginianus* Zimmermann) (McInnes et al. 1992) and beaver (*Castor canadensis* Kuhl) (Pastor & Naiman 1992). Red squirrels (*Tamiasciurus hudsonicus* Erxleben), hares and various bird species can also affect reproductive processes of boreal tree species (Zasada et al. 1992).

Selective foraging by beaver has long-term implications on boreal forest dynamics (Naiman 1988; Naiman et al. 1988). As 'central place foragers', beaver are limited to a much smaller foraging radius than most herbivores (Johnston & Naiman 1990). They fell large- and small-diameter, early-successional deciduous species such as trembling aspen and balsam poplar, as well as shrubs including beaked hazelnut and mountain maple (Zasada & Phipps 1990; Pastor & Naiman 1992; Johnston & Naiman 1990). In northern Minnesota, tree density and basal area were decreased by 43% within 1 ha. forage zones surrounding two beaver ponds over a 6 year period (Johnston & Naiman 1990). In Voyageurs National Park, Minnesota, where beaver densities are high (0.92 colonies · km<sup>-2</sup>), foraging has altered 12-15% of the forested landscape (Naiman et al. 1988). Canopy openings created through tree removal by beaver are often large enough to permit

light penetration to the forest floor (Pastor & Naiman 1992), releasing understory conifers from competition (Pastor et al. 1992). Alternatively, trembling aspen and balsam poplar may resprout in these gaps, perpetuating their occurrence at the site (Pastor et al. 1988).

#### 1.2.4 Gap Dynamics

In the absence of fire, large- or small-scale canopy openings or 'gaps', resulting from the mortality of one or more canopy trees, or large branches, break the continuity of the forest canopy and drive forest succession (Frelich & Reich 1995; Kneeshaw & Bergeron 1998; Bergeron 2000). Small (10-30 m diameter) gaps caused by wind, insect pests and fungal pathogens gradually “chip away” at a continuous forest canopy (Frelich & Reich 1995). Canopy openings increase resource availability (i.e. light) in lower plant canopies, facilitating the growth of understory species. An understanding of why some tree species utilize disturbed patches or gaps, while others do not, must be accomplished by considering species life-history traits.

Different rates of uprooting in forest stands are related to storm frequency, soil type, productivity, topographic position and presence of permafrost (Jonsson & Dynesius 1993). Species-specific characteristics such as growth rate, mean lifespan and disposition to uprooting versus stem breakage determine uprooting rates. Patches of forest floor disturbed by uprooted trees are important for the regeneration of both vascular plants and bryophytes (Jonsson & Dynesius 1993), and are important in tree gap-phase dynamics (Englemark et al. 1993). Wind damage creates a continuum of conditions that influence vegetative and sexual reproduction processes in secondary succession (Zasada et al. 1992).

Natural succession towards conifer dominance is frequently interrupted by outbreaks of spruce budworm (*Choristoneura fumiferana* Clemens), which kill balsam fir and white spruce and so result in a shift toward increased dominance of deciduous hardwoods (Bergeron & Dansereau 1993). As a result, mixed stands are often present after long fire intervals derived from periodic gap creation by spruce budworm. The response of understory species to gaps created by budworm outbreaks depends on seed source availability and site characteristics (DeGrandpré et al. 1993). In general, greatly increased light availability favours early successional species. Spruce budworm may have a beneficial role in balsam fir forests by decreasing aboveground biomass build-up and reducing structural deterioration (Zoladeski & Maycock 1990). Spruce budworm outbreaks progress more slowly and are of greater duration in the western boreal forests as a result of the wider dispersions of balsam fir stands (Zoladeski & Maycock 1990). An increased abundance of



hardwoods has been shown to reduce the degree to which forest stands are defoliated by spruce budworm (Su et al. 1996; Bergeron et al. 1995; Bergeron & Leduc 1998).

### 1.2.5 Human Activity

The effects of human activity are widespread throughout the Canadian boreal forest. The Claybelts of Québec and Ontario, the mixedwood forests of Manitoba and Saskatchewan, and the Peace River District of Alberta and British Columbia were settled primarily between 1890 and 1940 (Weir & Johnson 1998). These areas originated on lacustrine, glaciofluvial or glacial till deposits, and were preferred for their fine-textured soils and few stones (Tchir & Johnson 1999). Northern regions of these areas are characterized by logging practices for saw timber and pulp, whereas southern regions have been fragmented by land clearance or complete conversion to agriculture (Tchir & Johnson 1999).

The effects of human settlement on natural fire frequencies and the distribution of white spruce have been documented for the mixedwood boreal forest (Weir & Johnson 1998; Tchir & Johnson 1999; Weir et al. 1999). The time-since-fire distribution for northern regions consists of 3 epochs of different fire cycles, whereas the southern regions consist of 2 epochs (Weir et al. 1999). For the northern region, the fire cycle prior to 1890 was shorter than between 1890-1945, and increased after 1945. In southern regions, there was a short fire cycle prior to 1945 which subsequently increased. The differences in northern and southern fire frequencies between 1890 and 1945 result from landuse. Prior to settlement in the 1890s, southern regions were covered by continuous mixedwood forest. Between 1900-1940 land clearance in southern regions resulted in an increased frequency of escaped fires as settlers piled and burned debris. The increased area burned during settlement offset the increase in fire cycles as a result of climatic change as seen in northern regions. Settlement fires stopped once regional settlement was essentially complete (ca. 1945), with the largely unforested area acting as a massive fire break.

Frequent escaped settlement fires in the southern regions between 1890-1945, and several wildfires which took place at the time, resulted in a decrease in white spruce (Weir & Johnson 1998). This was accompanied by a corresponding increase in trembling aspen which resprouts vigorously after fire. The Dominion Lands Act of 1883 required that all 'merchantable' trees with a diameter >25 cm (10 in.) be harvested, with white spruce being the principal merchantable tree harvested in the mixedwood boreal forest (Dickson 1909). Smaller spruce and other species were more infrequently cut (Weir & Johnson 1998). Areas of the mixedwood boreal forest which were

frequently burned over and selectively logged had a larger reduction in white spruce than areas which were burned alone (Weir & Johnson 1998). Although frequent fires produced good seedbeds (e.g. exposed mineral soil) for white spruce, few seed sources were available on the landscape.

In northern regions of the boreal forest fires are regulated by natural factors (Zoladeski & Maycock 1990). However, fire suppression is actively practiced in southern areas where the majority of commercial harvesting and settlement occurs (Furyaev et al. 1983). Since fire shapes the forest mosaic, effective suppression may have a dramatic impact on boreal structure and dynamics (Bergeron & Dansereau 1993). Glenn-Lewin et al. (1992) suggest that the removal of fire as an environmental disturbance will result in large changes in vegetation composition and structure. In Alberta, extensive and frequent boreal wildfires have limited the distribution of uneven-aged populations of white spruce and balsam fir (Achuff & LaRoi 1977). In northwestern Ontario, frequent fires in jack pine stands have limited the development towards a canopy dominated by black spruce and balsam fir (Zoladeski & Maycock 1990). Fire suppression may lead to successional development towards a steady-state of “self-replacing forests” (Bergeron & Dubuc 1989), or may result in paludification and peatland formation (Heinselman 1973). Decreased fire frequency may also facilitate the regeneration of late-successional species such as white spruce and balsam fir, increasing the likelihood of spruce budworm outbreaks (Blais 1983).

Although fire suppression potentially has large and long-lasting implications on boreal forest structure and dynamics, its effectiveness has recently been questioned (Johnson 1992; Johnson et al. 1998). Climate has been demonstrated to be the overriding factor determining fire frequency in the boreal forest (Johnson 1992; Turner & Romme 1994; Nash & Johnson 1996) (see “*Fire Suppression and Climate Change*” in Section 1.2.2 of this chapter).

Other human activities include the control of herbivore and carnivore populations by hunting and trapping, and the spread of non-native and invasive plant species along roadways and corridors.

## **1.3 Succession And Vegetation Dynamics**

### 1.3.1 Introduction

Communities exist in a dynamic state “of continuous change in response to varying environmental and biological conditions” with recognizable patterns of recovery from disturbance (McCook 1994). Succession may undergo convergent, divergent, or cyclic trajectories, or may be suppressed. Predicting forest succession has been a major focus in ecological research, and is a controversial issue that has over time witnessed alterations and developments in its theory and application (Finnegan 1984).

### 1.3.2 A Chronological Review of Forest Succession Theory

Johnson (1979) considers succession theory to have developed over four distinct periods. The first period emerged between the years 1859-1900, during which time "most of the architecture of the theory was laid out" (Johnson 1979). Most notable during this period was the first fully described sequence of forest succession along the southern shores of Lake Michigan by Cowles (1899). A "developmental and elaborative" or "classical" period followed between the years 1900-1930, dominated by the works of Frederic Clements (1916, 1928, 1936). McCook (1994) considers "the most influential work on succession" to be the "copious description and interpretation" by Clements. Clements considered succession to be "the growth and development of a complex organism", or 'superorganism' (McCook 1994), almost certainly leading to a regional or climatic climax (Cook 1996). His theory is centred around 'reaction', wherein plants modify their environment. Succession occurs in a series of sequential steps, or through 'facilitation' (Finnegan 1984), whereby dominant plant species modify their environment (especially soil and light) to their own detriment, facilitating the invasion and domination of later-successional species (McCook 1994). The community thus develops unidirectionally and eventually reaches a fixed climax. Gleason's 'reductionist' theory advocated a very different view of succession from that proposed by Clements. He viewed plant communities as a largely fortuitous assemblage of species populations, "each with a unique behaviour" (Finnegan 1984). He considered communities to be highly individualistic in which successional changes is determined by floristic composition and stochastic factors (McCook 1994). Disturbance was regarded by both Clements and Gleason as uncommon and not an essential component of the successional process (Cook 1996). Disturbance is the adversary of classical succession theory because it introduced "heterogeneity and lack of compositional stability" (Johnson 1979). The

"scholastic interval", the third developmental period of succession theory, occurred between the years 1930-1947 (Johnson 1979). During this period, Gleasonian views were favoured over those advocated by Clements (Kenkel & Watson 1996). Following this period, several 'modern' theories emerged.

Johnson's (1979) "confused period" (post-1949) witnessed a major "loss in faith" in the conventional views of succession theory. Watt described community vegetation dynamics at the patch level (Cook 1996), in which patches are "dynamically related" and form a mosaic constituting the community (Watt 1947). Such patches undergo cyclical as opposed to seral succession (Kenkel & Watson 1996). Watt recognized the importance of stochasticity, plant life-histories, and biotic interactions in determining community structure and dynamics. Egler's (1954) "initial floristic composition" model explained succession as the differential rate of growth of species which are initially present at a site (McCook 1994). His paper was a "seminal break with the wide acceptance of Clements' concepts" (Wilson et al. 1992).

More modern perspectives on succession theory were beginning to emerge. Drury & Nisbit (1973) challenged Clementsian theory, arguing that the autoecological or physiological level (i.e. not the community level) was the most appropriate scale for explaining succession (Cook 1996). They suggested that vegetation patterns following disturbance should consider cycles and divergences in addition to successional replacement (McCook 1994). They also suggested that new theories of succession should consider evolution (Cook 1996). Pickett (1976) expanded on this evolutionary aspect, producing the first theory of succession based on the evolutionary strategies which are best suited to "environmental conditions along a successional continuum" (Cook 1996). He declared that disturbance is common and integral to the process of succession, that predation may be very influential, and that biotic pressures such as herbivore grazing are important (Cook 1996). Essentially, Pickett viewed the landscape as consisting of different patches which continually change in terms of their relative size, position, and geography in response to a given disturbance regime (Kenkel & Watson 1996). Different species are present during the succession, since their life history traits confer particular advantages or disadvantages at different times. A climax community was defined as one where the adaptation levels of species present are equal or greater than those of potential competitors.

Connell & Slatyer (1977) proposed three successional models (facilitation, tolerance and inhibition), each incorporating differing levels in the timing of species establishment, competition for space and resources, and autoecological characteristics such as species longevity and shade

tolerance (Cook 1996). They recognized disturbance as of "critical importance to the course of succession". The facilitation pathway is "essentially the classical, relay floristic pathway" (Noble & Slatyer 1980), where the presence of early colonizers enhance the invasion and growth of late-succession species (Connell & Slatyer 1977) so that successional processes are essentially controlled by the vegetation. The tolerance pathway suggests that changes in succession are mediated by the life history characteristics of species (e.g. growth rates, seed dispersal capabilities), and the relative efficiencies of resource use by species (Cook 1996). Early-successional species will suppress the rates of invasion and growth of late-successional species (Connell & Slatyer 1977). In the inhibition pathway, the first colonizers of a site inhibit the establishment of all other species (Cook 1996) until the colonizers are damaged or die. According to Cook (1996), this pathway deviates the most from Clementsian views since the initial species group is superior, and succession can be arrested or multidirectional (Cook 1996). McCook (1994) suggests that these three pathways only model the net effect of early successional species on later ones. The pathways only represent extreme conditions along a continuum, since the strength and direction of these pathways could vary as succession proceeds.

Grime (1977) expanded on the ideas of Pickett by classifying species life-history strategies based on their adaptations to various levels of disturbance (McCook 1994). Plants having a 'ruderal' strategy dominate in early succession and 'stress-tolerant' species dominate in later succession (Cook 1996). Species with a 'competitive strategy' increase in importance in undisturbed habitats during the intermediate stages of succession as site productivity increases (Cook 1996).

Horn (1976) indicates that analytical models show "that the general pattern of succession is largely determined by biologically interpretable properties" of individual species in the succession. He used estimates of probabilities of species replacement by "another of its kind or by another species" to predict the future composition of forests. Replacement probabilities are held constant over time, and the model leads to a single climax for all successional communities. Horn (1976) suggests that the rate of convergence on a climax can be slow or rapid, depending upon the type of disturbance, species replacement and regeneration trends, and whether species interactions are competitive or facilitative.

Noble & Slatyer (1980) use a set of life-history characteristics to model vegetation dynamics in communities with recurrent disturbance. Disturbances of various intensities and frequencies exist. The 'vital attributes' of a dominant species are "those attributes of a species which are vital to its

role in a vegetation replacement sequence". These attributes determine the method by which a species arrives and persists at a site following disturbance, the ability to establish and mature in the developing post-disturbance community, and the time required to reach critical life history stages (e.g. reproduction). In effect, certain species attributes can be either beneficial or detrimental under different disturbance regimes. Generally, species with high dispersal capabilities are at an advantage following catastrophic disturbance, and will usually comprise the suite of pioneer species in a succession sequence. Their model demonstrates that a given environment can have multiple successional pathways (Cook 1996). McCune & Allen (1985) demonstrate that chance and/or stand history are important factors determining vegetational change, and that succession can be stochastic and have multiple endpoints (Cook 1996). The 'life history' model of Huston & Smith (1987) suggests that most successional patterns in communities can be explained by species-by-species replacement (Cook 1996).

Although much research has been conducted on forest succession over the past two decades, the concept is still "in a state of definition", and traditional (pre-1947) theories are no longer considered in their original form (Cook 1996). Presently, there is no one theory of succession that is widely accepted, indicating that succession is an "unfinished revolution" (Johnson 1979). However, there are several commonalities that consolidate the prevailing views on succession (Cook 1996):

- (i) Disturbance is frequent enough to exert a significant influence on vegetation dynamics, and disturbances operate at various spatial and temporal scales.
- (ii) Many systems do not reach a stable climax, multiple successional pathways are common, retrogression is possible, and succession may be arrested.
- (iii) Random factors play a significant role in vegetation dynamics at various spatial and temporal scales.
- (iv) Life-history traits and vital attributes of species must be utilized in explaining forest succession processes.
- (v) Various mechanisms drive succession at different spatial and temporal scales, and more than one mechanism may operate at one time.

### 1.3.3 Studies on Boreal Forest Succession

Forest succession models were originally developed from observations in temperate deciduous forest ecosystems. These forests have a high diversity of tree species with varied life history characteristics and infrequent catastrophic natural disturbances (Kenkel & Watson 1996). By contrast, boreal ecosystems are comparatively species-poor and fire disturbance is the most important community process determining vegetation development (Payette 1992, Johnson 1992). Until relatively recently, few studies had been conducted on boreal forest succession. A chronology of key studies on this topic is presented below, based on a general outline by Kenkel & Watson (1996).

Rowe (1961) questioned the justification of “transferring generalities about vegetation from region to region”, noting that some concepts in temperate deciduous ecosystems are “unrealistic” in boreal ecosystems. Rowe (1956, 1961) was the first to apply concepts of succession theory to the boreal forest. He “vigorously challenged” Clementsian views of succession by recognizing that the boreal forests of central and northern Canada do not have a single climax community type (Rowe 1961). He notes that no one species possesses the full range of silvic characteristics required to achieve a self-replacing climax, that the boreal forest is characterized by recurrent disturbance (particularly fire), and gap creation favours an irregular forest structure. He also criticizes the concept of succession as a unidirectional process with a predetermined endpoint, suggesting that edaphic conditions and the proximity of various seed sources promote multiple successional pathways. Stochasticism, site history, edaphic conditions and species life-history attributes are therefore important determinants of boreal forest composition, structure and dynamics (Rowe 1961).

Dix & Swan (1971) enumerated 89 stands at Candle Lake, Saskatchewan, and examined the life-history characteristics and vital attributes of boreal tree species to infer stand structure and successional trends. At their site, they explain that fire is a major disturbance factor, with fire cycles of approximately 100 years tending to “stabilize forest composition so that the pre-fire forest will predominate after fire”. They found that relative age data, size-age relationships, and internal stand structure all indicate that trembling aspen, jack pine, balsam poplar and paper birch are 'pioneer' species (i.e. species which do not establish beneath themselves, Kenkel & Watson 1996). They also found that white spruce and black spruce can establish in stands immediately after disturbance, but do not have the ability to invade. Balsam fir was found to be the only

species capable of continual establishment. However, they noted the “unimportance of succession in the landscape” since balsam fir very infrequently dominated the upper and sub-canopies.

Achuff & La Roi (1977) examined 30 mature white spruce-balsam fir stands in the highlands of northern Alberta. Unlike lowland forests, the Alberta highlands are characterized by moist and short summers, and conifer species generally dominate the seral and climax forests. The authors described these stands based on the life-histories and vital attributes of the tree species. They note that wildfires are extensive in the western regions of the boreal forest, precluding the development of uneven-aged populations of white spruce or balsam fir. The climax population age structure of balsam fir is different from that of white spruce. Balsam fir has a shorter lifespan, establishes at a higher rate, and has a much higher mortality of saplings. The authors note that these attributes serve to maintain the presence of both species in climax stands.

Carleton & Maycock (1978) enumerated 152 closed-canopied boreal forest stands in northern Ontario. Size-class ordination was conducted using 8 boreal tree species. With the exceptions of balsam fir, the ‘succession vectors’ tended to be short, circular and divergent in their configuration rather than long, linear and convergent. This suggests that species do not show a tendency to progress towards a single climax type. Short vectors indicate that interspecies associations are neither strong nor subject to dramatic change during succession. Circular vectors indicate that tree species are adapted to establishment on deforested (burned) areas. Balsam fir has a linear vector, suggesting it does not form a self-regenerating climax. Balsam fir does not demonstrate an affinity for any one tree species when young, and associates (essentially) with white spruce, balsam poplar, paper birch and trembling aspen in older stands. Upland forests tended to be young, monospecific, and composed of early-successional species adapted to rapid post-fire colonization. Young to medium-aged stands of jack pine often showed invasion and establishment of black spruce and/or balsam fir. In contrast, older stands tended to become open and “savanna-like”, displaying little regeneration of black spruce and balsam fir. Although black spruce and balsam fir regenerated under stands of trembling aspen, few stands appeared to be dominated by these species. The authors demonstrate that fire is an integral component of forest systems, that a self-regenerating climax is absent in boreal forests, and that boreal forest composition and dynamics are influenced by “adjustments” made by the vegetation to recurrent fire disturbance. These adjustments include increased flammability of species on fire-prone sites, serotinous cones in jack pine and the semi-serotinous cones in black spruce, and vegetative regeneration following fire.



Zoladeski & Maycock (1990) enumerated 212 stands in northwestern Ontario, using age structure analysis to infer trends in forest dynamics. Most stands were relatively young and composed of post-fire pioneer species. They found regeneration patterns indicating a continuation of the initial tree composition (c.f. Egler 1954) “consistent with a report for the region by Carleton & Maycock (1978)” who found that each tree species “tended to form a climax in its own right”. Sites dominated by rapid colonizers such as trembling aspen and jack pine are fire-prone and therefore subject to limited compositional change. Balsam fir showed continuous recruitment in most stands, but spruce budworm infestations are expected to periodically kill white spruce and balsam fir individuals. Balsam fir forests, which occurred on sites that were the least subject to burning, form self-perpetuating communities. Black spruce lowlands and bogs were the most stable forest type, since vegetative layering will allow these stands to retain their present composition. Upland black spruce stands are dense and likely to burn before deteriorating. Stands of jack pine and trembling aspen often had recruitment of black spruce and balsam fir in the understory, but fires are frequent enough to prevent them from reaching the canopy.

Taylor et al. (1987) examined upland black spruce stands in eastern Ontario. Following fire, the feathermoss *Pleurozium schreberi* forms a continuous mat which persists until the stand is approximately 60 years old. After this time, other large pleurocarpous mosses as well as some vascular herbs and low shrubs become established. After 100 years, the site becomes paludified as peat mosses (*Sphagnum* spp.) begin to invade. The authors indicate that *Alnus* may establish in mineral soils exposed by windthrown trees. Kenkel (1986) notes that fire and water level changes may lead to multidirectional and irregular cycles in boreal wetland vegetation.

Shafi & Yarranton (1973) examined areas of the Clay Belt of northern Ontario in order to detect the presence and duration of successional stages, and study the nature of changes between stages. They discovered four stages in the succession: initial heterogeneity, early phase, heterogeneous phase and late phase. The authors note that initial heterogeneity is attributable to spatial variation in the intensity of the burn, and heterogeneity in prefire vegetation composition. The early phase is less heterogeneous since it is rapidly dominated by plants which spread rapidly in the absence of competition. As more species “recover from the effects of fire” (e.g. vegetative regeneration) or colonize the post-fire site, competition becomes more intense. During these early phases ephemerals colonize the area (e.g. fireweed, graminoids). The interaction between increased competition and environmental heterogeneity increases the heterogeneity of vegetation. The last phase of succession is initiated by the development of a tree canopy. The authors note

that this last phase, depending on local physiographic conditions, will become dominated by black spruce on poorly-drained areas and jack pine on very well-drained areas. On some upland clay sites, trembling aspen may become locally dominant. Temporal changes between phases vary spatially in the landscape, since some sites develop faster than others. The authors note that evolutionary pressures in repeatedly disturbed boreal systems are different from those of more stable systems. Evolutionary pressures in boreal systems favour rapid regeneration and reproduction, and post-fire survival (e.g. suckering and sprouting).

Cogbill (1985) aged 1,785 trees from 145 forest stands in the Laurentian Highlands of central Québec to determine forest history and stand dynamics. He found that 71% of all trees that were cored established within the first 30 years following disturbance. Cogbill suggests that succession is an expression of “differential longevity and conspicuousness of species”. Black spruce bogs witnessed a decrease in the abundance of eastern larch with age and a minor increase in balsam fir. Upland black spruce stands showed a nearly constant proportion of black spruce, with slight increases in balsam fir and paper birch over time. After 100 years, jack pine stands were almost equally composed of black spruce. The author notes that this mixed condition results through the mortality of older jack pine individuals and the slow growth of black spruce. Canopy openings in the oldest stands may result in balsam fir and paper birch establishment. Stands of trembling aspen and paper birch have increasing conifer (white spruce, black spruce, balsam fir) content with time, and may eventually develop into black spruce or balsam fir stands. The oldest upland stands suffer from severe deterioration and are characterized by a lack of regeneration and a “ragged appearance, common openings, and fallen trees”. Very old white spruce stands witness “rapid deterioration or degeneration”, with poor growth, limited reproduction, and shrubby undergrowth in canopy openings. Stands of balsam fir in the region are regularly disturbed by windthrow and spruce budworm outbreaks, and mixed fir stands are subject to severe deterioration at a cycle equivalent to their lifespan (typically 100 years). Sites generally maintain similar vegetation after major disturbances (sensu Noble & Slatyer 1980) and succession is expressed by differential longevity and conspicuousness of species (sensu Egler 1954). Accumulation of humus and feathermoss in the understory tends to retard seedling establishment, which slows down change or replacement in these systems. In many sites, dense shrub cover establishes (e.g. *Alnus* thickets, ericaceous shrubs, mountain maple and beaked hazelnut), “excluding trees for decades and preserving pioneer communities in various habitats”.

Yves Bergeron and colleagues have undertaken numerous studies on boreal forest vegetation dynamics in Québec. Bergeron & Bouchard (1983) analyzed and classified 167 plots in the Lake Abitibi region. Communities varied according to surficial material (organic vs. mineral), drainage, relative abundance of soil bases, flooding, presence of bedrock outcrops, fire disturbance and microclimate. Bergeron & Dubuc (1989) studied boreal succession in northwestern Québec using 'size-class ordination' techniques (see Section 1.3.4 this chapter). Specifically, they described successional pathways using communities of different post-fire age, and examined the convergence of successional pathways and the effects of fire suppression on communities. The authors compensated for the fact that "abiotic differences between stands mask the relationships between the composition of forest communities and time elapsed since the last fire" by stratifying their sites into abiotically homogeneous subsets. On the ordination diagram, "points representing diameter classes of the same stand were linked in decreasing order of diameter classes" for xeric exposed bedrock, xeric-mesic morainic, and mesic-hydric clayey surface deposits. All communities, regardless of the dominant species following fire, tend to converge towards the shade-tolerant and late-successional species balsam fir and eastern white cedar on mesic and hydric substrates, and eastern white cedar and black spruce on xeric substrates. Non-converging patterns may be observed when seed sources for shade-tolerant species are not present or abundant. Self-replacing (climax) communities are not likely because recurrent fire disturbance and gap dynamics, caused by spruce budworm and windthrow, alter successional pathways. All species are present at a site within the first 50 years following fire, and the pre-fire forest composition was similar to post-fire composition. The authors note that their results were consistent with Egler's (1954) initial floristic composition model and Connell & Slatyer's (1977) tolerance model. Essentially, early successional species disappear as they are unable to reproduce under a closed canopy, and shade tolerant species become more abundant over time. Bergeron & Dubuc (1989) explain that along this successional gradient, species are sorted in relation to their time of persistence in the forest, and by their vital attributes (Noble & Slatyer 1980). Kenkel & Watson (1996) note that eastern white cedar and balsam fir are the only boreal species in this region having the vital attributes characteristic of late-successional species (i.e. longevity, shade tolerance) and the ability to regenerate on organic substrates.

Bergeron & Dansereau (1993) reconstructed post-fire successional trajectories for forests of the Lake Abitibi region in Québec. They found a transition from deciduous-dominated canopies in young post-fire stands towards a mixed deciduous composition in mid-succession and a mixed coniferous and coniferous-dominated canopy in the oldest post-fire stands. They note that this

post-fire successional pattern has been documented for southern Canadian boreal forests by Dix & Swan (1971), Heinselman (1981), Cogbill (1985), and Bergeron & Dubuc (1989). This successional scheme relates to the replacement of shade-intolerant species (e.g. trembling aspen, paper birch) with more shade-tolerant species (e.g. balsam fir, eastern white cedar, black spruce, and white spruce). However, large variations in species replacement were witnessed due to factors such as substrate type and availability (distance) of seed sources. Availability of seed sources may be related to the size, intensity and season of fires. As well, Bergeron & Dansereau (1993) found that spruce budworm outbreaks may periodically halt the trend towards coniferous-dominated communities in forests with fire cycles >200 years. Although succession favours an increase in conifer abundance, mixed stands will be present for long time periods in the absence of fire due to the creation of forest gaps.

DeGrandpré et al. (1993) examined post-fire compositional change and abundance of understory species in the boreal forests surrounding Lake Duparquet, Québec. The authors found that post-fire regeneration succession in herb and shrub composition is closely related to Egler's (1954) initial floristic composition model and Connell & Slatyer's (1977) tolerance model. Balsam fir gradually increased in abundance over time while deciduous abundance decreased. This coincided with a decrease in richness, diversity and evenness in the vascular understory species. However, spruce budworm outbreaks, and other small-scale disturbance, reversed these trends in later stages of succession. Succession was predicted from species life-history traits such as longevity, establishment ability, light tolerance and ability to resprout vegetatively following fire. The authors note that post-fire heterogeneity may be related to the spatial variability in fire intensity and the degree of survival of below-ground plant parts. As many as 70% of the species at a site were capable of resprouting following fire. DeGrandpré et al. (1993) did not find changes in understory species composition after canopy closure and disappearance of early-successional species. As well, the authors mention that only mosses and lichens underwent successional change after canopy closure in northern black spruce forests. Moss species richness increased with stand age, but abundance remained constant.

Bergeron & Charron (1994) also conducted a study at Lake Duparquet, Québec. They examined species and stand dynamics over a 230 year period using a 'dendroecological' approach (see Section 1.3.4 this chapter), in which tree-ring analysis was used in combination with species life-history characteristics (e.g. growth rates). Although the pre-fire forest composition was dominated by eastern white cedar and balsam fir, trembling aspen immediately dominated post-fire stands through vegetative suckering. Post-fire recruitment of balsam fir and white spruce was

continuous, but large increases in abundance were not seen until individuals matured and produced seed. The understory was dominated by shade-tolerant conifers, suggesting that they will eventually replace the deciduous canopy. Once the first cohort of trees has been replaced, a mixed composition of deciduous and coniferous species may persist for 150 years or more. These stands may develop into a coniferous-dominated community over time as gaps are created by the death of overmature trembling aspen, insect defoliation (e.g. tent caterpillar, *Malacosoma disstria* Hübner) or spruce budworm outbreaks.

Heinselman (1973) emphasized that fire and other disturbances "maintain a dynamic mosaic of forest-age classes and community types" in the boreal-Great Lakes forest ecotone of the Boundary Waters Canoe Area Wilderness in northeastern Minnesota. However, fire suppression since ca. 1900 has resulted in "widespread successional changes". He found that jack pine communities exhibit succession towards a fir-spruce-birch or black spruce-feathermoss type. The author attests that the climax vegetation would not be 'stable', or self-replacing, as frequent disturbance (e.g. spruce budworm outbreaks, wind breakage and uprooting) alter forest dynamics. In the same region, Frelich and Reich (1995) examined the relationships between spatial patchiness, spatial scale, and canopy succession. Like Heinselman (1973), they indicate that the dominant successional pathways in the region have changed as a result of a dramatically reduced fire frequency following European settlement. High fire frequencies maintained even-aged stands of jack pine and trembling aspen. With the advent of fire suppression, stands of jack pine (and occasionally red pine) or trembling aspen change towards old-growth, uneven-aged mixture of black spruce, balsam fir, paper birch and eastern white cedar. Small canopy openings influence the direction of succession in these older stands. At large regional scales (1-16 ha), gap-dynamic succession leads to convergence toward stands of mixed composition, whereas at smaller scales (0.01-0.1 ha) succession diverges towards monodominant forest stands. Few studies have attempted to link processes occurring at the individual tree scale with processes occurring at the stand level and at larger spatial scales.

Fastie (1995) notes that the existence of multiple successional pathways at similar sites at Glacier Bay, Alaska demonstrates that no single sequence of species replacements or mechanistic model of plant community change is mandatory. He found multiple successional pathways to be a function of landscape in conjunction with species life-history traits, especially dispersal capability and generation time. These factors affect seed rain to newly deglaciated surfaces, altering the arrival sequence of species. McCune & Allen (1985a,b) found pronounced differences in climax vegetation in sites with similar conditions in the Bitterroot Canyons of western Montana. They

attribute site “historical factors” (e.g. weather, seed production, disease) to be the dominant mechanisms driving forest succession.

Bergeron (2000) extended the past studies conducted at Lake Duparquet, Québec by using a combination of chronosequencing and ‘stand reconstruction’ methods (see Section 1.3.4 of this chapter) to test for temporal changes in forest composition. A total of 8 plots with similar edaphic conditions were reconstructed, one plot for each of the major fires that have burned through the area over the past 230 years. The results of this study corroborate previous studies at this location. Stand development follows a multi-cohort process characterized by 1) a post-fire hardwood (aspen) dominance, 2) the dismissal of the initial aspen cohort (stand ‘breakup’) which facilitates the recruitment of subsequent cohorts of aspen, and the development of birch, balsam fir and white spruce which established after fire, and 3) spruce budworm outbreaks in which stands are increasingly dominated by conifers, with a minor hardwood component being maintained through small canopy disturbances. Each of these stages in forest development correspond to a decrease in hardwood abundance, with a corresponding increase in conifer abundance. Suppressed understory white spruce, recruited contemporaneously with aspen after fire, experience growth release with the senescence of the initial aspen cohort. The recruitment of white spruce in stands is mostly limited to the post-fire cohort, and is subsequently very low. The progression of forest succession involving several successive aspen cohorts is more complex than the simple replacement of hardwoods by more shade-tolerant conifers previously reported in the literature.

#### 1.3.4 Methods for Studying Boreal Forest Succession

Numerous methods have been utilized to study past changes in forest structure and dynamics at different spatial scales. These are summarize below:

##### *Pollen and Charcoal Stratigraphy*

Lakebeds throughout the boreal forest contain annually laminated sediments of fossil pollen. These layers have been examined to reconstruct fine-resolution chronologies of vegetation change within and between regions of the boreal forest since deglaciation (Ritchie & Yarranton 1978a,b; Ritchie 1964, 1969, 1985, 1987, 1989). Investigations are typically for the purposes of 1) making direct and indirect links from micropalaeontological data to reconstructions of climate, 2) examining spatial variation in pollen frequencies of major species at specific time intervals, and 3) detecting patterns of vegetation change across large regions, thereby promoting an understanding of broad-scale vegetation dynamics and chronology (Ritchie & Yarranton 1978a).

Charcoal stratigraphic analyses have often been conducted in conjunction with pollen studies to compare patterns of large-scale disturbance (fire) with climatic and vegetation change (Clark 1990a, 1997; Larsen & MacDonald 1998). Results of these techniques must be interpreted carefully, as they vary widely according to sampling methodology and site selection (Ritchie 1985). Although these methods provide information on changes in the relative abundance of plant species and assemblages over large temporal and (sometimes) spatial scales, the results obtained are too coarse to provide specific and comprehensive information on forest succession at small spatial scales.

#### *Long-Term Monitoring Using Permanent Plots*

Permanent plots offer the most comprehensive approach for the study of boreal forest succession, allowing for the direct observation of forest dynamics over time. However, no direct study of forest succession has been possible so far because of the long lifespan of trees (Finnegan 1984). In the absence of permanent plot data, boreal forest dynamics must be inferred by comparing present stand characteristics (Bergeron & Charron 1994).

#### *Chronosequencing*

A chronosequence represents a series of stands (static age distributions) of increasing post-fire age (Gutsell & Johnson 1999). This method assumes that younger stands represent earlier stages of succession whereas older stands represent later stages. Chronosequencing assumes that sites are only different in terms of their age, and not in substrate, climatic history, past disturbance or propagule availability, and that there is one underlying successional trajectory (Finnegan 1984). However, such assumptions must be questioned when studying boreal forest dynamics given the importance of Egler's (1954) initial floristic composition theory (Kenkel & Watson 1996). Bergeron & Dansereau (1993) indicate that different pre-fire compositions, as well as different fire intensities and size, may result in variable post-fire successional trajectories. Furthermore, older stands are often poorly represented in the boreal forest, especially in fire-prone areas (Heinselman 1973). If environmental heterogeneity exists between stands or if multiple succession pathways are possible, chronosequencing may provide erroneous or overly simplistic trajectories. However, adequate replication of stands (i.e. large sample sizes of plots of various ages) will improve the reliability and accuracy of chronosequencing, since the expected variation can be quantified. Chronosequencing has been applied in the examination of boreal forest dynamics (Shafi & Yarranton 1973; Taylor et al. 1987; Bergeron & Dansereau 1993; DeGrandpré

et al. 1993; Frelich & Reich 1995), often in conjunction with the examination of size- and age-class relationships (see below). Chronosequence re-sampling can potentially give other insights into successional processes that are not available through a static survey alone (Foster & Tilman 2000). For example, rates of change in species richness and diversity, and in forest structure and composition, can be inferred for each site by measuring changes over the re-sampling interval.

#### *Size- and Age-Class Relationships*

Size- and/or age-class distributions of tree species are often used to infer successional trends. Bergeron & Dubuc (1989) explain that large and small diameter classes represent the past and future successional stages of the forest, respectively. For example, a stand dominated by species *A* in the canopy and species *B* in the understory implies that species *B* will dominate the future canopy of the stand. Such a sequence assumes that species mortality, natality and growth rates, and life-history strategies are similar (Kenkel & Watson 1996). However, such assumptions may be questionable under certain circumstances (Bergeron & Dubuc 1989). There may be differential mortalities of young individuals (e.g. interspecific competition, selective herbivory) which does not represent successional change (Bergeron & Dubuc 1989). For example, Rowe (1956) notes that a thick shrub canopy may induce mortality in trembling aspen suckers. As well, balsam fir is a common understory component of many eastern boreal forest stands, yet is a preferred browse of moose (McInnes et al. 1992). Cogbill (1985) witnessed a high mortality rate of young stems of black spruce in upland stands. To circumvent the problems associated with differential mortality of young individuals, Bergeron & Dubuc (1989) excluded individuals <5 cm in diameter from their analysis. Boreal tree species also have differential growth rates. The importance of understory black spruce may be underestimated as a result of its slow rate of growth (Cogbill 1985). Generally, boreal tree species are characterized by a wide range of life-history strategies and vital attributes. Despite these limitations, canopy-subcanopy relationships have been used, largely in conjunction with chronosequencing, to infer successional trends in the boreal forest (e.g. Dix & Swan 1971; Cogbill 1985; Zoladeski & Maycock 1990). Size-class analysis (e.g. Carleton & Maycock 1978, 1980; Bergeron & Dubuc 1989) has "previously been used successfully for the study of succession" (Bergeron & Dubuc 1989).



### *Dendroecology and Stand Reconstruction*

Forest ecologists commonly rely on static stand structures or chronosequencing to make inferences about the dynamics of forest systems (Johnson et al. 1994). Stand reconstruction does not infer successional processes from a static series of forest stands. Instead, the method directly observes the history of recruitment and mortality for (essentially) all individuals within stands (Bergeron & Charron 1994; Johnson et al. 1994; Gutsell & Johnson 1999; Bergeron 2000). Within each stand, all live and dead (standing, fallen and buried) trees are aged using dendrochronological techniques at the root collar and every subsequent meter. The decomposition of individuals limits how far back in time a given stand can be reconstructed (Gutsell & Johnson 1999). The large sample sizes required to create a detailed historical reconstruction of a region are often not obtained, as this method is very labour-intensive (Bergeron & Charron 1994). Dendroecology is the study of ring structure and how this relates to spatial and temporal changes in environmental conditions (e.g. climate), and may be an alternative tool to facilitate stand history reconstruction and examine species dynamics. However, very few studies in the southern boreal forest have utilized the technique (Bergeron & Charron 1994).

Bergeron & Charron (1994) and Bergeron (2000) used stand reconstruction to examine post-fire stand dynamics near Lake Duparquet, Québec. These studies involved the reconstruction of one mid-succession (75 year old) mixedwood stand, and a chronosequence of 8 mixedwood stands ranging in age from 26–230 years, respectively. Johnson et al. (1994) and Gutsell & Johnson (1999) used stand reconstruction to test the assumptions made by static size- and age-class methods. Reconstruction was conducted in 5 coniferous plots in the southern Canadian Rockies (Kananaskis River watershed), Alberta, and 4 mixedwood plots in Prince Albert National Park, Saskatchewan, respectively.

By aging each tree at the root collar and at each subsequent meter ‘cumulative height-date’ curves can be produced (Johnson et al. 1994; Bergeron 2000). These curves are used to study the frequency of sharp increases and decreases in growth of individuals over time. ‘Lexis’ diagrams are also produced to trace individual trees from birth to the time of sampling or mortality, with each line in the diagram representing one or more live or dead individuals. Height-date curves and Lexis diagrams clearly illustrate the problems associated with the use of static age structures to infer stand dynamics (Johnson et al. 1994).

## CHAPTER 2 RIDING MOUNTAIN NATIONAL PARK

### 2.1 Introduction

Riding Mountain National Park (RMNP), Manitoba covers an area of 2,976 km<sup>2</sup> (297,600 ha; Parks Canada 1977), and is located in the southeastern extension of either the Mixedwood Section (B.18a) of the Boreal Forest Region (Rowe 1972) or the Mid-Boreal Upland Ecoregion of the Boreal Plains Ecozone (Ecological Stratification Working Group 1995). The Mixedwood Section is roughly triangular in outline, having its base in northwestern Alberta and its apex in southwestern Manitoba (**Fig. 2.1**). RMNP is bounded to the south and east by the Aspen-Oak Region and to the west by the Aspen Region. The Park has been described as an ecological island in a sea of agriculture (Bailey 1968). RMNP is situated on a plateau marking the transition from the first prairie level (the Manitoba Plain) to the second prairie level or Saskatchewan Plain. The park is bounded to the east by a portion of the Manitoba Escarpment, to the north by the broad valley occupied by the Wilson and Valley rivers, and to the south by a plain that slopes gradually towards the Assiniboine valley (Lang 1974). The upper reaches of the Assiniboine River form a broad valley separating the west end of RMNP from the rest of the Saskatchewan Plain (Lang 1974). RMNP encompasses three major ecosystems: the northern boreal forest, the central grasslands, and the eastern deciduous forest. Post-glacial climate change, landscape-landform and disturbance history have substantially influenced the temporal and spatial development of the forest mosaic in the Park.

### 2.2 Climate

RMNP lies within Köppen's Dfc or Humid Microthermal Climatic zone, and is characterized by a rain-snow climate with cold winters and warm summers (Waldron 1966). Marked differences in climatic conditions may occur within RMNP (Bailey 1968). Total summer precipitation decreases from higher to lower elevations on the Escarpment, likely resulting from a "precipitation-shadow" which exists along the lower portion of the Escarpment (Tunstall 1940; Ritchie 1964; Parks Canada 1977). **Fig. 2.2** illustrates the relationship between elevation (m a.s.l.), maximum monthly temperature (°C) and total precipitation (June-September; mm) for meteorological stations at similar latitude in and around the Park (Environment Canada 1993). Although trends should be interpreted with caution, maximum monthly temperature decreases and total precipitation increases with increasing elevation.

Annual rainfall in the Park ranges from 40.6-50.8 cm, with approximately 80% falling between April and October (Bailey 1968). June is the wettest month, having a mean rainfall of 9.8 cm (Environment Canada 1990). Mean winter snowfall is 127.0 cm at elevations of 731.5 m a.s.l., dropping to 25.4 cm at 335.3 m a.s.l. (Parks Canada 1977). Wasagaming (50°39'N 99°58'W; 622 m a.s.l.) has a temperature range of -19.7°C (mean January) to 16.5°C (mean July), with a mean daily temperature of 0.0°C (Environment Canada 1993). Mean annual growing season is between 160-180 days (Waldron 1966). The area has an average of 105 frost-free days from May 25-30 to September 10-15 (Bailey 1968).

### 2.3 Quaternary Ecology: Post-Glacial Development of the Flora

A reconstruction of the Holocene vegetation of the Riding Mountain area was conducted by Ritchie (1969) who examined the changing patterns of relative and absolute pollen frequencies in cores of sediment recovered from three small kettle lakes in the Park. Trends from the three sites showed sufficient similarity to allow for a reconstruction of the Riding Mountain region as a whole.

The flora of Manitoba was entirely eliminated during the last glacial period, the Wisconsin Ice Age. The last remnants of this ice sheet retreated from northern Manitoba ca. 3000-4000 years ago (Löve 1959) and from the Riding Mountain area ca. 12,500 years ago (Lang 1974). Following deglaciation, a spruce-dominated forest invaded the Riding Mountain area from the south, although a pioneer treeless phase probably existed immediately after ice-wasting (Ritchie 1969). This early Holocene spruce forest was present before 11,500 years BP in southern Manitoba and Saskatchewan, as well as adjacent regions of northwestern Minnesota and the Dakotas. Pollen records indicate that this forest was dominated by *Picea* in association with *Artemisia*, *Shepherdia canadensis*, Cyperaceae, and to a lesser extent *Juniperus*, *Fraxinus*, *Larix*, *Populus*, *Pinus*, *Betula* and *Alnus* (Ritchie 1985). These xeric floristic elements indicate that the climate during this immigrant forest phase was comparatively dry.

By ca. 10,000 years BP the climate became even warmer and drier (Ritchie 1969). Spruce abundance declined sharply, and the forest was replaced by a treeless vegetation dominated by grasses, forbs and shrubs (*Salix*, *Juniperus*, *Shepherdia argentea*). This change in floral composition was coincident with the Hypsithermal period or 'long drought' (Löve 1959). By ca. 6,500 years BP there was an increase in the abundance of bur oak (*Quercus macrocarpa* Michx.), and beaked hazelnut (*Corylus cornuta* Marsh.) had appeared (Ritchie 1985). After this time, the

abundance of xeric grassland species began to decline, indicating cooler and moister conditions. The regional flora changed dramatically ca. 2,500 years BP, with an immigration of boreal trees and shrubs and a further decrease in grassland species (Ritchie 1969). Floristic change likely resulted from a “marked deterioration in regional climate”. The forests of RMNP took their present form at this time, with increasing abundance of *Picea*, *Pinus*, *Larix*, *Alnus* and *Abies*. Although small amounts of jack pine (*Pinus banksiana* Lamb.) pollen were present in the park before 2,500 years BP, its presence was most likely due to long-distance dispersal from the Cordilleran foothills and/or the southeast (Ritchie 1969). Current evidence suggests that jack pine first arrived in RMNP ca. 2,500 years BP, likely from a western refugium (Ritchie & Yarranton 1978).

## **2.4 Landscape and Landform**

### *Landform*

RMNP occurs mainly on the rolling 'uplands' of the Saskatchewan Plain, but also includes portions of the Manitoba Escarpment and the Manitoba Plain. The Riding Mountain upland and Escarpment developed from preglacial erosion of the soft Cretaceous shales, followed by the effects of continental glaciation (Ritchie 1964) and subsequent erosion, transport and deposition (Lang 1974). The Escarpment witnesses the greatest relief in the park, with an elevational change of approximately 365 m over 6 km distance. Streams and rivers in the park are typically small and shallow, and the patterns of drainage are poorly developed (Parks Canada 1977). Streams have cut into the Escarpment to form deep gullies (Ritchie 1964). The Birdtail Valley in the northwest and McFadden Valley in the southeast were cut by large channels of meltwater from retreating glaciers (Parks Canada 1977). The major river systems include the Vermillion and Wilson rivers, which are the largest of the north-flowing rivers; the upper reaches of the Little Saskatchewan River, which drains the southeastern portion of the park; and Birdtail Creek, which drains the western portion of the park southward towards the Assiniboine River (Lang 1974).

### *Bedrock and Glacial Deposits*

The bedrock of RMNP originated from silt deposits laid down in shallow Cretaceous seas between 136-65 million years ago (Lang 1974). The bedrock of the area has been divided into six geological formations. From the north-east to the south-west (oldest to youngest) lie the Swan River, Ashville, Favel, Vermillion River, Riding Mountain and Boissevain formations (Parks Canada 1997). The Riding Mountain formation is the largest and deepest, covering most of

southwestern Manitoba including the Porcupine Hills, as well as Duck Mountain and Riding Mountain. This formation has a width of up to 200 km and a maximum depth of 310 m, and is composed of non-calcareous gray shale.

The upland region of the park has a rolling topography, with extensive deposits of calcareous glacial till (Ritchie 1964). The same author notes that conspicuous terminal moraines are rare, but that hummocky disintegration moraines, till plains and local deposits of glaciofluvial gravels and alluvium are extensive. Sand and gravel beach ridges formed by glacial Lake Agassiz occur near the base of the Manitoba Escarpment.

#### *Edaphic Factors*

The predominant soils on the Riding Mountain upland belong to the Luvisolic soil order of the Canadian System of Soil Classification (CSSC) (Agriculture Canada Expert Committee on Soil Survey 1987). These soils vary considerably in their drainage, texture and calcareousness (Ritchie 1964). Other major soils include the CSSC Brunisolic, Chernozemic, Gleysolic, Organic and Regosolic Orders.

## **2.5 Disturbance**

#### *Logging Activity*

Peak logging activity in the Park was coincident with settlement and railway construction near the end of the 19th century (Bailey 1968), when "...railways required large quantities of timber for bridges, culverts, cross-ties station houses, etc., and the settlers required even larger quantities to erect houses and barns" (Tunstall 1940). The Canadian Pacific rail line through Minnedosa was built in 1883-1884, the Canadian National (CN) rail line through Dauphin was officially opened in 1897, and the Rosburn subdivision of the CN was completed to Russel in 1908 (Tunstall 1940).

Pre-logging descriptions of the Riding Mountain forests are unfortunately not available. However, white spruce (*Picea glauca* (Moench) Voss) may have been more abundant in the park than at the present. Evans (1923) noted that in the western portion of the park "...the original forest type on the reserve was coniferous. It consisted principally of white spruce".

Milling operations began in Riding Mountain in the 1870s, and were concentrated close to settlement activity on the periphery of the Manitoba Escarpment (Sentar 1992). Fires often accompanied timber harvesting, and were often set by loggers and settlers burning hay meadows or clearing land (Sentar 1992). White spruce was the most heavily exploited species in the park, but jack pine, balsam fir (*Abies balsamea* (L.) Mill.), aspen (*Populus tremuloides* Michx.), bur oak, green ash (*Fraxinus pennsylvanica* Fern) and black spruce (*Picea mariana* (Mill.) BSP) were also taken (Bailey 1968). Construction of the railway to Dauphin in the late 1890s incurred a heavy demand for jack pine rail way ties which were obtained by logging in the southeastern corner of the Park (Bailey 1968). Trembling aspen, black spruce, green ash and bur oak were removed on a continual basis from the periphery of the Park for fuelwood and fenceposts (Bailey 1968).

The Riding Mountain Forest Reserve was officially established by Departmental Order on July 13, 1895. The Forest and Parks Act transferred control of this area from the Lands Branch to the Forestry Branch of the then Department of the Interior, and changed its designation from Timber Reserve to Forest Reserve (Tunstall 1940). Designation of the Forest Reserve withdrew settlement from the region in order to protect the depleting timber resources. However, logging practices remained essentially unchanged. In 1906 an Order-in-Council established cutting regulations for the Reserve, although illegal timber cutting continued (Sentar 1992). At this time, reports indicated that timber resources were becoming scarce, including white spruce (Sentar 1992). The resource extraction policy was modified in 1930 when the area was given National Park status, although limited timber harvesting continued until the mid-1960s.

### *Fire*

Previous fire events have strongly influenced the development of the forest mosaic in the Park. Unfortunately, little work has been conducted on the reconstruction of historic fire frequencies in the area (but refer to Sentar 1992).

Very few old forests are found in the Park, except for some hygic sites and areas where topographical features have provided protection from fire (Rowe 1955). Records from fire scars on old white spruce, and ages of *Populus* stands, indicate that fires were prevalent in the area around the years 1822, 1853-1855, 1889-1891 and 1918-1919 (Rowe 1955). Tunstall (1940) indicated that fires became prevalent in the Riding Mountain area with settlement, as settlers "made free use of this agency to help clear land". He indicated that fires were particularly

common between 1885-1889, burning several hundred thousand acres. Dickson (1909) noted that two fires in close succession ca. 1890 burned over 70 percent of the area west of the Strathclair trail, "...not leaving even a spruce seed-tree over large tracts". Evans (1923) also attributed the decrease in spruce abundance in the western portion of the Park to these two successive fires which followed white spruce logging. Before these fires, Dickson (1909) notes that there were a number of white spruce stands "...of several square miles" and small areas "...a few acres in extent are scattered everywhere among the poplar". He recalled the abundant post-fire regeneration of aspen "...in the once solid spruce forest". Major fires in close succession will eliminate conifers from a region, resulting in vegetative regeneration of species such as trembling aspen, balsam poplar (*Populus balsamifera* L.) and paper birch (*Betula papyrifera* Marsh.) (Heinselman 1973). Large areas of jack pine forest in the southeastern portion of the Park have burned repeatedly since the turn of the century (Sentar 1992).

Several factors act to control the frequency and extent of fire in the Park. Extensive land clearance around the Park and intensive fire-fighting efforts since the 1930s have had a direct effect on the incidence and extent of forest fires within the Park boundary. However, major fires have occurred in 1940 (Whitewater Lake, apx. 21,000 ha), 1961 (Gunn Lake, apx. 9,000 ha) and 1980 (Rolling River, apx. 21,000 ha) (Parks Canada 1997).

#### *Herbivory and Granivory*

Elk (*Cervus elaphus* L.), moose (*Alces alces* L.) and mule deer (*Odocoileus hemionus* crooki) were abundant in the Riding Mountain area prior to European settlement (Bird 1961). Elk and bison (*Bison bison* L.) were thought to have summered in the Riding Mountain uplands and wintered in the surrounding parkland (Green 1933; Trottier et al. 1983). Mule deer were extirpated from the area as the range of white-tailed deer (*Odocoileus virginianus* Zimmermann) expanded westward with increased land clearance associated with agriculture and settlement in the late 19th century (Trottier et al. 1983).

There are few detailed accounts of ungulate population densities in the region before European settlement. Historical documents describe the dramatic depletion of elk, white-tailed deer and moose numbers in Riding Mountain concomitant with settlement in the late 19th century (Trottier et al. 1983). At this time, Department of the Interior reports described the decline of elk and moose along the southern boundary of Forest Reserve as a result of indiscriminant hunting by

settlers (Trottier et al. 1983). Dominion Land Surveys between 1894-1896 reported that ungulate populations were more abundant in northeastern portions of the Park (Trottier et al. 1983).

A moratorium on hunting was imposed in 1895 with the establishment of the Riding Mountain Forest Reserve, which withdrew people from the area. This ban was soon lifted in 1900 when the Province of Manitoba administered the area open to regulated hunting with the exception of a 500 km<sup>2</sup> game preserve (Trottier et al. 1983). In combination with periodic severe winters, the lifting of the hunting ban resulted in major declines in ungulate populations. By 1914, the elk populations in the Reserve were crudely estimated at 500 individuals (Trottier et al. 1983). Consequently, a legislative decree closed the Forest Reserve to hunting in 1917, facilitating a recovery of ungulate populations.

Although elk populations witnessed a large crash in the late 1940s as a result of severe winter conditions, recoveries were generally rapid, reaching an estimated 12,000 individuals by 1946 (Trottier et al. 1983). In contrast, moose populations were slower to increase, with an estimated 250 individuals in the Park in 1950. By 1979, however, elk and moose densities were almost equal at approximately 3,900 and 5,100 individuals, respectively (Trottier et al. 1983; Parks Canada 1997). Recent (1996) estimates of elk and moose population densities in the Park are 5,000 and 4,500 individuals, respectively (Parks Canada 1997).

In RMNP, ungulate herbivores selectively browse shrubs and saplings of trembling aspen, balsam poplar, paper birch, green ash, Manitoba maple (*Acer negundo* L.), American elm (*Ulmus americana* L.), bur oak and balsam fir (pers. obs.). Rowe (1955) has previously indicated that white-tailed deer and elk heavily browse balsam fir but that they largely avoid white and black spruce. Mountain maple (*Acer spicatum* Lam.), beaked hazelnut, and trembling aspen are important components in moose diet in southern Manitoba (Trottier et al. 1983). Hazelnut is also an important dietary component for elk, white-tailed deer and hare in the Park (Trottier et al. 1983). Intense selective herbivory by ungulate herbivores in forest systems has been shown to have long-term implications on forest structure and development (McInnes et al. 1992; Pastor et al. 1988, 1993). Unfortunately, few studies have examined these effects in RMNP.

Beaver (*Castor canadensis* Kuhl) modify habitats through foraging and water impounding activities. Removal of deciduous trees (especially trembling aspen) along watercourses favours conifer growth, and damming kills low-lying vegetation and modifies local hydrology (Naiman 1988; Naiman et al. 1988). The history of beaver in the Riding Mountain area is similar to that of



most Canadian regions. Trapping and land clearance during European settlement resulted in the near extinction of beaver. Extensive fires during the 1890s further disrupted beaver populations, but eventually enhanced their habitat by promoting aspen regeneration (Trottier 1980). In 1936 the number of colonies was estimated to be less than 50 (Green 1936). When the Forest Reserve was given national park status in 1930 the remnant beaver population began to expand. By the early 1960s the population size had risen, but formal surveys were not conducted to monitor these trends. The drought of 1961 and the associated Gunn Lake fire, in combination with the active elimination of beaver during the haying of meadows prior to 1969, placed further limitations on population growth (Trottier 1980). However, colonization increased rapidly after 1961, as there was higher than normal precipitation and a moratorium on haying was imposed. Since 1976 the population has stabilized at approximately 3,400 colonies ( $1.1 \text{ colonies} \cdot \text{km}^{-2}$ ), where each colony may contain 4-7 beaver (Parks Canada 1997). In 1980 this density was one of the highest measured in Canada as a result of complete protection from harvest (Trottier 1980). The stabilization of the beaver population in the Park is the result of habitat saturation and a corresponding decrease in reproductive rates (Trottier 1980). The escarpment and lowland regions support the lowest density of colonies in the Park, whereas the hummocky western upland and plateau regions support the greatest densities (Trottier 1980).

### *Pests and Pathogens*

Numerous agents of disease have influenced the structure of the forest mosaic in RMNP. An outbreak of eastern larch sawfly (*Pristiphora erichsonii* Hartig) became epidemic in the Park around 1913, "...killing all the tamarack (larch) in this area" (Tunstall 1940). Evans (1923) placed the estimate of larch mortality at 30-40%. Records indicate that spruce budworm (*Choristoneura fumiferana* Clemens) has caused considerable damage to stands of white spruce and balsam fir in certain regions of the province (e.g. Duck Mountain Provincial Park) (Brandt 1993). However, historical and recent records for RMNP indicate that the species has not been an agent of major disturbance, occasionally resulting in the partial or full mortality of individual white spruce and balsam fir trees (Tunstall 1940; Brandt 1993; W. Vanderschiut pers. comm. 1998). The bronze birch borer (*Agrilus anxius* Gory) has previously caused extensive damage to birch in the Park (Tunstall 1940), and Dutch elm disease (*Ophiostoma ulmi* (Buisson) Nannf.) has recently resulted in the widespread mortality of mature American elm, leaving few healthy individuals on the landscape (pers. obs.).

The effects of other insect and fungal agents are discussed for individual tree species in Section 2.6 of this chapter.

### *Human Activity*

Since settlement began in the region, Park history is replete with accounts of human disturbance at various spatial scales. In combination with the above-mentioned examples, grazing and haying of plant communities and gravel extraction have influenced plant community assemblages on the landscape (Tunstall et al. 1922; Tunstell 1940; Bailey 1968). The construction of roadways and trail systems has facilitated the spread of non-native and invasive species, and has possibly altered the migration patterns of large mammals.

## **2.6 Ecology of Major Tree Species in RMNP**

The life-history characteristics of boreal and eastern deciduous tree and shrub species vary considerably. Species 'vital attributes' (Noble & Slatyer 1980) are important determinants of the temporal and spatial development of forests communities. In addition, Bergeron & Dubuc (1989) stress the importance of regional variations in species attributes on boreal forest succession. The biology of dominant trees in RMNP are discussed below:

### White Spruce (*Picea glauca* (Moench) Voss)

Rowe (1955) stresses that "it is difficult to generalize about the reproduction of white spruce as the process is complex at any one place and varies according to location". In mixed stands of trembling aspen and white spruce, seed production begins when spruce are 45-60 years old (Rowe 1955, 1956; Waldron 1965), although seed may be produced "in quantity" after 30 years (Sutton 1969; Nienstaedt & Zasada 1990). White spruce is a prolific seed producer, with good seed crops every 2-6 years and light crops in the intervening years (Sutton 1969). Records of cone production over a 40 year period in the Duck Mountain and Porcupine Forest Reserves showed that there were heavy crops every 3-4 years, with the longest interval without a heavy crop being 4 years (Rowe 1955). In Alberta, heavy seed crops occur on average every 7 years (Dix & Swan 1971). Waldron (1965) notes that in Ontario and Saskatchewan 24-50 percent of potentially good seed is viable in good cone crop years, whereas little to no viable seed is produced in poor cone crop years. Large, mature white spruce may produce up to 184,000 viable seeds from 8,000 cones (Waldron 1965). Rowe (1956) notes that a single individual of white spruce may produce up to 15,000 cones.

Higher than average day and night temperatures, as well as higher than average sunshine, are conducive to the production of cone primordia (Waldron 1965). Pollen shedding occurs between late May and mid-June in RMNP. Cones mature during the first summer, with seed ripening by the end of August. The release of most seed occurs during the first two weeks of September (Waldron 1966), although a small amount of seed has been found in cones which remained on trees into the following summer (Rowe 1955). Seed dispersal distances have been measured at 100-300 m (Galipeau et al. 1997), but seed may travel much further as a result of turbulence and convection currents, and the skidding of seed on top of a snow crust (Ritchie & MacDonald 1986).

Many factors influence the germination of white spruce seed and the survival of seedlings. The reproduction of white spruce at any one location depends on seed production and distribution, seed-bed quality, and favourable climatic and biotic factors. "Only when a favourable coincidence of the fluctuating variables occurs is there likely to be establishment and survival on a large scale" (Rowe 1955). The chances of unfavourable conditions increase westwards across the continent, largely as a result of increasing chances of drought (Sutton 1969). Most seed germinates in July during the first summer, although seed may remain on the ground for one year before germinating (Rowe 1955). Germination may be delayed until autumn or following years if conditions are too dry, and may be delayed as a result of below normal temperatures (Waldron 1966). Litter of trembling aspen may reduce surface soil moisture loss and may increase white spruce germination, although heavy leaf accumulation before or after natural seedfall reduces germination (Waldron 1963, 1966). Death of seedlings may result from spring and winter frost heaving, summer drought and trampling by elk (Waldron 1966; Sutton 1969). Crushing of seedlings under leaves of herbs, shrubs and other hardwoods "...may be an important cause of mortality in the first few years" (Rowe 1955). However, once established mortality of white spruce is low (Galipeau et al. 1997).

Galipeau et al. (1997) note that white spruce is able to colonize burned sites through long distance dispersal of seed. Although white spruce is characteristic of late successional stands, it has a colonization pattern that is similar to a pioneer species since it establishes best during the initial phase of forest development (Carleton & Maycock 1978). White spruce demonstrates two waves of recruitment. The first peak occurs during the initial phase of stand establishment, while a second (smaller) peak occurs later in succession. Immediately after fire, the two factors found to have the greatest predictive power in determining regeneration of both white spruce and balsam fir are distance from seed source and soil parent material (Galipeau et al. 1997).

Growth rates of white spruce are much greater on mineral soil than on decayed wood (Rowe 1955). However, in the absence of exposed mineral soil (from fire or windthrow), decayed wood is a favoured seedbed for white spruce since it holds more moisture than humus (Liefers et al. 1996). In mixedwood stands, 20-30 years are required for fallen trees to decay sufficiently to provide a suitable seedbed (Rowe 1955). Decaying white spruce wood is a preferred substrate over aspen and balsam poplar as it holds more moisture (Rowe 1955). However, feathermoss and associated organic layers are common seedbeds in mature stands (Nienstaedt & Zasada 1990).

The climate over the range of white spruce is cool temperate to subarctic. White spruce occurs on a wide range of soil types, including those of glacial, lacustrine, marine and alluvial origin. Parent materials include limestones, Precambrian and Devonian granites and gneisses, Silurian sediments, schists and slates (Sutton 1969). Textures range from clays to sand flats and coarse soils. White spruce may also be present on deep organic soils. Best development occurs on alluvial soils, moist sandy loams and calcareous lacustrine silts. Growth is best on moist, strongly leached tills (Rowe 1956; Galipeau et al. 1997). Although soils with a sandy texture are less fertile, they have good aeration and drainage and are more stable over the growing season (Galipeau et al. 1997). Growth is optimal on soils of pH 4.0-7.0 and possibly higher (Nienstaedt & Zasada 1990). White spruce matures at approximately 120 years (Rowe 1956), with a lifespan of 250-300 years (Sutton 1969).

White spruce is rarely browsed by moose or white-tailed deer, but snowshoe hare (*Lepus americanus* Erxleben) may cause extensive damage to saplings and young trees. Red squirrels (*Tamiasciurus hudsonicus* Erxleben) sever leaders and branch ends, especially when cones are scarce, and annually take most of the cones and seed of white spruce except during heavy seed years (Rowe 1955; Nienstaedt & Zasada 1990). This may have an important impact on white spruce seed dispersal and seedling establishment. Porcupines (*Erethizon dorsatum* L.) and black bears (*Ursus americanus* Pallas) may strip the bark. White spruce is not normally susceptible to windthrow, but windthrown trees are sometimes encountered in RMNP (pers. obs.).

Trembling Aspen (*Populus tremuloides* Michx.)

Trembling aspen is the most widely distributed tree species in North America (Perala 1990). Climatic conditions are extremely varied over the range, especially winter minimum temperature and annual precipitation. Trembling aspen is generally restricted to areas where annual precipitation exceeds evapotranspiration. The species grows on soils ranging from shallow and rocky to deep loamy sands and heavy clays, and is occasionally encountered on coarse, sandy glacial outwash and shallow soils on rock outcrops. Best growth is on soils developed from basic igneous rock such as basalt, and from neutral to calcareous shales and limestones, with poorest growth occurring on acidic, granitic substrates. Trembling aspen does not grow well on organic soils (Rowe 1956). Perala (1990) indicates that good soils for growth are well drained, loamy, and high in organic matter, calcium, magnesium, potassium and nitrogen. Growth on sandy soils is poor as a result of low moisture and nutrient levels. Water tables less than 0.6 m limit growth, as do heavy clay soils with poor aeration. In Alaska and western Canada, trembling aspen is most abundant and grows best on warm south to southwest aspects (Rowe 1956; Perala 1990).

Good seed crops are produced every 4-5 years, with light crops in intervening years. Minimum age for large seed crops is 10-20 years, with optimal production at 50-70 years (Perala 1990). Seed may be produced annually by 2-3 years of age. Seeds ripen and within a few days begin to disperse over a 3-5 week period. Seeds can be carried for several kilometers by air currents, and water often serves as a dispersal agent (Perala 1990; Zasada et al. 1992). Viability of fresh seed is high but lasts only 2-4 weeks after maturity, or less in unfavourable conditions (Perala 1990). Exposed mineral soils are the best seedbeds and litter is poorest. Despite prolific seed production, few survive as a result of short viability, unfavourable moisture conditions during dispersal, high soil surface temperatures, fungi, adverse diurnal temperature fluctuations during initial stages of seedling growth, and unfavourable chemical balance in some seeds. Height growth is rapid for the first 20 years but slows thereafter. Trembling aspen is highly shade-intolerant, and high mortality (self-thinning) characterizes young aspen stands.

One year old aspen seedlings are capable of producing root sprouts, or 'suckers', and mature stands show vigorous vegetative propagation through suckering (Perala 1990). Suckers grow faster than natural seedlings. Clone size is a function of age, the number of seedlings initially established, and the frequency and degree of disturbance since seedling establishment. Reserves of carbohydrates supply the energy needed for suckering until the suckers emerge from the soil surface to self-photosynthesize. Excess soil moisture severely inhibits sucker production, and

clones subject to fungal heart rot usually produce few suckers. Light attenuation from a heavy shrub cover may limit suckering in older stands (Rowe 1956). Aspen suckers <1 m tall are common in mature mixedwood stands, but they rarely develop further (Rowe 1955).

Repeated burning increases stand density by stimulating suckering and preparing mineral soil seedbeds for seedling establishment (Rowe 1955, 1956; Perala 1990). However, surface fires may result in the loss of shallow feeder roots and create “fire wounds” that reduce aspen productivity (Perala 1990). Death of aspen does not necessarily result in the death of the root system, as a substantial root system may persist even in the absence of aspen in the canopy (Peterson & Peterson 1992).

Trembling aspen is a short-lived tree, growing to 36.5 m and 137 cm diameter at breast height (DBH; 1.3 m) (Perala 1990). Trees may attain a maximum age of 200 years. Rowe (1956) indicates that aspen rarely reaches ages greater than 150 years as it is very susceptible to fungal trunk rot (particularly *Fomes igniarius* (L.) Gill.). In the eastern and western portions of its range, aspen is classified as highly shade intolerant throughout its lifespan (Perala 1990). The species is an aggressive pioneer that readily colonizes burns and can be self-perpetuating in the absence of a major disturbance. However, in the absence of shade-tolerant trees, pure aspen stands often deteriorate into “shrubwood” characterized by a few overmature individuals, a dense shrub cover and few aspen suckers (Perala 1990). Old stands may lose their ability to sucker, and as individuals die and the canopy opens the site may be entirely overtaken by shrubs (Rowe 1955). Fire may be necessary to renew such stands. However, severe fires may eliminate aspen entirely “...resulting in a weed-grass vegetation on what had been a well-forested site” (Rowe 1955).

Young trees are often killed by bark-eating mammals such as meadow mice (*Zapus hudsonius* Zimmermann) and snowshoe hares (Perala 1990). In addition, moose, elk, mule deer and white-tailed deer may kill or damage young trees by rubbing, browsing and debarking (Heinselman 1973). Beaver feed on young, tender bark and shoots and cut down large numbers of trees (Perala 1990). As well, porcupines (*Erethizon dorsatum* L.) can damage tree crowns directly by feeding, and indirectly by increasing susceptibility of aspen to disease.

Trunk, butt and root rots are common forms of mortality. The most common decay-causing fungal species of mature trees in Alberta is *Fomes igniarius* (L.) Gill (Peterson & Peterson 1992). Hoof-shaped ‘conks’ on the outside of the tree are characteristic indicators of the fungus. *Armillaria* spp. is the most common cause of butt rot in Alberta. Common infectious foliage and

stem diseases in the prairie provinces include gall, canker, leaf blight, leaf spot, leaf rust and mildew.

The forest tent caterpillar (*Malacosoma disstria* Hübner) is the most serious defoliator of trembling aspen, but causes little lasting damage (Peterson & Peterson 1992). Outbreaks typically last 4-5 years, with some lasting several years longer. Light defoliation has little effect on tree growth, although two years of moderate to severe defoliation may cause a severe reduction in radial growth and a considerable mortality of branches.

#### Balsam Poplar (*Populus balsamifera* L.)

Precipitation varies throughout the range of balsam poplar, but prolonged summer droughts are uncommon (Zasada & Phipps 1990). In younger stands, the roots of balsam poplar can extract water from near the water table and the capillary zone above it. As stands age, the importance of water supplied by rainfall and snow increases. In the eastern portion of its range and on upland sites in the western portion, balsam poplar grows on soils developed from lacustrine deposits, glacial till, outwash and loess. In Saskatchewan, balsam poplar is frequently associated with trembling aspen on moderately well-drained sites, but its distribution is restricted to local depressions or drainage channels. In Ontario, balsam poplar occurs on soils that are relatively nutrient-rich and less acidic. The species grows on dry, sandy, south facing sites near the treeline in Canada. The litter of balsam poplar may be "soil improving" since it has high concentrations of calcium carbonate (Rowe 1956).

Balsam poplar usually reaches flowering age by 8-10 years of age (Zasada & Phipps 1990). Flowering usually occurs in April-May prior to leafing out, but may be delayed until June in northern areas and at high elevation. The species produces large seed crops almost annually, although large annual variation in production occurs in individual stands and trees. Seed dispersal occurs in May-June (July in northern stands). Rapid dispersal is initiated by warm, dry weather, and lasts for a minimum of two weeks. Viable seeds have been found on trees 4-6 weeks after the onset of dispersal. The small, light seeds are dispersed over long distances by wind and water. Seeds usually die within a few weeks following dispersal, although some may remain viable for 4-5 weeks. Cooler and drier conditions prolong seed viability.

Seed does not exhibit dormancy, and germination occurs over temperatures ranging from 5-35°C provided moisture is adequate (Zasada & Phipps 1990). Moist mineral soil seedbeds are optimal substrates for germination. Germination may occur on moist organic seedbeds, but survival is poor.

Balsam poplar is one of the most versatile members of the Salicaceae in its vegetative reproduction. New stems may originate from intact or broken roots, preformed or adventitious buds on stumps or at the base of trees, and buried stems or side branches (Zasada & Phipps 1990). Production of suckers after disturbance varies, although response is "...less than that of aspen". The density of suckers is greatest where the organic layer is disturbed, as this layer may normally inhibit sprouting by controlling soil temperature (Zasada & Phipps 1990).

Balsam poplar is an early successional species. The species is highly shade-intolerant, undergoes rapid growth when young, is a prolific seed producer, and has a relatively short life span. As stands develop, it is gradually replaced by more shade-tolerant species such as white spruce (Zasada & Phipps 1990). Balsam poplar is similar to trembling aspen in its shade tolerance, modes of regeneration, and rapid initial growth (Rowe 1956). However, balsam poplar is more aggressive on moist sites and is better adapted to colonization and regeneration on silty alluvial deposits. The species often outlives aspen as it is less susceptible to fungal decay (Rowe 1956). Large balsam poplar may reach 90-180 cm DBH and 23-30 m in height (Zasada & Phipps 1990), and have a maximum longevity of approximately 200 years (Zasada & Phipps 1990).

Moose, deer and elk browse on balsam poplar stems but generally avoid the foliage (Zasada & Phipps 1990). Stems as large as 5 cm DBH may be broken by moose and have their tops browsed. Snowshoe hares eat internodes of twigs and stems but not the resin-containing buds. The high terpene and phenolic resin content of balsam poplar makes it less palatable than trembling aspen. Balsam poplar suckers are more tolerant to frost damage than those of trembling aspen which may influence their consociation. Girdling by hares and rodents can kill saplings and small trees, and individuals are cut by beaver along watercourses (Zasada & Phipps 1990).

The most common decay-causing fungal species of mature trees is the fungus *Fomes igniarius* (L.) Gill., followed by *Pholiota destruens* (Peterson & Peterson 1992). *Choristoneura conflictana* (Wlk.) is a common defoliator of balsam poplar, commonly preceding outbreaks of forest tent caterpillar. Numerous other insects cause damage to balsam poplar and trembling aspen, although damage is typically minimal.



Paper Birch (*Betula papyrifera* Marsh.)

Paper birch is a northern species that is adapted to cold climates (Safford et al. 1990). The range of the species is bounded to the north by the 13°C July isotherm. In the south the species seldomly grows naturally where average July temperatures exceed 21°C. Generally, paper birch is found in climates where summers are short and cool, and winters are long and cold. In Alaska, paper birch is found growing on cool north- and east-facing aspects, while trembling aspen is found on warmer south- and west-facing slopes. Paper birch tolerates a wide range of moisture conditions, from 300 mm in Alaska to 1,520 mm at higher elevations in the eastern mountains.

Paper birch grows on "...almost any soil and topographic situation ranging from steep rocky outcrops of the mountains to flat muskegs of the boreal forest" (Safford et al. 1990). However, optimal growth is on deep, moderately well-drained soils that are free of shallow permafrost. Vigorous growth of paper birch has been noted on north-facing slopes with a mean annual depth of thaw in permafrost of 64-76 cm.

The rapid decomposition of paper birch litter contributes to the nutrient status of the forest floor (Safford et al. 1990). The litter is rich in calcium, potassium, magnesium, phosphorous, boron, as well as reduced manganese, aluminum, iron and zinc. Nutrient enrichment may extended to a depth of 3 cm into the mineral soil, where concentrations of calcium, nitrogen, phosphorous, magnesium, potassium, and volatile matter and pH increase. The rain throughfall of paper birch stands contains one-half to one-third the calcium and magnesium and twice the manganese of throughfall of trembling aspen. Soils under birch and aspen tend to be warmer and drier than soils under coniferous species.

Paper birch flowers from mid-April to June, depending on site location (Safford et al. 1990). Seed ripens from early August to mid-September, and dispersal begins soon after ripening. Timing of dispersal depends on weather conditions, and occurs sooner in injured trees. Dispersal usually lasts from September-November in eastern and western portions of the range. Birds feeding on catkins may cause seeds to fall as early as July. Paper birch usually begins producing seed at 15 years of age, with optimum seed production at 60-70 years. Good seed crops are usually produced every second year. Seeds are wind-dispersed and can travel great distances, although the majority of seed falls within a short distance of the parent tree. Seed viability varies according to year, location and individual.

Optimal germination occurs on mineral soil (Safford et al. 1990). Germination on humus is reduced by 50%, and germination on undisturbed litter is only 10% of that on mineral soil. Shaded sites produce approximately twice as many germinants as those under full light. Germination may occur on windthrow mounds, although the majority of germinants occur on rotting logs, stumps and tree boles. Rowe (1956) notes that paper birch may occur over a wide soil moisture range, from jack pine stands on dry, sandy sites to wet peaty stands dominated by eastern larch and black spruce. Birch has been described as having a regeneration pattern that is similar to white spruce and balsam fir (Kneeshaw & Bergeron 1996).

Paper birch can regenerate from sprouts after fire (Safford et al. 1990). Sprouting is usually not abundant enough to replace mature stands, but can facilitate regeneration on dry or “difficult” sites. The ability to sprout decreases after 50 years, and by 125 years only 30-40% of trees have the ability to sprout (Zasada et al. 1992). Sprouts mature sooner (50-60 years) and die earlier (70-90 years) than trees initiated by seed (Safford et al. 1990).

Young paper birch grows quickly, often attaining a DBH of 20 cm by age 30 (Safford et al. 1990). Growth rates decline and become “almost negligible” in old age. In mature stands, trees average 25-30 cm DBH and 21 m high. Paper birch is relatively short-lived, maturing at 60-70 years. Few individuals live longer than 140-200 years. The species is shade-intolerant, and suppressed trees quickly die if they are not soon released. Only trembling aspen is more shade intolerant.

Paper birch has a shallow root system, with the majority of roots occurring within 60 cm of the soil surface (Safford et al. 1990). The species does not form taproots. High winds often break the boles rather than uprooting the tree, but the broken boles will often resprout. When growing in mixture with spruce and/or fir, birch will often “retain a position” in the stand. In some Alaskan spruce stands, birch persists as its leaf litter physically smothers spruce seedlings.

Many animals cause damage to paper birch, including white-tailed deer, porcupines, moose and hares. Heavy browsing by white-tailed deer and moose is a major cause of sprout mortality. Yellow-bellied sapsuckers (*Sphyrapicus varius* L.) bore holes through the bark and facilitate secondary infections. In a study in Maine, over half of all trees bored by sapsuckers died. Red squirrels may girdle stems or bite trees to obtain sap.

Balsam Fir (*Abies balsamea* (L.) Mill.)

Optimal growth of balsam fir occurs in the eastern portions of its range (southeast Canada and northeast United States), where temperatures are cooler and moisture is more abundant (Frank 1990). The species grows on a variety of inorganic and organic substrates, but growth is slow on gravelly sands and in peat swamps. Optimal habitats have near-neutral substrates (pH 6.5-7.0).

Seed is produced regularly after 20-30 years, with good seed crops occurring every 2-4 years (Frank 1990). Timing of seedfall is long and dissemination distances vary. Seedfall begins in late August, peaks in September and October, and continues into November. In addition, some seeds fall throughout the winter and early spring. Seeds are wind-dispersed and may travel up to 100-160 m, although common distances are 25-60 m. Typically, many seeds fall close to the parent tree with the cone scales (Frank 1990; Galipeau et al. 1997). Small mammals may play a role in dispersing seed over larger distances, but this is probably negligible (Frank 1990; Galipeau et al. 1997). Seed viability is lost within one year (Frank 1990).

High moisture retention capacity makes mosses and rotten wood preferred substrates for balsam fir establishment (McLaren & Janke 1996). Moisture is thought to be more important than light in determining germination success (Frank 1990). Germination usually occurs from late May to early July. The probability of survival of the first winter decreases if germination occurs after mid-July. Optimal seedbed conditions are somewhat shaded, moist mineral substrates. However, almost any seedbed is satisfactory if enough moisture is available. Seedlings are commonly smothered or crushed by ice, snow and deciduous leaf litter. Mortality of balsam fir seedlings can be high during the first year, especially under a deciduous canopy or dense cover (McLaren & Janke 1996), although seedling losses after the first year are minimal (Frank 1990).

Balsam fir seedlings are very shade-tolerant, develop quickly, and have a deep taproot to reach the moist soil stratum (Galipeau et al. 1997). The species is more shade-tolerant than white and black spruce (Frank 1990). Seedlings 15 cm tall can be considered established, especially if secondary branching has started. Like spruce, balsam fir can survive many years of suppression and responds well to release.

Balsam fir is small- to medium-sized at maturity, depending on location and growing conditions (Frank 1990). Heights generally range from 12-18 m, and bole size from 30-46 cm DBH. Balsam fir can live for more than 100 years (Galipeau et al. 1997), and may attain a maximum age of approximately 200 years (Frank 1990). Growth rates of balsam fir are related to

climate, soil conditions, age and stand composition. The root systems of balsam fir are mostly confined to the upper 60-75 cm of soil, making them prone to windthrow.

Balsam fir is a highly prolific seeder that shows strong recruitment during intermediate stages of succession (Galipeau et al. 1997). The species does not regenerate well during the early stages of stand recolonization, since seedlings are intolerant of dry conditions and strong competition from light-demanding species. The species is also susceptible to frost damage, which may limit survival until a partial canopy has developed. Regeneration patterns of balsam fir are closely related to gap disturbance, since seedlings aggressively colonize windfall gaps (McLaren & Janke 1996).

Several small mammal and bird species consume balsam fir seeds (Frank 1990). Birds and squirrels can destroy the buds, and black bears sometimes girdle mature trees. Fungal rot increases with stand age, and over half the trees in a stand are infected by age 70. Drier sites have a higher incidence of rot. Red heart fungus (*Stereum sanguinolentum* (Albertini & Schwein.:Fr.) Fr.) causes decay in living balsam fir, entering through injuries in the trunk and branches. Spruce budworm can be a serious damaging agent in balsam fir stands (Blais 1983). Balsam fir saplings are heavily browsed by ungulate herbivores. However, the species can develop a protective morphology that is resistant to heavy browsing (McLaren & Janke 1996). The flammable needles, shallow root system, and resinous bark of balsam fir make the species highly susceptible to fire.

#### Jack Pine (*Pinus banksiana* Lamb.)

Jack pine occurs in climates characterized by short, warm to cool summers, very cold winters, and low rainfall (Rudolph & Laidly 1990). The northern range limit of the species closely parallels the 20°C mean annual maximum isotherm. Annual precipitation ranges from 380-890 mm, with summer droughts being common in the south-central and western portions of the range. Temperature, rainfall, and frost-free days increase from the northwestern to southeastern portions of the range.

Jack pine is usually found on sandy loam soils, thin soils over granites and metamorphosed rocks of the Canadian Shield, limestones, peats, and soil over permafrost (Rudolph & Laidly 1990). The species can grow on very dry sandy or gravelly soils, but has optimal growth on well-drained loamy sands with a midsummer water table at 1.2-1.8 m depth. Jack pine does not grow well on alkaline soils, but does occur on soils overlying limestone. Growth on calcareous soils (pH>8.0) can take place if a normal mycorrhizal association is present. Jack pine is found as pure

stands wherever there are extensive sandy soils, but it is common on heavier-textured calcareous soils in association with trembling aspen, paper birch and white spruce (Rowe 1956). In low-lying areas, it may occur with black spruce. Jack pine commonly grows on level to gently rolling sand plains of glacial outwash, fluvial or lacustrine origin (Rudolph & Laidly 1990). The species occurs less commonly on eskers, sand dunes, rock outcrops and bald rock ridges.

Jack pine produces cones at an earlier age than most other pine species (Rudolph & Laidly 1990). Cones are produced at 10-15 years of age, which gives the species an advantage in areas with short fire cycles (Heinselman 1973). Cone production is fairly regular, but declines with increasing crown competition (Rudolph & Laidly 1990). Seed production is annual but variable. Jack pine has predominantly serotinous cones over most of its range, but in some southern portions of its range cones may be non-serotinous. Some cones may open when temperatures reach 27°C, but the majority remain closed until they are exposed to fire.

Jack pine seed usually germinates within 15-60 days under favourable conditions. Optimum conditions for seedling establishment are exposed mineral substrates (where competition from other plants is not severe), a high water table, and some shading to reduce surface temperatures and evapotranspiration (Rudolph & Laidly 1990). On clay soils in Manitoba and Saskatchewan, competition from trembling aspen and beaked hazelnut limits survival. Seedlings develop a taproot that is maintained to maturity, however, the majority of the root system consists of lateral roots that occur in the upper 50 cm of the mineral soil (Rudolph & Laidly 1990).

Jack pine is highly shade-intolerant, but is considered to be slightly more shade-tolerant than trembling aspen, paper birch or eastern larch. In its native range, jack pine is the fastest growing conifer (other than eastern larch) in the first 20 years. Typically, trees grow to 17-20 m in height and 20-25 cm DBH. Stands often begins to deteriorate after 80 years on the best sites and after 60 years on poorer sites. Jack pine matures by 60-80 years on dry sandy soils, and may not mature until 100 years on more clay loams (Rowe 1956). Vigorous trees up to 185 years in age occur in northwestern Minnesota (Rudolph & Laidly 1990), and the species can persist as a scattered overstory element for 200 years or more (Hienselman 1973).

Jack pine seedlings are damaged by elk, and meadow voles (*Microtus pennsylvanicus* Ord) and rabbits may kill seedlings by gnawing off the bark of lower stems and branches (Rudolph & Laidly 1990). In Riding Mountain, porcupines may strip large sections of bark from the boles of

mature trees (pers. obs.). Granivores, particularly the red squirrel, can remove large numbers of serotinous cones from mature trees (Rudolph & Laidly 1990).

Black Spruce (*Picea mariana* (Mill.) B.S.P.)

Black spruce occurs in cold, humid to dry subhumid climates in which total annual precipitation ranges from 380-760 mm (Viereck & Johnston 1990). Black spruce usually grows on wet organic soils, but productive stands have been found on deep humus, clays, loams, sands, coarse till, boulder pavements and shallow soil mantles over bedrock. Optimum growth is on dark brown to blackish peats which have a large amount of decayed wood. Stands with the lowest productivity are found on thick deposits of partially decomposed *Sphagnum*. Mixed stands occur with eastern larch on wet peats, and with trembling aspen, white spruce, balsam fir and jack pine on uplands. In mixed jack pine-black spruce stands, jack pine usually occupies slight ridges between black spruce 'flats', so that the two species are alternating rather than evenly mixed (Rowe 1956). Black spruce is well-adapted to growing on permafrost soils because of its shallow root system, however, the shallow root system make the species susceptible to windthrow (Viereck & Johnston 1990).

Low nutrient levels slow the growth of seedlings on peat (*Sphagnum*) substrates, and fast-growing *Sphagnum* species may eventually overtop and smother young trees (Viereck & Johnston 1990). Feathermosses may provide an adequate seedbed during wet years, but they often dry out before root penetration occurs. Fires which completely remove the surface organic layer provide good seedbeds for black spruce.

Black spruce cones are semi-serotinous, gradually opening in the absence of fire (Zasada et al. 1992). When heated by fire, cone opening and seed dispersal occurs rapidly. There is geographic variation in the degree of cone serotiny (Zasada et al. 1992). The seeds of black spruce disperse 3 months after pollination, usually in late August or early September (Viereck & Johnston 1990). Heavy seed crops occur every 2-6 years, with peak crops every 4 years on average over most of the range. Black spruce cones remain partially closed and disperse seed for several years, thus providing an adequate supply of seed when fire occurs. Seed number and viability decline quickly, but some seeds may remain on cones for 25 years. Seeds remain viable on the forest floor for at least 10 months, with viability completely lost by 16 months. Seeds are dispersed throughout the year, with highest dispersal in the spring and lowest in autumn (Viereck & Johnston 1990).

Black spruce is shade-tolerant, but is less so than balsam fir (Viereck & Johnston 1990). Seedlings may develop in 10% of full light, but survival and growth are much better under full light. Black spruce is often a pioneer species after fire on uplands and peatlands, and fire usually results in the immediate reestablishment of black spruce if a seed source is available. Layering is an important method of vegetative propagation in sites where moss-covered lower branches develop adventitious roots and produce new vegetative shoots (Zasada et al. 1992). In dense upland stands, lower branches are “self-pruned” and layering does not occur (Rowe 1956).

Black spruce generally grows very slowly, often requiring 15-20 years to attain a height of 1.5 m (Zasada et al. 1992). At maturity, black spruce averages 12-20 m tall and 23 cm DBH on good sites (Viereck & Johnston 1990). Average maximum age is approximately 200 years, although trees as old as 280 years have been reported. Stunted trees growing in swamps may reach over 200 years of age, but rapidly growing trees in upland stands may mature at 100 years and die soon after (Rowe 1956).

Snowshoe hare can cause extensive damage to seedlings and saplings of black spruce (Viereck & Johnston 1990). Red squirrels gather cones in large quantities, consuming a high percentage of seeds in some areas during poor seed years (Zasada et al. 1992).

#### Eastern Larch (*Larix laricina* (Du Roi) K. Koch)

Eastern larch is one of the most widely distributed North American conifers (Johnston 1990). The species can tolerate a wide range of soil conditions, but is most commonly encountered on wet to moist organic soils (e.g. *Sphagnum* and woody peats). The species grows on soils ranging from heavy clay to coarse sand. Eastern larch can tolerate high soil moisture and acidity, and low temperatures. The species is found on peatlands ranging from rich swamp (forested rich fen) to raised bogs, but is most common in somewhat mesotrophic, hygic sites. Optimal growth occurs on moist well-drained loamy soils along water courses, in seepage areas, and on mineral soils with a thin organic layer.

Eastern larch begins to produce seed by 12-15 years, but high seed production does not begin until age 40 and optimum seed production typically begins after 75 years. On peatland in Saskatchewan and Manitoba, eastern larch does not produce cones in quantity until 50 years of age. Good seed crops are produced every 3-6 years, with seed dispersal occurring from

September to the following spring. Although seeds are small, few fall at a distance greater than twice the tree height.

Under normal conditions, seed dormancy is broken after the first winter. The best seedbed is a warm, moist mineral or organic soil. Hummocks of *Sphagnum* moss usually make a good seedbed. In Minnesota, germination is best on fine-textured mosses, especially *Mnium* spp., *Drepanocladus* spp., and *Helodium* spp. Seedling mortality is high during the initial 6-8 weeks following germination.

Layering is a common method of vegetative propagation at the northern limit of the species' range, but is uncommon further south. Mature trees usually attain heights of 15-23 m and 36-51 cm DBH. Maximum age is usually 150-180 years. The growth rate of eastern larch depends on nutrient status and moisture-aeration conditions. Under full sunlight, eastern larch is one of the fastest growing boreal conifers.

Eastern larch is a very shade tolerant pioneer species that is well-adapted to establishing on burned sites (Johnston 1990). Seedlings are very frost intolerant (Rowe 1956). Eastern larch is highly susceptible to recurrent outbreaks of larch sawfly throughout its range. The species is also susceptible to fire as a result of its thin bark and shallow root system, but larch habitat is usually wet enough to prevent mortality. Strong winds can uproot individuals with shallow root systems, but the species is relatively windfirm. Heavy mortality may be caused by snowshoe hare, white-tailed deer and moose (Beefink 1951; Rowe 1956). Over half the seed that fall are consumed by granivores (Johnston 1990).

#### Bur Oak (*Quercus macrocarpa* Michx.)

Bur oak is widely distributed in the eastern United States and the Great Plains region, and is one of the most drought-resistant North American oaks (Johnson 1990). The species is best adapted to sites that are dry to moderately moist. Upland bur oak stands most commonly occur on calcareous substrates. In prairie regions, bur oak is found on sandy plains, black prairie loams, and on south and west facing loamy slopes. The species often dominates extreme sites with thin soils, heavy clay soils, gravel ridges and coarse loess hills. In the Great Plains region, the species may also occur along stream bottoms and river terraces. Bur oak is the dominant tree in oak savannas or "oak openings" in the prairie-forest transition zones Manitoba, the Dakotas, Minnesota, Wisconsin, Iowa and Illinois.



Bur oak flowers in mid-June in the northern part of its range. Acorns ripen and fall from trees as early as August and as late as November. Germination occurs soon after seedfall, although acorns in northern regions may remain dormant until the following spring. Minimum seed-bearing age is 35 years, with optimum acorn production occurring between 75-150 years. Trees may produce seed until 400 years of age. Good seed crops occur every 2-3 years, with poor or no crops in intervening years. Acorns are typically dispersed short distances (10-30 m) by gravity, water, mice, squirrels, chipmunks (*Tamias striatus* L.) and birds. Rodents bury acorns close to their source which increases the chances for successful germination. Blue jays (*Cyanocitta cristata* L.) have been found to collect only viable acorns, and disperse them great distances from parent trees (Darley-Hill & Johnson 1981).

Acorns covered by leaf litter are susceptible to pilferage by rodents, and newly developed seedlings are susceptible to attack by fungi and insects. Optimal growth of seedlings occurs under daytime temperatures of approximately 30°C and overnight temperatures of approximately 20°C. The species is relatively flood intolerant, although seedlings can endure flooding for up to 30 consecutive days during the growing season. Rapid initial root growth and efficient water use may explain why bur oak can establish itself in competition with prairie shrubs and grasses. In prairie areas, roots of bur oak have been found at depths of 3-6 m, with a spread of >12 m.

Oak seedling germination is best on loose soil since the radicle cannot penetrate excessively compact surfaces (Carvell & Tryon 1961). Bur oak sprouts vigorously following burning or cutting. After five years of prescribed burning in Minnesota, 60% of mature bur oak individuals (10-41 cm DBH) produced an average of 21 live sprouts each (Johnson 1990). Bur oak is slow-growing, with an average maximum annual height growth of approximately 0.50 m and diameter growth of approximately 0.5 cm. On good sites, bur oak may reach a height of 24-30 m, 91-122 cm DBH and 200-400 years of age. The species has intermediate shade tolerance.

#### Green Ash (*Fraxinus pennsylvanica* Marsh.)

Green ash ranges from Cape Breton Island and Nova Scotia to southeastern Alberta, south to southeastern Texas, and east to northeastern Florida and Georgia (Kennedy 1990). The species is found over a wide range of substrates, from clay soils subject to frequent flooding to dry sandy or silty soils, with optimum growth on moist, well-drained soils. Green ash is most commonly found on alluvial soils along rivers and streams, and less frequently in swamps. In the western portion of its range, the species is largely restricted to watercourses and river valleys. The species is very

flood tolerant, and can tolerate flooding for approximately 40% of the growing season. Young green ash can develop adventitious water roots on the submerged stem, accelerate anaerobic respiration rates in the absence of oxygen, and oxidize its rhizospheres. These adaptations enable the species to withstand several months of flooding.

Seeds begin to fall as soon as they ripen in late September and October. Most are dispersed by wind within a short distance of the parent tree. Germination may occur in the spring following seedfall, but innate dormancy may delay germination for several years. In the northern part of its range, green ash seedlings grow 30 cm in height in the first year and an additional 46 cm in the second under optimal conditions. Stumps of saplings and “pole-size” green ash readily sprout (Kennedy 1990). Green ash reaches heights of 15-18 m in the northern parts of its range, and 46-61 cm DBH. Roots penetrate about 1 m deep and may extend laterally for 15 m or more. This extensive root system makes the species windfirm.

Green ash is an early successional species on alluvial soils, either as a pioneer or following invasion by cottonwood, trembling aspen and/or willow (*Salix* spp.). The species is shade tolerant in the northern portion of its range, and may grow less than 15 cm in height annually when suppressed under a canopy. However, the species responds well to release and outgrows most of its potential competitors. Deer commonly browse young trees and rabbits may sever the stems of saplings.

#### American Elm (*Ulmus americana* L.)

American elm is found throughout eastern North America, ranging from Nova Scotia to southeastern Saskatchewan, and south to central Texas and central Florida (Bey 1990). Within the range of American elm, the climate ranges from warm and humid to cold and dry. Throughout its range, American elm is most commonly found on flats and bottomlands, with optimal growth occurring on rich, well-drained loams. In the northwestern part of its range it is usually restricted to valley bottoms along watercourses. Soil moisture influences growth, with poor growth occurring on droughty sands and on soils with a high summer water table. The optimum soil pH range is 5.5-8.0. Leaves of the American elm have a high potassium and calcium content, and their decomposition may “improve” soil (Bey 1990).

Flowering, seed ripening and seedfall occur in spring throughout the range of the species. Seedfall is usually complete by mid-June in northern regions. Seed production begins by age 15, but abundant amounts of seed are not produced until age 40. Seeds are light and readily wind-

dispersed. Spring frosts can induce mortality in flowers and fruit, and small mammals and birds may reduce seed crops. Flower buds, flowers and fruit are commonly eaten by gray squirrels (*Sciurus carolinensis* Gmelin), and seeds are eaten by numerous small mammals and birds.

Seeds usually germinate within 6-12 days following dissemination, although they may remain dormant until the following spring. Seeds may germinate on moist litter, moss or decayed logs and stumps, but germination is best on exposed mineral soil. Optimum seedling growth occurs at one-third of full sunlight during the first year. American elm shows intermediate tolerance to flooding.

American elm is infrequently found in pure stands. The species may reach 30-38 m in height and 122-152 cm DBH, although on wet or very dry soils heights of 12-18 m are more typical. The species is long-lived, often reaching 175-200 years of age and occasionally exceeding 300 years. Small trees produce vigorous stump sprouts, and sucker production has been observed in bottom-land stands in Minnesota. The species is classified as intermediately shade tolerant. Once it is established in mixed forest stands, American elm is rarely overtaken by other species.

Throughout most of North America, American elm has essentially been eliminated from the overstory by the fungal pathogen Dutch elm disease. This fungus is introduced into the sap stream of twigs and small branches during feeding by the European elm bark beetle (*Scolytus multistriatus* Marsham) and/or the native elm bark beetle (*Hylurgopinus rufipes* Eichhoff).

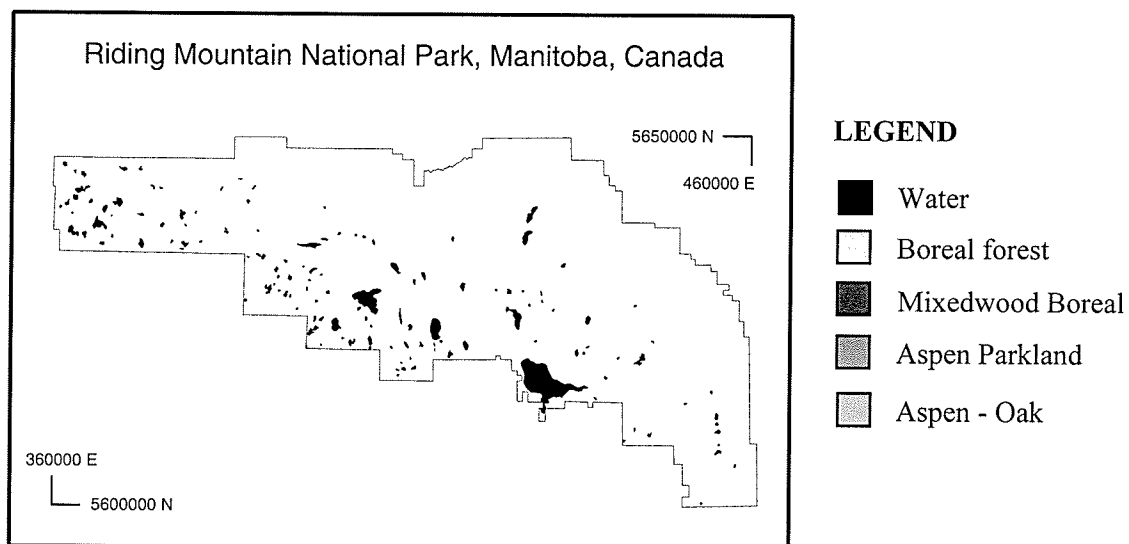
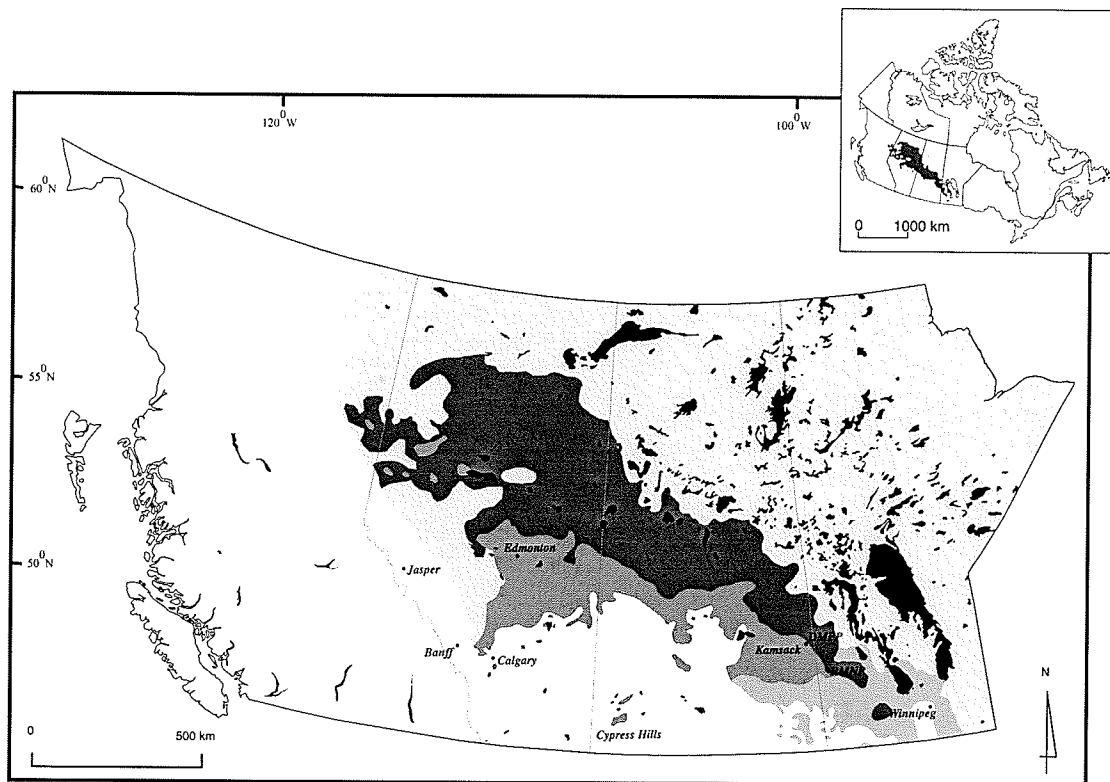
American elm is shallow-rooted on moist soils, but the widespread root system makes the species less susceptible to windthrow. The species may form a taproot 5.5-6.0 m in length when growing on well-drained substrates. The species is fairly drought resistant, although prolonged drought may induce mortality. Animal damage is not major except for injury by sapsuckers and woodpeckers.

#### Manitoba Maple (*Acer negundo* L.)

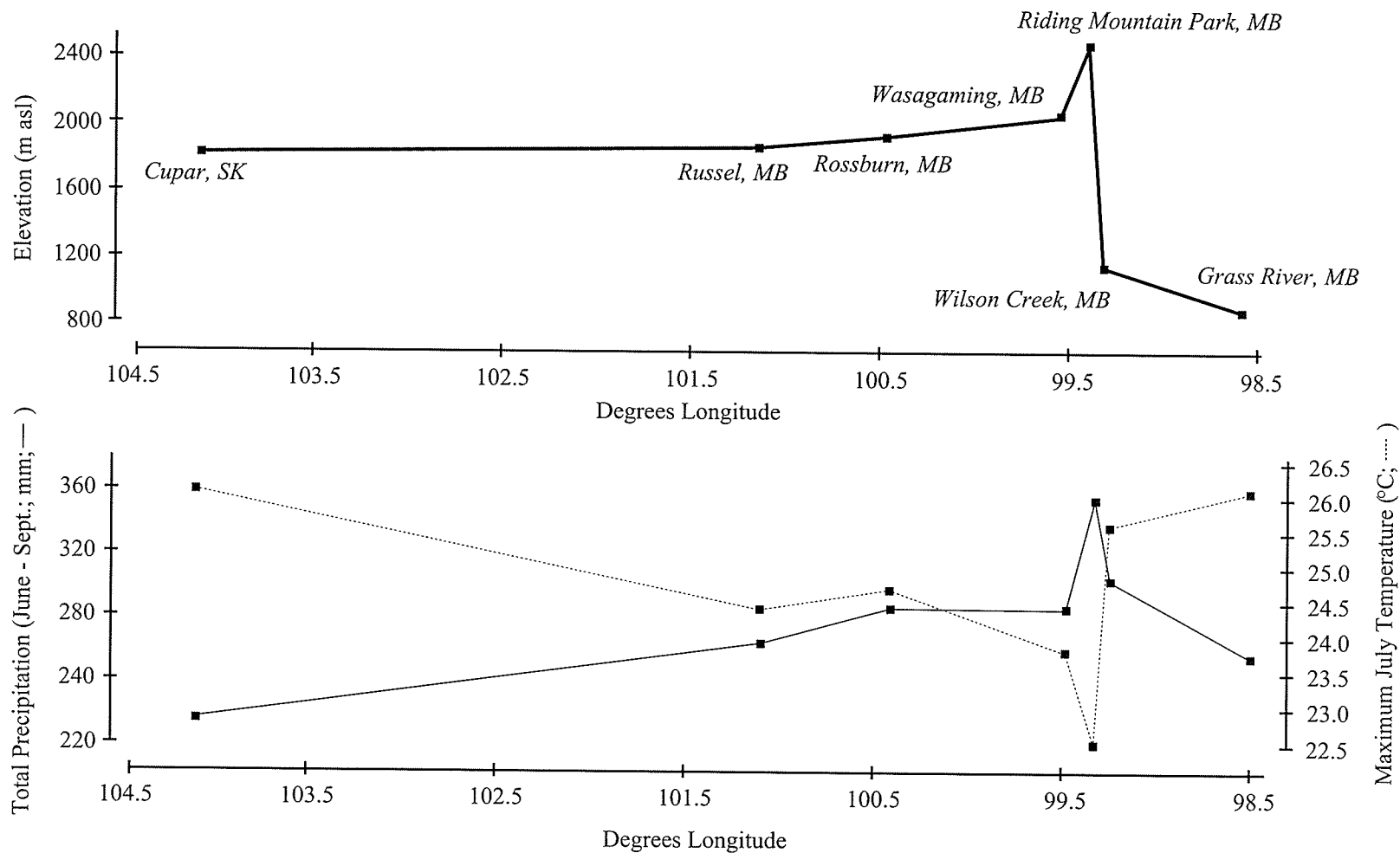
Manitoba maple is the most widely distributed of the North American maples, with disjunct ranges from the east to west coast and from Canada to Guatemala (Overton 1990). The species is most commonly found from New York to central Florida, west to southern Texas, and northwest through the Great Plains region to eastern Alberta, central Saskatchewan and Manitoba, and east into southern Ontario. The species is relatively drought tolerant, but is usually found on moist soils. It can survive inundation for up to 30 days.

Manitoba maple may occur as pure stands on heavy clay soil, although it is most commonly found on deep alluvial soils near streams. It may also occur on upland sites and on 'poor', dry soils. The species commonly develops a shallow, fibrous root system, although short taproots with strong laterals may develop on deep soils. Manitoba maple establishes over a wide range of seedbed conditions, but seedlings soon die if light levels are low. The species is generally classified as shade tolerant.

Seed crops are produced annually beginning at 8-11 years of age. Seeds ripen from August-October and are continuously distributed by wind until spring. Manitoba maple is a small- to medium-sized tree, reaching 15-23 m in height and 60-120 cm DBH. The species is short-lived, rarely achieving an age of 100 years. Growth during the first 15-20 years is very rapid, with annual increases of up to 2.5 cm DBH. In the south, young, vigorous trees frequently reproduce by stump and root sprouts. Trees are commonly damaged by ice and wind, and the species is susceptible to fire and mechanical damage as a result of its thin bark.



**Figure 2.1.** Top: The location of Riding Mountain National Park in relation to Rowe's (1972) Aspen - Oak, Aspen Parkland and Mixedwood Boreal Sections, and Boreal Forest Region. Bottom: Detailed map of the Park. Waterbodies are in black, whereas vegetation regions are highlighted in greyscale.



**Figure 2.2.** Top: elevation (m a.s.l.) and bottom: total precipitation (June - Sept.; mm) and maximum July temperature (°C) for 7 meteorological stations at similar latitude (latitudinal range=50.31-50.51) in and around Riding Mountain National Park. Meteorological station data: Cupar, SK, 1960-1990; Russel, MB, 1960-1990; Rossburn, MB, 1960-1990; Wasagaming, MB, 1966-1989; Riding Mountain Park, MB, 1960-1983; Wilson Creek, MB, 1971-1989; Grass River, MB, 1960-1990 (Environment Canada 1993).

## CHAPTER 3 CLASSIFICATION AND DESCRIPTION OF FOREST STANDS

### 3.1 Introduction

Species assemblages within a region are governed by a host of factors which operate at different spatial and temporal scales. Landform, which incorporates parent material and surficial topography, affects insolation, soil moisture and nutrient status, rates of decomposition, soil formation and disturbance regimes (Viereck 1983; Host et al. 1987). These factors exert a strong influence on the distribution of species communities on the landscape (Dix & Swan 1971; Killingbeck & Bares 1978; Carleton & Maycock 1980; Kenkel 1986, 1987; Bridge & Johnson 1999). Regional and local climatic conditions also control species distributions and associations (Bonan & Sirois 1992; Lenihan 1993; Hogg 1994) and influence the frequency, size and extent of disturbances, especially fire (Wein & Maclean 1983; Johnson 1992). Factors such as ungulate herbivory (McInnes et al. 1992) and insect pest and fungal pathogens (Morin 1994; Hubbes 1999) operate at smaller spatial scales (Frelich & Reich 1995).

The classification of species assemblages in a region, and the identification of vegetation-environment relationships, provides a framework for the summarization of forest community structure and composition across complex landscapes. Such an understanding is required to infer stand dynamic processes.

Classification and ordination are complementary techniques, permitting the classification of vegetation communities and facilitating the identification of relationships between these defined communities, respectively (Bergeron & Dubuc 1989). Maximal information in survey studies results from a dual strategy of classification and ordination (Orlóci 1978; Kenkel 1986). These methods have commonly been used in the literature to study the structure and dynamics of boreal forest communities (e.g. Grigal & Ohmann 1975; Achuff & La Roi 1977; Bergeron & Bouchard 1983; Bergeron & Dubuc 1989; La Roi 1992). Apart from the descriptive work of Rowe (1956) and reports from early surveyors in the Riding Mountain area (Dickson 1909; Tunstell et al. 1922; Evans 1923; Halliday 1932; Tunstell 1940), few studies have examined the structure of forest communities and vegetation-environment relationships in Riding Mountain National Park (RMNP). Studies on bur oak (Wolfe & Kenkel 2000) and spatio-temporal forest dynamics (Walker & Kenkel 1998) have recently been conducted in the Park, providing important information on forest community structure and dynamics. However, forest communities remain poorly understood.

The specific objectives of this chapter are 1) to characterize and describe recurrent forest-vegetation associations (or ‘stand types’) in the Park to summarize variation in forest composition and structure, and 2) to determine and quantify vegetation-environment relationships on the landscape. This information will be used in the creation of a synoptic model of forest stand dynamics for the Park (see Chapter 6).

### 3.2 Methods

#### 3.2.1 Data Collection

##### *Sampling Criteria*

A total of 202 plots were sampled across a wide range of forest associations in RMNP during the 1996-1997 growing seasons (May 31- Aug 31; **Fig. 3.1**). Plots were 10 x 10 m in size, and were sampled if there was no evidence of past logging or human disturbance, and if the vegetation and site conditions were representative over a larger area (typically >0.25 ha).

Plots were located using a combination of resources, including aerial photographs, David Walker’s LANDSAT-based vegetation classification of RMNP, topographic maps, a Global Positioning System, and guidance and advice from the RMNP warden service.

##### *Vegetation*

A complete inventory of all vascular and non-vascular (bryophytes and lichens) plants was conducted in each plot. Epiphytic lichens were not consistently collected in the field and were not included in this study. Within each 10 x 10 m plot, cover-abundance estimates were taken for each species within 6 discrete vegetation ‘canopies’. These canopies are:

<i>Canopy Composition</i>	<i>Canopy Height (m)</i>
Canopy Trees	>15
Subcanopy Trees	10-15
Low Trees, Tall Shrubs	2-10
Saplings, Low Shrubs	0.5-<2
Seedlings, Graminoids, Forbs, Ferns and Fern Allies	<0.5
Bryophytes and Lichens	On forest floor



These plant canopies were chosen to match those of Kenkel & Watson (1996) in order to facilitate interregional comparisons of forest structure and composition. Percent cover values of trees were estimated for the 10 x 10 m plot as a whole, and values for shrubs were obtained within each 5 x 5 m plot nested within the larger 10 x 10 m plot. Herb as well as bryophyte and lichen cover were estimated within a 1 x 1 m plot randomly placed within each 5 x 5 m plot. **Fig. 3.2** illustrates the tree and shrub strata as well as plot design used in this study. The 10 x 10 m plot was examined for any herb or bryophyte and lichen species not collected in the 1 x 1 m plots, and these specimens were noted as present. All vascular and non-vascular plants were identified (**Appendix 1**). Species nomenclature is based on Cody (1988) for vascular plants, Crum (1976) for mosses, Johnson et al. (1995) for liverworts, and Vitt (1988) for lichens. Voucher specimens are being held at the University of Manitoba herbarium (WIN).

Within each plot, diameter at breast height (DBH; 1.3 m) measurements were obtained for each tree, and density measures for all seedlings, saplings and mature stems were recorded. Moreover, herbivore browsing intensity on saplings and shrubs was determined for each plot. In year 2, browsing intensity was determined for each woody species in the understory of each plot. Measures were based on the estimated ratio of the number of twigs browsed / total number of twigs (Trottier 1983), and were placed on an ordinal scale of 1-5: (1) absent; (2) low-moderate; (3) moderate; (4) moderate-heavy; and (5) heavy.

### *Environment*

A soil pit was dug to a depth of 1 m close to the centre of each plot, and soil was taken from the upper 30 cm of the mineral or organic soil. Soils were air dried and brought to the Department of Soil Science at the University of Manitoba for analysis. Each sample was analyzed for pH, conductivity ( $\mu\text{S}/\text{cm}$ ) and particle size (percent sand, silt and clay). In the second field season the depth of the A horizon and depth to carbonates (using dilute 1:10 HCl) were recorded, and profiles were identified to Subgroup level of the Canadian System of Soil Classification (Agriculture Canada Expert Committee on Soil Survey 1987).

Soil pH was measured using the Fischer Scientific Accumet pH meter model 925, and conductivity was measured using the Orion conductivity meter model 160. A 'particle size analysis' was undertaken using the Bouyoucos hydrometer method (see Section 3.2.2; Kalra & Maynard 1991).

Site description data includes measures of percent bareground, degrees slope, aspect (degrees from magnetic north), and location (UTMs). The amount of decaying wood on the forest floor in the form of fallen boles or large branches was estimated for each plot on an ordinal scale of 0-3: (0) absent; (1) low; (2) moderate; (3) high. Wood was considered to be 'decayed' if spongy, and was capable of mechanical separation by hand. Moreover, an estimate of 'minimum stand age' was obtained for each plot by taking increment cores (35.6 cm long x 5 mm diameter) at breast height (1.3 m above ground level) from 2-3 of the largest individuals of each tree species in each plot. This provides a reasonably accurate measure of the time since the last catastrophic, stand-replacing fire. Estimates of minimum stand age are typically conservative since tree cores taken at breast height underestimate the age of the canopy tree by the length of time it takes for the specimen to grow to breast height. Minimum stand age fails to be conservative when 'residual' trees from past fire events are used for estimating plot age. Ages of cores obtained from specimens that were suffering from decay, most commonly trembling aspen (*Populus tremuloides* Michx.) and balsam poplar (*Populus balsamifera* L.), had to be partially estimated. All tree cores were mounted, labeled, finely sanded (using 400 grit sandpaper) and polished (using 600 grit sandpaper), and rings were counted using a dissecting microscope (Parker 1971).

### 3.2.2 Data Analysis: Methods

#### *Soil Particle Size Analysis*

Particle size analysis is a measure of the size distribution of individual particles in a soil sample, and provides a measure of soil texture. The Bouyous hydrometer method determines the proportion of sand (0.5-2 mm), silt (0.002-0.05 mm) and clay (<0.002 mm) particles in a soil sample based on their relative settling rates (using Stoke's Law) when dispersed in solution. Dispersion is obtained through mechanical and chemical separation of soil particles. Mechanical separation physically breaks down particle aggregates, whereas chemical separation disperses smaller particles, especially clay colloids, using sodium hexametaphosphate.

Mechanical and chemical separation were conducted at the same time for each soil sample. A mixture of 50 g of dried and sifted mineral soil, 250 mL of distilled water and 50 mL of dispersing agent (Calgon detergent,  $43 \text{ mg} \cdot \text{L}^{-1}$ ) was blended in a high-speed soil mixer for 10 minutes. The dispersed soil solution was then transferred to a 1000 mL graduated cylinder to begin suspension.

The amount of material held in suspension can be determined by the density of the suspension. Suspension densities were measured at two time intervals: 40 sec. to give the density of silt and clay in suspension, and again at 6 hours 20 minutes when (essentially) only clay is left in suspension. Suspension densities were calculated using a Fischer Scientific soil hydrometer (model 14-331-58) with a specific gravity range of 0.995-1.060. Density measures were adjusted for changes in water temperature, on the order of 0.36 graduation units added for every 1°C above 20°C.  $W_s$ , the weight of the soil particles remaining in suspension at a given time interval was calculated as follows:

$$W_s = \frac{V_t \cdot (D - D_w)}{\left(1 - \frac{D_w}{D_s}\right)}$$

where  $V_t$  is the total volume of water used to suspend the soil (1000 mL),  $D$  is the density of the soil suspension (hydrometer reading) at a given time,  $D_w$  is the density of water ( $1.0 \text{ mg} \cdot \text{m}^{-3}$ ), and  $D_s$  is the density of soil (which is reasonably assumed to be  $2.65 \text{ mg} \cdot \text{m}^{-3}$ ; Greg Morden pers. comm. 1997). From the value of  $W_s$ , proportions of sand, silt and clay were calculated for a given soil sample.

For comparative purposes, and to reduce error, each soil sample was analyzed twice. Measures of solution density were averaged across both trials before calculating proportions of sand, silt and clay.

#### *Effective Species Richness, N2*

Values of effective species richness ( $N_2$ ) were calculated using Simpson's index for the tree, shrub, herb and bryophyte strata for each of the 8 stand types. In order to make comparisons between stand types of different sample sizes, calculations were made using a randomized procedure. Within a given stand type, effective species richness was calculated from percent cover values of species from 10 randomly-selected plots, with  $s$  representing the number of species in the random sample and  $p_i$  representing the proportional cover of the  $i$ th species in the sample:

$$N_2 = \left[ \sum_{i=1}^s p_i^2 \right]^{-1}$$

This procedure was repeated 100 times for each stand type to provide a measure of the ‘mean effective species richness’ for a given category of vegetation (trees, shrubs, herbs, bryophytes).  $N^2$  approaches a maximum value of  $s$  if all species have equivalent cover values, and a minimum value of 1 if one species predominates.

#### *Stand Classification and Description*

Correspondence analysis (CA) is an ‘indirect gradient analysis’. The method is effective at summarizing data redundancy and is robust in handling non-linear data structures. However, CA is sensitive to outliers. This method partitions the total chi-squared ( $\chi^2$ ) of a data matrix  $\mathbf{F}$  into a series of linearly additive components. Partitioning is performed by eigenanalysis of a square symmetric matrix  $\mathbf{S}$ , the elements of which can be defined as:

$$\mathbf{S} = \mathbf{U}\mathbf{U}'$$

$$\text{where } U_{ij} = \left[ \frac{F_{ij}}{\sqrt{(F_i \cdot F_{\cdot j})}} \right] - \left[ \frac{\sqrt{(F_i \cdot F_{\cdot j})}}{F_{\cdot\cdot}} \right]$$

where  $F_{ij}$  is an element of data matrix  $\mathbf{F}$ ,  $F_i$  and  $F_{\cdot j}$  are row and column totals, respectively, and  $F_{\cdot\cdot}$  is the grand total. The first ordination axis consists of the ordering of sites and species to produce the maximum possible correlation between site and species scores (Palmer 1993). The second and higher axes also have maximal site-species correlation subject to the constraint that axes are orthogonal. The eigenvalue  $\lambda_i$  is the squared canonical correlation (‘redundancy’) between the row and column categories on the  $i$ th ordination axis, and ranges from 0-1 (Kenkel 1998).

In this study, CA was used to produce two-dimensional summarizations of the vegetation relationships of the sampled plots (CANOCO; ter Braak 1987b). A dataset of  $n = 196$  plots and  $p = 247$  ‘pseudospecies’ were originally entered into the analysis. Percent cover values were square-root transformed and rare species were ‘downweighted’. Six plots of regenerating jack pine (*Pinus banksiana* Lamb.) and trembling aspen located in the 1980 Rolling River burn were excluded from the analysis. Within each ordination diagram, unique or outlying groups of plots tended to be pulled away from the others, compressing them in the ordination space. A series of residual ordinations were created in order to resolve the variation between the compressed plots. Specifically, the unique groups of plots were removed from each ordination and the remaining plots were reordinated. This was done until major differences between groups of plots could be

visually assessed. Eight stand types were created by visually examining the ordinations and raw cover-data for groups of related plots.

The plots belonging to each of the 8 stand types were reordinated using CA in order to examine variation within each stand type (CANOCO; ter Braak 1987b). Percent cover values were square-root transformed and rare species were downweighted. For each stand type, distinct variants (usually based on moisture regime) were also described.

#### *Vegetation-Environment Relationships*

Canonical correspondence analysis (CCA), also referred to as a 'direct gradient analysis' or 'constrained ordination', is a canonical variant of CA (ter Braak 1986, 1987a; Palmer 1993). This method performs a multiple least-squares regression technique with quadrat scores as the dependant (**Y**) variables, and environmental variables as the independent (**X**) variables. Output describes how well the species information is predicted by the environmental information. The method assumes that species abundances are unimodal functions along environmental gradients.

CCA was used to examine the relationship between 171 species in 179 stands, and 6 edaphic-environmental variables (CANOCO; ter Braak 1987b). Species which occurred fewer than three times in the dataset were omitted before the analysis was conducted, to prevent rare species from dominating the analysis. Percent cover values of the remaining species were square-root transformed, and rare species were downweighted. Edaphic and environmental variables were depth of the LFH horizon, pH, electrical conductivity, soil texture (percent sand and clay), and degrees slope. Since some of these variables were only measured for mineral soils (percent sand and clay, and depth of the LFH horizon), the analysis excludes 17 stands on organic substrates. The 6 plots sampled in the 1980 Rolling River burn were also excluded since they differ dramatically from the remaining stands in terms of their structure and developmental stage. The variable degrees slope was log transformed as  $\log(p+1)$  to meet the assumptions of multivariate normality (Ter Braak 1986, 1987a). Weighted average (WA) scores were used instead of linear combination (LC) scores to place more emphasis on biotic data.

### 3.3 Results and Discussion

#### 3.3.1 Classification of Stand Types

In order to resolve the salient features of the vegetation data and form stand types, residual ordinations were created by sequentially removing outlier groups. The method used is summarized below:

##### 1. Initial Ordination

Correspondence analysis (CA) was used to display relationships among the 196 stands in two-dimensional ordination space (**Fig. 3.3a**). Several outlier plots of unique floristic composition were separated along the first CA ordination axis. These were assigned to stand type I (Black Spruce Organic,  $n = 15$ ) or stand type II (Jack Pine - Black Spruce,  $n = 17$ ) according to canopy composition and soil-environment characteristics. Specifically, black spruce (*Picea mariana* (Mill.) BSP) dominated stands on organic (peat-dominated) substrates were assigned to stand type I, while stands on mineral soil with jack pine in the upper canopy were assigned to stand type II. Note that the remaining  $196 - 32 = 164$  plots were compressed along the first ordination axis. In order to resolve the differences between the remaining plots, the 32 plots assigned to stand types I and II were removed and a residual ordination analysis performed.

##### 2. Residual Ordination I (Removal of Stand Types I and II)

The CA residual ordination (164 plots) is shown in **Fig. 3.3b**. Two distinct outlier groups are clearly separated on the first two ordination axes. Each of these 31 outlier plots were assigned to stand type III (Bur Oak,  $n = 15$ ) or stand type IV (Eastern Deciduous,  $n = 16$ ) based on floristic composition and soil-environmental characteristics. Plots of stand type III occur on well-drained substrates and are characterized by a monodominant bur oak (*Quercus macrocarpa* Michx.) canopy, whereas stand type IV are mixed stands dominated by green ash (*Fraxinus pennsylvanica* Fern), American elm (*Ulmus americana* L.), Manitoba maple and/or bur oak. The remaining  $164 - 31 = 133$  plots were poorly separated in the CA ordination space. A residual ordination was therefore performed after removing stand types III and IV.

##### 3. Residual Ordination II (Removal of Stand Types III and IV)

The CA residual ordination (133 plots) is shown in **Fig. 3.3c**. Plots dominated by balsam fir (*Abies balsamea* (L.) Mill) form a distinct outlier group in the upper right of the ordination space.

These plots were assigned to stand type V (Balsam Fir,  $n = 18$ ). Since the remaining  $133 - 18 = 115$  plots stands were poorly resolved in the ordination space, a final residual ordination was performed after the removing the plots assigned to stand type V.

#### *4. Residual Ordination III (Removal of Stand Type V)*

The residual CA ordination provided a useful resolution of the remaining 115 plots in ordination space (**Fig. 3.3d**). Three distinct groups of plots were recognized based on floristic composition and soil-environmental characteristics: stand type VI (Trembling Aspen – Birch - Mountain Maple,  $n = 22$ ), stand type VII (Trembling Aspen - Balsam Poplar,  $n = 46$ ), and stand type VIII (White Spruce,  $n = 47$ ).

#### *Ordination of Each Stand Type*

Following delineation of the eight stand types I-VIII, the plots belonging to each stand type were separately ordinated (using CA) to summarize the variation within each stand type and to describe stand type ‘variants’. Stand type variants were delineated in the CA ordination space by grouping plots according to their position along a strong underlying moisture gradient. Variants are described in terms of their floristic composition (Section 3.4.4 in this chapter) and successional trajectories (Section 6.3.3 in Chapter 6). The ordination results are not presented.

### 3.3.2 Stand Type Characteristics

#### *Soil-Environment*

Mean edaphic and environmental variables (**Table 3.1**) and soil profile classifications (**Table 3.2**) are summarized for each stand type.

Stand types III, and to a lesser extent stand types II, IV, and V, have more coarse-textured sandy soils. Stand types VI-VIII have the highest clay content and thickest A-horizon. Organic substrates occur in stand type I, and in two plots of stand type VIII. Conductivity and pH are generally low in stand type II, and conductivity is very low in stand type III. Highest values of pH and conductivity were encountered in stand type IV. Depth of the LFH horizon is greatest in stand types IV and V, and lowest in stand type III. Depth to carbonates, a general indicator of soil drainage, is greatest in types II, III, and V (good drainage), and lowest in stand types VII and VIII (poorest drainage). Bare ground cover tends to be highest in conifer-dominated stands (stand types II, V, and VIII). Stand types VI and VIII often occur on slopes.

Soils of stand type I are organic, and are predominantly of the Hydric Fibrisol Subgroup. In stand types II and V-VIII, Orthic Gray Luvisols and Gleyed Gray Luvisols are the most commonly encountered Subgroups. In the eastern stand types III and IV, in comparison, Orthic Eutric Brunisols, Cumulic Regosols and Orthic Regosols predominate.

In general, ungulate herbivore browsing intensity on understory shrub and tree species is heaviest in stand type III and moderately heavy in types IV-VIII. Browsing intensity is lowest in stand types I and II.

#### *Age-Class Distributions*

Age frequency histograms for each stand type are presented in **Fig. 3.4**, and the mean, range, and standard deviation of stand ages in **Table 3.3**. The oldest forests occur in stand type III (mean age >150 years), and in stand types I-II and IV-V (mean ages >100 years). Stand types VI-VIII generally contain younger forests (mean stand age <100 years).

#### *Floristics*

**Table 3.4** summarizes the mean effective species richness of trees, shrubs, herbs and bryophytes for each stand type. Overall effective species richness is greatest in stand types IV-VI, and is the lowest in stand types I and III. Stand types IV and VI have the highest effective richness for trees. Stand types I and III are dominated by black spruce and bur oak, respectively, resulting in the lowest effective richness for trees. Effective richness of shrubs is greatest in stand types II and III and the lowest in V-VII, which tend to be dominated by beaked hazelnut (*Corylus cornuta* Marsh.) and mountain maple (*Acer spicatum* Lam.). Herbaceous richness is greatest in stand type II, followed by VI-VIII, and is lowest in stand types III and IV. The high effective herbaceous richness in stand type II is largely the result of a high evenness of a relatively species-poor understory. Bryophytic richness is greatest in stand type V, and lowest in II and VII.

#### 3.3.3 Vegetation-Environment Relationships

The CCA species-environment biplots are presented in **Fig. 3.5a-g**. Corresponding positions of the 179 plots (stand types II-VIII) in the CCA ordination space are presented in **Fig. 3.5h**. The redundancy of the vegetation-environment relationship (ratio of the canonical inertia to total inertia =  $0.338/4.172$ ) is 8.1%. This indicates that a substantial proportion of the variation in floristic composition is unrelated to the 6 soil-environmental variables measured. The remaining



variation may be explained by a number of factors, including site disturbance history, stochastic events and unmeasured environmental variables.

The two-dimensional CCA ordination space reveals a trend of increasingly coarse soil texture from bottom to top, and a decline in soil pH and nutrient status (conductivity) from right to left. Bur oak is found on coarse-textured, nutrient poor soils in close association with stand type III and drier stands belonging to stand type IV. Bur oak is closely associated with the shrubs *Rhus radicans*, *Symphoricarpos occidentalis* and *Viburnum rafinesquianum*, and the herbs *Smilax herbacea*, *Geum rivale*, *Zizia aurea* and *Aster umbellatus*. The graminoids *Agropyron subsecundum*, *Calamagrostis canadensis* and *Schizachne purpurascens* are commonly associated with bur oak.

The eastern deciduous species Manitoba maple, green ash and American elm occur on less sandy, nutrient-rich substrates, and are largely associated with stand type IV. These species are closely associated with the shrubs *Parthenocissus inserta*, *Ribes hudsonianum* and *Celastrus scandens*, and the herbs *Urtica dioica*, *Humulus lupulus*, *Viola renifolia*, *Aquilegia canadensis* and *Geum aleppicum*. The clonal fern *Matteucia struthiopteris* and the graminoid *Elymus canadensis* are associated with stand type IV. The bryophytes *Anomodon minor*, *Thuidium delicatulum* and *Hypnum palustris* are associated with stand types III and IV.

Jack pine is most commonly found on relatively sandy soils with a low pH and conductivity, and is closely associated with black spruce, white spruce and trembling aspen. The shrubs *Vaccinium myrtilloides*, *Vaccinium vitis-idaea* and *Salix* spp. are commonly found in stands dominated by jack pine and black spruce (stand type II).

White spruce, trembling aspen, balsam poplar, paper birch and balsam fir are found on more fine-textured (silt-clay) soils, and are closely associated with stand types V-VIII. Balsam poplar occurs in more nutrient-rich, less-acidic habitats, and is commonly found in association with the shrubs *Cornus stolonifera* and *Alnus rugosa*. Paper birch, and to a lesser extent balsam fir, are commonly found on sites with a high slope. Beaked hazelnut is found in association with many species and over a broad edaphic range, and is therefore situated near the centre of the ordination space. By contrast, mountain maple has a distinct preference for more fine-textured (silt-clay) soils, and is most commonly found in association with balsam poplar and balsam fir.

### 3.3.4 Description of Stand Types

#### Stand Type I. Black Spruce Organic ( $n = 15$ )

##### *Edaphic - Environment*

These stands occur on poorly to moderately drained organic (peat) substrates. The pH is close to neutral in most stands (mean pH = 6.8), but some sites are quite acidic (**Table 3.1**). The most frequently encountered soil types were of the Hydric Fibrisol ( $f = 0.64$ ) and Hydric Mesisol ( $f = 0.27$ ) Subgroups (**Table 3.2**). Stands range in age from 79-163 years (**Table 3.3**). Herbivore browsing is essentially absent from these stands.

##### *Vegetation*

Black spruce is the dominant tree species in all the canopy layers (**Table 3.5, 3.6**), resulting in a low effective richness for trees in this stand type (mean = 1.2; **Table 3.4**). Total mean basal area per plot is quite high. Eastern larch is sometimes associated with black spruce in the canopy and subcanopy layers, and paper birch is very infrequent in the subcanopy. While black spruce dominates the lower canopy layers, eastern larch, paper birch, balsam fir and/or white spruce are infrequently encountered.

Ericaceous shrubs are common in most stands (**Table 3.7**). *Ledum groenlandicum* is the most frequently occurring shrub, and often occurs at moderate cover in hygric sites. *Vaccinium vitis-idaea*, *Oxycoccus microcarpus* and *Gaultheria hispidula* are also common, but usually occur at low cover. *Alnus rugosa*, *Betula pumila* and *Ribes* spp. are occasionally encountered at low cover in mesic sites.

Herbaceous cover is generally low, with species richness increasing along a hygric to mesic moisture gradient. *Carex* spp., *Rubus pubescens* and *Mitella nuda* are the most frequent and abundant species (**Table 3.8**). *Habenaria hyperborea* and *Equisetum* spp. are infrequent but occur at moderate cover when present.

The understory of most stands is dominated by bryophytes (mean effective richness = 5.0; **Table 3.4**), particularly *Pleurozium schreberi* and *Sphagnum* species (**Table 3.9**). *Aulacomium palustre* and *Hylocomium splendens* are also frequently encountered but generally occur at low cover. Lichens are infrequent in these stands.

#### Variant 1 - Hygric ( $n = 6$ )

Most of these stands were sampled in the eastern portion of the Park, and had a more open canopy (**Appendix 2.1**). Vegetative propagation of black spruce by layering is common. The dominant shrub is *Ledum groenlandicum*. Herb richness and cover are low, the most commonly encountered species being *Carex* spp. and *Habenaria hyperborea*. Moss cover is high and dominated by *Pleurozium schreberi*, *Sphagnum fuscum* and *Sphagnum warnstorffii*. These stands are comparatively oligotrophic and may be somewhat acidic.

#### Variant 2 - Mesic ( $n = 9$ )

Many of these stands are found in the western portion of the Park along the Birdtail River valley. These stands have a more closed canopy than the hygric sites. Black spruce density is very high in the canopy and subcanopy layers, but is greatly reduced in the lower tree strata as a result of heavy shading. Vegetative propagation by layering is not common in these dense stands. Balsam fir, paper birch and white spruce are very infrequently encountered in the lower tree strata. Shrub richness is relatively high, although total cover is low. *Ledum groenlandicum* is present in most stands at low cover. The dominant herbs are *Carex* spp., *Mitella nuda*, *Equisetum arvense* and *Rubus pubescens*. Moss cover is high, the most abundant species being *Pleurozium schreberi* and *Sphagnum warnstorffii*. *S. fuscum* is not present in these stands. *Helodium blandowii* is frequent but occurs at low cover. These stands are more nutrient-rich than the hygric stands.

#### Discussion

Several authors have described self-regenerating black spruce stands, including Rowe (1961) in Alberta, Ritchie (1956) in Manitoba, and Zoladeski & Maycock (1990) in northwestern Ontario. Ritchie (1956) notes that closed upland black spruce stands are the climax for the climatic and edaphic conditions of northern Manitoba. Young post-fire stands tend to be even-aged whereas older stands are open and uneven-aged (Cogbill 1985; Viereck & Johnston 1991). Bonan & Korzuhin (1989) suggest that the dynamic of black spruce stands reflects a complex feedback mechanism involving the forest floor moss-organic layer, the tree species present and prevailing site conditions. Taylor et al. (1987) suggest that succession in black spruce stands is related to stages of tree growth, mortality and thinning, combined with increases in site moisture levels. In upland stands, they note that *Pleurozium schreberi* and other pleurocarpous mosses form a continuous mat on the forest floor, increasing soil moisture and facilitating the invasion of peat mosses (*Sphagnum* species) and eventually leading to site paludification. Fire may reverse the

trend towards paludification in black spruce stands by promoting microbial activity (Viereck 1983).

#### Stand Type II. Jack Pine - Black Spruce ( $n = 17$ )

##### *Edaphic - Environment*

Soil texture in these sites ranges from sandy loam to clay, but most occur on clay loam (**Table 3.1**). Soils are moderately acidic (mean pH = 6.1), somewhat oligotrophic and poorly drained. The most frequently encountered soils belong to the Gleyed Gray Luvisol ( $f = 0.33$ ) and Orthic Luvic Gleysol ( $f = 0.33$ ) Subgroups (**Table 3.2**). The organic (LFH) horizon is poorly developed (mean depth = 5.4 cm) and bare ground cover is high (mean = 21%). Stands range in age from 58-151 years (**Table 3.3**). Herbivore browsing is generally low.

##### *Vegetation*

Younger stands are dominated by jack pine in the canopy, but in older stands black spruce, white spruce and trembling aspen are common co-dominants (**Table 3.10, 3.11**). Balsam poplar occurs infrequently as a canopy co-dominant. The subcanopy and lower tree strata are usually dominated by black spruce, although trembling aspen, white spruce and/or balsam poplar are occasional. Jack pine is not present in the lower canopy layers. Most stands are very dense and dominated by jack pine and black spruce. Species richness is low.

Shrubs are not very abundant in these stands (**Table 3.12**), but have a high mean effective richness (mean = 6.6; **Table 3.4**). The most frequently encountered species are *Rosa acicularis* (found in all stands at low cover) and *Symphoricarpos albus*. The tall shrubs *Amelanchier alnifolia* and beaked hazelnut are uncommon. The ericaceous shrubs *Vaccinium vitis-idaea* and *Ledum groenlandicum* are also infrequent, and generally occur at low cover when present. Herb cover is also low, the most frequently encountered species being *Linnaea borealis* (**Table 3.13**). *Maianthemum canadense*, *Cornus canadensis*, *Anemone canadensis* and *Fragaria virginiana* may also be present at low to moderate cover.

Mean effective bryophytic richness in these dense stands is low (mean = 2.3; **Table 3.4**), dominated by the pleurocarpous feathermosses *Pleurozium schreberi* and *Hylocomium splendens* (**Table 3.14**). *Ptilium-crista castrensis* and *Drepanocladus uncinatus* are fairly common, but they generally occur at low cover. Lichens are generally not abundant, although species of *Cladonia* and *Peltigera* are occasionally encountered.

#### Variant 1 – Mesic ( $n = 10$ )

The upper canopy of these stands is dominated by jack pine, although black spruce may also be encountered (**Appendix 2.2**). The subcanopy and lower tree strata are dominated by black spruce. Shrub cover is typically very low, the most abundant species being *Rosa acicularis*. Herb cover is also very low. The understory is dominated by the feathermosses *Pleurozium schreberi* and *Hylocomium splendens*. *Ptilium crista-castrensis* is frequent but occurs at low cover.

#### Variant 2 - Xeric-Mesic ( $n = 7$ )

These stands often occur on hummocky terrain. They are older jack pine stands in which black spruce, white spruce and/or trembling aspen have established more or less contemporaneously. White spruce, black spruce and/or trembling aspen are generally present in the subcanopy and lower tree strata as well. Balsam poplar is infrequent. Shrub and herb cover varies depending on stand density. In more open stands, *Rosa acicularis*, *Amelanchier alnifolia*, *Rubus idaeus* and/or beaked hazelnut may be present. Common herbs include *Aralia nudicaulis*, *Anemone canadensis*, and *Rubus pubescens*. Feathermoss cover is highest in dense stands.

#### Discussion

Recruitment of jack pine occurs during the first few years following fire, as has occurred in the 1980 Rolling River burn. Black spruce may establish contemporaneously with jack pine (Frelich & Reich 1995), or it may invade into established jack pine stands for 60 years or more (Dix & Swan 1971). In Québec, the majority of black spruce establishment in jack pine stands occurs during the first 30 years following fire (Cogbill 1985). Because black spruce is comparatively slow-growing it is often overtopped by jack pine and may take several years to reach the upper canopy (Frelich & Reich 1995). Black spruce in the lower tree strata remains in a 'suppressed', slow-growing condition until canopy opening occurs (Heinselman 1973).

Jack pine stands begin to deteriorate after 80 years on the best sites, and after 60 years on poor sites (Rudolph & Laidely 1990). Several authors have noted that in the absence of fire, jack pine stands are eventually succeeded by black spruce (Dix & Swan 1971; Carleton & Maycock 1978; Kenkel 1986; Frelich & Reich 1995) or mixed stands of black spruce, trembling aspen, paper birch, balsam fir and/or white cedar (Heinselman 1973). In Minnesota, reduced fire frequencies have changed dominant successional pathways in jack pine forests. Many stands are in transition from even-aged stands of fire origin to uneven-aged mixed stands (Frelich & Reich 1995). In these older stands, succession is driven by small canopy openings caused by wind, insects and

disease, which gradually “chip away” at a uniform jack pine canopy (Bergeron & Dubuc 1989; Frelich & Reich 1995). Jack pine may remain scattered in the canopy of stands for over 200 years, although the species may be extirpated from an area if fire frequencies exceed 200 years (Heinselman 1973; Cogbill 1985; Bergeron & Dubuc 1989). Bergeron & Dubuc (1989) suggest that steady-state black spruce forests are unlikely to occur under natural short fire cycles. If the seed source of jack pine is lost, a reintroduction of burning may lead to dominance by trembling aspen (Frelich & Reich 1995).

### Stand Type III. Bur Oak ( $n = 15$ )

#### *Edaphic - Environment*

These stands typically occur on shale-based alluvial deposits near the base of the Manitoba Escarpment. Soils are coarse-textured, moderately to excessively-drained sandy loams that are pH-neutral (mean pH = 6.7) and of low nutrient status (mean conductivity = 156.5  $\mu\text{S}/\text{cm}$ ; **Table 3.1**). Orthic Eutric Brunisols ( $f = 0.58$ ) and Orthic Regosols ( $f = 0.25$ ) are the most frequently encountered soil Subgroups (**Table 3.2**). The organic (LFH) layer is poorly developed (mean depth = 4.2 cm). Stands range in ages from 95-196 years, with a mean age of 152 years (**Table 3.3**). Oak saplings and seedlings, and the tall shrubs beaked hazelnut and *Viburnum rafinesquianum*, are heavily browsed by ungulate herbivores.

#### *Vegetation*

Trees in these stands are generally <15 m in height. The canopy is very open and is dominated almost exclusively by bur oak (mean effective tree species richness = 1.1; **Table 3.4**). Mean basal area per plot is low compared to other stands (**Table 3.15**). White spruce was found in the canopy of one stand. The lower tree strata are dominated by bur oak at low to moderate density. Green ash saplings are occasionally encountered, whereas balsam fir and trembling aspen saplings are rare (**Table 3.16**).

Shrub cover in these stands is generally very high (**Table 3.17**), and mean effective shrub richness is comparatively high (mean = 5.0; **Table 3.4**). The dominant species are *Viburnum rafinesquianum* and beaked hazelnut. *Amelanchier alnifolia*, *Prunus virginiana*, and *Rosa acicularis* are encountered in all plots but occur at lower cover. *Rhus radicans* is common and may occur at moderate cover when present.

The herb layer is dominated by *Aralia nudicaulis* (Table 3.18). Other frequently encountered species include *Maianthemum canadense*, *Galium boreale*, *Aster ciliolatus*, *Anemone quinquefolia*, *Oryzopsis asperifolia* and *Carex* spp. Bryophyte cover is very low (Table 3.19). The most commonly encountered moss is *Mnium cuspidatum*, which is found growing on decaying wood.

#### Variant 1 - Xeric-Mesic ( $n = 6$ )

These stands occur on substrates that are not excessively drained (lower sand content and depth to carbonates) and of somewhat greater nutrient status. Stand canopies are typically dominated by bur oak; white spruce was encountered in one stand. Green ash is commonly present in the lower tree strata at variable density. Total shrub cover is high, the dominant species being beaked hazelnut and *Viburnum rafinesquianum*. The dominant herb is *Aralia nudicaulis*. Bryophyte cover is low.

#### Variant 2 - Xeric ( $n = 9$ )

These stands occur on excessively drained, nutrient-poor sandy soils over coarse shale deposits (Appendix 2.3). The canopy and lower tree strata of these stands are completely dominated by bur oak. Total shrub cover is very high and dominated by *Viburnum rafinesquianum*. *Prunus virginiana*, *Amelanchier alnifolia* and beaked hazelnut occur at lower frequency and cover, and thickets of *Crataegus chrysocarpa* are occasionally encountered. The dominant herb is *Aralia nudicaulis*. Total herb cover is higher than the stand type mean. Bryophyte cover is low.

### Discussion

Variants 1 (Xeric-Mesic) and 2 (Xeric) of this stand type correspond to Wolfe & Kenkel's (2000) stand type 2A (Oak/Aspen/Green Ash: Subxeric) and stand type 1B (Oak - Low Shrub: Xeric), respectively.

Reduced fire frequencies since the early 1900s in Minnesota have resulted in a change "from scrub oak to oak woods" (White 1983). Previously, frequent fires were important in maintaining the structure and composition of oak communities along the forest-prairie transition zone. Tester (1989) notes that frequent fires are important for the natural regeneration of oak savanna, and should be recognized as a common natural event. In oak savanna, species richness is promoted by increased frequency of prescribed burns. In addition, frequent burning greatly reduces the abundance of competitive woody species, particularly shrubs (White 1983; Tester 1989). Wolfe & Kenkel (2000) have found that a lack of fire, in combination with intensive ungulate herbivory,

promotes shrub dominance in oak stands. A dense shrub canopy may promote the replacement of bur oak by more shade tolerant species such as green ash (Wolfe & Kenkel 2000).

In Minnesota, Ritchie et al. (1998) found that mammalian herbivores, particularly white-tailed deer (*Odocoileus virginianus* Zimmermann), indirectly control the productivity, nitrogen cycling and forest succession of oak stands by consuming nitrogen-fixing legumes and woody plants. Seven years of herbivore exclusion resulted in a five-fold increase in the cover and biomass of legumes and woody plant species, especially *Lathyrus venosus* and *Quercus* spp. Exclusion was also found to enhance nitrogen cycling.

#### Stand Type IV. Eastern Deciduous ( $n = 16$ )

##### *Edaphic - Environment*

These stands occur over a relatively wide range of edaphic-environmental conditions. Soil texture and drainage (depth to carbonates) vary according to stand location. Although many soils have a sandy loam texture, texture ranges from sandy loam to clay (**Table 3.1**). Soils are basic (mean pH = 7.2) and nutrient rich (mean conductivity = 378.1  $\mu\text{S}/\text{cm}$ ), and the organic (LFH) layer is well developed (mean depth = 7.1 cm). Cumulic Regosols ( $f = 0.38$ ) predominate, followed by Orthic Eutric Brunisols ( $f = 0.15$ ) and Orthic Regosols ( $f = 0.15$ ) (**Table 3.2**). Stands range in age from 76-170 years (**Table 3.3**). Herbivore browsing of saplings, seedlings and shrubs is heavy.

##### *Vegetation*

The canopy of these stands is generally dominated by a mixture of American elm, green ash and Manitoba maple, although trembling aspen, balsam poplar, bur oak, paper birch and/or cottonwood may also occur (**Table 3.20, 3.21**). Green ash, Manitoba maple and American elm are the most abundant species in the subcanopy and lower tree strata. Trembling aspen and balsam poplar do not occur in the lower tree canopies, and paper birch, bur oak and cottonwood are uncommon there. Total mean tree density per plot is high, attributable largely to strong regeneration in the subcanopy and sapling layers. Mean basal area per plot is relatively low. These stands are characterized by high per plot mean effective species richness (**Table 3.4**).



Shrub cover ranges from low to moderately high depending on stand location (**Table 3.22**). *Prunus virginiana* occurs in all plots. Beaked hazelnut is common and may occur at high cover when present. *Viburnum trilobum* and *Viburnum rafinesquianum* are less frequent and generally occur at low cover. The most common low shrub is *Rhus radicans*.

These stands typically have a species-rich herb layer that varies in composition and total cover (**Table 3.23**). *Carex* spp. and *Aralia nudicaulis* are often encountered at moderate cover. The fern *Matteucia struthiopteris* occurs in over half the stands and often occurs at high cover when present. Other common herb species include *Thalictrum dasycarpum*, *Rudbeckia laciniata* and *Maianthemum canadense*. A number of eastern deciduous herbs are at or near their northern and western distributional limits in these stands, including *Sanicula marilandica*, *Rudbeckia laciniata* and *Phryma leptostachya*.

Bryophytes are not abundant in these stands (**Table 3.24**), but have a comparatively high mean effective richness (mean = 4.5; **Table 3.4**). The most frequently encountered species are *Mnium cuspidatum* and *Brachythecium* spp., which are found growing on decaying wood. Mosses with an eastern floristic affinity were also encountered in these stands, including *Anomodon minor*, *Callicladium haldanianum* and *Rhodobryum ontariense*. Lichens are rare.

#### Variant 1 - Hygric-Mesic ( $n = 6$ )

These stands are found along the base of the Manitoba Escarpment on moist, nutrient-rich, basic substrates (**Appendix 2.4**). Soils are typically gleyed and have a low depth to carbonates, indicating impeded drainage. The canopy is typically dominated by Manitoba maple, green ash and American elm, with the occasional balsam poplar or trembling aspen. American elm, Manitoba maple and green ash are regenerating well in the subcanopy and lower tree strata. Shrub cover is low, the most commonly encountered species being *Prunus virginiana* and *Ribes triste*. The understory is usually dominated by an almost continuous cover of the clonal fern *Matteucia struthiopteris*. *Carex* spp. and *Osmorrhiza longistylis* are also common, but occur at low cover. Bryophytes are found on decaying wood at low cover.

#### Variant 2 - Mesic ( $n = 9$ )

These stands occur on moderately-drained, somewhat sandy soils along the Manitoba Escarpment, and occasionally along water courses in the central and western regions of the Park. They are characterized by a relatively open canopy that is typically dominated by American elm, green ash and/or Manitoba maple. Paper birch, trembling aspen, cottonwood and bur oak are

occasional associates. Green ash, and to a lesser extent Manitoba maple, are abundant in the subcanopy and lower tree strata layers. American elm and bur oak are also commonly encountered, and more rarely paper birch and cottonwood. Shrub cover is often high in these stands, the dominant species being beaked hazelnut. *Viburnum rafinesquianum* and *V. trilobum* are also common but usually occur at lower cover. The herb layer is dominated by *Aralia nudicaulis*, with *Carex* spp., *Maianthemum canadense* and *Oryzopsis asperifolia* occurring at lower cover. Bryophyte cover is low.

### Discussion

Many Great Lakes species reach their eastern and northern limits in northern Minnesota, western Ontario and eastern Manitoba (Swan & Dix 1966). As a result, the forests of Saskatchewan contain very few eastern deciduous elements. The eastern deciduous forests of Manitoba are poorly studied. Bailey (1968) suggests that the eastern deciduous forests of RMNP are self-perpetuating, since the constituent species are found in the subcanopy and sapling layers.

Several studies have examined the structure and dynamics of eastern deciduous 'gallery' forests along the Missouri River in North and South Dakota (Wilson 1970; Keammerer et al. 1975; Johnson et al. 1976; Reily & Johnson 1982). These forests are typically dominated by green ash, American elm, Manitoba maple and bur oak, while cottonwood and peach-leaved willow (*Salix amygdaloides* Anderss.) are less frequently encountered. The structure and composition of gallery forests are determined by both stand age and the relative flood-tolerance of tree species (Johnson et al. 1976). Green ash has a wide ecological amplitude and readily colonizes both floodplain habitats and mesic-xeric upland terraces (Killingbeck & Bares 1978). American elm enters the successional sequence later than green ash and Manitoba maple, and is generally restricted to more mesic, nutrient-rich stands. The species is highly tolerant of periodic flooding and saturated soils. Bur oak occurs only in the oldest stands, and is most abundant on mesic upland terraces. It is relatively flood-intolerant and does not occur in floodplain habitats.

The deciduous forests in northeastern North Dakota have been described as a western extension of the eastern deciduous forest, with some boreal species such as paper birch (Wikum & Wali 1974; Killingbeck & Bares 1978). There are pronounced differences in floristic composition and structure between floodplains and higher slopes (Wikum & Wali 1974). Aspect and elevation are important in determining stand characteristics, since they determine potential solar irradiation as well as soil water and nutrient status. Killingbeck & Bares (1978) found that topographic and

edaphic factors were both important determinants of forest community composition. Bur oak was most abundant on well-drained soils, while paper birch was only encountered on steep, north-facing slopes. Soils of higher nutrient status were found to support more dense forest stands.

In Iowa and southwestern Michigan, Dutch elm disease (*Ophiostoma ulmi* (Buism) Nannf.) has virtually eliminated American elm from the overstory (Bey 1990). However, the species continues to be a major component of the understory and seedling layers. Rapid mortality of American elm creates large canopy gaps that may be colonized by less shade-tolerant tree species.

#### Stand Type V. Balsam Fir ( $n = 18$ )

##### *Edaphic - Environment*

These stands are restricted to a small area in the north-eastern portion of the Park near the base of the Manitoba Escarpment. They are usually found on well-drained, slightly basic (mean pH = 6.7), moderately nutrient-rich (mean conductivity = 237.7  $\mu\text{S}/\text{cm}$ ) sandy loams (soil texture ranges from sandy loam to clay) (**Table 3.1**). The most frequently encountered soils belong to the Orthic Gray Luvisol Subgroup ( $f = 0.33$ ), followed by the Gleyed Gray Luvisol ( $f = 0.22$ ) and Orthic Gleysol ( $f = 0.22$ ) Subgroups (**Table 3.2**) The organic (LFH) layer is well developed (mean depth = 7.9 cm), and the understory is characterized by high percentage cover of bare ground (mean bareground = 20.2%). Stands range in age from 75-165 years (**Table 3.3**). Herbivore browsing of tree saplings and shrubs is moderately heavy.

##### *Vegetation*

Stands are characterized by a high density and canopy cover of balsam fir (**Tables 3.25, 3.26**). Paper birch, trembling aspen, balsam poplar and/or white spruce are commonly encountered as canopy co-dominants, while green ash and American elm are occasional. The subcanopy and lower tree strata are typically dominated by balsam fir, often at high density. Paper birch is common in the subcanopy but is rarely encountered in the lower tree strata. Balsam poplar, green ash and/or white spruce are found in the subcanopy at low frequency. Seedlings and saplings of balsam fir are abundant. White spruce and green ash are also occasionally encountered in the lower tree strata. Saplings of balsam fir are heavily browsed by herbivores. Mean effective species richness per plot is high (**Table 3.4**).

These stands have a well-developed tall shrub layer that is usually dominated by mountain maple (**Table 3.27**). Beaked hazelnut and *Prunus virginiana* are also frequently encountered but occur at lower cover. The low shrubs *Rosa acicularis* and *Symphoricarpos albus* are also found in most stands. Overall, the mean effective richness of shrubs is comparatively low (mean = 2.2; **Table 3.4**).

The herb layer is moderately species-rich (mean = 9.2; **Table 3.4**). *Aralia nudicaulis* is the most abundant species and occurs in all stands (**Table 3.28**). Other frequently encountered herbs include *Carex* spp., *Mitella nuda* and *Maianthemum canadense*, but they usually occur at low cover. *Cornus canadensis* and *Rubus pubescens* are encountered less frequently, but may have high cover when present.

Bryophytes typically occur at low cover (**Table 3.29**) but have a high mean effective richness in these stands (mean = 6.2; **Table 3.4**). Stands belonging to this stand type are relatively old, have coniferous-dominated canopies (i.e. low deciduous leaf litter), and have an abundance of decaying wood in various stages of decay on the forest floor (i.e. high microsite abundance). These factors promote a high mean effective bryophytic richness in these stands (Crites & Dale 1998). The most commonly encountered species are *Mnium cuspidatum*, *Brachythecium* spp., *Eurhynchium pulchellum*, *Hylocomium splendens* and *Pleurozium schreberi*. Lichens of the genera *Cladonia* and *Peltigera* are infrequent and occur at low cover.

#### Variant 1 - Mesic-Hygic ( $n = 5$ )

These stands are characterized by a canopy dominated by balsam fir, with paper birch, green ash, balsam poplar, American elm and/or trembling aspen as occasional canopy subdominants. Balsam fir also dominates the subcanopy, although green ash, trembling aspen, white spruce and/or paper birch are infrequently encountered. Both balsam fir and white spruce occur at moderate density in the lower tree strata, while green ash and Manitoba maple are less frequent. Paper birch is not found in the lower tree strata. The tall shrub mountain maple occurs at high cover in these stands, while moss and herb cover are low. Bareground cover is very high, which is likely attributable to the dense shrub canopy.

#### Variant 2 - Mesic ( $n = 13$ )

These stands occur on moderately-drained sandy loams, and have a well-developed organic (LFH) layer. They are dominated by balsam fir in the canopy (**Appendix 2.5**). Paper birch is a canopy co-dominant in some stands, while other stands have both white spruce and balsam poplar

as canopy co-dominants. Trembling aspen is also occasionally encountered in the canopy. Balsam fir is abundant in the subcanopy and lower tree strata layers of these stands. Balsam poplar is also abundant in the subcanopy layer of some stands. Paper birch, American elm, white spruce and/or green ash are less frequently found in the subcanopy and lower strata. These stands differ from those of the previous variant in having a much lower tall shrub cover. Mountain maple, beaked hazelnut and *Rosa acicularis* are the most commonly encountered shrub species. Herb cover is greater than in the previous variant. The dominant species are *Aralia nudicaulis*, *Cornus canadensis* and *Rubus pubescens*. Bryophyte cover is also greater than in the previous variant. The most frequently encountered species are *Hylocomium splendens*, *Brachythecium* spp., *Mnium cuspidatum* and *Pleurozium schreberi*.

### *Discussion*

Anecdotal evidence indicates that balsam fir was much more abundant in RMNP at the turn of the century than it is today. Dickson (1909) noted that it was difficult to prevent balsam fir “from seeding cut-over spruce lands” and that the species was “one of the forester’s chief problems”. He noted that 1.5% of all saw material (stems >20 cm DBH) in the Riding Mountain Forest Reserve was balsam fir, and recommended that seed trees of balsam fir be cut or girdled to prevent invasion of the species into white spruce stands.

Balsam fir does not regenerate during the initial stages of stand recolonization following fire (Dix & Swan 1971; Carleton & Maycock 1978), and has difficulty establishing on xeric substrates and in areas of strong competition from light-demanding species (Galipeau et al. 1997). Balsam fir seedlings begin to appear once a stand develops a closed canopy, usually after 30 to 50 years (MacLean 1960; Galipeau et al. 1997). Optimal regeneration of balsam fir occurs under a canopy cover of 40-80% (MacLaren & Janke 1996). The species is a highly prolific seeder that readily colonizes canopy gaps created through windfall and natural mortality (MacLaren & Janke 1996). Tall shrubs such as mountain maple may also colonize canopy openings in stands older than 120 years (DeGrandpré et al. 1993). On clayey and silty sites in Ontario, shrub cover increases as the canopy opens, making coniferous establishment difficult (MacLean 1960). Mixed fir stands are also constantly subject to disturbance by pathogens and windthrow (Cogbill 1985). Spruce budworm (*Choristoneura fumiferana* Clemens) causes mortality in balsam fir and to a lesser extent white spruce. Outbreaks may influence forest dynamics through gap creation (Bergeron & Dubuc 1989), favouring the regeneration of less shade-tolerant species such as white spruce, black spruce and paper birch (Bergeron & Dansereau 1993; Frelich & Reich 1995).

Severity of spruce budworm outbreaks are decreased in mixed forests of low balsam fir density (Bergeron et al. 1995; Su et al. 1996). Mixed stands of balsam fir, white spruce and paper birch, once established, are thought to be self-perpetuating (Buell & Niering 1957; Achuff & LaRoi 1977).

In Saskatchewan, the "relative unimportance of succession in the landscape" was attributed to high fire frequency (Dix & Swan 1971). Balsam fir commonly occurred in the seedling and sapling layers of these Saskatchewan stands, but rarely reached the canopy. Many authors suggest that balsam fir will become a dominant species in the absence of fire (Grigal & Ohmann 1975; Carleton & Maycock 1978; Bergeron & Dubuc 1989). When stands are overmature and begin to degenerate (typically after 200 years), balsam fir is the only species to increase in abundance since it readily reproduces under moderate shade and does not have demanding seedbed preferences. As a result, balsam fir may largely replace white spruce, trembling aspen and paper birch, since white spruce reproduction is often poor and windfalls may not provide enough light for the establishment of trembling aspen or paper birch (MacLean 1960). However, several recent studies indicate that paper birch can regenerate well in older stands (Grigal & Ohmann 1975; Kneeshaw & Bergeron 1996; Frelich & Reich 1995). Paper birch can establish in large gaps created by intermediary disturbances that are not light-limited (Frelich & Reich 1995). A dynamic stand equilibrium may exist at the landscape level if there is a stable pattern of gap formation over time (Bergeron & Dubuc 1989).

#### Stand Type VI. Trembling Aspen – Birch - Mountain Maple ( $n = 22$ )

##### *Edaphic - Environment*

These stands occur over a wide range of site conditions, although the majority are found on slightly acidic (mean pH = 6.6) clay loam soils with a well-developed A-horizon (mean depth = 14.9 cm) (**Table 3.1**). Many of these stands occur on slopes along the Manitoba Escarpment. Soil drainage and nutrient status vary widely. The most frequently encountered soils belong to the Orthic Gray Luvisol Subgroup ( $f = 0.44$ ), followed by Gleyed Gray Luvisols ( $f = 0.22$ ) and Orthic Gleysols ( $f = 0.22$ ) (**Table 3.2**). Most stands are comparatively young, ranging in age from 55-145 years (**Table 3.3**). Herbivore browsing is heavy.

## Vegetation

The canopy of these stands is typically quite open (**Tables 3.30, 3.31**). The dominant canopy species is trembling aspen. Balsam poplar and paper birch are commonly encountered canopy co-dominants, while green ash and white spruce are infrequent. In most stands paper birch dominates the subcanopy, but trembling aspen and/or balsam poplar may also be present. The lower tree strata usually have moderate densities of green ash and/or paper birch, although trembling aspen, Manitoba maple, American elm, white spruce, balsam poplar and/or bur oak are also occasional. Mean effective richness of tree species is high (mean = 3.2; **Table 3.4**).

Total shrub cover in these stands is high (**Table 3.32**), although mean effective richness is comparatively low (mean = 2.6; **Table 3.4**). Mountain maple is the dominant species, but beaked hazelnut is also frequent and may be abundant. Other common shrubs include *Prunus virginiana*, *Cornus stolonifera*, *Ribes triste*, and *Rosa acicularis*, but their cover is much lower.

The heavy tall shrub cover in these stands results in a poorly developed understory. As a result, total cover of herbs and bryophytes is quite low (**Tables 3.33, 3.34**). The most commonly encountered herb species are *Aralia nudicaulis*, *Rubus pubescens*, *Pyrola asarifolia*, *Maianthemum canadense*, and *Galium triflorum*. The mosses *Brachythecium* spp. and *Mnium cuspidatum* are commonly encountered but occur at very low cover.

### Variant 1 - Mesic ( $n = 12$ )

These stands are typically found near the base of the Manitoba Escarpment on level to gently sloping ground (**Appendix 2.6**). The canopy is dominated by trembling aspen, but balsam poplar is a frequent associate. Paper birch and green ash are infrequently encountered in the canopy. Trembling aspen and balsam poplar are occasionally found in the subcanopy and lower tree strata, while white spruce, Manitoba maple, bur oak, American elm and/or paper birch are less frequent. Green ash is often abundant in the lower tree strata, while Manitoba maple and American elm are occasional and bur oak, white spruce and paper birch are infrequent. Shrub cover is high and dominated by mountain maple. Total herb and moss cover are low.

### Variant 2 - Xeric ( $n = 10$ )

These stands typically occur on well-drained slopes along the steep portions of the Manitoba Escarpment (**Appendix 2.7**). The canopy is dominated by both trembling aspen and paper birch, with white spruce and balsam poplar as occasional associates. The subcanopy and lower tree strata are dominated by paper birch. Trembling aspen, white spruce and/or balsam poplar are

infrequent. Green ash, American elm, Manitoba maple and bur oak are rarely encountered in these stands. Shrub cover is high and dominated by beaked hazelnut. Herb and bryophyte cover are low.

### *Discussion*

In the mesic variant of this stand type, succession is toward increased abundance of green ash and Manitoba maple at the expense of trembling aspen and balsam poplar. Trembling aspen can remain in the canopy of boreal stands for over 200 years (Bergeron & Dansereau 1993), but it is highly shade-intolerant and does not normally regenerate beneath a closed canopy (Dix & Swan 1971; Perala 1990). Mature individuals of trembling aspen (>60 years in age) are very susceptible to trunk rot (especially *Fomes igniarius* (L.) Gill.), which reduces suckering (Rowe 1956). By contrast, green ash is relatively shade-tolerant at the northern limit of its range. Green ash grows slowly when suppressed, but responds well to release and outgrows its potential competitors (Kennedy 1990).

Mountain maple has medium moisture and nutrient requirements, and low heat and light requirements (Sullivan 1993). In the northern parts of its range, it prefers rich, moist soils on rocky slopes, flats and along streams. The understory light regime in which mountain maple most commonly occurs is characterized by low, diffuse light punctuated by short pulses of sunflecks (Lei & Lechowicz 1990). Green ash also has optimal growth in partial shade (Kennedy 1990), and is found growing in association with mountain maple in eastern parts of its range (Rossario 1988). Mountain maple is a common understory or subcanopy component in communities that are not susceptible to fire, such as eastern mixed spruce-fir forests and hardwood-conifer forests of lower slopes (Heinselman 1981). The species exhibits a density/age distribution that is similar to that of climax trees (Clark 1990). Germination and seedling establishment are improved on undisturbed soils, and are not enhanced by bare mineral soil (Sullivan 1993). Like green ash, mountain maple colonizes the understory of pioneer tree species (e.g. trembling aspen) as they decline in abundance, often dominating the understory along with beaked hazelnut (Sullivan 1993). The species has been found to inhibit the establishment of white spruce, balsam fir and paper birch (Vincent 1965; Kneeshaw & Bergeron 1996).

The xeric sites of this stand type usually occur on steep slopes of the Manitoba Escarpment. These stands will become increasingly dominated by paper birch as the abundance of trembling aspen declines. Paper birch is not abundant in RMNP, except along the north- and east-facing slopes of the Manitoba escarpment (Rowe 1956). These unstable slopes are subject to seepage



and so provide a moist mineral soil for seedling establishment. Unlike many other boreal tree species, the root system of paper birch can tolerate shifting soil. Although paper birch is a pioneer species that rapidly invades burned sites, it can also survive in long-established conifer stands (Rowe 1955; Swan & Dix 1966). Paper birch can regenerate from seed or vegetative sprouts. Sprouting is usually not prolific enough to replace mature stands, but it facilitates regeneration of the species on 'difficult' sites (Safford et al. 1990). Sprouting ability decreases with age, and sprouted individuals tend to die sooner than those initiated from seed (Zasada et al. 1992).

#### Stand Type VII. Trembling Aspen - Balsam Poplar ( $n = 46$ )

##### *Edaphic - Environment*

These stands occur on slightly acidic (mean pH = 6.3), fine-textured soils (clays or clay loams) in the central and western uplands of the Park (**Table 3.1**). Drainage ranges from moderate to poor, with soils of the Orthic Gray Luvisol Subgroup predominating ( $f = 0.60$ ) (**Table 3.2**). Most stands are relatively young, with stand ages ranging from 37-150 years (**Table 3.3**). The organic (LFH) layer is often poorly developed (mean depth = 5.8 cm). Herbivore browsing of saplings, seedlings and shrubs is moderate.

##### *Vegetation*

These are typically relatively open stands (**Tables 3.35, 3.36**). The canopy is dominated by trembling aspen and/or balsam poplar, with balsam poplar being favoured in more poorly drained sites. White spruce and paper birch are infrequent canopy associates. Trembling aspen and balsam poplar are also common in the subcanopy, with white spruce, paper birch, green ash and/or Manitoba maple occurring much less frequently. White spruce, green ash or Manitoba maple occur infrequently in the lower tree strata of some stands. Mean effective richness of trees is low (mean = 2.2; **Table 3.4**).

Shrub cover in these stands is typically very high (**Table 3.37**), but mean effective richness is low (mean = 2.5). The dominant tall shrub, beaked hazelnut, occurs at high frequency and cover (mean cover of approximately 31%). *Prunus virginiana*, *Amelanchier alnifolia* and *Rosa acicularis* are also common, but they occur at much lower cover.

Total herb cover is fairly low in these stands (**Table 3.38**), but mean effective richness is comparatively high (mean = 11.3). The most frequently encountered species are *Aralia nudicaulis*, *Fragaria virginiana*, *Maianthemum canadense*, *Aster ciliolatus*, *Viola rugulosa* and

*Rubus pubescens*. Bryophyte cover and is also low. *Brachythecium* spp. and *Mnium cuspidatum* are the most commonly encountered species (Table 3.39). A low mean effective bryophytic richness (mean = 2.4) in these stands is the combined result of heavy leaf litter, a dense understory shrub layer, and a low abundance of decaying wood substrates.

#### Variant 1 - Xeric-Mesic ( $n = 16$ )

Trembling aspen dominates the canopy in more well-drained xeric-mesic sites, although balsam poplar and white spruce occur infrequently as co-dominants. Trembling aspen also dominates the subcanopy, and vegetative suckers are often abundant in the lower tree strata. White spruce occurs in the subcanopy and lower tree strata of half the stands. Shrub cover is lower than the stand type mean, and the dominant species is *Rosa acicularis* although beaked hazelnut is also common. Herb cover is moderately high, the most frequently encountered species being *Fragaria virginiana*, *Carex* spp. and *Aster ciliolatus*. Bryophyte cover is low.

#### Variant 2 - Mesic ( $n = 17$ )

These stands are dominated by trembling aspen, with balsam poplar as an occasional co-dominant. Paper birch and white spruce are infrequently encountered in the upper canopies. Trembling aspen suckers are common in lower tree strata, while balsam poplar and white spruce are infrequent. A heavy cover of the tall shrub beaked hazelnut characterizes these stands. The heavy shade cast by the shrub layer reduces herb and bryophyte cover, resulting in high bare ground cover.

#### Variant 3 - Mesic-Hygic ( $n = 13$ )

These stands occur on more poorly-drained, nutrient-rich sites. The dominant canopy species is balsam poplar, although trembling aspen is a common co-dominant. Paper birch is infrequent in the canopy. Trembling aspen, white spruce and paper birch are absent from the subcanopy and occur infrequently in the lower strata. In some stands, green ash, Manitoba maple and/or balsam poplar are present in the lower strata. Shrub cover is heavy and dominated by beaked hazelnut. *Prunus virginiana* is also common but occurs at low cover. Herb and bryophyte cover are low.

### Discussion

Well-drained sites may be invaded and succeeded by white spruce. Others are being succeeded by eastern deciduous species such as green ash and Manitoba maple. However, many stands are expected to become increasingly shrub-dominated (mainly beaked hazelnut). This is attributable to the combined effects of the lack of a ready seed source of white spruce and other later-

successional species, and heavy ungulate browsing. Such shrub-dominated communities are common in older deciduous stands along the upper reaches of the Manitoba escarpment. These stands are characterized by a dense cover of beaked hazelnut interspersed with a few relict individuals of trembling aspen and/or paper birch (**Appendix 2.8**).

Trembling aspen is an aggressive pioneer that readily colonizes burned sites but rarely lives beyond 150 years (Perala 1990). The species is susceptible to trunk rot, and stands are considered 'overmature' by age 100 (Rowe 1956). Balsam poplar is similar to trembling aspen in terms of its shade tolerance, modes of regeneration, and rapid initial growth. However, it is more aggressive on moist sites and is better adapted to establishing and regenerating on silty alluvial deposits. In addition, balsam poplar outlives trembling aspen and is less susceptible to fungal decay (Rowe 1956).

Trembling aspen can be self-perpetuating in the absence of a major disturbance (Perala 1990). However, several authors have noted that in the absence of fire and seed sources of shade-tolerant tree species, pure aspen stands often deteriorate and become shrub-dominated (Rowe 1956, 1955, 1961; MacLean 1960; Dix & Swan 1971; Carleton & Maycock 1978; Zoladeski & Maycock 1990). In Québec, Cogbill (1985) noted that mountain maple or beaked hazelnut virtually dominate canopy openings to the exclusion of trees. An early study in RMNP noted that older trembling aspen individuals lose their ability to sucker, and as these trees die the stands become increasingly dominated by beaked hazelnut (Rowe 1955). In these stands tree cover is highly discontinuous and composed of scattered overmature trembling aspen, with the occasional white spruce, paper birch and/or balsam poplar (Bailey 1968). Heavy browsing of understory saplings by elk (*Cervus elaphus* L.) and moose (*Alces alces* L.) may indefinitely favour shrub dominance.

Beaked hazelnut is the dominant shrub species of the uplands of RMNP. High light intensity following canopy opening favours vegetative propagation of the species, while heavy shading by coniferous species results in high mortality (Tappeiner & John 1973; Trottier 1983; Kurmis & Sucoff 1989). Persistent beaked hazelnut populations have an 'all-aged' structure with the highest frequencies in the shorter (younger) stem classes (Kurmis & Sucoff 1989). Areas dominated by beaked hazelnut are capable of supporting dense ungulate populations, since the species is preferred browse for moose, elk and white-tailed deer (**Appendix 2.9**; Trottier 1983). Unlike mountain maple and trembling aspen, beaked hazelnut is highly resistant to heavy browsing.

## Stand Type VIII. White Spruce ( $n = 47$ )

### *Edaphic - Environment*

Most of these stands occur on gentle to steep slopes in the east-central portion of the Park. Most occur on moderately-drained, slightly acidic (mean pH = 6.4) clay loams, but soil texture ranges from sandy loam to clay (**Table 3.1**). A wide range of soil types were encountered, the most frequent being the Gleyed Gray Luvisol Subgroup ( $f = 0.20$ ), followed by the Orthic Gleysol ( $f = 0.16$ ), Orthic Gray Luvisol ( $f = 0.16$ ) and Orthic Luvic Gleysol ( $f = 0.16$ ) Subgroups (**Table 3.2**). Stands range in age from 44-180 years (**Table 3.3**). Herbivore browsing is moderate.

### *Vegetation*

These stands are characterized by a canopy dominated by white spruce (**Tables 3.40, 3.41**). Trembling aspen and balsam poplar are common associates but occur at much lower cover. Paper birch is infrequent and balsam fir, black spruce and bur oak are rarely encountered. The subcanopy and lower tree strata are generally dominated by white spruce as well. Trembling aspen, balsam poplar, paper birch and/or balsam fir may also occur in the lower canopy layers. Total basal area per plot is often high, and is dominated by white spruce. Stands typically have a high mean effective species richness.

Shrub cover is low to moderate (**Table 3.42**). The dominant species is beaked hazelnut, but the low shrubs *Rosa acicularis* and *Symphoricarpos albus* are also frequently encountered at lower cover.

Herb cover is moderate (**Table 3.43**), and mean effective richness is high (mean = 12.3; **Table 3.4**). *Fragaria virginiana*, *Mertensia paniculata*, *Rubus pubescens* and *Aralia nudicaulis* are frequently encountered at moderate cover. *Cornus canadensis*, *Mitella nuda*, *Viola rugulosa* and *Anemone canadensis* are less frequently encountered but may occur at moderate cover when present. Bryophyte cover is low to moderate (**Table 3.44**), but mean effective richness is high (mean = 4.9). The most frequently encountered species are *Brachythecium* spp. and *Mnium cuspidatum*. *Pleurozium schreberi* is found in almost half of the stands but is never abundant. Lichens of the genus *Peltigera* are common in these stands, but their cover is low.

### Variant 1 - Xeric-Mesic ( $n = 12$ )

These stands generally occur on well-drained sandy slopes. They are characterized by a dense mixed canopy of white spruce and trembling aspen (**Appendix 2.10**). In the upper canopy,

density of trembling aspen is generally higher than that of white spruce. Balsam poplar is uncommon. White spruce dominates the subcanopy layer of these stands, while trembling aspen, balsam poplar and paper birch are infrequent. The lower strata is dominated by trembling aspen suckers; white spruce saplings are present but not abundant. These stands typically have low cover in the shrub, herb and bryophyte layers. The most commonly encountered shrub is beaked hazelnut, although *Rosa acicularis* and *Symphoricarpos albus* are also common at low cover. The herb layer is dominated by *Fragaria virginiana*, *Maianthemum canadense*, *Galium boreale*, *Oryzopsis asperifolia* and/or *Aralia nudicaulis*.

#### Variant 2 - Mesic ( $n = 28$ )

The canopy of these stands is dominated by white spruce, with trembling aspen occurring at lower density and frequency. Balsam poplar is a common canopy associate at low density, while paper birch is less common. The subcanopy and lower tree strata are usually dominated by white spruce, with trembling aspen, balsam poplar and/or paper birch occurring occasionally at low density. The regenerating sapling layer is frequently dominated by suckers of trembling aspen and/or balsam poplar. White spruce saplings are infrequent and typically occur at low density. Shrub cover in these stands is low to moderate. Beaked hazelnut is the dominant species, but *Rosa acicularis* is also common at low cover. *Aralia nudicaulis*, *Mertensia paniculata*, *Rubus pubescens*, *Mitella nuda* and *Fragaria virginiana* are the most frequently encountered species in the herb layer. Bryophyte cover is low. Pleurocarpos feathermosses (*Pleurozium schreberi*, *Hylocomium splendens*) occur in some stands at low cover.

#### Variant 3 - Mesic-Hygic ( $n = 7$ )

The canopy of these stands is dominated by white spruce, with balsam poplar occurring as a canopy associate at lower density. Paper birch, balsam fir and trembling aspen are also occasionally found in the canopy. White spruce occurs at moderate density in the subcanopy and lower tree strata, while trembling aspen, balsam poplar and/or balsam fir occur at low density. Seedlings and saplings of paper birch, balsam poplar and/or balsam fir are common in these stands. Shrub cover is high and dominated by beaked hazelnut. The well-developed herb layer is dominated by *Aralia nudicaulis*, *Mertensia paniculata*, *Mitella nuda* and *Viola rugulosa*. Bryophytes are uncommon in these stands.

## *Discussion*

White spruce is considered to be both a pioneer and 'climax' species (Dix & Swan 1971). However, the species rarely forms pure stands throughout most of its range (Blais 1983; Grigal & Ohmann 1975). The timing of white spruce establishment in post-disturbance stands across the boreal forest is variable (Youngblood 1995; Lieffers et al. 1996). Establishment may occur immediately after disturbance or shortly afterwards (Dix & Swan 1971; Heinselman 1978; Cogbill 1985), although it is frequently delayed for approximately 10 years (Rowe 1955). For upland conifer-hardwood stands in interior Alaska, hardwoods and white spruce commonly establish as a single cohort within 30 years after fire (Youngblood 1995). Stand development in this region was affected by the composition of plant communities establishing immediately after fire. Delayed recruitment may occur in sites which are not producing seed at the time of disturbance or in sites with poor seedbeds (Lieffers et al. 1996). White spruce may not regenerate well in open, post-disturbance areas, likely requiring site modification by protective vegetation before establishing in high densities (Achuff & LaRoi 1977; Whipple & Dix 1979; Kneeshaw & Burton 1997). In the mixedwood region, in comparison, establishment may continue for decades, producing an uneven-aged understory (Achuff & La Roi 1977; Lieffers et al. 1996), or extend for more than 100 years in some subalpine regions (Kneeshaw & Burton 1997). Sites with good seedbeds and an abundant supply of seed tend to have rapid and heavy white spruce recruitment (Lieffers et al. 1996). In comparison, sites with poor seedbeds tend to have sporadic and delayed recruitment.

In eastern Canada, white spruce has demonstrated a two-wave recruitment pattern (Kneeshaw & Bergeron 1996; Gallipeau et al. 1997). The first wave occurs during the initial stages of stand development, whereas the second occurs later in stand development after the first cohort begins to produce seed. The initial cohort density was found to be the most important factor explaining the distribution in abundance of the second cohort (Gallipeau et al. 1997).

Early investigators believed that the aspen, aspen-white spruce, and white spruce forests of RMNP represented a successional continuum of increased environmental stability (Dickson 1909; Evans 1923; Tunstall et al. 1922). They suggested that initial post-disturbance forests are usually dominated by trembling aspen. These stands are colonized by white spruce, eventually leading to a self-perpetuating white spruce climax. Dickson (1909) indicated that back-to-back catastrophic fires in the 1890's resulted in abundant regeneration of aspen "in the once solid spruce forest". However, he claimed that white spruce is "in the future destined to be the most important" of all

tree species in RMNP, being able to “endure at all stages of its life-history the greater amount of shading” (Dickson 1909).

Rowe (1961) proposed that in the absence of catastrophic disturbance, the climax forest on many upland sites in the western boreal forest is “open, unhealthy, ragged, and frequently brush-filled, awaiting the rejuvenating touch of fire, flood, or windfall ploughing of the soil” (**Appendix 2.11**). In Québec, older (>200 years) white spruce stands have poor growth and limited reproduction, and are “shrub-filled under canopy openings” (Cogbill 1985). It was suggested that a catastrophic fire may be required to rejuvenate these stands and increase nutrient mobility. Carleton & Maycock (1978) noted similar 'decadent' white spruce stands in northern Ontario. In RMNP, Rowe (1955) hypothesized that trembling aspen and balsam poplar will die out in very old conifer forests, leaving paper birch as the only hardwood species. Paper birch can regenerate from sprouts, and can seed into older stands with establishment occurring in large forest gaps created by intermediary disturbances (Frelich & Reich 1995). The species has similar seedbed preferences to white spruce, and can be found growing on decayed logs and stumps, on wet humus, and on moist light-textured soils. Mixed mature stands of white spruce and paper birch are therefore not uncommon (Rowe 1955).

### **3.4 Conclusion**

Overall, the classification of sampled forest stands resulted in the delineation of eight unique stand types, and will facilitate an examination of landscape-level forest stand dynamics. Before successional trajectories are created for each of the eight stand types in Chapter 6, Chapters 4 and 5 examine the growth response of understory green ash and white spruce, respectively, to different habitat conditions.

In Chapter 4, understory green ash growth is examined in boreal (aspen-dominated) and adjacent mixed eastern deciduous stands, to better understand the future development of these communities. Green ash is found in the understory of stands along the Cretaceous escarpment, most commonly in stands belonging to stand types IV (Eastern Deciduous), V (Balsam Fir) and VI (Aspen-Birch-Mountain Maple). Stands with understory green ash have the potential to undergo dramatic compositional and structural change, warranting examination.

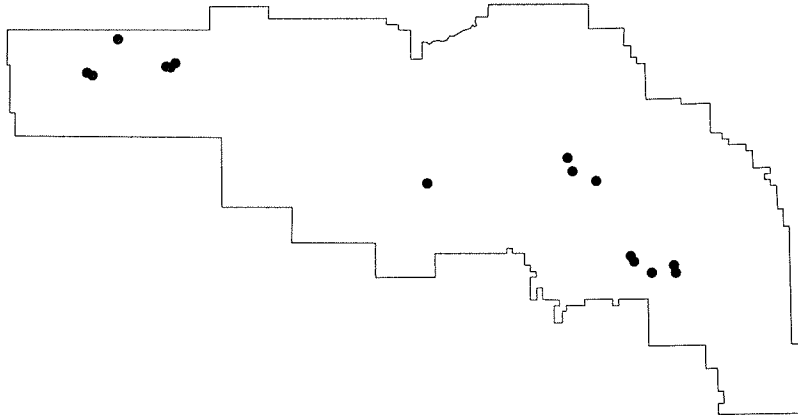
In Chapter 5, understory white spruce growth is examined across a broad range of habitat conditions. White spruce is the most widespread and abundant conifer in the Park, and is expected to have a large influence on future forest development. The species is most commonly

found in the understory of stand types V (Balsam Fir), VII (Aspen-Balsam Poplar) and VIII (White Spruce). Numerous studies have examined the growth of understory white spruce, demonstrating that white spruce growth and subsequent stand development is dependant on prevailing habitat conditions. Understanding the growth response of white spruce to different habitat conditions is integral for a more complete understanding of forest change across the landscape.

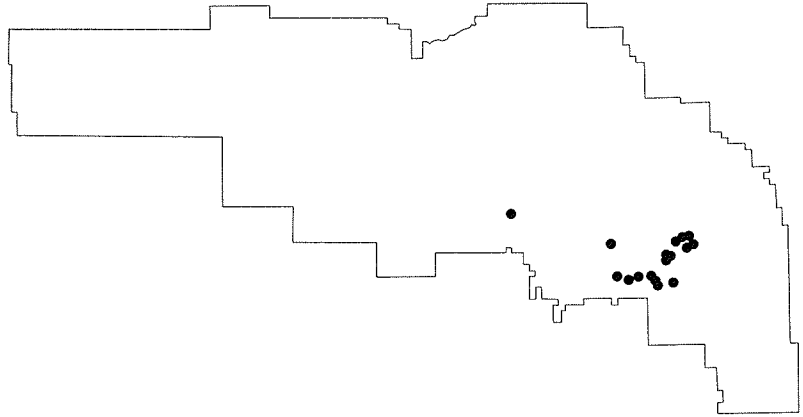
Chapters 4 and 5 provide an in-depth background on the growth of green ash and white spruce across complex landscapes, and provide a framework for the development of successional trajectories for each of the eight stand types in Chapter 6.



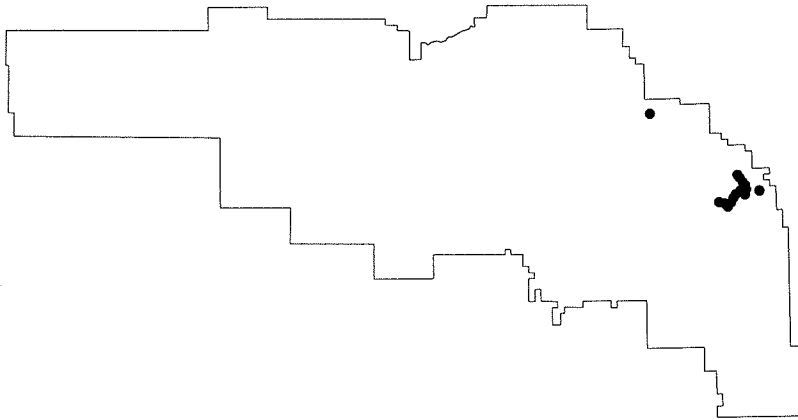
**I. Black Spruce Organic**  $n=15$



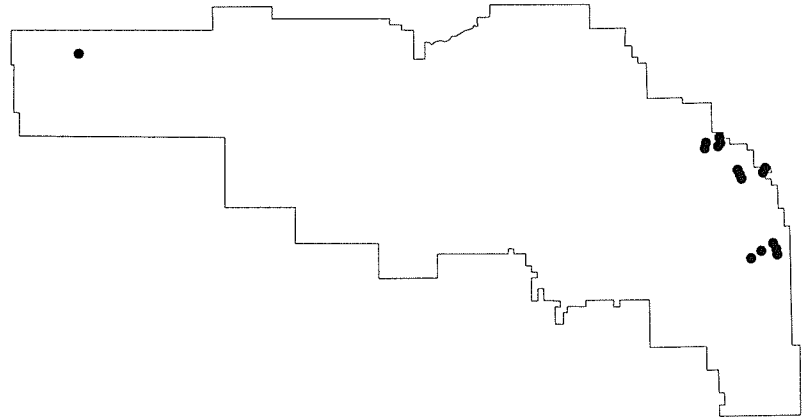
**II. Jack Pine - Black Spruce**  $n=17$



**III. Bur Oak**  $n=15$

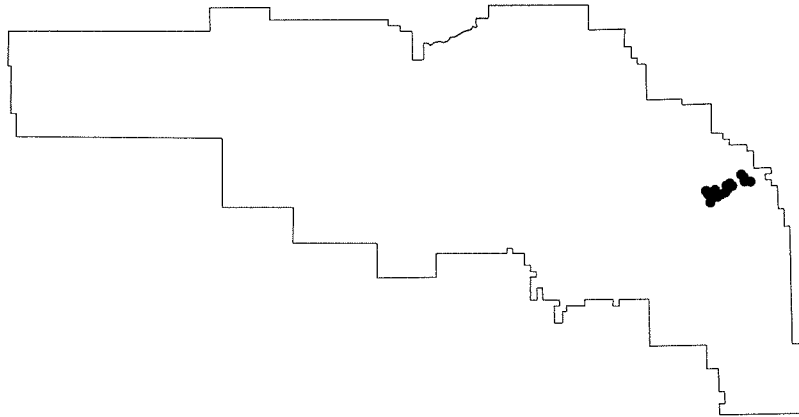


**IV. Eastern Deciduous**  $n=16$

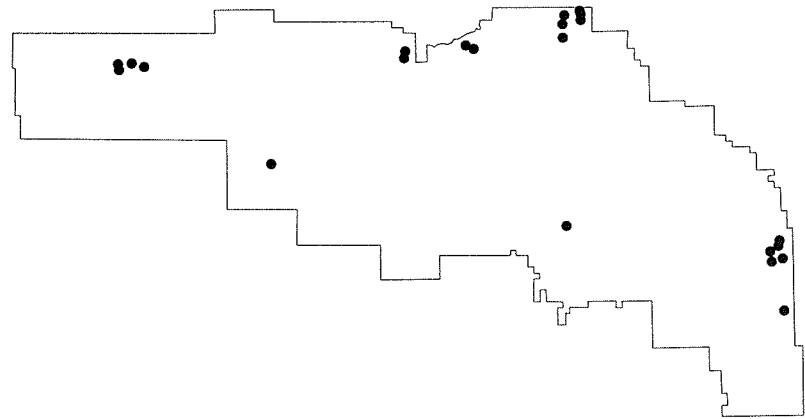


102 **Figure 3.1.** Location of plots sampled within RMNP between 1996-1997 for stand types I-VIII.

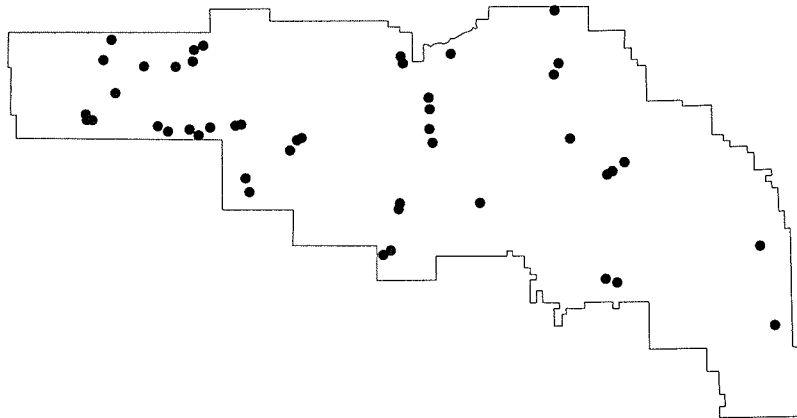
V. Balsam Fir  $n=18$



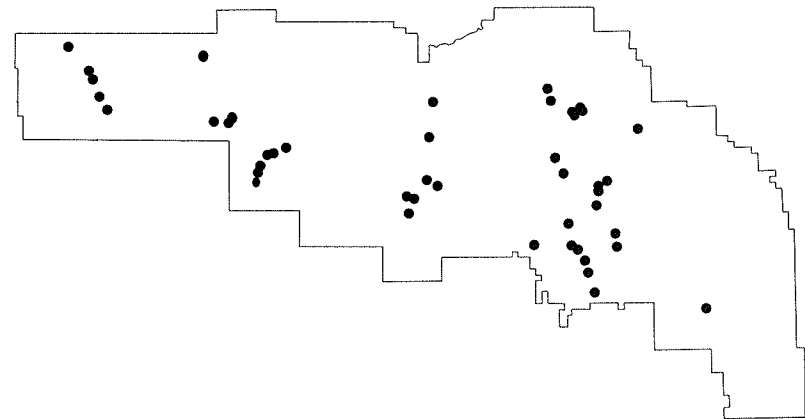
VI. Aspen - Birch - Mountain Maple  $n=22$



VII. Aspen - Balsam Poplar  $n=46$



VIII. White Spruce  $n=47$



103 Figure 3.1 cont'd. Location of plots sampled within RMNP between 1996-1997 for stand types I-VIII.

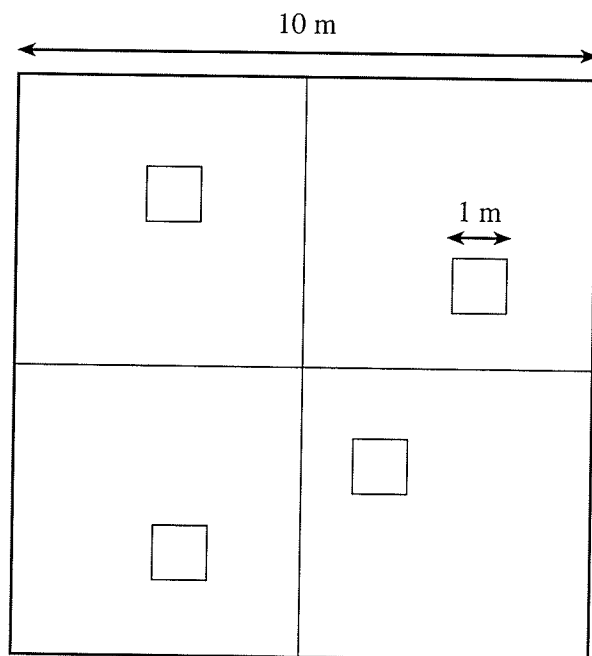
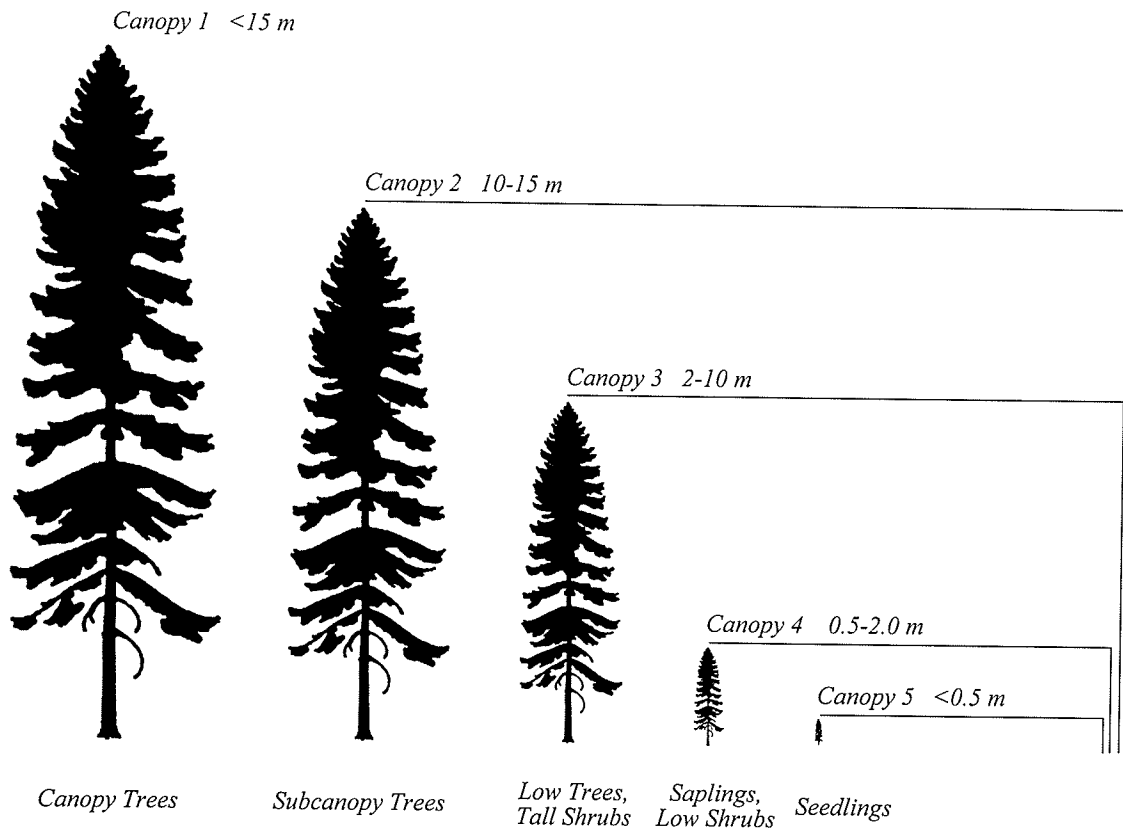
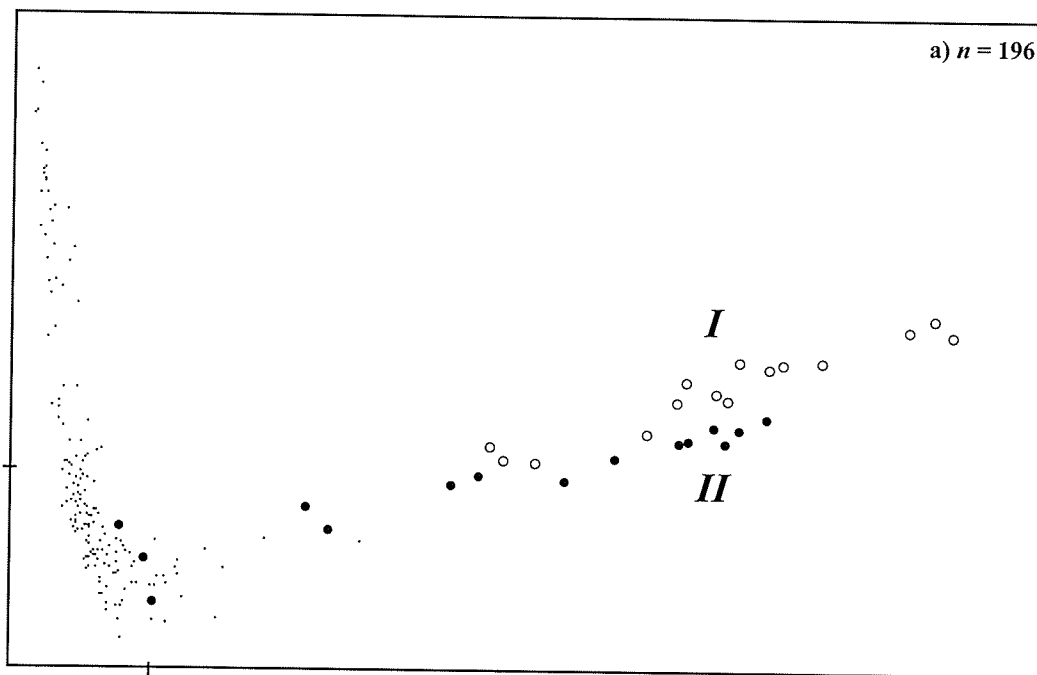
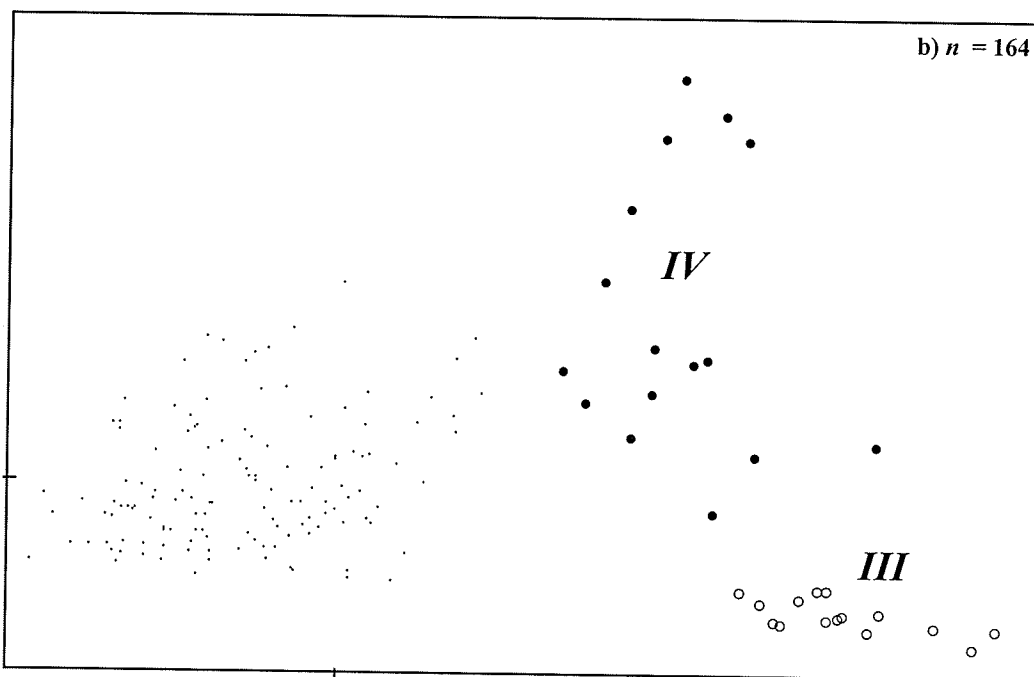


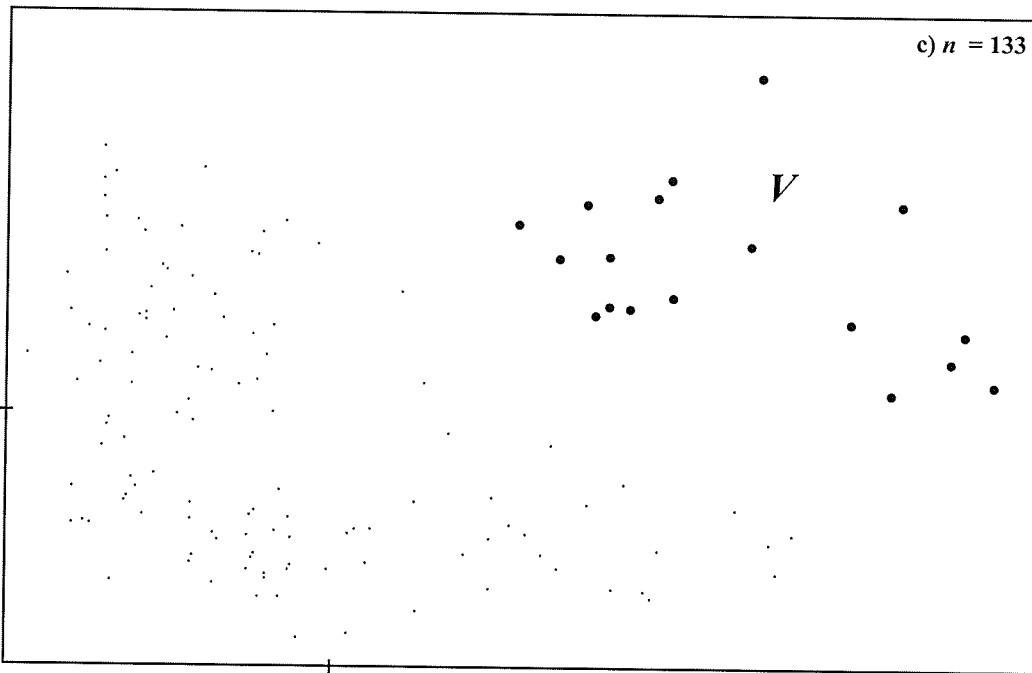
Figure 3.2. Height ranges for each tree canopy (top); Quadrat design (bottom).



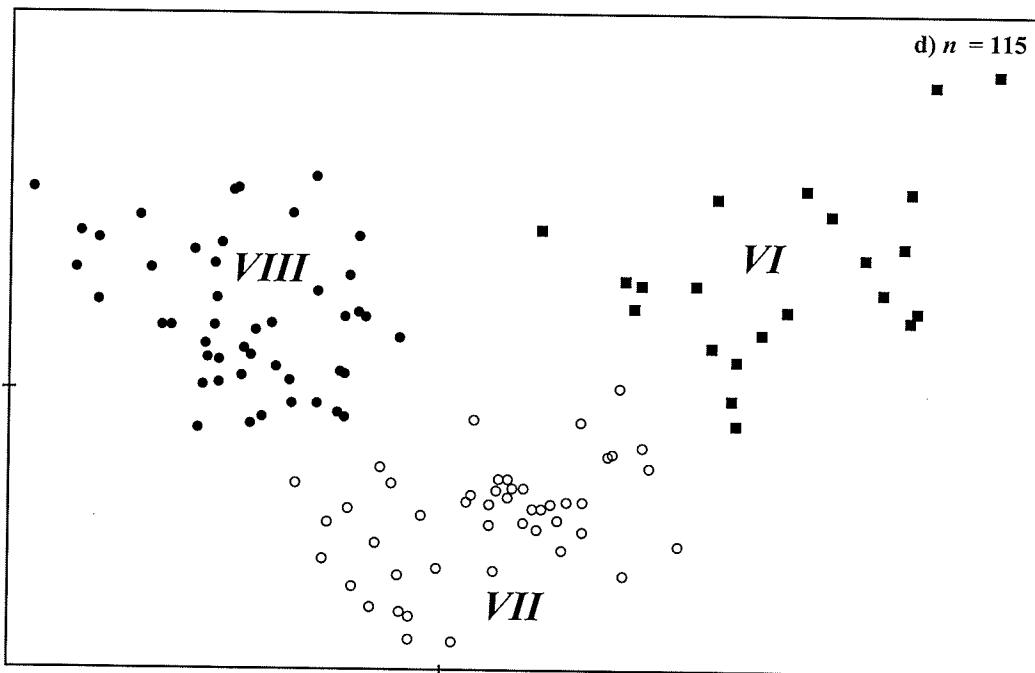
**Figure 3.3 a.** Correspondence analysis ordination of  $n = 196$  stands. Stand types I (Black Spruce Organic) and II (Jack Pine - Black Spruce) are indicated by larger open and closed circles, respectively. Eigenvalues and percent inertia:  $\lambda = 0.643$  (14.1%),  $\lambda = 0.362$  (7.9%). The horizontal axis is ordination axis 1. The vertical axis is ordination axis 2.



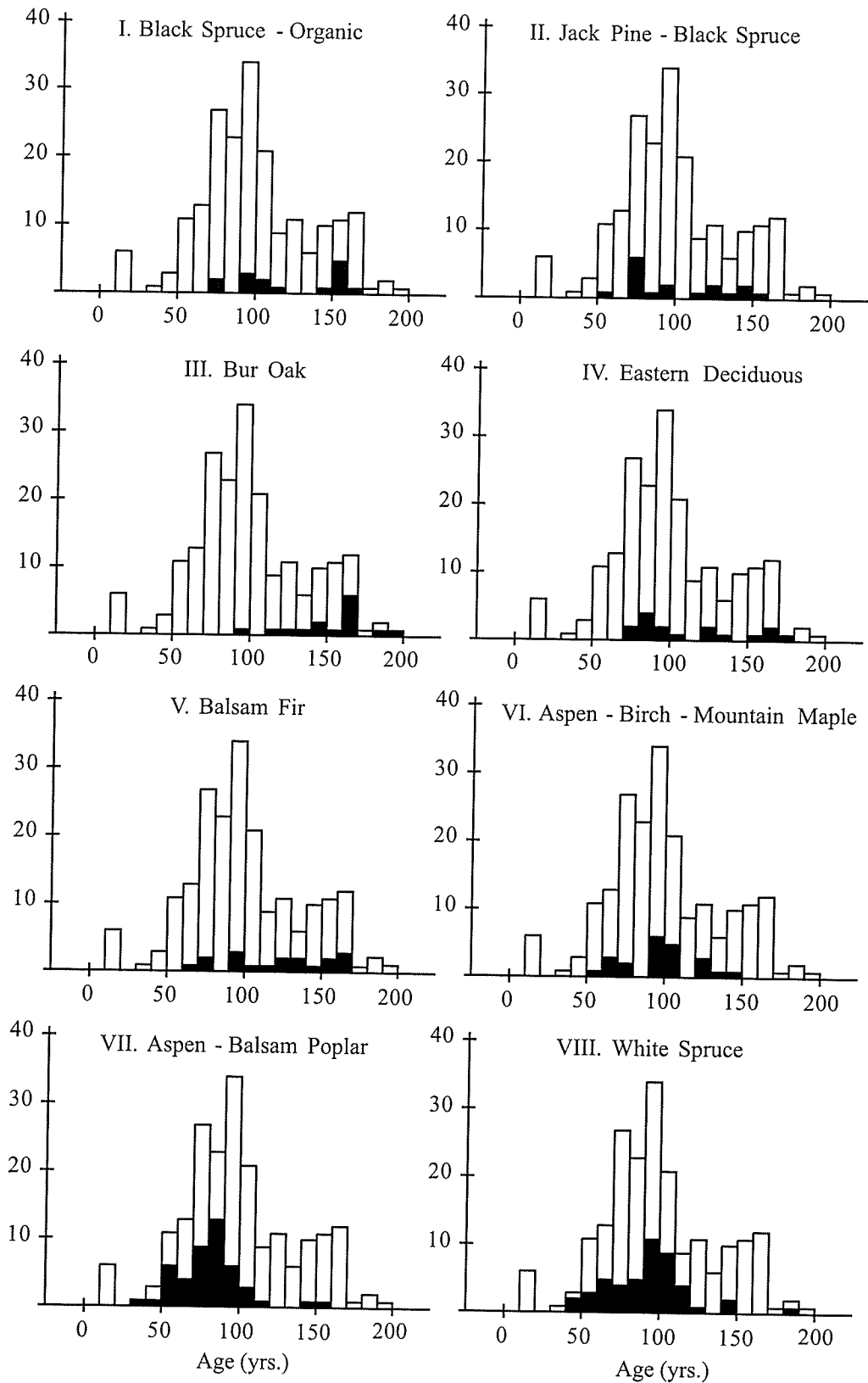
**Figure 3.3 b.** Correspondence analysis ordination of  $n = 164$  stands, after removal of Stand types I (Black Spruce Organic) and II (Jack Pine - Black Spruce). Stand types III (Bur Oak) and IV (Eastern Deciduous) are indicated by the open and closed circles, respectively. Eigenvalues and percent inertia:  $\lambda_1 = 0.383$  (11.2%),  $\lambda_2 = 0.317$  (9.3%). The horizontal axis is ordination axis 1. The vertical axis is ordination axis 2.



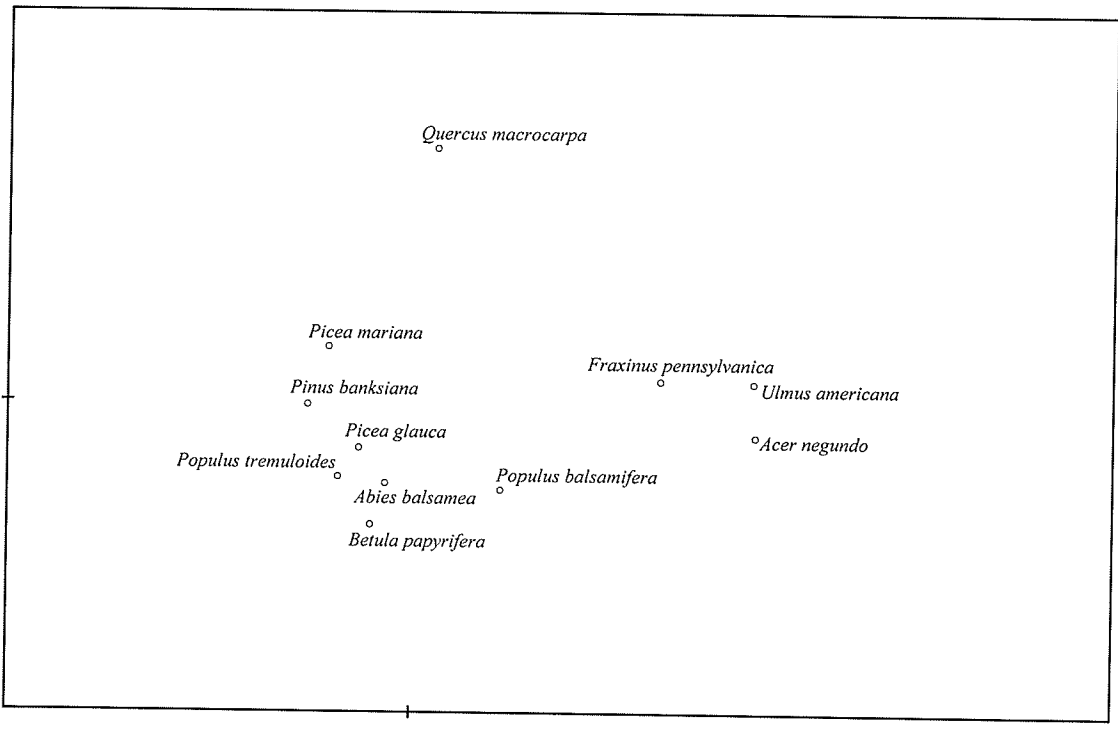
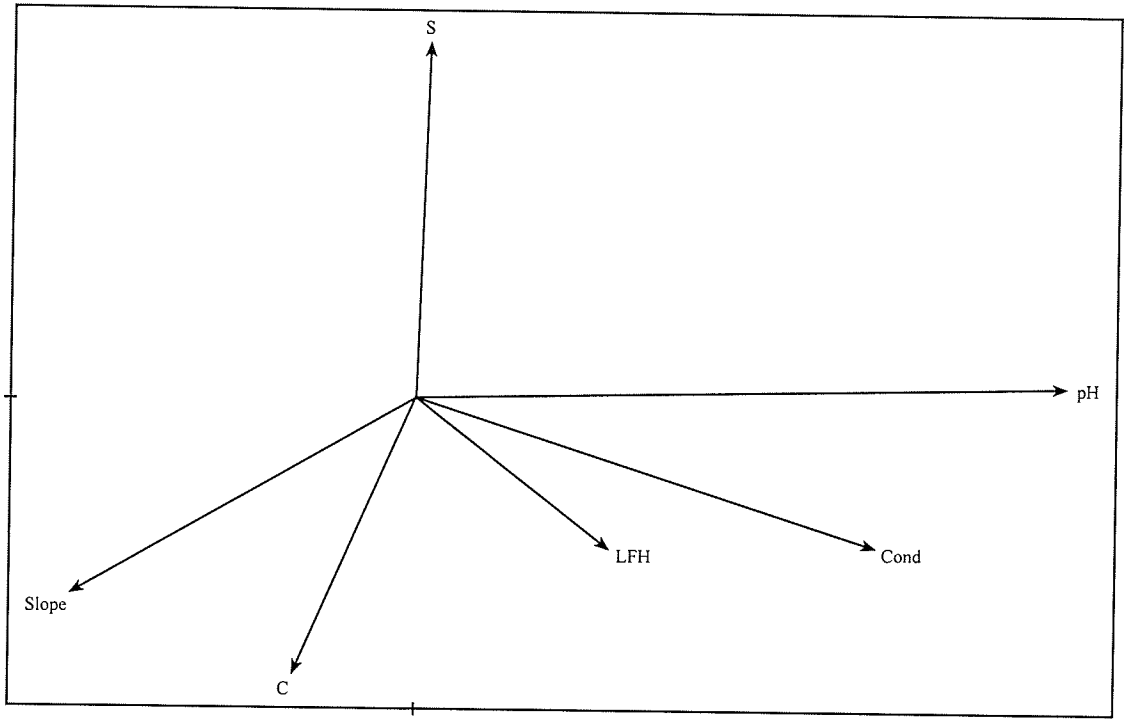
**Figure 3.3 c.** Correspondence analysis ordination of  $n = 133$  stands, after removal of stand types I-IV. Stand type V (Balsam Fir) is indicated by the large closed circles. Eigenvalues and percent inertia:  $\lambda_1 = 0.294$  (10.8%),  $\lambda_2 = 0.233$  (8.6%). The horizontal axis is ordination axis 1. The vertical axis is ordination axis 2.



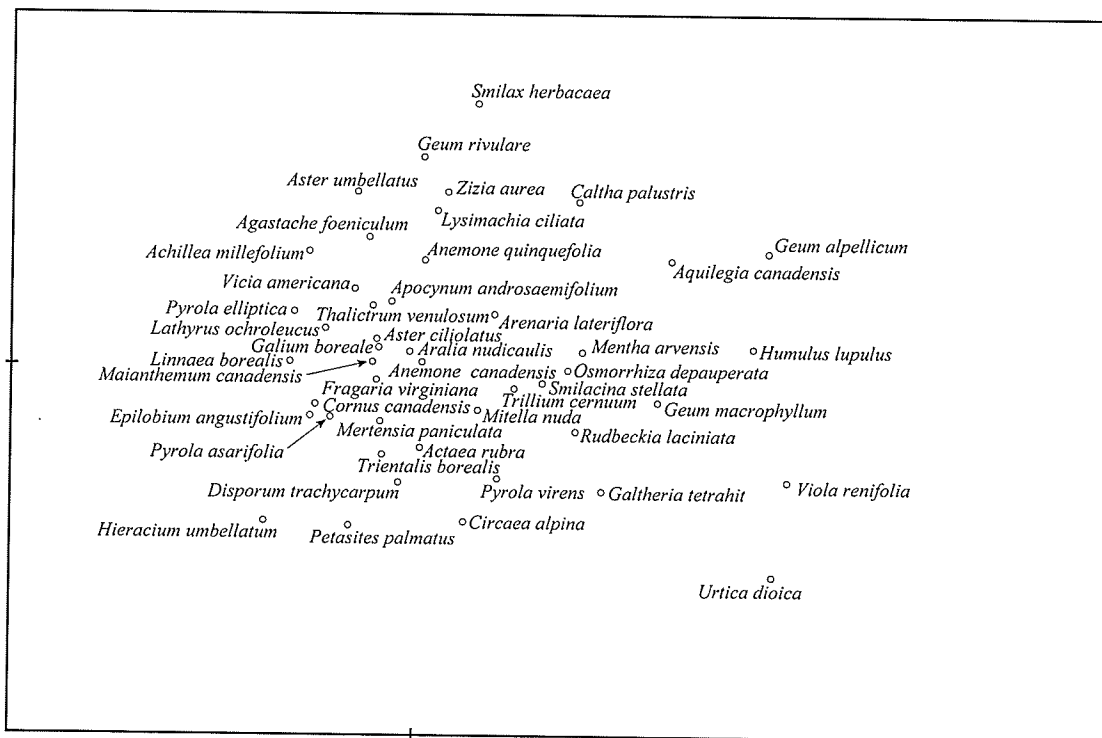
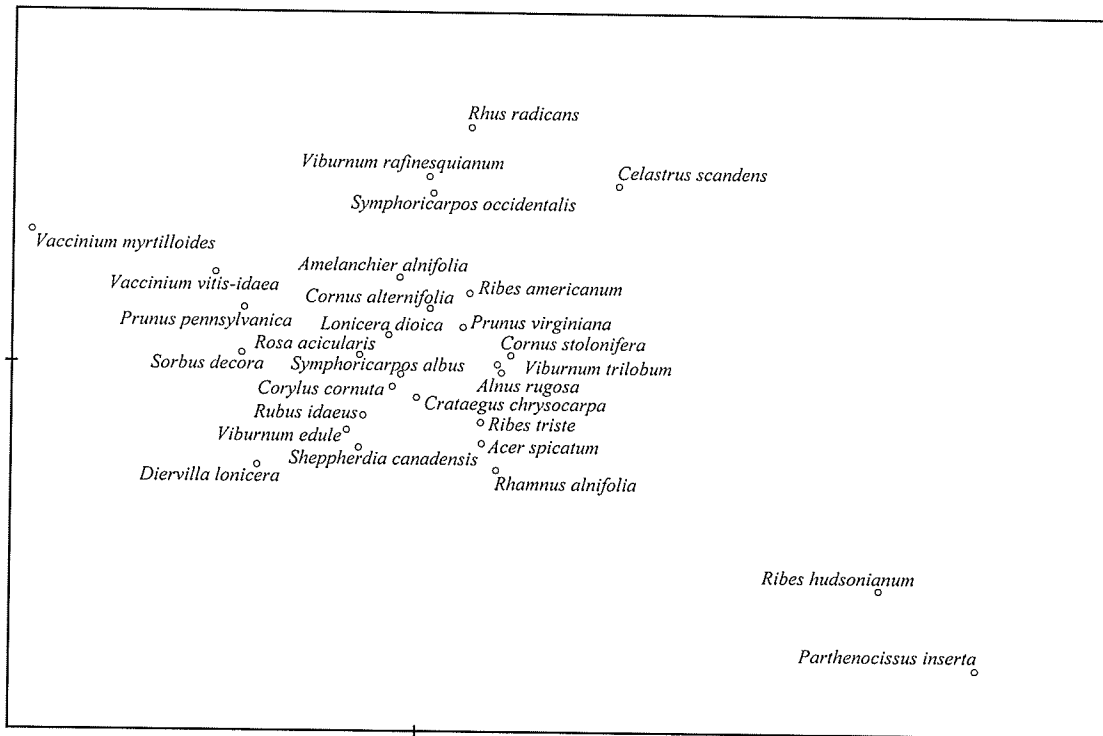
**Figure 3.3 d.** Correspondence analysis ordination of  $n = 115$  stands, after removal of stand types I-V. Stand types VI (Trembling Aspen - Birch - Mountain Maple), VII (Trembling Aspen - Balsam Poplar), and VIII (White Spruce) are indicated by closed circles, open circles and closed squares, respectively. Eigenvalues and percent inertia:  $\lambda_1 = 0.248$  (11.1%),  $\lambda_2 = 0.181$  (8.2%). The horizontal axis is ordination axis 1. The vertical axis is ordination axis 2.



**Figure 3.4.** Minimum stand age frequency histograms for each of the eight stand types I-VIII.

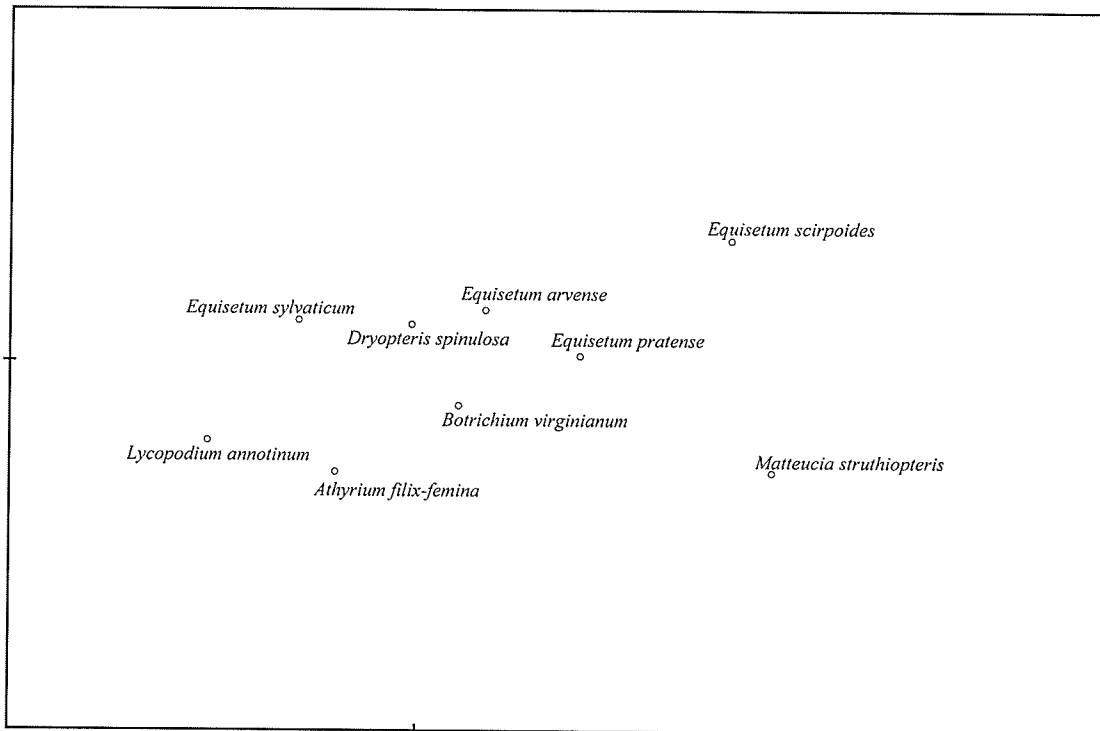
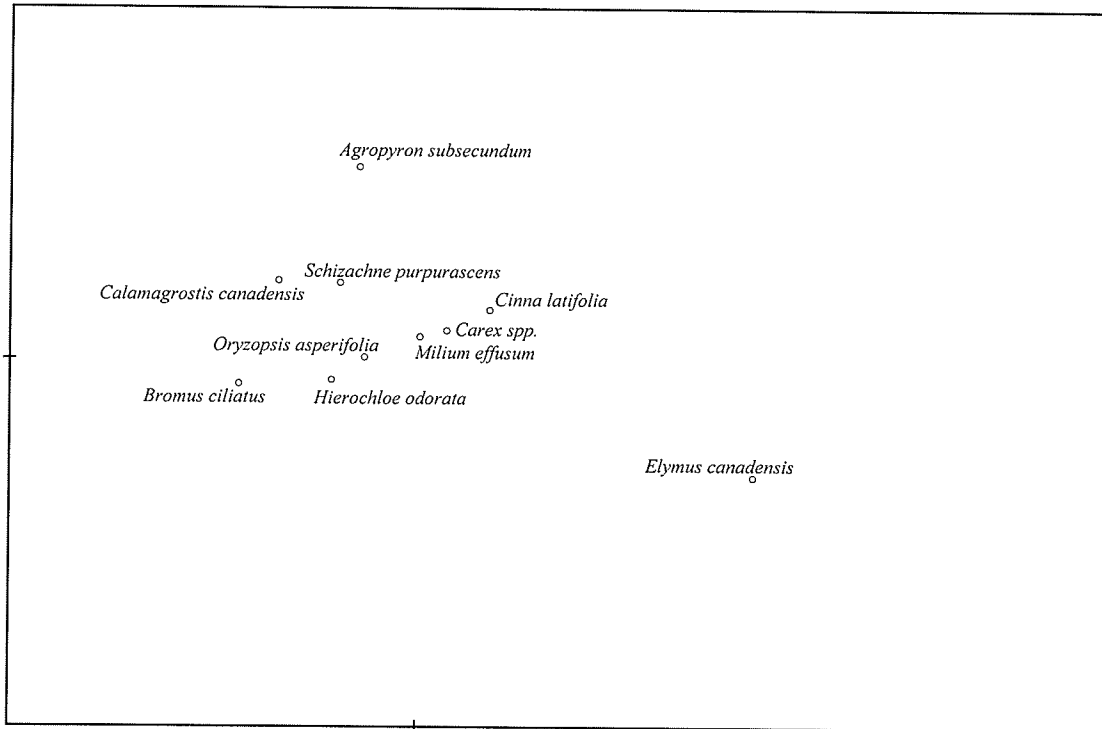


**Figure 3.5 a (top) and b (bottom).** Canonical correspondence analysis of  $n=179$  stands on mineral soil, utilizing 171 species and 6 environmental variables. Top: Environmental variable biplot. Bottom: species ordination dual, illustrating major tree species. Horizontal axis is axis 1, vertical axis is axis 2. The redundancy of the vegetation-environment relationship (ratio of the canonical inertia to the total inertia  $0.338/4.172$ ) = 8.1%. Environmental variable codes: C = percent clay content of soil; Cond = electrical conductivity (uS) of soil; LFH = depth of LFH soil horizon; pH = soil pH; S = percent sand content of soil; Slope = degrees slope of plot.

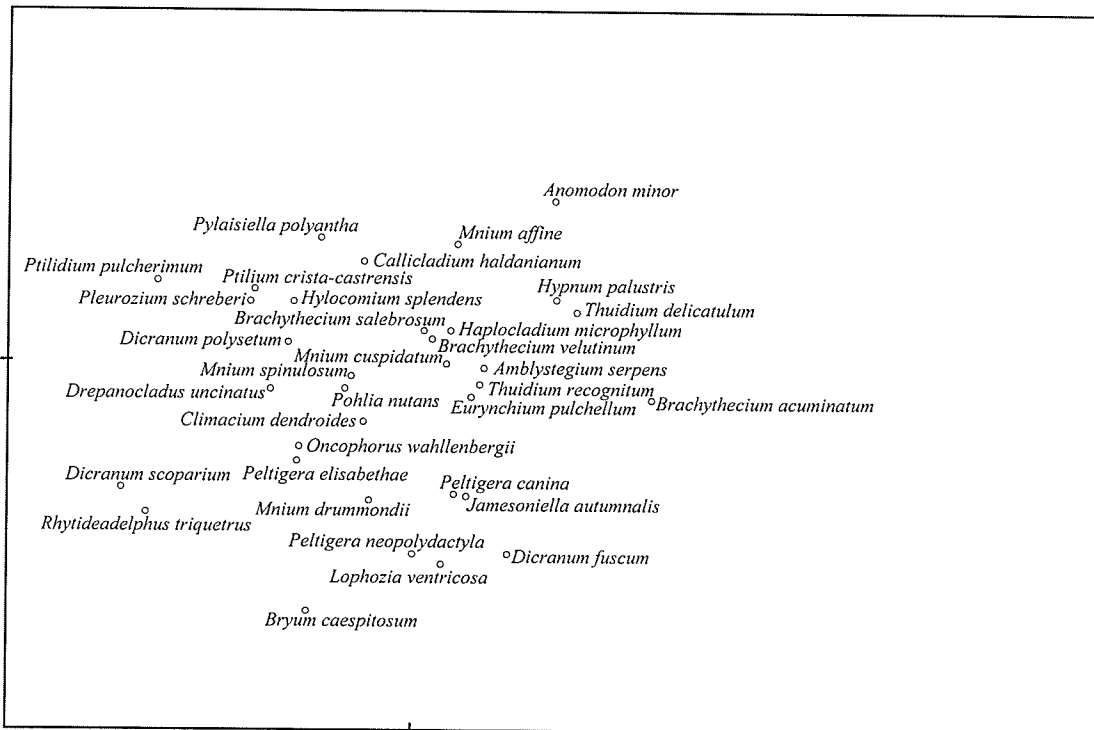


**Figure 3.5 c (top) and d (bottom).** Canonical correspondence analysis of  $n=179$  stands on mineral soil, utilizing 171 species and 6 environmental variables. Top: species ordination dual, illustrating major shrub species. Bottom: species ordination dual, illustrating major herb species. Horizontal axis is axis 1, vertical axis is axis 2. The redundancy of the vegetation-environment relationship (ratio of the canonical inertia to the total inertia  $0.338/4.172$ ) = 8.1%.



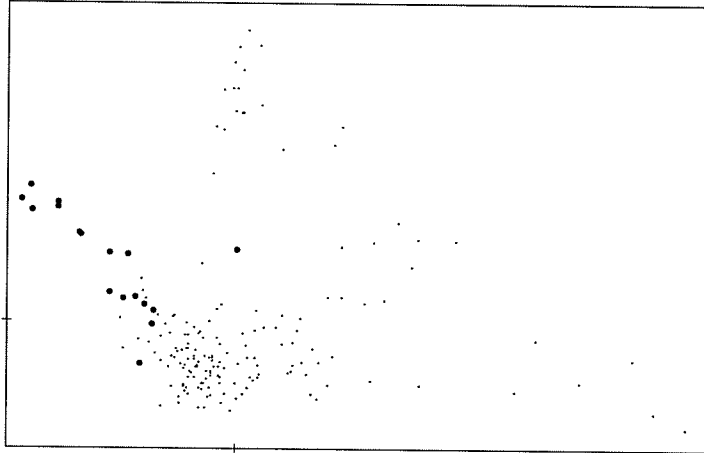


**Figure 3.5 e (top) and f (bottom).** Canonical correspondence analysis of  $n=179$  stands on mineral soil, utilizing 171 species and 6 environmental variables. Top: species ordination dual, illustrating major graminoid species. Bottom: species ordination dual, illustrating major fern species. Horizontal axis is axis 1, vertical axis is axis 2. The redundancy of the vegetation-environment relationship (ratio of the canonical inertia to the total inertia  $0.338/4.172 = 8.1\%$ ).

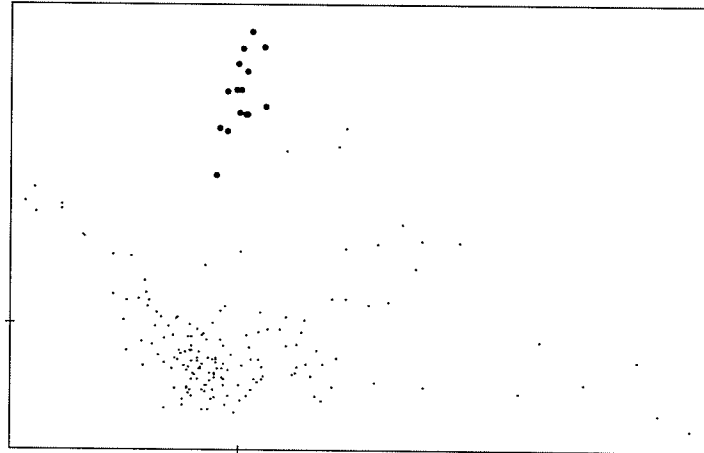


**Figure 3.5 g.** Canonical correspondence analysis of  $n=179$  stands on mineral soil, utilizing 171 species and 6 environmental variables. Species ordination dual, illustrating major bryophyte species. Horizontal axis is axis 1, vertical axis is axis 2. The redundancy of the vegetation-environment relationship (ratio of the canonical inertia to the total inertia  $0.338/4.172 = 8.1\%$ ).

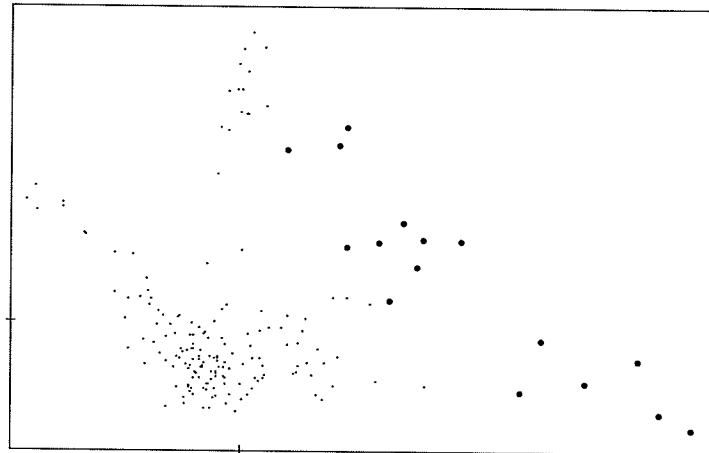
Stand Type II. Jack Pine - Black Spruce



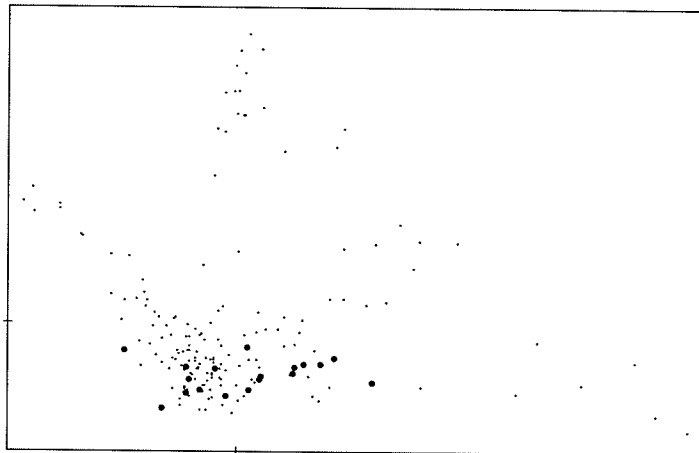
Stand Type III. Bur Oak



Stand Type IV. Eastern Deciduous



Stand Type V. Balsam Fir

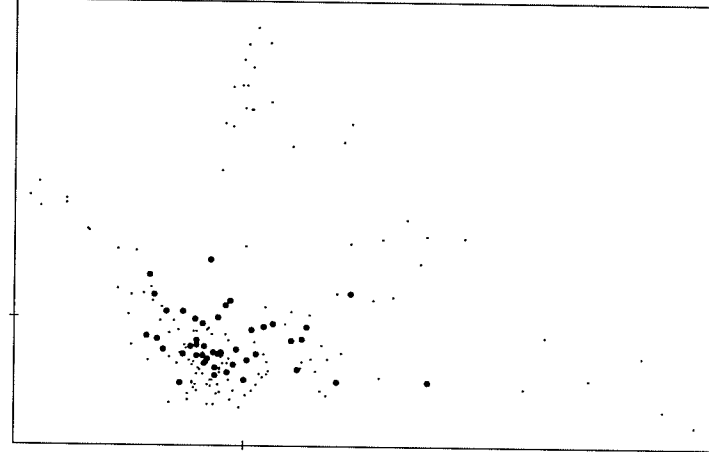


**Figure 3.5 h.** Plot positions of stand types II-V for the canonical correspondence analysis of  $n=179$  stands on mineral soil, utilizing 171 species and 6 environmental variables. Horizontal axis is axis 1, vertical axis is axis 2. The redundancy of the vegetation-environment relationship (ratio of the canonical inertia to the total inertia  $0.338/4.172$ ) = 8.1%. Corresponding environmental and species biplots are presented in **Figures 3.5 a-g**.

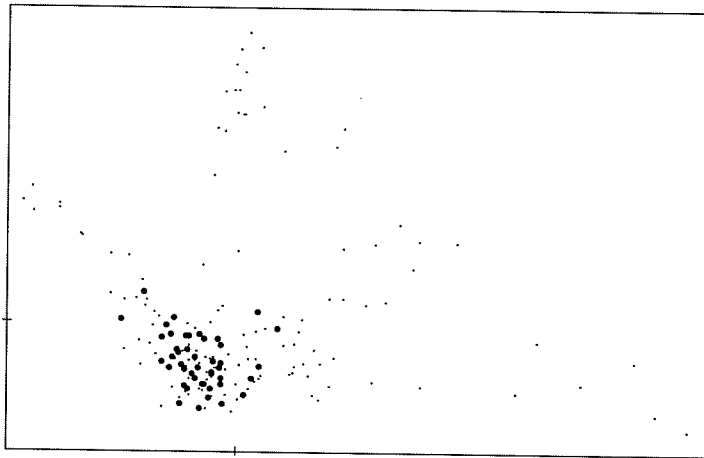
Stand Type VI. Aspen - Birch - Mountain Maple



Stand Type VII. Trembling Aspen - Balsam Poplar



Stand Type VIII. White Spruce



**Figure 3.5 h continued.** Plot positions of stand types VI-VIII for the canonical correspondence analysis of  $n=179$  stands on mineral soil, utilizing 171 species and 6 environmental variables. Horizontal axis is axis 1, vertical axis is axis 2. The redundancy of the vegetation-environment relationship (ratio of the canonical inertia to the total inertia  $0.338/4.172$ ) = 8.1%. Corresponding environmental and species biplots are presented in **Figures 3.5 a-g**.

Table 3.1. Mean, range and standard deviation of edaphic and environmental variables measured for each of the 8 stand types. Depth of A horizon and depth to carbonates are based on data collected in year 2.

Stand Type	<i>n</i>	Sand (%)	Silt (%)	Clay (%)	pH	Conductivity (µS/cm)	LFH Depth (cm)	Depth of A (cm)	Depth to Carb (cm)	Bareground (%)	Slope (degrees)	Herbivore Browse (ordinal scale, 1-5)
I. Black Spruce Organic	15	-	-	-	6.8	239.6	-	-	-	2.3	0.5	1.7
					(3.88 - 7.87)	(110 - 680)				(2.0 - 20.0)	(0.0 - 5.0)	(1.0 - 3.0)
II. Jack Pine - Black Spruce	17	41.3	28.8	29.9	6.1	215.5	5.4	8.7	24.1	21.1	3.9	2.5
		(27.7 - 67.9)	(19.3 - 43.4)	(12.8 - 45.0)	(5.0 - 7.8)	(92.0 - 480.0)	(2.0 - 10.0)	(1.0 - 14.0)	(6.0 - 67.0)	(1.0 - 60.0)	(0.0 - 15.0)	(1.0 - 5.0)
		9.0	7.5	7.5	0.8	105.2	1.9	3.7	18.8	17.4	3.4	1.1
III. Bur Oak	15	62.7	19.8	17.5	6.7	156.5	4.2	5.2	20.0	5.7	2.4	4.5
		(34.2 - 79.1)	(9.6 - 40.2)	(8.0 - 30.5)	(5.8 - 7.6)	(58.0 - 350.0)	(0.5 - 6.0)	(1.0 - 12.0)	(1.0 - 43.0)	(1.0 - 20.0)	(0.8 - 5.0)	(3.0 - 5.0)
		13.6	8.8	5.8	0.5	83.2	1.5	3.4	11.4	6.3	1.3	0.6
IV. Eastern Deciduous	16	45.3	30.0	24.7	7.2	378.1	7.1	5.1	15.9	7.8	2.4	4.0
		(8.5 - 77.5)	(13.5 - 64.2)	(9.0 - 49.8)	(5.9 - 7.8)	(170.0 - 740.0)	(4.0 - 11.0)	(0.0 - 20.0)	(0.0 - 66.0)	(1.0 - 30.0)	(0.7 - 5.0)	(3.0 - 5.0)
		23.7	14.9	13.3	0.6	162.0	2.3	6.2	23.3	7.9	1.4	0.5
V. Balsam Fir	18	43.6	28.3	28.1	6.7	237.7	7.9	8.1	21.6	20.2	5.3	3.3
		(24.5 - 69.5)	(11.2 - 40.2)	(17.7 - 45.0)	(5.1 - 8.0)	(75.0 - 505.0)	(3.0 - 18.0)	(0.0 - 15.0)	(0.0 - 49.0)	(1.0 - 50.0)	(2.0 - 15.0)	(2.0 - 5.0)
		15.6	9.2	8.8	1.0	112.2	4.6	4.0	16.7	15.5	3.6	1.0
VI. Aspen - Birch - Mountain Maple	22	38.8	29.3	32.0	6.6	243.7	5.9	14.9	16.1	18.0	6.6	3.4
		(19.7 - 80.7)	(4.8 - 38.2)	(14.5 - 46.6)	(4.8 - 8.1)	(100.0 - 480.0)	(0.5 - 11.5)	(0.5 - 53.0)	(0.0 - 53.0)	(1.0 - 50.0)	(2.0 - 27.0)	(1.0 - 5.0)
		17.2	9.2	9.3	0.7	96.5	2.5	14.4	16.1	14.9	6.9	1.1
VII. Aspen - Balsam Poplar	46	34.0	31.9	34.0	6.3	242.6	5.8	11.6	11.9	11.6	4.9	3.5
		(11.7 - 74.3)	(8.0 - 49.8)	(14.8 - 67.5)	(5.0 - 7.7)	(40.0 - 520.0)	(1.0 - 13.0)	(2.0 - 40.0)	(0.0 - 34.0)	(1.0 - 70.0)	(1.0 - 20.0)	(1.0 - 5.0)
		15.2	8.0	12.2	0.7	122.7	2.8	9.8	11.4	15.0	3.7	1.1
VIII. White Spruce	47	39.9	29.5	30.7	6.4	279.6	6.0	11.3	10.4	21.0	6.3	3.3
		(19.7 - 75.9)	(12.8 - 43.4)	(8.0 - 54.6)	(4.6 - 8.4)	(50.0 - 920.0)	(0.5 - 12.0)	(3.0 - 30.0)	(0.0 - 35.0)	(1.0 - 80.0)	(0.1 - 30.0)	(1.0 - 5.0)
		14.5	7.4	10.5	0.8	171.6	3.0	6.6	9.0	22.2	6.7	1.0

Table 3.2. Frequency of soil types (classified according to the Canadian System of Soil Classification) for stands sampled during the second field season.

Stand Type	n	Order	Great Group	Subgroup	Classification Code	Frequency
I. Black Spruce Organic	11	Organic	Fibrisol	Hydric Fibrisol	HY.F	0.64
		Organic	Mesisol	Hydric Mesisol	HY.M	0.27
		Organic	Humisol	Hydric Humisol	HY.H	0.09
II. Jack Pine - Black Spruce	12	Luviosolic	Gray Luvisol	Gleyed Gray Luvisol	GL.GL	0.33
		Gleysolic	Luvic Gleysol	Orthic Luvic Gleysol	O.LG	0.33
		Gleysolic	Gleysol	Orthic Gleysol	O.G	0.17
		Brunisolic	Eutric Brunisol	Gleyed Eutric Brunisol	GL.EB	0.08
		Luviosolic	Gray Luvisol	Orthic Gray Luvisol	O.GL	0.08
III. Bur Oak	12	Brunisolic	Eutric Brunisol	Orthic Eutric Brunisol	O.EB	0.58
		Regosolic	Regosol	Orthic Regosol	O.R	0.25
		Luviosolic	Gray Luvisol	Orthic Gray Luvisol	O.GL	0.08
		Regosolic	Humic Regosol	Orthic Humic Regosol	O.HR	0.08
IV. Eastern Deciduous	13	Regosolic	Regosol	Cumulic Regosol	CU.R	0.38
		Brunisolic	Eutric Brunisol	Orthic Eutric Brunisol	O.EB	0.15
		Regosolic	Regosol	Orthic Regosol	O.R	0.15
		Chernozemic	Dark Brown	Orthic Dark Brown	O.DB	0.08
		Gleysolic	Gleysol	Orthic Gleysol	O.G	0.08
		Brunisolic	Melanic Brunisol	Orthic Melanic Brunisol	O.MB	0.08
		Gleysolic	Gleysol	Rego Gleysol	R.G	0.08
V. Balsam Fir	18	Luviosolic	Gray Luvisol	Orthic Gray Luvisol	O.GL	0.33
		Luviosolic	Gray Luvisol	Gleyed Gray Luvisol	GL.GL	0.22
		Gleysolic	Gleysol	Orthic Gleysol	O.G	0.22
		Brunisolic	Eutric Brunisol	Orthic Eutric Brunisol	O.EB	0.11
		Regosolic	Regosol	Cumulic Regosol	CU.R	0.06
		Gleysolic	Luvic Gleysol	Orthic Luvic Gleysol	O.LG	0.06
VI. Trembling Aspen - Birch - Mountain Maple	16	Luviosolic	Gray Luvisol	Orthic Gray Luvisol	O.GL	0.44
		Luviosolic	Gray Luvisol	Gleyed Gray Luvisol	GL.GL	0.13
		Gleysolic	Gleysol	Orthic Gleysol	O.G	0.13
		Gleysolic	Humic Gleysol	Orthic Humic Gleysol	O.HG	0.06
		Gleysolic	Luvic Gleysol	Orthic Luvic Gleysol	O.LG	0.06
		Regosolic	Regosol	Orthic Regosol	O.R	0.06
		Gleysolic	Gleysol	Rego Gleysol	R.G	0.06
		Gleysolic	Humic Gleysol	Rego Humic Gleysol	R.HG	0.06
VII. Trembling Aspen - Balsam Poplar	25	Luviosolic	Gray Luvisol	Orthic Gray Luvisol	O.GL	0.60
		Luviosolic	Gray Luvisol	Gleyed Gray Luvisol	GL.GL	0.12
		Brunisolic	Eutric Brunisol	Orthic Eutric Brunisol	O.EB	0.08
		Brunisolic	Eutric Brunisol	Gleyed Eutric Brunisol	GL.EB	0.04
		Regosolic	Regosol	Gleyed Regosol	GL.R	0.04
		Gleysolic	Gleysol	Orthic Gleysol	O.G	0.04
		Gleysolic	Humic Gleysol	Orthic Humic Gleysol	O.HG	0.04
		Gleysolic	Luvic Gleysol	Orthic Luvic Gleysol	O.LG	0.04
VIII. White Spruce	25	Luviosolic	Gray Luvisol	Gleyed Gray Luvisol	GL.GL	0.20
		Gleysolic	Gleysol	Orthic Gleysol	O.G	0.16
		Luviosolic	Gray Luvisol	Orthic Gray Luvisol	O.GL	0.16
		Gleysolic	Luvic Gleysol	Orthic Luvic Gleysol	O.LG	0.16
		Brunisolic	Eutric Brunisol	Orthic Eutric Brunisol	O.EB	0.12
		Gleysolic	Humic Gleysol	Orthic Humic Gleysol	O.HG	0.08
		Brunisolic	Eutric Brunisol	Gleyed Eutric Brunisol	GL.EB	0.04
		Gleysolic	Luvic Gleysol	Humic Luvic Gleysol	HU.LG	0.04
Gleysolic	Humic Gleysol	Rego Humic Gleysol	R.HG	0.04		

**Table 3.3.** Minimum stand ages (mean, range, and standard deviation) by stand type, and for all stands.

Stand Type	n	Stand Age (years)			
		Mean	Min	Max	S.D.
I. Black Spruce Organic	15	123	79	163	33.98
II. Jack Pine - Black Spruce	17	102	58	151	29.72
III. Bur Oak	15	152	95	196	26.68
IV. Eastern Deciduous	16	112	76	170	34.83
V. Balsam Fir	18	121	66	165	32.64
VI. Aspen - Birch - Mountain Maple	22	97	55	145	23.98
VII. Aspen - Balsam Poplar	46	80	37	150	21.28
VIII. White Spruce	47	92	44	180	25.50
All Stands	202	100	16	196	35.90

Table 3.4. Effective species richness (calculated using Simpson's Index) and standard deviation for various plant canopies for stand types I-VIII. Calculations are based on species cover.

Stand Type	<i>n</i>	All Species	Trees	All Understory	Shrubs	Herbs	Bryophytes
I. Black Spruce Organic	15	6.7	1.2	10.1	4.5	6.4	5.0
		<i>1.0</i>	<i>0.2</i>	<i>2.0</i>	<i>1.6</i>	<i>1.1</i>	<i>1.0</i>
II. Jack Pine - Black Spruce	17	7.5	3.0	5.2	6.6	13.6	2.3
		<i>1.4</i>	<i>0.6</i>	<i>1.5</i>	<i>1.2</i>	<i>2.3</i>	<i>0.2</i>
III. Bur Oak	15	6.6	1.1	8.2	5.0	3.3	4.2
		<i>0.5</i>	<i>0.0</i>	<i>0.9</i>	<i>0.7</i>	<i>0.9</i>	<i>1.5</i>
IV. Eastern Deciduous	16	11.2	3.9	8.9	4.6	4.7	4.5
		<i>1.1</i>	<i>0.5</i>	<i>1.5</i>	<i>1.2</i>	<i>1.0</i>	<i>1.4</i>
V. Balsam Fir	18	9.2	2.5	8.5	2.2	9.2	6.2
		<i>1.4</i>	<i>0.5</i>	<i>2.9</i>	<i>0.5</i>	<i>1.2</i>	<i>1.7</i>
VI. Aspen - Birch - Mountain Maple	22	8.0	3.2	4.9	2.6	10.5	3.3
		<i>0.9</i>	<i>0.5</i>	<i>0.9</i>	<i>0.3</i>	<i>3.2</i>	<i>0.8</i>
VII. Aspen - Balsam Poplar	46	7.3	2.2	5.7	2.5	11.3	2.4
		<i>1.6</i>	<i>0.5</i>	<i>2.3</i>	<i>0.8</i>	<i>3.9</i>	<i>0.5</i>
VIII. White Spruce	47	7.2	1.9	17.2	4.1	12.3	4.9
		<i>1.3</i>	<i>0.2</i>	<i>4.6</i>	<i>1.3</i>	<i>2.4</i>	<i>1.1</i>



**Table 3.5.** Stand Type I. Black Spruce Organic ( $n = 15$ )

Tree species relative frequency, and mean density and mean basal area per 10 x 10 m plot.

(a) Relative Frequency

Species	Common Name	Canopy Layer					
		Total	1	2	3	4	5
<i>Picea mariana</i>	Black Spruce	1.00	0.67	1.00	0.93	0.73	0.33
<i>Larix laricina</i>	Eastern Larch	0.40	0.13	0.27	0.07	0.07	0.07
<i>Betula papyrifera</i>	White Birch	0.20		0.07		0.07	0.07
<i>Abies balsamea</i>	Balsam Fir	0.13				0.07	0.13
<i>Picea glauca</i>	White Spruce	0.13				0.07	0.07

(b) Mean Density Per Plot

Species	Common Name	Canopy Layer					
		Total	1	2	3	4	5
<i>Picea mariana</i>	Black Spruce	75.47	11.60	24.60	20.80	14.80	3.67
<i>Larix laricina</i>	Eastern Larch	2.87	1.13	0.87	0.07	0.20	0.60
<i>Betula papyrifera</i>	White Birch	0.47		0.07		0.07	0.33
<i>Abies balsamea</i>	Balsam Fir	0.33				0.07	0.27
<i>Picea glauca</i>	White Spruce	0.47				0.07	0.40
		79.60	12.73	25.53	20.87	15.20	5.27

(c) Mean Basal Area ( $m^2$  per Plot)

Species	Common Name	Canopy Layer					
		Total	1	2	3	4	5
<i>Picea mariana</i>	Black Spruce	0.839	0.376	0.364	0.095	0.005	-
<i>Larix laricina</i>	Eastern Larch	0.040	0.029	0.010	-	-	-
<i>Betula papyrifera</i>	White Birch	-		-		-	-
<i>Abies balsamea</i>	Balsam Fir	-				-	-
<i>Picea glauca</i>	White Spruce	-				-	-
		0.879	0.405	0.374	0.095	0.005	-

Note: Dashes (-) indicate values < 0.0005

**Table 3.6.** Stand type I. Black Spruce Organic ( $n = 15$ )  
Frequency, mean cover, and variance of tree species.

Species	Common Name	Frequency	Mean Cover (%)	Variance
<i>Picea mariana</i>	Black Spruce	1.00	36.57	279.66
<i>Larix laricina</i>	Eastern Larch	0.40	2.63	60.15
<i>Betula papyrifera</i>	Paper Birch	0.20	0.12	0.08
<i>Abies balsamea</i>	Balsam Fir	0.13	0.05	0.02
<i>Picea glauca</i>	White Spruce	0.13	0.07	0.04

**Table 3.7.** Stand type I. Black Spruce Organic ( $n = 15$ )  
Frequency, mean cover, and variance of common shrubs ( $f > 0.1$ ).

Species	Common Name	Frequency	Mean Cover (%)	Variance
<b>Tall Shrubs</b>				
<i>Alnus rugosa</i>	Speckled Alder	0.40	1.47	11.10
<i>Betula pumila</i>	Swamp Birch	0.40	0.23	0.14
<i>Cornus stolonifera</i>	Red-Osier Dogwood	0.33	0.10	0.03
<i>Corylus cornuta</i>	Beaked Hazelnut	0.27	0.10	0.04
<i>Sorbus decora</i>	Western Mountain-Ash	0.20	0.12	0.08
<i>Viburnum trilobum</i>	High Bush-Cranberry	0.20	0.05	0.01
<b>Low Shrubs</b>				
<i>Ribes oxycanthoides</i>	Northern Gooseberry	0.40	0.15	0.04
<i>Lonicera dioica</i>	Twining Honeysuckle	0.33	0.10	0.03
<i>Rhamnus alnifolia</i>	Alder-Leaved Buckthorn	0.33	0.23	0.27
<i>Ribes triste</i>	Wild Red Currant	0.27	0.12	0.04
<i>Ribes glandulosum</i>	Skunk Currant	0.13	0.10	0.11
<i>Ribes lacustre</i>	Black Gooseberry	0.13	0.12	0.10
<i>Rubus idaeus</i>	Wild Red Raspberry	0.13	0.07	0.04
<i>Salix myrtillifolia</i>	Myrtle-Leaved Willow	0.13	0.07	0.04
<i>Shepherdia canadensis</i>	Canada Buffaloberry	0.13	0.03	0.01
<b>Ericaceous Shrubs</b>				
<i>Ledum groenlandicum</i>	Common Labrador Tea	0.87	3.55	21.22
<i>Vaccinium vitis-idaea</i>	Bog Cranberry	0.73	0.57	0.49
<i>Oxycoccus microcarpus</i>	Small Bog Cranberry	0.53	0.38	0.17
<i>Gaultheria hispidula</i>	Creeping-Snowberry	0.33	0.13	0.05

Table 3.8. Stand type I. Black Spruce Organic ( $n = 15$ )  
 Frequency, mean cover, and variance of common herb, fern and fern-ally taxa ( $f > 0.1$ ).

Species	Common Name	Frequency	Mean Cover (%)	Variance
<i>Carex</i> spp.	Sedge Species	0.93	5.07	10.92
<i>Rubus pubescens</i>	Dewberry	0.87	0.93	1.13
<i>Mitella nuda</i>	Bishop's-Cap	0.80	1.20	1.38
<i>Linnaea borealis</i>	Twinflower	0.67	0.32	0.09
<i>Caltha palustris</i>	Yellow Marsh-Marigold	0.67	0.60	1.04
<i>Equisetum scirpoides</i>	Dwarf Scouring-Rush	0.67	0.52	0.32
<i>Habenaria hyperborea</i>	Northern Green Bog-Orchid	0.60	1.87	6.01
<i>Equisetum arvense</i>	Common Horsetail	0.53	1.03	2.72
<i>Mertensia paniculata</i>	Tall Lungwort	0.33	0.18	0.16
<i>Galium triflorum</i>	Sweet-Scented Bedstraw	0.33	0.13	0.04
<i>Cornus canadensis</i>	Bunchberry	0.33	0.33	0.65
<i>Smilacina trifolia</i>	Three-Leaved False Solomon's-Seal	0.27	0.47	1.19
<i>Smilacina stellata</i>	Star Flowered False Solomon's-Seal	0.27	0.07	0.01
<i>Calamagrostis canadensis</i>	Bluejoint	0.27	0.13	0.06
<i>Viola renifolia</i>	Kidney-Leaved Violet	0.20	0.10	0.07
<i>Polygonum amphibium</i>	Water Smartweed	0.20	0.05	0.01
<i>Fragaria virginiana</i>	Wild Strawberry	0.20	0.10	0.07
<i>Aster ciliolatus</i>	Fringed Aster	0.20	0.05	0.01
<i>Aralia nudicaulis</i>	Wild Sarsaparilla	0.20	0.05	0.01
Grass spp.	Grass species	0.20	0.07	0.02
<i>Glyceria striata</i>	Fowl Manna Grass	0.20	0.05	0.01
<i>Cinna latifolia</i>	Drooping Wood-Reed	0.20	0.05	0.01
<i>Pyrola secunda</i>	One-Sided Wintergreen	0.13	0.05	0.02
<i>Potentilla palustris</i>	Marsh Cinquefoil	0.13	0.12	0.15
<i>Petasites vitifolius</i>	Vine-Leaved Coltsfoot	0.13	0.03	0.01
<i>Petasites sagittatus</i>	Arrow-Leaved Coltsfoot	0.13	0.10	0.11
<i>Petasites palmatus</i>	Palmate-Leaved Coltsfoot	0.13	0.05	0.02
<i>Monenses uniflora</i>	One-Flowered Wintergreen	0.13	0.03	0.01
<i>Maianthemum canadense</i>	Wild Lily-of-the-Valley	0.13	0.03	0.01
<i>Geum rivale</i>	Purple Avens	0.13	0.18	0.41
<i>Drosera rotundifolia</i>	Round-Leaved Sundew	0.13	0.07	0.03
<i>Coptis trifolia</i>	Goldthread	0.13	0.08	0.05
<i>Aster puniceus</i>	Purple-Stemmed Aster	0.13	0.03	0.01
<i>Aster junciformis</i>	Marsh Aster	0.13	0.03	0.01

Table 3.9. Stand type I. Black Spruce Organic ( $n = 15$ )

Frequency, mean cover, and variance of common bryophyte and lichen taxa ( $f > 0.1$ ).

Species	Common Name	Frequency	Mean Cover (%)	Variance
<b>Bryophytes</b>				
<i>Pleurozium schreberi</i>	Big Red Stem	0.93	16.50	198.35
<i>Sphagnum warnstorfi</i>	Warnstorf's Peat Moss	0.80	11.15	123.18
<i>Aulacomnium palustre</i>	Tufted Moss	0.80	1.22	2.08
<i>Hylocomium splendens</i>	Stair-Step Moss	0.73	1.79	10.64
<i>Helodium blandowii</i>	Blandow's Feather Moss	0.67	1.37	4.27
<i>Ptilium crista-castrensis</i>	Knight's Plume	0.60	1.82	11.10
<i>Bracethecium velutinum</i>	Velvet Feather Moss	0.53	0.06	0.02
<i>Tomenthypnum nitens</i>	Golden Fuzzy Fen Moss	0.47	0.75	2.91
<i>Climacium dendroides</i>	Common Tree Moss	0.47	0.57	1.67
<i>Thuidium delicatulum</i>	Common Fern Moss	0.40	1.24	13.12
<i>Mnium affine</i>	Marsh Magnificent Moss	0.40	1.02	5.58
<i>Dicranum polysetum</i>	Electric Eels	0.40	0.36	1.04
<i>Sphagnum fuscum</i>	Rusty Peat Moss	0.33	3.54	63.98
<i>Mnium cuspidatum</i>	Woodsy Leafy Moss	0.33	0.65	1.93
<i>Mnium medium</i>	Common Leafy Moss	0.27	0.97	7.00
<i>Polytrichum juniperinum</i>	Juniper Hair-Cap	0.20	0.10	0.07
<i>Hypnum lindbergii</i>	Clay Pigtail Moss	0.20	0.08	0.03
<i>Drepanocladus uncinatus</i>	Sickle Moss	0.20	0.09	0.10
<i>Campylium chrysophyllum</i>	Campylium	0.20	0.07	0.04
<i>Bracethecium</i> spp.	Bracethecium Species	0.20	0.44	2.59
<i>Sphagnum recurvum</i>	Poor-Fen Peat Moss	0.13	4.08	145.64
<i>Polytrichum commune</i>	Common Hair Cap	0.13	0.04	0.01
<i>Pohlia nutans</i>	Copper Wire Moss	0.13	0.02	0.00
<i>Lepidozia reptans</i>	Little Hands Liverwort	0.13	0.00	0.00
<i>Dicranum flagellare</i>	Whip Fork Moss	0.13	0.02	0.00
<i>Calliergon stramineum</i>	Straw-Coloured Water Moss	0.13	0.00	0.00
<i>Amblystegium serpens</i>	Amblystegium	0.13	0.01	0.00
<b>Lichens</b>				
<i>Cladina rangiferina</i>	Grey Reindeer Lichen	0.20	0.22	0.50
<i>Peltigera aphthosa</i>	Freckle Pelt	0.13	0.03	0.01

**Table 3.10.** Stand Type II. Jack Pine - Black Spruce ( $n = 17$ )

Tree species relative frequency, and mean density and mean basal area per 10 x 10 m plot.

(a) Relative Frequency

Species	Common Name	Canopy Layer					
		Total	1	2	3	4	5
<i>Pinus banksiana</i>	Jack Pine	0.88	0.88	0.53	0.18		
<i>Picea mariana</i>	Black Spruce	0.82	0.29	0.82	0.71	0.18	0.18
<i>Picea glauca</i>	White Spruce	0.41	0.41	0.24	0.18	0.12	
<i>Populus tremuloides</i>	Trembling Aspen	0.35	0.29	0.06	0.06	0.24	0.18
<i>Populus balsamifera</i>	Balsam Poplar	0.24	0.06	0.06	0.06	0.12	0.12
<i>Betula papyrifera</i>	White Birch	0.06					0.06
<i>Abies balsamea</i>	Balsam Fir	0.02					0.02

(b) Mean Density Per Plot

Species	Common Name	Canopy Layer					
		Total	1	2	3	4	5
<i>Pinus banksiana</i>	Jack Pine	9.71	6.41	3.12	0.18		
<i>Picea mariana</i>	Black Spruce	28.12	3.06	11.29	12.18	1.35	0.24
<i>Picea glauca</i>	White Spruce	4.76	2.41	0.82	1.41	0.12	
<i>Populus tremuloides</i>	Trembling Aspen	5.76	1.76	0.06	0.35	2.41	1.18
<i>Populus balsamifera</i>	Balsam Poplar	2.29	0.12	0.06	0.24	1.29	0.59
<i>Betula papyrifera</i>	White Birch	0.59					0.59
<i>Abies balsamea</i>	Balsam Fir	0.12					0.12
		51.35	13.76	15.35	14.35	5.18	2.71

(c) Mean Basal Area ( $m^2$  per Plot)

Species	Common Name	Canopy Layer					
		Total	1	2	3	4	5
<i>Pinus banksiana</i>	Jack Pine	0.402	0.348	0.052	0.002		
<i>Picea mariana</i>	Black Spruce	0.357	0.114	0.170	0.073	-	-
<i>Picea glauca</i>	White Spruce	0.122	0.101	0.014	0.007	-	
<i>Populus tremuloides</i>	Trembling Aspen	0.090	0.090	-	-	-	-
<i>Populus balsamifera</i>	Balsam Poplar	0.007	0.006	0.001	-	-	-
<i>Betula papyrifera</i>	White Birch	-					-
<i>Abies balsamea</i>	Balsam Fir	-					-
		0.979	0.660	0.237	0.082	-	-

Note: Dashes (-) indicate values < 0.0005

**Table 3.11.** Stand type II. Jack Pine - Black Spruce ( $n = 17$ )

Frequency, mean cover, and variance of tree species.

Species	Common Name	Frequency	Mean Cover (%)	Variance
<i>Pinus banksiana</i>	Jack Pine	0.88	12.82	120.90
<i>Picea mariana</i>	Black Spruce	0.82	26.15	337.86
<i>Picea glauca</i>	White Spruce	0.41	9.34	261.17
<i>Populus tremuloides</i>	Trembling Aspen	0.35	6.54	165.43
<i>Populus balsamifera</i>	Balsam Poplar	0.24	0.54	2.16
<i>Betula papyrifera</i>	Paper Birch	0.06	0.01	-
<i>Abies balsamea</i>	Balsam Fir	0.02	0.01	-

**Table 3.12.** Stand type II. Jack Pine - Black Spruce ( $n = 17$ )

Frequency, mean cover, and variance of common shrub taxa ( $f > 0.1$ ).

Species	Common Name	Frequency	Mean Cover (%)	Variance
<b>Tall Shrubs</b>				
<i>Amelanchier alnifolia</i>	Saskatoon	0.47	0.51	2.61
<i>Corylus cornuta</i>	Beaked Hazelnut	0.47	0.60	0.88
<i>Betula pumila</i>	Dwarf Birch	0.18	0.34	1.61
<i>Viburnum edule</i>	Low Bush-Cranberry	0.18	0.07	0.04
<i>Prunus virginiana</i>	Choke Cherry	0.12	0.06	0.04
<b>Low Shrubs</b>				
<i>Rosa acicularis</i>	Prickly Rose	1.00	1.74	8.03
<i>Symphoricarpos albus</i>	Common Snowberry	0.65	0.54	0.51
<i>Ribes triste</i>	Wild Red Currant	0.35	0.13	0.04
<i>Lonicera dioica</i>	Twining Honeysuckle	0.29	0.16	0.08
<i>Ribes oxycanthoides</i>	Northern Gooseberry	0.24	0.10	0.05
<i>Rubus idaeus</i>	Wild Red Raspberry	0.24	0.50	2.29
<i>Vaccinium myrtilloides</i>	Velvet-Leaved Blueberry	0.18	0.16	0.13
<i>Ribes lacustre</i>	Black Gooseberry	0.12	0.04	0.02
<b>Ericaceous Shrubs</b>				
<i>Vaccinium vitis-idaea</i>	Bog Cranberry	0.41	0.21	0.10
<i>Ledum groenlandicum</i>	Common Labrador Tea	0.35	0.09	0.02

Note: Dashes (-) indicate values  $< 0.005$

Table 3.13. Stand type II. Jack Pine - Black Spruce ( $n = 17$ )

Frequency, mean cover, and variance of common herbs, ferns, and fern-ally taxa ( $f > 0.1$ ).

Species	Common Name	Frequency	Mean Cover (%)	Variance
<i>Linnaea borealis</i>	Twinflower	0.94	0.93	0.74
<i>Maianthemum canadense</i>	Wild Lily-of-the-Valley	0.82	0.56	0.25
<i>Cornus canadensis</i>	Bunchberry	0.82	1.60	3.51
<i>Anemone canadensis</i>	Canada Anemone	0.82	1.03	1.33
<i>Fragaria virginiana</i>	Wild Strawberry	0.71	1.29	3.87
<i>Rubus pubescens</i>	Dewberry	0.65	0.71	0.83
<i>Oryzopsis asperifolia</i>	Rough-Leaved Rice Grass	0.59	0.65	1.41
<i>Mitella nuda</i>	Bishop's-Cap	0.53	0.53	0.69
<i>Galium boreale</i>	Northern Bedstraw	0.47	0.24	0.10
<i>Carex</i> spp.	Sedge Species	0.47	0.44	0.95
<i>Pyrola asarifolia</i>	Common Pink Wintergreen	0.41	0.18	0.06
<i>Pyrola secunda</i>	One-Sided Wintergreen	0.35	0.12	0.03
<i>Mertensia paniculata</i>	Tall Lungwort	0.35	0.26	0.26
Grass spp.	Grass Species	0.35	0.13	0.05
<i>Thalictrum venulosum</i>	Veiny Meadow Rue	0.29	0.31	0.54
<i>Galium triflorum</i>	Sweet-Scented Bedstraw	0.29	0.13	0.06
<i>Aster ciliolatus</i>	Fringed Aster	0.29	0.28	0.34
<i>Aralia nudicaulis</i>	Wild Sarsaparilla	0.24	0.99	6.01
<i>Lathyrus venosus</i>	Purple Peavine	0.18	0.09	0.05
<i>Schizachne purpurascens</i>	Purple Oat Grass	0.18	0.07	0.03
<i>Equisetum scirpoides</i>	Dwarf Scouring Rush	0.18	0.22	0.53
<i>Equisetum pratense</i>	Meadow Horsetail	0.18	0.22	0.46
<i>Equisetum arvense</i>	Common Horsetail	0.18	0.10	0.07
<i>Viola renifolia</i>	Kidney-Leaved Violet	0.12	0.04	0.02
<i>Viola adunca</i>	Early Blue Violet	0.12	0.04	0.02
<i>Vicia americana</i>	American Vetch	0.12	0.04	0.02
<i>Pyrola</i> spp.	Wintergreen Species	0.12	0.06	0.04
<i>Pyrola elliptica</i>	White Wintergreen	0.12	0.06	0.04
<i>Actaea rubra</i>	Red and White Baneberry	0.12	0.03	0.01
<i>Cinna latifolia</i>	Drooping Wood-Reed	0.12	0.04	0.02
<i>Lycopodium complanatum</i>	Ground-Cedar	0.12	0.04	0.02
<i>Lycopodium annotinum</i>	Stiff Club-Moss	0.12	0.16	0.37
<i>Dryopteris spinulosa</i>	Spinulose Shield Fern	0.12	0.03	0.01

**Table 3.14.** Stand type II. Jack Pine - Black Spruce ( $n = 17$ )

Frequency, mean cover, and variance of common bryophyte and lichen taxa ( $f > 0.1$ ).

Species	Common Name	Frequency	Mean Cover (%)	Variance
<b>Bryophytes</b>				
<i>Pleurozium schreberi</i>	Big Red Stem	0.88	17.29	376.79
<i>Hylocomium splendens</i>	Stair-Step Moss	0.88	16.60	191.14
<i>Ptilium crista-castrensis</i>	Knight's Plume	0.65	1.67	10.10
<i>Drepanocladus uncinatus</i>	Sickle Moss	0.59	0.11	0.02
<i>Dicranum polysetum</i>	Electric Eels	0.35	0.15	0.06
<i>Mnium cuspidatum</i>	Woodsy Leafy Moss	0.29	0.29	0.50
<i>Brachythecium</i> spp.	Brachythecium Species	0.29	0.19	0.25
<i>Mnium spinulosum</i>	Red-Mouthed Mnium	0.24	0.02	-
<i>Mnium drummondii</i>	Drummond's Leafy Moss	0.24	0.06	0.02
<i>Brachythecium velutinum</i>	Velvet Feather Moss	0.24	0.02	-
<i>Pohlia nutans</i>	Copper Wire Moss	0.18	0.02	-
<i>Eurhynchium pulchellum</i>	Common Beaked Moss	0.18	0.05	0.02
<i>Amblystegium serpens</i>	Amblystegium	0.18	0.01	-
<i>Thuidium delicatulum</i>	Common Fern Moss	0.12	0.03	0.01
<i>Rhytidiadelphus triquetrus</i>	Shaggy Moss	0.12	0.03	0.01
<i>Dicranum fuscescens</i>	Curly Heron's-Bill Moss	0.12	0.02	-
<i>Brachythecium oxycladon</i>	Brachythecium	0.12	0.04	0.02
<b>Lichens</b>				
<i>Cladonia</i> spp.	Club Lichens	0.24	0.03	0.01
<i>Peltigera aphthosa</i>	Freckle Pelt	0.12	0.03	0.01

Note: Dashes (-) indicate values  $< 0.005$



Table 3.15. Stand Type III. Bur Oak ( $n = 15$ )

Tree species relative frequency, and mean density and mean basal area per 10 x 10 m plot.

(a) Relative Frequency

Species	Common Name	Total	Canopy Layer				
			1	2	3	4	5
<i>Quercus marcocarpa</i>	Bur Oak	1.00		1.00	1.00	0.67	0.53
<i>Fraxinus pennsylvanica</i>	Green Ash	0.20			0.20	0.13	
<i>Picea glauca</i>	White Spruce	0.07	0.07				
<i>Abies balsamea</i>	Balsam Fir	0.07				0.07	
<i>Populus tremuloides</i>	Trembling Aspen	0.07					0.07

(b) Mean Density Per Plot

Species	Common Name	Total	Canopy Layer				
			1	2	3	4	5
<i>Quercus marcocarpa</i>	Bur Oak	27.93		9.67	8.53	6.07	3.67
<i>Fraxinus pennsylvanica</i>	Green Ash	1.40			0.40	1.00	
<i>Picea glauca</i>	White Spruce	0.07	0.07				
<i>Abies balsamea</i>	Balsam Fir	0.07				0.07	
<i>Populus tremuloides</i>	Trembling Aspen	0.13					0.13
		29.60	0.07	9.67	8.93	7.13	3.80

(c) Mean Basal Area ( $m^2$  per Plot)

Species	Common Name	Total	Canopy Layer				
			1	2	3	4	5
<i>Quercus marcocarpa</i>	Bur Oak	0.400		0.320	0.078	0.001	-
<i>Fraxinus pennsylvanica</i>	Green Ash	0.001			0.001	-	
<i>Picea glauca</i>	White Spruce	0.003	0.003				
<i>Abies balsamea</i>	Balsam Fir	-				-	
<i>Populus tremuloides</i>	Trembling Aspen	-					-
		0.404	0.003	0.320	0.079	0.001	-

Note: Dashes (-) indicate values < 0.0005

**Table 3.16.** Stand type III. Bur Oak ( $n = 15$ )  
Frequency, mean cover, and variance of tree taxa.

Species	Common Name	Frequency	Mean Cover (%)	Variance
<i>Quercus macrocarpa</i>	Bur Oak	1.00	33.42	137.11
<i>Fraxinus pennsylvanica</i>	Green Ash	0.20	0.22	0.28
<i>Populus tremuloides</i>	Trembling Aspen	0.07	0.02	-
<i>Abies balsamea</i>	Balsam Fir	0.07	0.02	-
<i>Picea glauca</i>	White Spruce	0.07	0.67	6.67

**Table 3.17.** Stand type III. Bur Oak ( $n = 15$ )  
Frequency, mean cover, and variance of common shrub taxa ( $f > 0.1$ ).

Species	Common Name	Frequency	Mean Cover (%)	Variance
<b>Tall Shrubs</b>				
<i>Viburnum rafinesquianum</i>	Downy Arrowwood	1.00	12.55	43.96
<i>Prunus virginiana</i>	Choke Cherry	1.00	6.40	36.28
<i>Amelanchier alnifolia</i>	Saskatoon	1.00	6.23	25.66
<i>Corylus cornuta</i>	Beaked Hazelnut	0.87	13.52	251.13
<i>Crataegus chrysocarpa</i>	Hawthorn	0.20	0.12	0.11
<i>Prunus pennsylvanica</i>	Pin Cherry	0.07	0.03	0.02
<b>Low Shrubs</b>				
<i>Rosa acicularis</i>	Prickly Rose	1.00	2.00	8.75
<i>Symphoricarpos occidentalis</i>	Western Snowberry	0.87	1.95	6.23
<i>Lonicera dioica</i>	Twining Honeysuckle	0.80	0.50	0.16
<i>Rhus radicans</i>	Poison Ivy	0.80	3.62	15.06
<i>Symphoricarpos albus</i>	Common Snowberry	0.67	1.50	2.62

Note: Dashes (-) indicate values  $< 0.005$

**Table 3.18.** Stand type III. Bur Oak ( $n = 15$ )

Frequency, mean cover, and variance of common herb, fern, and fern-ally taxa ( $f > 0.1$ ).

Species	Common Name	Frequency	Mean Cover (%)	Variance
<i>Maianthemum canadense</i>	Wild Lily-of-the-Valley	1.00	0.72	0.21
<i>Galium boreale</i>	Northern Bedstraw	1.00	0.63	0.05
<i>Aster ciliolatus</i>	Fringed Aster	0.93	1.13	0.84
<i>Aralia nudicaulis</i>	Wild Sarsaparilla	0.93	14.17	154.35
<i>Anemone quinquefolia</i>	Wood Anemone	0.93	0.50	0.07
<i>Oryzopsis asperifolia</i>	Rough-Leaved Rice Grass	0.93	0.97	0.15
<i>Carex</i> spp.	Sedge Species	0.93	1.18	0.50
<i>Sanicula marilandica</i>	Snakeroot	0.87	0.40	0.10
<i>Lathyrus venosus</i>	Purple Peavine	0.87	0.50	0.11
<i>Fragaria virginiana</i>	Wild Strawberry	0.80	0.82	1.60
<i>Thalictrum venulosum</i>	Veiny Meadow Rue	0.73	0.97	1.28
Grass spp.	Grass Species	0.73	0.28	0.07
<i>Vicia americana</i>	American Vetch	0.67	0.22	0.03
<i>Osmorhiza longistylis</i>	Smooth Sweet-Cicely	0.60	0.57	0.75
<i>Thalictrum dasycarpum</i>	Tall Meadow Rue	0.53	0.75	1.28
<i>Smilax herbacea</i>	Carrionflower	0.53	0.22	0.14
<i>Apocynum androsaemifolium</i>	Spreading Dogbane	0.47	0.40	0.60
<i>Agastache foeniculum</i>	Giant Hyssop	0.47	0.40	0.62
<i>Solidago canadensis</i>	Canada Goldenrod	0.40	0.28	0.31
<i>Lathyrus ochroleucus</i>	Creamy Peavine	0.33	0.38	1.05
<i>Arenaria lateriflora</i>	Blunt-Leaved Sandwort	0.27	0.08	0.02
<i>Viola rugulosa</i>	Western Canada Violet	0.20	0.07	0.02
<i>Lysimachia ciliata</i>	Fringed Loosestrife	0.20	0.08	0.03
<i>Achillea millefolium</i>	Common Yarrow	0.20	0.05	0.01
<i>Anemone canadensis</i>	Canada Anemone	0.13	0.12	0.15

**Table 3.19.** Stand type III. Bur Oak ( $n = 15$ )

Frequency, mean cover, and variance of common bryophyte and lichen taxa ( $f > 0.1$ ).

Species	Common Name	Frequency	Mean Cover (%)	Variance
<i>Mnium cuspidatum</i>	Woodsy Leafy Moss	0.47	0.06	0.01
<i>Brachythecium oxycladon</i>	Brachythecium	0.27	0.15	0.15
<i>Haplocladium microphyllum</i>	Haplocladium	0.20	0.01	-
<i>Pylaisiella polyantha</i>	Stocking Moss	0.13	0.03	0.01
<i>Callicladium haldanianum</i>	Shiny-Leaf Moss	0.13	0.03	-
<i>Brachythecium velutinum</i>	Velvet Feather Moss	0.13	0.01	-
<i>Brachythecium</i> spp.	Brachythecium Species	0.13	0.15	0.18
<i>Brachythecium acuminatum</i>	Brachythecium	0.13	0.02	-

Note: Dashes (-) indicate values  $< 0.005$

Table 3.20. Stand Type IV. Eastern Deciduous ( $n = 16$ )

Tree species relative frequency, and mean density and mean basal area per 10 x 10 m plot.

(a) Relative Frequency

Species	Common Name	Total	Canopy Layer				
			1	2	3	4	5
<i>Fraxinus pennsylvanica</i>	Green Ash	0.94	0.56	0.81	0.81	0.63	0.56
<i>Ulmus americana</i>	American Elm	0.88	0.63	0.56	0.56	0.31	0.50
<i>Acer negundo</i>	Manitoba Maple	0.88	0.38	0.63	0.63	0.69	0.69
<i>Quercus marcocarpa</i>	Bur Oak	0.56	0.06	0.25	0.19	0.25	0.38
<i>Populus tremuloides</i>	Trembling Aspen	0.31	0.19				0.13
<i>Populus balsamifera</i>	Balsam Poplar	0.25	0.13				0.19
<i>Betula papyrifera</i>	Paper Birch	0.13	0.06	0.06	0.06		
<i>Populus deltoides</i>	Cottonwood	0.06	0.06	0.06			

(b) Mean Density Per Plot

Species	Common Name	Total	Canopy Layer				
			1	2	3	4	5
<i>Fraxinus pennsylvanica</i>	Green Ash	15.81	1.63	3.06	3.75	2.31	5.06
<i>Ulmus americana</i>	American Elm	11.50	0.94	1.00	4.69	1.19	3.69
<i>Acer negundo</i>	Manitoba Maple	18.44	0.75	2.38	2.44	1.69	11.19
<i>Quercus marcocarpa</i>	Bur Oak	3.44	0.06	0.94	0.56	0.63	1.25
<i>Populus tremuloides</i>	Trembling Aspen	0.56	0.25				0.31
<i>Populus balsamifera</i>	Balsam Poplar	2.13	0.44				1.69
<i>Betula papyrifera</i>	Paper Birch	0.44	0.13	0.19	0.13		
<i>Populus deltoides</i>	Cottonwood	0.31	0.25	0.06			
		52.63	4.44	7.63	11.56	5.81	23.19

(c) Mean Basal Area ( $m^2$  per Plot)

Species	Common Name	Total	Canopy Layer				
			1	2	3	4	5
<i>Fraxinus pennsylvanica</i>	Green Ash	0.177	0.100	0.061	0.016	-	-
<i>Ulmus americana</i>	American Elm	0.130	0.089	0.025	0.017	-	-
<i>Acer negundo</i>	Manitoba Maple	0.136	0.050	0.071	0.015	-	-
<i>Quercus marcocarpa</i>	Bur Oak	0.034	0.002	0.029	0.004	-	-
<i>Populus tremuloides</i>	Trembling Aspen	0.021	0.021				-
<i>Populus balsamifera</i>	Balsam Poplar	0.061	0.061				-
<i>Betula papyrifera</i>	Paper Birch	0.012	0.008	0.004	-		
<i>Populus deltoides</i>	Cottonwood	0.041	0.040	0.001			
		0.612	0.370	0.191	0.051	-	-

Note: Dashes (-) indicate values < 0.0005

**Table 3.21.** Stand type IV. Eastern Deciduous ( $n = 16$ ).  
Frequency, mean cover, and variance of tree species.

Species	Common Name	Frequency	Mean Cover (%)	Variance
<i>Fraxinus pennsylvanica</i>	Green Ash	0.94	20.14	163.08
<i>Ulmus americana</i>	American Elm	0.88	16.53	167.84
<i>Acer negundo</i>	Manitoba Maple	0.88	15.80	188.67
<i>Quercus macrocarpa</i>	Bur Oak	0.56	3.88	56.69
<i>Populus tremuloides</i>	Trembling Aspen	0.31	0.73	2.85
<i>Populus balsamifera</i>	Balsam Poplar	0.25	1.05	8.58
<i>Betula papyrifera</i>	Paper Birch	0.13	2.66	52.89
<i>Populus deltoides</i>	Cottonwood	0.06	1.94	60.06

**Table 3.22.** Stand type IV. Eastern Deciduous ( $n = 16$ ).  
Frequency, mean cover, and variance of common shrub taxa ( $f > 0.1$ ).

Species	Common Name	Frequency	Mean Cover (%)	Variance
<b>Tall Shrubs</b>				
<i>Prunus virginiana</i>	Choke Cherry	1.00	4.73	24.57
<i>Corylus cornuta</i>	Beaked Hazelnut	0.75	14.50	223.12
<i>Viburnum trilobum</i>	American Bush-Cranberry	0.69	3.77	41.75
<i>Viburnum rafinesquianum</i>	Downy Arrowwood	0.63	3.09	38.73
<i>Amelanchier alnifolia</i>	Saskatoon	0.56	1.14	5.96
<i>Cornus stolonifera</i>	Red-Osier Dogwood	0.31	1.16	3.89
<i>Acer spicatum</i>	Mountain Maple	0.19	0.77	4.71
<i>Viburnum edule</i>	Low Bush-Cranberry	0.06	0.02	-
<b>Low Shrubs</b>				
<i>Rhus radicans</i>	Poison Ivy	0.63	1.81	4.73
<i>Ribes triste</i>	Wild Red Currant	0.50	0.81	2.10
<i>Symphoricarpos albus</i>	Common Snowberry	0.50	0.59	1.00
<i>Rosa acicularis</i>	Prickly Rose	0.44	0.48	0.84
<i>Lonicera dioica</i>	Twining Honeysuckle	0.38	0.33	0.22
<i>Ribes hudsonianum</i>	Northern Black Currant	0.38	0.72	2.07
<i>Rubus idaeus</i>	Wild Red Raspberry	0.31	0.22	0.23
<i>Symphoricarpos occidentalis</i>	Western Snowberry	0.25	1.03	5.84
<i>Ribes oxycanthoides</i>	Northern Gooseberry	0.19	0.11	0.07
<i>Celastrus scandens</i>	Climbing Bittersweet	0.13	0.03	0.01
<i>Ribes americana</i>	Wild Black Currant	0.06	0.02	-
<i>Ribes glandulosum</i>	Skunk Currant	0.06	0.03	0.02
<i>Ribes lacustre</i>	Black Gooseberry	0.06	0.05	0.04

Note: Dashes (-) indicate values  $< 0.005$

**Table 3.23.** Stand type IV. Eastern Deciduous ( $n = 16$ ).  
Frequency, mean cover, and variance of common herb, fern, and fern-ally taxa ( $f > 0.1$ ).

Species	Common Name	Frequency	Mean Cover (%)	Variance
<i>Carex</i> spp.	Sedge Species	0.94	2.94	14.99
<i>Aralia nudicaulis</i>	Wild Sarsaparilla	0.88	12.19	238.41
<i>Thalictrum dasycarpum</i>	Tall Meadow Rue	0.75	0.53	0.42
<i>Rudbeckia laciniata</i>	Coneflower	0.75	0.25	0.06
<i>Maianthemum canadense</i>	Wild Lily-of-the-Valley	0.75	1.33	3.01
<i>Galium triflorum</i>	Sweet-Scented Bedstraw	0.69	0.30	0.09
<i>Trillium cernuum</i>	Nodding Trillium	0.56	0.16	0.02
<i>Osmorhiza longistylis</i>	Smooth Sweet-Cicely	0.56	1.44	6.69
<i>Anemone quinquefolia</i>	Wood Anemone	0.56	0.19	0.05
<i>Actaea rubra</i>	Red and White Baneberry	0.56	0.27	0.16
<i>Oryzopsis asperifolia</i>	Rough-Leaved Rice Grass	0.56	0.52	0.24
<i>Matteucia struthiopteris</i>	Ostrich Fern	0.56	7.92	169.84
<i>Rubus pubescens</i>	Dewberry	0.50	0.83	2.01
<i>Fragaria virginiana</i>	Wild Strawberry	0.50	0.27	0.13
<i>Aster ciliolatus</i>	Fringed Aster	0.50	0.36	0.55
<i>Solidago canadensis</i>	Canada Goldenrod	0.44	0.14	0.03
<i>Smilacina stellata</i>	Star-Flowered False Solomon's Seal	0.44	0.27	0.25
<i>Galium boreale</i>	Northern Bedstraw	0.44	0.16	0.04
<i>Thalictrum venulosum</i>	Veiny Meadow Rue	0.38	0.31	0.25
<i>Viola rugulosa</i>	Western Canada Violet	0.31	0.20	0.15
<i>Smilax herbacea</i>	Carrionflower	0.31	0.08	0.01
<i>Sanicula marilandica</i>	Snakeroot	0.31	0.13	0.05
<i>Botrychium virginianum</i>	Virginia Grape Fern	0.31	0.08	0.01
<i>Urtica dioica</i>	Stinging Nettle	0.25	0.13	0.06
<i>Lathyrus venosus</i>	Purple Peavine	0.25	0.06	0.01
<i>Humulus lupulus</i>	Common Hop	0.25	0.08	0.02
<i>Circaea alpina</i>	Small Enchanter's Nightshade	0.25	0.16	0.19
<i>Viola renifolia</i>	Kidney-Leaved Violet	0.19	0.31	0.89
<i>Pyrola asarifolia</i>	Common Pink Wintergreen	0.19	0.11	0.07
<i>Parthenocissus inserta</i>	Virginia Creeper	0.19	0.05	0.01
<i>Mitella nuda</i>	Bishop's-Cap	0.19	0.17	0.19
<i>Lathyrus ochroleucus</i>	Creamy Peavine	0.19	0.06	0.02
Grass spp.	Grass species	0.19	0.09	0.07
<i>Equisetum pratense</i>	Meadow Horsetail	0.19	0.08	0.04
<i>Zizia aurea</i>	Golden Alexander	0.13	0.05	0.02
<i>Viola</i> spp.	Viola species	0.13	0.17	0.39
<i>Galeopsis tetrahit</i>	Hemp-Nettle	0.13	0.03	0.01
<i>Arenaria lateriflora</i>	Blunt-Leaved Sandwort	0.13	0.06	0.04
<i>Aquilegia canadensis</i>	Canada Columbine	0.13	0.03	0.01
<i>Apocynum androsaemifolium</i>	Spreading Dogbane	0.13	0.03	0.01
<i>Dryopteris spinulosa</i>	Spinulose Shield Fern	0.13	0.03	0.01

**Table 3.24.** Stand type IV. Eastern Deciduous ( $n = 16$ ).  
Frequency, mean cover, and variance of common bryophyte and lichen taxa.

Species	Common Name	Frequency	Mean Cover (%)	Variance
<b>Bryophytes</b>				
<i>Mnium cuspidatum</i>	Woodsy Leafy Moss	0.44	0.10	0.04
<i>Brachythecium</i> spp.	Brachythecium Species	0.44	0.19	0.15
<i>Haplocladium microphyllum</i>	Haplocladium	0.25	0.06	0.03
<i>Brachythecium acuminatum</i>	Brachythecium	0.19	0.03	0.01
<i>Anomodon minor</i>	Anomodon	0.19	0.01	-
<i>Amblystegium serpens</i>	Amblystegium	0.19	0.02	-
<i>Pylaisiella polyantha</i>	Stocking Moss	0.13	0.02	-
<i>Brachythecium salebrosum</i>	Golden Ragged Moss	0.13	0.02	-
<i>Brachythecium oxycladon</i>	Brachythecium	0.13	0.05	0.04
<i>Hypnum pallescens</i>	Stump Pigtail Moss	0.06	0.01	-
<i>Callicladium haldanianum</i>	Shiny-Leaf Moss	0.06	0.04	0.02

Note: Dashes (-) indicate values  $< 0.005$

**Table 3.25.** Stand Type V. Balsam Fir ( $n = 18$ )

Tree species relative frequency, and mean density and mean basal area per 10 x 10 m plot.

(a) Relative Frequency

Species	Common Name	Total	Canopy Layer				
			1	2	3	4	5
<i>Abies balsamea</i>	Balsam Fir	1.00	0.94	1.00	0.67	0.22	1.00
<i>Picea glauca</i>	White Spruce	0.83	0.22	0.11	0.50	0.22	0.39
<i>Populus balsamifera</i>	Balsam Poplar	0.72	0.33	0.22	0.06	0.06	0.67
<i>Betula papyrifera</i>	Paper Birch	0.67	0.44	0.39			0.44
<i>Fraxinus pennsylvanica</i>	Green Ash	0.67	0.11	0.17	0.22	0.06	0.44
<i>Populus tremuloides</i>	Trembling Aspen	0.50	0.28	0.06			0.50
<i>Ulmus americana</i>	American Elm	0.44	0.11	0.06			0.33
<i>Acer negundo</i>	Manitoba Maple	0.06			0.06		0.06

(b) Mean Density Per Plot

Species	Common Name	Total	Canopy Layer				
			1	2	3	4	5
<i>Abies balsamea</i>	Balsam Fir	57.22	4.17	4.50	1.83	3.67	43.06
<i>Picea glauca</i>	White Spruce	2.83	0.44	0.11	1.00	0.67	0.61
<i>Populus balsamifera</i>	Balsam Poplar	7.78	0.50	0.61	0.06	0.06	6.56
<i>Betula papyrifera</i>	Paper Birch	3.83	0.56	0.61			2.67
<i>Fraxinus pennsylvanica</i>	Green Ash	4.94	0.11	0.22	0.61	0.22	3.78
<i>Populus tremuloides</i>	Trembling Aspen	2.67	0.56	0.11			2.00
<i>Ulmus americana</i>	American Elm	1.06	0.17	0.06			0.83
<i>Acer negundo</i>	Manitoba Maple	0.33			0.17		0.17
		80.67	6.50	6.22	3.67	4.61	59.67

(c) Mean Basal Area ( $m^2$  per Plot)

Species	Common Name	Total	Canopy Layer				
			1	2	3	4	5
<i>Abies balsamea</i>	Balsam Fir	0.335	0.199	0.116	0.017	0.001	0.001
<i>Picea glauca</i>	White Spruce	0.054	0.047	0.003	0.004	-	-
<i>Populus balsamifera</i>	Balsam Poplar	0.075	0.052	0.023	0.001	-	-
<i>Betula papyrifera</i>	Paper Birch	0.071	0.055	0.016			-
<i>Fraxinus pennsylvanica</i>	Green Ash	0.014	0.008	0.004	0.001	-	-
<i>Populus tremuloides</i>	Trembling Aspen	0.045	0.043	0.003			-
<i>Ulmus americana</i>	American Elm	0.013	0.010	0.003			-
<i>Acer negundo</i>	Manitoba Maple	0.001			0.001		-
		0.607	0.413	0.168	0.024	0.001	0.001

Note: Dashes (-) indicate values < 0.0005



Table 3.26. Stand type V. Balsam Fir ( $n = 18$ )

Frequency, mean cover, and variance of tree species.

Species	Common Name	Frequency	Mean Cover (%)	Variance
<i>Abies balsamea</i>	Balsam Fir	1.00	25.54	92.66
<i>Picea glauca</i>	White Spruce	0.83	2.89	12.65
<i>Populus balsamifera</i>	Balsam Poplar	0.72	3.76	39.42
<i>Betula papyrifera</i>	Paper Birch	0.67	4.53	39.20
<i>Fraxinus pennsylvanica</i>	Green Ash	0.67	1.71	9.78
<i>Populus tremuloides</i>	Trembling Aspen	0.50	2.75	31.01
<i>Ulmus americana</i>	American Elm	0.44	1.04	6.92
<i>Acer negundo</i>	Manitoba Maple	0.06	0.58	6.13

Table 3.27. Stand type V. Balsam Fir ( $n = 18$ )

Frequency, mean cover, and variance of common shrub taxa ( $f > 0.1$ ).

Species	Common Name	Frequency	Mean Cover (%)	Variance
<b>Tall Shrubs</b>				
<i>Acer spicatum</i>	Mountain Maple	1.00	20.76	333.64
<i>Corylus cornuta</i>	Beaked Hazelnut	0.89	4.96	26.60
<i>Prunus virginiana</i>	Choke Cherry	0.89	1.15	1.13
<i>Viburnum edule</i>	Low Bush-Cranberry	0.50	0.54	0.73
<i>Viburnum rafinesquianum</i>	Downy Arrowwood	0.50	0.25	0.15
<i>Viburnum trilobum</i>	American Bush-Cranberry	0.44	0.13	0.02
<i>Cornus stolonifera</i>	Red-Osier Dogwood	0.33	0.22	0.15
<i>Amelanchier alnifolia</i>	Saskatoon	0.22	0.11	0.07
<i>Sorbus decora</i>	Western Mountain-Ash	0.17	0.04	0.01
<i>Alnus rugosa</i>	River Alder	0.11	0.10	0.13
<b>Low Shrubs</b>				
<i>Rosa acicularis</i>	Prickly Rose	0.67	0.85	0.97
<i>Symphoricarpos albus</i>	Common Snowberry	0.67	0.26	0.08
<i>Ribes triste</i>	Wild Red Currant	0.56	0.35	0.20
<i>Diervilla lonicera</i>	Bush Honeysuckle	0.50	0.96	3.49
<i>Cornus alternifolia</i>	Green Osier	0.33	0.31	0.31
<i>Lonicera dioica</i>	Twining Honeysuckle	0.33	0.14	0.05
<i>Rubus idaeus</i>	Wild Red Raspberry	0.33	0.19	0.11
<i>Rhamnus alnifolia</i>	Alder-Leaved Buckthorn	0.17	0.08	0.06
<i>Ribes lacustre</i>	Black Gooseberry	0.17	0.04	0.01
<i>Rhus radicans</i>	Poison Ivy	0.11	0.03	0.01
<b>Ericaceous Shrubs</b>				
<i>Ledum groenlandicum</i>	Common Labrador Tea	0.11	0.03	0.01

**Table 3.28.** Stand type V. Balsam Fir ( $n = 18$ )

Frequency, mean cover, and variance of common herb, fern, and fern-ally taxa ( $f > 0.1$ ).

Species	Common Name	Frequency	Mean Cover (%)	Variance
<i>Galium triflorum</i>	Sweet-Scented Bedstraw	1.00	0.42	0.05
<i>Aralia nudicaulis</i>	Wild Sarsaparilla	1.00	6.53	26.09
<i>Carex</i> spp.	Sedge Species	0.94	1.39	1.24
<i>Mitella nuda</i>	Bishop's Cap	0.89	1.96	1.95
<i>Maianthemum canadense</i>	Wild Lily-of-the-Valley	0.89	1.19	1.20
<i>Cornus canadensis</i>	Bunchberry	0.83	2.44	5.02
<i>Anemone quinquefolia</i>	Wood Anemone	0.78	0.30	0.06
<i>Viola rugulosa</i>	Western Canada Violet	0.72	1.04	2.30
<i>Rubus pubescens</i>	Dewberry	0.72	3.72	19.71
<i>Fragaria virginiana</i>	Wild Strawberry	0.72	0.74	0.97
<i>Oryzopsis asperifolia</i>	Rough-Leaved Rice Grass	0.72	0.44	0.13
<i>Pyrola asarifolia</i>	Common Pink Wintergreen	0.67	0.76	0.75
<i>Galium boreale</i>	Northern Bedstraw	0.67	0.29	0.09
<i>Mertensia paniculata</i>	Tall Lungwort	0.56	0.72	0.85
<i>Anemone canadensis</i>	Canada Anemone	0.56	1.11	2.27
<i>Linnaea borealis</i>	Twinflower	0.50	0.86	2.19
<i>Aster ciliolatus</i>	Fringed Aster	0.50	0.50	0.63
<i>Disporum trachycarpum</i>	Fairybells	0.44	0.11	0.02
<i>Trientalis borealis</i>	Northern Starflower	0.39	0.32	0.37
<i>Osmorhiza longistylis</i>	Smooth Sweet-Cicely	0.39	0.10	0.02
<i>Pyrola secunda</i>	One-Sided Wintergreen	0.33	0.11	0.03
<i>Equisetum scirpoides</i>	Dwarf Scouring-Rush	0.33	0.31	0.30
<i>Equisetum pratense</i>	Meadow Horsetail	0.33	0.36	0.66
<i>Trillium cernuum</i>	Nodding Trillium	0.28	0.07	0.01
<i>Sanicula marilandica</i>	Snakeroot	0.28	0.14	0.10
<i>Smilacina stellata</i>	Star Flowered False Solomon's Seal	0.22	0.08	0.03
<i>Actaea rubra</i>	Red and White Baneberry	0.22	0.06	0.01
Grass spp.	Grass Species	0.22	0.11	0.05
<i>Viola renifolia</i>	Kidney-Leaved Violet	0.17	0.06	0.02
<i>Taraxacum officinale</i>	Common Dandelion	0.17	0.04	0.01
<i>Lathyrus venosus</i>	Purple Peavine	0.17	0.06	0.02
<i>Lathyrus ochroleucus</i>	Creamy Peavine	0.17	0.06	0.02
<i>Matteuccia struthiopteris</i>	Ostrich Fern	0.17	0.10	0.09
<i>Rudbeckia laciniata</i>	Coneflower	0.11	0.03	0.01
<i>Pyrola virens</i>	Green Wintergreen	0.11	0.03	0.01
<i>Petasites vitifolius</i>	Vine-Leaved Coltsfoot	0.11	0.03	0.01
<i>Caltha palustris</i>	Yellow Marsh-Marigold	0.11	0.03	0.01
<i>Equisetum arvense</i>	Common Horsetail	0.11	0.03	0.01

**Table 3.29.** Stand type V. Balsam Fir ( $n = 18$ )  
 Frequency, mean cover, and variance of common bryophyte and lichen taxa ( $f > 0.1$ ).

Species	Common Name	Frequency	Mean Cover (%)	Variance
<b>Bryophytes</b>				
<i>Mnium cuspidatum</i>	Woodsy Leafy Moss	0.67	0.13	0.03
<i>Brachythecium</i> spp.	Brachythecium Species	0.61	0.75	2.39
<i>Eurhynchium pulchellum</i>	Common Beaked Moss	0.56	1.40	6.59
<i>Hylocomium splendens</i>	Stair-Step Moss	0.50	0.97	8.88
<i>Pleurozium schreberi</i>	Big Red Stem	0.39	1.08	9.54
<i>Mnium spinulosum</i>	Red-Mouthed Mnium	0.33	0.09	0.03
<i>Amblystegium serpens</i>	Amblystegium	0.33	0.01	-
<i>Rhytidiadelphus triquetrus</i>	Shaggy Moss	0.28	0.22	0.27
<i>Mnium drummondii</i>	Drummond's Leafy Moss	0.28	0.12	0.10
<i>Drepanocladus uncinatus</i>	Sickle Moss	0.28	0.09	0.09
<i>Brachythecium salebrosum</i>	Golden Ragged Moss	0.28	0.21	0.27
<i>Thuidium delicatulum</i>	Common Fern Moss	0.22	0.26	0.53
<i>Oncophorus wahlenbergii</i>	Mountain Curved-Back Moss	0.22	0.02	-
<i>Brachythecium velutinum</i>	Velvet Feather Moss	0.22	0.56	3.18
<i>Brachythecium acuminatum</i>	Brachythecium	0.22	0.47	2.76
<i>Ptilium crista-castrensis</i>	Knight's Plume	0.17	0.03	0.01
<i>Haplocladium microphyllum</i>	Haplocladium	0.17	-	-
<i>Callicladium haldanianum</i>	Shiny-Leaf Moss	0.17	0.01	-
<i>Mnium longirostrum</i>	Mnium	0.11	0.33	1.19
<i>Jamesoniella autumnalis</i>	Jameson's Liverwort	0.11	-	-
<i>Climacium dendroides</i>	Common Tree Moss	0.11	0.03	0.01
<b>Lichens</b>				
<i>Cladonia</i> spp.	Club Lichens	0.33	0.02	-
<i>Peltigera elisabethae</i>	Dog Lichen	0.17	0.04	0.01

Note: Dashes (-) indicate values  $< 0.005$

**Table 3.30.** Stand Type VI. Trembling Aspen - Birch - Mountain Maple ( $n = 22$ )

Tree species relative frequency, and mean density and mean basal area per 10 x 10 m plot.

(a) Relative Frequency

Species	Common Name	Canopy Layer					
		Total	1	2	3	4	5
<i>Populus tremuloides</i>	Trembling Aspen	0.91	0.82	0.23	0.18	0.27	0.50
<i>Populus balsamifera</i>	Balsam Poplar	0.50	0.45	0.14	0.09	0.09	0.27
<i>Betula papyrifera</i>	Paper Birch	0.50	0.32	0.50	0.41	0.14	0.14
<i>Fraxinus pennsylvanica</i>	Green Ash	0.50	0.05	0.09	0.41	0.36	0.27
<i>Ulmus americana</i>	American Elm	0.32		0.05	0.09	0.14	0.14
<i>Acer negundo</i>	Manitoba Maple	0.32		0.05	0.23	0.09	0.09
<i>Quercus macrocarpa</i>	Bur Oak	0.23		0.09	0.05	0.18	0.09
<i>Picea glauca</i>	White Spruce	0.14	0.09	0.09	0.09	0.05	
<i>Abies balsamea</i>	Balsam Fir	0.09				0.05	0.05

(b) Mean Density Per Plot

Species	Common Name	Canopy Layer					
		Total	1	2	3	4	5
<i>Populus tremuloides</i>	Trembling Aspen	11.77	5.68	0.68	1.14	0.91	3.36
<i>Populus balsamifera</i>	Balsam Poplar	3.00	1.46	0.23	0.09	0.14	1.09
<i>Betula papyrifera</i>	Paper Birch	8.86	1.05	2.50	3.32	0.46	1.55
<i>Fraxinus pennsylvanica</i>	Green Ash	9.86	0.05	0.41	2.55	2.05	4.82
<i>Ulmus americana</i>	American Elm	1.73		0.05	0.14	0.50	1.05
<i>Acer negundo</i>	Manitoba Maple	1.14		0.05	0.36	0.27	0.46
<i>Quercus macrocarpa</i>	Bur Oak	1.46		0.14	0.09	0.77	0.46
<i>Picea glauca</i>	White Spruce	0.50	0.14	0.18	0.14	0.05	
<i>Abies balsamea</i>	Balsam Fir	2.64				0.27	2.36
		40.95	8.36	4.23	7.82	5.41	15.14

(c) Mean Basal Area ( $m^2$  per Plot)

Species	Common Name	Canopy Layer					
		Total	1	2	3	4	5
<i>Populus tremuloides</i>	Trembling Aspen	0.349	0.329	0.014	0.005	-	-
<i>Populus balsamifera</i>	Balsam Poplar	0.143	0.136	0.006	0.001	-	-
<i>Betula papyrifera</i>	Paper Birch	0.169	0.055	0.094	0.020	-	-
<i>Fraxinus pennsylvanica</i>	Green Ash	0.017	0.002	0.003	0.011	-	-
<i>Ulmus americana</i>	American Elm	0.003		0.003	-	-	-
<i>Acer negundo</i>	Manitoba Maple	0.001		-	0.001	-	-
<i>Quercus macrocarpa</i>	Bur Oak	0.004		0.004	0.001	-	-
<i>Picea glauca</i>	White Spruce	0.026	0.021	0.005	0.001	-	
<i>Abies balsamea</i>	Balsam Fir	-				-	-
		0.711	0.544	0.128	0.039	-	-

Note: Dashes (-) indicate values  $< 0.0005$

Table 3.31. Stand type VI. Trembling Aspen - Birch - Mountain Maple ( $n = 22$ )

Frequency, mean cover, and variance of tree species ( $n = 22$ ).

Species	Common Name	Frequency	Mean Cover (%)	Variance
<i>Populus tremuloides</i>	Trembling Aspen	0.91	13.22	103.66
<i>Populus balsamifera</i>	Balsam Poplar	0.50	3.47	28.47
<i>Betula papyrifera</i>	Paper Birch	0.50	12.49	221.02
<i>Fraxinus pennsylvanica</i>	Green Ash	0.50	3.10	26.23
<i>Ulmus americana</i>	American Elm	0.32	0.35	0.65
<i>Acer negundo</i>	Manitoba Maple	0.32	0.42	0.84
<i>Quercus macrocarpa</i>	Bur Oak	0.23	0.65	2.92
<i>Picea glauca</i>	White Spruce	0.14	1.32	16.44
<i>Abies balsamea</i>	Balsam Fir	0.09	0.07	0.05

Table 3.32. Stand type VI. Trembling Aspen - Birch - Mountain Maple ( $n = 22$ )

Frequency, mean cover, and variance of common shrub taxa ( $f > 0.1$ ).

Species	Common Name	Frequency	Mean Cover (%)	Variance
<b>Tall Shrubs</b>				
<i>Acer spicatum</i>	Mountain Maple	1.00	24.20	447.50
<i>Corylus cornuta</i>	Beaked Hazelnut	1.00	17.70	183.06
<i>Prunus virginiana</i>	Choke Cherry	0.91	1.51	2.59
<i>Cornus stolonifera</i>	Red-Osier Dogwood	0.77	0.67	0.54
<i>Amelanchier alnifolia</i>	Saskatoon	0.55	0.26	0.10
<i>Viburnum trilobum</i>	American Bush-Cranberry	0.55	0.93	2.29
<i>Viburnum rafinesquianum</i>	Downy Arrowwood	0.45	0.28	0.23
<i>Viburnum edule</i>	Low Bush-Cranberry	0.41	0.26	0.23
<i>Prunus pensylvanica</i>	Pin Cherry	0.23	0.13	0.11
<b>Low Shrubs</b>				
<i>Ribes triste</i>	Wild Red Currant	0.77	0.68	0.58
<i>Rosa acicularis</i>	Prickly Rose	0.73	0.69	0.63
<i>Symphoricarpos albus</i>	Common Snowberry	0.59	0.44	0.26
<i>Lonicera dioica</i>	Twining Honeysuckle	0.50	0.35	0.19
<i>Rubus idaeus</i>	Wild Red Raspberry	0.27	0.28	0.47
<i>Rhus radicans</i>	Poison Ivy	0.23	0.35	1.01
<i>Ribes oxycanthoides</i>	Northern Gooseberry	0.23	0.10	0.05
<i>Cornus alternifolia</i>	Green Osier	0.18	0.49	2.67
<i>Diervilla lonicera</i>	Bush Honeysuckle	0.18	0.26	0.83
<i>Rhamnus alnifolia</i>	Alder-Leaved Buckthorn	0.14	0.07	0.04

Table 3.33. Stand type VI. Trembling Aspen - Birch - Mountain Maple ( $n = 22$ )  
 Frequency, mean cover, and variance of common herb, fern, and fern-ally taxa ( $f > 0.1$ ).

Species	Common Name	Frequency	Mean Cover (%)	Variance
<i>Rubus pubescens</i>	Dewberry	0.91	1.33	1.54
<i>Pyrola asarifolia</i>	Common Pink Wintergreen	0.91	0.91	0.83
<i>Maianthemum canadense</i>	Wild Lily-of-the-Valley	0.91	0.92	0.88
<i>Galium triflorum</i>	Sweet-Scented Bedstraw	0.91	0.40	0.07
<i>Aralia nudicaulis</i>	Wild Sarsaparilla	0.91	4.33	35.02
<i>Aster ciliolatus</i>	Fringed Aster	0.86	0.99	1.13
<i>Cornus canadensis</i>	Bunchberry	0.73	0.28	0.06
<i>Mitella nuda</i>	Bishop's Cap	0.64	0.76	1.26
<i>Mertensia paniculata</i>	Tall Lungwort	0.64	0.93	3.05
<i>Galium boreale</i>	Northern Bedstraw	0.64	0.28	0.08
<i>Fragaria virginiana</i>	Wild Strawberry	0.64	0.44	0.62
<i>Oryzopsis asperifolia</i>	Rough-Leaved Rice Grass	0.64	0.33	0.12
<i>Sanicula marilandica</i>	Snakeroot	0.59	0.39	0.46
<i>Viola rugulosa</i>	Western Canada Violet	0.55	0.84	3.71
<i>Actaea rubra</i>	Red and White Baneberry	0.50	0.17	0.07
<i>Osmorhiza longistylis</i>	Smooth Sweet-Cicely	0.45	0.15	0.04
<i>Lathyrus venosus</i>	Purple Peavine	0.45	0.13	0.02
<i>Carex</i> spp.	Sedge Species	0.45	0.33	0.26
<i>Trillium cernuum</i>	Nodding Trillium	0.41	0.13	0.03
<i>Disporum trachycarpum</i>	Fairybells	0.41	0.13	0.03
<i>Pyrola secunda</i>	One-Sided Wintergreen	0.36	0.13	0.04
<i>Anemone canadensis</i>	Canada Anemone	0.27	0.23	0.25
<i>Solidago canadensis</i>	Canada Goldenrod	0.23	0.08	0.03
<i>Smilacina stellata</i>	Star Flowered False Solomon's-Seal	0.23	0.10	0.05
<i>Thalictrum venulosum</i>	Veiny Meadow Rue	0.18	0.05	0.01
<i>Thalictrum dasycarpum</i>	Tall Meadow Rue	0.18	0.11	0.11
<i>Matteucia struthiopteris</i>	Ostrich Fern	0.18	1.27	9.02
<i>Equisetum pratense</i>	Meadow Horsetail	0.18	0.09	0.06
<i>Rudbeckia laciniata</i>	Coneflower	0.14	0.18	0.42
<i>Petasites sagittatus</i>	Arrow-leaved Coltsfoot	0.14	0.06	0.03
<i>Petasites palmatus</i>	Palmate-Leaved Coltsfoot	0.14	0.06	0.02
<i>Linnaea borealis</i>	Twinflower	0.14	0.03	0.01
<i>Lathyrus ochroleucus</i>	Creamy Peavine	0.14	0.05	0.02
<i>Heracleum lanatum</i>	Cow Parsnip	0.14	0.09	0.08
<i>Apocynum androsaemifolium</i>	Spreading Dogbane	0.14	0.07	0.03
Grass spp.	Grass species	0.14	0.07	0.04

**Table 3.34.** Stand type VI. Trembling Aspen - Birch - Mountain Maple ( $n = 22$ )  
 Frequency, mean cover, and variance of common bryophyte and lichen taxa.

Species	Common Name	Frequency	Mean Cover (%)	Variance
<b>Bryophytes</b>				
<i>Brachythecium</i> spp.	Brachythecium Species	0.77	0.41	0.26
<i>Mnium cuspidatum</i>	Woodsy Leafy Moss	0.59	0.18	0.08
<i>Haplocladium microphyllum</i>	Haplocladium	0.55	0.15	0.16
<i>Brachythecium velutinum</i>	Velvet Feather Moss	0.18	0.03	0.01
<i>Amblystegium serpens</i>	Amblystegium	0.18	-	-
<i>Lophozia ventricosa</i>	Leafy Liverwort	0.14	-	-
<i>Brachythecium salebrosum</i>	Golden Ragged Moss	0.14	0.05	0.03
<i>Brachythecium acuminatum</i>	Brachythecium	0.14	0.01	-
<i>Hypnum pallescens</i>	Stump Pigtail Moss	0.09	0.02	0.01
<i>Climacium dendroides</i>	Common Tree Moss	0.09	0.02	-
<i>Callicladium haldanianum</i>	Shiny-Leaf Moss	0.09	-	-
<b>Lichens</b>				
<i>Peltigera canina</i>	Dog Pelt	0.18	0.05	0.01
<i>Peltigera scabrosa</i>	Rough Pelt	0.05	0.01	-
<i>Peltigera neopolydactyla</i>	Frog Pelt	0.05	0.01	-
<i>Cladonia coniocraea</i>	Tiny Toothpick Cladonia	0.05	-	-

Note: Dashes (-) indicate values <0.005

**Table 3.35.** Stand Type VII. Trembling Aspen - Balsam Poplar ( $n = 46$ )

Tree species relative frequency, and mean density and mean basal area per 10 x 10 m plot.

(a) Relative Frequency

Species	Common Name	Canopy Layer					
		Total	1	2	3	4	5
<i>Populus tremuloides</i>	Trembling Aspen	0.93	0.85	0.50	0.39	0.41	0.48
<i>Populus balsamifera</i>	Balsam Poplar	0.67	0.50	0.39	0.11	0.30	0.20
<i>Picea glauca</i>	White Spruce	0.28	0.07	0.17	0.13	0.13	0.02
<i>Acer negundo</i>	Manitoba Maple	0.13		0.07	0.07	0.09	0.04
<i>Quercus macrocarpa</i>	Bur Oak	0.13				0.11	0.02
<i>Betula papyrifera</i>	Paper Birch	0.11	0.04	0.02	0.11		0.04
<i>Fraxinus pennsylvanica</i>	Green Ash	0.09		0.07	0.09	0.07	0.04
<i>Ulmus americana</i>	American Elm	0.02				0.02	

(b) Mean Density Per Plot

Species	Common Name	Canopy Layer					
		Total	1	2	3	4	5
<i>Populus tremuloides</i>	Trembling Aspen	18.20	7.98	2.39	1.91	1.61	4.30
<i>Populus balsamifera</i>	Balsam Poplar	7.89	3.48	1.33	0.28	0.78	2.02
<i>Picea glauca</i>	White Spruce	1.04	0.09	0.44	0.30	0.20	0.02
<i>Acer negundo</i>	Manitoba Maple	0.61		0.20	0.15	0.15	0.11
<i>Quercus macrocarpa</i>	Bur Oak	0.39				0.28	0.11
<i>Betula papyrifera</i>	Paper Birch	0.65	0.11	0.04	0.26		0.24
<i>Fraxinus pennsylvanica</i>	Green Ash	2.17		0.11	0.85	1.07	0.15
<i>Ulmus americana</i>	American Elm	0.41				0.41	
		31.37	11.65	4.50	3.76	4.50	6.96

(c) Mean Basal Area ( $m^2$  per Plot)

Species	Common Name	Canopy Layer					
		Total	1	2	3	4	5
<i>Populus tremuloides</i>	Trembling Aspen	0.461	0.407	0.048	0.006	-	-
<i>Populus balsamifera</i>	Balsam Poplar	0.210	0.179	0.030	0.001	-	-
<i>Picea glauca</i>	White Spruce	0.020	0.007	0.011	0.001	-	-
<i>Acer negundo</i>	Manitoba Maple	0.006		0.005	0.001	-	-
<i>Quercus macrocarpa</i>	Bur Oak	-				-	-
<i>Betula papyrifera</i>	Paper Birch	0.011	0.008	0.001	0.001		-
<i>Fraxinus pennsylvanica</i>	Green Ash	0.004		0.003	0.002	-	-
<i>Ulmus americana</i>	American Elm	-				-	-
		0.712	0.602	0.098	0.012	-	-

Note: Dashes (-) indicate values  $< 0.0005$



**Table 3.36.** Stand type VII. Trembling Aspen - Balsam Poplar ( $n = 46$ )

Frequency, mean cover, and variance of tree species.

Species	Common Name	Frequency	Mean Cover (%)	Variance
<i>Populus tremuloides</i>	Trembling Aspen	0.93	21.77	212.18
<i>Populus balsamifera</i>	Balsam Poplar	0.67	10.76	180.05
<i>Picea glauca</i>	White Spruce	0.28	2.18	29.28
<i>Acer negundo</i>	Manitoba Maple	0.13	1.00	15.54
<i>Quercus macrocarpa</i>	Bur Oak	0.13	0.04	0.01
<i>Betula papyrifera</i>	Paper Birch	0.11	0.34	1.96
<i>Fraxinus pennsylvanica</i>	Green Ash	0.09	0.99	20.23
<i>Ulmus americana</i>	American Elm	0.02	0.04	0.07

**Table 3.37.** Stand type VII. Trembling Aspen - Balsam Poplar ( $n = 46$ )

Frequency, mean cover, and variance of common shrub taxa ( $f > 0.1$ ).

Species	Common Name	Frequency	Mean Cover (%)	Variance
<b>Tall Shrubs</b>				
<i>Corylus cornuta</i>	Beaked Hazelnut	0.98	31.18	564.40
<i>Prunus virginiana</i>	Choke Cherry	0.89	2.19	12.06
<i>Amelanchier alnifolia</i>	Saskatoon	0.80	1.45	6.53
<i>Viburnum trilobum</i>	American Bush-Cranberry	0.59	0.83	1.85
<i>Cornus stolonifera</i>	Red-Osier Dogwood	0.50	0.83	3.31
<i>Crataegus chrysoarpa</i>	Hawthorn	0.24	0.66	8.03
<i>Salix bebbiana</i>	Beaked Willow	0.20	0.16	0.18
<i>Viburnum edule</i>	Low Bush-Cranberry	0.15	0.15	0.29
<i>Acer spicatum</i>	Mountain Maple	0.11	0.09	0.12
<i>Viburnum rafinesquianum</i>	Downy Arrowwood	0.11	0.13	0.22
<b>Low Shrubs</b>				
<i>Rosa acicularis</i>	Prickly Rose	0.96	4.78	40.94
<i>Symphoricarpos albus</i>	Common Snowberry	0.67	0.60	0.35
<i>Rubus idaeus</i>	Wild Red Raspberry	0.59	1.02	3.81
<i>Ribes oxycanthoides</i>	Northern Gooseberry	0.57	0.45	0.85
<i>Ribes triste</i>	Wild Red Currant	0.54	0.39	0.25
<i>Lonicera dioica</i>	Twining Honeysuckle	0.50	0.28	0.13
<i>Symphoricarpos occidentalis</i>	Western Snowberry	0.22	0.92	6.10
<i>Rhamnus alnifolia</i>	Alder-Leaved Buckthorn	0.20	0.16	0.24
<i>Diervilla lonicera</i>	Bush Honeysuckle	0.11	0.15	0.56

**Table 3.38.** Stand type VII. Trembling Aspen - Balsam Poplar ( $n = 46$ )  
 Frequency, mean cover, and variance of common herb, fern, and fern-ally taxa ( $f > 0.1$ ).

Species	Common Name	Frequency	Mean Cover (%)	Variance
<i>Fragaria virginiana</i>	Wild Strawberry	0.98	1.80	2.98
<i>Maianthemum canadense</i>	Wild Lily-of-the-Valley	0.93	1.00	0.58
<i>Aster ciliolatus</i>	Fringed Aster	0.87	1.72	8.64
<i>Viola rugulosa</i>	Western Canada Violet	0.83	1.11	2.97
<i>Rubus pubescens</i>	Dewberry	0.83	1.29	1.54
<i>Galium boreale</i>	Northern Bedstraw	0.80	0.49	0.11
<i>Aralia nudicaulis</i>	Wild Sarsaparilla	0.80	6.67	100.81
<i>Carex</i> spp.	Sedge Species	0.80	1.43	7.40
<i>Oryzopsis asperifolia</i>	Rough-Leaved Rice Grass	0.74	0.72	0.86
<i>Sanicula marilandica</i>	Snakeroot	0.72	0.39	0.22
<i>Mertensia paniculata</i>	Tall Lungwort	0.63	1.40	5.20
<i>Thalictrum venulosum</i>	Veiny Meadow Rue	0.61	0.41	0.32
<i>Pyrola asarifolia</i>	Common Pink Wintergreen	0.59	0.77	1.29
<i>Galium triflorum</i>	Sweet-Scented Bedstraw	0.59	0.29	0.10
<i>Smilacina stellata</i>	Star Flowered False Solomon's Seal	0.54	0.20	0.05
<i>Lathyrus venosus</i>	Purple Peavine	0.50	0.29	0.25
<i>Solidago canadensis</i>	Canada Goldenrod	0.48	0.65	1.98
<i>Cornus canadensis</i>	Bunchberry	0.48	0.31	0.19
<i>Heracleum lanatum</i>	Cow-Parsnip	0.41	0.59	5.59
<i>Actaea rubra</i>	Red and White Baneberry	0.39	0.15	0.07
<i>Thalictrum dasycarpum</i>	Tall Meadow Rue	0.37	0.23	0.37
<i>Mitella nuda</i>	Bishop's-Cap	0.30	0.52	1.83
<i>Anemone canadensis</i>	Canada Anemone	0.30	0.45	1.15
<i>Epilobium angustifolium</i>	Fireweed	0.28	0.26	0.53
<i>Vicia americana</i>	American Vetch	0.26	0.09	0.03
<i>Osmorhiza longistylis</i>	Smooth Sweet-Cicely	0.26	0.10	0.03
<i>Bromus ciliatus</i>	Fringed Brome	0.26	0.15	0.09
<i>Taraxacum officinale</i>	Common Dandelion	0.22	0.15	0.23
<i>Petasites palmatus</i>	Palmate-Leaved Coltsfoot	0.20	0.08	0.03
<i>Lathyrus ochroleucus</i>	Creamy Peavine	0.20	0.07	0.03
<i>Apocynum androsaemifolium</i>	Spreading Dogbane	0.20	0.15	0.18
<i>Agastache foeniculum</i>	Giant Hyssop	0.20	0.09	0.05
<i>Pyrola secunda</i>	One-Sided Wintergreen	0.17	0.05	0.01
<i>Pyrola elliptica</i>	White Wintergreen	0.17	0.08	0.04
<i>Disporum trachycarpum</i>	Fairybells	0.17	0.04	0.01
<i>Achillea millefolium</i>	Common Yarrow	0.17	0.05	0.02
<i>Calamagrostis canadensis</i>	Bluejoint	0.17	0.22	0.66
<i>Botrychium virginianum</i>	Virginia Grape Fern	0.17	0.04	0.01
<i>Rudbeckia laciniata</i>	Coneflower	0.15	0.29	1.45
<i>Equisetum pratense</i>	Meadow Horsetail	0.15	0.04	0.01
<i>Equisetum arvense</i>	Common Horsetail	0.15	0.17	0.36
<i>Petasites sagittatus</i>	Arrow-Leaved Coltsfoot	0.11	0.09	0.17
<i>Monotropa uniflora</i>	Indian-Pipe	0.11	0.03	0.01
<i>Hieracium umbellatum</i>	Narrow-Leaved Hawkweed	0.11	0.05	0.02
<i>Aster umbellatus</i>	Flat-Topped White Aster	0.11	0.23	1.27
<i>Arenaria lateriflora</i>	Blunt-Leaved Sandwort	0.11	0.03	0.01
Grass spp.	Grass species	0.11	0.06	0.05

**Table 3.39.** Stand type VII. Trembling Aspen - Balsam Poplar ( $n = 46$ )  
 Frequency, mean cover, and variance of common bryophyte and lichen taxa .

Species	Common Name	Frequency	Mean Cover (%)	Variance
<b>Bryophytes</b>				
<i>Brachythecium</i> spp.	Brachythecium Species	0.76	0.36	0.15
<i>Mnium cuspidatum</i>	Woodsy Leafy Moss	0.35	0.12	0.05
<i>Haplocladium microphyllum</i>	Haplocladium	0.17	0.06	0.05
<i>Brachythecium oxycladon</i>	Brachythecium	0.15	0.01	-
<i>Brachythecium velutinum</i>	Velvet Feather Moss	0.11	0.01	-
<i>Mnium drummondii</i>	Drummond's Leafy Moss	0.07	0.02	-
<i>Amblystegium serpens</i>	Amblystegium	0.07	-	-
<i>Pylaisiella polyantha</i>	Stocking Moss	0.04	0.01	-
<i>Jamesoniella autumnalis</i>	Jameson's Liverwort	0.04	-	-
<b>Lichens</b>				
<i>Peltigera neopolydactyla</i>	Frog Pelt	0.09	0.02	-
<i>Peltigera canina</i>	Dog Pelt	0.09	0.02	-
<i>Lichen</i> spp.	Lichens	0.02	0.01	-

Note: Dashes (-) indicate values <0.005

**Table 3.40.** Stand Type VIII. White Spruce ( $n = 47$ )

Tree species relative frequency, and mean density and mean basal area per 10 x 10 m plot.

(a) Relative Frequency

Species	Common Name	Total	Canopy Layer				
			1	2	3	4	5
<i>Picea glauca</i>	White Spruce	1.00	0.98	0.94	0.77	0.40	0.13
<i>Populus tremuloides</i>	Trembling Aspen	0.79	0.64	0.32	0.15	0.36	0.36
<i>Populus balsamifera</i>	Balsam Poplar	0.62	0.36	0.26	0.02	0.26	0.34
<i>Betula papyrifera</i>	Paper Birch	0.34	0.19	0.26	0.06	0.04	0.21
<i>Abies balsamea</i>	Balsam Fir	0.17	0.02	0.04	0.02	0.13	0.11
<i>Picea mariana</i>	Black Spruce	0.02		0.02	0.02		
<i>Quercus macrocarpa</i>	Bur Oak	0.02			0.02		
<i>Ulmus americana</i>	American Elm	0.02					0.02

(b) Mean Density Per Plot

Species	Common Name	Total	Canopy Layer				
			1	2	3	4	5
<i>Picea glauca</i>	White Spruce	16.70	6.19	5.47	3.60	0.83	0.62
<i>Populus tremuloides</i>	Trembling Aspen	15.13	4.23	1.23	0.49	3.47	5.70
<i>Populus balsamifera</i>	Balsam Poplar	8.13	0.81	0.40	0.04	2.38	4.49
<i>Betula papyrifera</i>	Paper Birch	2.83	0.36	0.43	0.17	0.04	1.83
<i>Abies balsamea</i>	Balsam Fir	5.62	0.02	0.04	0.11	0.45	5.00
<i>Picea mariana</i>	Black Spruce	0.06	0.04	0.02			
<i>Quercus macrocarpa</i>	Bur Oak	0.02			0.02		
<i>Ulmus americana</i>	American Elm	0.02					0.02
		48.51	11.66	7.60	4.43	7.17	17.66

(c) Mean Basal Area ( $m^2$  per Plot)

Species	Common Name	Total	Canopy Layer				
			1	2	3	4	5
<i>Picea glauca</i>	White Spruce	0.673	0.500	0.138	0.034	-	-
<i>Populus tremuloides</i>	Trembling Aspen	0.214	0.187	0.026	0.001	-	-
<i>Populus balsamifera</i>	Balsam Poplar	0.083	0.067	0.016	-	-	-
<i>Betula papyrifera</i>	Paper Birch	0.044	0.026	0.018	-	-	-
<i>Abies balsamea</i>	Balsam Fir	0.006	0.003	0.003	-	-	-
<i>Picea mariana</i>	Black Spruce	0.002	0.002	0.001			
<i>Quercus macrocarpa</i>	Bur Oak	-			-		
<i>Ulmus americana</i>	American Elm	-					-
		1.023	0.785	0.202	0.036	-	-

Note: Dashes (-) indicate values  $< 0.0005$

Table 3.41. Stand type VIII. White Spruce ( $n = 47$ )  
Frequency, mean cover, and variance of tree species.

Species	Common Name	Frequency	Mean Cover (%)	Variance
<i>Picea glauca</i>	White Spruce	1.00	33.13	140.76
<i>Populus tremuloides</i>	Trembling Aspen	0.79	10.89	144.81
<i>Populus balsamifera</i>	Balsam Poplar	0.62	2.94	26.61
<i>Betula papyrifera</i>	Paper Birch	0.34	1.91	13.23
<i>Abies balsamea</i>	Balsam Fir	0.17	0.28	1.02
<i>Picea mariana</i>	Black Spruce	0.02	0.13	0.77
<i>Quercus macrocarpa</i>	Bur Oak	0.02	0.01	-
<i>Ulmus americana</i>	American Elm	0.02	0.01	-

Table 3.42. Stand type VIII. White Spruce ( $n = 47$ )  
Frequency, mean cover, and variance of common shrubs ( $f > 0.1$ ).

Species	Common Name	Frequency	Mean Cover (%)	Variance
<b>Tall Shrubs</b>				
<i>Corylus cornuta</i>	Beaked Hazelnut	0.94	8.06	126.18
<i>Amelanchier alnifolia</i>	Saskatoon	0.62	0.40	0.21
<i>Prunus virginiana</i>	Choke Cherry	0.60	0.65	1.20
<i>Viburnum trilobum</i>	American Bush-Cranberry	0.57	0.49	0.69
<i>Cornus stolonifera</i>	Red-Osier Dogwood	0.55	0.55	0.70
<i>Viburnum edule</i>	Low Bush-Cranberry	0.23	0.49	2.58
<i>Alnus rugosa</i>	River Alder	0.21	0.51	3.60
<i>Acer spicatum</i>	Mountain Maple	0.11	0.11	0.17
<b>Low Shrubs</b>				
<i>Rosa aciculais</i>	Prickly Rose	0.98	1.72	3.05
<i>Symphoricarpos albus</i>	Common Snowberry	0.79	0.94	1.37
<i>Ribes triste</i>	Wild Red Currant	0.53	0.43	0.69
<i>Ribes oxycanthoides</i>	Northern Gooseberry	0.51	0.39	0.79
<i>Rubus idaeus</i>	Wild Red Raspberry	0.47	0.40	0.42
<i>Ribes lacustre</i>	Black Gooseberry	0.36	0.14	0.05
<i>Lonicera dioica</i>	Twining Honeysuckle	0.34	0.17	0.09
<i>Rhamnus alnifolia</i>	Alder-Leaved Buckthorn	0.21	0.13	0.12
<i>Symphoricarpos occidentalis</i>	Western Snowberry	0.21	0.09	0.05
<i>Ribes glandulosum</i>	Skunk Currant	0.13	0.12	0.24
<i>Cornus alternifolia</i>	Green Osier	0.11	0.16	0.44

Note: Dashes (-) indicate values  $< 0.005$

Table 3.43. Stand type VIII. White Spruce ( $n = 47$ )

Frequency, mean cover, and variance of common herb, fern, and fern-ally taxa ( $f > 0.1$ ).

Species	Common Name	Frequency	Mean Cover (%)	Variance
<i>Fragaria virginiana</i>	Wild Strawberry	0.98	1.32	1.40
<i>Mertensia paniculata</i>	Tall Lungwort	0.91	2.94	9.39
<i>Rubus pubescens</i>	Dewberry	0.87	2.11	3.49
<i>Maianthemum canadense</i>	Wild Lily-of-the-Valley	0.87	0.64	0.26
<i>Aster ciliolatus</i>	Fringed Aster	0.85	0.95	1.93
<i>Galium boreale</i>	Northern Bedstraw	0.83	0.50	0.13
<i>Aralia nudicaulis</i>	Wild Sarsaparilla	0.83	5.34	45.96
<i>Cornus canadensis</i>	Bunchberry	0.79	1.03	1.06
<i>Mitella nuda</i>	Bishop's-Cap	0.74	2.13	18.71
<i>Carex</i> spp.	Sedge Species	0.72	0.92	2.41
<i>Pyrola asarifolia</i>	Common Pink Wintergreen	0.68	0.61	0.78
<i>Galium triflorum</i>	Sweet-Scented Bedstraw	0.68	0.30	0.08
<i>Viola rugulosa</i>	Western Canada Violet	0.66	1.53	6.28
<i>Anemone canadensis</i>	Canada Anemone	0.66	1.28	2.21
<i>Oryzopsis asperifolia</i>	Rough-Leaved Rice Grass	0.64	0.67	0.79
<i>Thalictrum venulosum</i>	Veiny Meadow Rue	0.51	0.19	0.05
<i>Actaea rubra</i>	Red and White Baneberry	0.51	0.26	0.26
<i>Sanicula marilandica</i>	Snakeroot	0.45	0.14	0.05
<i>Linnaea borealis</i>	Twinflower	0.45	0.55	1.70
<i>Equisetum pratense</i>	Meadow Horsetail	0.38	1.76	53.21
<i>Smilacina stellata</i>	Star Flowered False Solomon's-Seal	0.36	0.21	0.25
<i>Disporum trachycarpum</i>	Fairybells	0.32	0.12	0.05
<i>Petasites vitifolius</i>	Vine-Leaved Coltsfoot	0.30	0.09	0.03
<i>Lathyrus venosus</i>	Purple Peavine	0.30	0.09	0.02
<i>Pyrola secunda</i>	One-Sided Wintergreen	0.26	0.08	0.02
<i>Osmorhiza longistylis</i>	Smooth Sweet-Cicely	0.23	0.21	0.39
<i>Heracleum lanatum</i>	Cow-Parsnip	0.23	0.21	0.85
<i>Taraxacum officinale</i>	Common Dandelion	0.19	0.05	0.01
<i>Lathyrus ochroleucus</i>	Creamy Peavine	0.19	0.08	0.06
<i>Circaea alpina</i>	Small Enchanter's Nightshade	0.19	0.19	0.38
Grass spp.	Grass species	0.19	0.15	0.17
<i>Epilobium angustifolium</i>	Fireweed	0.17	0.10	0.09
<i>Apocynum androsaemifolium</i>	Spreading Dogbane	0.17	0.06	0.02
<i>Equisetum arvense</i>	Common Horsetail	0.17	0.30	2.15
<i>Solidago canadensis</i>	Canada Goldenrod	0.15	0.07	0.06
<i>Petasites palmatus</i>	Palmate-Leaved Coltsfoot	0.15	0.15	0.30
<i>Monenses uniflora</i>	One-Flowered Wintergreen	0.15	0.04	0.01
<i>Galeopsis tetrahit</i>	Hemp-Nettle	0.13	0.03	0.01
<i>Anemone quinquefolia</i>	Wood Anemone	0.13	0.04	0.01
<i>Botrychium virginianum</i>	Virginia Grape Fern	0.13	0.04	0.01
<i>Pyrola elliptica</i>	White Wintergreen	0.11	0.04	0.02

Table 3.44. Stand type VIII. White Spruce (n =47)

Frequency, mean cover, and variance of common bryophyte and lichen taxa (>0.1).

Species	Common Name	Frequency	Mean Cover (%)	Variance
<b>Bryophytes</b>				
<i>Brachythecium</i> spp.	Brachythecium Species	0.91	1.16	1.91
<i>Mnium cuspidatum</i>	Woodsy Leafy Moss	0.81	0.77	2.27
<i>Pleurozium schreberi</i>	Big Red Stem	0.47	0.60	2.14
<i>Mnium drummondii</i>	Drummond's Leafy Moss	0.40	0.31	0.90
<i>Hylocomium splendens</i>	Stair-Step Moss	0.34	1.01	6.01
<i>Brachythecium velutinum</i>	Velvet Feather Moss	0.32	0.15	0.83
<i>Brachythecium oxycladon</i>	Brachythecium	0.28	0.02	-
<i>Eurhynchium pulchellum</i>	Common Beaked Moss	0.23	0.22	0.84
<i>Amblystegium serpens</i>	Amblystegium	0.23	0.01	-
<i>Ptilium crista-castrensis</i>	Knight's Plume	0.19	0.44	6.70
<i>Drepanocladus uncinatus</i>	Sickle Moss	0.19	0.01	-
<i>Climacium dendroides</i>	Common Tree Moss	0.19	0.07	0.04
<i>Thuidium delicatulum</i>	Common Fern Moss	0.17	0.16	0.31
<i>Haplocladium microphyllum</i>	Haplocladium	0.15	0.00	0.00
<i>Oncophorus wahlenbergii</i>	Mountain Curved-Back Moss	0.13	0.00	0.00
<i>Callicladium haldanianum</i>	Shiny-Leaf Moss	0.13	0.00	0.00
<i>Mnium affine</i>	Marsh Magnificent Moss	0.11	0.03	0.03
<b>Lichens</b>				
<i>Peltigera canina</i>	Dog Pelt	0.21	0.05	0.01
<i>Peltigera neopolydactyla</i>	Frog Pelt	0.11	0.03	0.01
<i>Peltigera elisabethae</i>	Dog Lichen	0.11	0.02	0.01

Note: Dashes (-) indicate values <0.005

**CHAPTER 4**  
**GROWTH RESPONSE OF GREEN ASH (*FRAXINUS PENNSYLVANICA* MARSH.) IN**  
**BOREAL AND MIXED EASTERN DECIDUOUS FOREST COMMUNITIES**

**4.1 Introduction**

Green ash (*Fraxinus pennsylvanica* Marsh.) approaches its northern and western distributional limits in Riding Mountain National Park (RMNP). Within the Park, the distribution of the species on the landscape is spatially explicit. In northern and eastern portions of the Park, green ash is abundant along the lower slopes of the Cretaceous escarpment, and is most frequently encountered in the understory of mixed eastern deciduous forest communities and adjacent stands of aspen-dominated boreal forest. These forest communities have not been previously described in the Park.

Mixed eastern deciduous forest communities are common along the base of the eastern escarpment. The canopy and understory strata are dominated by a mixture of green ash, American elm (*Ulmus americana* L.) and Manitoba maple (*Acer negundo* L.), and to a lesser extent trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.) and bur oak (*Quercus macrocarpa* Michx.). Eastern cottonwood (*Populus deltoides* var. *occidentalis* Rydb.) is uncommon. These stands are found in sand type IV (Eastern Deciduous). In comparison, boreal stands are vertically stratified. Stands are typically found adjacent to the mixed eastern forests, and have canopies that are dominated by a single cohort of trembling aspen, occasionally in mixture with balsam poplar. Understories of these boreal stands are dominated by green ash, Manitoba maple, American elm and the tall shrub mountain maple (*Acer spicatum* Lam.). These stands are found in VI (Aspen-Birch-Mountain Maple). Green ash is the most abundant tree species in the understory of both communities in the Park, and is the species which has the potential to dramatically influence stand structure at various spatial and temporal scales.

Both boreal and mixed eastern deciduous stands are currently exhibiting dramatic structural and compositional change on the landscape. These stands will continue to undergo further change as a result of altered disturbance regimes. The expansion of agriculture along the periphery of the Park, in combination with active fire suppression, may reduce the frequency of future catastrophic (i.e. stand replacing) fires (Clark 1989; Johnson et al. 1998; Weir & Johnson 1998; Tchir & Johnson 1999; Weir et al. 1999). Increasing temperatures in certain portions of the boreal forest as a result of global warming (Bergeron & Archambault 1993; Bergeron et al. 1998; Flannigan et al. 1998) will influence the growth response of green ash (Carter 1996). Moreover,



the senescence of canopy American elm due to the extensive expansion of Dutch elm disease (*Ophiostoma ulmi* (Buism) Nannf.) in the Park will modify resource availability (e.g. light) (Naidu & DeLucia 1998) in mixed eastern stands. The spatial and temporal alteration of habitat conditions will determine the propensity for understory green ash to reach the canopy and produce seed (Bartlett & Remphrey 1998; Naidu & DeLucia 1998). In the absence of major disturbance, aspen-dominated boreal stands have a strong propensity to develop canopies dominated by eastern deciduous species, most notably green ash. Mixed eastern deciduous systems will also increase in the abundance of green ash at the expense of reduced numbers of canopy elm.

Habitat conditions, including light quality and quantity, nutrient and moisture availability, interspecific competition, topographic position and climate, have been shown to strongly influence the growth (e.g. radial and height) and morphology (e.g. branching patterns and canopy architecture) of understory boreal and eastern deciduous tree species (Borges & Chaney 1989; Tardif & Bergeron 1993; Pacala et al. 1994; Remphrey & Davidson 1994; Tardif et al. 1994; Bartlett & Remphrey 1998; Naidu & DeLucia 1998; Aubin et al. 2000; Drobyshev & Nihlgård 2000).

Radial growth of trees depends on local environmental conditions (Clark 1991). Widths of growth rings and changes in ring width over time contain useful information regarding past climatic trends and habitat conditions (Clark 1991; D'Arrigo et al. 1992; Tardif & Bergeron 1993; Cho 1995; Tardif & Bergeron 1997; Lebourgeois et al. 2000; Wright et al. 2000). However, one must be cautious when interpreting results of ring-width analyses since such data contain biases resulting from accumulated mortality over time. Namely, trees that survive to be sampled constitute a highly biased subset of a juvenile cohort, as cohort density commonly declines by several orders of magnitude from juvenile to canopy classes (Kenkel et al. 1997; Clark 1991).

The goal of this chapter is to improve the understanding of future stand development in both boreal (aspen-dominated) stands with an ash-dominated eastern deciduous understory, and mixed eastern deciduous communities in RMNP. Specific objectives are to 1) examine the current distribution of green ash on the landscape, and 2) to assess the influence of habitat quality (stand composition and canopy position) on incremental radial growth. The following specific questions will be addressed: i) What are the dominant variables influencing the distribution of green ash on the landscape? ii) Are there differences in the annual incremental radial growth of green ash growing beneath boreal and mixed eastern deciduous canopies? iii) What implications does this

have for stand development in both communities? iv) In mixed eastern deciduous communities, are canopy green ash growing at a different rate than understory ash? Understanding the present growth responses of green ash to habitats in which it is found will facilitate a more complete understanding of forest change on the landscape.

## 4.2 Methods

### 4.2.1 Data Collection

Of the 202 - 10 x 10 m forest stands that were enumerated in RMNP (see Chapter 3), a total of 75 were analyzed to examine patterns of green ash distribution on the landscape. Numerous variables were collected for each stand, including percent cover of all plant species in 5 vegetation canopies (1 canopy trees, >15 m; 2 subcanopy trees, 10-15 m; 3 lower subcanopy trees and tall shrubs, 2-10 m; 4 saplings and low shrubs, 0.5-2 m; 5 tree seedlings, herbs and bryophytes, <0.5 m), edaphic information including percent sand, silt and clay content (Bouycous hydrometer method, Kalra & Maynard 1991), pH, electrical conductivity ( $\mu\text{S}/\text{cm}$ ) and LFH depth (cm), tree density and DBH, and an estimate of minimum stand age (years). Minimum stand age was determined for each 'stand' from which green ash were harvested by taking increment cores at 1.3 m (breast height) above ground level from two of the largest individuals of each tree species.

Incremental radial growth of green ash growing beneath aspen and mixed eastern deciduous canopies was examined by randomly selecting and harvesting a total of 44 understory (<10 m in height) green ash from these two forest communities. Specifically, 28 individuals were harvested at ground level from 7 aspen-dominated stands (belonging to stand type VI), and 16 individuals were harvested from 3 mixed eastern deciduous stands (belonging to stand type IV). At the time of harvest, the height, diameter and health of each individual were recorded. Within a 5 x 5 m area centred around each harvested individual, ocular estimates of canopy, shrub and decaying wood cover were recorded.

All tree sections were finely sanded (using 400 grit sandpaper) and polished (using 600 grit sandpaper), and rings were counted to 0.01 mm along 4 perpendicular axes from the centre of each section (**Fig. 4.1**). Increment cores were obtained at 0.3 m above ground level from 8 canopy green ash found in the 3 mixed eastern deciduous stands. Only cores that could be confidently aged were kept for the analyses. Cores were mounted, finely sanded and polished, and rings were counted to 0.01 mm along the one axis. The most recent growth ring for each tree section and

core was included in the analysis, since radial growth was nearly complete for that year (i.e. collections were made in late October). Proper surface preparation of tree sections and cores facilitated the distinction between 'true' and 'false' rings. True rings exhibit an abrupt change in cell size between the last-formed cells of the previous ring and the first-produced vessels of the current ring, whereas false rings tend to display a gradual transition in vessel diameter on both ring margins (Wimmer et al. 2000).

#### 4.2.2 Data Analysis

##### *Landscape-Level Patterns of Green Ash Regeneration*

Multiple Discriminant Analysis (MDA) is used to maximally distinguish among groups of individuals (determined *a priori*). A total of  $p$  variables are measured on each of the  $N$  individuals, where  $N = n_1 + n_2 + n_3 + \dots + n_g$ . Here,  $g$  is the number of pre-defined groups and  $n$  are the number of individuals belonging to each of the groups. This method obtains linear composites which maximize the variance between groups relative to the variance within groups, thereby maximizing group discrimination (Kenkel 1998).

In this study MDA is used to assess which habitat conditions best discriminate among forest communities with and without the presence of green ash (SYNTAX, Podani 1994). A total of 75 of the 202 enumerated forest stands (see Chapter 3) were pooled and then divided into 3 groups (determined *a priori*): 1) aspen-dominated boreal stands from the western 'upland' of RMNP that lack green ash in both the understory (vegetation strata 3, 4 and 5) and overstory (vegetation strata 1 and 2),  $n=45$ ; 2) aspen-dominated boreal stands at lower elevations along the escarpment with green ash in the understory but lacking in the canopy,  $n=10$ ; and 3) mixed eastern deciduous stands at lower elevations along the escarpment with green ash present in both the understory and canopy,  $n=20$ . The remaining 127 enumerated forest stands were excluded from the analysis as they were dominated by black spruce (*Picea mariana* (Mill.) BSP), jack pine (*Pinus banksiana* Lamb.), bur oak, balsam fir (*Abies balsamea* (L.) Mill) and white spruce (*Picea glauca* (Moench) Voss) (i.e. habitats in which green ash is typically absent). 14 variables were used to discriminate against the 3 groups of stands. These discriminating variables are percent cover of all shrubs, beaked hazelnut (*Corylus cornuta* Marsh.), mountain maple, herbs, bryophytes and bareground, amount of decaying wood on the forest floor (ordinal scale of 0-3), soil pH, conductivity ( $\mu\text{S}/\text{cm}$ ), LFH depth (cm), and percent sand and clay, degrees slope of the plot, and minimum stand age (years). Of these variables, percent cover of shrubs, beaked hazelnut, mountain maple, bryophytes

and bareground were transformed as  $\log(p+1)$  to meet the assumptions of multivariate normality (ter Braak 1986, 1987a).

### *Growth of Green Ash in Two Communities*

For descriptive purposes, differences in community structure and composition are illustrated for the  $n=7$  boreal and  $n=3$  mixed eastern deciduous stands from which understory green ash were harvested and canopy green ash were cored. Trends were illustrated using bar charts of mean tree density within each of the 5 height classes. Within both community types, relationships between age, height and diameter of harvested understory green ash are compared, and ring-width analyses were conducted on harvested and cored individuals. Annual rates of growth were calculated as the slope of the regression line through the scatter of incremental radius (mm) over time (years) (**Fig. 4.2**). All ring widths were included in the calculations (i.e. youngest and oldest rings). Out of the original 44 harvested understory green ash, 35 were kept for ring-width analyses. Omitted specimens were either very young and/or had indistinct ring structures making measurements difficult and unreliable. For the final analysis, box plots were used to compare differences in incremental radial growth among  $n=21$  understory green ash harvested from  $n=7$  aspen-dominated boreal stands,  $n=14$  understory green ash harvested from  $n=3$  mixed eastern deciduous stands, and  $n=8$  cored green ash from the canopy of the same  $n=3$  mixed eastern deciduous stands. Understory growth in the two forest communities was compared using a 2-sample t-test of  $\mu_1 - \mu_2$ . Overstory and understory growth was compared using an ANOVA.

## **4.3 Results**

### 4.3.1 Landscape-Level Patterns of Green Ash Regeneration

Results of the multiple discriminant analysis are presented in **Fig. 4.3**. Both axes 1 and 2 significantly discriminate among the 3 groups ( $\chi^2$  axis 1=76.79,  $P<0.0001$ ;  $\chi^2$  axis 2=26.09,  $P<0.016$ ). Eigenvalues as a percentage: axis 1=70.49; axis 2=29.51. The most discriminating variables along axis 1 are soil pH, site age, amount of decaying wood on the forest floor and slope. **Table 4.1** presents the mean and standard deviation for each of the  $n=14$  variables for the  $n=3$  groups.

The 95% confidence interval around the mean for group 1 is situated on the far left side of axis 1. As compared to groups 2 and 3, stands belonging to group 1 are characterized as being younger stands which occur on the rolling till deposits of RMNP's upland, having soils with a relatively

low pH and conductivity, and high clay content. In contrast, the 95% confidence intervals around the means of groups 2 and 3 are situated on the right side of axis 1. Stands belonging to groups 2 and 3 are older, are situated on the more gentle slopes of the lower escarpment, have less clayey soils with high pH and conductivity, and have a greater abundance of decaying wood on the forest floor. Group 2 is separated from group 3 along axis 2. Group 2 is typified by a high cover of mountain maple, low cover of shrubs excluding beaked hazelnut and mountain maple, and low herbaceous cover.

#### 4.3.2 Growth of Green Ash in Two Communities

Boreal stands and mixed eastern deciduous stands from which understory ash have been harvested are described in terms of their composition and structure in **Figs. 4.4a and 4.4b**. Boreal stands ( $n=7$  stands; **Fig. 4.4a**) are characterized as having a canopy dominated by a single cohort of aspen, occasionally in mixture with balsam poplar, with an understory dominated by eastern deciduous species, especially green ash. Mixed eastern deciduous stands ( $n=3$  stands; **Fig. 4.4b**), in comparison, exhibit multiple cohorts of eastern deciduous tree species, with green ash being the most abundant canopy species. Lower numbers of aspen or balsam poplar and American elm are commonly found in the canopy of these stands. The understory is comprised of a mixture of eastern deciduous species, with green ash and elm being understory dominants.

Harvested understory green ash ( $n=44$ ) have established in stands several decades following stand establishment (**Fig. 4.5**), suggesting that habitat conditions have been conducive to seed propagation, germination, establishment and survival. Relationships between age, height and diameter of all ( $n=44$ ) harvested understory green ash are presented in **Fig. 4.6**. Relationships in decreasing order of association (using Pearson's product-moment correlation) are height and diameter ( $r=0.921$ ,  $P<0.01$ ), diameter and age ( $r=0.909$ ,  $P<0.01$ ), and height and age ( $r=0.851$ ,  $P<0.01$ ). Specimens from each community type have been separately highlighted on each biplot.

Ring width analyses were undertaken for green ash in aspen-dominated boreal ( $n=7$  stands) and mixed eastern deciduous communities ( $n=3$  stands). These stands have mean tree covers of 30% and 75%, respectively. Incremental ring widths (**Fig. 4.7**) and calculated growth rates (**Fig. 4.8**) are presented for specimens belonging to both communities. Mean incremental radial growth ( $\text{mm} \cdot \text{yr}^{-1}$ ) of understory green ash beneath aspen ( $n=21$ ) and mixed eastern deciduous ( $n=14$ ) canopies are  $0.685 \pm 0.154$  and  $0.588 \pm 0.118$ , respectively. A 2-sample t-test indicates that incremental radial growth of green ash beneath an aspen canopy is significantly greater than

specimens beneath a mixed eastern deciduous canopy ( $P=0.0445$ ). The mean annual radial growth ( $\text{mm} \cdot \text{yr}^{-1}$ ) of canopy green ash ( $1.612 \pm 0.425$ ) is significantly greater than understory green ash in either community (ANOVA,  $P < 0.0001$ ).

#### 4.4 Discussion

Boreal and mixed eastern deciduous stands containing green ash advanced regeneration differ both biotically and abiotically from western upland stands which lack green ash. The spatial distribution of green ash in RMNP is therefore restricted to a specific subset of habitat conditions, including high soil pH and conductivity, and low slope (reduced drainage), where the cover of beaked hazelnut is low and cover of mountain maple is high. Stands containing green ash are typically restricted to the lower slopes of the Cretaceous escarpment. Historically recurrent fires on the upland of the Park (Bird 1961; Sentar 1992), perhaps as frequently as every 2-15 years in the southern boreal forest of western Canada (Heinselman 1978), may have been a limiting factor in the distribution of green ash in the Park. Moreover, although the Saskatchewan Plain or upland of the Park has a higher moisture index ( $P$ -PET, i.e. the difference between precipitation and potential evapotranspiration) than the surrounding Manitoba Plain (Hogg 1994), lower mean July and annual minimum temperatures on the adjacent upland (Environment Canada 1993; Hogg 1994) may limit the distribution of green ash into these areas. The health of green ash advanced regeneration typically deteriorates with increased elevation in the Park, where specimens at the highest elevations (closest to the Saskatchewan Plain or upland) exhibit a low-growing, prostrate form (pers. obs.). This suggests that the presently observed distribution of green ash in the Park approaches its limits of habitat tolerance, and that any future changes in habitat conditions may have a dramatic influence on the species' distribution and growth.

This study reveals that understory green ash growing in aspen-dominated boreal stands tend to have a greater mean incremental radial growth than understory ash in mixed eastern deciduous stands. In comparison, canopy green ash in the mixed eastern deciduous stands have a greater mean incremental radial growth than individuals growing in the understory of either community. These results have direct implications on future stand development. The propensity for an understory individual to attain maturity and reach the canopy, and ultimately produce seed, is largely determined by its performance as a sapling (Canham 1988). Habitat quality has previously been shown to exert a strong influence on growth and morphology of *Fraxinus* spp., especially light availability (Pacala et al. 1994; Bartlett & Remphrey 1998; DeLucia et al. 1998; Naidu & DeLucia. 1998).

Green ash is well-adapted to shaded conditions, and has previously been classified as moderately shade tolerant (Bartlett & Remphrey 1998; Kennedy 1990). For most woody plants under conditions of very low photosynthetically active radiation (PAR), there is typically a reduction in the amount of assimilates produced through photosynthesis, and consequently, a reduction in available carbon energy (Smith 1982). However, certain species, including green ash, are able to compensate for reduced levels of PAR through modifications in leaf and shoot structure, and biomass allocation. Under shaded conditions, green ash has been shown to produce thinner leaves at decreased angles of elevation, fewer and shorter shoots, as well as reduced branching frequency and lateral shoot growth, and decreased biomass (Bartlett & Remphrey 1998). Under less heavy shade, shoot numbers and length increase, and branch numbers increase (Bartlett & Remphrey 1998).

White ash (*Fraxinus americana*) is a closely-related species that is also well adapted to shaded understory conditions. This species is capable of allocating more photosynthate to attributes that promote survivorship under low light conditions, including accumulated carbohydrate stores and high measurements of specific leaf area (i.e. leaf area/leaf mass) and leaf area ratio (i.e. leaf area/sapling mass) (Pacala et al. 1994; DeLucia et al. 1998). The species demonstrates slow radial growth under low light conditions and high radial growth under high light conditions (Pacala et al. 1994, DeLucia et al. 1998; Naidu & DeLucia 1998), and is capable of tolerating suppression for several decades (Cho 1995). While the large compound leaves of white ash allow for a greater shade tolerance than 'early succession' species during the early stages of growth, its architecture promotes rapid trunk growth at later stages (Millet & Bouchard 1999).

The formation of canopy gaps from the mortality of canopy trees or large branches results in increased light penetration to the forest floor (Pickett & White 1985; Canham 1988; Clark 1991; Naidu & DeLucia 1998; Drobyshev & Nihlgård 2000). The ability of understory species to acclimate to such increases in PAR may be important for the filling of these canopy openings (Connell 1989). Acclimation can be defined as the process by which physiological and morphological changes increase carbon gain within the new environment (Naidu et al. 1998). White ash has been shown to produce new flushes of leaves and increase photosynthetic rates of existing shade-developed leaves to levels that do not differ from gap-grown individuals within 4 weeks of gap exposure (Naidu et al. 1998).

In the present study, understory green ash from both communities, which have established several years after stand establishment, or after the establishment of canopy trees (**Fig. 4.5**), are growing much slower than canopy ash. This may be a result of reduced understory light availability. Previous studies have shown that light availability is the overriding factor determining the growth of understory advanced regeneration (Pacala et al. 1994). However, *Fraxinus* has the ability to maintain slow growth rates under conditions of low PAR (DeLucia et al. 1998). In this study, mean incremental radial growth of understory green ash is greater beneath open aspen canopies as compared to closed mixed eastern canopies. This suggests that the greater understory light availability in aspen stands may have a positive influence on the radial growth of green ash advanced regeneration. The adaptive response of *Fraxinus* to canopy openings is well documented (Naidu & DeLucia 1998), suggesting that understory green ash in this study will respond to future canopy openings with increased rates of growth.

The comparatively rapid incremental radial growth witnessed for the canopy green ash warrants further consideration. If these canopy ash first established in the understory of post-disturbance aspen-dominated or mixed eastern deciduous stands, a slower incremental radial growth during initial life stages would be expected as a result of reduced PAR. However, since incremental radial growth has been rapid and consistent since the onset of measured growth (**Fig. 4.7**), this suggests that the canopy green ash presently found in mixed eastern deciduous stands may have established under conditions of high PAR. There is the potential that establishment may have taken place contemporaneously with other species after disturbance, or in large canopy openings created by the active harvesting of large canopy trees near the turn of the century (Dickson 1909; Tunstall 1922, 1940; Evans 1923; Sentar 1992). Regardless of when canopy green ash recruitment occurred, results of this study illustrate that the species has the potential to attain rapid incremental radial growth under certain habitat conditions. Understory ash, therefore, may have the potential to attain similar patterns of growth under similar conditions.

The sampled boreal stands originated ca. 100 years ago, during the extensive fires that swept through the west end of the Park (and other regions of western Canada) in the late 19th and early 20th century (Dickson 1909; Tunstall 1922, 1940; Evans 1923 Rowe 1955; Clark 1990). In addition, active harvesting of eastern deciduous forests along the periphery of the Park near the turn of the century may have influenced the present forest structure of these communities (SENTAR 1992). Prefire composition of stands sampled in this study are difficult to determine, however aspen was almost certainly present in both boreal and eastern deciduous communities. The single cohort of *Populus* found in the boreal stands is indicative of post-fire vegetative



suckering from underground rootstocks that would have been present before fire (Zasada et al. 1992). A few mature aspen per hectare produce a sufficient number of root suckers to regenerate a pure aspen stand (Lavertu et al. 1994). The lack of residual trees and the homogeneity of the aspen canopy cohort in the boreal stands would suggest that the stand-initiating fire was intense (i.e. high heat output; Johnson 1992) and severe (i.e. the removal of a large proportion of the aboveground biomass, including canopy trees, advanced regeneration and organic matter; Greene et al. 1999). Mixed eastern deciduous stands have large aspen and balsam poplar in the canopy, which may have established after the last stand-replacing fire or are the result of post-fire vegetative suckering. The presence of numerous large, decayed boles of *Populus* on the forest floor of these mixed eastern stands indicates that members of this genus were more abundant at an earlier stage of succession. There is the possibility, therefore, that boreal stands may eventually witness a decline in the density of canopy *Populus*, and develop into communities of mixed eastern deciduous composition.

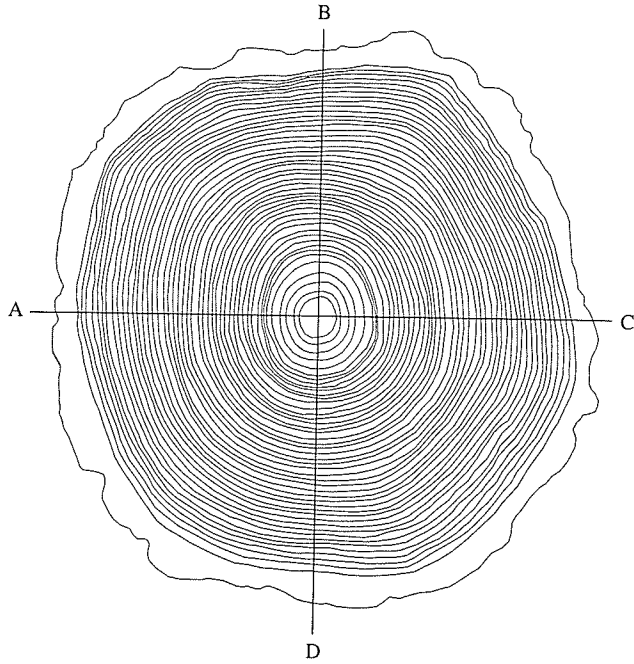
There is already clear evidence that aspen-dominated boreal stands are undergoing rapid canopy development. The single cohort of canopy aspen is senescent, and dying individuals are creating large canopy openings. The canopy aspen are not being replaced by members of its own species but by eastern deciduous species, most notably green ash (**Fig. 4.4**). The low density of shade-intolerant *Populus* regeneration in the understory may be the result of numerous factors. Ungulate herbivory has previously been shown to result in large decreases in understory seedling and sapling density, dramatically altering the size class distribution of stands (Whitney 1984). In addition, low levels of PAR beneath a dense laminar canopy of mountain maple may have an inhibitory effect on shade-intolerant *Populus* regeneration (Messier et al. 1999; Aubin et al. 2000). Dense shrub layers may not allow for heat and light to reach the forest floor to stimulate suckering and/or to sustain growth (Burns & Honkala 1990). Moreover, an increase in the LFH soil horizon inhibits aspen suckering (Lavertu et al. 1994). The ability of *Fraxinus* to survive beneath a closed canopy, and grow rapidly in canopy openings or in conditions of increased PAR, means that aspen-dominated boreal stands in the Park have the propensity to change rapidly in structure and composition over time. As the aspen canopy cohort is removed, the understory ash will become increasingly dominant as it responds to increased light levels. A similar pattern of stand development has been described in a permanent aspen-northern hardwoods stand in northern lower Michigan (Roberts 1992), where a canopy of senescent aspen is being replaced by a discontinuous subcanopy of mid- and shade-tolerant eastern hardwoods.

There are numerous factors which have the potential to drive the structural and compositional change of forests in the Park. The most important factor is fire (Heinselman 1973; Wein & MacLean 1983; Johnson 1992). Changes in land use patterns around the Park periphery, including increased land clearance, in combination with active fire suppression, may result in decreased fire frequencies within the Park boundary (Clark 1989; Johnson et al. 1998; Weir & Johnson 1998; Tchir & Johnson 1999; Weir et al. 1999). Reduced fire frequencies may result in the loss of *Populus* from the canopy of boreal stands with an eastern deciduous understory, and allow for stand development towards a predominantly eastern forest composition.

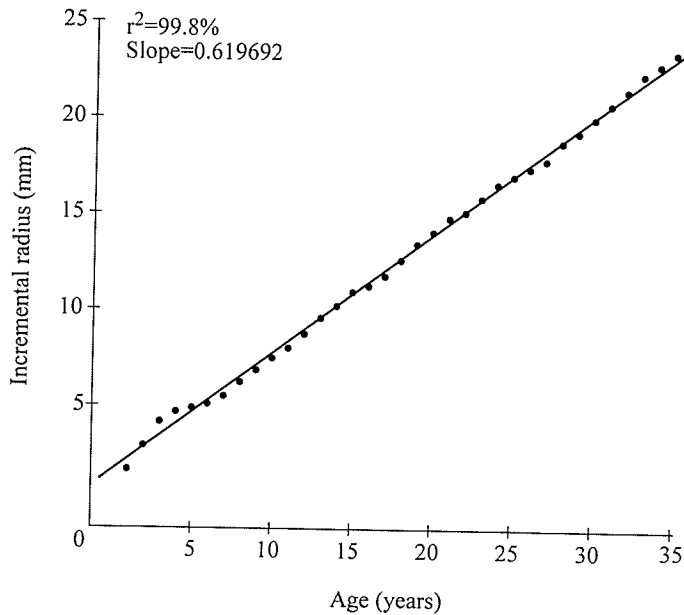
In RMNP, Dutch elm disease is dramatically altering resource availability in mixed eastern forests through the mortality of nearly all large canopy American elm (pers. obs.). The death of canopy elm will increase the availability of understory PAR (**Fig. 4.9**). Although increased PAR will result in a rapid increase in radial and height growth of understory green ash, it may also result in the proliferation of tall understory shrubs, especially *Acer spicatum* (Kneeshaw & Bergeron 1996, 1998; Aubin et al. 2000; Bergeron 2000). Heavy shrub cover may limit the growth of green ash at local spatial scales. Rapid, episodic recruitment of *Fraxinus americana* has been tied to large canopy disturbances created by Dutch elm disease in mixed eastern forests in Ohio (Cho 1995). In the northern Great Plains (e.g. North Dakota), green ash has been described as a climax species in regions where Dutch elm disease has resulted in the mortality of American elm (Girard et al. 1989).

Moreover, the potential impacts of global warming on green ash growth are substantial. Most tree species are genetically variable, with much of this variation attributable to provenance (seed source) adaptation to long-term local evolutionary conditions (Carter 1996). With climate models projecting an increase in average global temperature by 1-5°C within the next 100 years (Roberts 1989, Flannigan et al. 1998), increases in average annual minimum temperature in the northern portions of the green ash range are expected to result in increased annual height growth of the species (Carter 1996). As well, increased soil temperatures may result in more rapid green ash growth, and would directly influence detritivore activity and nutrient cycling, mycorrhizal infection of roots and plant respiration (Borges & Chaney 1989).

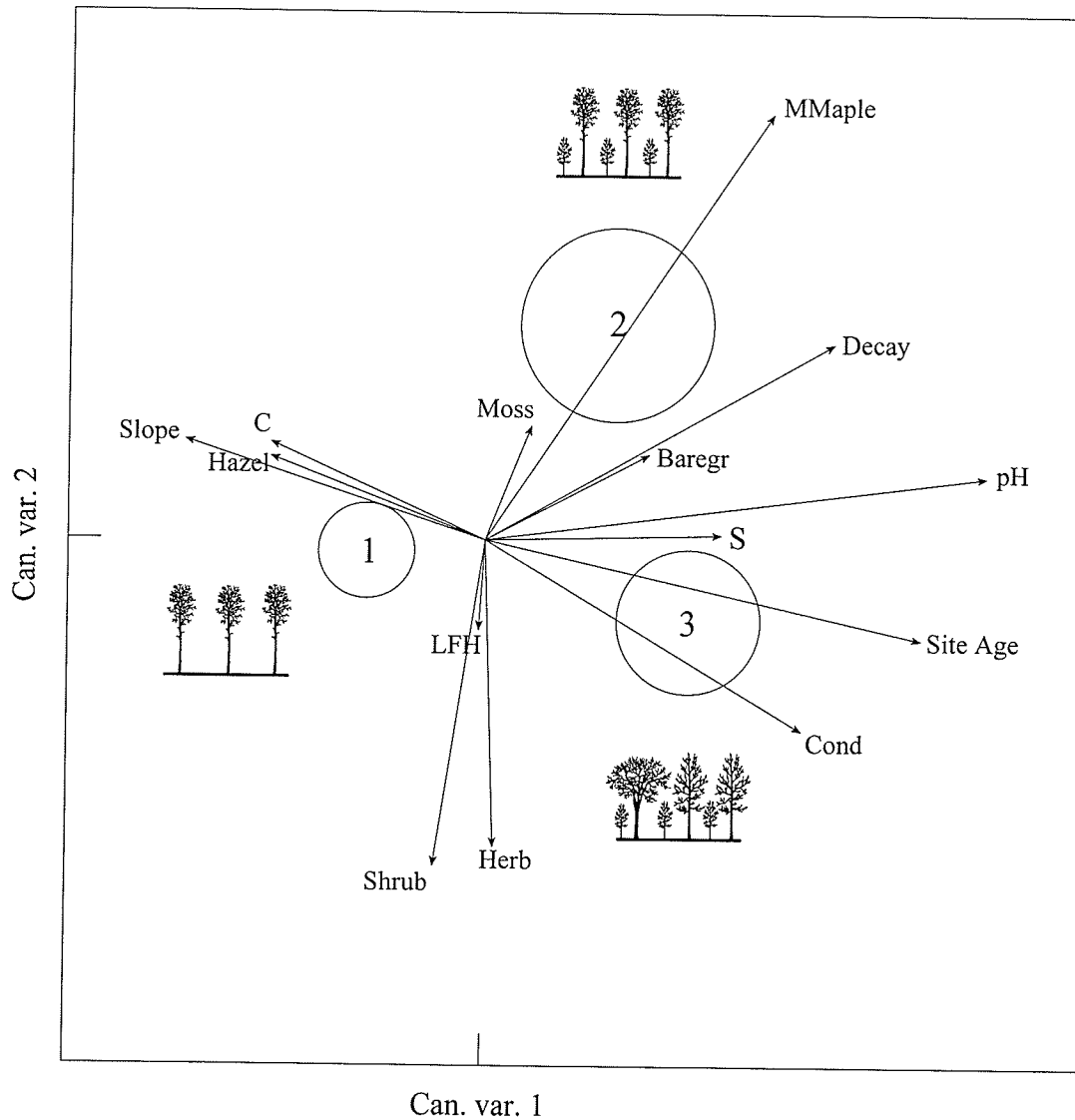
The implications of an extensive change in forest structure and composition at the landscape level in RMNP warrants further study. Future studies should focus on recruitment and mortality rates of understory green ash in boreal and mixed eastern deciduous forests to facilitate a broader understanding of stand development at differing spatial and temporal scales.



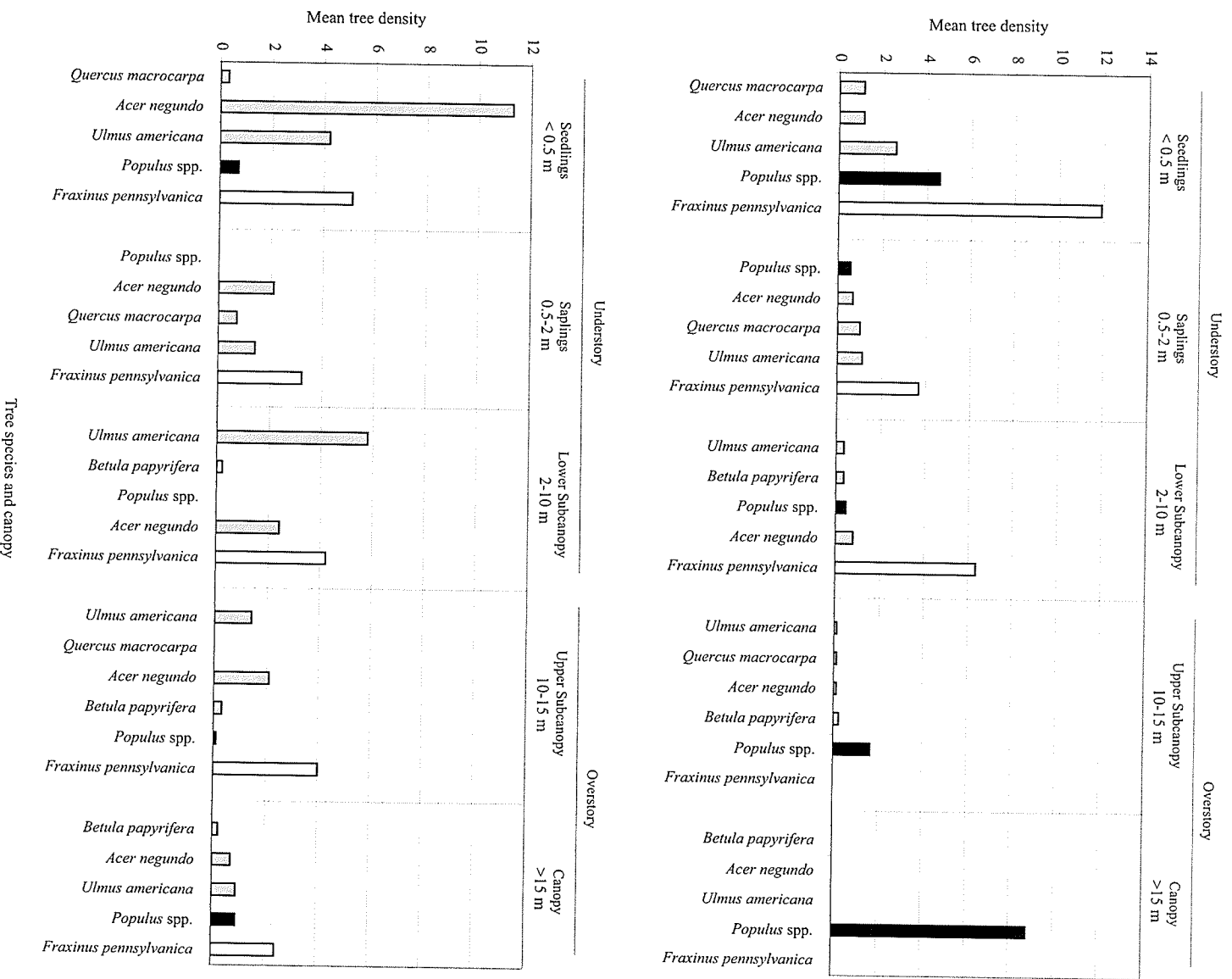
**Figure 4.1.** A section of green ash taken at ground level. Ring widths (mm) were measured along each of 4 perpendicular radii (A-D) from the center of the section. This illustration was created from a section of green ash which was scanned and vectorized, and is displayed at actual size. The specimen used in this figure is not the same as that used in **Figure 4.2** (see below).



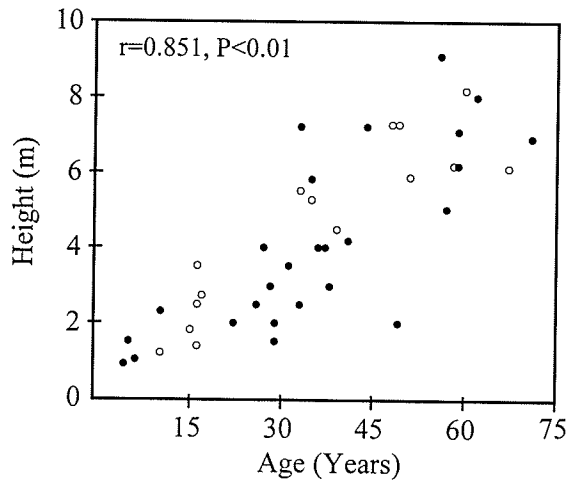
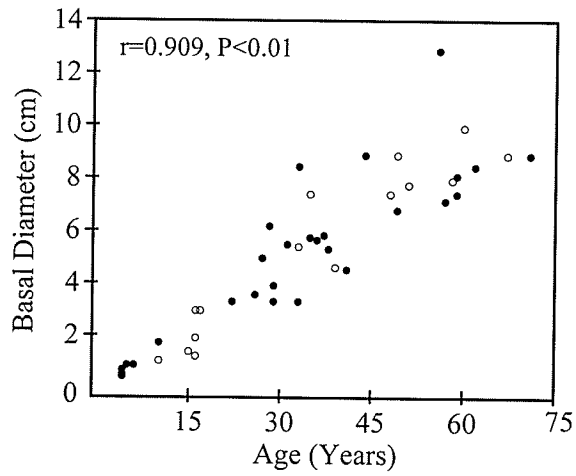
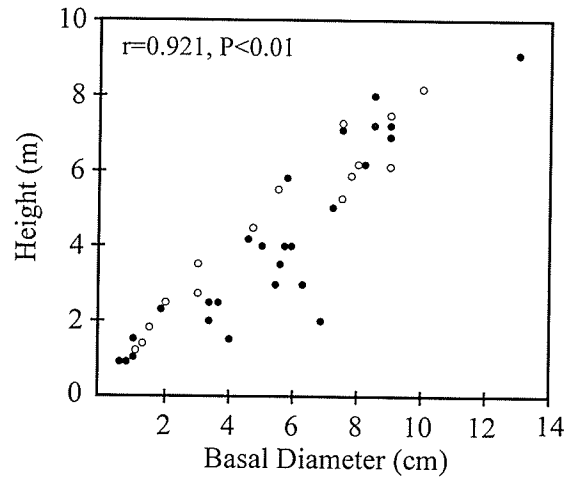
**Figure 4.2.** Calculation of mean annual incremental radial growth for a specimen of green ash harvested from the understory of a mixed eastern deciduous stand. The slope of the regression line (0.619692) taken from the biplot of incremental radius (mm) against ring number or age (years) represents the mean annual incremental radial growth ( $\text{mm} \cdot \text{yr}^{-1}$ ) for the specimen.



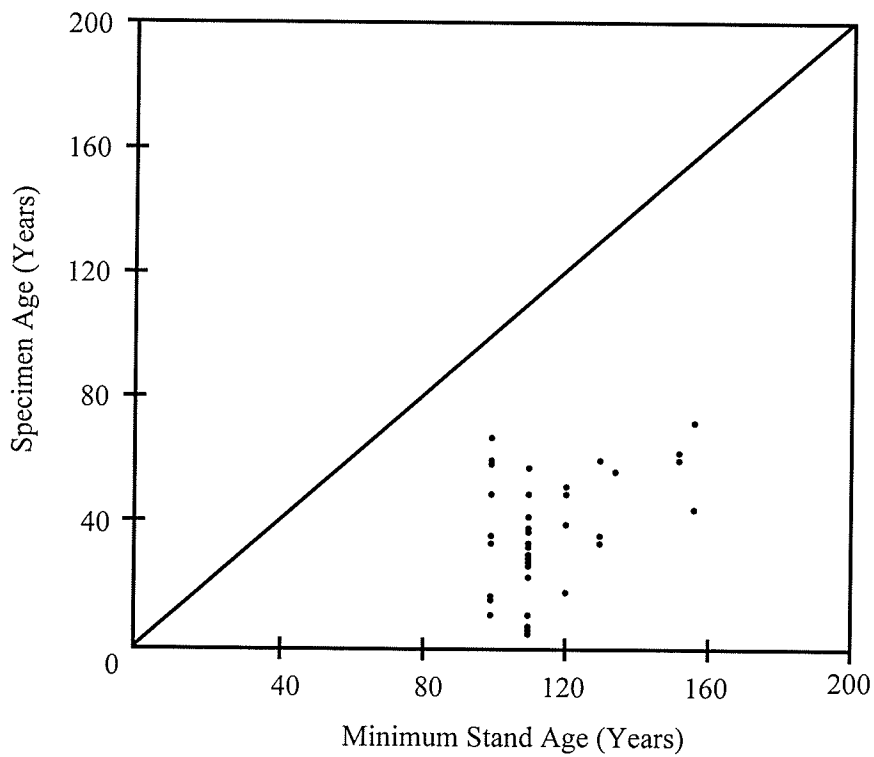
**Figure 4.3.** Multiple discriminant analysis (MDA) of 3 groups of stands using 14 variables of which Baregr, Slope, Shrub, Hazel, MMaple and Moss were transformed as  $\log(p+1)$ . 75 stands were divided *a priori* into 3 groups: 1) stands lacking green ash in both the understory and canopy ( $n=45$ ); 2) stands with green ash in the understory but lacking in the canopy ( $n=10$ ); and 3) stands with green ash present in both the understory and canopy ( $n=20$ ). Eigenvalues as a percentage: axis 1 = 70.49; axis 2 = 29.51. Variable codes: Baregr = total bareground cover; Slope = percent slope; Decay = amount of decaying wood on the forest floor; Site Age = minimum age of stand; S = sand content of mineral soil; C = Clay content of mineral soil; pH = soil pH; Cond = soil electrical conductivity ( $\mu\text{S}/\text{cm}$ ); LFH = depth of the LFH horizon; Hazel = total cover of beaked hazelnut; MMaple = total cover of mountain maple; Shrub = total shrub cover excluding beaked hazelnut and mountain maple; Moss = total bryophyte cover; Herb = total herbaceous cover.



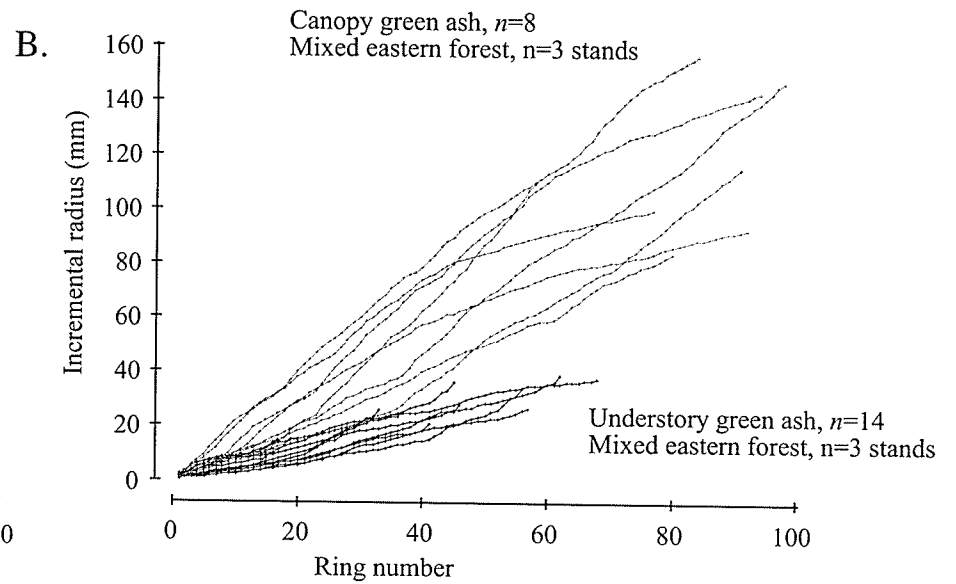
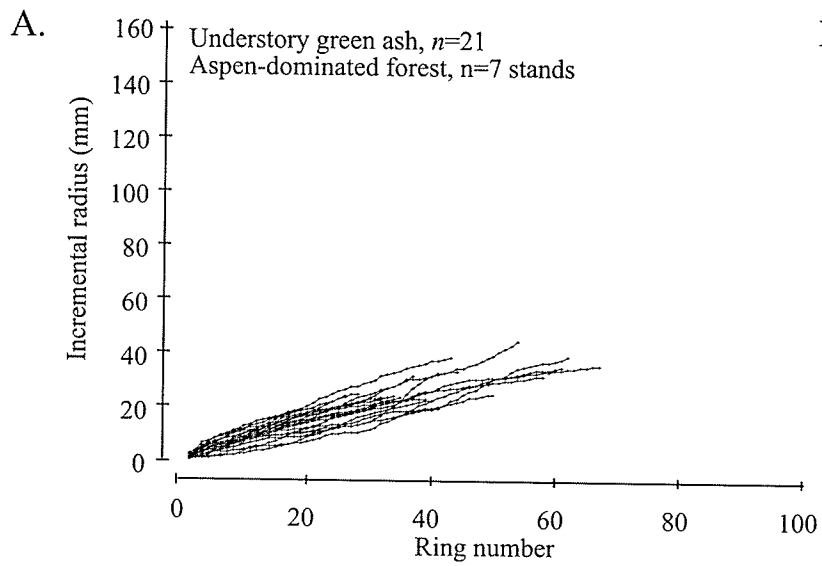
**Figure 4.4.** Mean density and height class of tree species from aspen-dominated boreal (top;  $n=7$ ) and mixed eastern deciduous (bottom;  $n=3$ ) stands from which understory and overstory green ash were sampled.



**Figure 4.5.** Age (years), basal diameter (cm) and height (m) relationships for  $n=44$  understory (<10 m height) green ash harvested from  $n=7$  aspen-dominated boreal (•) stands and  $n=3$  mixed eastern deciduous (◦) stands. All green ash were harvested at ground level.

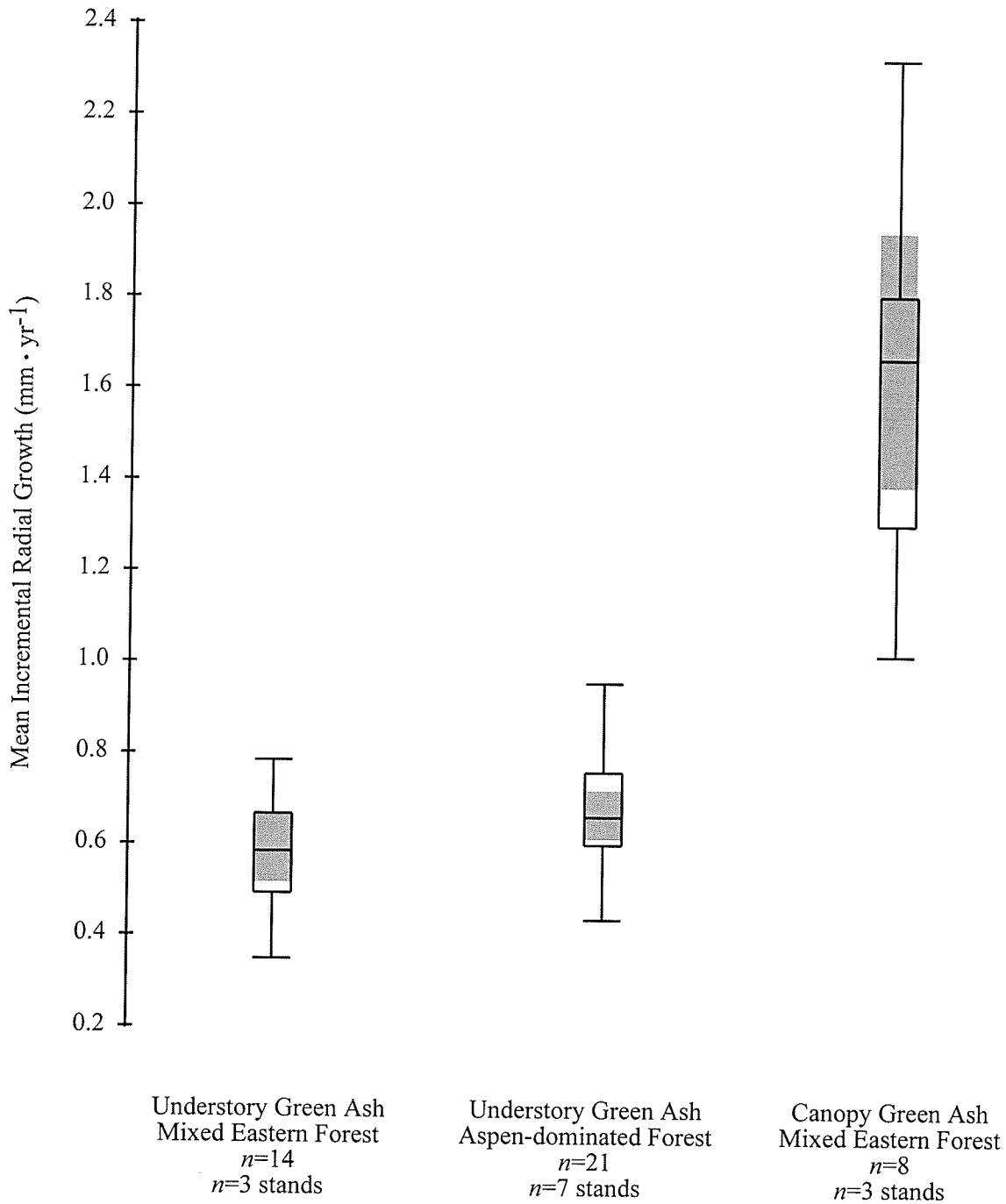


**Figure 4.6.** Age of understory (<10 m in height) green ash ( $n=44$ ) in relation to the minimum age of the stand (years) from which they were harvested. All green ash were harvested at ground level. Specimens falling below the line have been recruited after stand establishment.



**Figure 4.7.** Comparison of incremental radial growth ( $\text{mm} \cdot \text{yr}^{-1}$ ) for A)  $n=21$  harvested understory green ash from  $n=7$  aspen-dominated boreal stands and B)  $n=8$  canopy green ash from  $n=3$  mixed eastern deciduous stands and  $n=14$  harvested understory green ash from the same  $n=3$  mixed eastern deciduous stands.





**Figure 4.8.** Mean incremental radial growth ( $\text{mm} \cdot \text{yr}^{-1}$ ) for understory and canopy green ash sampled from  $n=7$  aspen-dominated boreal and  $n=3$  mixed eastern deciduous stands.



**Figure 4.9.** The effects of Dutch elm disease on two mixed eastern deciduous forest canopies. These stands are situated near the base of the eastern Cretaceous escarpment.

**Table 4.1.** Means and standard deviations for  $n = 14$  variables used to discriminate between 3 groups of forest stands: 1) stands lacking green ash in both the understory (canopies 3, 4 and 5) and overstory (canopies 1 and 2) ( $n = 45$ ); 2) stands with green ash in the understory but lacking in the canopy ( $n = 10$ ); and 3) stands with green ash present in both the understory and canopy ( $n = 20$ ). Variable codes: Bareground = total bareground cover; Slope = percent slope; Decay = amount of decaying wood on the forest floor; Age = minimum stand age; S = sand content of mineral soil; C = Clay content of mineral soil; pH = soil pH; Conductivity = soil electrical conductivity ( $\mu\text{S}/\text{cm}$ ); LFH = depth of LFH layer; Hazel = total cover of beaked hazelnut; MMaple = total cover of mountain maple; Shrub = total shrub cover excluding beaked hazelnut and mountain maple; Moss = total bryophyte cover; Herb = total herbaceous cover.

Group	$n$	Bareground (percent)	Slope (degrees)	Decay (0-3)	Age (years)	S (percent)	C (percent)	pH	Conductivity ( $\mu\text{S}/\text{cm}$ )	LFH (cm)	Hazel (percent)	MMaple (percent)	Shrub (percent)	Moss (percent)	Herb (percent)
1	45	11.98	5.09	0.60	80.62	34.47	33.75	6.18	230.84	5.94	28.34	4.77	15.82	0.78	25.65
		14.25	3.92	0.62	18.78	14.69	11.76	0.72	121.66	2.82	22.82	15.86	14.75	0.87	14.81
2	10	13.50	3.70	1.30	94.70	42.18	31.80	6.98	250.00	5.45	17.87	16.60	7.63	0.96	17.15
		10.55	1.83	0.48	20.97	24.40	12.44	0.66	86.41	2.03	11.71	16.18	7.10	0.67	9.76
3	20	15.45	2.78	1.05	108.35	44.27	26.82	7.06	347.65	6.05	16.64	9.56	17.60	0.99	29.26
		16.55	1.42	0.76	33.64	22.50	14.59	0.69	166.73	2.09	16.18	18.36	15.30	1.84	17.03

**CHAPTER 5**  
**GROWTH RESPONSE OF WHITE SPRUCE (*PICEA GLAUCA* (MOENCH) VOSS)**  
**ACROSS A BROAD RANGE OF HABITAT CONDITIONS**

**5.1 Introduction**

Differences in habitat conditions appear to be the major determinant in the successful germination, establishment and subsequent growth of white spruce (*Picea glauca* (Moench) Voss) in mixedwood stands of the boreal forest. The growth and survival of understory white spruce depends on the functional response of saplings to spatial and temporal changes in biotic and abiotic stand conditions (Messier et al. 1999).

Germination and establishment of white spruce is dependant on a combination of factors, including seed source proximity, seedbed quality and the spatial arrangement of safe- or microsites (Kneeshaw & Bergeron 1996; DeLong et al. 1997; Galipeau et al. 1997; Simard et al. 1998; Greene et al. 1999), and site disturbance history (McCune & Allen 1985a). Radial and height growth of understory white spruce is largely determined by the direct and indirect effects of light availability beneath the canopy (Yang 1991; Lieffers & Stadt 1994; Constabel & Lieffers 1996; Lieffers et al. 1996; Groot 1999; Lieffers et al. 1999, Messier et al. 1999; Drobyshhev & Nihlgård 2000; Walters & Reich 2000), although individuals are also exposed to a correlated set of environmental conditions, including contrasting air movement, temperature, CO<sub>2</sub>, moisture and nutrient regimes, and competition with surrounding vegetation for moisture and nutrients (Marsden et al. 1996; Kneeshaw & Bergeron 1998; Greene et al. 1999; Messier et al. 1999; Drobyshhev & Nihlgård 2000).

The understory light environment of forest stands is influenced by numerous factors. The species composition of forest canopies, in combination with the spatial arrangement of canopy trees, strongly influences the quality and quantity of understory photosynthetically active radiation, or PAR. Several studies have shown that there is an intrinsic difference in the quantity, and spatial and temporal variability, of light penetrating deciduous, mixed deciduous-coniferous and coniferous-dominated canopies (Lieffers & Stadt 1994; Constabel & Lieffers 1996; Lieffers et al. 1996; Comeau et al. 1998; Messier et al. 1998; Lieffers et al. 1999; Aubin et al. 2000; Walters & Reich 2000). In addition, large- or small-scale canopy openings or 'gaps', resulting from the mortality of one or more canopy trees, or large branches, break the continuity of the forest canopy structure. Gap size, architectural geometry of trees immediately adjacent to the gap, diurnal and seasonal changes of the sun, and geographic latitude influence the spatial variation and quantity of understory PAR in and around the canopy gap (Runkle 1982; Canham 1998;

Cumming et al. 2000; Drobyshev & Nihlgård 2000). Large gaps increase understory PAR, facilitating the proliferation of a dense understory shrub canopy (Constabel & Lieffers 1996; Kneeshaw & Bergeron 1998; Aubin et al. 2000). Dense shrub canopies, in turn, limit white spruce growth and establishment by attenuating ground-level PAR and increasing deciduous leaf litter (Lieffers et al. 1996; Aubin et al. 2000).

The amount of light intercepted by forest stands is one of the driving variables controlling forest dynamics (Aubin et al. 2000), and influences the rate at which understory conifers are initiated into the canopy (Lieffers et al. 1996; Drobyshev & Nihlgård 2000). White spruce is a shade tolerant species (Marsden et al. 1996), capable of growing in a 'suppressed' condition in the understory for several decades under conditions of low PAR (Yang 1991; Wright et al. 2000). Messier et al. (1999) adopt a comparative and functional definition of shade tolerance, emphasizing the morphological and physiological characteristics of a species that confer a greater or lesser capacity to grow under conditions of low PAR. As compared to shade intolerant conifers (e.g. *Pinus*), shade tolerant species (e.g. *Picea* and *Abies*) tend to have lower values of specific leaf mass, live crown ratio and leader over lateral length ratio, and have higher values of STAR (shoot silhouette area to total needle surface area), leaf area ratio and root over shoot ratio. Shade tolerant conifers have been described as having a "maximum sustainable height", whereby height growth stops under conditions where light interception does not meet the costs of maintaining new tissues (Messier et al. 1999). Although white spruce can survive in a slow growing condition for prolonged periods, the species responds well to 'release' following canopy disturbances which increase understory PAR (Neinstadt & Zasada 1990; Yang 1991; Bergeron 2000). Generally, saplings in gaps benefit from higher resource availability, and obtain higher growth rates as compared to suppressed saplings growing beneath a dark canopy (Clark 1991; Bergeron 2000).

White spruce (*Picea glauca* (Moench) Voss) approaches its southern distributional limits in the province in RMNP. The regional distribution of the species is most likely determined by moisture availability (i.e. the *P*-PET index, the difference between precipitation and potential evapotranspiration; see Hogg 1994), as well as the cumulative effects of past fires and logging (Clark 1989; Hogg 1994; Johnson et al. 1998; Weir & Johnson 1998; Tchir & Johnson 1999; Weir et al. 1999). Several studies have postulated that white spruce will become more abundant in mixedwood stands of boreal forest in the absence of fire, thereby affecting stand composition and structure, and influencing the persistence of the species on the landscape (Bergeron & Dubuc 1989; Carleton & Maycock 1991; Bergeron 2000). In RMNP, the expansion of agriculture along the Park periphery, in combination with active fire suppression, may reduce the frequency of

stand-replacing fires (Clark 1989; Johnson et al. 1998; Weir & Johnson 1998; Tchir & Johnson 1999; Weir et al. 1999), and facilitate the transition to gap-driven forest dynamics (Frelich & Reich 1995; Kneeshaw & Bergeron 1998; Walker & Kenkel 1998). White spruce is the most abundant and widely-distributed conifer in RMNP, and therefore has the potential to greatly influence forest structure and dynamics at the landscape level.

Measures of radial and height growth have previously been used in the literature to effectively quantify the growth of white spruce advanced regeneration. The widths of the last few (youngest) rings of a specimen, and most recent changes in height growth, are typically used to calculate individual growth responses (Lieffers & Stadt 1994; Lieffers et al. 1996; Drobyshev & Nihlgård 2000). Measuring the most recent growth of a specimen, as compared to earlier (older) growth, more accurately reflects the prevailing habitat conditions in which that individual is found, and alleviates the problems associated with the inherent changes in architectural geometry of a tree over time.

This study examines incremental radial growth and height of harvested understory white spruce along a continuum of habitat conditions in the RMNP. Post-fire stand composition and subsequent formation of canopy openings are expected to account for intraspecific differences in patterns of white spruce growth. The objectives of this chapter are twofold: 1) to examine the habitat conditions which are conducive to (or limit) white spruce regeneration on the landscape, and 2) to assess the differences in white spruce radial and height growth across a broad range of habitat conditions. Addressing these issues will improve the understanding of how spatial and temporal changes in habitat structure and composition influence growth of white spruce advanced regeneration. The propensity for successful white spruce regeneration in different forest stands is discussed.

## **5.2 Methods**

### **5.2.1 Data Collection**

Of the 202 - 10 x 10 m forest stands that were enumerated in RMNP (see Chapter 3), a total of 119 were analyzed to examine distribution patterns of white spruce on the landscape. Numerous variables were collected in each stand, including percent cover of all plant species in 5 vegetation canopies (1 canopy trees, >15 m; 2 subcanopy trees, 10-15 m; 3 lower subcanopy trees and tall shrubs, 2-10 m; 4 saplings and low shrubs, 0.5-2 m; 5 tree seedlings, herbs and bryophytes, <0.5 m), edaphic information including percent sand, silt and clay content (Bouycous hydrometer

method, Kalra & Maynard 1991), pH, electrical conductivity ( $\mu\text{S}/\text{cm}$ ) and LFH horizon depth (cm), tree density and DBH, and an estimate of minimum stand age (years). Minimum stand age was determined for each 'stand' from which white spruce was harvested by taking increment cores at 1.3 m (breast height) above ground level from two of the largest individuals of each tree species.

A total of  $n=92$  understory (<10 m in height) white spruce were randomly selected and harvested from a total of  $n=20$  stands throughout central and eastern portions of the Park. These 20 stands were sampled in addition to the 202 enumerated forest stands in the Park, corresponding most closely with stand types VII (Aspen-Balsam Poplar) and VIII (White Spruce). Specimens showed no signs of physical damage, and were harvested at ground level according to one of three canopy types (defined *a priori*) beneath which they were found: 1) coniferous-dominated, 2) deciduous and 3) mixed deciduous-coniferous. The inherent structural and compositional differences between these 3 groups, and their dramatic effects on understory light quality and quantity (Lieffers & Stadt 1994; Constabel & Lieffers 1996), facilitates the examination of understory white spruce growth across a wide range of habitat conditions. A canopy was deemed to be coniferous-dominated if six or more (i.e. 75-100%) of the eight closest live canopy trees to a specimen were coniferous (white spruce and/or balsam fir (*Abies balsamea* (L.) Mill.). A canopy was deemed to be deciduous if all (i.e. 100%) of the eight closest live canopy trees to the specimen were deciduous (trembling aspen (*Populus tremuloides* Michx.) in all cases). A mixed deciduous-coniferous canopy did not satisfy either of these criteria, having from 1 to 5 (i.e. 12.5-62.5%) of the closest 8 live canopy trees to the specimen being coniferous. At the time of harvest, measures of diameter, height and growth form were recorded for each specimen. Growth form was noted as being either monopodial (i.e. conic) or sympodial. A monopodial growth form refers to a tree axis that has been constructed from a single meristem, whereas a sympodial growth form is constructed from a series of modules (Millet & Bouchard 1999).

Numerous variables which directly influence the immediate understory light environment were measured within a 5 x 5 m area centred around each harvested white spruce. These measurements include ocular estimates of percent canopy cover, the proportion of deciduous and coniferous trees comprising the canopy, percent shrub cover by species, the amount of decaying wood on the forest floor (ordinal scale of 0-3), an estimate of minimum stand age (years), plot slope (which is closely related to insolation; in degrees) and whether or not the specimen was growing beneath a canopy opening or 'gap'. A gap was defined as a distinct break in the continuity of the forest

canopy, caused by the past mortality of a canopy tree. A white spruce specimen was considered to be growing in a gap only if there was evidence of canopy tree mortality, or mortality of large canopy branche(s), and if the mean distance from a given specimen to the closest six live canopy trees was greater than 6 m.

All white spruce sections were finely sanded (using 400 grit sandpaper) and polished (using 600 grit sandpaper) and rings were counted to 0.01 mm along 4 perpendicular axes from the centre of each section (Fig. 5.1). The most recent growth ring for each tree section was included in the analysis, since radial growth was nearly complete for that year (i.e. collections were made in late October). Proper surface preparation of tree sections and cores facilitated the distinction between 'true' and 'false' rings. True rings exhibit an abrupt change in tracheid size between the last-formed tracheids of the previous ring and the first-produced tracheids of the current ring. False rings, in comparison, tend to display a gradual transition in tracheid diameter on both ring margins (Wimmer et al. 2000).

### 5.2.2 Data Analysis

#### *Landscape-Level Patterns of White Spruce Regeneration*

Multiple discriminant analysis was used to assess differences in habitat conditions in which white spruce is found in the Park. A total of 4 groups were examined: 1) deciduous stands from the western 'upland' of the Park that lack white spruce regeneration in both the understory (vegetation strata 3, 4 and 5) and overstory (vegetation strata 1 and 2),  $n=55$ ; 2) deciduous stands with white spruce present in the understory but absent in the canopy,  $n=15$ ; 3) mixed deciduous-coniferous stands with white spruce present in both the overstory and understory,  $n=28$ ; 4) coniferous-dominated stands (>75% of all overstory trees are coniferous) with white spruce present in both the understory and overstory,  $n=21$ . A total of 119 out of the 202 previously sampled stands were entered into the analysis, excluding 71 black spruce (*Picea mariana* (Mill.) BSP), jack pine (*Pinus banksiana* Lamb.), eastern deciduous and bur oak (*Quercus macrocarpa* Michx.) plots (i.e. habitats in which white spruce is commonly absent), and 12 mixed deciduous-coniferous and coniferous plots lacking white spruce regeneration. 14 variables were used to discriminate among the 4 groups of stands. These discriminating variables are percent cover of the shrubs beaked hazelnut (*Corylus cornuta* Marsh.) and mountain maple (*Acer spicatum* Lam.), all shrubs excluding beaked hazelnut and mountain maple, herbs, bryophytes and bareground, the amount of decaying wood on the forest floor (ordinal scale of 0-3), soil pH, conductivity ( $\mu\text{S}/\text{cm}$ ),



LFH horizon depth (cm), and percent sand and clay, plot slope (degrees), and minimum stand age (years). Of these variables, percent cover of shrubs, beaked hazelnut, mountain maple, bryophytes and bareground were transformed as  $\log(p+1)$  to meet the assumptions of multivariate normality (ter Braak 1986, 1987a).

#### *Growth of White Spruce Under Different Habitat Conditions*

Out of the  $n=92$  sampled understory white spruce, ring-width analyses were conducted on  $n=67$  individuals. All cored specimens were omitted from the dataset, as well as specimens that were very old (i.e. strong outliers) and those that had indistinct ring structures making measurements difficult and unreliable.

Mean incremental radial growth of white spruce was calculated using the 5 most recent growth rings of each specimen. The slope of the regression line through the scatter of incremental radius (mm) over time (years) was used as a mean measure of growth over time (**Fig. 5.2**). These most recent growth rings closely reflect the presently-observed habitat conditions from which specimens were harvested. Comparing understory white spruce growth should be done with caution, however, since age differences preclude them from being at the same stage of development.

Principal Components Analysis (PCA) was used to distinguish differences in habitat conditions for the white spruce used in the study. Five variables were used to summarize habitat conditions for the  $n=67$  individuals, using a correlation matrix (SYNTAX, Podani 1994). These variables are percent canopy cover, percent cover of the shrubs mountain maple and beaked hazelnut, the presence or absence of a canopy gap, and plot slope. To determine if white spruce growth is influenced by its habitat conditions, PCA axis 1 object scores were compared with i) the calculated mean incremental radial growth for each specimen and ii) the residual height value of each specimen from the 'expected' height for a given age. A value of residual height was determined by first forcing a regression line through zero on the biplot of the square root of height (m) and age (years) (**Fig. 5.3**). Using the square root of specimen height provided a more normal height distribution. The positive or negative difference between expected and observed height represents the residual height value for a given specimen.

Differences in radial and height growth of understory white spruce were compared between coniferous-dominated, mixed deciduous-coniferous and deciduous forest canopies using boxplots.

### 5.3 Results

#### 5.3.1 Landscape-Level Patterns of White Spruce Regeneration

Results of the MDA are presented in **Fig. 5.4**. Both axes 1 ( $\chi^2$  axis 1=146.92,  $P<0.0001$ ) and 2 ( $\chi^2$  axis 2=47.18,  $P=0.0067$ ) significantly discriminate between the 4 groups of stands. Eigenvalues as a percentage: axis 1=75.10; axis 2=18.84. The most discriminating variables along axis 1 are the abundance of beaked hazelnut, bryophytes, total shrub cover (excluding beaked hazelnut and mountain maple) and mountain maple. The most discriminating variables along axis 2 are the abundance of decaying wood, minimum stand age, LFH horizon depth and the abundance of mountain maple. **Table 5.1** presents the mean and standard deviation for each of the  $n=14$  variables for the  $n=4$  groups.

The 95% confidence interval around the mean for group 1 is situated on the left side of MDA axis 1. Group 1 contains 'upland' stands that lack white spruce regeneration. These stands are relatively young (mean age=87±24 years), are shrub-dominated (especially by beaked hazelnut and occasionally mountain maple), and have a low ground cover of bryophytes and decaying wood. Stands belonging to group 2 (stands with white spruce regeneration beneath a canopy of *Populus*) are older stands (mean age=114±35 years) with a high abundance of decaying wood on the forest floor and a deep LFH horizon. Regeneration density is typically low (mean density=2.13±1.88), and stands occasionally contain a high abundance of the tall shrub mountain maple. Group 3, comprised of mixed deciduous-coniferous stands with understory white spruce regeneration, is spatially separated from group 2 along MDA axis 2. These stands are relatively young (mean age=83±25 years) with little decaying wood on the forest floor, have a shallow LFH horizon and occur on less clayey soils. These stands have a lower abundance of beaked hazelnut as compared to group 1, and a lower abundance of mountain maple as compared to groups 1 and 2. Regeneration density is higher than groups 1 or 2 (mean density=3.86±2.62). Group 4 is situated on the right side of MDA axis 1. These stands are older (mean age=105±28 years), with a high abundance of decaying wood on the forest floor, a deep LFH horizon and a high abundance of bryophytes. Regeneration density is high when compared to groups 1-3 (mean density=5.95±3.98).

### 5.3.2 Growth of White Spruce Under Various Habitat Conditions

The harvested understory white spruce ( $n=92$ ) have established in stands several years following stand establishment (**Fig. 5.5**), suggesting that habitat conditions have been conducive to seed dispersal (or viability in the seed bank), germination, establishment and survival. Of the total  $n=92$  harvested understory white spruce,  $n=67$  were utilized in growth analyses.

Results of the PCA are presented in **Fig. 5.6**. The  $n=67$  specimens are labeled according to the type of canopy from beneath which they were harvested (i.e. deciduous, mixed deciduous-coniferous or coniferous-dominated). The positions of some white spruce individuals in the ordination space are overlapping (making there appear to be fewer than 67 points in the ordination space) as a result of having very similar habitat conditions. Eigenvalues as a percentage: axis 1=58.87; axis 2=17.58. From left to right, PCA axis 1 separates specimens along a gradient of increasing understory light availability.

Understory white spruce harvested from coniferous-dominated stands ( $n=24$  specimens; mean stand age= $143\pm 27$  years) tend to occur on the left side of the ordination space. The left side of the ordination space is characterized by stands with a closed canopy, a high abundance of mountain maple (and usually a low abundance of beaked hazelnut), and relatively large slope. A few specimens belonging to this group occur in canopy gaps ( $n=8$  of the 24), and are situated on the right side of the ordination space. Specimens found growing in gaps have a lower canopy cover, but the extent of canopy cover depends on the size of a given gap.

Understory white spruce harvested from deciduous stands ( $n=23$  specimens; mean stand age= $120\pm 23$  years), in comparison, tend to occur on the right side of the ordination space. The right side of the ordination space is characterized by stands with an open canopy, the presence of a canopy gap, an abundance of beaked hazelnut (and conversely a lack of mountain maple), and relatively low slope. These stands are old, and have canopies punctuated by gaps formed from the mortality of individual aspen. Of the specimens belonging to this group,  $n=22$  of the 23 were situated in canopy gaps.

Specimens harvested from mixed deciduous-coniferous stands ( $n=20$  specimens; mean stand age= $105\pm 19$  years) are widely distributed throughout the ordination space, encompassing a wide range of habitat conditions. Several specimens harvested from this group occur on the right side of the ordination space, under conditions of lower canopy cover. However, canopy gaps were not

commonly encountered in this group. Of the specimens belonging to this group,  $n=1$  of the 20 was situated in a canopy gap.

Habitat conditions are strongly trended with white spruce incremental radial growth and residual height. Regressions are presented in **Fig. 5.7**. PCA axis 1 object scores are significantly related to mean incremental radial growth ( $r^2=41.3\%$ ,  $P<0.0001$ ) and residual height ( $r^2=49.1\%$ ,  $P<0.0001$ ) for understory white spruce.

Mean incremental radial growth ( $\text{mm} \cdot \text{yr}^{-1}$ ) during each of the last 5 years of growth is illustrated for specimens growing beneath each of the predetermined canopy types: 1) coniferous-dominated (gap and non-gap), 2) mixed deciduous-coniferous and 3) deciduous (**Fig. 5.8**). Within the coniferous group, specimens are categorized as to whether or not they are growing beneath a canopy gap. **Fig. 5.9** presents the raw incremental radial growth curves for specimens belonging to each of the predefined groups. Several specimens belonging to the closed- and mixed deciduous-coniferous groups have undergone numerous episodes of suppression and release over time. Specimens belonging to the deciduous and coniferous-gap groups, in comparison, do not demonstrate these trends as readily.

**Figs. 5.10 and 5.11** utilize boxplots to compare mean incremental radial growth and residual height, respectively, among the 3 dominant canopy types. The coniferous-dominated canopy category has been separated into gap and non-gap. Recent mean incremental radial growth (calculated from the 5 most recent growth rings, in  $\text{mm} \cdot \text{yr}^{-1}$ ) is greatest for individuals growing beneath open deciduous canopies ( $2.3779 \pm 0.9232$ ), followed by mixed deciduous-coniferous stands ( $0.8058 \pm 0.6495$ ) and closed coniferous stands ( $0.8468 \pm 0.7079$ ). In coniferous stands, mean incremental radial growth of understory white spruce is significantly higher (using a 2-sample t-test of  $\mu_1 - \mu_2$ ,  $P<0.0001$ ) for individuals growing beneath a canopy gap ( $1.6983 \pm 0.5057$ ) as compared to a closed canopy conditions ( $0.4210 \pm 0.2628$ ). Residual height of white spruce is greatest for individuals growing beneath open deciduous canopies ( $0.6683 \pm 0.3496$ ), followed by mixed deciduous-coniferous stands ( $-0.0985 \pm 0.4421$ ) and closed coniferous stands ( $-0.1785 \pm 0.5215$ ). In coniferous stands, residual height of understory white spruce is significantly higher (using a 2-sample t-test of  $\mu_1 - \mu_2$ ,  $P=0.0372$ ) for individuals growing beneath a canopy gap ( $0.1686 \pm 0.5472$ ) as compared to closed canopy conditions ( $-0.3521 \pm 0.4254$ ). Specimen ages are similar for each of the coniferous-dominated (mean= $39 \pm 13$  years), mixed deciduous-coniferous (mean= $34 \pm 10$  years) and deciduous (mean= $24 \pm 7$  years) groups, minimizing the confounding effects of age and size.

A final model of white spruce incremental radial growth and residual height is presented in **Fig. 5.12**. Mean incremental radial growth and mean residual height increase monotonically along a continuum of canopy types:

closed coniferous < mixed deciduous-coniferous < coniferous gap < deciduous

This continuum of canopy types generally corresponds to an increase in understory light availability, and can be interpreted as a good predictor of understory white spruce growth (Lieffers & Stadt 1994; Constabel & Lieffers 1996; Lieffers et al. 1996, 1999; Aubin et al. 2000, Drobyshev & Nihlgård 2000). Canopy conditions will therefore be a major determinant in forest stand dynamics on the landscape.

## **5.4 Discussion**

### 5.4.1 Patterns of White Spruce Regeneration on the Landscape

Differences in habitat conditions will determine the propensity for white spruce to disperse, germinate, grow and reach the canopy. The spatial arrangement of white spruce on the landscape has major implications on the future composition and structure of forest stands.

Results of the MDA (**Fig. 5.4**) indicate that the spatial distribution of white spruce on the landscape is influenced by habitat conditions including the abundance of beaked hazelnut and mountain maple, minimum stand age, and the abundance of decaying wood and bryophytes. These factors were able to effectively discriminate among deciduous, mixed deciduous-coniferous and coniferous-dominated stands with and without understory white spruce advanced regeneration. Deciduous stands lacking understory white spruce are young, have a high abundance of understory shrubs and have little decaying wood on the forest floor. In contrast, deciduous and coniferous-dominated stands with white spruce regeneration are older, have a deep LFH horizon, a large abundance of decaying wood on the forest floor, and a relatively low cover of beaked hazelnut, mountain maple and other shrub species. The coniferous-dominated stands are mostly found in central and eastern regions of the Park, as well as along the Cretaceous escarpment where a reticulation of stream valleys provide protection from frequent fires. Older deciduous stands with white spruce regeneration are also common in central and eastern regions of the Park, as well as along mid to upper slopes of the northern and eastern escarpment which have burned less frequently in the recent past than the adjacent upland (Sentar 1992). Mixed

deciduous-coniferous stands, in comparison, tend to be younger stands with a low cover of beaked hazelnut. These stands most commonly occur in central and western regions of the Park, although older mixedwood stands are found along the eastern escarpment.

Post-fire recruitment of white spruce in mixedwood stands of the boreal forest is most successful when there is a proximate seed supply, a high abundance of decomposing boles on the forest floor and a low abundance of understory shrubs (Kneeshaw & Bergeron 1996; DeLong et al. 1997; Simard et al. 1998). Recruitment commonly occurs immediately after fire when mineral soil is exposed and an abundant seed supply is present (Lieffers et al. 1996). Sites with poor seedbed conditions and where seed trees are absent, immature or are not producing seed at the time of the disturbance, often have sporadic and delayed recruitment patterns.

A dense shrub layer dominated by beaked hazelnut or mountain maple may form beneath deciduous stands as a result of high PAR transmittance through the canopy and an abundance of rapidly-decomposing, nutrient-rich leaf litter (Messier et al. 1998). A thick shrub canopy is also supported beneath large gaps in mixed deciduous-coniferous and coniferous-dominated forests (Bergeron 2000). Shrubs may limit conifer growth and establishment by dramatically decreasing ground-level PAR and increasing the amount of smothering deciduous leaf litter (Vincent 1965; Sullivan 1993; Lieffers & Stadt 1994; Constabel & Lieffers 1996; Kneeshaw & Bergeron 1996, 1998; Messier et al. 1998; Aubin et al. 2000). Decomposing boles act as elevated seedbeds, and have been described as necessary for the effective post-fire recruitment of white spruce (Rowe 1955; Waldron 1966; Lieffers et al. 1996; DeLong et al. 1997). Although they do not provide an advantage for sapling radial or height growth as compared to growth on mineral soil (Lieffers et al. 1996), they have a higher soil temperature, lower soil strength and accumulate less deciduous leaf litter than exposed patches of mineral soil and the LFH horizon of the forest floor (DeLong et al. 1997). The abundance of decaying wood on the forest floor is related to stand senescence, and increases with stand age (Sturtevant et al. 1997). Simard et al. (1998) have found that the abundance of decaying wood is greatest in mid-successional stands.

All of the understory white spruce aged from deciduous, mixed deciduous-coniferous and coniferous-dominated stands in this study have recruited after fire (Fig. 5.5). This implies that stand conditions are conducive to the successful germination, establishment and growth of the species in these areas. The stands from which regeneration was obtained have a proximate seed supply, and the interfire period has been long enough to allow for the accumulation of decaying wood on the forest floor. The propensity for understory white spruce to reach the canopy in these

stands will be determined by prevailing habitat conditions and the timing and scale of disturbance.

#### 5.4.2 Growth of White Spruce Under Various Habitat Conditions

Light has previously been shown to be one of the most influential factors regulating the growth and survival of understory white spruce regeneration. The availability of understory PAR is directly and indirectly affected by the species composition and spatial complexity of the forest canopy, as well as the formation of small- and large-scale canopy gaps. In this study, white spruce growth is strongly trended with prevailing habitat conditions. Both incremental radial growth and residual height of understory white spruce increase along a gradient of increasing light availability. Namely, specimens growing beneath coniferous-dominated canopies without a gap exhibit slow incremental radial growth and low residual height. Growth in these habitats is similar to that beneath mixed deciduous-coniferous canopies. In comparison, incremental radial growth and residual height are dramatically increased beneath coniferous-dominated canopies with a canopy gap. Growth of white spruce in coniferous gaps is similar to that beneath deciduous canopies, where recent growth is optimized. Variation in white spruce growth within gaps may be accounted for by differences in gap size and the location of regeneration within the gap (Kneeshaw & Bergeron 1998; Drobyshev & Nihlgård 2000).

Studies have shown that there is an intrinsic difference in light quantity, and the spatial and temporal variability of light, penetrating the forest canopy in different boreal forest communities. Typically, canopies dominated by shade-intolerant hardwoods such as trembling aspen, balsam poplar (*Populus balsamifera* L.) and/or paper birch (*Betula papyrifera* Marsh.) transmit a greater percent Photosynthetic Photon Flux Density (%PPFD,  $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$ ) than canopies containing shade-tolerant conifers such as white spruce and/or balsam fir (Lieffers & Stadt 1994; Constabel & Lieffers 1996; Lieffers et al. 1996; Comeau et al. 1998; Messier et al. 1998; Lieffers et al. 1999; Aubin et al. 2000; Walters & Reich 2000). White spruce has previously been shown to demonstrate the most rapid growth beneath deciduous as compared to mixed deciduous-coniferous or coniferous-dominated canopies (Lieffers & Stadt 1994; Lieffers et al. 1996). Height increment, the number of buds, diameter of the current leader and height to diameter ratio increase with increasing understory PAR (Lieffers & Stadt 1994). White spruce survival has also been shown to increase with increasing PAR (Walters & Reich 2000).

In forest systems where gap dynamics represent an important mode of canopy recruitment, shade-tolerant species such as white spruce typically undergo multiple episodes of suppression and release before reaching higher canopy layers (Wright et al. 2000). The relative abilities of saplings of different tree species to survive periods of suppression and respond to release are critical determinants in the development of forests. White spruce is considered to be in a suppressed state when incremental radial growth rates fall below a threshold of  $0.6 \text{ mm} \cdot \text{yr}^{-1}$  (Wright et al. 2000). This value was based the functional relationship between growth and mortality. Namely, the growth rate associated with a sapling mortality rate of 10% after 3 years was chosen as the threshold, coinciding with a steep inflection in the probability of specimen mortality.

Understory white spruce is well-adapted to take advantage of changes in light availability. Past periods of suppression have been shown to have no effect on the current response of white spruce to release (Wright et al. 2000). In addition, white spruce demonstrates a gradual increase in growth rate at a given light level during the course of release. Release events have therefore been described as “ameliorative” to the effects of past suppression (Wright et al. 2000). In contrast, shade intolerant species (e.g. trembling aspen and paper birch) respond differently to suppression and release. There is generally a lag in response to release, especially if individuals have been suppressed, with the effects of suppression disappearing during the course of release for all species except trembling aspen. Overall, shade intolerant species are suppressed under higher light conditions than their more shade tolerant counterparts.

Canopy gaps markedly influence the growth of understory regeneration (Runkle 1982; Pickett & White 1985; Kneeshaw & Burton 1997; Cumming et al. 2000; Drobyshev & Nihlgård 2000), and the reorganization of existing understory vegetation (Castelli et al. 1999). Although there is an obvious increase in understory PAR following the creation of a canopy opening, quantifying the effects of such openings is difficult (Canham 1988). For example, microclimate, including moisture availability and temperature, may be substantially altered in larger gaps (Marsden et al. 1996; Drobyshev & Nihlgård 2000), and gap size influences the abundance of competing understory vegetation (Kneeshaw & Bergeron 1996, 1998; Aubin et al. 2000). In addition, large diurnal and seasonal changes in the position of the sun produce large changes in the amount of direct beam radiation received at a point in or around the gap (Canham 1988). There is substantial spatial variation in understory light levels as a result of the geometry of shading by canopy trees adjacent to the gap, making gap size alone an inadequate measure of the amount of light received by plants in or around the gap (Canham 1988). The "extended" gap, therefore, may be a more



meaningful measure than the "projected" gap (Runkle 1982; Canham 1988; Cumming et al. 2000). Gap size is closely related to the radial and height growth of white spruce (Drobyshev & Nihlgård 2000). However, large gaps may perpetuate the regeneration of competing shade intolerant species and promote the formation of a dense shrub canopy (Kneeshaw & Bergeron 2000). Gap formation, therefore, may not necessarily result in direct increases in light availability for smaller saplings because of shading by competing vegetation (Wright et al. 2000).

The direct effects of understory shrub competition are an important consideration when describing patterns of white spruce growth. The spatial arrangement of stems and leaves may have a greater effect on the understory light regime than the quantity of foliage itself (Brown & Parker 1994). Horizontal leaf orientation is associated with higher light extinction coefficient ( $k$ ) values than other orientations, and canopies with clumped and heterogeneous foliage have lower  $k$  values than canopies with homogeneous foliage arrangements (Aubin et al. 2000). Mountain maple canopies are homogeneous with a horizontal leaf orientation, often with foliage located in the upper stratum, giving the species high light extinction properties (Aubin et al. 2000). A regime of heavy ungulate herbivory promotes shoot proliferation (Bédard et al. 1978; Sullivan 1993; pers. obs.) which may further accentuate the attenuation of understory light. Ultimately, shrub competition inhibits white spruce establishment and reduces growth during early post-establishment periods (Lieffers et al. 1996; Kneeshaw & Bergeron 1996). White spruce regeneration below 0.5 m in height may be at or below the photosynthetic light compensation point for much of the growing season in systems dominated by deciduous tree and shrub species (Constabel & Lieffers 1996). A large portion of its annual carbon fixation may occur during the spring and autumn, when leaf-off periods of over- and understory deciduous species increase understory PAR (Constabel & Lieffers 1996; Comeau et al. 1998).

In this study, shrub abundance and composition varies between stands from which white spruce was sampled. Mountain maple is most abundant in sampled coniferous-dominated and mixed deciduous-coniferous stands, whereas beaked hazelnut is most abundant in sampled deciduous stands. Stand-level differences in the spatial arrangement of shrubs may influence understory PAR and in turn, early growth phases of white spruce regeneration. Since only the most recent radial growth (last 5 years) was measured for each white spruce specimen, and since the majority of all white spruce were growing at a height above the understory shrub canopy, it is difficult to assess the direct impact of the shrub canopy on white spruce growth.

### 5.4.3 Implications on Stand Dynamics

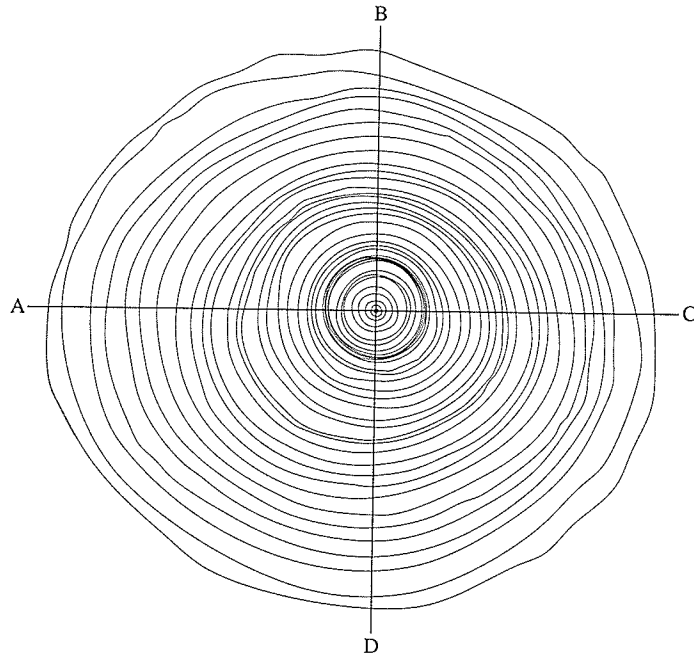
Understanding patterns of growth and mortality is integral for the prediction of forest dynamics (Wright et al. 2000). This study suggests that the regeneration of white spruce on the landscape, and subsequent recruitment into the canopy, ultimately depends on prevailing habitat conditions at smaller spatial scales. Regeneration is generally limited to stands with a proximate seed source, a relatively low shrub cover and a high abundance of decaying wood on the forest floor. In these stands, light conditions will determine the rate at which understory regeneration will grow into successively higher plant canopies. Light availability is largely determined by canopy composition and heterogeneity, the presence or absence of a canopy gap and interspecific competition. The successful recruitment of white spruce regeneration into the canopy is dependant on numerous factors, and will therefore be spatially limited on the landscape.

In RMNP, deciduous stands and coniferous-dominated stands with large canopy gaps are expected to witness the most rapid recruitment of white spruce into the canopy. Closed mixed deciduous-coniferous and coniferous-dominated stands (i.e. without canopy gaps), in comparison, will witness slower compositional change. In these communities, small-scale disturbances will be required to open the canopy to increase understory PAR. The ability of white spruce to remain in a suppressed condition in the understory for extended periods of time and then take advantage of canopy openings by rapidly increasing its growth rate suggests that gap dynamic processes will be a critical factor in forest stand development.

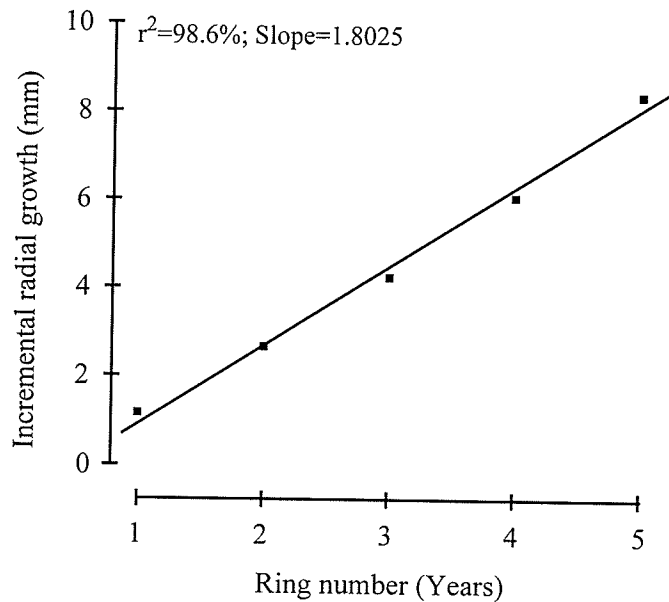
The role of disturbance in mediating the dynamics of many natural forests is well recognized (Kuuluvainen 1994; Kneeshaw & Bergeron 1998; Aubin et al. 2000; Cumming et al. 2000; Drobyshv & Nihlgård 2000). Scale can determine whether disturbances tend towards the homogenization or diversification of stand structure (Parish et al. 1999; Walker & Kenkel 1998). Large, intense fires alter much of the patch structure within stands, homogenizing not only individual stands but extensive areas of forest. In comparison, low intensity, small-scale disturbances caused by insect attack, disease or blowdown may create patchiness and spatial heterogeneity within stands (Parish et al. 1999). With increasing time since fire, the proportion of a forest canopy in gap has been found to increase dramatically (Kuuluvainen 1994; Kneeshaw & Bergeron 1998). The spatial patterning of forests becomes increasingly entropic with time since fire, where small-scale canopy gaps result in a distinctive 'peppering' effect in predominant land-cover classes (Walker & Kenkel 1998). Intermittent, small-scale disturbances are critical in modifying post-fire canopy structure, and are a dominant driving force behind stand development

in the absence of initiating catastrophic (stand-replacing) fire (Frelich & Reich 1995; Kneeshaw & Bergeron 1998, Wright et al. 2000).

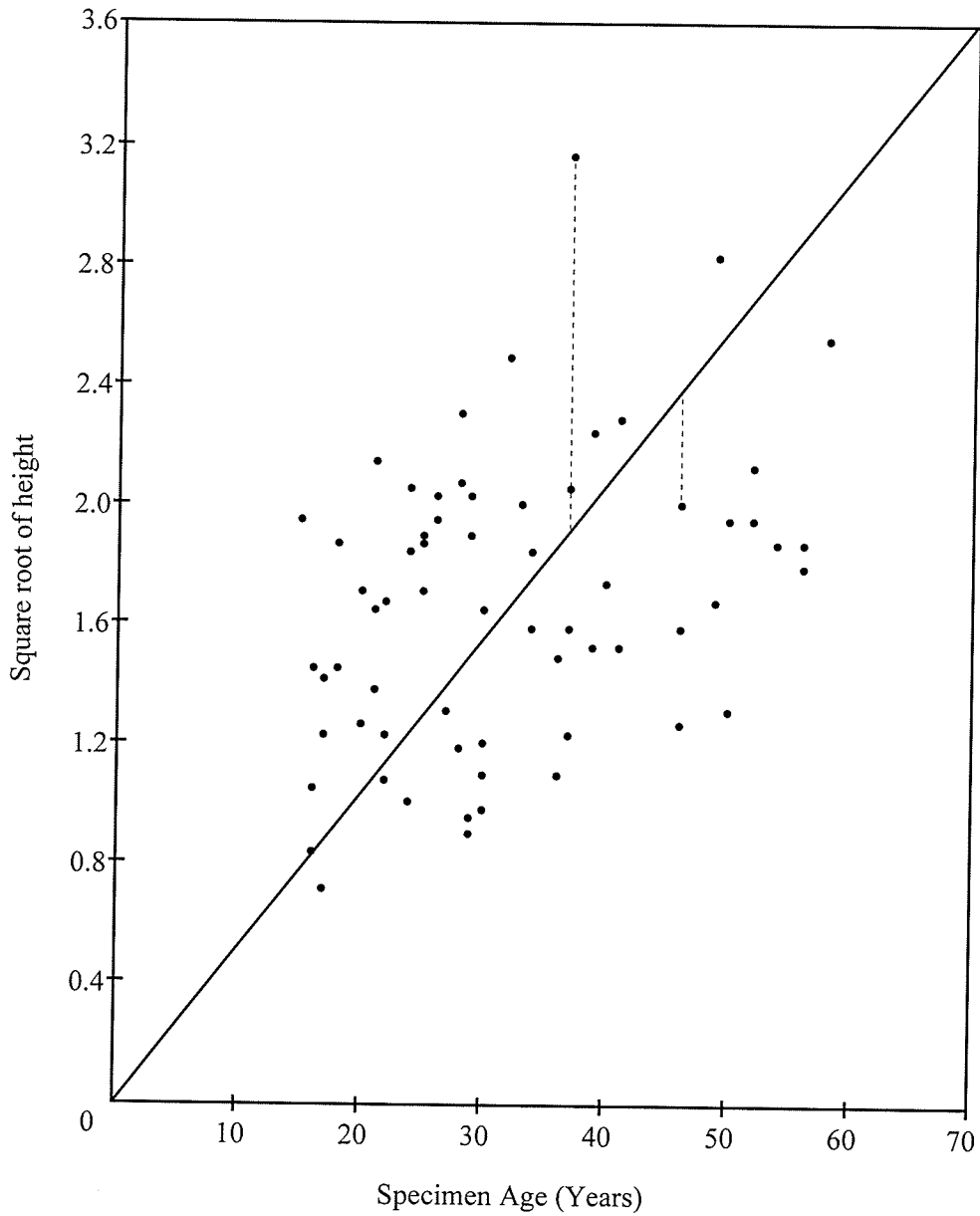
The recruitment of white spruce regeneration into the canopy has implications on landscape-level forest dynamics, resulting in the modification of local stand conditions and providing a seed source for dissemination into surrounding habitats. Changes in forest structure and composition at the stand level, therefore, will have direct implications on landscape-level processes.



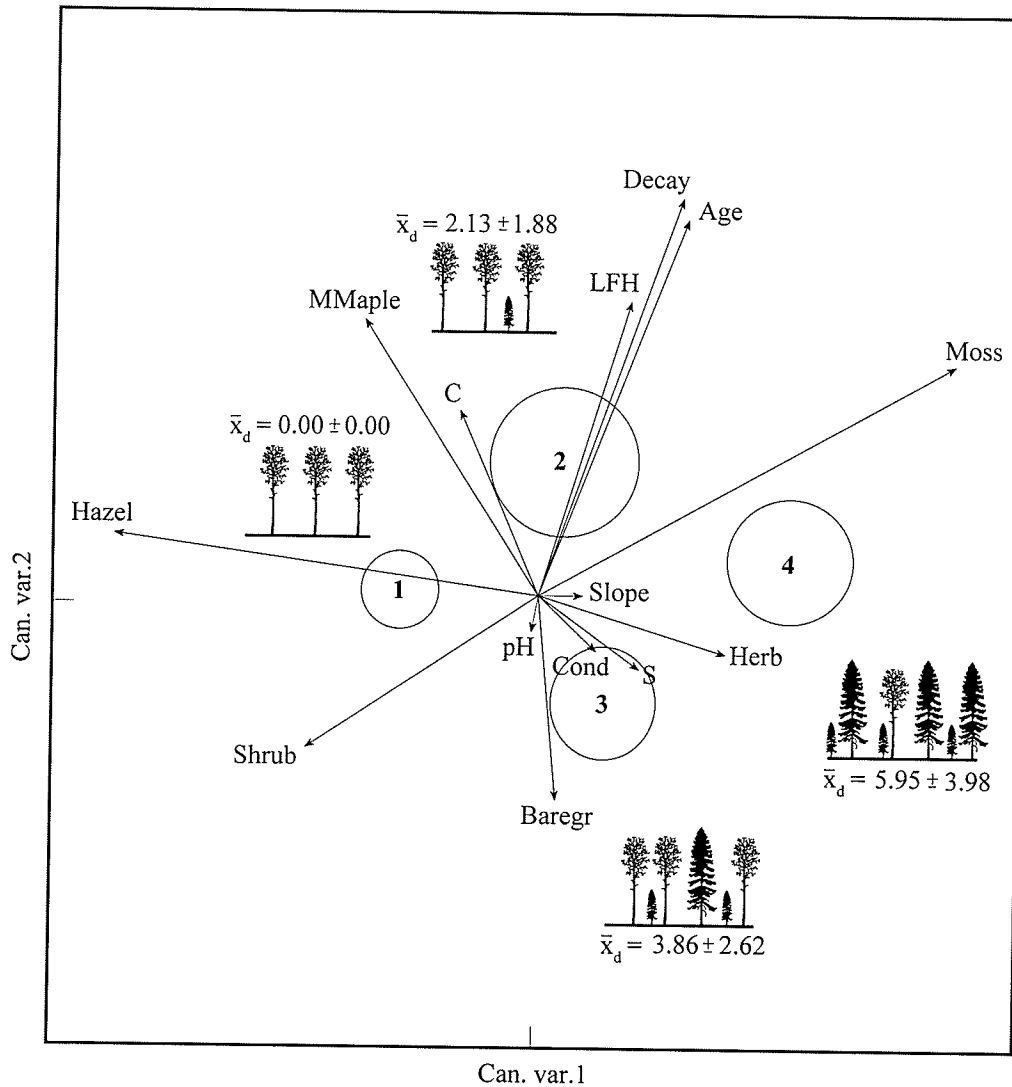
**Figure 5.1.** A section of white spruce taken at ground level. Ring widths (mm) were measured along each of 4 perpendicular radii (A-D) from the center of the section. This illustration was created from a section of white spruce which was scanned and vectorized, and is displayed at actual size. The specimen used in this figure is not the same as that used in **Figure 5.2** (see below).



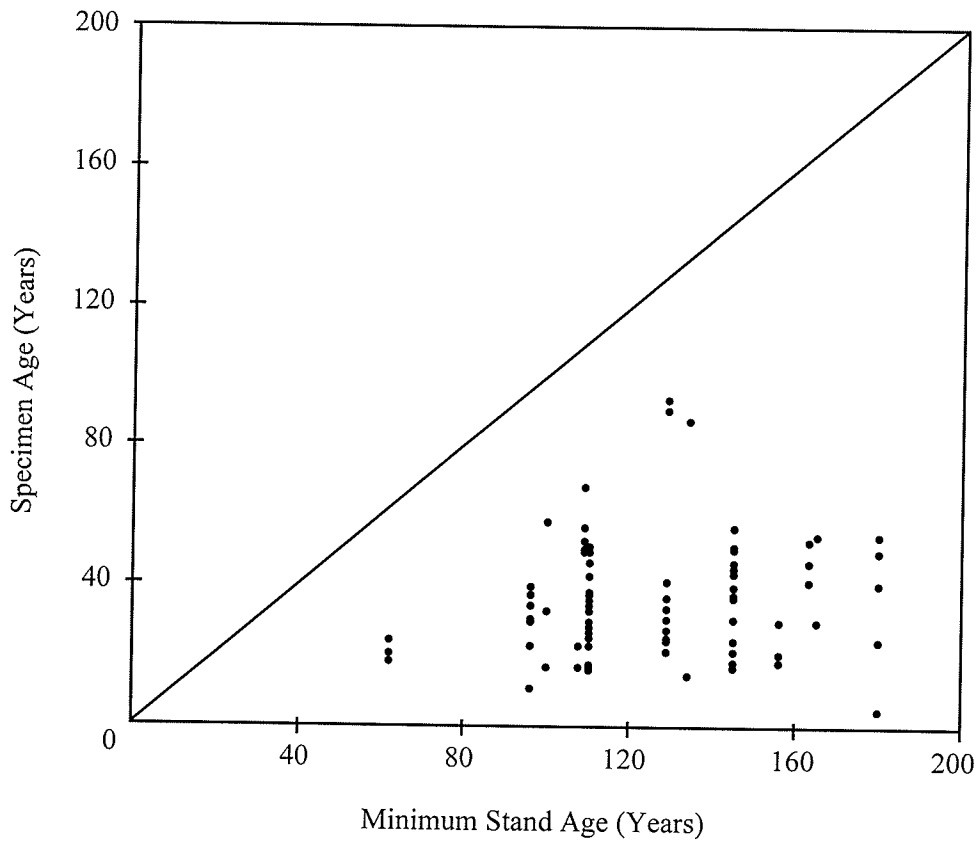
**Figure 5.2.** Calculation of mean incremental radial growth over the last 5 years for a representative understory white spruce. The slope of the regression line through the biplot of incremental radius (mm) against ring number or time (years) provides a measure of mean incremental radial growth ( $\text{mm} \cdot \text{yr}^{-1}$ ).



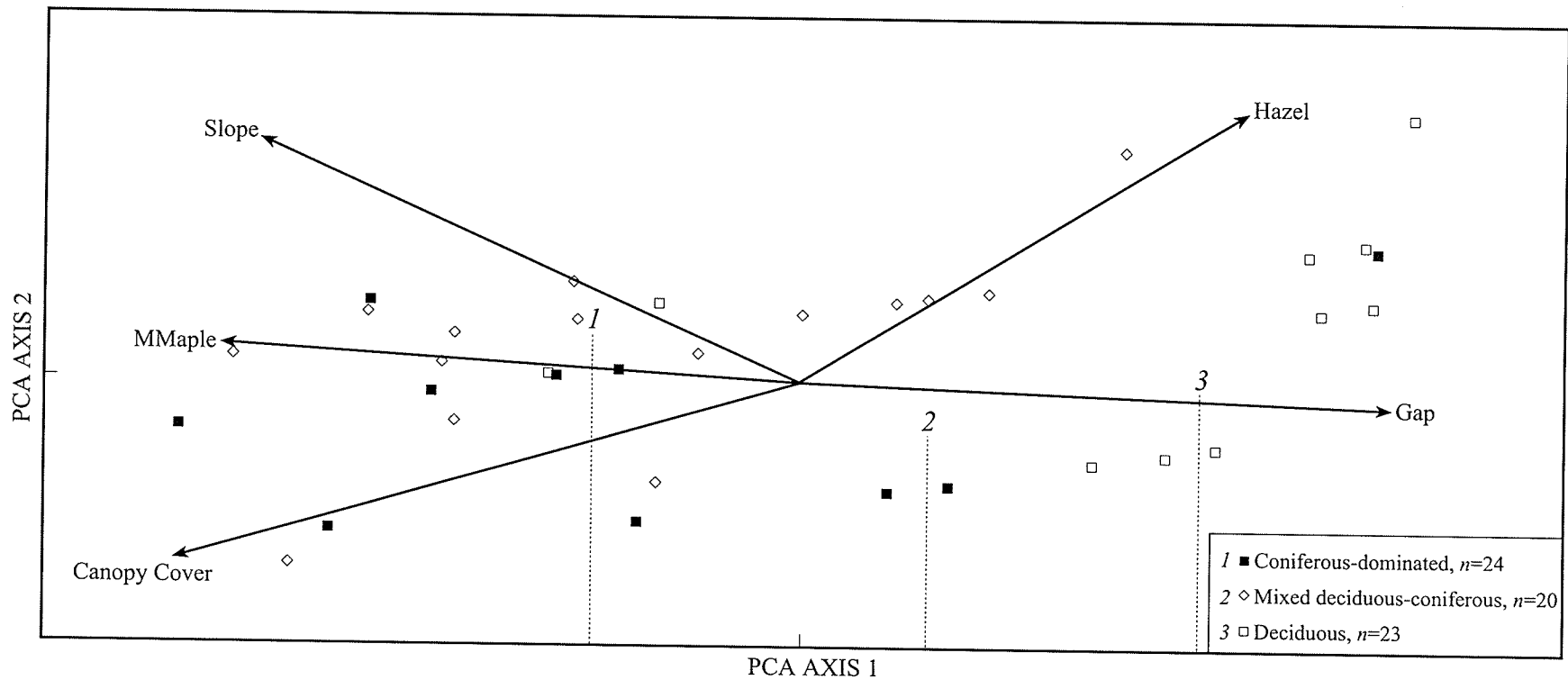
**Figure 5.3.** Specimen age (years) against square root of height for  $n=67$  harvested understory (<10 m tall) white spruce. Residual height values were calculated as the positive and negative deviations from the regression line which was forced through the origin.



**Figure 5.4.** Multiple discriminant analysis of 4 groups of stands using 14 variables (of which Baregr, Slope, Shrub, Hazel, MMaple and Moss were transformed as  $\log(p+1)$ ). 119 stands were divided *a priori* into 4 groups: 1) stands with the absence of white spruce in canopies 1+2 and 3, 4 and 5 ( $n=55$ ); 2) deciduous stands with the absence of white spruce in canopies 1+2 but presence in 3, 4 and 5 ( $n=15$ ); 3) mixed coniferous stands with the presence of white spruce in canopies 1+2 and 3, 4 and 5 ( $n=28$ ); 4) coniferous stands with the presence of white spruce in canopies 1+2 and 3, 4 and 5 ( $n=21$ ). Mean density ( $\bar{x}_d$ ) of white spruce regeneration (canopies 3, 4 and 5) is given for each group. Eigenvalues as a percentage: axis 1 = 75.10; axis 2 = 18.84. Variable codes: Baregr = total bareground cover; Slope = percent slope; Decay = amount of decaying wood on forest floor; Age = minimum site age; S = sand content of mineral soil; C = clay content of mineral soil; pH = soil pH; Cond = soil electrical conductivity ( $\mu\text{S}/\text{cm}$ ); LFH = depth of LFH horizon; Hazel = total cover of beaked hazelnut; MMaple = total cover of mountain maple; Shrub = total shrub cover excluding beaked hazelnut and mountain maple; Moss = total bryophyte cover; Herb = total herbaceous cover.

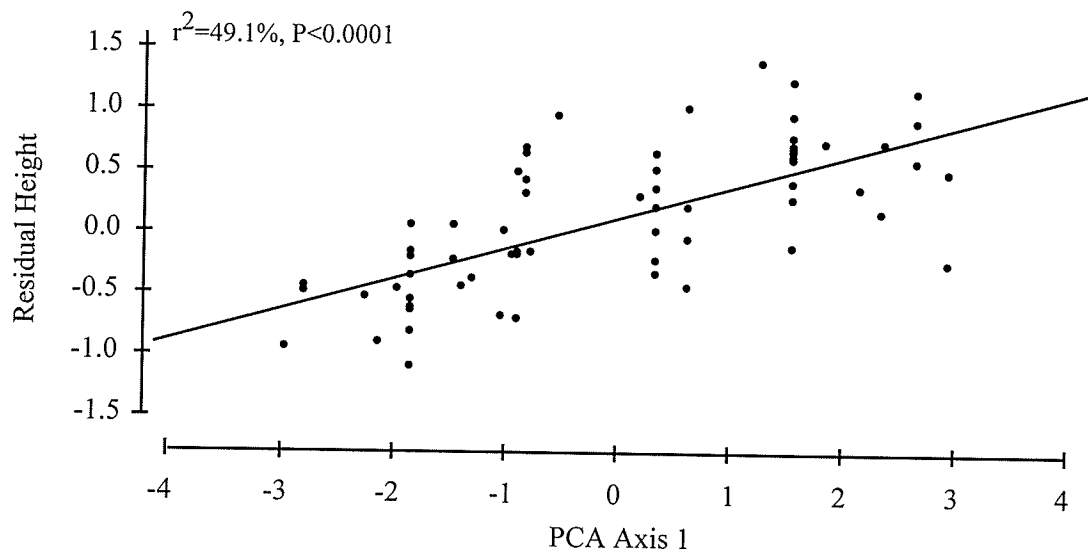
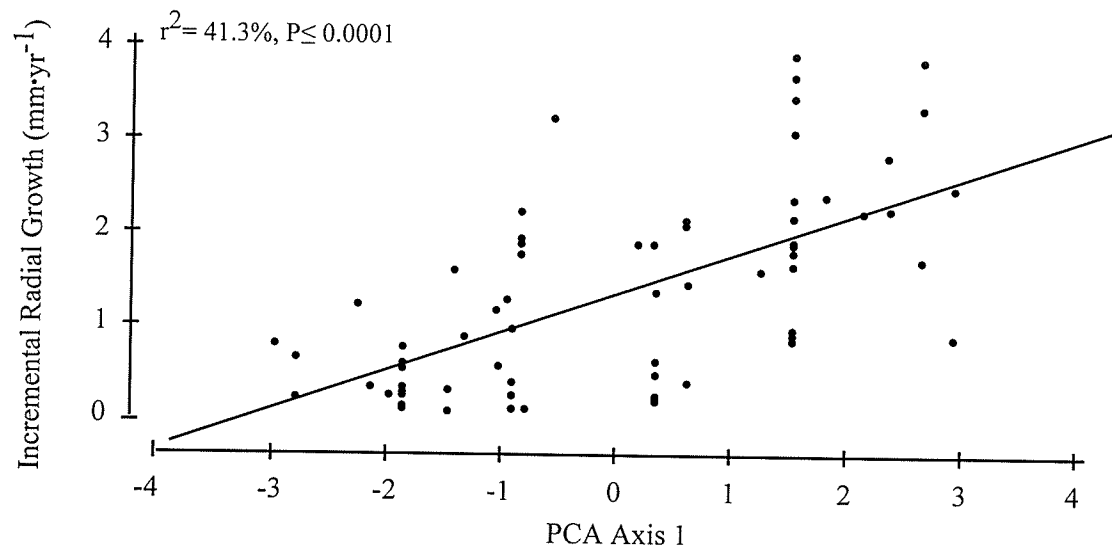


**Figure 5.5.** Age of understory (<10 m in height) white spruce ( $n=92$ ) in relation to the minimum age of the stand (years) from which they were harvested. Specimens were harvested from a total of  $n=20$  stands throughout central and eastern portions of the Park. Specimens falling below the line have been recruited after stand establishment.

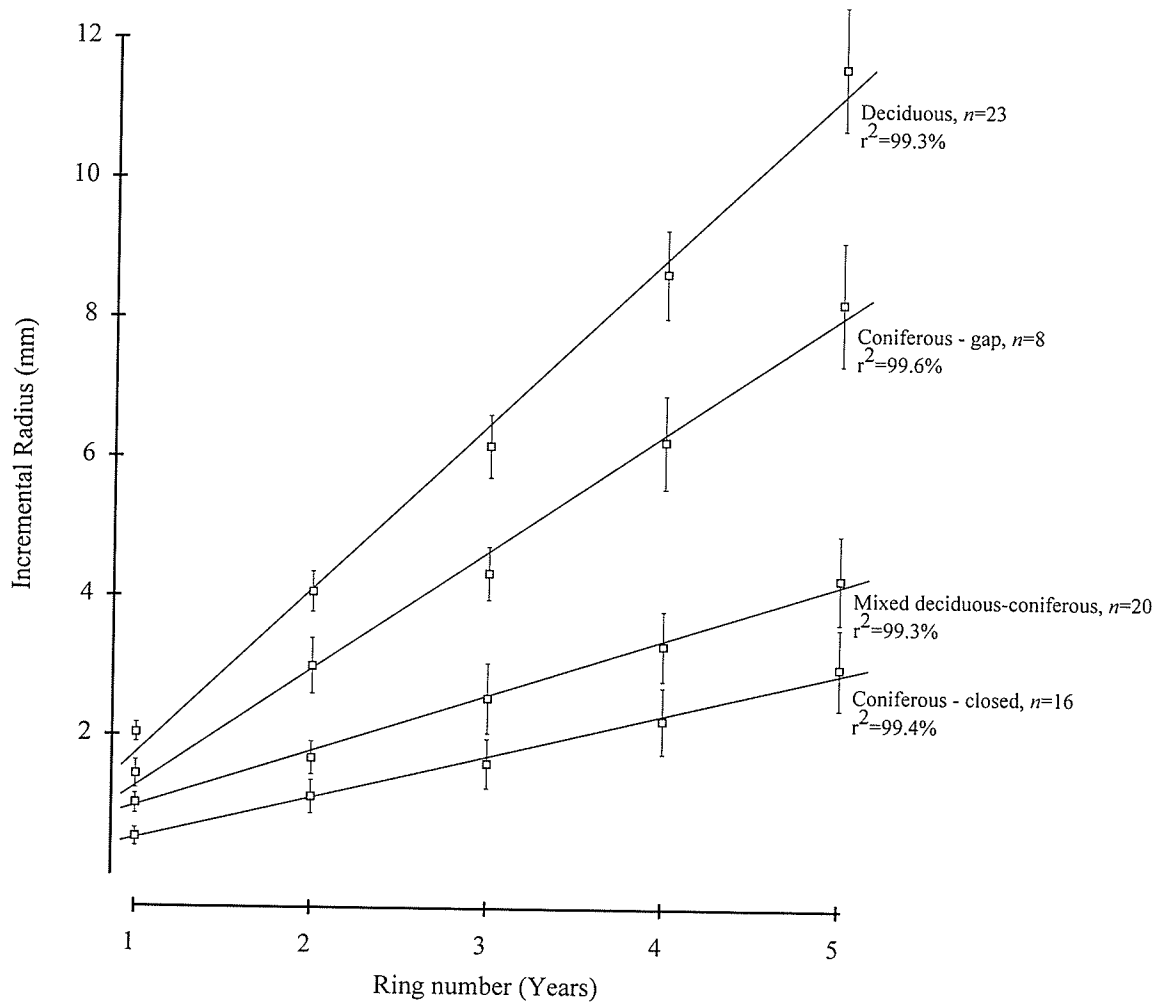


**Figure 5.6.** Principal Components Analysis (PCA) of  $n=67$  understory white spruce using 5 variables. Variables codes: Hazel=percent cover of beaked hazelnut; Gap=the presence or absence of a canopy opening; Canopy cover=percent cover of all canopy trees; MMaple=percent cover of mountain maple; Slope=degrees slope of the plot. Each white spruce in the ordination space has been assigned a symbol (see ordination legend) to signify whether it was sampled from a coniferous-dominated, mixed-coniferous or deciduous forest stand. The numbers in the ordination space are the group means for each forest stand type. Please note that several points in the ordination space are overlapping.

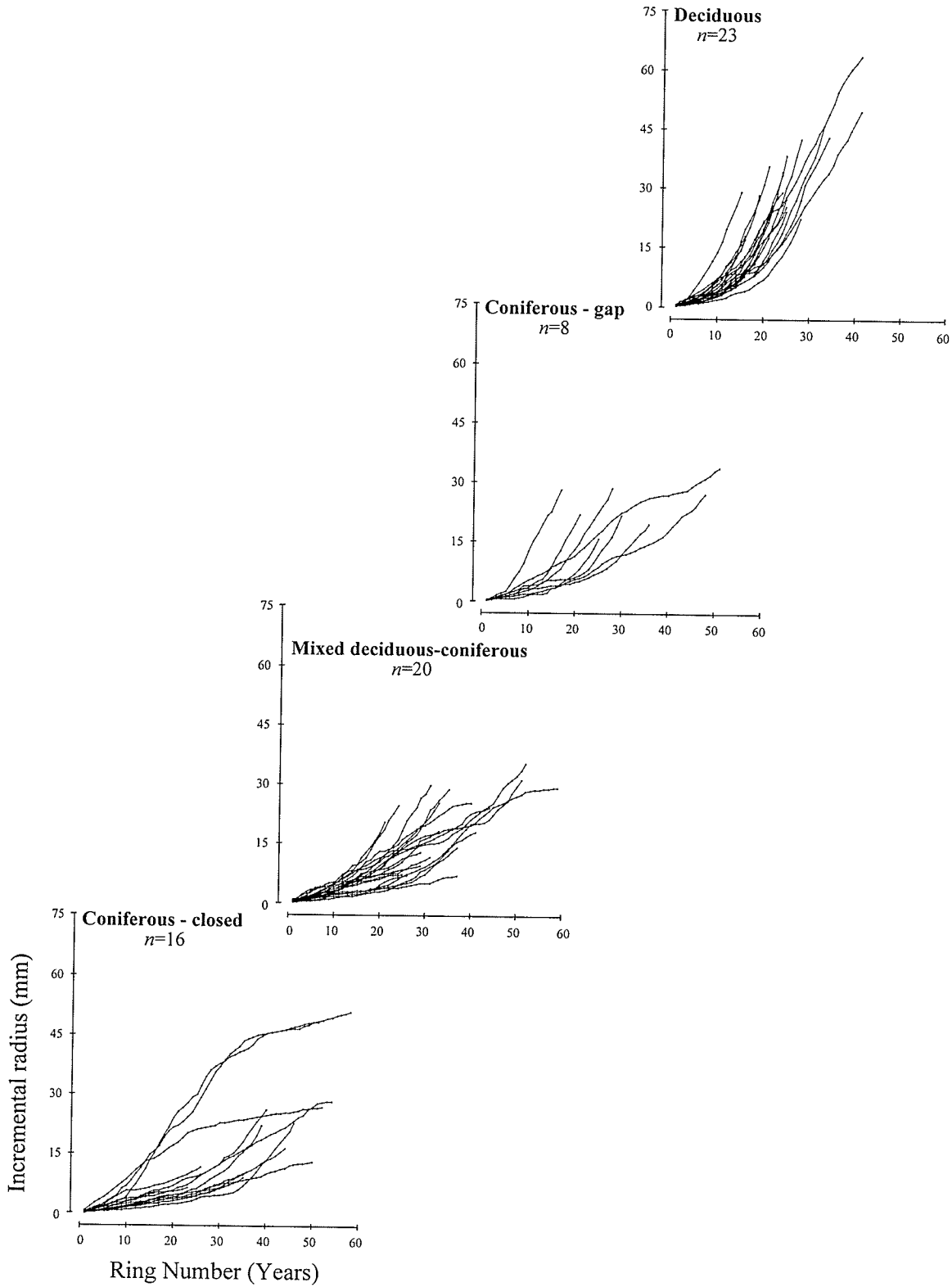




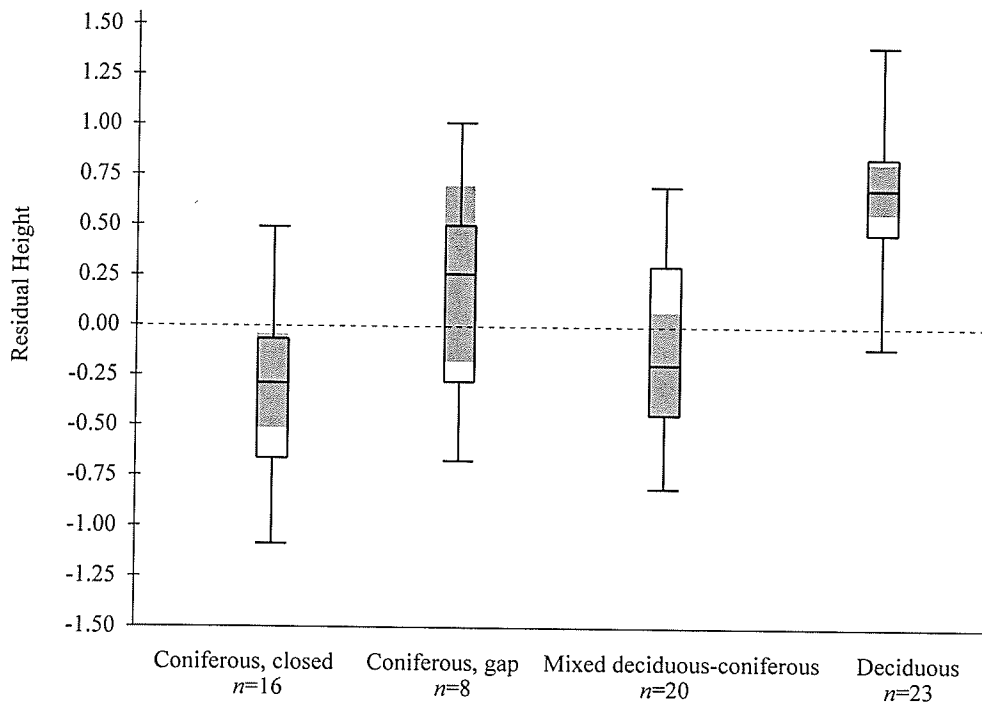
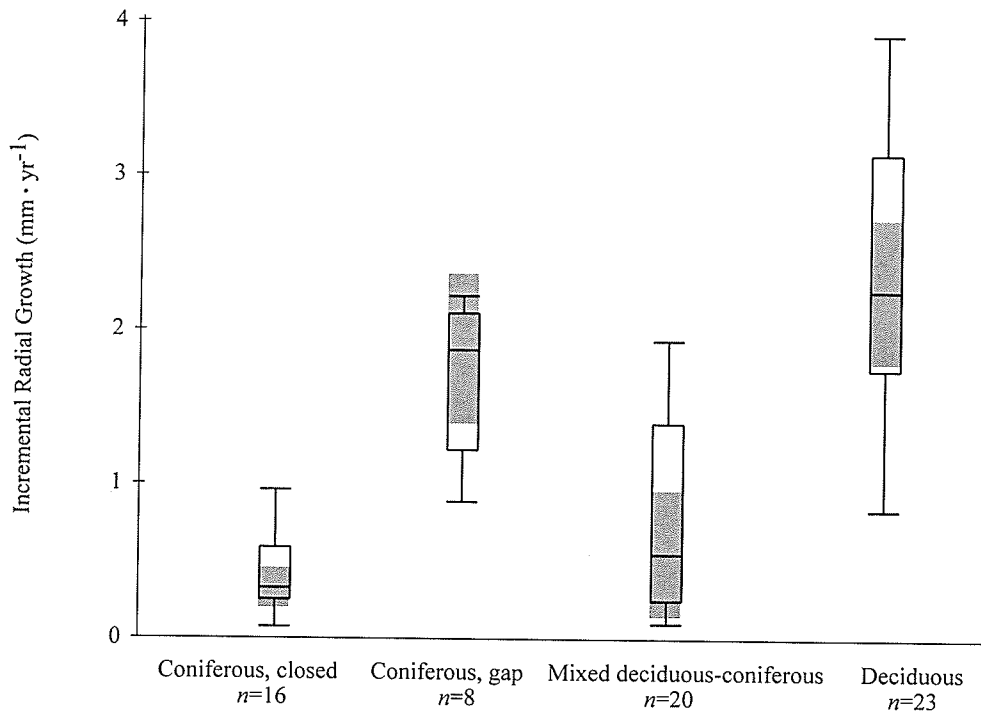
**Figure 5.7.** PCA axis 1 scores vs incremental radial growth ( $\text{mm}\cdot\text{yr}^{-1}$ ; top) and residual height (bottom) for the  $n=67$  sampled white spruce.



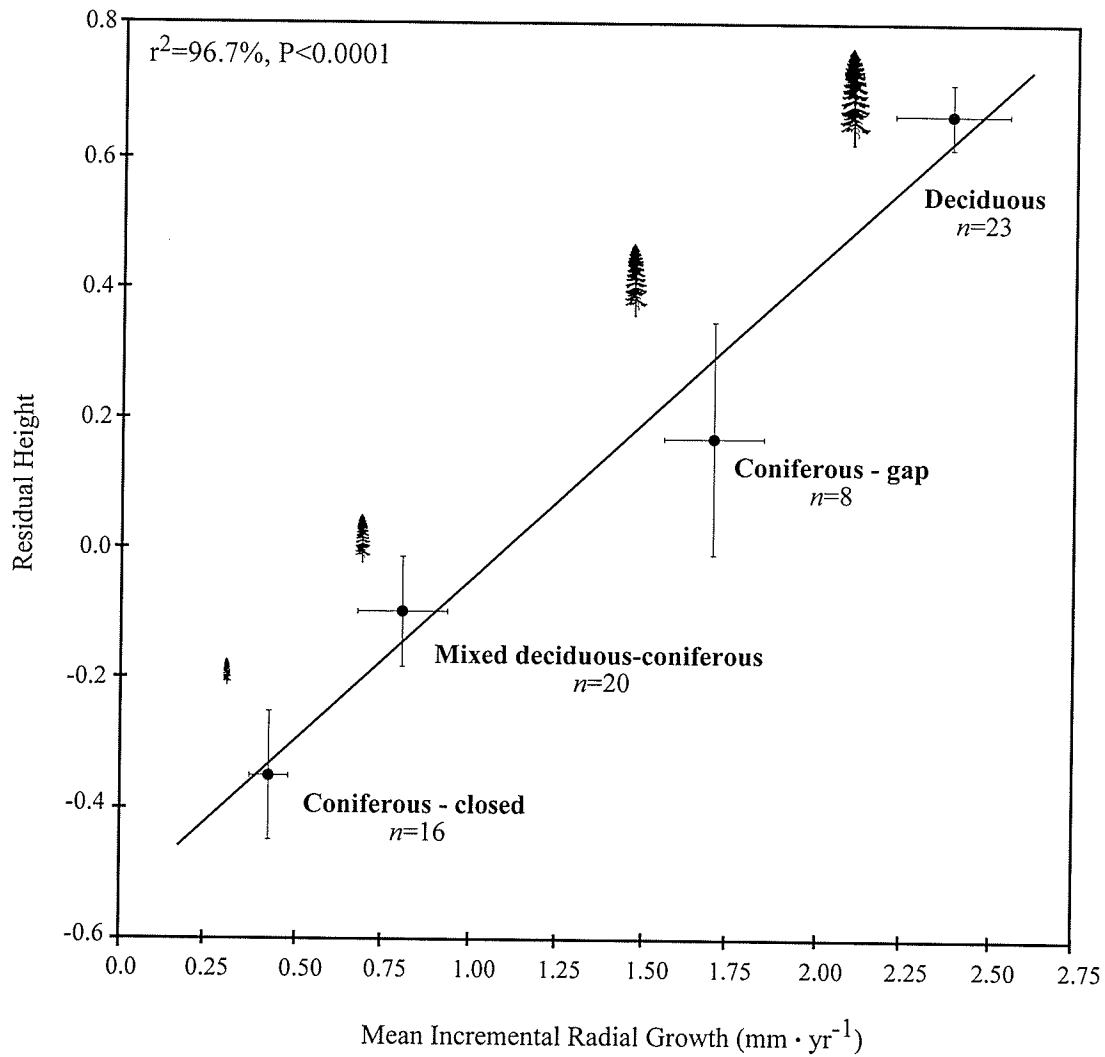
**Figure 5.8.** Mean Incremental radius (mm) for the last 5 years of growth for white spruce belonging to deciduous, mixed deciduous-coniferous, coniferous-gap and closed-coniferous forest stand types. Standard deviation bars are presented around the mean for each group.



**Figure 5.9.** Incremental radius (mm) for understory white spruce harvested from deciduous ( $n=23$ ), mixed deciduous-coniferous ( $n=20$ ) and coniferous-dominated ( $n=24$ ) forest stands. Coniferous-dominated stands have been broken into closed canopy (no gap present,  $n=16$ ) and open canopy (gap present,  $n=8$ ).



**Figures 5.10 (top) and 5.11 (bottom).** Boxplots of incremental radial growth ( $\text{mm} \cdot \text{yr}^{-1}$ ) and residual height for white spruce belonging to closed-coniferous ( $n=16$ ), coniferous-gap ( $n=8$ ), mixed deciduous-coniferous ( $n=20$ ) and deciduous ( $n=23$ ) forest stand types.



**Figure 5.12.** Mean incremental radial growth ( $\text{mm} \cdot \text{yr}^{-1}$ ) and mean residual height for white spruce regeneration along a continuum of canopy types: closed coniferous ( $n=16$ ) < mixed deciduous-coniferous ( $n=20$ ) < coniferous - gap ( $n=8$ ) < deciduous ( $n=23$ ) canopies. Standard error bars are presented around the mean for each group. The white spruce icon above each group represents the mean relative size of individuals belonging to each group.

**Table 5.1.** Means and standard deviations for  $n = 14$  variables used to discriminate between 4 groups of forest stands: 1) stands with the absence of white spruce in canopies 1+2 and 3, 4 and 5 ( $n = 55$ ); 2) deciduous stands with the absence of white spruce in canopies 1+2 but presence in 3, 4 and 5 ( $n = 15$ ); 3) mixed coniferous stands with the presence of white spruce in canopies 1+2 and 3, 4 and 5 ( $n = 28$ ); 4) coniferous stands with the presence of white spruce in canopies 1+2 and 3, 4 and 5 ( $n = 21$ ). Variable codes: Bareground = total bareground cover; Slope = percent slope; Decay = amount of decaying wood on forest floor; Age = minimum stand age; S = sand content of mineral soil; C = clay content of mineral soil; pH = soil pH; Conductivity = soil electrical conductivity ( $\mu\text{S}/\text{cm}$ ); LFH = depth of LFH horizon; Hazel = total cover of beaked hazelnut; MMaple = total cover of mountain maple; Shrub = total shrub cover excluding beaked hazelnut and mountain maple; Moss = total bryophyte cover; Herb = total herbaceous cover.

Group	$n$	Bareground (percent)	Slope (degrees)	Decay (0-3)	Age (years)	S (percent)	C (percent)	pH	Conductivity ( $\mu\text{S}/\text{cm}$ )	LFH (cm)	Shrub (percent)	Hazel (percent)	MMaple (percent)	Moss (percent)	Herb (percent)
1	55	14.47	5.44	0.84	87.31	35.49	33.16	6.40	244.27	5.95	13.38	26.30	9.36	1.05	20.82
		14.85	4.99	0.66	24.09	16.54	11.05	0.78	115.78	2.49	13.61	18.91	16.79	1.61	11.89
2	15	15.60	4.80	1.53	114.20	38.97	33.62	6.44	228.73	7.00	8.90	15.87	14.15	4.52	26.31
		16.37	2.78	0.74	35.09	17.22	12.34	0.88	126.45	3.78	6.19	24.02	18.43	6.64	11.23
3	28	21.32	7.44	0.64	82.71	41.64	28.06	6.47	258.36	4.79	11.37	8.78	5.10	1.95	29.14
		16.89	8.36	0.78	24.79	14.21	11.43	0.85	128.77	2.72	10.37	12.09	15.70	2.19	17.04
4	21	14.95	6.00	1.33	105.00	39.58	31.40	6.35	272.48	7.45	5.20	4.70	1.48	7.28	27.94
		19.44	4.64	0.80	27.90	12.86	7.60	0.80	199.16	3.48	2.84	5.67	4.65	8.16	15.10

## CHAPTER 6 STAND DYNAMICS

### 6.1 Introduction

#### 6.1.1 Background

The complex physiography and disturbance history of Riding Mountain National Park (RMNP), has resulted in a unique assemblage of aspen parkland, eastern deciduous and boreal forest communities on the landscape. Few forest studies have been undertaken in the Mixedwood Section (B.18a) of the Boreal Forest Region (Rowe 1972) in western Manitoba. Early studies by surveyors in the Park were largely descriptive in nature (Dickson 1909; Tunstell et al. 1922; Evans 1923; Halliday 1932; Tunstell 1940). Although later studies examined more specific aspects of forest communities (Rowe 1955, 1956; Ritchie 1957; Waldron 1963, 1965, 1966; Bailey 1968; Walker & Kenkel 1998; Wolfe & Kenkel 2000), much remains to be understood (Shugart et al. 1992).

The boreal forest is a disturbance-driven biome, with fire being widely recognized as the primary disturbance agent (Heinselman 1973; Wein & MacLean 1983; Johnson 1992). Catastrophic fire is so frequent that classical Clementsian concepts of succession are probably not realistic (Rowe 1961; Johnson 1992). The majority of studies on boreal forest succession in North America suggest that Egler's (1954) model of 'initial floristic composition' is generally applicable. According to this model change in forest structure and composition over time is an expression of differential growth rates of tree species which have established contemporaneously after a catastrophic, stand initiating disturbance (the 'complete' Egler model, cf. Wilson et al. 1992). In east-central Québec, for example, "apparent succession is simply an expression of differential longevity and conspicuousness of species" (Cogbill 1985). Bergeron (2000) concludes that initial floristic composition and Connell and Slayter's (1977) 'tolerance' model describe succession in boreal forest ecosystems. The tolerance model suggests that subordinate species remain in a suppressed or slow-growing state in the understory until resource availability (e.g. light) increases by the removal of adjacent dominant individuals.

Although the initial floristic composition and tolerance models have gained acceptance, paradigms on boreal forest succession vary regionally across the North American biome. In western regions fire frequencies are typically short enough to destroy stands before major changes in canopy composition occur (Johnson 1992; Johnson et al. 1994; Youngblood 1995; Gutsell & Johnson 1999). Young, post-fire stands dominated by early succession 'pioneers' such

as jack pine (*Pinus banksiana* Lamb.), trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.) and paper birch (*Betula papyrifera* Marsh.) will typically burn before developing into late-succession stands dominated by balsam fir (*Abies balsamea* (L.) Mill.), white spruce (*Picea glauca* (Moench) Voss) and/or black spruce (*Picea mariana* (Mill.) BSP). Studies in the boreal, boreal montane and near-boreal forest indicate that forests burn frequently enough to leave only 5-10% of the landscape as 'old-growth' (Johnson et al. 1995; Johnson et al. 1998). At Candle Lake, SK, Dix & Swan (1971) indicate that white spruce and balsam fir establish as late succession species in established forest stands, but suggest that fire will inevitably revert forests to an earlier stage of succession.

As one travels eastward, studies indicate that young, post-fire stands will eventually become dominated by balsam fir, white spruce, black spruce and/or eastern white cedar (Boundary Waters Canoe Area, MN (Heinselman 1981); northwestern ON (Kenkel & Watson 1996), Laurentian Highlands, QB (Bergeron & Dansereau 1993); and Lake Duparquet, QB (Bergeron & Dubuc 1989; Bergeron 2000; Larocque et al. 2000)). Older stands, however, commonly tend to exhibit "deterioration and degeneration" (Cogbill 1985), becoming shrub-dominated and showing limited advanced regeneration (Dix & Swan 1971; Carleton & Maycock 1978). Fire may be required to renew these systems (Rowe 1961). Although studies demonstrate that early succession stands are developing canopies dominated by black spruce and balsam fir, authors again indicate that fire will reverse these floristic trends (Carleton & Maycock 1978; Zoladeski & Maycock 1990). In the absence of fire for long periods of time, stands at Lake Duparquet, QB (Bergeron & Dubuc 1989, Bergeron 2000) have become dominated by white spruce, balsam fir and/or eastern white cedar. However, small-scale disturbances and insect outbreaks (especially spruce budworm, *Choristoneura fumiferana* Clemens) alter 'ideal' pathways. 'Gap dynamics' are an important mechanism in the development of late-succession boreal forest, controlling the growth of understory advanced regeneration and shrubs (Kneeshaw & Bergeron 1998; Bergeron 2000; see also Chapters 4 and 5).

In RMNP, the forest succession paradigm falls between the extremes of western and eastern regions. Fire frequency, controlled largely by climate (Wein & MacLean 1983; Johnson 1992), is greater in RMNP than eastern regions which receive high annual rainfall, and is lower than the much drier western Interior Plains (Heinselman 1978). In the absence of frequent fire, gap dynamics are expected to be an important factor in the development of forests in the Park, especially along the eastern Escarpment where heavier precipitation and complex topography dramatically reduce the frequency of stand-replacing fire.



Overall, succession in the boreal forest is an extremely variable process, resulting in multiple potential pathways (Fastie 1995; McCune & Allen 1985a,b). Factors such as disturbance type, size, frequency and intensity, seed source availability and dispersal, seedbed quality, interspecific competition, edaphic and topographic variability, ungulate herbivory, granivory, insect pest and fungal pathogens, and changes in climate have profound and long-term impacts on forest dynamics (Johnson 1992; McInnes et al. 1992; Zasada et al. 1992; Greene & Johnson 1995, 1996, 1997; Cornett et al. 1998; Stewart et al. 1998; Morin 1994; Kneeshaw & Bergeron 1998; Bergeron 2000). The result is a complex mosaic of stands of different age, structure and composition on the landscape.

#### 6.1.2 Patterns of Natural Regeneration on the Landscape

Although authors in western regions of the biome have indicated that fire is frequent enough to destroy stands before understory regeneration has a chance to reach the canopy (Johnson 1992), research in central and eastern regions has indicated that canopy replacement occurs given prolonged inter-fire periods (Lieffers et al. 1996; Bergeron & Kneeshaw 1998; Bergeron 2000). In order to improve the understanding of post-fire stand dynamic processes in RMNP, patterns of natural regeneration on the landscape must be examined.

Recent literature has suggested that the fire frequency in the North American boreal forest since the end of the Little Ice Age (ca. AD 1550-1850) has decreased as a result of a wetter climate (Bergeron & Archambault 1993; Flannigan et al. 1998; Weir et al. 1999). Short-term changes in fire frequency, in comparison, are controlled by local climate, landform, and human land-use patterns (Heinselman 1978; Johnson 1992). For example, agriculture practices since the turn of the century have resulted in the removal of a continuous canopy cover in the mixedwood boreal forest of central Saskatchewan, consequently decreasing the local fire frequency (Johnson et al. 1998; Weir & Johnson 1998). In the absence of fire as a major controlling process of forest development, reduced fire frequencies may allow for understory regeneration to control canopy replacement (Johnson et al. 1994). Under these circumstances, the creation of forest gaps by wind, pathogens and other damaging agents, results in the mortality of single or multiple overstory trees, controlling stand dynamics and the development of understory regeneration (Roberts & Richardson 1985; Johnson et al. 1995; Su et al. 1996; Foré et al. 1997; Bergeron et al. 1998; Bergeron & Leduc 1998; Kneeshaw & Bergeron 1998). The regeneration of a species within a post-disturbance forest patch may occur by germination of buried seeds, rhizomes, spores, or other propagules, the dispersal of propagules into the area (i.e. colonization), and clonal

encroachment (Rydgren et al. 1998). Factors which affect the distribution and abundance of understory regeneration have not yet been examined in the Riding Mountain area.

There are numerous factors at various spatial and temporal scales that influence the dispersal, germination and subsequent establishment of tree regeneration in the boreal forest. Dispersal and germination are most influenced by the proximity of conspecific adults (i.e. seed source), primary and secondary mechanisms of seed dispersal, edaphic and seedbed conditions, stand age, competition from understory species, and seed viability and predation (Dix & Swan 1971; Johnson 1992; Kneeshaw & Burton 1997; Kneeshaw & Bergeron 1996; Lieffers et al. 1996; McLaren & Janke 1996; Galipeau et al. 1997; Morin & Laprise 1997; Cornett et al. 1998; Foré et al. 1997; Kneeshaw et al. 1998; Messier et al. 1998; Rydgren et al. 1998; Simard et al. 1998; Stewart et al. 1998). Conifer seedlings are rarely randomly distributed on the forest floor (Maguire & Forman 1983), as regeneration is commonly associated with safe microsites (Simard et al. 1998). Microsite abundance varies with stand composition (deciduous or coniferous dominated, or mixed) and successional stage (Simard et al. 1998). The distribution of understory white spruce and balsam fir, for example, is strongly influenced by the abundance of decomposing logs on the forest floor, which provide protection from herbaceous vegetation and leaf litter (Simard et al. 1998; Lieffers et al. 1996).

After dissemination and germination, the establishment and growth of understory regeneration is largely related to light and moisture availability, and damaging agents such as insect and fungal pathogens, and ungulate herbivory (Zasada et al. 1992). Light and moisture levels at the forest floor are largely regulated by canopy composition and heterogeneity, the presence or absence and size of canopy gaps, and interspecific competition (Zasada et al. 1992; Lieffers & Stadt 1994; Drobyshév & Nihlgård 2000).

The objectives of this chapter are 1) to summarize patterns of natural regeneration on the landscape for 9 dominant tree species in RMNP (trembling aspen, white spruce, balsam poplar, paper birch, balsam fir, green ash (*Fraxinus pennsylvanica* Fern), Manitoba maple (*Acer negundo* L.), American elm (*Ulmus americana* L.), bur oak (*Quercus macrocarpa* Michx.)), and 2) to use static size structures of forests to infer successional processes for each of the stand types delineated in Chapter 3. This information is used to create a holistic model of forest stand dynamics for the Park.

## 6.2 Methods

### 6.2.1 Data Collection

A total of 202 – 10 x 10 m plots were sampled between the 1996-1997 growing seasons in various forest communities throughout RMNP. Plots were sampled if there was no evidence of past logging or human disturbance, and if the vegetation and site conditions were representative of a larger area (>0.25 ha). Within each plot, a complete inventory of all vascular and non-vascular plant species was conducted. Vegetation was enumerated in 6 height classes: 1) canopy trees (>15 m); 2) subcanopy trees (10-15 m); 3) low trees and tall shrubs (2-10 m); 4) saplings and low shrubs (0.5-2 m); 5) tree seedlings, graminoids, forbs, ferns and fern allies (typically <0.5 m); and 6) bryophytes and lichens (on the forest floor). Within each plot, diameter at breast height (DBH) measurements were obtained for each tree, and density measures of all trees were recorded. Herbivore browsing intensity was measured for each tree and shrub species on an ordinal scale of 1 (absent) to 5 (heavy).

A soil pit was dug near the center of each plot to a depth of 1 m. Soil horizons were textured and identified, and their depths recorded. Soil profiles were classified according to the Canadian System of Soil Classification to Subgroup (Soil Classification Working Group 1998). Each sample was air dried and sifted with a 2 mm sieve, and analyzed for pH, electrical conductivity ( $\mu\text{S}/\text{cm}$ ), and particle size (percent sand, silt, and clay) using the Bouyoucos hydrometer method (Kalra & Maynard 1991).

Site description data includes a measure of percent bareground, percent slope, aspect (degrees from true north), and geographical (UTM) coordinates. The amount of decaying wood on the forest floor was estimated on an ordinal scale of 0 (absent) to 3 (high) for each plot. Moreover, increment cores were taken at breast height from 2-3 of the largest individuals of each tree species in each plot to obtain a minimum age of stand establishment (i.e. time since catastrophic fire). Ages of seedlings, saplings and low trees were obtained by sections at ground level. Tree cores and sections were mounted, finely sanded (using 400 grit sandpaper) and polished (using 600 grit sandpaper), and rings were counted using a dissecting microscope (Parker 1971).

## 6.2.2 Data Analysis

### *Patterns of Natural Regeneration on the Landscape*

Canonical correspondence analysis (CCA) was used to describe the distribution and abundance of understory regeneration (<10 m in height) for 9 tree species using 3 variable sets. Prior to this analysis, a total of  $n=265$  understory individuals were aged at ground level to determine general patterns in the timing of recruitment. **Fig. 6.1** demonstrates that understory recruitment continues to occur several years to decades after the establishment of the initial canopy cohort.

CCA has not been previously used in the boreal literature to examine factors influencing the distribution of understory regeneration. Commonly, stepwise multiple regressions, linear regressions and/or correlations have been used (Kneeshaw & Bergeron 1996; Gallipeau et al. 1997; Kneeshaw & Burton 1997). CCA allows for the simultaneous examination of both species and environmental datasets, and is robust with non-linear data (ter Braak 1986, 1987a). Basal areas of all seedlings (<0.5 m in height), saplings (0.5-2 m) and low trees (2-10 m) were used to describe the abundance of regeneration for each understory tree species for a total of  $n=154$  stands where regeneration was present. For the purposes of this study, all seedlings, saplings and low trees are defined as 'advanced regeneration'; regeneration which has the potential to grow into successively higher plant canopies. The first set of variables was related to stand composition, and used the total basal area of each overstory tree species (trees >10 m in height) as a measure of their abundance. The second variable set includes 9 abiotic and biotic site and seedbed conditions. These variables are the total cover of bryophytes, herbs, mountain maple (*Acer spicatum* Lam.), beaked hazelnut (*Corylus cornuta* Marsh.), other shrubs (shrubs excluding beaked hazelnut and mountain maple) and bareground, as well as an estimate of herbivore browsing intensity (on an ordinal scale of 1-5) and minimum stand age. The third variable set includes 6 edaphic factors. These are soil pH, electrical conductivity, percent sand and clay content, depth of the LFH horizon and the degrees slope of the plot. The variables degrees slope and total cover of bryophytes, herbs, hazel, mountain maple, other shrubs and bareground were log transformed as  $\log(p+1)$  for all CCA analyses to meet the assumptions of multivariate normality (ter Braak 1986, 1987a).

Stand development will ultimately depend on the propensity for tree species to disperse on the landscape by seed or vegetative propagation. These factors were examined for each of the 9 tree species in this study. Specifically, the relative propensity for a tree species to disperse on the landscape was measured by examining the proportion of stands in which regeneration of a species

was present but lacked conspecific canopy trees for a distance of at least 100 m. In addition, the relative ability of a tree species to establish beneath its own canopy was measured by examining the proportion of stands in which regeneration of a species was present beneath conspecific canopy trees.

#### *Size-Class Analysis of Tree Species (Successional Trajectories)*

For each of the 8 stand types defined in Chapter 3, the frequency of occurrence was determined for the 12 most abundant tree species in the 3 upper tree strata (canopy, >15 m; subcanopy, 10-15 m; lower trees, 2-10 m). The lowest tree stratum (saplings, <2 m) was excluded from the analysis. Since there is differential mortality of saplings, this tree stratum may not reflect the future composition of the stand type. Correspondence analysis (CANOCO; ter Braak 1987b) was used to summarize the relationships between the stand types. Successional trajectories were inferred for stand types I-VIII by connecting the 3 tree strata in the order canopy, subcanopy, lower trees. The lower canopies can be assumed to represent the future successional stages of the stand type (cf. 'size-class' ordination analysis, Carleton & Maycock 1978; Bergeron & Dubuc 1989). Short vectors indicate that interspecies association is neither strong nor does it change much during stand history (Carleton & Maycock 1978).

#### *Landscape Model of Stand Dynamics*

The above analyses were used to create a synoptic, conceptual model of forest stand dynamics for RMNP. The following information was also considered:

i) Seed source availability - The direction of forest succession is largely dependent on the proximity of seed sources. White spruce is common in the understory of trembling aspen and balsam poplar stands in western portions of the Park. However, as distance from seed-bearing white spruce increases regeneration of understory white spruce becomes increasingly limited. Succession may be limited in areas where late successional species are absent (Heinselman 1973; Cogbill 1985, McClanahan 1986).

ii) Differential mortality of understory regeneration - Authors have recognized that understory regeneration commonly shows greater rates of mortality than trees in higher canopies (Heinselman 1973, 1981; Cogbill 1985). Seedlings and saplings, therefore, do not necessarily reflect the future composition of forest stands (Bergeron & Dubuc 1989). Factors such as decreased light levels at the forest floor, interspecific competition, insect pests and fungal

pathogens, and ungulate herbivory increase the likelihood of mortality (Zasada et al. 1992), and must be incorporated into a model of forest dynamics.

iii) Disturbance - Stand structure will tend towards homogenization or diversification depending on the size, frequency and intensity of disturbance (Parish et al. 1999). Large, intense fires alter much of the patch structure within stands, homogenizing large areas of forest. In comparison, low-intensity, small-scale disturbances (e.g. wind damage) create patchiness and spatial heterogeneity within stands (Frelich & Reich 1995). The proportion of a forest canopy in gap has been found to increase with increasing time since fire (Kuuluvainen 1994; Kneeshaw & Bergeron 1998), and the spatial patterning of the forest canopy becomes increasingly entropic (Walker & Kenkel 1998). Intermittent, small-scale disturbances such as selective browsing of shrubs and saplings by ungulate herbivores can result in long-term community changes (Belovsky 1981; McLaren & Peterson 1994).

iv) Life-history characteristics - The modelling of forest dynamics requires a pluralistic approach, incorporating the life history characteristics of species in the ecosystem (Pickett et al. 1987). Species life-history characteristics determine the method by which a species arrives and persists at a site following disturbance, the ability to establish and mature in the post-disturbance community, and the time required to reach critical life-history stages (e.g. reproduction) (Noble & Slatyer 1980; Rydgren et al. 1998).

v) Interspecific competition - The majority of boreal forest succession models only consider changes in tree species composition (Kenkel & Watson 1996). However, shrub, herb and bryophyte strata strongly influence forest dynamics. Heavy seedling mortality of balsam fir during the first year is attributable to smothering by deciduous leaves (McLaren & Janke 1996). Herbaceous competition (Galipeau et al. 1996) and leaf litter from shrub and tree layers (Rowe 1955, 1956; Waldron 1966) limit the germination and development of white spruce. Heavy canopies of beaked hazelnut and mountain maple inhibit the establishment of white spruce and trembling aspen (Vincent 1965; Trottier 1981).

vi) Landform - Landform, which incorporates parent material and surficial topography, determines patterns of insolation and drainage on the landscape (Host et al. 1987). These patterns, in turn, influence soil development, species composition, community structure, and disturbance regimes (Ritchie 1956; Viereck 1983; Host et al. 1987). Landform is therefore an important determinant in the distribution and regeneration of vegetation on the landscape, influencing the

direction of forest succession (Heinselman 1973, 1981; Host et al. 1987). Sites which have similar environmental conditions, however, may not always develop similar vegetation (McCune & Allen 1985a). Large differences in vegetation in sites with similar conditions may be explained by site history (e.g. ungulate herbivory, frost, seed production and dispersal, insect pests and fungal pathogens, wind damage).

vii) Moisture and nutrient availability - Moisture and nutrient gradients are important determinants of the spatial distribution of species on the landscape (Carleton & Maycock 1978; Kenkel 1987; Zoladeski & Maycock 1990), but are not commonly incorporated into models of forest dynamics. Variation in soil moisture, nutrient status and nutrient cycling influences species composition at a site and their competitive interactions (Heinselman 1981; Pastor et al. 1987).

viii) Spatial scale - Frelich and Reich (1995) indicate that several factors limit the ability to predict the direction of boreal forest succession, including lack of spatial context, inadequate consideration of spatial scale, and inadequate knowledge of successional mechanisms. They note that many studies concentrate on processes which occur at a single spatial scale (e.g. individual tree gaps, stands, landscapes), and that few studies attempt to link processes occurring at the individual tree scale with stand and larger spatial scales. The direction of forest succession is necessarily dependent upon the scale at which the study is conducted. At large spatial scales (1-16 ha) succession appears to converge toward a mixture of species, whereas at smaller scales (0.01-0.1 ha) succession appears to diverge to monodominant stands (Frelich & Reich 1995).

## 6.3 Results

### 6.3.1 Patterns of Natural Regeneration on the Landscape

Results of the CCA indicate that the first variable set, the abundance of conspecific canopy trees (i.e. potential seed sources), was the greatest predictor of understory regeneration abundance for the 9 species examined (the ratio of constrained to unconstrained eigenvalues, or variable redundancy=54.43%) (**Fig. 6.2a**). Axis 1 and 2 separate eastern deciduous species from the boreal coniferous and deciduous species. Axis 3 separates balsam fir and paper birch from the remainder of the species.

The second variable set, which includes biotic and abiotic site conditions, is also important in describing the abundance of understory regeneration (variable redundancy=31.65%) (**Fig. 6.2b**), although not to the same extent as the abundance of parental trees. Total shrub cover (excluding

beaked hazelnut and mountain maple), total moss cover and minimum stand age were most strongly trended with axis 1, while total cover of beaked hazelnut, total herbaceous cover and the amount of decaying wood on the forest floor were most strongly trended with axis 2. Total moss and herbaceous cover are strongly trended with axis 3. The abundance of white spruce and balsam fir regeneration are associated with high total moss cover and amount of decaying wood on the forest floor, with balsam fir tending to occur in older stands. Most stands with balsam fir regeneration ( $f=0.78$ ) have decaying wood on the forest floor. Although mountain maple is found in some stands, white spruce and balsam fir are found where the abundance of beaked hazelnut and other shrub species are low. Conversely, trembling aspen and paper birch are found in younger stands with a high cover of beaked hazelnut, where total moss cover and amount of decaying wood are low. Balsam poplar regeneration is most abundant in young stands with low shrub abundance. The eastern deciduous species green ash, Manitoba maple, American elm and bur oak typically regenerate in older stands. Manitoba maple, green ash and American elm are abundant in stands with a high herbaceous cover (axis 3), whereas bur oak is common in older forest stands with a high shrub cover (excluding beaked hazelnut and mountain maple).

Edaphic variables were the least effective in describing the abundance of understory regeneration, explaining only a small proportion of the variation in seedling distribution (variable redundancy=18.13%) (**Fig. 6.2c**). The variables most highly trended with axis 1 are percent slope, clay and sand content of the mineral soil, and soil pH, while soil electrical conductivity, pH and depth of the LFH horizon are most highly trended with axis 2. Balsam fir, white spruce and balsam poplar regeneration are typically found on fine-textured soils with a thick LFH horizon. Trembling aspen and paper birch regeneration are also found on fine-textured soils, but paper birch is commonly found on steeper slopes. In comparison, the regeneration of eastern deciduous species tends to be found on more coarse-textured soils. American elm and Manitoba maple are abundant on soils with a high pH and conductivity, whereas green ash and bur oak regeneration are more common on soils with a higher sand content and lower electrical conductivity.

### 6.3.2 Ranking the Dispersal and Regeneration of Tree Species

The results of the CCA analyses indicate that the abundance of conspecific canopy trees is the greatest predictor of understory regeneration abundance. **Table 6.1** compares the relative propensity for each species to disperse and establish into stands with and without parental trees. When considering regeneration in both canopies 3 and 4, green ash and balsam fir demonstrate the highest ranking to disperse into stands that do not have conspecific parent trees ( $f=0.50$  and



0.43, respectively), whereas balsam poplar and trembling aspen demonstrate the lowest rankings ( $f=0.11$  and  $0.08$ , respectively). Interestingly, balsam fir demonstrates a high ranking for canopy 4 ( $f=0.69$ ) but not for canopy 3 ( $f=0.08$ ), since very few stands without parental trees have the presence of balsam fir in canopy 3. The eastern deciduous trees American elm, bur oak and Manitoba maple have relatively high rankings for the combined canopies 3 and 4, ( $f=0.43$ ,  $0.35$  and  $0.35$ , respectively) with white spruce and paper birch having lower rankings ( $f=0.21$  and  $0.20$ , respectively).

The eastern deciduous species Manitoba maple, bur oak and green ash have the highest rankings for the ability to establish underneath conspecific canopy trees for each of the understory canopy categories, with values of  $f=1.00$ ,  $0.95$  and  $0.82$ , respectively, for the combined canopies 3 and 4. In comparison, balsam poplar, American elm and paper birch have the lowest rankings for the combined canopies 3 and 4 ( $f=0.47$ ,  $0.47$  and  $0.39$ , respectively). Whereas both trembling aspen and balsam poplar have relatively high rankings for canopy 4 ( $f=0.40$  and  $0.37$ , respectively), these species rank lowest for canopy 3 ( $f=0.28$  and  $0.12$ , respectively).

### 6.3.3 Succession Trajectories

The initial ordination of all 8 stand types is presented in **Fig. 6.3a**. The horizontal axis is ordination axis 1 ( $\lambda_1=0.860$ ; percent inertia=26.8%) and the vertical axis is axis 2 ( $\lambda_2=0.733$ ; percent inertia=22.9%). Stand types I (Black Spruce Organic), II (Jack Pine - Black Spruce), and III (Bur Oak) are outliers. The vector for stand type I is circular and very short, suggesting that these stands will be self-replacing in the future. The species ordination dual shows that black spruce and eastern larch (*Larix laricina* (Du Roi) K. Koch) are closely associated species. Stands do not show convergence towards an association with other tree species. Stand type II has a longer vector, which converges towards black spruce. Stands will generally become dominated by black spruce, however some stands will increase in abundance of white spruce and trembling aspen. Stand type III will remain dominated by bur oak as the vector is relatively short and is distant from other species.

The trajectories for stand types IV-VIII were obscured by stand types I-III, so the analysis was reformed after removing the outliers (**Fig. 6.3b**). The horizontal axis is ordination axis 1 ( $\lambda_1=0.669$ ; percent inertia=46.9%) and the vertical axis is axis 2 ( $\lambda_2=0.391$ ; percent inertia=27.4%). The vector for stand type IV (Eastern Deciduous) is fairly short and turns in on itself, suggesting that stands will remain dominated by American elm, Manitoba maple, bur oak,

and green ash. Stand type V (Balsam Fir) has a short, circular vector centered around balsam fir. These stands will become increasingly dominated by balsam fir, while white spruce and paper birch may only have a minor role in future stand composition. Stand type VI (Trembling Aspen - Birch - Mountain Maple) has a long vector, indicating a strong change in species composition over time. There will be an increased dominance of green ash as well as other eastern deciduous species, however paper birch will also dominate locally. Trembling aspen and balsam poplar will decrease in abundance over time as the vector moves a large distance away from them in the ordination space. Stand type VII (Trembling Aspen - Balsam Poplar) has a fairly short vector indicating little compositional change over time. Stands will remain dominated by trembling aspen and balsam poplar, with a potential increase in abundance of white spruce. The vector for stand type VIII (White Spruce) is short, and begins to curve in on itself. These stands are proceeding towards a dominance of white spruce, possibly in association with paper birch and to a lesser extent balsam fir. The vector is directed away from trembling aspen and balsam poplar as they will become less abundant over time.

Stand dynamics are described below for each of the 8 stand types and their variants delineated in Chapter 3:

#### Stand Type I. Black Spruce Organic ( $n=15$ )

The floristic composition of these stands is relatively stable, suggesting that they will undergo only minor changes over time. Stands will tend to become more open and uneven-aged over time as vegetative layering of black spruce increases in abundance. Eastern larch will probably disappear from older stands.

#### Hygric ( $n=6$ )

These stands are expected to undergo very little change over time. The canopy may become more open, but regeneration of black spruce by layering will continue. Eastern larch will probably decrease in abundance over time.

#### Mesic ( $n=9$ )

These stands will become more open-canopied and uneven-aged over time. As the density of black spruce in the canopy and subcanopy layers declines over time, vegetative layering may become more abundant. Total shrub cover may increase as the canopy opens. Paper birch, balsam fir and white spruce may become established in some stands, but the rate of invasion is expected to be very low. Eastern larch is expected to become less frequent over time.

### Stand Type II. Jack Pine - Black Spruce ( $n=17$ )

Jack pine will become less abundant in the canopy over time, although a few relict jack pine may survive in the canopy for many years. In most stands, jack pine will be replaced by black spruce as it is usually the most abundant species in the lower canopy layers. In some upland stands, white spruce or trembling aspen (occasionally balsam poplar) may replace jack pine in the canopy. Stands will become more open-canopied and uneven-aged over time, and shrub cover will probably increase.

#### Mesic ( $n=10$ )

In these stands, jack pine will eventually be replaced by a monodominant canopy of black spruce. However, relict individuals of jack pine may remain in the upper canopy for many years. Stands will become more open-canopied and uneven-aged over time. Shrub cover will remain low, and feathermosses mosses will continue to dominate the understory.

#### Xeric-Mesic ( $n=7$ )

These stands will become more open-canopied and uneven-aged over time. Relict jack pine trees may persist in the canopy for many years, but stands will succeed toward mixed stands of white spruce, black spruce, trembling aspen and/or balsam poplar. Canopy openings are expected to result in increased shrub cover, and may allow for the regeneration of trembling aspen, balsam poplar and paper birch from seed or vegetative suckering.

### Stand Type III. Bur Oak ( $n=15$ )

These stands will undergo little change over time, remaining as essentially monodominant bur oak stands with the occasional green ash, white spruce, or trembling aspen. The canopy may open slightly as succession proceeds, since heavy ungulate herbivory of bur oak saplings and seedlings may limit regeneration. Shrub cover will remain high, and may increase in response to canopy openings and heavy ungulate herbivory.

#### Xeric-Mesic ( $n=6$ ).

These stands will remain uneven-aged and dominated by bur oak. The green ash saplings present in the lower tree strata may eventually reach the canopy, but will likely occur at low abundance due to extreme moisture limitation. The canopy may open up slightly as a result of heavy ungulate browsing of tree saplings and seedlings. Shrub cover will remain high.

Xeric ( $n=9$ ).

These monodominant, uneven-aged stands of bur oak will undergo little change over time. Shrub cover will remain high. The canopy may become more open over time, since heavy ungulate herbivory on bur oak saplings and seedlings may limit regeneration.

#### Stand Type IV. Eastern Deciduous ( $n=16$ )

These stands are expected to undergo little change over time, since green ash, American elm, and Manitoba maple are all regenerating well. Bur oak will remain an associated species on well-drained soils, while trembling aspen and balsam poplar will decrease in abundance. In the short term, the canopy of these stands will open somewhat as the mature individuals of American elm succumb to Dutch elm disease. Canopy openings may result in increased shrub cover, or may facilitate the establishment of more shade-intolerant species such as trembling aspen, balsam poplar, and paper birch.

Hygric-Mesic ( $n=6$ )

Strong regeneration of green ash, Manitoba maple and American elm suggest that these stands will undergo little compositional and structural change over time. Trembling aspen and balsam poplar abundance will decline as 'overmature' individuals die. Green ash and Manitoba maple will likely colonize the canopy gaps created by the loss of mature individuals of American elm to Dutch elm disease.

Mesic ( $n=9$ )

These stands are expected to undergo little structural and compositional change over time, since green ash and Manitoba maple are regenerating well. However, American elm will decline in abundance as Dutch elm disease kills mature individuals. Bur oak may become an increasingly important component of some stands. Trembling aspen is uncommon in the canopy and will decline in importance as overmature individuals die.

#### Stand Type V. Balsam Fir ( $n=18$ )

These stands will become somewhat more open and uneven-aged over time. Balsam fir will continue to dominate the canopy of these stands, since the species is abundant in all the lower tree strata. However, heavy herbivore browsing of balsam fir saplings may prevent the species from completely dominating these stands. In addition, these stands are driven by gap-dynamic processes since balsam fir is a relatively short-lived species. Forest gaps opened by the death of an individual may be colonized by a number of tree species, thus ensuring that these stands will

retain a mixed canopy composition. Trembling aspen and paper birch will probably decrease in abundance as overmature individuals die, since these species are not common in the lower canopy layers. Balsam poplar will decrease in abundance, but it may remain an important canopy associate since it is frequently encountered in the subcanopy layer. American elm will be largely extirpated from these stands as the larger trees succumb to Dutch elm disease. The relatively high shade tolerance of balsam fir saplings allows the species to regenerate prolifically and establish quickly in forest gaps. Forest gaps created by factors including natural senescence, disease and windthrow may also be invaded by the shade-tolerant tall shrub mountain maple.

#### Mesic-Hygic ( $n=5$ )

These stands are expected to undergo relatively minor changes over time, and are expected to retain a mixture of boreal and eastern deciduous elements in both the tree canopy and understory. Stands will become more open and uneven-aged, and the dominance of balsam fir is expected to increase. The abundance of green ash and white spruce will also increase in some stands, since they are often found in the subcanopy and lower tree strata. Paper birch will continue to be a minor but important component of these stands, but trembling aspen and balsam poplar are expected to decline in abundance.

#### Mesic ( $n=13$ )

The successional trajectory for these stands is toward an uneven-aged mixed canopy. Balsam fir is expected to dominate the canopy over the long term, but gap dynamics processes will ensure that it will continue to occur in mixture with balsam poplar, white spruce and/or paper birch. Canopy openings may result in an increase in shrub cover over time.

#### Stand Type VI. Trembling Aspen - Birch - Mountain Maple ( $n=22$ )

These stands will become more open and uneven-aged over time, and are expected to change in floristic composition and structure. Density and cover of trembling aspen and balsam poplar will decrease as overmature individuals die. Although these species are not abundant in the regenerating layers, they may remain in these stands by vegetative suckering. Green ash and/or paper birch will increase in abundance in these stands, since they currently form an important component of the subcanopy and lower stratal layers. Manitoba maple, American elm and/or white spruce will also enter the canopy but at lower density. Tall shrub cover (mountain maple and/or beaked hazelnut) will increase as the canopy opens, and this increased shrub cover may inhibit the regeneration of shade-intolerant tree species.

Mesic ( $n=12$ )

Succession in these stands is toward increased abundance of eastern deciduous species, particularly green ash. Trembling aspen and balsam poplar will gradually disappear from the canopy, but they may be perpetuated by vegetative suckering in canopy gaps. Green ash will increase in abundance since it is abundant in the lower canopy layers. Manitoba maple and American elm are also expected to increase in abundance, although Dutch elm disease will limit American elm colonization. Bur oak and white spruce will enter the canopy at low density and frequency. Cover of the tall shrubs mountain maple and beaked hazelnut will increase as the canopy opens.

Xeric ( $n=10$ )

These stands are succeeding toward more open, uneven-aged stands dominated by paper birch. Trembling aspen will decrease in abundance over time, as it typically occurs at low density in the subcanopy and lower tree strata. By contrast, paper birch occurs at high density in all strata below the canopy, indicating strong regeneration. Balsam poplar is infrequent and will decrease in abundance over time. White spruce will enter the canopy of some stands. Cover of the dominant shrub beaked hazelnut will increase as the canopy opens. Heavy ungulate browsing also promotes a dense shrub layer, inhibiting the establishment of shade-intolerant tree species.

#### Stand Type VII. Trembling Aspen - Balsam Poplar ( $n=46$ )

These stands will become more open and uneven-aged over time. Although the density and cover of trembling aspen and balsam poplar are expected to decline over time, these species will remain an important component of these forests through vegetative suckering. Alone or in combination, these two species are often the only tree species present in this stand type. White spruce is occasionally present in the lower canopy layers, and will eventually dominate the canopy in these situations. In some mesic stands, green ash and Manitoba maple are present in the lower canopy and are expected to eventually dominate. The tall shrub beaked hazelnut will increase in cover as the canopy opens. Ungulate browsing also promotes a dense shrub layer. A heavy cover of beaked hazelnut may inhibit the establishment and regeneration of shade-intolerant tree species such as trembling aspen and balsam poplar.

Xeric-Mesic ( $n=16$ )

These stands will become more open and uneven-aged over time. Trembling aspen and balsam poplar will decline in importance, although the presence of aspen suckers in the lower canopy layers suggest that the species will persist for many decades. However, heavy ungulate browsing

of these suckers may limit regeneration. Shrub cover will increase as the canopy opens, and succession will be toward more open 'parkland' stands. In those stands where white spruce has established in the lower canopy, succession will be toward open stands dominated by white spruce (see stand type VIII).

#### Mesic ( $n=17$ )

These stands will become more open and uneven-aged over time, although both trembling aspen and balsam poplar may persist through vegetative suckering. Heavy ungulate herbivory will limit suckering of trembling aspen and balsam poplar, while favouring the expansion of beaked hazelnut thickets. As a result, many of these stands may eventually become shrub-dominated 'parklands' of low tree cover.

#### Mesic-Hygic ( $n=13$ )

Balsam poplar and trembling aspen density will decline over time, resulting in stands that are more open and uneven-aged. However, the abundance of balsam poplar in the subcanopy layer indicates that it will remain an important component of these stands for some time. Heavy ungulate browsing may limit the propagation of trembling aspen and balsam poplar from vegetative suckers. Green ash and Manitoba maple will eventually dominate the canopy of some of these stands. Others may become shrub-dominated since heavy browsing favours the development of dense beaked hazelnut thickets.

#### Stand Type VIII. White Spruce ( $n=47$ )

These stands will continue to be dominated by white spruce, but they will become more open and multi-aged over time. Successful regeneration of white spruce in these stands is indicated by its ubiquity in the subcanopy and lower strata layers. Trembling aspen and balsam poplar will decline in abundance over time as overmature individuals lose their ability to sucker and eventually die. Paper birch and/or balsam fir are found in the subcanopy and lower strata of some stands, and will increase in abundance at these locations. Shrub cover will increase over time as the canopy opens.

#### Xeric-Mesic ( $n=12$ )

These stands will become more open and uneven-aged over time. They will become increasingly dominated by white spruce, since it currently occurs at high density in the subcanopy layer and is present in the lower strata as well. Trembling aspen will decline in abundance over time, but may persist in stands for many years since it suckers prolifically and occurs at moderate

density in the subcanopy of some stands. The tall shrub beaked hazelnut will increase in cover over time as the canopy opens.

#### Mesic ( $n=28$ )

These stands will become more open and uneven-aged over time, and will be increasingly dominated by white spruce. Trembling aspen and balsam poplar will decline in importance and will be a minor component of older stands. Paper birch will invade into gaps as the canopy opens, and is expected to increase in abundance. Shrub cover will also increase as the canopy opens.

#### Mesic-Hygric ( $n=7$ )

These stands are succeeding towards more open, uneven-aged stands of mixed composition. Trembling aspen and balsam poplar, which are infrequent in the subcanopy and lower tree strata, will decline over time. However, suckering may allow balsam poplar to persist in these stands. The high density of white spruce in the subcanopy and lower strata indicates that it will increase in abundance. Paper birch is also common in the subcanopy layer and will increase in abundance over time as the canopy opens. Balsam fir saplings are abundant in stands where it occurs in the canopy. Such stands will succeed toward balsam fir stands of mixed composition (stand type V). Shrub cover is expected to increase as the canopy opens.

### 6.3.4 Landscape Model of Stand Dynamics

A long-term synoptic model of forest succession for RMNP is presented in **Fig. 6.4**. This model is a summarization of analyses in this and previous chapters. The model excludes black spruce, jack pine, and bur oak, focusing only on the dominant forest associations of the Park.

Post-fire stands are generally dominated by early-succession hardwood species. In the absence of a seed source of later-successional tree species, post-fire stands will 'degenerate' into open-canopied, shrub-dominated systems. Most stands will become dominated by beaked hazelnut, particularly under a regime of heavy ungulate herbivory. Mountain maple occurs more locally in areas of higher soil nutrient status. In these stands, canopy tree cover is highly discontinuous, composed of scattered 'overmature' trembling aspen with the occasional white spruce, paper birch and/or balsam poplar. Alternative successional trajectories occur when a seed source of later successional tree species is present. Xeric to mesic, mesotrophic habitats succeed towards paper birch (particularly on seepage slopes) or green ash. Mesic to hygric, mesotrophic habitats show succession toward eastern deciduous forest stands dominated by American elm, green ash and Manitoba maple. In less nutrient-rich habitats, xeric to mesic sites succeed towards dominance of



white spruce, whereas more mesic to hygric sites succeed towards mixed stands dominated by balsam fir in association with white spruce, paper birch, trembling aspen and/or balsam poplar. Fire and gaps created in the forest canopy will revert stands towards earlier hardwood-dominated stages of succession.

## **6.4 Discussion**

### 6.4.1 Patterns of Natural Regeneration on the Landscape

#### *Abundance of Conspecific Canopy Trees*

In RMNP, the abundance of understory regeneration is best explained by the abundance of conspecific canopy trees. Similar results have been observed in the literature in eastern hardwood systems (Abrams 1986; McClanahan 1986) and the boreal forest (Kneeshaw & Bergeron 1996; Galipeau et al. 1997; Cornett et al. 1998; Kneeshaw & Burton 1997). Parental trees provide a proximate source of seed which can disperse and germinate in favorable surrounding microsites. Seed dispersal distances are species-specific, and will be influenced by different environmental conditions (Johnson 1992). Overstory composition can also contribute directly to seedbed characteristics such as the quality of the forest floor (e.g. light conditions, amount and types of litter, soil moisture and temperature), and indirectly such as the levels of seed predation and understory competition (Cornett et al. 1998). Forest floor quality will determine the number of potential sites available for seedling establishment (Galipeau et al. 1997; Kneeshaw & Burton 1997; Cornett et al. 1998; Messier et al. 1998; Rydgren 1998; Simard et al. 1998). The basal area of overstory species provides an indirect measure of understory conditions that directly determine the potential for advanced regeneration to establish (Greene et al. 1999).

#### *Site Conditions*

As compared to the abundance of overstory seed trees, site conditions were also able to explain a large proportion of the variation in regeneration abundance. Kneeshaw & Bergeron (1996) found similar results for boreal tree species in eastern Canada. However, the same authors suggest that the predictive value of these variables may be fairly low due to the rapid rate at which some of them change over time (e.g. cover of beaked hazelnut, mountain maple and other dominant shrub species, as well as bryophytes, herbaceous plants, bareground, and the amount of decaying wood on the forest floor), particularly as compared to the slower rates of change in seed-tree abundance or edaphic conditions. In addition, Cornett et al. (1998) suggest that many

environmental variables can fluctuate interannually (e.g. temperature, precipitation), which may influence the density of understory regeneration at different temporal and spatial scales.

The results of the CCA demonstrate that the regeneration of white spruce and balsam fir is lowest in stands with a high cover of beaked hazelnut and other abundant shrubs. The presence of a thick shrub canopy (especially beaked hazelnut) has been previously documented as inhibiting regeneration densities of understory white spruce and balsam fir (Rowe 1955; Vincent 1965; Lieffers et al. 1996; Galipeau et al. 1997; Morin & Laprise 1997; Kneeshaw & Bergeron 1996, 1998; Stewart et al. 1998). Thick herbaceous and shrub canopies in trembling aspen stands have been shown to reduce % photosynthetic photon flux density at the level of the forest floor, inhibiting conifer seedling establishment and growth (Messier et al. 1998). 'Safe sites' (sensu Harper 1977) or 'microsites' (Simard et al. 1998) are often necessary for the germination and establishment of white spruce and balsam fir. Determining what constitutes a safe site for different conifer species will improve the understanding of how the coniferous component of forests is maintained in different stands (Cornett et al. 1998). Although exposed mineral soil is a preferred germination substrate for boreal conifers (Johnson 1992; Zasada et al. 1992), both white spruce and balsam fir (Waldron 1966; Lieffers et al. 1996; McLaren & Janke 1996; Kneeshaw & Burton 1997; Simard et al. 1998) have been found to readily germinate on decaying wood and moss in undisturbed areas. The abundance of decaying wood on the forest floor is greatest in mid-successional as compared to early-successional deciduous or late-successional coniferous stands (Simard et al. 1998). Increased tree cover (up to 80%), reduced deciduous leaf litter and north-facing aspects favor balsam fir regeneration (Galipeau et al. 1997; Kneeshaw & Burton 1997; Simard et al. 1998). In eastern Canada, the formation of small gaps in mixed stands promotes the regeneration of balsam fir, whereas large, slow-forming gaps in fir-dominated forests typically become infilled with shrubs and limit the regeneration of balsam fir and white spruce (Kneeshaw & Bergeron 1996, 1998).

Trembling aspen, paper birch, and to a lesser extent balsam poplar regeneration is typically abundant in younger stands dominated by beaked hazelnut and other shrub species. These stands are also characterized by low levels of decaying wood on the forest floor and low total moss cover. Decomposition and nutrient cycling rates are more rapid in more mesic sites, especially when deciduous litter predominates (Kneeshaw & Bergeron 1996). The high levels of light transmitted through the canopy and nutrient-rich litter of shade intolerant species such as trembling aspen may allow for the development of a dense tall understory vegetation cover (Messier et al. 1998). This dense understory, in turn, may reduce light levels at the forest floor

and impede the establishment of white spruce and balsam fir (Lieffers et al. 1996; Kneeshaw & Bergeron 1996).

Hardwood forests in Ohio, USA, have been shown to demonstrate a temporally dynamic understory while the overstory remains stable (Foré et al. 1997). The same authors observed that different understory species increased or decreased in abundance based on their species characteristics (e.g. shade tolerance and ability to colonize gaps). Increased shrub cover in eastern deciduous gallery forests were found to be negatively correlated with stand basal area and total reproduction (Abrams 1986; Lorimer et al. 1994). In RMNP, Dutch elm disease (*Ophiostoma ulmi* (Buism) Nannf.) is resulting in the mortality of mature American elm trees along the Manitoba Escarpment (pers. obs.). As a result, the understory light environment of stands with senescent American elm will be altered. Whether these canopy openings will promote the development of dense shrub growth in the understory is uncertain at this time, and will require further examination. In southwestern North Dakota, green ash has been found to eventually dominate stands in which Dutch elm disease has eliminated American elm from the canopy (Girard et al. 1989).

#### *Edaphic Conditions*

Edaphic factors were the least effective at describing the abundance of understory tree regeneration in RMNP. Similar results were obtained by Kneeshaw & Bergeron (1996) in eastern Canada, who found that abiotic factors explained only a small proportion of the variation for conifer and hardwood seedling distribution. In particular, trees which reproduce vegetatively (e.g. trembling aspen) were shown to have a weak relationship to abiotic factors since regeneration is highly dependent on the presence of adult trees. In another study, soil parent material best explained the density of the initial cohort of white spruce, whereas the second cohort was best explained by distance to seed source and organic layer thickness (Galipeau et al. 1997). The distribution of eastern deciduous species have been described by edaphic and topographic factors, including soil particle size and electrical conductivity, slope and aspect (Killingbeck & Bares 1978). However, few studies have examined the distribution of understory regeneration in these communities (Foré et al. 1998).

#### 6.4.2 Ranking the Dispersal and Regeneration of Tree Species

In RMNP, tree species of both boreal and eastern deciduous affinity demonstrate different propensities to establish in stands without conspecific canopy trees (or to 'disperse' on the landscape), and to regenerate beneath their own canopy. Sexual reproduction and vegetative regeneration are important processes for the invasion, colonization and maintenance of species at a site (Zasada et al. 1992). These processes differ in the genetic composition of the resultant population, growth rates and potential for plant dispersal, which will influence the spatial and temporal distribution of species on the landscape.

All boreal forest trees germinate best on exposed mineral soil, while having differing success on duff (Johnson 1992). The recolonization of species in a burned area will depend on the extent and severity of disturbance, species composition of adjacent unburned areas, individual survivors and site conditions (Zasada et al. 1992; Galipeau et al. 1997). Trembling aspen (Peterson & Peterson 1992), balsam poplar (Zasada & Phipps 1990) and paper birch (Safford et al. 1990) may survive fire and resprout from underground vegetative organs. The most common mode of regeneration for trembling aspen and balsam poplar is vegetative regeneration in the form of clonal expansion and vegetative regrowth from roots, basal buds or stem fragments (Zasada et al. 1992). Paper birch will commonly produce basal sprouts, but this ability declines after 50 years (Zasada et al. 1992). White spruce and balsam fir, in contrast, have no alternative but to disperse seed into burned or unburned areas (Heinselman 1981).

The eastern deciduous species green ash, Manitoba maple and American elm are commonly found in eastern hardwood forests which are not frequently subject to fire (Heinselman 1978), and have a thin bark which does not confer protection from fire (Rosario 1988; Tirmenstein 1988; Coladonato 1992). Although post-disturbance colonization of stands is most frequently by seed dispersed from adjacent areas, these species will sprout from the root crown following non-lethal fires (Bey 1990; Johnson 1990; Kennedy 1990; Overton 1990). As compared to white spruce and balsam fir which produce heavy seed crops every few years, mature green ash, Manitoba maple and American elm produce heavy seed crops annually. Bur oak has a thick, fire-resistant bark at maturity, often allowing large trees to survive fire (Johnson 1990). Surviving bur oak will vigorously sprout from the root crown or sucker vegetatively (Tirmenstein 1988). Regeneration in post-disturbance stands may occur by dispersal of seed, heavy crops of which are produced every 2-3 years, although vegetative regeneration (epicormic propagation) is much more common (Tirmenstein 1988).

### *Species Dispersal*

Green ash, balsam fir and American elm demonstrate the greatest propensities to colonize stands without a proximate conspecific seed source for the combined regeneration layers (canopies 3+4). The winged samaras of green ash are wind-dispersed during the fall and winter months, the majority falling within a few hundred feet of the parent tree (Rosario 1988). Winged seeds of American elm may be wind-carried in excess of 400 m from a parent tree, or may be transported several kilometers by water (Coladonato 1992). The high ranking for balsam fir is interesting. Despite being a prolific seed producer (Frank 1990), previous studies have suggested that balsam fir has poor seed dispersal capabilities (Galipeau et al. 1997). The effectiveness of secondary dispersal mechanisms, however, has rarely been addressed in the literature. Interestingly, balsam fir is frequently found in the sapling stage (canopy 4) but infrequently in the low tree (canopy 3) stage. The absence of balsam fir in the low tree height class may be due to numerous factors, including the inherent problems of enumerating static stand structures (Johnson et al. 1994; Gutsell & Johnson 1999), intensive herbivore browse on saplings (McInnes et al. 1992; pers. obs.) or inoptimal habitat conditions (McLaren & Janke 1996; Galipeau et al. 1997; Cornett et al. 1998).

Since regeneration of trembling aspen, balsam poplar and paper birch is most commonly in the form of vegetative propagation (Zasada et al. 1992), these species demonstrate the poorest ability to colonize stands when a parental tree is not present. White spruce also has a relatively low ranking. Several authors have suggested that white spruce regeneration may be limited by a low density of microsites (Simard et al. 1998), competing understory vegetation (Kneeshaw & Bergeron 1996; Lieffers et al. 1996), and climatic factors including drought and frost (Waldron 1966; Sutton 1969) and wind speed and direction (Stewart et al. 1998). In the Interior Plains, very strong wind events tend to be much more common from the west, northwest and southwest than from the east, northeast and southeast (Stewart et al. 1998). Very little is known about the process of seed dispersal (Green & Johnson 1996). Dispersal of white spruce seed has only been studied in clearings or into clearings from neighboring stands, which differs from seed dispersal within stands (Stewart et al. 1998). Observed seed densities display an approximately negative exponential decrease with distance from the edge of an area source (Greene & Johnson 1996). However, white spruce seed released from an area source into a clearing has been found to travel distances of up to 1 km (Greene & Johnson 1995). Long distance (>250 m) seed dispersal, therefore, may be an important mechanism for the persistence of white spruce in fire-prone ecosystems (Stewart et al. 1998). The importance of secondary dispersal of seed on snow depends

on the percentage of seed crop that abscises during winter months and on the percentage of winter months that are expected to have snow cover (Zasada et al. 1992; Greene & Johnson 1997). Whereas primary dispersal is dependent upon release height, secondary dispersal is not (Greene & Johnson 1997). Long-distance dispersal of seed on snow may be possible, but may be unlikely. Notably, the majority of North American trees complete abscission by the end of October, and seeds become trapped in surface depressions or buried by subsequent snowfalls (Greene & Johnson 1995).

#### *Regeneration Beneath Conspecific Canopy Trees*

The species with the greatest propensities to germinate beneath conspecific parental trees are the eastern deciduous species Manitoba maple, bur oak and green ash. Regeneration of American elm, interestingly, is not as frequently encountered beneath its own canopy. Green ash (Kennedy 1990), American elm (Bey 1990) and especially Manitoba maple (Overton 1990) are capable of germinating on a thick horizon of deciduous leaf litter. Rapid, early root development of bur oak may confer an advantage for regeneration in areas of dense vegetation, but acorns buried by litter are susceptible to pilferage by rodents, and the newly developed seedlings are more liable to fungus and insect attack (Johnson 1990). The ability of eastern deciduous species to establish on litter will be advantageous for both the colonization of nearby stands and regeneration beneath conspecific adults. In comparison, deciduous leaf litter is not a preferred seedbed for either white spruce or balsam fir, as seedlings of these species tend to be easily smothered or subject to desiccation (Rowe 1955; Sutton 1963, 1966; McLaren & Janke 1996).

Trembling aspen and balsam poplar saplings (canopy 4) are frequently encountered beneath their own canopies. However, low trees (canopy 3) are not commonly encountered. In addition, both saplings and low trees of paper birch are infrequent. Heavy herbivory, barking and rubbing of saplings and low trees by ungulate herbivores is common throughout the Park, which may limit development of these species into higher regeneration layers (Rowe 1956; Trottier et al. 1981; McInnes et al. 1992; pers. obs.). In comparison, low trees (canopy 3) of white spruce and balsam fir are frequently found beneath conspecific adults, with saplings being more infrequent. The understory of mixed or coniferous-dominated stands may be more conducive to conifer regeneration than deciduous stands, since these stands have lower shrub cover, less deciduous leaf litter and increased moss cover. Moreover, white spruce has improved germination rates on decomposing wood of its own species, as compared to that of trembling aspen or balsam poplar, due to its greater moisture retaining capacity (Rowe 1955).

### 6.4.3 Succession Trajectories

Canopy-subcanopy relationships (Dix & Swan 1971; Cogbill 1985; Zoladeski & Maycock 1990) and size-class analysis (Carleton & Maycock 1978, 1980; Bergeron & Dubuc 1989) have previously been used to infer successional trends in the boreal forest. These methods assume that species mortality, natality and growth rates, and life-history strategies are similar. However, such assumptions may be questionable under certain circumstances (Bergeron & Dubuc 1989; Johnson et al. 1994). In particular, there may be differential growth and mortality rates of understory regeneration. Black spruce, for example, can remain in a slow-growing or 'suppressed' condition underneath a jack pine canopy until canopy opening occurs (Heinselman 1973; Cogbill 1985; Frelich & Reich 1995). Height and diameter growth of white spruce is reduced under a thick shrub or canopy layer (Lieffers et al. 1996). Suckers of trembling aspen <1 m in height are abundant in mixedwood stands, but rarely develop further (Rowe 1955, 1956). In addition, the effects of herbivory on forest development are potentially large and long-lasting. Ungulate herbivores selectively browse saplings and seedlings of trembling aspen, balsam poplar, paper birch, green ash, Manitoba maple, American elm, bur oak and balsam fir in RMNP, whereas white and black spruce are largely avoided (Rowe 1956; pers. obs.). Due to strong differential mortality in the lowest tree strata, saplings and seedlings do not necessarily reflect future successional stages. To circumvent problems associated with differential mortality (e.g. interspecific competition, selective herbivory), saplings and seedlings are commonly excluded from analyses (Cogbill 1985; Bergeron & Dubuc 1989).

Generally, short, non-directional vectors are indicative of self-regenerating stands, in which interspecies associations are neither strong nor subject to dramatic change during succession (Carleton & Maycock 1978; Rydgren et al. 1998). The successional vectors for stand types I, III-V, VII and VIII are relatively short (**Figs. 2 a,b**), suggesting that these stands will undergo little compositional change over time. Stand type I (Black Spruce Organic) is self-replacing over time. There is typically an abundant regeneration of black spruce by vegetative layering, although layering is more abundant in open, nutrient-poor stands (Viereck & Johnston 1990). Self-regenerating black spruce stands have been described by Rowe (1961) in Alberta, Ritchie (1956) in Manitoba and Zoladeski & Maycock (1990) in northwestern Ontario. Stand type III (Bur Oak) will undergo little compositional change, as there is typically an abundant regeneration of bur oak in the lower tree strata. However, heavy ungulate herbivory of saplings and seedlings may limit regeneration, resulting in a more open canopy in the future (Ritchie et al. 1998). Stand type IV (Eastern Deciduous) is characterized by an abundant regeneration of American elm, Manitoba

maple, green ash and bur oak in the lower tree strata. The successional vector moves away from trembling aspen and balsam poplar as these species are occasionally present in the canopy but are uncommon in the lower tree strata. In stand type V (Balsam Fir), balsam fir will largely replace balsam poplar, trembling aspen, white spruce and paper birch since it is the only species capable of abundant regeneration in moderate shade and does not have demanding seedbed preferences (McLaren & Janke 1996). Paper birch and to a lesser extent white spruce may remain associated species in these stands, regenerating in large gaps created by windblown balsam fir (Frelich & Reich 1995; Kneeshaw & Bergeron 1998). Mixed stands of balsam fir, white spruce and paper birch, once established, are thought to be self-perpetuating (Buell & Niering 1957; Achuff & La Roi 1977). In stand type VII (Trembling Aspen - Balsam Poplar), trembling aspen and balsam poplar can be self-perpetuating in the absence of major disturbance by vegetative suckering. However, in the absence of a seed source of white spruce stands often deteriorate, becoming open and dominated by shrubs, especially beaked hazelnut (Rowe 1955, 1956, 1961; MacLean 1960; Bailey 1968; Dix & Swan 1971; Carleton & Maycock 1978; Cogbill 1985; Zoladeski & Maycock 1990). Stands of stand type VIII (White Spruce) will continue to be dominated by white spruce as it is typically abundant below the canopy. Old stands, however, have been witnessed (pers. obs.) and described (Carleton & Maycock 1978; Cogbill 1985) as open and shrub-dominated.

Stand types II (Jack Pine - Black Spruce) and VI (Aspen - Birch - Mountain Maple) have longer, directional vectors, indicating compositional (successional) change over time. Jack pine stands begin to deteriorate at an early age, approximately 60-80 years (Rudolph & Laidley 1990), and are typically succeeded by black spruce in the absence of fire (Dix & Swan 1971; Kenkel 1986; Frelich & Reich 1995). Steady-state black spruce forests are unlikely to occur under natural short fire rotations (Bergeron & Dubuc 1989). However, reduced fire frequencies in northern Minnesota are changing even-aged post-fire stands of jack pine to uneven-aged mixed stands (Heinselman 1973; Frelich & Reich 1995). In stand type VI, trembling aspen and balsam poplar dominate the canopy as a result of post-fire sprouting from an existing rootstock. Green ash, and more occasionally American elm and Manitoba maple, are abundant in the lower tree strata, and will gradually replace trembling aspen and balsam poplar in the absence of major disturbance. In other stands of this stand type, paper birch dominates the lower tree canopies and will eventually replace trembling aspen in the canopy. The successional vector for stand type VI is therefore a 'composite' of stands of somewhat different vegetation composition. The vector tip does not completely extend to the eastern deciduous elements at the far right of axis 1 (Fig. 6.2b), since its length is limited by stands with paper birch in the lower tree strata.



Cyclical succession has been reported for boreal communities dominated by jack pine and black spruce (Ritchie 1956; Rowe 1961; Shafi & Yarranton 1973; Carleton & Maycock 1978; Zoladeski & Maycock 1990; Frelich & Reich 1995). Directional succession involving species replacement has been described in regions where post-fire communities converge towards forests dominated by white spruce, black spruce and/or balsam fir (Heinselman 1973; Bergeron & Dubuc 1989; Zoladeski & Maycock 1990; Bergeron 2000). High fire frequencies in many regions of the boreal forest typically does not allow for the development of steady-state forests (Heinselman 1973; Gutsell & Johnson 1998). Southern and eastern portions of the boreal forest have low fire frequencies which may allow for directional succession (Heinselman 1981; Bergeron & Charron 1994; Larocque et al. 2000).

At any one site, multiple or individualistic successional pathways may occur depending on disturbance history and episodic stochastic events (Fastie 1995). Recruitment of white spruce, for example, is dependent upon seed source proximity, which is in turn dependent upon the size, intensity and seasonality of past fires (Heinselman 1973; Grigal & Ohmann 1975; Bergeron & Dansereau 1993 Galipeau et al. 1997). Stand history (e.g. past frost, drought, herbivory, fire) influences vegetation dynamics, although it leaves “no direct, independent and measurable evidence on the site” (McCune & Allen 1985a).

#### 6.4.4 Landscape Model of Stand Dynamics

Post-fire stand composition is largely dependent on fire size and intensity (Johnson 1992; Bergeron 2000), propagule availability and past floristic composition (Shafi & Yarranton 1973). Post-fire stands in the Park are typically dominated by trembling aspen, balsam poplar and to a lesser extent paper birch (Dickson 1909; Dix & Swan 1971). This is indicated by the shaded box (**Fig. 6.4**). Trembling aspen is more common in sites with a lower moisture and nutrient status, whereas balsam poplar is more frequent in mesic-hygic, nutrient-rich sites. However, a continuum of composition occurs (Rowe 1956; Perala 1990; Zasada & Phipps 1990). Paper birch is characteristic of well-drained seepage slopes in the Park.

Seed source availability is an important determinant in the direction of forest succession (Heinselman 1973; Grigal & Ohmann 1975; Bergeron & Dubuc 1989; Bergeron & Dansereau 1993; Fastie 1995; Kneeshaw & Bergeron 1996; Galipeau et al. 1997). In the absence of a seed source of later-successional tree species (e.g. white spruce, balsam fir), post-fire hardwood stands 'degenerate' into open-canopied, shrub-dominated systems (vertical arrows in **Fig. 6.4**) (Rowe

1955, 1956, 1961; MacLean 1960; Bailey 1968; Dix & Swan 1971; Carleton & Maycock 1978; Cogbill 1985; Perala 1990; Zoladeski & Maycock 1990). Most stands in the Park become dominated by beaked hazelnut, particularly under heavy ungulate browsing (Rowe 1955; Trotter 1981). Mountain maple occurs more locally in areas of higher nutrient status (Vincent 1965; Galipeau et al. 1997) (**Appendix 2.12**), particularly in the east end of the Park near the base of the Manitoba Escarpment. Tree cover is highly discontinuous, composed of scattered overmature trembling aspen with the occasional white spruce, paper birch and/or balsam poplar (Bailey 1968). In the absence of disturbance, trembling aspen and balsam poplar can maintain themselves in the canopy of these stands for many years by vegetative sprouting (Perala 1990; Zasada & Phipps 1990; Bergeron & Dansereau 1993), although older stands lose their ability to sucker (Rowe 1955, 1956; Peterson & Peterson 1992).

Alternative successional trajectories occur when a seed source of later-successional tree species is present (horizontal arrows in **Fig. 6.4**). In xeric to mesic, mesotrophic habitats, succession is toward paper birch (particularly on seepage slopes) or green ash. Mesic to hygric, mesotrophic sites show succession toward eastern deciduous forest stands dominated by green ash, American elm and/or Manitoba maple. In less nutrient-rich habitats, xeric to mesic sites succeed toward dominance by white spruce, while more mesic to hygric sites succeed toward stands dominated by balsam fir. These balsam fir stands will retain a mixed canopy composition of white spruce, paper birch, trembling aspen and/or balsam poplar in the canopy (Buell & Niering 1957; Achuff & LaRoi 1977; Kneeshaw & Bergeron 1996) as they are driven by gap dynamic processes (Sprugel 1976; Bergeron & Dubuc 1989; Bergeron & Dansereau 1993; Frelich & Reich 1995).

The time required to reach later successional stages will vary, depending on seed source availability, intensity of ungulate herbivory, and the frequency, size and intensity of disturbance. Herbivory has been shown to increase the rate at which coniferous dominated systems are reached (Naiman 1988), whereas fire, windthrow and disease may revert the forest to an earlier stage of succession (Heinselman 1973; Pastor et al. 1993). The double arrows in **Fig. 6.4** indicate that transitions between forest associations may occur, and that a continuum of conditions are possible. Shrub-dominated systems may eventually become colonized by trees if seed sources become available, although fire may be necessary to renew these systems (Rowe 1961). Conversely, forests may become increasingly shrub-dominated as they mature and become more open-canopied (**Appendix 2.13**). Mature white spruce forests often show a lack of regeneration and may become open and shrub-filled (Rowe 1961; Dix & Swan 1971; Cogbill 1985). White

spruce and balsam fir are commonly found in association with paper birch, and occasionally with the eastern deciduous elements green ash, American elm and Manitoba maple.

Following fire, later-successional stands will often revert to an earlier, hardwood-dominated stage of succession (shaded box in **Fig. 6.4**) (Dix & Swan 1971; Shafi & Yarranton 1973; Heinselman 1973; Carleton & Maycock 1978; Bergeron & Charron 1994; Frelich & Reich 1995). Deciduous species have been shown to return as principal components in the post-fire cohort even when old-growth conifer stands have burned (Bergeron 2000). Trembling aspen, balsam poplar and paper birch (Oechel & Lawrence 1985; Zasada et al. 1992), as well as beaked hazelnut and mountain maple (Heinselman 1973) vigorously resprout after fire from an established rootstock. Composition of post-fire stands is usually similar to pre-fire composition (Dix & Swan 1971; Carleton & Maycock 1978; Cogbill 1985; Bergeron & Dubuc 1989; Zoladeski & Maycock 1990). In addition, gap creation in forest canopies (e.g. wind, disease, pathogens) may favor the establishment of shade-intolerant hardwood species, reverting succession to earlier stages (Pastor et al. 1988; Bergeron & Dubuc 1989; Bergeron & Dansereau 1993; Frelich & Reich 1995).

### **6.5 A Summary of Disturbance and Stand Dynamics**

The modelling of forest dynamics is a complex process, as numerous factors operate at various spatial and temporal scales. Successional trajectories for stand types in the Park do not converge towards a single self-perpetuating 'climax' community. Instead, vectors diverge, converge and remain cyclical, with multiple potential pathways recognized for each stand type. This study demonstrates that species assemblages, and the propensity for change, are governed by the cumulative and synergistic effects of climate, topography, disturbance frequency, size and intensity, edaphic conditions and the proximity of parental seed sources. These factors have resulted in a patchwork mosaic of forest stands on the landscape of varying structure, composition and seral stage.

Historical fire frequencies have played a critical role in the distribution and development of forests in the Park. As compared to western regions, the eastern uplands are cooler and have higher precipitation, resulting in fewer and less extensive fires. In addition, the dramatic relief and reticulation of stream valleys along the Cretaceous escarpment prevents the movement of fire (which spreads primarily from the south and west with prevailing winds), resulting in protected areas which burn infrequently. Mature stands of white spruce are more common at higher elevations throughout eastern regions (**Appendix 2.14**). Balsam fir is also widespread throughout

this area, but tends to be most prevalent in stands which burn very infrequently - in stream valleys traversing the escarpment (**Appendix 2.15**) and the leeward side of large bodies of water which block the spread of fire.

In contrast, the western upland of the Park is drier and hotter, which has resulted in a greater frequency of fire. Apart from large wetlands and bodies of water, the relatively flat terrain of this region provides few barriers against the spread of fire. The result is a much greater dominance of species which are well-adapted to large-scale disturbance, such as trembling aspen, balsam poplar and beaked hazelnut (**Appendix 2.16**). Life-history characteristics of these species include vegetative and clonal propagation, high establishment density, rapid growth, shade intolerance and short lifespans. Balsam fir is essentially absent from western regions of the Park as a result of recurrent catastrophic fires which eliminate parental seed sources from extensive areas.

Mid to lower slopes of the escarpment have an increased abundance of eastern deciduous species. These portions of the escarpment burn less frequently than the western upland of the Park, allowing for the expansion of species which are poorly adapted to recurrent fire. On occasion fires do burn these areas, resulting in stands with an aspen-dominated canopy cohort and an eastern deciduous understory. These stands will develop into eastern-dominated stands given long enough interfire periods (see also Chapter 4).

Gap dynamics processes are an important factor in the development of forest stands which have not burned for extended periods of time (especially stands belonging to the Bur Oak, Eastern Deciduous, Balsam Fir and White Spruce stand types). The mortality of individual canopy trees drives the development of understory vegetation and advanced regeneration (Kneeshaw & Bergeron 1998; see also Chapter 5). Large gaps facilitate the perpetuation of early succession deciduous species in old-growth mixedwood and conifer forests (Kneeshaw & Bergeron 1998). Fire suppression and the expansion of agriculture along the Park's periphery will decrease the frequency of future fires (Johnson et al. 1998; Weir & Johnson 1998), resulting in a greater proportion of old-growth stands on the landscape.

Overall, results of this study are in general agreement with studies from central and eastern regions of the boreal forest. Post-fire stands are dominated by pioneering hardwoods such as aspen, balsam poplar and paper birch (Bergeron 2000). Mid-succession stands show an increasingly greater proportion of white spruce in the canopy, whereas late-succession stands are dominated by white spruce and balsam fir and are driven by gap dynamic processes. The oldest

stands are commonly open and shrub-dominated, especially by beaked hazelnut and mountain maple (Cogbill 1985). In areas of dense shrub cover and/or areas without a proximate seed source, regeneration of white spruce and balsam fir is dramatically reduced (Vincent 1965; Kneeshaw & Bergeron 1996). Ungulate herbivores selectively browse trees and shrubs, impacting the long-term dynamics of forest systems (McInnes et al. 1992).

## **6.6 Management Considerations and Implications**

Riding Mountain National Park consists of patchwork mosaic of forest stands which are the biological legacy of a complex landscape and disturbance history. Pollen and charcoal stratigraphy have illustrated that since deglaciation species assemblages in the region have undergone consistent change in response to a continually changing climate and associated disturbance regimes. More recently, land clearance for settlement and agriculture, active fire suppression, control of wildlife populations and the introduction of non-native and invasive species have impacted forest communities since European settlement.

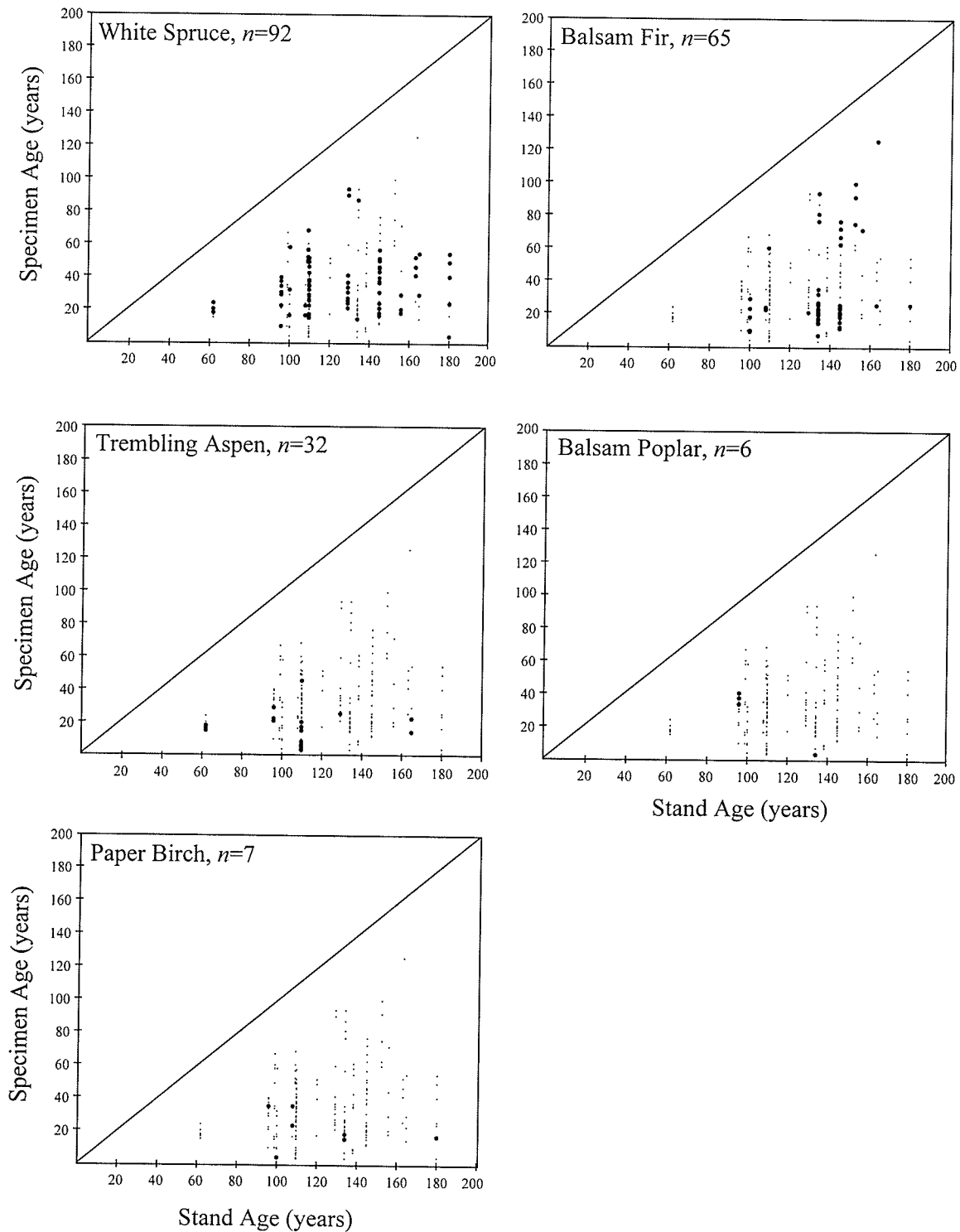
The mandate of Parks Canada is to “conserve, restore and maintain ecological integrity”, by ensuring that parks “remain areas with whole and complete biological systems, including species, landscape elements and processes” (Parks Canada 2000). The inherent complexity of biological systems would dictate that a hands-off approach to management would be appropriate. However, this may not always be the most appropriate solution given the extent to which humans have altered and manipulated these systems.

The maintenance of a biological system in its ‘natural’ state, however, is problematic. Studies have demonstrated that the fire frequency of a region is always in a state of change, correlated with changes in climatic conditions (Clark 1990; Johnson 1992; Flannigan et al. 1998; Johnson et al. 1998). The overriding importance of weather in determining fire frequency indicates that natural processes which produce landscape patterns are operating on scales much larger than the size of the management unit (Johnson et al. 1998).

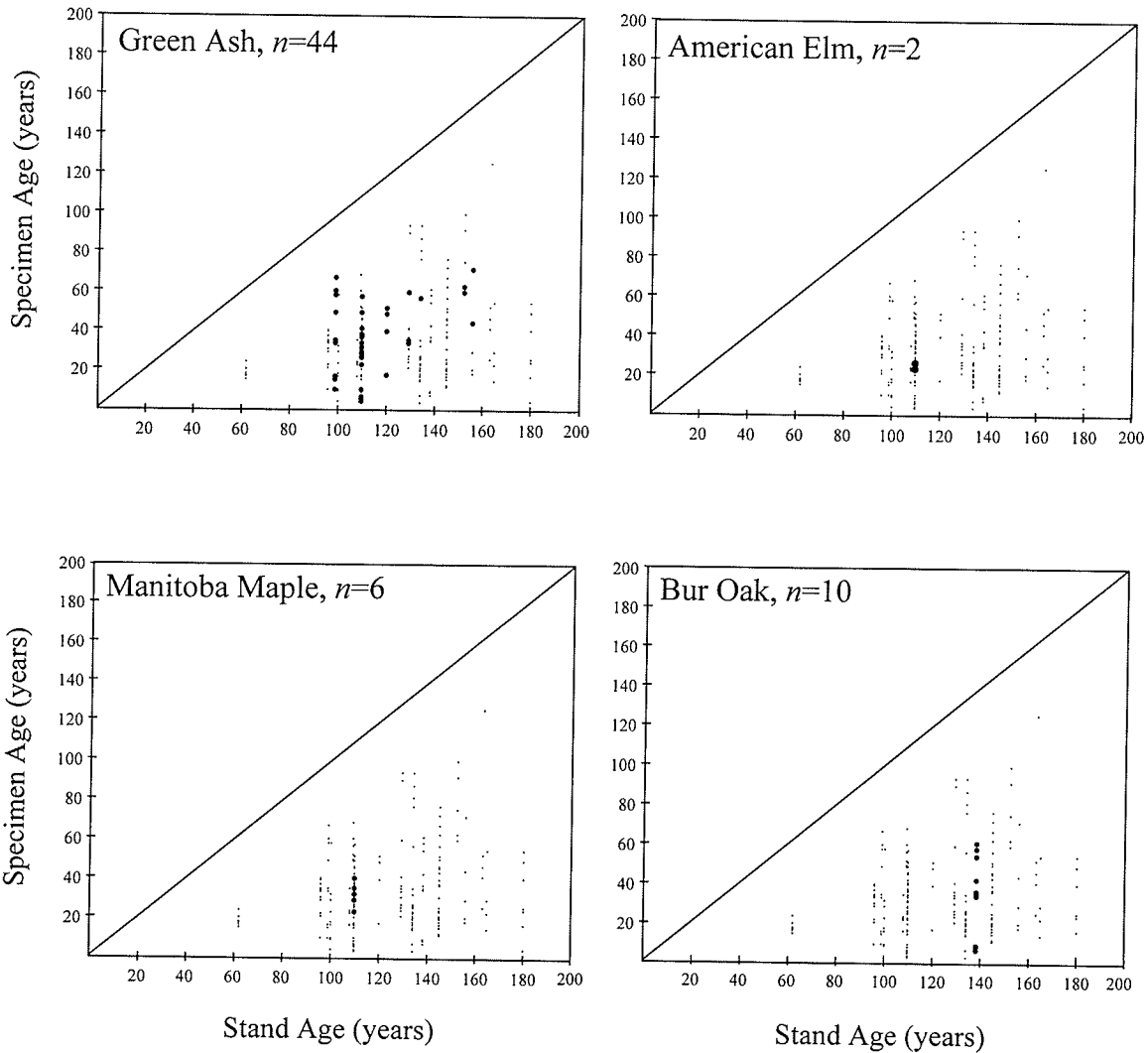
The management of ecosystems presents the hypothesis that we are able to develop a more ecologically sound basis for management by emulating the effects of natural disturbances, such as fire (Weir et al. 1999). Natural processes of disturbance are often used as ‘benchmarks’ for the establishment of a management policy (Lertzman et al. 1998). Disturbance regimes for a region are often defined as having specific spatial and temporal reference scales (e.g. region *X* has a fire

cycle of  $Y$  years). However, it is difficult to identify non-arbitrary reference scales that allow one to distinguish between the 'signal and noise' in the variability of data (Lertzman et al. 1998).

Ecosystem management must incorporate a long-term mandate, recognizing the inherent complexity of biological systems and the fact that they are in a state of continual change. Policies must be based more on scientific data and less on intuition (Johnson et al. 1998). Research is needed to better document the ways in which climate and fire influence the response of organisms with differing life-history traits, and influence other ecosystem-level processes such as predator-prey interactions, watershed dynamics and nutrient cycling. The fragmentation of the surrounding landscape by humans will influence the frequency and extent of fire, the immigration and emigration of animals, predator-prey interactions and the spread of disease. Active fire suppression, as a result of threats to infrastructure and private land, will also affect forest structure. All of these factors must be considered when developing a holistic management scenario.



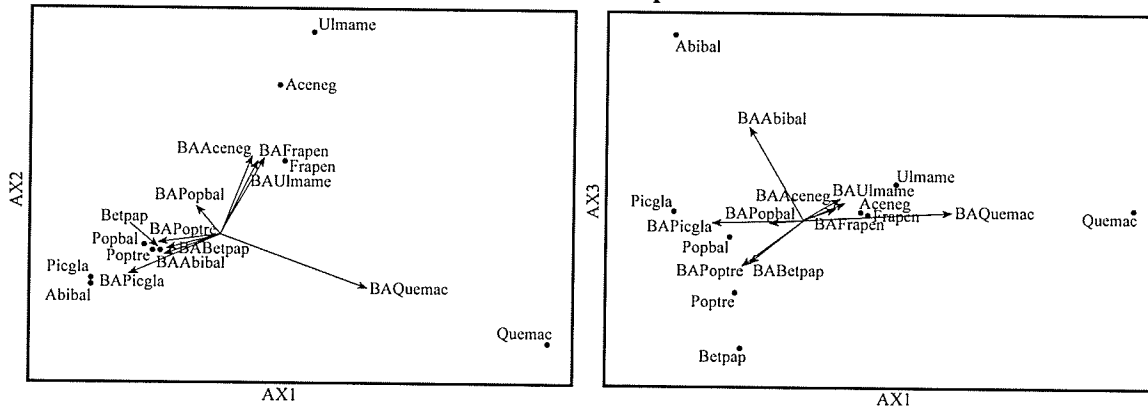
**Figure 6.1a.** Timing of recruitment for 9 dominant boreal (this page) and eastern deciduous (next page) tree species sampled throughout RMNP. Specimens below the line have established after the canopy cohort. All specimens are <10 m in height, and were aged at ground-level. Specimens belonging to each species have been separately highlighted for each illustration.



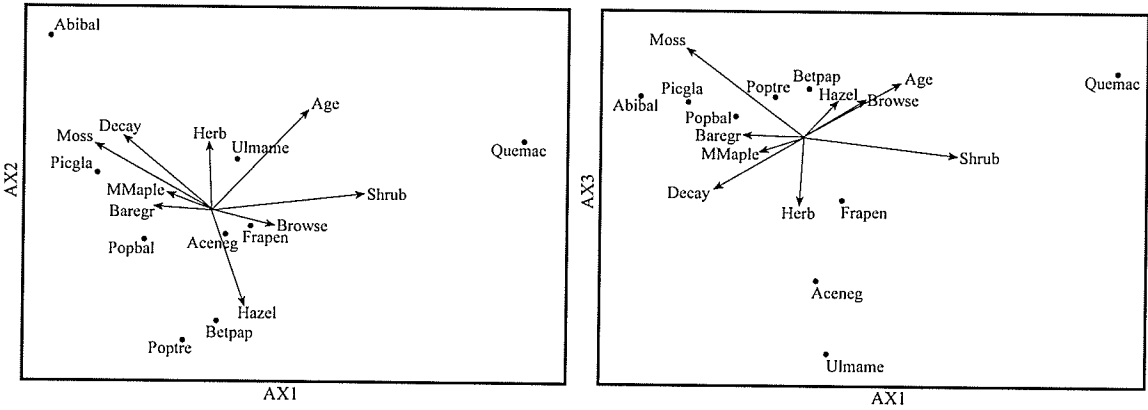
**Figure 6.1b.** Timing of recruitment for 9 dominant boreal (previous page) and eastern deciduous (this page) tree species sampled throughout RMNP. Specimens below the line have established after the canopy cohort. All specimens are <10 m in height, and were aged at ground-level. Specimens belonging to each species have been separately highlighted for each illustration.



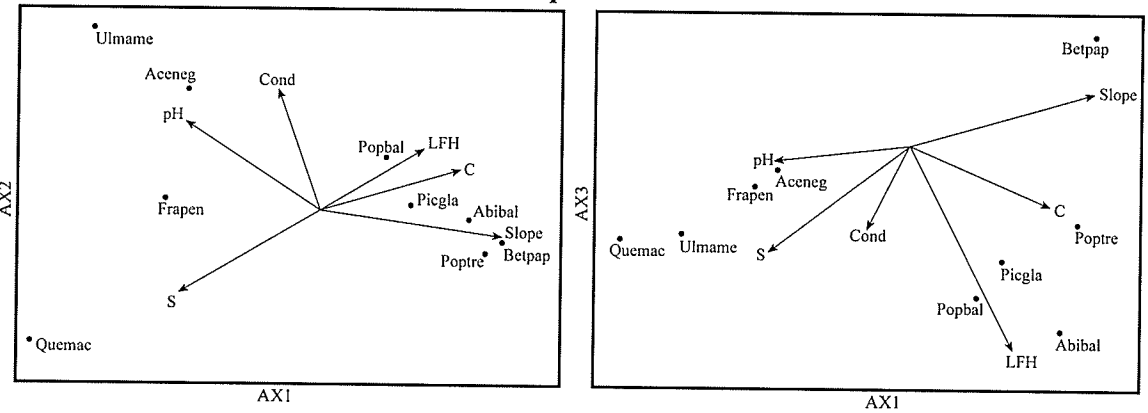
### A. Abundance of Conspecific Adult Trees



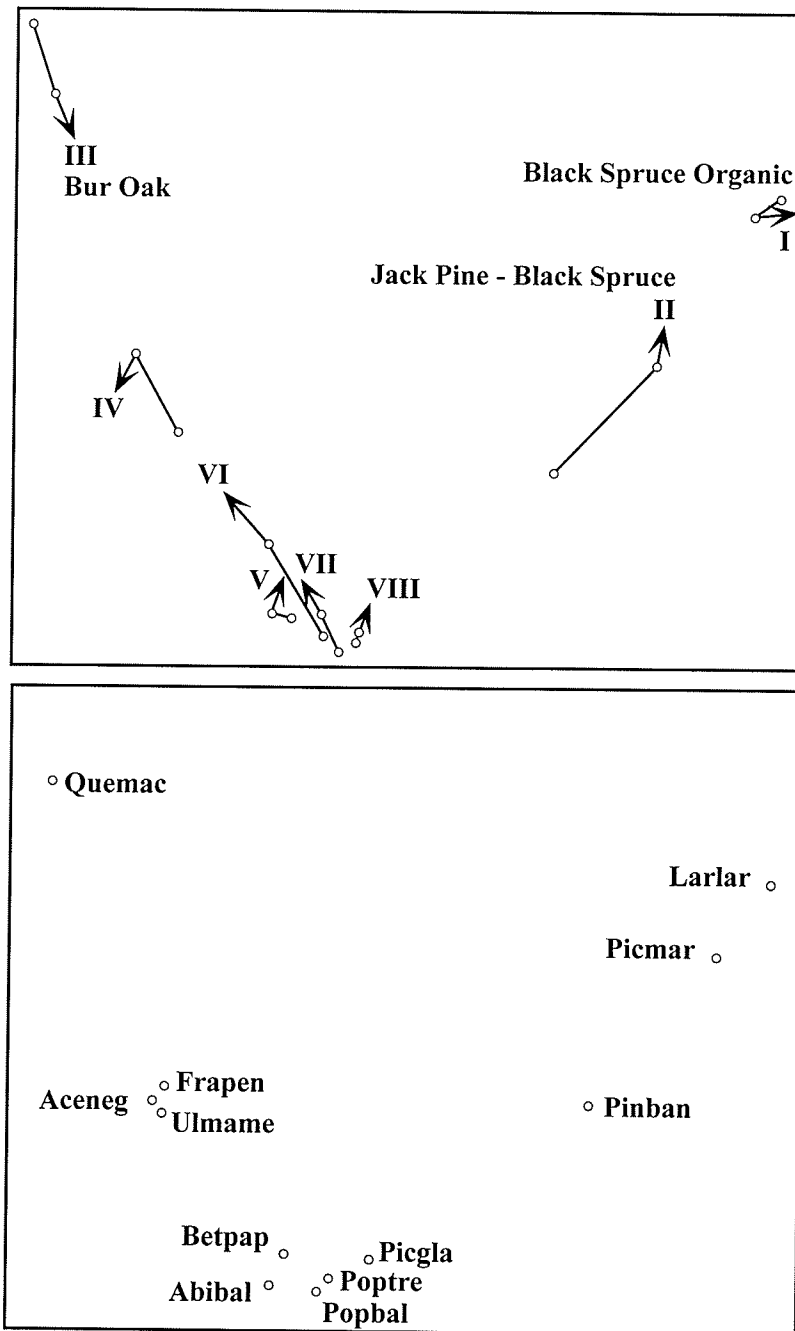
### B. Site Conditions



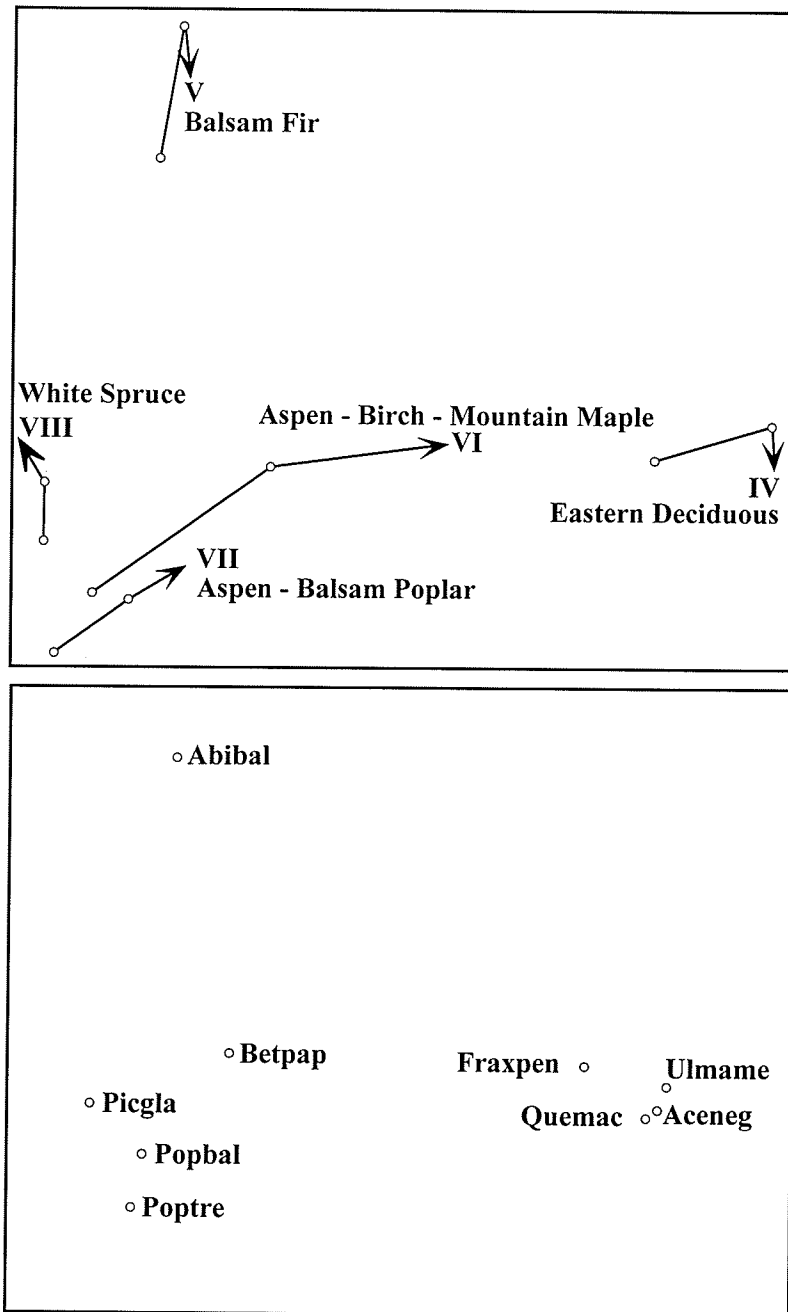
### C. Edaphic Conditions



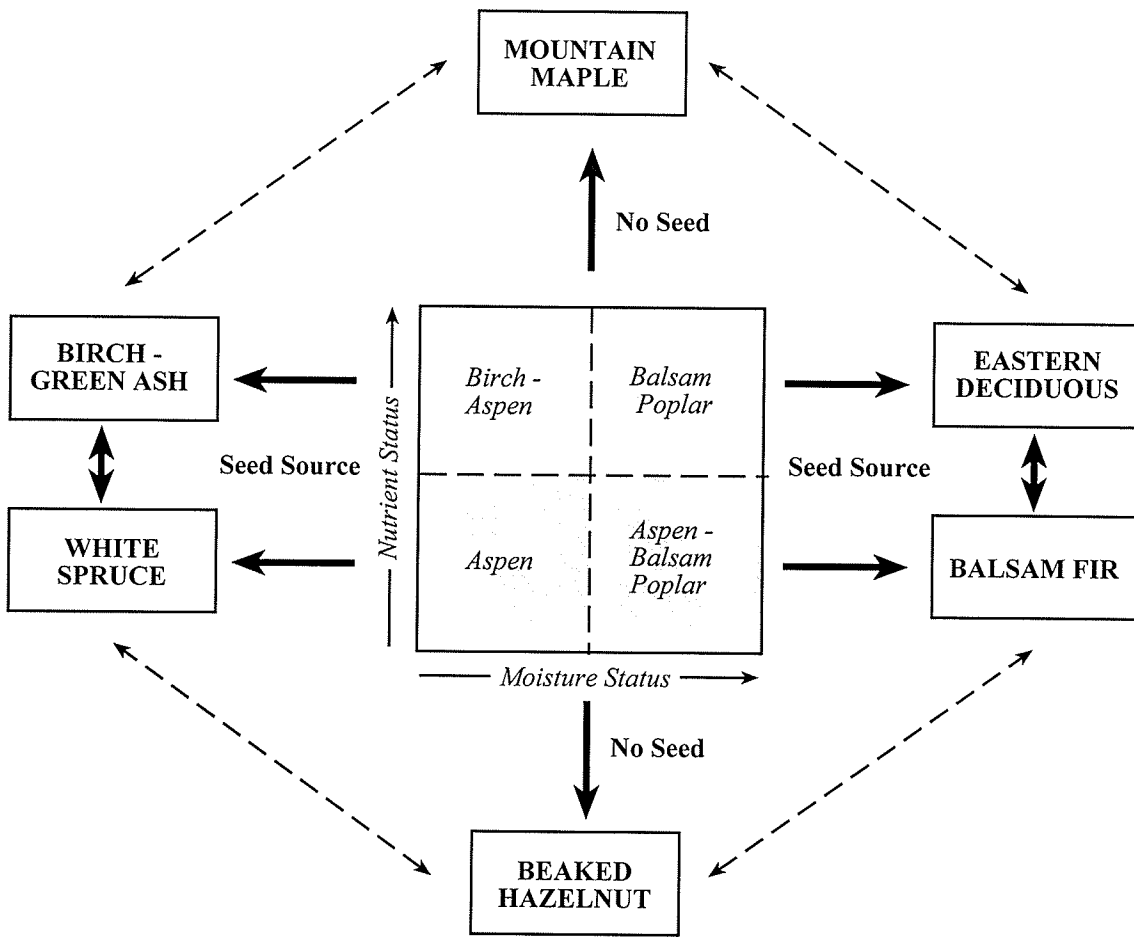
**Figure 6.2 (a-c).** Canonical correspondence analysis results for 3 variable groups and  $n=154$  stands. Groups of variables are as follows: A) the abundance of conspecific canopy trees, B) site conditions and C) edaphic conditions. Species codes: Abibal = balsam fir; Aceneg = Manitoba maple; Betpap = *Betula papyrifera* (paper birch); Frapen = *Fraxinus pennsylvanica* (green ash); Picgla = *Picea glauca* (white spruce); Popbal = *Populus balsamifera* (balsam poplar); Poptre = *Populus tremuloides* (trembling aspen); Quemac = *Quercus macrocarpa* (bur oak); Ulmane = *Ulmus americana* (American elm). Variable codes: BA = basal area; Moss = total moss cover; Decay = amount of decaying wood on forest floor; Hazel = total cover of *Corylus cornuta*; MMaple = total cover of *Acer spicatum*; Age = minimum stand age; Browse = herbivore browsing intensity; Baregr = total bareground cover; Shrub = total shrub cover excluding *Corylus cornuta* and *Acer spicatum*; S = sand content of mineral soil; C = clay content of mineral soil; LFH = depth of LFH soil horizon; Cond = soil electrical conductivity ( $\mu\text{S}$ ); pH = soil pH; Slope = percent slope.



**Figure 6.3a.** Correspondence analysis ordination of stand types I-VIII by three tree canopy strata (top) and the corresponding species ordination dual (bottom). The horizontal axis is ordination axis 1 ( $\lambda_1=0.860$ ; percent inertia=26.8%) and the vertical axis is axis 2 ( $\lambda_2=0.733$ ; percent inertia=22.9%). The endpoint of each trajectory is designated by the arrow tip. Species codes: Abibal = *Abies balsamea* (Balsam Fir); Aceneg = *Acer negundo* (Manitoba Maple); Betpap = *Betula papyrifera* (Paper Birch); Frapen = *Fraxinus pennsylvanica* (Green Ash); Larlar = *Larix laricina* (Eastern Larch); Picgla = *Picea glauca* (White Spruce); Picmar = *Picea mariana* (Black Spruce); Pinban = *Pinus banksiana* (Jack Pine); Popbal = *Populus balsamifera* (Balsam Poplar); Poptre = *Populus tremuloides* (Trembling Aspen); Quemac = *Quercus marocarpa* (Bur Oak); Ulmame = *Ulmus americana* (American Elm).



**Figure 6.3b.** Correspondence analysis (CA) ordination of stand types IV-VIII by three tree canopy strata (top) and the corresponding species ordination dual (bottom). The horizontal axis is ordination axis 1 ( $\lambda_1=0.669$ ; percent inertia=46.9%) and the vertical axis is axis 2 ( $\lambda_2=0.391$ ; percent inertia=27.4%). The endpoint of each trajectory is designated by the arrow tip. Species codes: Abibal = *Abies balsamea* (Balsam Fir); Aceneg = *Acer negundo* (Manitoba Maple); Betpap = *Betula papyrifera* (Paper Birch); Fraxpen = *Fraxinus pennsylvanica* (Green Ash); Picgla = *Picea glauca* (White Spruce); Popbal = *Populus balsamifera* (Balsam Poplar); Poptre = *Populus tremuloides* (Trembling Aspen); Quemac = *Quercus marcocarpa* (Bur Oak); Ulmame = *Ulmus americana* (American Elm).



**Figure 6.4.** A synoptic forest succession model for RMNP (excluding jack pine, black spruce and bur oak stands). Post-fire stands (shaded box) are generally dominated by early-succession hardwood species. In the absence of a seed source of later-successional tree species, post-fire stands will 'degenerate' into open-canopied, shrub dominated systems (vertical arrows). Most stands will become dominated by beaked hazelnut, particularly under heavy ungulate browsing. Mountain maple occurs more locally in areas of higher nutrient status, especially in the east end of the Park near the base of the Manitoba Escarpment. In these stands tree cover is highly discontinuous, composed of scattered 'overmature' trembling aspen with the occasional white spruce, paper birch and/or balsam poplar. Alternative successional trajectories occur when a seed source of later-successional tree species is present (horizontal arrows). Xeric to mesic, mesotrophic habitats succeed towards paper birch (particularly on seepage slopes) or green ash. Mesic to hygric, mesotrophic sites show succession toward eastern deciduous forest stands dominated by American elm, green ash and Manitoba maple. In less nutrient-rich habitats, xeric to mesic sites succeed towards dominance of white spruce, whereas more mesic to hygric sites succeed towards mixed stands dominated by balsam fir in association with white spruce, paper birch, trembling aspen and/or balsam poplar. Double arrows indicate that transition between forest associations may occur, and that a continuum of conditions are possible. Fire and gaps created in the forest canopy will revert stands towards earlier hardwood-dominated stages of succession (shaded box).

**Table 6.1.** The relative propensity for 9 boreal and eastern deciduous tree species to a) establish in sites without conspecific adult trees in the canopy, and to b) establish in sites with conspecific adult trees in the canopy.

PROPENSITY TO ESTABLISH IN STANDS WITHOUT CONSPECIFIC ADULTS			PROPENSITY TO ESTABLISH IN STANDS WITH CONSPECIFIC ADULTS		
Species	p	n	Species	p	n
<b>Canopy 3 + 4 regeneration</b>					
<i>Fraxinus pennsylvanica</i>	0.50	36	<i>Acer negundo</i>	1.00	17
<i>Abies balsamea</i>	0.43	21	<i>Quercus macrocarpa</i>	0.95	21
<i>Ulmus americana</i>	0.43	14	<i>Fraxinus pennsylvanica</i>	0.82	22
<i>Quercus macrocarpa</i>	0.35	31	<i>Picea glauca</i>	0.73	71
<i>Acer negundo</i>	0.35	26	<i>Abies balsamea</i>	0.60	20
<i>Picea glauca</i>	0.21	66	<i>Populus tremuloides</i>	0.56	103
<i>Betula papyrifera</i>	0.20	20	<i>Populus balsamifera</i>	0.47	73
<i>Populus balsamifera</i>	0.11	38	<i>Ulmus americana</i>	0.47	17
<i>Populus tremuloides</i>	0.08	63	<i>Betula papyrifera</i>	0.39	41
<b>Canopy 3 regeneration</b>					
<i>Fraxinus pennsylvanica</i>	0.48	33	<i>Quercus macrocarpa</i>	0.86	21
<i>Acer negundo</i>	0.32	19	<i>Fraxinus pennsylvanica</i>	0.77	22
<i>Ulmus americana</i>	0.27	11	<i>Acer negundo</i>	0.76	17
<i>Betula papyrifera</i>	0.17	18	<i>Picea glauca</i>	0.66	71
<i>Picea glauca</i>	0.16	56	<i>Abies balsamea</i>	0.60	20
<i>Quercus macrocarpa</i>	0.10	20	<i>Ulmus americana</i>	0.47	17
<i>Populus balsamifera</i>	0.10	10	<i>Betula papyrifera</i>	0.37	41
<i>Abies balsamea</i>	0.08	13	<i>Populus tremuloides</i>	0.28	103
<i>Populus tremuloides</i>	0.03	30	<i>Populus balsamifera</i>	0.12	73
<b>Canopy 4 regeneration</b>					
<i>Abies balsamea</i>	0.69	13	<i>Acer negundo</i>	0.76	17
<i>Fraxinus pennsylvanica</i>	0.46	24	<i>Quercus macrocarpa</i>	0.62	21
<i>Ulmus americana</i>	0.44	9	<i>Fraxinus pennsylvanica</i>	0.59	22
<i>Quercus macrocarpa</i>	0.43	23	<i>Populus tremuloides</i>	0.40	103
<i>Acer negundo</i>	0.24	17	<i>Populus balsamifera</i>	0.37	73
<i>Picea glauca</i>	0.21	33	<i>Picea glauca</i>	0.37	71
<i>Betula papyrifera</i>	0.17	6	<i>Ulmus americana</i>	0.29	17
<i>Populus balsamifera</i>	0.13	31	<i>Abies balsamea</i>	0.20	20
<i>Populus tremuloides</i>	0.09	45	<i>Betula papyrifera</i>	0.12	41

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**APPENDIX 1**

**A LIST OF ALL VASCULAR AND NON-VASCULAR  
PLANT SPECIES ENUMERATED IN RMNP**

Appendix 1.1. A List of all vascular and non-vascular plant species enumerated in RMNP during the 1996-1997 field seasons.

Plant Form	Genus	Species and Variety	Common Name
Trees	<i>Abies</i>	<i>balsamea</i>	Balsam Fir
	<i>Acer</i>	<i>negundo</i>	Manitoba Maple
	<i>Betula</i>	<i>papyrifera</i>	Paper Birch
	<i>Fraxinus</i>	<i>pennsylvanica</i> var. <i>austini</i>	Green Ash
	<i>Larix</i>	<i>laricina</i>	Eastern Larch; Tamarack
	<i>Picea</i>	<i>glauca</i>	White Spruce
	<i>Picea</i>	<i>mariana</i>	Black Spruce
	<i>Pinus</i>	<i>banksiana</i>	Jack Pine
	<i>Populus</i>	<i>deltoides</i>	Cottonwood
	<i>Populus</i>	<i>balsamifera</i>	Balsam Poplar
	<i>Populus</i>	<i>tremuloides</i>	Trembling Aspen
	<i>Quercus</i>	<i>macrocarpa</i>	Bur Oak
	<i>Ulmus</i>	<i>americana</i>	American Elm; White Elm
	Shrubs	<i>Acer</i>	<i>spicatum</i>
<i>Alnus</i>		<i>crispa</i>	Green Alder
<i>Alnus</i>		<i>rugosa</i> var. <i>americana</i>	Speckled Alder; River Alder
<i>Amelanchier</i>		<i>alnifolia</i>	Saskatoon; Serviceberry; Juneberry
<i>Arctostaphylos</i>		<i>uva-ursi</i>	Common Bearberry; Kinnikinnick
<i>Betula</i>		<i>occidentalis</i>	Water Birch; River Birch
<i>Betula</i>		<i>pumila</i> var. <i>glandulifera</i>	Swamp Birch; Dwarf Birch
<i>Celastrus</i>		<i>scandens</i>	Climbing Bittersweet
<i>Cornus</i>		<i>alternifolia</i>	Green Osier
<i>Corylus</i>		<i>cornuta</i>	Beaked Hazelnut
<i>Cornus</i>		<i>stolonifera</i>	Red-Osier Dogwood; Red Willow
<i>Crataegus</i>		<i>chrysoarpa</i>	Hawthorn
<i>Diervilla</i>		<i>lonicera</i>	Bush Honeysuckle
<i>Gaultheria</i>		<i>hispidula</i>	Creeping-Snowberry
<i>Ledum</i>		<i>groenlandicum</i>	Common Labrador Tea
<i>Lonicera</i>		<i>dioica</i> var. <i>glaucescens</i>	Twining Honeysuckle; Red Honeysuckle
<i>Oxycoccus</i>		<i>microcarpus</i>	Small Bog Cranberry
<i>Parthenocissus</i>		<i>inserta</i>	Virginia Creeper
<i>Potentilla</i>		<i>fruticosa</i>	Shrubby Cinquefoil
<i>Prunus</i>		<i>americana</i>	Wild Plum
<i>Prunus</i>		<i>nigra</i>	Canada Plum
<i>Prunus</i>		<i>pennsylvanica</i>	Pin Cherry
<i>Prunus</i>		<i>virginiana</i>	Choke Cherry
<i>Rhamnus</i>		<i>alnifolia</i>	Alder-Leaved Buckthorn
<i>Rhus</i>		<i>radicans</i> var. <i>rydbergii</i>	Poison Ivy
<i>Ribes</i>		<i>americanum</i>	Wild Black Currant
<i>Ribes</i>		<i>glandulosum</i>	Skunk Currant
<i>Ribes</i>		<i>hudsonianum</i>	Northern Black Currant
<i>Ribes</i>		<i>lacustre</i>	Black Gooseberry; Bristly Black Currant
<i>Ribes</i>		<i>oxycanthoides</i>	Northern Gooseberry
<i>Ribes</i>		<i>triste</i>	Wild Red Currant; Swamp Red Currant
<i>Rosa</i>		<i>acicularis</i>	Prickly Rose
<i>Rosa</i>		<i>woodsii</i>	Common Wild Rose
<i>Rubus</i>		<i>idaeus</i> var. <i>strigosus</i>	Wild Red Raspberry
<i>Salix</i>		<i>bebbiana</i>	Beaked Willow; Bebb's Willow
<i>Salix</i>		<i>discolor</i>	Pussy Willow
<i>Salix</i>		<i>myrtilifolia</i>	Myrtle-Leaved Willow; Low Blueberry Willow
<i>Salix</i>		<i>pseudomonticola</i>	Mountain Willow
<i>Salix</i>		spp.	Willow Species
<i>Shepherdia</i>		<i>canadensis</i>	Soapberry; Soopolallie; Canada Buffaloberry
<i>Sorbus</i>		<i>decora</i>	Western Mountain-Ash
<i>Symphoricarpos</i>		<i>albus</i>	Common Snowberry; Few-Flowered Snowberry
<i>Symphoricarpos</i>		<i>occidentalis</i>	Western Snowberry; Buckbrush
<i>Vaccinium</i>		<i>cespitosum</i>	Dwarf Bilberry; Dwarf Blueberry
<i>Vaccinium</i>		<i>myrtilloides</i>	Velvet-Leaved Blueberry; Common Blueberry
<i>Vaccinium</i>		<i>vitis-idaea</i> var. <i>minus</i>	Lingonberry; Bog Cranberry
<i>Viburnum</i>		<i>edule</i>	Low Bush-Cranberry; Squashberry; Mooseberry
<i>Viburnum</i>		<i>rafinesquianum</i>	Downy Arrowwood
<i>Viburnum</i>		<i>trilobum</i>	High Bush-Cranberry; American Bush-Cranberry; Pembina

Plant Form	Genus	Species and Variety	Common Name
Herbs	<i>Achillea</i>	<i>millefolium</i>	Common Yarrow; Milfoil
	<i>Actaea</i>	<i>rubra</i>	Red and White Baneberry
	<i>Agastache</i>	<i>foeniculum</i>	Giant Hyssop
	<i>Agrimonia</i>	<i>striata</i>	Agrimony
	<i>Alisma</i>	<i>triviale</i>	Water-Plantain
	<i>Amphicarpa</i>	<i>bracteata</i>	Hog Peanut
	<i>Anemone</i>	<i>canadensis</i>	Canada Anemone
	<i>Anemone</i>	<i>multifida</i>	Cut-Leaved Anemone
	<i>Anemone</i>	<i>quinquefolia</i> var. <i>interior</i>	Wood Anemone
	<i>Anemone</i>	<i>virginiana</i>	Thimbleweed
	<i>Apocynum</i>	<i>androsaemifolium</i>	Spreading Dogbane
	<i>Aquilegia</i>	<i>canadensis</i>	Canada Columbine; Wild Columbine
	<i>Arabis</i>	<i>drummondii</i>	Drummond's Rock Cress
	<i>Aralia</i>	<i>nudicaulis</i>	Wild Sarsaparilla
	<i>Arctium</i>	<i>minus</i>	Common Burdock
	<i>Arenaria</i>	<i>lateriflora</i>	Blunt-Leaved Sandwort
	<i>Astragalus</i>	<i>canadensis</i>	Milk-Vetch
	<i>Aster</i>	<i>ciliolatus</i>	Fringed Aster; Lindley's Aster
	<i>Aster</i>	<i>junciformis</i>	Marsh Aster; Rush Aster
	<i>Aster</i>	<i>laevis</i>	Smooth Aster
	<i>Aster</i>	<i>puniceus</i>	Purple-Stemmed Aster
	<i>Aster</i>	spp.	Aster Species
	<i>Astragalus</i>	<i>striatus</i>	Ascending Purple Milk-Vetch
	<i>Aster</i>	<i>umbellatus</i> var. <i>pubens</i>	Flat-Topped White Aster
	<i>Caltha</i>	<i>palustris</i>	Yellow Marsh-Marigold
	<i>Castilleja</i>	<i>minata</i>	Red Indian Paintbrush
	<i>Cicuta</i>	<i>maculata</i>	Water-Hemlock
	<i>Circaea</i>	<i>alpina</i>	Small Enchanter's Nightshade
	<i>Convolvulus</i>	<i>sepium</i>	Wild Morning Glory; Hedge-Bindweed
	<i>Coptis</i>	<i>trifolia</i> var. <i>groenlandica</i>	Goldthread
	<i>Corydalis</i>	<i>aurea</i>	Golden Corydalis
	<i>Cornus</i>	<i>canadensis</i>	Bunchberry
	<i>Disporum</i>	<i>trachycarpum</i>	Fairybells; Rough-Fruited Fairybells
	<i>Drosera</i>	<i>rotundifolia</i>	Round-Leaved Sundew
	<i>Epilobium</i>	<i>angustifolium</i>	Fireweed
	<i>Epilobium</i>	<i>glandulosum</i> var. <i>adenocaulon</i>	Purple-Leaved Willowherb
	<i>Epilobium</i>	<i>palustre</i>	Marsh Willowherb
	<i>Erigeron</i>	<i>philadelphicus</i>	Philadelphia Fleabane
	<i>Fragaria</i>	<i>vesca</i> var. <i>americana</i>	Woodland Strawberry
	<i>Fragaria</i>	<i>virginiana</i>	Wild Strawberry; Smooth Wild Strawberry
	<i>Galium</i>	<i>boreale</i>	Northern Bedstraw
	<i>Galeopsis</i>	<i>tetrahit</i> var. <i>bifida</i>	Hemp-Nettle
	<i>Galium</i>	<i>triflorum</i>	Sweet-Scented Bedstraw
	<i>Gentiana</i>	<i>amarella</i>	Northern Gentian; Felwort
	<i>Geum</i>	<i>aleppicum</i> var. <i>strictum</i>	Yellow Avens
	<i>Geum</i>	<i>macrophyllum</i> var. <i>perincisum</i>	Large-Leaved Avens
	<i>Geum</i>	<i>rivale</i>	Purple Avens
	<i>Goodyera</i>	<i>repens</i> var. <i>ophioides</i>	Lesser Rattlesnake-Plantain
	<i>Habenaria</i>	<i>hyperborea</i>	Northern Green Bog-Orchid; Green-Flowered Bog-Orchid
	<i>Habenaria</i>	<i>obtusata</i>	Blunt-Leaved Bog-Orchid; One-Leaved Rein-Orchid
	<i>Hedysarum</i>	<i>alpinum</i> var. <i>americanum</i>	Alpine Hedysarum; Alpine Sweet-Vetch
	<i>Heracleum</i>	<i>lanatum</i>	Cow-Parasnip
	<i>Heuchera</i>	<i>richardsonii</i>	Richardson's Alumroot
	<i>Hieracium</i>	<i>umbellatum</i>	Narrow-Leaved Hawkweed
	<i>Humulus</i>	<i>lupulus</i>	Common Hop
	<i>Lathyrus</i>	<i>ochroleucus</i>	Creamy Peavine; Cream-Colored Vetchling
	<i>Lathyrus</i>	<i>palustris</i>	Marsh Vetchling
	<i>Lathyrus</i>	<i>venosus</i> var. <i>intonsus</i>	Purple Peavine; Veined Peavine
	<i>Lilium</i>	<i>philadelphicum</i>	Western Wood Lily
	<i>Linnaea</i>	<i>borealis</i> var. <i>americana</i>	Twinflower
	<i>Listera</i>	<i>cordata</i>	Heart-Leaved Twayblade
	<i>Lysimachia</i>	<i>ciliata</i>	Fringed Loosestrife
	<i>Lysimachia</i>	<i>thyrsiflora</i>	Tufted Loosestrife
	<i>Maianthemum</i>	<i>canadense</i>	Wild Lily-of-the-Valley
	<i>Mentha</i>	<i>arvensis</i> var. <i>villosa</i>	Wild Mint
	<i>Mertensia</i>	<i>paniculata</i>	Tall Lungwort; Tall Bluebells
	<i>Mitella</i>	<i>nuda</i>	Bishop's-Cap; Common Mitrewort
	<i>Monenses</i>	<i>uniflora</i>	One-Flowered Wintergreen; Single Delight
	<i>Monotropa</i>	<i>uniflora</i>	Indian-Pipe
	<i>Orchis</i>	<i>rotundifolia</i>	Round-Leaved Orchid
	<i>Osmorhiza</i>	<i>longistylis</i>	Smooth Sweet-Cicely
	<i>Petasites</i>	<i>palmatus</i>	Palmate-Leaved Coltsfoot

Plant Form	Genus	Species and Variety	Common Name
	<i>Petasites</i>	<i>sagittatus</i>	Arrow-Leaved Coltsfoot
	<i>Petasites</i>	<i>vitifolius</i>	Vine-Leaved Coltsfoot
	<i>Phryma</i>	<i>leptostachya</i>	Lopseed
	<i>Polygonum</i>	<i>amphibium</i> var. <i>stipulaceum</i>	Water Smartweed
	<i>Potentilla</i>	<i>palustris</i>	Marsh Cinquefoil
	<i>Pyrola</i>	<i>asarifolia</i>	Common Pink Wintergreen
	<i>Pyrola</i>	<i>elliptica</i>	White Wintergreen
	<i>Pyrola</i>	<i>minor</i>	Lesser Wintergreen
	<i>Pyrola</i>	<i>secunda</i>	One-Sided Wintergreen
	<i>Pyrola</i>	spp.	Wintergreen Species
	<i>Pyrola</i>	<i>virens</i>	Green Wintergreen; Greenish-Flowered Wintergreen
	<i>Ranunculus</i>	<i>abortivus</i>	Small-Flowered Buttercup
	<i>Ranunculus</i>	<i>macounii</i>	Macoun's Buttercup
	<i>Rubus</i>	<i>chamaemorus</i>	Cloudberry; Baked-Apple Berry
	<i>Rubus</i>	<i>pubescens</i>	Dewberry; Trailing Raspberry
	<i>Rudbeckia</i>	<i>laciniata</i>	Coneflower
	<i>Sanicula</i>	<i>marilandica</i>	Snakeroot; Black Sanicle
	<i>Smilax</i>	<i>herbacea</i> var. <i>lasioneura</i>	Carrionflower
	<i>Smilacina</i>	<i>stellata</i>	Star Flowered False Solomon's-Seal
	<i>Smilacina</i>	<i>trifolia</i>	Three-Leaved False Solomon's-Seal
	<i>Solidago</i>	<i>canadensis</i>	Canada Goldenrod
	<i>Solidago</i>	<i>decumbens</i> var. <i>oreophila</i>	Mountain Goldenrod; Spike-Like Goldenrod
	<i>Solidago</i>	spp.	Goldenrod Species
	<i>Stachys</i>	<i>palustris</i> var. <i>pilosa</i>	Marsh Hedge-Nettle; Swamp Hedge-Nettle
	<i>Stellaria</i>	<i>longifolia</i>	Long-Leaved Chickweed; Long-Leaved Starwort
	<i>Taraxacum</i>	<i>officinale</i>	Common Dandelion
	<i>Thalictrum</i>	<i>dasy carpum</i>	Tall Meadow Rue
	<i>Thalictrum</i>	<i>venulosum</i>	Veiny Meadow Rue
	<i>Trientalis</i>	<i>borealis</i>	Northern Starflower
	<i>Trillium</i>	<i>cernuum</i>	Nodding Trillium
	<i>Urtica</i>	<i>dioica</i> var. <i>procera</i>	Stinging Nettle; Common Nettle
	<i>Vicia</i>	<i>americana</i>	Wild Vetch; American Vetch
	<i>Vicia</i>	<i>cracca</i>	Tufted Vetch; Canada Pea
	<i>Viola</i>	<i>adunca</i>	Early Blue Violet
	<i>Viola</i>	<i>pennsylvanica</i> var. <i>leiocarpa</i>	Smooth Yellow Violet
	<i>Viola</i>	<i>renifolia</i>	Kidney-Leaved Violet
	<i>Viola</i>	<i>rugulosa</i>	Western Canada Violet; Canada Violet
	<i>Viola</i>	spp.	Violet Species
	<i>Zizia</i>	<i>aurea</i>	Golden Alexander
<b>Graminoids</b>	<i>Agropyron</i>	spp.	Wheatgrass Species
	<i>Agropyron</i>	<i>subsecundum</i>	Awned Wheatgrass
	<i>Agropyron</i>	<i>trachycaulum</i>	Slender Wheat Grass
	<i>Bromus</i>	<i>ciliatus</i>	Fringed Brome
	<i>Bromus</i>	<i>inermis</i>	Northern Brome; Pumpelly Brome
	<i>Calamagrostis</i>	<i>canadensis</i>	Bluejoint; Marsh Reed Grass
	<i>Cinna</i>	<i>latifolia</i>	Drooping Wood-Reed; Wood Reedgrass
	<i>Elymus</i>	<i>canadensis</i>	Canada Wild Rye
	<i>Elymus</i>	<i>innovatus</i>	Hairy Wild Rye; Fuzzy-Spiked Wild Rye
	<i>Elymus</i>	spp.	Rye Species
	<i>Glyceria</i>	<i>striata</i>	Fowl Manna Grass
	<i>Grass</i>	spp.	Grass Species
	<i>Hierochloe</i>	<i>odorata</i>	Common Sweet Grass
	<i>Milium</i>	<i>effusum</i>	Millett Grass
	<i>Oryzopsis</i>	<i>asperifolia</i>	Rough-Leaved Rice Grass; White-Grained Mountain Rice Grass
	<i>Poa</i>	<i>pratensis</i>	Kentucky Bluegrass
	<i>Poa</i>	spp.	Bluegrass Species
	<i>Schizachne</i>	<i>purpurascens</i>	False Medic; Purple Oat Grass
<b>Sedges and Rushes</b>	<i>Carex</i>	<i>assiniboinensis</i>	Assiniboia Sedge
	<i>Carex</i>	<i>deweyana</i>	Dewey's Sedge
	<i>Carex</i>	<i>disperma</i>	Two-Seeded Sege; Soft-Leaved Sedge
	<i>Carex</i>	<i>gynocrates</i>	Northern Bog Sedge; Yellow Bog Sedge
	<i>Carex</i>	<i>lacustris</i>	Lakeshore Sedge
	<i>Carex</i>	<i>paupercula</i>	Bog Sedge
	<i>Carex</i>	<i>peckii</i>	Bent Sedge
	<i>Carex</i>	<i>pedunculata</i>	Peduncled Sedge
	<i>Carex</i>	<i>pennsylvanica</i>	Yellow Sedge
	<i>Carex</i>	<i>prairea</i>	Prairie Sedge
	<i>Carex</i>	spp.	Sedge Species
	<i>Carex</i>	<i>sprengellii</i>	Sprenger's Sedge
	<i>Carex</i>	<i>vaginata</i>	Sheathed Sedge
	<i>Juncus</i>	<i>balticus</i>	Baltic Rush
	<i>Luzula</i>	<i>acuminata</i>	Woodrush

Plant Form	Genus	Species and Variety	Common Name
Ferns	<i>Athyrium</i>	<i>filix-femina</i> var. <i>michauxii</i>	Lady Fern
	<i>Botrychium</i>	<i>virginianum</i>	Virginia Grape Fern; Rattlesnake Fern
	<i>Dryopteris</i>	<i>cristata</i>	Crested Shield Fern
	<i>Dryopteris</i>	<i>spinulosa</i>	Spinulose Shield Fern; Spiny Wood Fern
	<i>Gymnocarpium</i>	<i>dryopteris</i>	Oak Fern
	<i>Matteuccia</i>	<i>struthiopteris</i> var. <i>pennsylvanica</i>	Ostrich Fern
Fern-Allies	<i>Equisetum</i>	<i>arvense</i>	Common Horsetail
	<i>Equisetum</i>	<i>fluviatile</i>	Swamp Horsetail
	<i>Equisetum</i>	<i>hyemale</i> var. <i>affine</i>	Common Scouring-Rush
	<i>Equisetum</i>	<i>pratense</i>	Meadow Horsetail
	<i>Equisetum</i>	<i>scirpoides</i>	Dwarf Scouring-Rush
	<i>Equisetum</i>	<i>sylvaticum</i>	Woodland Horsetail; Wood Horsetail
	<i>Lycopodium</i>	<i>annotinum</i>	Stiff Club-Moss
<i>Lycopodium</i>	<i>complanatum</i>	Ground-Cedar	
Bryophytes	<i>Amblystegium</i>	<i>serpens</i>	Amblystegium
	<i>Anomodon</i>	<i>minor</i>	Anomodon
	<i>Aulacomnium</i>	<i>palustre</i>	Tufted Moss; Glow Moss; Ribbed Bog Moss
	<i>Brachythecium</i>	<i>acuminatum</i>	Brachythecium
	<i>Brachythecium</i>	<i>oxycladon</i>	Brachythecium
	<i>Brachythecium</i>	<i>populeum</i>	Brachythecium
	<i>Brachythecium</i>	<i>salebrosum</i>	Golden Ragged Moss; Smooth-Stalked Yellow Feather Moss
	<i>Brachythecium</i>	spp.	Brachythecium Species
	<i>Brachythecium</i>	<i>velutinum</i>	Velvet Feather Moss
	<i>Bryum</i>	<i>caespiticium</i>	Bryum
	<i>Bryum</i>	<i>pseudotriquetrum</i>	Tall Clustered Thread Moss
	<i>Callicladium</i>	<i>haldanianum</i>	Shiny-Leaf Moss
	<i>Calliergon</i>	<i>richardsonii</i>	Richardson's Water Moss; Golden Spoon Moss
	<i>Calliergon</i>	<i>stramineum</i>	Straw-Coloured Water Moss; Straw-Like Feather Moss
	<i>Campylium</i>	<i>chrysophyllum</i>	Campylium
	<i>Campylium</i>	<i>hispidulum</i>	False Willow Moss
	<i>Cinclidium</i>	<i>stygium</i>	Common Northern Lantern Moss
	<i>Climacium</i>	<i>dendroides</i>	Common Tree Moss
	<i>Ctenidium</i>	<i>molluscum</i>	Ctenidium
	<i>Dicranum</i>	<i>flagellare</i>	Whip Fork Moss
	<i>Dicranum</i>	<i>fuscescens</i>	Curly Heron's-Bill Moss; Dusty Fork Moss
	<i>Dicranum</i>	<i>polysetum</i>	Electric Eels; Wavy Dicranum
	<i>Dicranum</i>	<i>scoparium</i>	Broom Moss
	<i>Dicranum</i>	spp.	Broom Mosses
	<i>Drepanocladus</i>	<i>uncinatus</i>	Sickle Moss; Hook Moss
	<i>Entodon</i>	<i>seductrix</i>	Entodon
	<i>Eurhynchium</i>	<i>pulchellum</i>	Common Beaked Moss
	<i>Haplocladium</i>	<i>microphyllum</i>	Haplocladium
	<i>Helodium</i>	<i>blandowii</i>	Blandow's Feather Moss
	<i>Hylocomium</i>	<i>splendens</i>	Stair-Step Moss
	<i>Hypnum</i>	<i>impotens</i>	Hypnum
	<i>Hypnum</i>	<i>lindbergii</i>	Clay Pigtail Moss
	<i>Hypnum</i>	<i>pallenscens</i>	Stump Pigtail Moss
	<i>Jamesoniella</i>	<i>autumnalis</i>	Jameson's Liverwort
	<i>Lepidozia</i>	<i>reptans</i>	Little Hands Liverwort
	<i>Leskea</i>	<i>gracilescens</i>	Leskea
	<i>Lophozia</i>	<i>ventricosa</i>	Leafy Liverwort
	<i>Mnium</i>	<i>affine</i>	Marsh Magnificent Moss
	<i>Mnium</i>	<i>cuspidatum</i>	Woodsy Leafy Moss; Woodsy Mnium
	<i>Mnium</i>	<i>drummondii</i>	Drummond's Leafy Moss
	<i>Mnium</i>	<i>longirostrum</i>	Mnium
	<i>Mnium</i>	<i>medium</i>	Common Leafy Moss
	<i>Mnium</i>	<i>punctatum</i>	Mnium
	<i>Mnium</i>	<i>spinulosum</i>	Red-Mouthed Mnium
	<i>Mnium</i>	spp.	Mnium Species
	Moss	spp.	Moss Species
	<i>Oncophorus</i>	<i>wahlenbergii</i>	Mountain Curved-Back Moss
	<i>Orthotrichum</i>	<i>obtusifolium</i>	Blunt-Leaved Bristle Moss
	<i>Orthotrichum</i>	<i>speciosum</i> var. <i>elegans</i>	Showy Bristle Moss
	<i>Platydictya</i>	spp.	Platydictya species
<i>Platydictya</i>	<i>subtile</i>	Platydictya	
<i>Pleurozium</i>	<i>schreberi</i>	Big Red Stem; Red-Stemmed Feathermoss	
<i>Pohlia</i>	<i>nutans</i>	Copper Wire Moss; Nodding Pohlia	
<i>Polytrichum</i>	<i>commune</i>	Common Hair Cap	
<i>Polytrichum</i>	<i>juniperinum</i>	Juniper Hair-Cap; Juniper Moss	
<i>Polytrichum</i>	<i>strictum</i>	Slender Hair-Cap; Bog Hair Cap	
<i>Ptilium</i>	<i>crista-castrensis</i>	Knight's Plume	
<i>Ptilidium</i>	<i>pulcherrimum</i>	Naugehyde Liverwort	
<i>Pylaisiella</i>	<i>polyantha</i>	Stocking Moss; Aspen Moss	

Plant Form	Genus	Species and Variety	Common Name
	<i>Rhodobryum</i>	<i>ontariense</i>	Rhodobryum
	<i>Rhytidiadelphus</i>	<i>triquetrus</i>	Shaggy Moss; Electrified Cat's Tail Moss
	<i>Sphagnum</i>	<i>fuscum</i>	Rusty Peat Moss; Common Brown Sphagnum
	<i>Sphagnum</i>	<i>magellanicum</i>	Midway Peat Moss
	<i>Sphagnum</i>	<i>recurvum</i>	Poor Fen Peat Moss; Yellow-Green Peat Moss
	<i>Sphagnum</i>	<i>warnstorffii</i>	Warnstorff's Peat Moss
	<i>Splachnum</i>	<i>luteum</i>	Yellow Collar Moss; Fairy Parasols
	<i>Tetraphis</i>	<i>pellucida</i>	Common Four-Tooth Moss
	<i>Thuidium</i>	<i>delicatulum</i>	Common Fern Moss
	<i>Thuidium</i>	<i>recognitum</i>	Hook-Leaf Fern Moss
	<i>Tomenthypnum</i>	<i>nitens</i>	Golden Fuzzy Fen Moss; Golden Moss
<b>Lichens</b>	<i>Cladonia</i>	<i>chlorophaea</i>	False Pixie-Cup
	<i>Cladonia</i>	<i>coniocraea</i>	Tiny Toothpick Cladonia; Awl-Shaped Stump Lichen
	<i>Cladonia</i>	<i>gracilis</i>	Brown-Foot Cladonia; Slender Cup Lichen
	<i>Cladonia</i>	<i>rangiferina</i>	Grey Reindeer Lichen; True Reindeer Lichen
	<i>Cladonia</i>	spp.	Club Lichen Species
	<i>Lichen</i>	spp.	Lichen Species
	<i>Peltigera</i>	<i>aphthosa</i>	Freckle Pelt; Studded Leather Lichen
	<i>Peltigera</i>	<i>canina</i>	Dog Pelt; Dog Ear
	<i>Peltigera</i>	<i>elisabethae</i>	Dog Pelt Lichen
	<i>Peltigera</i>	<i>neckeri</i>	Dog Pelt Lichen
	<i>Peltigera</i>	<i>neopolydactyla</i>	Frog Pelt; Finger Felt Lichen
	<i>Peltigera</i>	<i>scabrosa</i>	Rough Pelt
	<i>Peltigera</i>	spp.	Dog Pelt Lichen Species



**APPENDIX 2**

**SELECTED PHOTOGRAPHS OF FIELD OBSERVATIONS**



**Appendix 2.1.** (Top) A hygric, open-canopied black spruce stand south of Moon Lake. Ground cover is dominated by *Pleurozium schreberi* and *Sphagnum* species. Vegetative reproduction by layering is common.

**Appendix 2.2.** (Bottom) An old jack pine stand along Tea Creek, north of Whirlpool Lake. Jack pine are falling from the canopy, and will be replaced by black spruce which is abundant in all tree strata beneath the canopy. Ground cover is dominated by the pleurocarpous bryophytes *Hylocomium splendens* and *Pleurozium schreberi*.



**Appendix 2.3.** (Top) An open-canopied monodominant stand of bur oak along the Manitoba Escarpment escarpment (the North Escarpment trail system). The understory is dominated by a heavily browsed cover of beaked hazelnut. Bur oak seedlings and saplings are abundant but are heavily browsed by ungulate herbivores.

**Appendix 2.4.** (Bottom) An eastern deciduous forest at the base of the Manitoba Escarpment near the Henderson pickup. American elm, green ash and Manitoba maple dominate the canopy, and regeneration of these species is abundant in the lower tree strata. The herbaceous stratum is dominated by a continuous cover of the clonal fern *Matteucia struthiopteris*.



**Appendix 2.5.** (Top) A balsam fir stand south of Scott's Creek at the base of the Manitoba Escarpment. There are several windblown balsam fir in the area, commonly as a result of trunk rot at an early age. A large, decaying bole of *Populus* spp. is present in the foreground, and other fallen trees have created numerous canopy openings throughout the area. Shrub cover is low.

**Appendix 2.6.** (Bottom) A stand situated near the base of the Manitoba Escarpment along Kelwood trail system. The stand is characterized by a senescing post-fire canopy cohort of trembling aspen, and a predominantly eastern deciduous understory. The understory is dominated by the tall shrub mountain maple and an abundance of green ash (visible as dark trunks in the photo), Manitoba maple and American elm regeneration. Trembling aspen regeneration is not abundant.



**Appendix 2.7.** (Top) A monodominant stand of paper birch on a steep, north-facing portion of the J.E.T. trail system along the Manitoba Escarpment. Shrub cover is heavy and is dominated by beaked hazelnut. Paper birch regeneration is abundant.

**Appendix 2.8.** (Bottom) A typical system dominated by beaked hazelnut along the upper portions of the Manitoba Escarpment. Remnant paper birch, trembling aspen and white spruce are visible in these old stands. Tree regeneration is extremely limited as a result of the dense shrub cover and heavy ungulate herbivory.





**Appendix 2.9.** (Top) Heavy ungulate herbivory on beaked hazelnut along the South Escarpment trail system, near Muskrat Lake. Note the proliferation of secondary branches.

**Appendix 2.10.** (Bottom) A relatively young 'mixedwood' stand of trembling aspen and white spruce in the western region of the Park. The subcanopy of white spruce has established contemporaneously with the post-fire canopy cohort of trembling aspen, and will remain in a slow-growing condition until canopy opening occurs. Cover of beaked hazelnut in these stands is relatively low.



**Appendix 2.11.** (Top) An old stand of white spruce along the Strathclair trail system. The canopy is very open and the understory is dominated by a moderate-heavy cover of beaked hazelnut. Paper birch has established in the understory.

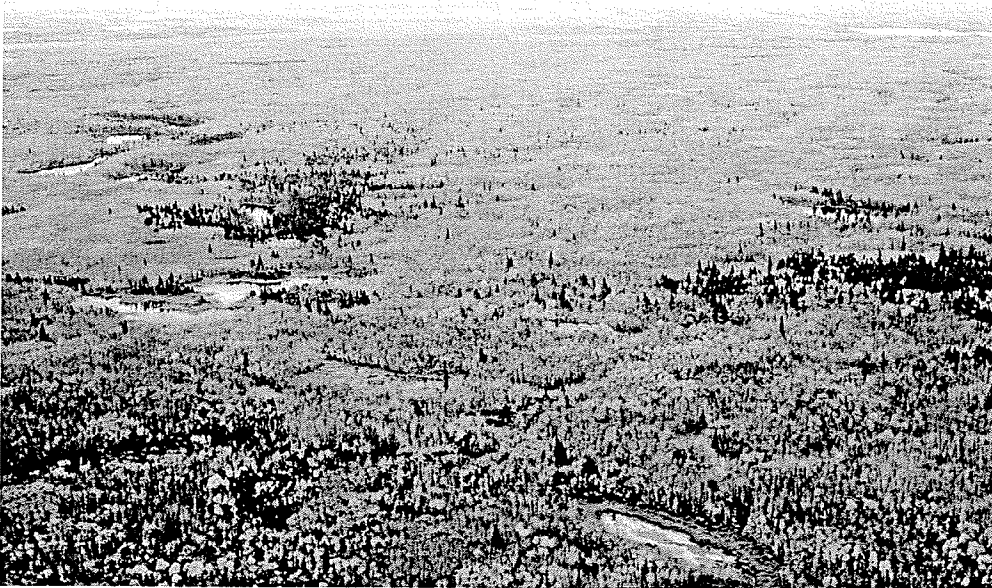
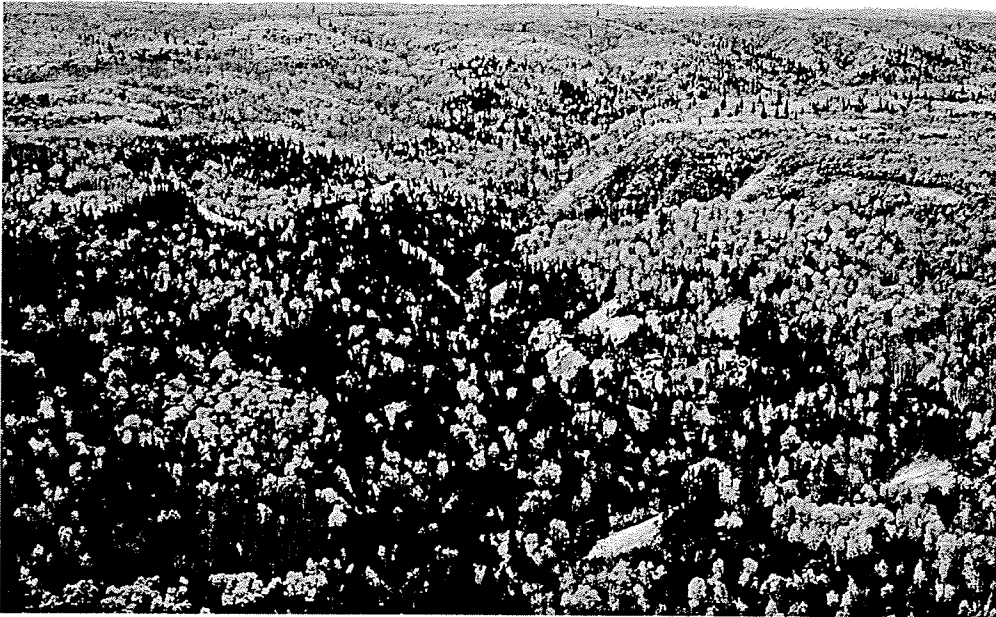
**Appendix 2.12.** (Bottom) A stand dominated by the tall understory shrub mountain maple. This stand is located along the Manitoba Escarpment and has a remnant canopy of trembling aspen. Regeneration trembling aspen is not abundant, and no seed sources of white spruce and balsam fir are present in the area.



**Appendix 2.13.** (Top) An old stand of white spruce and trembling aspen along the Manitoba Escarpment. The canopy is very open, with an understory dominated by beaked hazelnut. Regeneration of trembling aspen and white spruce is not abundant. Ungulate herbivory is heavy.

**Appendix 2.14.** (Bottom) An aerial photograph of the eastern upland of the Park. This region is relatively old, and is dominated by white spruce, trembling aspen and balsam poplar.





**Appendix 2.15.** (Top) An aerial photograph of the Manitoba Escarpment south of the Norgate road. Communities of balsam fir, white spruce and paper birch commonly occur in localized areas that are well-protected from fire, such as north-facing slopes along stream valleys traversing the Escarpment.

**Appendix 2.16.** (Bottom) An aerial photograph of the western upland of the Park. The Park boundary (defined by the beginning of agricultural clearance) can be seen in the distance. This region is relatively young, and is dominated by a canopy of trembling aspen and balsam poplar. White spruce is not as abundant, occurring in localized pockets and in the understory of stands.