

**THE IMPACT OF CATTLE GRAZING ON ASPEN REGENERATION ON  
CROWN LANDS IN WESTERN MANITOBA**

by

Jeffrey Charles Renton

A Thesis submitted to the Faculty of Graduate Studies, The University of Manitoba In  
Partial Fulfillment of the requirements for the degree of

**MASTER OF SCIENCE**

Department of Biological Sciences, University of Manitoba, Winnipeg, Manitoba

**COPYRIGHT © 2010 BY JEFFREY CHARLES RENTON**

## TABLE OF CONTENTS

### TABLE OF FIGURES IV

### LIST OF TABLES V

### ACKNOWLEDGEMENTS VI

### ABSTRACT 1

### GENERAL INTRODUCTION 3

<i>Objectives</i> .....	5
-------------------------	---

### CHAPTER 1 - LITERATURE REVIEW 6

1.1. INTRODUCTION.....	6
1.1.1. <i>Aspen Range and Distribution</i> .....	6
1.1.2. <i>Life History of Aspen</i> .....	6
1.1.3. <i>Hormone Control in Regeneration</i> .....	9
1.1.4. <i>Common Stressors</i> .....	10
1.1.5. <i>Grazing and Aspen Regeneration</i> .....	13
1.1.6. <i>Forest Harvesting and Regeneration</i> .....	15
1.1.7. <i>Grazing and Timber Removal on the Same Land Base</i> .....	17
1.2. STATISTICAL ANALYSES .....	17
1.2.1. <i>Measures of Diversity</i> .....	17
Alpha Diversity.....	18
Species Evenness .....	19
1.2.2. <i>Indicator Species Analysis</i> .....	21
1.2.3. <i>Mantel's Test</i> .....	21
1.2.4. <i>Rarefaction</i> .....	22
1.2.5. <i>Ordination</i> .....	23

### CHAPTER 2 - THE INFLUENCE OF CATTLE GRAZING ON ASPEN

#### REGENERATION AND HEALTH 25

2.1. INTRODUCTION.....	25
2.1.1. <i>Objectives</i> .....	27
2.2. METHODS.....	28
2.2.1. <i>Study area and site selection</i> .....	28
2.2.2. <i>Plot Establishment</i> .....	29
2.2.3. <i>Tree Regeneration</i> .....	30
2.2.4. <i>Health Indices</i> .....	31
2.2.5. <i>Soil Compaction</i> .....	32
2.2.6. <i>Soil Characteristics</i> .....	35
2.2.7. <i>Coarse Woody Debris</i> .....	36

2.3. DATA ANALYSIS .....	<b>36</b>
2.3.1. <i>Tree Regeneration</i> .....	36
<i>Comparison with other Regeneration Studies</i> .....	37
2.3.2. <i>Tree Health</i> .....	37
2.3.3. <i>Soil Moisture Correction</i> .....	38
2.3.4. <i>Multivariate Analysis</i> .....	38
2.4. RESULTS .....	<b>40</b>
2.4.1. <i>Tree Regeneration</i> .....	40
2.4.2. <i>Comparison with other Regeneration Studies</i> .....	42
2.4.3. <i>Tree Health</i> .....	42
2.4.4. <i>Soil Variables</i> .....	46
2.4.5 <i>Principle Components Analysis (PCA)</i> .....	47
2.4.6. <i>Redundancy Analysis (RDA)</i> .....	48
2.5.7. <i>Partial RDA</i> .....	49
2.5. DISCUSSION.....	<b>65</b>
2.5.1. <i>Tree Density</i> .....	65
2.5.2. <i>Tree Health</i> .....	67
2.5.3. <i>Environmental Variables</i> .....	68
2.5.4. <i>Conclusion</i> .....	70

### **CHAPTER 3 - GRAZING EFFECTS ON ASPEN UNDERSTORY   71**

3.1. INTRODUCTION.....	<b>71</b>
3.1.1. <i>Aspen Harvest and Agricultural Land</i> .....	72
3.1.2. <i>Objectives</i> .....	73
3.2. METHODS.....	<b>73</b>
3.2.1 <i>Study Area and Site Selection</i> .....	73
3.2.2. <i>Data collection</i> .....	73
<i>Plant Species Diversity</i> .....	73
3.2.3. <i>Grazing Pressure</i> .....	75
3.2.4. <i>Soil Compaction</i> .....	75
3.2.5. <i>Soil Characteristics</i> .....	75
3.2.6 <i>Coarse Woody Debris</i> .....	75
3.3. DATA ANALYSIS.....	<b>76</b>
3.3.1. <i>Plant Species Diversity</i> .....	76
<i>Diversity Indices</i> .....	76
<i>Indicator Species Analysis</i> .....	76
<i>Rarefaction Analysis</i> .....	77
<i>Cluster Analysis</i> .....	78
<i>Site Proximity</i> .....	78
3.3.2. <i>Soil Moisture Correction</i> .....	79
<i>Reference section 2.3.3</i> .....	79
3.3.3. <i>Multivariate Analysis</i> .....	79
3.4. RESULTS.....	<b>80</b>
3.4.1. <i>Diversity Indices and Rarefaction</i> .....	80
3.4.2. <i>Cluster Analysis and Mantel's Test</i> .....	81
3.4.3. <i>Indicator Species Analysis</i> .....	82
3.4.4. <i>Principle Components Analysis</i> .....	83
3.4.5. <i>Redundancy Analysis</i> .....	84
3.5. DISCUSSION.....	<b>103</b>
3.5.1. <i>Effects of Grazing and Harvest Year</i> .....	103
3.5.2. <i>Site Factors</i> .....	105
3.5.3. <i>Conclusion</i> .....	106

**CHAPTER 4 - SYNOPSIS 107**

<i>4.1. ASPEN DENSITY AND HEIGHT</i> .....	107
<i>4.2. TREE HEALTH</i> .....	108
<i>4.3. ASPEN REGENERATION AND THE SOIL ENVIRONMENT</i> .....	109
<i>4.4. GRAZING AND THE ASPEN UNDERSTORY</i> .....	109
<i>4.5. CONCLUSION</i> .....	110

**LITERATURE CITED 111****APPENDIX 126**

## List of Figures

Figure 1-1: Distribution of the Aspen-Parkland region (shaded in grey) in the western Prairie Provinces of Canada (Davis 2009). .....	7
Figure 2-1: Distribution of study sites in the Duck Mountain area (Davis 2009). .....	30
Figure 2-2: Boxplots of total stems $\text{ha}^{-1}$ of all commercial tree species (aspen, balsam poplar, and white birch) .....	51
Figure 2-3: Boxplots of stems $\text{ha}^{-1}$ of all commercial tree species (aspen, balsam poplar, and white birch). .....	52
Figure 2-4: Boxplots of total stems $\text{ha}^{-1}$ of aspen within each treatment. ....	54
Figure 2-5: Boxplots of stems $\text{ha}^{-1}$ of aspen of each height class within each treatment. ....	55
Figure 2-6: A comparison of stand density of aspen stems amongst naturally regenerating clear-cut stands from multiple studies, and the grazed and ungrazed stands from this study. ....	56
Figure 2-7: Scatter plot of crown dieback (%) and stem density (stems $\text{ha}^{-1}$ ) of aspen in all plots. ....	59
Figure 2-8: Total stem density for each tree species observed – PCA Ordination diagram. .	60
Figure 2-9: Individual height classes of all tree species observed – PCA Ordination diagram. ....	61
Figure 2-10: Total stem density for each tree species observed – RDA Ordination diagram. ....	62
Figure 2-11: Individual height classes of all tree species observed – RDA Ordination diagram. ....	63
Figure 3-1: Species accumulation curves of all species in the first eight sites sampled .....	75
Figure 3-2: Rarefaction curve of the number of herbaceous species found in grazed and ungrazed sites. ....	87
Figure 3-3: Rarefaction curve of the number of herbaceous species found in each stand age. ....	88
Figure 3-4: Rarefaction curve of the number of shrub species found in grazed and ungrazed sites. ....	89
Figure 3-5: Rarefaction curve of the number of shrub species found in each year-class treatment. ....	90
Figure 3-6: Ward method dendrogram of each site using herbaceous species data. ....	93
Figure 3-7: Distribution of study sites in the Duck Mountain area (Davis 2009). ....	94
Figure 3-8: Correlogram of Mantel's Test, relating species composition data to inter-site geographical distances. ....	95
Figure 3-9: Ward method dendrogram of each site using shrub species data. ....	96
Figure 3-10: Herbaceous species observed amongst all sites – PCA Ordination diagram. ....	99
Figure 3-11: Shrub species observed amongst all sites – PCA Ordination diagram. ....	100
Figure 3-12: Herbaceous species observed amongst all sites – RDA Ordination diagram. ....	101
Figure 3-13: Shrub species observed amongst all sites – RDA Ordination diagram .....	102

## List of Tables

Table 2-1: Definitions of tree health indices for aspen and balsam poplar .....	34
Table 2-2: Coding and definition of pest types noted on health trees. ....	35
Table 2-3: Contrast table of mean stem densities (stems ha <sup>-1</sup> ) and standard deviations (in brackets) for all commercial species (aspen, balsam poplar, and white birch) between grazing treatments within each age class.....	50
Table 2-4: Contrast table of mean stem densities (stems ha <sup>-1</sup> ) and standard deviations (in brackets) for aspen between grazing treatments within each age class. ....	53
Table 2-5: Mean health indices and standard deviations (in brackets) for aspen. Values with different letters indicate significant differences (Mann-Whitney U test, $P \leq 0.1$ ). ....	57
Table 2-6: Mean health indices and standard deviations (in brackets) for balsam poplar. Values with different letters indicate significant differences (Mann-Whitney U test, $P \leq 0.1$ ). ....	57
Table 2-7: Mean pest indices and standard deviations (in brackets) for aspen. Values with different letters indicate significant differences (Mann-Whitney U test, $P \leq 0.1$ ). ....	58
Table 2-8: Mean pest indices and standard deviations (in brackets) for balsam poplar. Values with different letters indicate significant differences (Mann-Whitney U test, $P \leq 0.1$ ). ..	58
Table 2-9: Results of RDA partial ordination of stem totals. ....	64
Table 2-10: Results of RDA partial ordination of pseudospecies. ....	64
Table 3-1: Mean alpha diversity indices and standard deviations (in brackets) for herbaceous species (n = 3 for all treatments).....	86
Table 3-2: Mean alpha diversity indices and standard deviations (in brackets) for shrub species (n = 3 for all treatments).....	86
Table 3-3: Jaccard's Similarity Matrix (% Similarity) for herbs for all sites. Similarity ranges from 0-1, 0 being completely dissimilar and 1 being completely similar.....	91
Table 3-4: Jaccard's Similarity Matrix (% Similarity) of shrubs for all sites. Similarity ranges from 0-1, 0 being completely dissimilar and 1 being completely similar.....	92
Table 3-5: Herbaceous indicator species by grazing treatment. ....	97
Table 3-6: Herbaceous indicator species by year class. ....	97
Table 3-7: Herbaceous indicator species by grazing and stand age combinations.....	98
Table 3-8: Shrub indicator species by grazing treatment. ....	98
Table 3-9: Shrub indicator species by year class.....	98

## Acknowledgements

Wow, it is hard to believe that I have finally finished this degree. This has been more than just a project; it has been a life altering journey. Along the way I have met and worked with some wonderful people that have provided me with invaluable guidance.

To my supervisors Andrew Park and Richard Westwood, I would like to thank you for all of the help you have provided over the years. I feel that your assistance not only helped me complete this project, but become a better scientist. With all of your valuable advice over the years I no longer see the world as a mess I have to make sense of, but rather it is composed of many paths that I can navigate.

Thanks for my sponsors, NSERC, Manitoba Agriculture, Manitoba Hydro, Louisiana Pacific Canada Limited for providing funding for this project.

I would also like to thank my committee members Brian Amiro and John Markham for their assistance, your advice over the years has been extremely helpful and I appreciate it.

Thanks for Jeff Babb for his statistical help in the data analysis portion of my project. Both Richard Staniforth and Karen Jones provided great assistance in identifying the great many plants I brought back from my field seasons.

This project would not have happened without my crack team of field researchers; Lyndsay Goldstein, Tim Davis, Kristen Adair, Foster Karcha, Alana Westwood, Stephanie Janz, Pam Godin, Amanda Dumont, and the others who worked on my project before my time. They were worked very hard and seldom complained, although Foster argued way too much.

During the field and off-season Paul LeBlanc from Louisiana Pacific and Robert Fleming from Manitoba Agriculture assisted me greatly with all aspects of this project.

Furthermore, to all of the leaseholders allowed me to sample on their leased land, I greatly appreciate all of the assistance and kindness that you showed my field assistants and I.

During the field season my assistants and I stayed at a lodge on Wellman Lake, which was operated by two of the most wonderful people that I have ever met, Blaine and Judy Hart welcomed us with open arms and made everyone feel as if at home.

I would also like to thank the relatives of the deer I hit with a van for not seeking out revenge. It was a complete accident.

To everyone in the office that has tolerated me over the years, advised me, and kept my spirits up, I would like to thank you. This includes Candice Grant, Rob Au, Jaimee Dupont, Keri LaFrance, Tim Davis, Sarah Kuleza, Susanne Kames and the many others.

Lastly, to the woman who has been with me every step of the way, in the field, in the lab, and at home, thank you so much for accompanying me. Thanks for enduring my infamous and grueling humor. Thanks for always being there Jenny.



## Abstract

In North America there has been an increasing appreciation for the value of trembling aspen (*Populus tremuloides* Michx.) as a source of timber. Moreover, trembling aspen stands and the understory vegetation that they support also provide valuable forage for livestock and wildlife. Timber harvesting and cattle grazing are often done on the same area of land in western Manitoba, though not simultaneously. The purpose of this project is to summarize the effects cattle grazing has on regeneration numbers and forest health in post-harvest aspen stands in the Aspen Parkland of western Manitoba.

Stem density, tree health, and understory diversity were compared in nine grazed and nine ungrazed sites spread across a 10 year harvesting chronosequence. Experimental design consisted of three stand age classes (2-3 years, 5-8 years and 9-11 years-old), of either grazed or ungrazed harvested aspen stands. Environmental data were collected to establish supplementary correlates of species performance, and account for inter-site differences among species and site conditions. These variables included soil compaction, soil texture, soil drainage class and an index of grazing pressure.

Commercial stems density was significantly lower in grazed than ungrazed stands ( $P < 0.1$ ); although grazing did not reduce overall stem density of trembling aspen ( $P > 0.1$ ). Ungrazed 9-11 year-old stands had a greater significantly density of trembling aspen stems, and in particular, those  $> 4\text{m}$  tall ( $P < 0.1$ ). Tree health appeared to have no biologically significant differences between grazed and ungrazed treatments within any stand age. Presence of grazing did not significantly influence alpha diversity for either herbaceous or shrub species. Herbaceous species composition was found to vary as a function of distance between sites, stand age, and presence/absence of grazing according to one of the beta

diversity indices. Analysis of shrubs species diversity revealed few trends, which may be a function of their greater tolerance of disturbance and a lower level of shrub species richness in the area. Based on these results, it appears that cattle grazing and forestry are compatible on the same land base.

## General Introduction

Since 1995 there has been an increased exploitation of forested rangelands containing trembling aspen (*Populus tremuloides* Michx., hereafter referred to as aspen) by the forest industry in western Manitoba. Mature and developing aspen stands provide valuable forage for livestock, elk, and deer, and are a source of timber for the manufacture of oriented strand board (OSB) and pulp (Hilton and Bailey 1974, Bailey *et al.* 1990, Peterson and Peterson 1992, Beck and Peek 2005). Increased timber harvesting on leased agricultural crown lands in Manitoba raises the prospect of user conflicts because there is currently limited planning to effectively integrate livestock grazing and timber extraction on the same land base.

Louisiana Pacific Canada Limited (LP) opened an OSB mill in Minitonas, Manitoba in 1995 to exploit underused aspen fibre in the region. Louisiana Pacific harvests aspen from Forest Management License 3 (FML 3, licensed to LP) and the southern portion of FML 2 (licensed to Tolko Industries Ltd). In addition to aspen, LP also harvests balsam poplar (*Populus balsamifera* L.), white birch, (*Betula papyrifera* Marsh.) and tamarack, (*Larix laricina* Du Roi). Forest Management License 3 covers a total of 6.3 million ha., of which 33% is crown forest, 22% agricultural crown land, and 45% privately owned land (Donnelly 2003). Forest Management License 3 is also used extensively for the production of oil seed and cereal crops, as well as cattle ranching and other livestock enterprises.

Louisiana Pacific obtains fibre from both crown agricultural and forestry coded land parcels in western Manitoba. A considerable amount of LP's harvesting occurs on agricultural crown land where livestock grazing occurs. Although livestock grazing is generally not permitted on forestry coded crown land, it is common for local agricultural

crown land leaseholders to graze livestock on freshly harvested stands due to their open nature and high levels of palatable forage in the regenerating understory. Louisiana Pacific foresters, forestry staff at Manitoba Conservation and agronomists at Manitoba Agriculture are concerned that the presence of cattle in recently harvested areas may have a negative influence on the regenerative capacity of aspen. They are particularly concerned that grazed stands will fail to reach provincial silvicultural stocking standards for deciduous and mixed wood stands. Moreover, it is suspected that some crown land leaseholders may be exceeding the recommended carrying capacity for cattle in grazed, leased agricultural parcels (K. Broughton LP, 2006 – personal communication).

Approximately 22% of the land area in FML 3 that has been included in the annual allowable harvest calculations for LP by the Manitoba Government is on agricultural crown land (Donnelly 2003). In a situation where the allowable developmental limit on a land parcel has been exceeded as a result of timber harvest, the forestry company must ensure that there is a forest regeneration plan in place for that particular area. The regeneration plan must ensure that the harvested stand reaches provincial stocking guidelines within seven years post-harvest (Manitoba Conservation 2001, Crown Land Classification Committee 2004). Failure to meet these guidelines by the forestry company may result in penalties. In the past LP may have employed a lower harvesting quota on leased agricultural crown land that is likely be grazed after harvest to i) avoid penalties and ii) attempt to ensure the stability of future wood supply. These measures may result in a lower volume of timber being available for harvest by LP than actually forecast by Forestry Branch of Manitoba Conservation.

### *Objectives*

The purpose of this study was to investigate the impact of livestock grazing on post-harvest aspen regeneration on agricultural crown lands. There were four objectives addressed within this study: 1) Assess the impact of cattle grazing on stem density of aspen and other commercial tree species across a chronosequence of harvests, 2) Characterize the relationship of tree health indicators and presence of pests with cattle grazing in harvested areas, 3) Assess impact of cattle grazing on the diversity and composition of herb and shrub communities in a chronosequence of timber harvests, and 4) Investigate the influence of local site factors (i.e., soil variables) on the density of commercial tree species and understory plant communities.

This thesis is divided into four chapters. There are two research chapters included in this thesis; the first chapter is primarily concerned with tree regeneration density and health, and how it is influenced by cattle presence and the surrounding environment. Stem density and health are compared between grazed and ungrazed stands among similar stand ages to assess the compatibility of cattle foraging and forestry activities on the same land base. The second research chapter explores the effect of cattle grazing and local environmental factors on the understory community within harvested aspen stands. Differences in the understory species composition and diversity in response to treatment (time since harvest and presence of cattle), environmental factors and inter-site distance are analyzed in depth within this chapter. This thesis also includes a general literature review that sets the context of the study, and a general conclusion at the end of the document.

## **Chapter 1 - Literature Review**

### **1.1. Introduction**

#### *1.1.1. Aspen Range and Distribution*

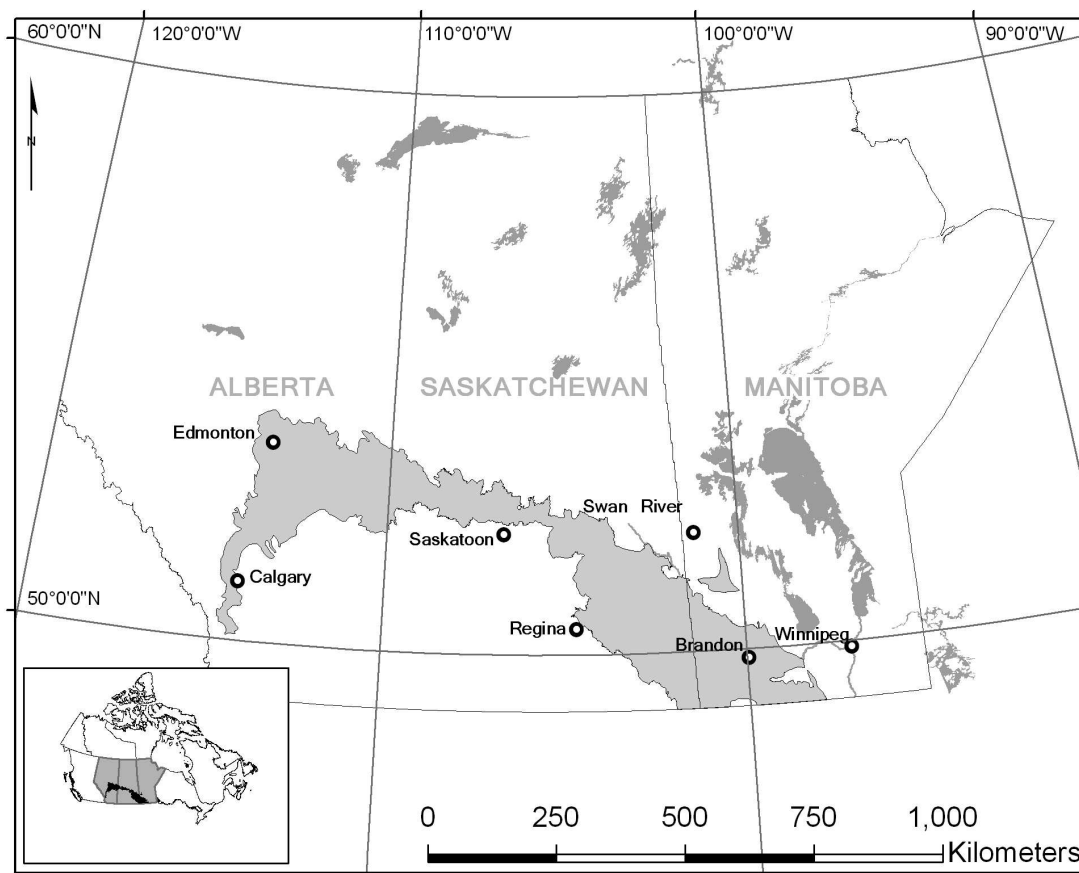
Poplar species represent approximately 56% of the hardwood volume in Canadian forests. Aspen comprises nearly 61% of that proportion, making it a valuable wood source (Forestry Canada 1988). Aspen has the widest latitudinal range of any tree in North America, occurring as far north as north-western Alaska, and as far south as the Sierra Madre Occidental of Mexico (Perala 1990). In Canada aspen occurs from north-western Yukon to eastern Newfoundland (Peterson and Peterson 1992, Wang 2003). It grows abundantly in the Aspen Parkland ecoregion, an area that extends from south-eastern Manitoba, into central Saskatchewan and much of Alberta (Figure 1-1).

Aspen grows in a wide-variety of environmental conditions. It grows best in well drained uplands; with soil textures that vary from loam to clay-loam; and a water table between one and two and a half meters in depth (Stenecker 1976a, Haeussler and Coates 1986, Perala 1990). There is anecdotal evidence that soil rich in calcium is also important to aspen development, influencing quality and quantity of stems within a stand (Heeney *et al.* 1975, Krajina *et al.* 1982, Perala 1990, Frey *et al.* 2003). The effect of calcium has not, however, been quantitatively demonstrated under field conditions.

#### *1.1.2. Life History of Aspen*

Aspen is shade intolerant, which is characteristic of early successional tree species (Stoekeler and Macon 1956, Shepperd and Engelby 1983, Perala 1990). Stoekler and Macon (1956) found aspen stocking to be higher in harvested areas with fewer residual trees. They reported that clear cut four and five year-old aspen stands with a residual basal

area of  $1.5 \text{ m}^2 \text{ ha}^{-1}$  and  $10.9 \text{ m}^2 \text{ ha}^{-1}$  had an average aspen density of  $1144 \text{ stems ha}^{-1}$  and  $152.6 \text{ stems ha}^{-1}$ , respectively.



**Figure 1-1:** Distribution of the Aspen-Parkland ecoregion (shaded in grey) in the western Prairie Provinces of Canada. Map prepared by Tim Davis, University of Manitoba.

Similar results were found by Prévost and Pothier (2003) where five year-old partially harvested aspen stands with 0%, 35% and 50% of the basal area removed had stem densities lower than  $1000 \text{ stems ha}^{-1}$ . Whereas stands with 65% and 100% of basal area removed, stem densities were approximately  $8\,000 \text{ stems ha}^{-1}$  and  $10\,000 \text{ stems ha}^{-1}$ , respectively (Prévost and Pothier 2003).

Huffman *et al.* (1999) used percent canopy cover and residual basal area as measures of potential light competition in regenerating aspen along a chronosequence of harvests. These authors compared the two measures as accurate predictors of regenerating aspen stem density, and found that they were highly correlated ( $r = 0.88$ ,  $P < 0.001$ ). Although, residual canopy cover was much more effective in determining density of regenerating stems than residual basal area in stands younger than nine years-old. Huffman *et al.* (1999) found that for every one percent increase in residual canopy cover, aspen stem density decreased by 210 stems  $\text{ha}^{-1}$ . Nine years after harvest, however, residual canopy cover began to show less of an effect on stem density (Huffman *et al.* 1999).

Reproduction by *Populus* species can be achieved by both sexual and vegetative means. Mature aspen produce large seed crops every four to five years, and these may have a viability of up to 95% (Maini and Cayford 1968). Despite having high seed production, successful cases of seedling establishment are thought to be rare (Perala 1990, Turner *et al.* 2003). The low success rate might be related to the lack of an endosperm in aspen seeds (Peterson and Peterson 1992). The endosperm is a common component of many tree seeds that supplies nutrients during development. Without it, successful germination may require a substrate of continually moist, exposed mineral soil (Maini 1968, Perala and Russell 1983, Peterson and Peterson 1992). These conditions are usually caused by a natural disturbance, such as a fire, or by clear-cut harvests (with appropriate site preparation) that would also remove potentially competing species (Perala and Russell 1983, Navratil 1991). However, fire prevention has been practiced by humans for many years, and may have become an obstacle to large scale aspen sexual reproduction (Romme *et al.* 1997, Quinn and Wu 2001).



Aspen propagates vegetatively through root suckering, an ability favoring early establishment after a disturbance. Root suckers (or ramets) are produced by a large colonial root system that provides them with resources essential for development (DeByle 1964, Tew *et al.* 1969, Shepperd 1990, Quinn and Wu 2001). After a large disturbance such as a fire, the newly developing suckers enjoy a growth advantage over seedlings of competing species (Frey *et al.* 2003). Almost all root suckers are initiated within 30 cm of the soil surface, and the majority between four and eight cm below the surface in mineral soil, which allows root suckers to tolerate light to moderate levels of above-ground disturbance (Maini and Horton 1964, Heeney *et al.* 1975, Shepperd 1990, Wang 2003).

Root suckers are able to grow faster than aspen seedlings and as they do not require planting, thus from a commercial aspect, suckers are more important in regenerating aspen than seedlings (Heeney *et al.* 1975). Aspen seedlings are rarely planted in western Canada (Peterson and Peterson 1992).

### *1.1.3. Hormone Control in Regeneration*

Root suckering is initiated when the ratio between the hormones auxin and cytokinin in the tree roots decreases (Frey *et al.* 2003). Auxin is produced in the above ground tissues (i.e., apical meristems in the shoots) and acts to inhibit suckering in the roots. Cytokinin is produced in the root tips and functions to encourage growth of root suckers. A decrease in auxin levels, followed by an increase cytokinin levels in the roots will result in the growth of root suckers once a specific ratio of cytokinin to auxin has been reached (Farmer 1962, Eliasson 1971a, Eliasson 1971b, Schier 1972, Wan *et al.* 2006). Such a situation arises from removal of the auxin producing stems by fire or harvesting (Farmer 1962, Eliasson 1971a, Eliasson 1971b, Schier 1972, Schier 1981).

A common side-effect of fire or timber harvesting is the loss of the top organic matter on the soil, which can affect the levels of suckering in regenerating aspen stands (Perala 1974, Haeussler and Kabzems 2005). Removal of this layer can lead to an increase in soil temperature, which may cause the degradation of the remnant auxin in the roots; as well as increasing production of cytokinins, further promoting the growth of root suckers (Horton and Maini 1964, Maini and Horton 1966, Williams 1972, Steneker 1974, Schier 1976, Navratil 1991, Landhausser *et al.* 2006).

#### *1.1.4. Common Stressors*

When aspen regenerates successfully, there are a multitude of stressors that may reduce vigor and growth rate, or lead to dieback. The most economically and ecologically important insect pest of aspen in the Prairies is the forest tent caterpillar (*Lepidoptera: Malacosoma disstria* Hübner). Outbreaks of the forest tent caterpillar typically last three to six years, and occur on average every 10 years, with a range of 6-16 years (Hildahl and Reeks 1960, Hildahl and Campbell 1975, Ives and Wong 1988, Hogg and Schwarz 1999). Populations of forest tent caterpillar are usually kept at low density by winter death of the eggs and spring freezing of larvae as well as by parasitic insects and song birds (Hildahl and Campbell 1975, Ives 1981, Holling 1988, Williams *et al.* 1996).

Forest tent caterpillar outbreaks are more common when summers and winters are unseasonably warm (Hildahl and Campbell 1975, Ives 1981), although, these outbreaks are unlikely to cause widespread mortality of aspen. Multiple years of heavy defoliation are needed to cause significant mortality in aspen stands (Hildahl and Campbell 1975). More often, aspen crowns are mildly affected by several years of light to moderate defoliation, with occasional years of heavy defoliation. An aspen tree responds to defoliation by

developing another flush of leaves, resulting in loss of radial growth due to the redirection of carbohydrates to produce new leaf tissue (Hildahl and Campbell 1975, Mattson and Addy 1975, Ives and Wong 1988).

The large aspen tortrix (*Lepidoptera: Choristoneura conflicta* Wlk.) may also be a significant defoliator of aspen. Outbreaks of the large aspen tortrix typically last two to three years and often precede those of the forest tent caterpillar (Ives and Wong 1988). In some years the large aspen tortrix may cause considerable economic damage, resulting in a decrease in the radial increment of aspen stems. As with outbreaks of forest tent caterpillar, several years of heavy defoliation by the large aspen tortrix are required to cause significant stem mortality (Ives and Wong 1988).

Insect pests can also have indirect affects on aspen health. The poplar borer (*Coleoptera: Saperda calcarata* Say.) inhabits young aspen stems, roots, and crowns. Poplar borer larvae bore into the tree and feed on sapwood and heartwood during its multiyear lifecycle (Ives and Wong 1988). Holes created by the poplar borer and other boring beetles in the same feeding guild provide a point of entry into sapwood for other pests and disease (Graham and Harrison 1954, Churchill *et al.* 1964, Hubbes 1966, Hildahl and Campbell 1975, Anderson *et al.* 1979, Houston 1992).

Outbreaks of wood boring insects and the forest tent caterpillar are known to precede infection by fungal pathogens such as hypoxylon canker (*Sphaeriales*). Aspen is quite susceptible to hypoxylon canker, and infected stems usually die within five years of initial infection (Peterson and Peterson 1992). Other fungal pathogens commonly affecting aspen include white trunk rot (*Hymenochaetales*), aspen shoot blight (*Dothideales*), and armillaria

root rot (*Agaricales*), which can cause internal stem and root decay, and decrease leaf longevity (Gross and Basham 1981, Stanosz and Patton 1987, Hiratsuka *et al.* 1990).

The presence of cankers and certain wood-boring insects (e.g., Coleoptera: *Agrilus spp.*) have been related to the occurrence of drought in the Prairies (Bagga and Smalley 1974, Ives and Wong 1988, Belanger *et al.* 1989, Haack 1996). Drought is believed to reduce tree vigour through reduction of photosynthetic activity, which may eventually deplete carbohydrate reserves, leading to decrease in stem vigour and an increase in the rate of mortality (Zoltai *et al.* 1991, Hogg and Hurdle 1995, Frey *et al.* 2004, Hogg *et al.* 2008).

Moisture is thought to be a critical determinant of the location of the Aspen Parkland ecoregion (Hogg 1994, Hogg 1997). Critical moisture levels for the occurrence of the Aspen Parkland have been defined using the climate moisture index (CMI), which is defined as precipitation (P) minus potential evapotranspiration (PET). The CMI throughout the Aspen Parkland ranges from -15 to 0 cm (Hogg 1994, Hogg 1997). To provide context, the boreal region to the north has a moisture surplus greater than 0 cm/year of precipitation, while the drier prairie grassland region to the south has a net loss of at least 15 cm/year of soil moisture according to the CMI (Hogg and Hurdle 1995).

Flooding, caused either by rising water tables post-harvest or exceptionally wet weather can also cause aspen mortality after disturbance, although the effects are seldom mentioned in the literature (Crouch 1986). Spring and early summer frosts are also of concern to aspen health. They often occur after the critical temperature threshold for bud burst and branch development has been exceeded (Hiratsuka and Zalasky 1993). Developing bud and leaf tissues are very susceptible to frost damage, symptoms include cracking of branches; bud damage leading to branch forking; and necrosis of foliage (Cayford *et al.*

1959, Hiratsuka and Zalasky 1993). This type of event, can affect stands on a massive scale, causing widespread dieback of trees (Cayford *et al.* 1959, Hogg *et al.* 2002).

#### *1.1.5. Grazing and Aspen Regeneration*

Mature and developing aspen stands are a very productive source of forage for livestock and wildlife. Mature stands are able to produce more than 2000 kg ha<sup>-1</sup> of palatable forage each year, which is significantly more than a coniferous forest, but less than a typical grassland (Reynolds 1969, DeByle 1985). In addition, the aspen canopy provides shade to cattle and protection to plants in the understory during times of drought (Powell and Bork 2007). During such conditions, when grassland vegetation is adversely affected, cattle may change their grassland foraging preference towards aspen stands (Hilton and Bailey 1972).

Grazing in aspen stands has the potential to cause considerable stress to aspen stems when managed poorly (Ellison and Houston 1958, Willoughby and Lane 2004). Cattle and large wild ungulates may trample young aspen stems as they move through regenerating stands. Damage caused by trampling may cause stem mortality or create an entry point for pathogens (Hinds 1972, Krebill 1972, DeByle 1985, Dockrill *et al.* 2004). It can be difficult to separate the effects of cattle browsing in an aspen stand from those caused by trampling (DeByle 1985). Attempts have been made to separate the two in previous studies, either through very careful observation or construction of apparatuses such as hydraulically powered hooves (Sampson 1919, Drewry *et al.* 2001). Observations confirmed that cattle may cause damage (through stem breakage or bark removal) to approximately 4.3-18.3% of stems in a regenerating stand depending on the duration of grazing period (Sampson 1919, Dockrill 2004).

Aspen stems are increasingly browsed later in the summer as abundance of desired forage decreases (Fitzgerald and Bailey 1984, Fitzgerald *et al.* 1986). During the spring and early summer, when there is little herbaceous biomass in aspen stands, suckers may be preferentially browsed by livestock (Arthur 1983, Arthur 1984, Bailey and Arthur 1985, Bailey *et al.* 1990, Lane and Willoughby 2000, Dockrill *et al.* 2004). Fresh leaves and shoots are vulnerable during this period because they have a higher protein content and shoots are less lignified than later in the year, when they become more lignified, giving them an increased resistance to the shearing force of cattle teeth (Bailey and Arthur 1985, Dockrill *et al.* 2006). Conversely, cattle if put out to pasture in proximity to an aspen stand during the early to mid summer will mostly graze their preferred forage species (e.g., grasses, Fitzgerald *et al.* 1986).

The aspen understory is sensitive to disturbance, and grazing may simplify or alter the understory community if cattle selectively graze the more palatable species. Over time species composition may shift to the less palatable species and foster the introduction of invasive species (Houston 1954, Kay and Bartos 2000, Willoughby and Lane 2004). Trampling by cattle has also been identified as an agent of change in the composition of the understory community in aspen stands (Weatherill and Keith 1969, DeByle 1985).

Intense grazing of the herbaceous layer in the aspen understory has the potential to reduce the amount of organic matter in the soil (Naeth *et al.* 1991). Typically, leaf litter would decompose slowly, but the animal pathway (i.e., digestion followed by excretion) converts live plant material directly to nutrients (mineralization, Floate 1970). The organic matter layer has an insulating effect on the soil. Therefore, if the thickness of the organic matter layer is reduced, surface mineral soil layers may warm up, further promoting the

growth and initiation suckering (Maini and Horton 1964, Schier *et al.* 1985). Root suckers can be adversely affected by the loss of this layer because it also serves to moderate soil compaction caused by cattle (Ferrero 1991).

Repeated travel by cattle may lead to localized compaction and increased bulk density in soils (Lull 1959, Bezkorowajnyj *et al.* 1993, Ferrero 1991). As soil bulk density increases, the proportion of macropores in the soil decreases, impeding infiltration of water (Lull 1959, Rauzi and Hanson 1966, Patric and Helvey 1986, Abdelmagid *et al.* 1987, Wood and Blackburn 1989, Greenwood and McKenzie 2001, Sharrow 2007). Additionally, reduced pore space decreases oxygen concentration, allowing carbon dioxide levels from root respiration to increase, which may create conditions that foster increased soil denitrification (Greacen and Sands 1980, Bezkorowajnyj *et al.* 1993, Sharrow 2007). This process may lead to an overall decrease in the levels of plant available nitrogen in the soil as demonstrated by Bezkorowajnyj *et al.* (1993). These authors found that poplar seedlings subjected to medium-high levels of soil compaction caused by cattle experienced lower growth rates than those subjected to low levels of compaction. The growth rate of stems in non-compacted soils was similar to compacted soils with applications of nitrogen rich slurry, thus negating the apparent effects of denitrification caused by soil compaction on stem growth rate.

#### *1.1.6. Forest Harvesting and Regeneration*

Clear cutting is the most common method of harvest for aspen, and it is widely considered to be the most successful method to secure abundant regeneration (Perala and Russel 1983, Schier *et al.* 1985). Levels of soil compaction resulting from the machinery used in timber removal have been found to vary depending on season of harvest, as a result

influencing the density of regenerating aspen stems (Bates *et al.* 1993, Stone and Elioff 1998, Berger *et al.* 2004). Bates *et al.* (1993) and Berger *et al.* (2004) found that summer harvests on unfrozen soils caused greater levels of soil compaction than was the case for frozen soils during winter harvests. Bates *et al.* (1993) compared disturbed and undisturbed areas (i.e., landings vs. non-traveled cutover areas) in both winter and summer harvests. They found that soils in disturbed and undisturbed areas from summer harvests were respectively 25% and 16%, more compacted than sites harvested in the winter where soils were frozen.

Summer harvested soils regularly experience loss of the top organic layer. Loss of this layer leaves soils less able to rebound from compaction, a situation similar to that of cattle grazing (Kabzems and Haeussler 2005). As mentioned earlier, soils with a shallow or absent organic matter layer are more likely to experience higher soil temperatures. Higher temperatures initially promote increased rates of suckering, but these newly developing suckers have been found to have higher mortality rates and are shorter than those growing in harvested areas with an intact organic matter layer (Kabzems and Haeussler 2005).

Aspen root carbohydrate levels vary according to season and may have an impact on levels of aspen regeneration (Tew 1970, Landhausser *et al.* 2003, Shepperd *et al.* 2004 ). Total levels of root carbohydrates are highest immediately before winter, and following a winter harvest can be mobilized to produce abundant suckers during the spring (Tew 1970). In contrast, during the summer, root carbohydrate levels are low, and carbohydrates in the leaves and branches are higher than in winter (Tew 1970, Heeney *et al.* 1975, Landhausser and Lieffers 2003, Mundell *et al.* 2008). Summer harvests can result in lower aspen sucker densities and shorter stems, however, opinions differ as to whether these effects arise due to



soil compaction, lower root carbohydrate levels, or from other causes (Schier 1976, Fitzgerald and Bailey 1984, Tyson Gills/Bill Gardner - Manitoba Agriculture personal communication 2009, Paul LeBlanc – Louisiana Pacific Canada Limited personal communication 2009).

#### *1.1.7. Grazing and Timber Removal on the Same Land Base*

Because grazing and forestry are increasingly combined on the same land base, concern has arisen about their compatibility. Although it is a versatile species, aspen already encounters stress from natural sources (e.g., insect pests, fungal pathogens, drought, unseasonable frosts, etc.). By adding additional stresses through livestock grazing, regeneration of harvested aspen stands may be further affected. Therefore, knowledge of how livestock grazing and local environmental variables influence aspen regeneration will be useful in assessing long term growth of aspen stands harvested in western Manitoba.

#### *1.2. Statistical Analyses*

Several analyses employed within this thesis, such as various diversity indices, aligned rank transform test, and multivariate analysis, may be unfamiliar to the reader. The following section summarizes some of the statistical techniques found in the thesis.

##### *1.2.1. Measures of Diversity*

In this study, plant species diversity was compared at the stand and landscape level to assess the impact of livestock grazing on understory flora in aspen stands. Diversity at the individual stand level, or alpha diversity, is the diversity within a spatially defined area. Beta diversity, or landscape level diversity is the degree of similarity between sites or stands across a landscape (Magurran 2004). Both alpha and beta diversity are common diversity measures in the ecological literature (MacArthur 1965, Whittaker 1977, Magurran 2004). It

should be mentioned that alpha and beta diversity are independent of each other. For instance, two sites with high alpha diversity values may have a rather low beta diversity value (Kimmins 1997). Therefore, when information is required on stand and landscape diversity, employment of both alpha and beta indices would be required.

### *Alpha Diversity*

Alpha diversity indices include measurements such as species richness (number of species present), a combination of species abundance and presence, and species evenness (Magurran 2004). There are several common indices used to measure alpha diversity of plants, examples include Simpson's Reciprocal Index, and Shannon's  $H'$  (Magurran 2004). Simpson's Reciprocal Index ( $1/D$ ) is a measure of alpha diversity as well as a heterogeneity index (Magurran 2004). It is based on the Simpson Index ( $D$ ), with the numerator and denominator reversed, so increased index values represent increasing rather than decreasing levels of species diversity (Magurran 2004). The index is calculated using the following equation:

$$1/D = \frac{N(N-1)}{\sum n_i(n_i-1)} \quad \text{Equation 1}$$

where,  $N$  = total number of individuals, and  $n_i$  = the number of individuals found in the  $i^{\text{th}}$  species. Simpson's Reciprocal Index is weighted by the abundance of the most common species, where the abundance of species relative to the total number of individuals sampled is the main driver of the index value (Magurran 2004). This index may also lead to a loss of information of rare species that occur only once in a sampling area, and is therefore less suited to studies where rare species are an important consideration.

The Shannon-Wiener Index (Shannon's  $H'$ ) combines measures of species richness and evenness (Magurran 2004). Shannon's  $H$  is calculated using the following equation:

$$H' = -\sum_{i=1}^S p_i \ln p_i \quad \text{Equation 2}$$

where,  $p_i$  = the proportion of individuals found in the  $i^{\text{th}}$  species. The values of diversity range from 0 - ~4.5, with zero representing low complexity, and ~ 4.5 representing a complex diverse plant community. This index relies on the assumption that all species within an area are sampled. If sample intensity decreases, a lower proportion of species within an area will be sampled, thus decreasing the accuracy of this index (Peet 1974). Shannon's  $H'$  also relies on the assumption that species are randomly sampled from an infinitely large population (Pielou 1975). Thus, any sampling method that would influence species distribution and create a non-random distribution of sample organisms (e.g., light traps for moths) would violate assumptions made by this index (Magurran 2004). Consequently, it is better suited to stationary organisms (i.e., plants) that will remain randomly distributed during sampling procedures.

#### *Species Evenness*

Species evenness was measured using Shannon's Evenness measure (Magurran 2004), and was calculated using the following equation:

$$J' = H' / H_{\max} \quad \text{Equation 3}$$

where,  $H'$  = value of Shannon's  $H'$ , and  $H_{\max}$  = maximum diversity possible with  $H'$  (all species are equally abundant).  $J'$  ranges from zero to one, zero is observed when there is only one species is represented, and one representing a situation where all species are equally abundant (Magurran 2004) This evenness measure provides a ratio of measured diversity to the maximum diversity possible (Magurran 2004).

#### *Beta Diversity*

Beta diversity indices may be helpful in comparing the diversity levels of sites of a

similar habitat that have undergone different types or severities of disturbance (e.g. comparing similarly aged grazed and ungrazed sites). Beta diversity can be measured qualitatively (presence/absence of species), where the number of species shared between sites is compared (i.e., Jaccard's Similarity Index, Shmida and Wilson 1985, Magurran 2004). The Jaccard Similarity Index is calculated as follows:

$$C_j = \frac{j}{a + b - j} \quad \text{Equation 4}$$

where,  $j$  = total number of species shared by both sites,  $a$  = the number of species in Site A, and  $b$  = the number of species in Site B. The values of similarity range from zero to one, zero indicating no shared species and one indicating all species present exist in both sites. Because it does not use species abundance, all species within a site regardless of abundance are weighted equally. It consequently lacks the precision of fully quantitative measures, but it does provide a good measure of how species composition varies between sites (Shmida and Wilson 1985, Magurran 2004).

Species similarity shared between sites can also be compared quantitatively, using the number of species shared between sites and their abundances. Hierarchical cluster analysis is often used to group sites based on similarities in species composition and abundance. The site values of each species and its abundance can be translated into Bray-Curtis space, where they are plotted relative to each other according to proportion of species not shared between sites (McCune and Grace 2002, pp 46-92). The sites can be "clustered" or linked using the Ward's linkage method (McCune and Grace 2002, pp 46-92). Ward's linkage method clusters sites based on shortest error sum of squares distance between clusters. The error sum of squares is defined as sum of the squares of distances in Bray-

Curtis space between each individual point and the centroid within its particular cluster (McCune and Grace 2002, pg 92).

### 1.2.2. Indicator Species Analysis

Indicator species analysis (ISA) is often used to determine species which are characteristic of a particular habitat type (Defrêne and Legendre 1997). The indicator value is calculated using the following equation adopted from Defrêne and Legendre (1997):

$$\text{INDVAL}_{ij} = A_{ij} \times B_{ij} \times 100 \quad \text{Equation 5}$$

where,  $A_{ij}$  = relative frequency of species  $i$  in group  $j$ , and  $B_{ij}$  = relative abundance of species  $i$  in group  $j$ . Significance of the indicators can be determined using a Monte-Carlo permutation test. The tests randomly arrange the data in each permutation, and each time calculates an indicator value for each species. The type I error probability is based on the proportion of times that the randomized indicator values for species  $i$  exceed the indicator value calculated from actual data (Defrêne and Legendre 1997, McCune and Mefford 1999).

### 1.2.3. Mantel's Test

Similarity of species composition is frequently a function of distance between areas sampled (Gilbert and Lechowicz 2004). This spatial bias, known as autocorrelation, implies that species composition or abundance at one site can be partially predicted by the values of the same variables at a site nearby (positive autocorrelation usually exists between proximally located sites and negative autocorrelation between sites further apart, Legendre and Legendre 1998, pg 9). Autocorrelation is an important concern when considering the relative distance between sites within a study. Where sites are close enough that they may be related through biological processes (e.g., dispersion), a Mantel test can be used to probe the data for positive autocorrelation (McCune and Mefford 1999). The test is calculated using

two dissimilarity matrices, such as species presence/absence and inter-site distance, to determine the effect distance has on species composition. Mantel's statistic is a correlation coefficient calculated from inter-site species distance using a standard distance matrix, such as Bray-Curtis space and inter-site geographical distance (McCune and Mefford 1999). The Mantel's statistic for each site is taken as the empirical data for comparison against subsequent permutations (Legendre and Legendre 1998). To arrive at a type I error rate, the rows and columns of one of the matrices are permuted repeatedly at random, preserving the relative cell addresses (Legendre and Legendre 1998). The probability of type I error is based on the proportion of permuted Mantel's statistics that equal or exceed the Mantel's statistic calculated from the original data (McCune and Mefford 1999).

Mantel's Test is calculated using the following equation:

$$r_m = \frac{1}{d-1} \sum_{i=1}^{n-1} \sum_{j=i+1}^n \left( \frac{x_{ij} - \bar{x}}{s_x} \right) \left( \frac{y_{ij} - \bar{y}}{s_y} \right) \quad \text{Equation 6}$$

where, n = total number of distances in within matrix Y, the distance matrix (excluding where j = i), y = values from matrix Y, x = values from matrix X, i and j are column and row indices,  $s_x$  and  $s_y$  are standard deviations for matrices X and Y (Legendre and Fortin 1989).

#### 1.2.4. Rarefaction

The density of individuals is known to vary by site, and this often results in unequal numbers of species being sampled among sites regardless of the sample size within a site (Magurran 2004). To standardize the accumulation of species observations by species density, a technique called rarefaction may be employed. Species richness from all sites is standardized to the number of observations made in the site with the smallest sample size (N) (Magurran 2004). A rarefaction curve is created through random selection of individuals

from the total species pool in each site, to a maximum of N observations. The average number species found at each observation is calculated from multiple permutations (Gotelli and Colwell 2001).

#### *1.2.5. Ordination*

The structures of communities in nature are inherently complex. Multivariate analysis can be useful in reducing complexity and highlighting underlying trends and associations in large data sets. The point of multivariate analysis is to reduce multivariate variation into a few meaningful axes that capture major trends in the data. In ordination analysis, multivariate data are simplified into N-dimensional space for graphical representation of species, site and environmental variables (biplot or triplot) to aid in representing any underlying structures or trends within the data (Jongman *et al.* 1995, pg 127-130).

In the ordination biplot the first axis is rotated to encompass the maximum amount of data, and the second axis will encompass the second largest amount of linear variation (Legendre and Legendre 1998). The variation encompassed by each axis is referred to as its eigenvalue (Kenkel *et al.* 2002). The larger the eigenvalue of an axis relative to the sum of all eigenvalues, the larger the fraction of data variability explained by that axis.

#### *Principal Components Analysis*

Principal Components Analysis (PCA) is an indirect gradient analysis. A PCA ordination of species represents a weighted average of species abundances among the pool of sites. Positions of sites are weighted averages on their species abundances. Position of species represents a function of weighting of species abundances from all sites (Jongman *et al.* 1995, pg 127-129). Both species and sites are mapped within a type of plot called a

biplot, which refers to the representation of both species and sites (Jongman *et al.* 1995, pg 127). Any trends observed in the positioning of the species or sites within the biplot, are taken to reflect underlying trends within the actual species and sites observed (Jongman *et al.* 1995, pg 127-130).

### *Redundancy Analysis*

Redundancy Analysis (RDA) is a direct gradient analysis because it explicitly regresses the data against the environmental variables (ter Braak and Smilauer 2002, pp 28-60). Species data are constrained through a multiple linear regression of the environmental variables, after which the fitted multiple regression values are run through a PCA (Kenkel *et al.* 2002). These data may be represented graphically in an ordination triplot (species, site and environmental data). In addition, environmental variables are represented as arrows originated from the center of the axes. The greater the arrow length for a particular vector (species, site or environmental variable) the greater its contribution to the eigenvalues of the respective axes. Species and site data positioning relative the other environmental variables can be related to its influence on their positioning within the ordination triplot.



## Chapter 2 - The Influence of Cattle Grazing on Aspen Regeneration and Health

### 2.1. Introduction

Poplar species represent approximately 56% of the hardwood volume in Canadian forests, of which nearly 61% is comprised of aspen (*Populus tremuloides* Michx., Forestry Canada 1988, Peterson and Peterson 1992). Aspen has the largest range of any tree species in North America, occurring as far north as north-western Alaska, and as far south as the Sierra Madre Occidental of Mexico (Perala 1990). It is particularly abundant in the Aspen Parkland ecoregion of the Prairie ecozone (Environment Canada 1996), an area that extends from south-eastern Manitoba, into central Saskatchewan, and much of Alberta (Bird 1961, McCartney 1993). The central and northern parts of the ecoregion are primarily composed of extensive tracts of forests dominated by aspen with minor components of balsam poplar (*Populus balsamifera* L.) and white birch (*Betula papyrifera* Marsh., Bird 1961).

Aspen is a shade intolerant early succession tree species (Stoekeler and Macon 1956, Shepperd and Engelby 1983, Perala 1990). Aspen propagates vegetatively through root suckering, which favors early establishment after disturbance (Perala and Russel 1983, Navratil 1991). However, aspen suckers require canopy closure of 30% or less after disturbance to regenerate without a potential loss of growth (Huffman *et al.* 1999).

Mature and developing aspen stands sustain valuable forage for cattle, domestic sheep, elk, and deer, (Hilton and Bailey 1974, Bailey *et al.* 1990, Peterson and Peterson 1992, Beck and Peek 2005). Mature stands may produce as much as 2000 kg ha<sup>-1</sup> of palatable forage (i.e., forbs and grass) each year, which is significantly greater than most coniferous forests, but less productive than typical grasslands (Houston 1954, Reynolds 1969). In addition, the aspen canopy provides protective cover to grazing animals and to

plants in the understory during times of drought and heat stress (Powell and Bork 2006, Powell and Bork 2007). Under these conditions, grassland vegetation often has a lower moisture content than aspen understory, and given the opportunity, cattle may spend more time grazing in aspen stands than adjacent grasslands (Springfield and Reynolds 1951, Hilton and Bailey 1972).

Since 1995, the forest industry in western Manitoba has increased its timber harvesting activities in aspen-dominated rangelands. Louisiana Pacific Canada Limited (LP) opened an oriented strand board (OSB) mill in Minitonas, Manitoba in 1995 to take advantage of a large supply of under-utilized aspen fibre in the region. Timber for this mill comes from Forest Management License 3 (FML 3, licensed to LP) and the southern portion of FML 2 (licensed to Tolko Industries Ltd). Forest Management License 3 covers a total of 6.3 million ha., 22% is classified as agricultural crown land under the Provincial land use system (Donnelly 2003). In addition to aspen, LP also harvests balsam poplar, white birch, and tamarack (*Larix laricina* Du Roi).

A portion of LP's wood supply comes from agricultural crown land that may also be used for livestock grazing. It is common for local crown agricultural land leaseholders to graze livestock on freshly harvested aspen stands because of high levels of palatable forage in the regenerating understory. Grazing in regenerating aspen stands if poorly managed, has the potential to cause considerable damage and reduction to the vigour of a large proportion tree stems with the stand (Nordstrom 1984, Pitt *et al.* 1998, Willoughby and Lane 2004). A poorly managed grazing regime may involve stocking of cattle beyond the capacity of an area of rangeland and having inadequate rest periods for a rangeland between periods of use (Heitschmidt and Walker 1983, Holechek *et al.* 1998).

Louisiana Pacific foresters, forestry staff at Manitoba Conservation and agronomists at Manitoba Agriculture have therefore become concerned that cattle grazing in recently harvested areas may reduce the quantity and quality of aspen regeneration. A working hypothesis discussed with LP was that browsing and mechanical damage caused by cattle would open up regenerating aspen to secondary health effects or secondary pathologies.

Each crown-lease land parcel has a maximum area that can be modified from the original wooded state without additional permission from the crown (Crown Land Classification Committee Guidelines 2004). When a section of leased agricultural land has been harvested in excess of this amount, a regeneration plan must be in place to ensure that the harvested stand within the section reaches the minimum provincial silvicultural stocking guidelines of 6299 hardwood stems  $\text{ha}^{-1}$  seven years post-harvest (Manitoba Conservation 2001, Crown Land Classification Committee Guidelines 2004). Failure to meet the required stocking levels may result in penalties for the forestry company. Therefore, LP has often reduced its harvest levels on leased lands grazed after harvest to avoid penalties and to ensure the stability of future wood supply in the region. Moreover, Manitoba Conservation and LP foresters have suggested that insufficient forest regeneration is occurring on some grazed sections in FML 2 and 3 based on company regeneration surveys. These concerns have led to uncertainty regarding the ability of grazed aspen stands to reach sufficient stem densities to meet provincial deciduous and mixed-wood stocking standards.

### *2.1.1. Objectives*

The purpose of this study was to investigate the impact of livestock grazing on aspen regeneration after timber harvest on agricultural crown lands. The objectives were: 1) Assess the impact of cattle grazing on stem density of aspen and other commercial tree species

across a chronosequence of harvests, 2) Characterize the relationships of tree health indicators and presence of pests with cattle grazing in harvested areas, and 3) Investigate the influence of local site factors (i.e., soil variables) on stem density of commercial tree species.

## **2.2. Methods**

### *2.2.1. Study area and site selection*

Eighteen study sites were located in and adjacent to Duck Mountain Provincial Forest, in Forest Management License Areas 2 and 3 (51.71- 51.80° N and 101.03-101.14° W, Figure 2-1). The sites were located in the Aspen Parkland, an ecoregion in the Prairie ecozone between the Boreal Plains ecozone to the north and grassland ecoregions to the south. The topography ranged from rolling hills in the south western portion of the study area to flat, open areas in the northern and eastern portions. The region is dominated by stands of aspen, intermixed with balsam poplar and white birch, with minor components of red alder (*Alnus rugosa* Bong.), bur oak (*Quercus macrocarpa* Michx.), and various *Salix* spp. (Rowe 1956). Common understory shrubs include prickly rose (*Rosa acicularis* Lindl.), pin cherry (*Prunus pensylvanica* L.f.), choke cherry (*Prunus virginiana* L.), red-osier dogwood (*Cornus stolonifera* Michx.), saskatoon (*Amelanchier alnifolia* Nutt.) and beaked hazel nut (*Corylus cornuta* Marsh.) (Hamel and Kenkel 2001). Mean annual precipitation (based on data from weather stations in Cowan, Swan River and Gilbert Plains, Manitoba from 1971 – 2000) is 553.4 mm, with average temperatures of -16.2°C in January and 20.0°C in July (Environment Canada 1996).

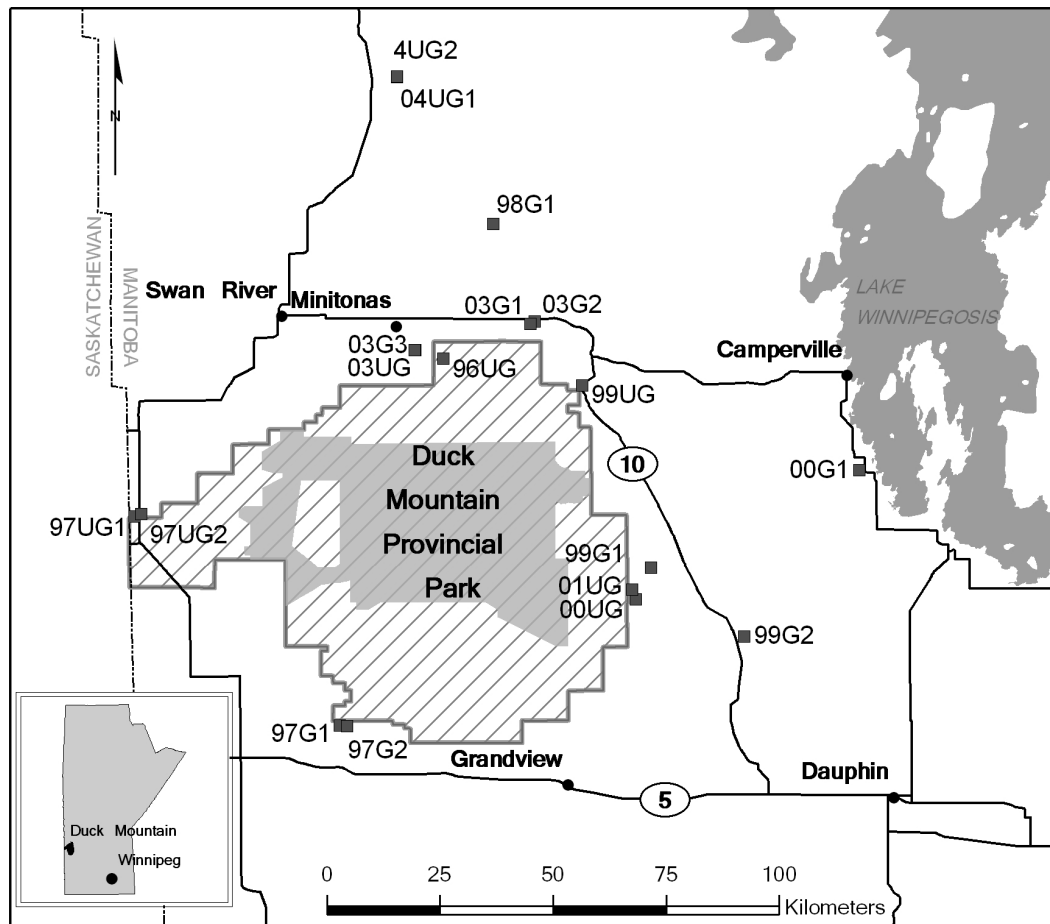
Mature aspen and balsam poplar were clear felled in each study site by contractors using a variety of harvesting and skidding equipment. Season of harvest could not be

verified for most of the sites surveyed. The sites were located on either agricultural or forestry coded crown land. The forestry coded crown land was not grazed, and all of the agricultural coded crown land was prior to harvest, and in most cases post harvest (some ungrazed sites were located on agricultural crown land). Grazing status, history and stocking rate (animal unit months ha<sup>-1</sup>) were based on records provided by Manitoba Agriculture and individual agricultural crown land leaseholders. Descriptions of each study site are listed in Appendix 2.

The eighteen study sites were separated into three stand age classes; 2-3 years, 5-8 years, and 9-11 years post harvest, with six sites per stand age class - three that were grazed after harvest and three with no post-harvest grazing. Three sites with no post-harvest grazing may have been grazed before the timber was harvested (i.e., 2-3UG1, 2-3UG2, and 2-3UG3).

### *2.2.2. Plot Establishment*

A one hectare plot was established within each of the 18 sites. The corners of each plot were located at least 20 m from mature forest. In most sites square plots were established, but on several occasions, the shape of the plot had to be modified to maintain an adequate buffer zone from the mature forest. Within each plot, 36 circular 24.6 m<sup>2</sup> subplots were placed on a grid with 20 m spacing. The corners of the plot and center of subplots were marked with wooden stakes (grazed sites) or metal pigtailed (ungrazed sites).



**Figure 2-1:** Distribution of study sites in the Duck Mountain area. Map prepared by Tim Davis, University of Manitoba.

### 2.2.3. Tree Regeneration

All trees and tall shrubs within a 2.8 m radius of the center of each subplot were identified, counted, and placed into one of five height classes: 0-0.5 m, 0.5-1.0 m, 1-2 m, 2-4 m, > 4 m (referred to as HC1 - HC5). Height classes were estimated by eye after a suitable period of calibration in which the height of each stem was measured. Stem density (stems  $\text{ha}^{-1}$ ) was calculated for each height class and for all height classes combined. Stem height, diameter at breast height (DBH), root collar diameter (RCD), crown depth, and crown

diameter (measured across the widest axis of the crown and perpendicular to this axis) were also recorded.

#### 2.2.4. Health Indices

We divided subplots into quadrants, using the point centered quarter technique (Mueller-Dombois and Ellenberg 1974) and selected the tallest living tree (aspen or balsam poplar) in each quadrant for health analysis. Tree health was characterized by a series of indices; including vigour; crown dieback; defoliation; necrosis and chlorosis of the leaves; and mechanical damage to the stem and root collar (Table 2-1). The indices used were modified by Boone and Westwood (2006) from methods previously established by Haapalla *et al.* (1996) and Stolte (1997). Health indices for individual stems assessed were then converted into a site health index by weighting the indices based on severity and averaging them from all trees surveyed within a site for each specific index using the procedure outlined in the following example:

$$\text{Site health index} = [(1 \times P_1) + (2 \times P_2) + \dots + (I \times P_b)] / N \quad \text{Equation 7}$$

where,  $P_b$  = number of trees in a site with a given value of a given health index,  $I$  = the maximum value for health index, and,  $N$  = number of trees sampled within a site. The range of the indices was 0 - 1, with 0 indicating an absence of symptoms of the particular health index, and 1 indicating a 100 percent incidence of the health index in question.

Indices were also constructed to assess the severity of insect pests and pathogens (Boone and Westwood 2006). Insect guilds and disease symptoms that were noted on the stems and leaves of health trees are shown in Table 2-2. All of the site pest indices were calculated as percentage of the total health tree population where a given pest was

present within each site. The range of site pest indices was 0 - 1, with 0 indicating an absence of a particular pest among measured trees, and 1 indicating the pest was present in all measured trees.

#### 2.2.5 Grazing Pressure.

Animal unit months  $ha^{-1}$  (AUM  $ha^{-1}$ ) was used as a measure of grazing pressure in the regenerating aspen stands. This metric is a standardized grazing intensity measurement, and was calculated using the following equation (Ziegler 2001):

$$AUM \cdot ha^{-1} = \left( \frac{AU * D}{A} \right) \quad \text{Equation 8}$$

where, AU = animal units, D = months of grazing and A = land area (ha). An animal unit month is the amount of forage required to feed a 453.6 kg cow and suckling calf for a month, which is approximately 353.8 kg of forage. The value for animal unit months was adjusted to account for bulls and horses that were feeding alongside the cow/calf pairs in some plots using conversion values provided by Ziegler (2001).

#### 2.2.5. Soil Compaction

Levels of soil compaction were measured using digital and analogue soil penetrometers (Field Scout SC-900 Soil Compaction Meter and Soil Compaction Tester Model 6100) with cone diameter and angles 1.27 cm at 30° and 1.91 cm at 30°, respectively (Spectrum Technologies Plainsfield, IL). Three series of measurements were taken in each subplot at N, SW and SE directions approximately 2 m from the center. Compaction (in kilopascals, kPa) was measured at 2.5 cm intervals to a depth of 22.5 cm.

Soil moisture and bulk density are known to influence resistance to penetration (compaction; see Section 2.3.3. in Data Analysis). Soil samples were therefore collected to determine moisture content and bulk density. Soil samples for determining moisture content



were taken at every fourth subplot in each plot ( $n = 9$ ). The samples were collected to a depth of approximately 20 cm using a bucket auger (core dimensions 20.0 x 6.2 cm), and their moisture content was determined gravimetrically. Bulk density samples ( $n = 9$ ) were taken using a custom built hammer corer (10.6 x 6.0 cm volume) owned by the University of Winnipeg. As with moisture, bulk density samples were taken to a depth of 20 cm, by extracting two samples within the same core, after removing the top organic matter layer. Bulk density samples were evenly distributed through the varying types of terrain and levels of disturbance (i.e., apparently undisturbed, moderate and heavy disturbance (e.g., cow path)). Bulk density samples were oven dried at approximately 80°C for 24 hr. Coarse fragments larger than approximately 2 mm were separated from the sample and weighed. Their volume was then estimated using the standard density assumption of 2.65g cm<sup>-2</sup>, coarse fragment volume was then subtracted from the total sample volume (Burt 2004).

**Table 2-1:** Definitions of tree health indices for aspen and balsam poplar

Variable	Descriptors	Definition
Vigour	1	Tree is healthy, without signs of stress
	2	Tree is stressed, but likely to recover
	3	Tree is stressed, not likely to recover
Defoliation	1	0-25% of crown is defoliated
	2	26-50% of crown is defoliated
	3	51-75% of crown is defoliated
	4	>75% of crown is defoliated
Crown Dieback	1	0-25% of crown showing dieback
	2	26-50% of crown showing dieback
	3	51-75% of crown showing dieback
	4	>75% of crown showing dieback
Mechanical Damage 1 (Stem)	1	Stem has no mechanical damage
	2	1-25% of stem has mechanical damage
	3	26-50% of stem has mechanical damage
	4	51-75% of stem has mechanical damage
	5	>75% of stem has mechanical damage
Mechanical Damage 2 (Root Collar)	1	Root collar has no mechanical damage
	2	1-25% of root collar has mechanical damage
	3	26-50% of root collar has mechanical damage
	4	51-75% of root collar has mechanical damage
	5	>75% of root collar has mechanical damage
Necrosis	1	0-25% of leaves are necrotic
	2	26-50% of leaves are necrotic
	3	51-75% of leaves are necrotic
	4	>75% of leaves are necrotic
Chlorosis	1	0-25% of leaves are chlorotic
	2	26-50% of leaves are chlorotic
	3	51-75% of leaves are chlorotic
	4	>75% of leaves are chlorotic

**Table 2-2:** Coding and definition of pest types noted on health trees.

<b>Variable</b>	<b>Descriptors</b>	<b>Definition</b>
Insect Damage	DEF	Defoliating insects (e.g., caterpillars)
	SUC	Sucking insects (e.g., lace bugs, aphids)
	SKEL	Skeletonizing insects (e.g., sawflies, leaf beetles)
	LM	Leaf miners (e.g., moths, beetles)
	GA	Gall forming insects (e.g., mites, aphids)
Disease	CA	Cankers on stem or branches
	CO	Conks on stem (Sign of decay)
	LS	Leaf spots (Sign of poor health)
	LR	Leaf rust (Sign of poor health)
	SR	Stem rust

#### 2.2.6. Soil Characteristics

Samples were taken for soil texture and organic matter content at every fourth plot using a bucket auger (core dimensions 20.0 x 6.2 cm). Soil texture was determined using the pipette method (Day 1965). Organic matter content was measured by percent weight lost at ignition, at a furnace temperature of 550°C (Federer *et al.* 1993). Soil pH was measured using a symPHony pH meter (VWR Batavia, IL). Samples were put in a beaker with a 4:1 ratio of 20 ml of 0.01 M of CaCl<sub>2</sub> to soil. The solution was stirred three times over 30 minutes, and then allowed to settle out for 20 minutes. A calibrating solution with a pH of 4 was used to calibrate the electrodes prior to measuring soil pH. The electrode was washed with distilled water between each measurement.

To determine the soil drainage class, a 1.0 x 1.5 m soil pit was dug down to the beginning of the C horizon near the center of each plot. Soil drainage class was determined from horizon depth, humus type, texture, and the presence or absence of mottling and

gleying at various depths using the protocol contained in the Manitoba Forest Ecosystem Classification Manual (Zoladeski *et al.* 1995).

### 2.2.7. Coarse Woody Debris

Optimal transect spacing and length for the measurement of coarse woody debris (CWD) volume were estimated using calibrating transects, which were established at several sites to determine the range of debris size classes present (Marshall *et al.* 2000). The diameter and shape class (round, semi-round and irregular) were recorded for each piece of debris 5 cm or larger in diameter that intersected the transect line. Unseasonable weather and time limitations prevented the measurement of CWD at every site; this variable was therefore not included in statistical analysis but is summarized in Appendix 3.

## 2.3. Data Analysis

### 2.3.1. Tree Regeneration

The average number of stems  $\text{ha}^{-1}$  for aspen and all commercial species were calculated for each plot from the subplot data. Stem density of pooled and separated height classes were compared using two-way analyses of variance (ANOVA) with grazing and stand age class as fixed factors. The ANOVAs were calculated within the General Linear Model (GLM) framework. Planned comparisons were used to compare stem density between grazed and ungrazed sites within each stand age class. Because of the high type I and type II error associated with low sample sizes, the type I error rate was set to  $\alpha = 0.1$  to decrease type II error, since management decisions in LP may be based on the findings of this study, and accepting a false hypothesis (type II error) would have more negative results than rejecting a hypothesis that is true (type I error).

### *Comparison with other Regeneration Studies*

To provide a comparative context for the stands surveyed in this study, data were compiled from a series of post-harvest aspen density surveys conducted in Canada and the United States (Pollard 1971, Bella and De Franceschi 1980, Weingartner 1980, Crouch 1981, Crouch 1983, Perala 1984, Bella 1986, Steneker 1976b, Dockrill 2001, DesRochers and Lieffers 2001, Berger et al. 2004). The aspen regeneration data from the Duck Mountains study were compared to the data collected from the comparison studies in a scatter plot to provide a qualitative analysis of density trends through time.

#### *2.3.2. Tree Health*

Tree health and pest data consisted of ratio variables in treatments with multiple replicates. A non-parametric, aligned rank transform test was used to analyze weighted averages of each index to test for main effects and their interaction (Higgins 2004, pp 309-314). The aligned rank transform test is a modified rank transform method that allows for the testing of effects of interaction in addition to the main effects, unlike typical rank transform tests (Higgins 2004, pp 309-314). The aligning procedure allows for each main effect and its interactions to be tested individually by subtracting the effect that is not being tested from the analysis (Higgins 2004, pp 309-314). Each health index could be described by the following equation:

$$Y_{ijk} = \mu + \alpha_i + \beta_j + \gamma_{ij} \quad \textbf{Equation 9}$$

where,  $Y_{ijk}$  = the value of the health index in the  $i^{\text{th}}$  stand age of the  $j^{\text{th}}$  grazing treatment under the  $k^{\text{th}}$  plot,  $\mu$  = global mean,  $\alpha_i$  = stand age mean,  $\beta_j$  = grazing treatment mean, and  $\gamma_{ij}$  = interaction mean.

By sequentially subtracting residual and main effects from each of the main effects and interactions and then ranking them, and a main effect or the interaction was tested exclusively in a two-way ANVOA. For example, to test for effect of interaction the following equation was used to align all values prior to ranking:

$$AB_{ijk} = Y_{ijk} - \mu - \alpha_i - \beta_j \quad \text{Equation 10}$$

The ranked data were then analyzed using a two-way ANOVA, the critical type I error rate was set to  $\alpha = 0.1$ , as a threshold for rejection of the null hypotheses that grazing and age had no influence on the value of the indices. If any main effect or interaction returned a Type I error  $\leq 0.1$ , a Mann-Whitney U test was employed to determine differences between treatment means. All ANOVA tests and post-hocs were calculated using SPSS 14.0 (SPSS Inc, 2005).

### 2.3.3. Soil Moisture Correction

Soil moisture and bulk density are known to influence resistance to penetration (compaction, Busscher and Sodjka 1987). To allow for this relationship a linear regression can be used to relate soil compaction to bulk density and soil moisture content. Since bulk density is held to be invariate within a site, variations in penetrometer resistance over time at any location will be influenced mainly by soil moisture. Penetrometer readings can then be standardized using a reference soil moisture content (usually the average of moisture readings, Krzic *et al.* 2003).

### 2.3.4. Multivariate Analysis

Multivariate ordinations were used to explore the influence between grazing, harvest year and local site factors on stem density. Ordinations were performed on both stem densities of pooled height classes for each species and on height classes represented in the

species matrix as pseudospecies (e.g., balsam poplar would be BP1, BP2, BP3, etc.). Initially, a Detrended Correspondence Analysis (DCA) was used to assess the gradient length (in standard deviations) of the primary ordination axes. This procedure is commonly used when choosing between multivariate techniques that presuppose either linear or univariate responses to underlying environmental gradients (Jongman *et al.* 1995, pp 106-108). As a rule of thumb, if the axis length is less than ~2.0 standard deviations, the underlying responses of the variables being analyzed are assumed to be roughly linear, and methods that assume linear responses (i.e., Principle Components Analysis (PCA) and Redundancy Analysis (RDA)) can be used (Jongman *et al.* 1995, pp 154). All ordinations were done using CANOCO 4.5 for Windows (ter Braak and Smilauer 2002, pg 125), and species data were log-transformed using  $x' = \log_{10}(x+1)$ .

The gradient lengths in the DCAs ranged from 0.148 – 1.671 standard deviations, PCA and RDA were therefore used in subsequent analyses. Principle Components Analysis and Redundancy Analysis covariance matrices were centered by species and samples (sites). Centering by species will plot sites relative to an origin based on the mean species composition of all sites, whereby how a site deviates from this “theoretical site” indicates how a species population within a site departs from the average (Dray *et al.* 2003). Centering by site creates an origin where sites are plotted relative to an origin based on equal abundance of all species (Dray *et al.* 2003). How a species deviates from equal species abundance will provide a measure of its relative proportion within the study (Dray *et al.* 2003). Furthermore, sites that differ from equal abundance of all species will also be indicative of their species evenness (Dray *et al.* 2003). The environmental variables used in the RDAs were soil drainage class, organic matter content, clay fraction, pH, soil

compaction, bulk density, and grazing pressure. The statistical significance of the first ordination axis and of all axes pooled together ( $\alpha = 0.1$ ) was tested using 9999 Monte Carlo permutation tests under the reduced model (ter Braak and Smilauer 2002, pp. 139-143).

A series of partial RDAs were used to partition environmental effects into pure and shared variance components from grazing pressure and soil characteristics (Borcard *et al.* 1992). To determine the magnitude of the pure and shared variance contributions of the soil variables and grazing pressure, they were alternately used as explanatory variables and covariates in a series of full and partial ordinations. The ordinations that were run were: 1) Soil variables with grazing pressure as a covariate, 2) Grazing pressure with soil variables as covariates, 3) Soil variables with no covariates, and 4) Grazing pressure with no covariates. Ordination 1 explained environmental variation, ordination 2 explained the variation caused by grazing, and shared variation was the difference between ordinations 1 and 3 or 2 and 4. An example of the partial ordination calculations is shown in Appendix 2. Total variation explained by all environmental variables was determined as the sum of the variance explained from ordinations of 1 and 4 or 2 and 3. The remaining (residual) variance was calculated by subtracting explained variance from 100%.

## **2.4. Results**

### *2.4.1. Tree Regeneration*

Ungrazed stands had a significantly greater density of commercial stems (pooled population of aspen, balsam poplar, and white birch) than grazed stands, with an average of 19,092 stems ha<sup>-1</sup> compared to 13,482 stems ha<sup>-1</sup> ( $F_{1,16} = 5.01$ ,  $P = 0.045$ , Table 2-3, Figure 2-2)). Moreover, pooled commercial stems greater than four meters in height in ungrazed stands 9-11 year-old stands were significantly more abundant than in similarly aged grazed



stands. In ungrazed stands there were 6,774 stems ha<sup>-1</sup> taller than 4 m compared to 1,350 stems ha<sup>-1</sup> in grazed stands ( $F_{1,4} = 6.97$ ,  $P = 0.022$ , Table 2-3, Figure 2-3). Regarding aspen stems, grazing had no overall influence on total stem density or density of individual height classes (Total stem,  $F_{1,16} = 3.31$ ,  $P > 0.10$ ; Height Classes  $F_{1,16} = 0.26-2.92$ ,  $P > 0.10$ ; Table 2-4, Figure 2-4). Planned comparisons revealed that aspen stem density was significantly greater in the 9-11 year-old ungrazed stands than grazed stands (17,167 stems ha<sup>-1</sup> in ungrazed stands compared to 9,600 stems ha<sup>-1</sup> grazed stands,  $F_{1,4} = 3.45$ ,  $P = 0.088$ , Table 2-4, Figure 2-5). Among individual height classes, the density of HC5 stems in 9-11 year-old ungrazed stands was significantly greater than that of grazed stands of the same age class (4,829 stems ha<sup>-1</sup> in ungrazed stands compared to 900 stems ha<sup>-1</sup> in grazed stands,  $F_{1,4} = 1.33$ ,  $P = 0.021$ , Table 2-4 and Figure 2-5). Density of HC1 aspen stems in 5-8 year-old grazed stands was twice that of ungrazed stands ( $F_{1,4} = 0.39$ ,  $P < 0.001$ ). The density of HC3 and HC4 stems were two times and four times greater, respectively in ungrazed than grazed 2-3 year-old stands ( $F_{1,4} = 6.75$ ,  $P = 0.023$ , and  $F_{1,4} = 0.15$ ,  $P = 0.090$ , respectively). No significant difference was found for cumulative stem density for all commercial stems between grazed and ungrazed 9-11 year-old stands ( $F_{1,4} = 3.04$ ,  $P = 0.107$ , Table 2-3, Figure 2-2).

Total stem density was lower in older stands, as time since harvest had a significant effect on aspen density ( $F_{2,12} = 4.99$ ,  $P = 0.026$ , Table 2-4 and Figure 2-4). Stem density of individual height classes was significantly different between many stand age classes (HC1 –  $F_{2,12} = 19.98$ ,  $P < 0.001$ ; HC2 –  $F_{2,12} = 23.59$ ,  $P < 0.001$ ; HC3 –  $F_{2,12} = 8.33$ ,  $P = 0.005$ ; HC4 –  $F_{2,12} = 16.95$ ,  $P < 0.001$ ; and HC5 –  $F_{2,12} = 92.36$ ,  $P < 0.001$ , Table 2-4 and Figure 2-4). Small height classes dominated 2-3 year-old stands, and larger height classes were more

prevalent in the 9-11 year-old stands (Table 2-3 and Table 2-4, Figure 2-3 and Figure 2-5).

#### *2.4.2. Comparison with other Regeneration Studies*

Aspen stem density compiled from a series of comparison studies (Pollard 1971, Bella and De Franceschi 1980, Weingartner 1980, Crouch 1981, Crouch 1983, Perala 1984, Bella 1986, Steneker 1976b, Dockrill 2001, DesRochers and Lieffers 2001, Berger et al. 2004) was higher than in the sites surveyed in and around Duck Mountain for the stands less than six years post-harvest (Figure 2-6). Rates of mortality were higher in most of the comparison studies, with an average stem decline between 2-3 year-old and 7-8 year-old stands of 73% over in the 2-3 stands from the comparison studies compared to an average stem decline of 18% in the Duck Mountain sites. Furthermore, seven to eight years after harvest, average stem density between the stands within the Duck Mountains and the comparison studies was quite similar (Figure 2-6). Beyond this point both grazed and ungrazed stands from the Duck Mountains appeared to have a higher average stem density than in the comparison studies (Figure 2-6).

#### *2.4.3. Tree Health*

Crown dieback was the only health index affected by grazing or time since harvest in aspen stems. There was an interaction between grazing and stand age in the crown dieback index for aspen ( $F_{2,12} = 4.68$ ,  $P = 0.031$ ). Aspen crown dieback was greater in ungrazed than grazed 2-3 year-old stands (41% vs. 30%, respectively, Table 2-5). In 9-11 year-old stands however, incidence of aspen crown dieback was greater in grazed than in ungrazed stands (34 vs. 29% respectively, Table 2-5). Aspen density was positively correlated with crown dieback ( $r = 0.52$ ,  $P = 0.028$ , Figure 2-7); but grazing pressure had no effect on incidence of crown dieback or stem density ( $P > 0.10$ ). The value of the vigour index for aspen ranged

from 17-30%, suggesting that aspen stands were stressed, although only one stand during sampling appeared to be in decline (Site – 2-3 G3, Table 2-5).

Balsam poplar in grazed stands had a significantly greater incidence of crown dieback (ungrazed  $25\% \pm 1\%$ , and grazed  $29\% \pm 4\%$ ,  $F_{1,12} = 9.2$ ,  $P = 0.010$ ) and necrosis (ungrazed  $28\% \pm 4\%$ , and grazed  $38\% \pm 9\%$ ,  $F_{1,12} = 20.66$ ,  $P < 0.001$ ) than in ungrazed stands (Table 2-6). In addition, levels of defoliation (2-3 year-old stands  $25\% \pm 0\%$ , 5-8 year-old stands  $26\% \pm 1\%$ , and 9-11 year-old stands  $28\% \pm 3\%$ ,  $F_{2,12} = 5.58$ ,  $P = 0.019$ ), damage to the stem (2-3 year-old stands  $27\% \pm 4\%$ , 5-8 year-old stands  $32\% \pm 12\%$ , and 9-11 year-old stands  $46\% \pm 8\%$ ,  $F_{2,12} = 5.31$ ,  $P = 0.022$ ), damage to the root collar (2-3 year-old stands  $26\% \pm 8\%$ , 5-8 year-old stands  $29\% \pm 11\%$ , and 9-11 year-old stands  $43\% \pm 2\%$ ,  $F_{2,12} = 5.47$ ,  $P = 0.021$ ), and leaf chlorosis (2-3 year-old stands  $26\% \pm 1\%$ , 5-8 year-old stands  $26\% \pm 6\%$ , and 9-11 year-old stands  $33\% \pm 11\%$ ,  $F_{2,12} = 5.60$ ,  $P = 0.019$ ) were all higher in 2-3 year-old stands than in 5-8 or 9-11 year-old stands (Table 2-6). A significant difference in levels of crown dieback was detected in the aligned rank transform test between stand ages ( $F_{2,12} = 36.00$ ,  $P < 0.001$ ), but no differences in crown dieback were detected for individual age classes in the post-hoc. A significant interaction between grazing and stand age for necrosis in balsam poplar was also found ( $F_{2,12} = 4.87$ ,  $P = 0.028$ ). Incidence of necrosis was 15% greater in 5-8 and 9-11 year-old grazed stands than similarly aged ungrazed stands ( $Z = -1.96$ ,  $P = 0.050$ , and  $Z = -2.09$ ,  $P = 0.37$  respectively, Table 2-6).

Gall-forming insects were more prevalent in ungrazed than grazed aspen stands, with an average incidence in aspen health tress of 15% in grazed and 4% in ungrazed sites ( $F_{1,12} = 12.04$ ,  $P = 0.003$ , Table 2-7). Conversely incidence of stem rust and leaf spot was higher on aspen in grazed sites (ungrazed  $10\% \pm 15\%$ , and grazed  $26\% \pm 27\%$ ,  $F_{1,12} = 9.63$ ,  $P = 0.007$ ;

and ungrazed  $29\% \pm 24\%$ , and grazed  $64\% \pm 36\%$ ,  $F_{1,12} = 41.16$ ,  $P < 0.001$ , respectively, Table 2-7).

Time since harvest also affected the presence of pests in aspen. Gall-forming insects were more prevalent on aspen stems in 5-8 year-old stands than 2-3 year-old stands (2-3 year-old stands  $3\% \pm 1\%$ , and 5-8 year-old stands  $17\% \pm 17\%$ ,  $Z = -2.08$ ,  $P = 0.037$ ). Symptoms of canker were less frequent in 2-3 year-old stands than 5-8 and 9-11 year-old stands, respectively (2-3 year-old stands  $0\%$ , 5-8 year-old stands  $47\% \pm 35\%$ , and 9-11 year-old stands  $70\% \pm 27\%$ ,  $Z = -2.99$ ,  $P = 0.002$ , and  $Z = -2.48$ ,  $P = 0.015$ , respectively). In 2-3 year-old stands incidence of stem rust was lower than 9-11 and 5-8 year-old stands (2-3 year-old stands  $0\%$ , 5-8 year-old stands  $17\% \pm 25\%$ , and 9-11 year-old stands  $37\% \pm 18\%$ ,  $Z = -2.29$ ,  $P = 0.065$ , and  $Z = -3.08$ ,  $P = 0.002$ , respectively). Incidence of leaf spot averaged was significantly greater in 2-3 year-old stands compared to 5-8 year-old stands (2-3 year-old stands  $20\% \pm 11\%$ , 5-8 year-old stands  $58\% \pm 33\%$ , and 9-11 year-old stands  $48\% \pm 52\%$ ,  $Z = -2.08$ ,  $P = 0.041$ , Table 2-7). Incidence of defoliators differed between stand ages ( $F_{2,12} = 10.33$ ,  $P = 0.002$ ), but the Mann-Whitney U test failed to detect differences between the specific age-classes ( $P > 0.10$ ).

Incidence of leaf rust differed significantly between treatments in aspen stems, ( $F_{2,12} = 5.87$ ,  $P = 0.017$ ). Incidence ranged from 0-65% of stems surveyed, but there was no consistent pattern within stand age or grazing status (Table 2-7). There was a greater abundance of leaf spot in the 9-11 year-old grazed than ungrazed stands (65% and 0%, respectively,  $F_{2,12} = 29.14$ ,  $P < 0.001$ , Table 2-7).

Forest tent caterpillar (*Lepidoptera: Malacosoma disstria* Hübner), a significant aspen defoliator, was observed in only one site (5-8 UG1), where heavy defoliation was

evident during the forest health assessment. The same stand was surveyed approximately the same time during the following year, and showed no signs of major defoliation.

The incidences of pests in balsam poplar were on average greater in grazed than ungrazed aspen stands (Table 2-8). These pests included leaf rollers (ungrazed  $2\% \pm 4\%$ , and grazed  $22\% \pm 33\%$ ,  $F_{1,12} = 30.03$ ,  $P < 0.001$ ); mining insects (ungrazed  $3\% \pm 7\%$ , and grazed  $11\% \pm 18\%$ ,  $F_{1,12} = 7.32$ ,  $P = 0.016$ ); skeletonizing insects (ungrazed  $9\% \pm 21\%$ , and grazed  $43\% \pm 43\%$ ,  $F_{1,12} = 9.01$ ,  $P = 0.008$ ); leaf rolling insects (ungrazed  $2\% \pm 5\%$ , and grazed  $15\% \pm 22\%$ ,  $F_{1,12} = 4.65$ ,  $P = 0.047$ ); and leaf spots (ungrazed  $50\% \pm 42\%$ , and grazed  $83\% \pm 12\%$ ,  $F_{1,12} = 25.41$ ,  $P < 0.001$ , Table 2-8). Only gall forming insects were present in greater numbers on balsam poplar stems in ungrazed than grazed stands ( $F_{1,12} = 13.70$ ,  $P = 0.002$ , Table 2-8).

Time since harvest had a significant effect on the presence on pests on balsam poplar stems, where there was usually a greater incidence of pests in 9-11 year-old stands than in 5-8 or 2-3 year-old stands. This included leaf rollers (2-3 year-old stands 0%, 5-8 year-old stands  $19\% \pm 34\%$ , and 9-11 year-old stands  $17\% \pm 26\%$ , 9-11 vs. 5-8:  $Z = -1.71$ ,  $P = 0.087$ , 9-11 vs. 2-3  $Z = -2.29$ ,  $P = 0.022$ ), skeletonizing insects (2-3 year-old stands 0%, 5-8 year-old stands  $37\% \pm 39\%$ , and 9-11 year-old stands  $40\% \pm 46\%$ , %, 9-11 vs. 2-3  $Z = -2.89$ ,  $P = 0.004$ ), gall-forming insects (2-3 year-old stands 0%, 5-8 year-old stands  $1\% \pm 2\%$ , and 9-11 year-old stands  $8\% \pm 6\%$ , %, 9-11 vs. 5-8:  $Z = -2.13$ ,  $P = 0.033$ , 9-11 vs. 2-3  $Z = -2.48$ ,  $P = 0.013$ ), incidence of canker (2-3 year-old stands 0%, 5-8 year-old stands  $32\% \pm 30\%$ , and 9-11 year-old stands  $23\% \pm 32\%$ , %, 9-11 vs. 2-3  $Z = -3.08$ ,  $P = 0.002$ , 5-8 vs. 2-3:  $Z = -2.29$ ,  $P = 0.022$ ), and stem rust (2-3 year-old stands 0%, 5-8 year-old stands  $10\% \pm 16\%$ , and 9-11 year-old stands  $32\% \pm 13\%$ , %, 9-11 vs. 5-8:  $Z = -1.96$ ,  $P = 0.050$ , 9-11 vs. 2-3  $Z = -3.07$ ,  $P =$

0.002). Incidence of pests was greatest in 9-11 year-old stands (Table 2-8). Only leaf rust was present in greater numbers on balsam poplar stems in the younger stands, averaging 42.8% in 9-11 year-old stands and 80% in 5-8 year-old stands compared to 76% in 2-3 year-old stands (9-11 vs. 2-3  $Z = -2.29$ ,  $P = 0.022$ , 5-8 vs. 2-3:  $Z = -1.89$ ,  $P = 0.059$ ). Leaf spots on balsam poplar were present in all treatments except for 9-11 year-old ungrazed sites.

Most treatment effects for balsam poplar were found between grazed and ungrazed sites in the 9-11 year-old age class (Table 2-8). Presence of leaf rollers, leaf miners, skeletonizing insects, and leaf spots in balsam poplar was significantly greater in grazed 9-11 year-old stands, where differences between grazed and ungrazed stands ranged from 14-86% ( $P < 0.10$ ). Gall forming insects were more prevalent on balsam poplar stems in the 9-11 year-old ungrazed than similarly aged grazed stands ( $Z = 2.09$ ,  $P = 0.037$ , Table 2-8).

#### 2.4.4. Soil Variables

Most sites were classified as poorly drained, and there was a wide range in organic matter content. The clay fraction in the soil varied between 5 -35% (Appendix 3). Soil pH among sites had an average of  $6.89 \pm 0.49$ , although 10 of the 16 sites sampled for pH were slightly basic (Appendix 3).

Grazing pressure was not significantly correlated with either bulk density ( $r = -0.18$ ,  $P = 0.670$ ) or soil compaction ( $r = 0.13$ ,  $P = 0.756$ , Appendix 3). Values of soil compaction appeared to be independent of soil moisture content and bulk density at all soil depths, although regressions of the three variables were statistically significant ( $P < 0.017$ ), the  $r^2$  values ranged from 0.02 to 0.08 (Appendix 3). Since no biologically significant relationships were observed among the three variables (observed from the non-significance of the

regression), raw soil compaction data were used in subsequent analyses instead of standardizing them using a soil moisture correction factor. Average levels of soil compaction within a profile were  $699 \pm 233$  kPa in ungrazed stands and  $739 \pm 184$  kPa in grazed stands.

#### 2.4.5 Principle Components Analysis (PCA)

In the PCA of species stem totals, the first two axes (PCA-1 and PCA-2) explained 55.2% of the variation in the species abundances (Figure 2-8). There were not any obvious gradients in either stand age or grazing class. Aspen density was not closely associated with the densities of the other two commercial species, balsam poplar and white birch. Furthermore, aspen was negatively associated with non-commercial species, such as *Salix* spp., *Alnus rugosa* and *Prunus virginiana*.

Both the PCA of total stem density of pooled height classes and the PCA of height class pseudospecies separated commercial poplar species from non-commercial trees and tall shrubs (Figure 2-8 and Figure 2-9). In the PCA with height class pseudospecies, the first two axes explained 42.9% of the variation in the species data (Figure 2-9). The first axis separated plots based on time since harvest, with 9-11 year-old stands located on the right side of the axis, transitioning to the more recent harvests on the left side of the axis. The younger harvests were associated with the three smallest height classes of the three commercial species. In addition, the same sites were negatively associated with HC4 and HC5 of the commercial species, which were principally associated with the 9-11 year-old stands. With the exception of HC2 of *Quercus macrocarpa*, all other non-commercial pseudospecies were distributed on the right side of PCA-1. The second axis of the

pseudospecies PCA separated the HC1-3 from HC4-5 of aspen. However, the height class distribution was not reflected in the distribution of sites by stand age.

#### 2.4.6. Redundancy Analysis (RDA)

In the RDA of pooled height classes, the first two axes explained 25.5% of the variation in the species data (Figure 2-10). However, neither the patterns observed in the first axis (RDA-1) nor the pooled axes were statistically significant ( $P > 0.10$ ), and therefore we used this analysis for exploratory purposes only. Aspen density was higher in soils with relatively high values soil compaction, relatively high clay content, and poorer soil drainage. Soil organic matter content, pH and bulk density were positively associated with balsam poplar and white birch, while the other environmental variables displayed no obvious patterns of association with either species. The majority of environmental variables were negatively associated with non-commercial species. Aspen density was negatively associated with all other species excluding the other commercial species and *Acer spicatum*. With the exception of soil drainage class, all soil environmental variables were positively associated with each other.

The first two axes of the RDA of height class pseudospecies explained 25.3% of the variation in the species data (Figure 2-11). The RDA was marginally significant based on the Monte Carlo permutation test ( $P = 0.078$ ), but individual environmental variables were not significant. Similar to the PCA of pseudospecies (Figure 2-9), the first axis (RDA-1) separated stand age classes, although the transition between the 5-8 and 9-11 year-old stands was less distinct (Figure 2-11). The non-commercial and shrub species (i.e., *Alnus rugosa*, *Quercus macrocarpa*, *Prunus pennsylvanica*, *Salix* spp., etc.) were mostly present on the left side of the axis, and were associated with 9-11 year-old stands, whereas most of the smaller



commercial stems were on the upper right quadrant in proximity to most of the 2-3 year-old stands. The tallest stems of aspen and balsam poplar were negatively associated with the environmental variables, and the three smallest height classes of commercial species.

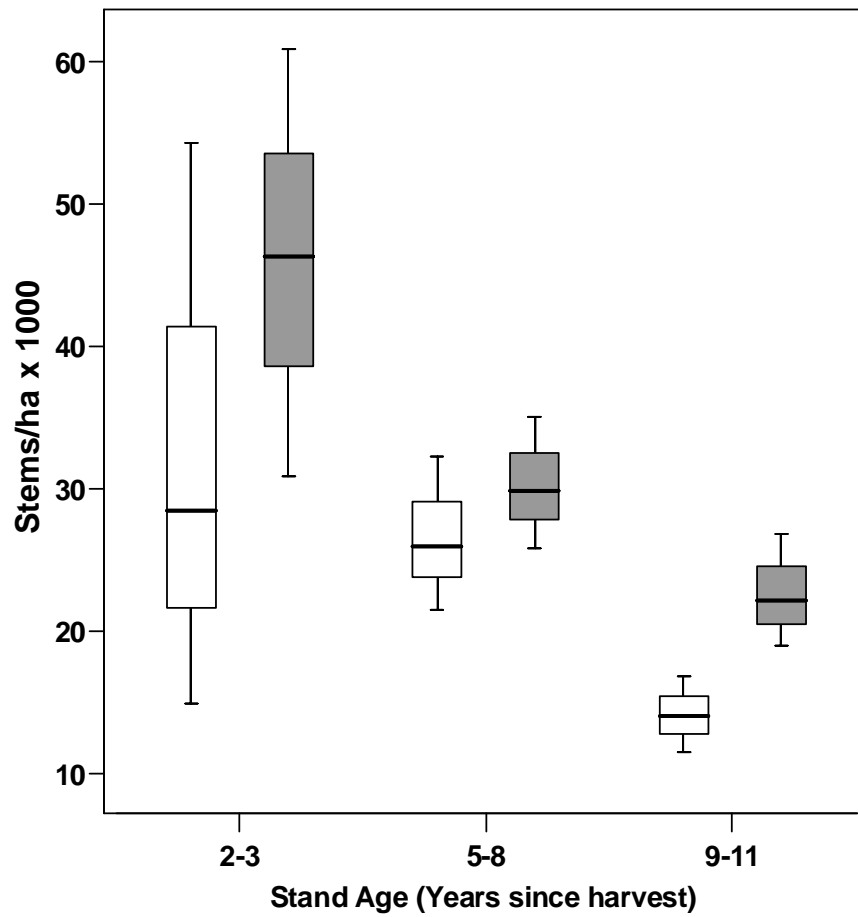
#### *2.5.7. Partial RDA*

In the partial RDA of species stem totals, 41.4% of the total variance in species assemblages was explained (Table 2-9). Grazing pressure explained only 3.5% of the variance in cumulative stem density, and environmental variables explained 36.1 % of the total variance. Shared variation of grazing pressure and soil variables explained only 1.7% of total variation, implying that the two sets of variables were operating almost independently of each other. The pattern of explained variation was repeated in the height class pseudospecies partial RDA. In this case, 42.8% of the variation of species assemblages was explained. Of this total, soil variables explained 36.8 % of the variation, 4.3% was explained by grazing pressure and 1.7 % by the shared variance of grazing pressure and soil variables (Table 2-10).

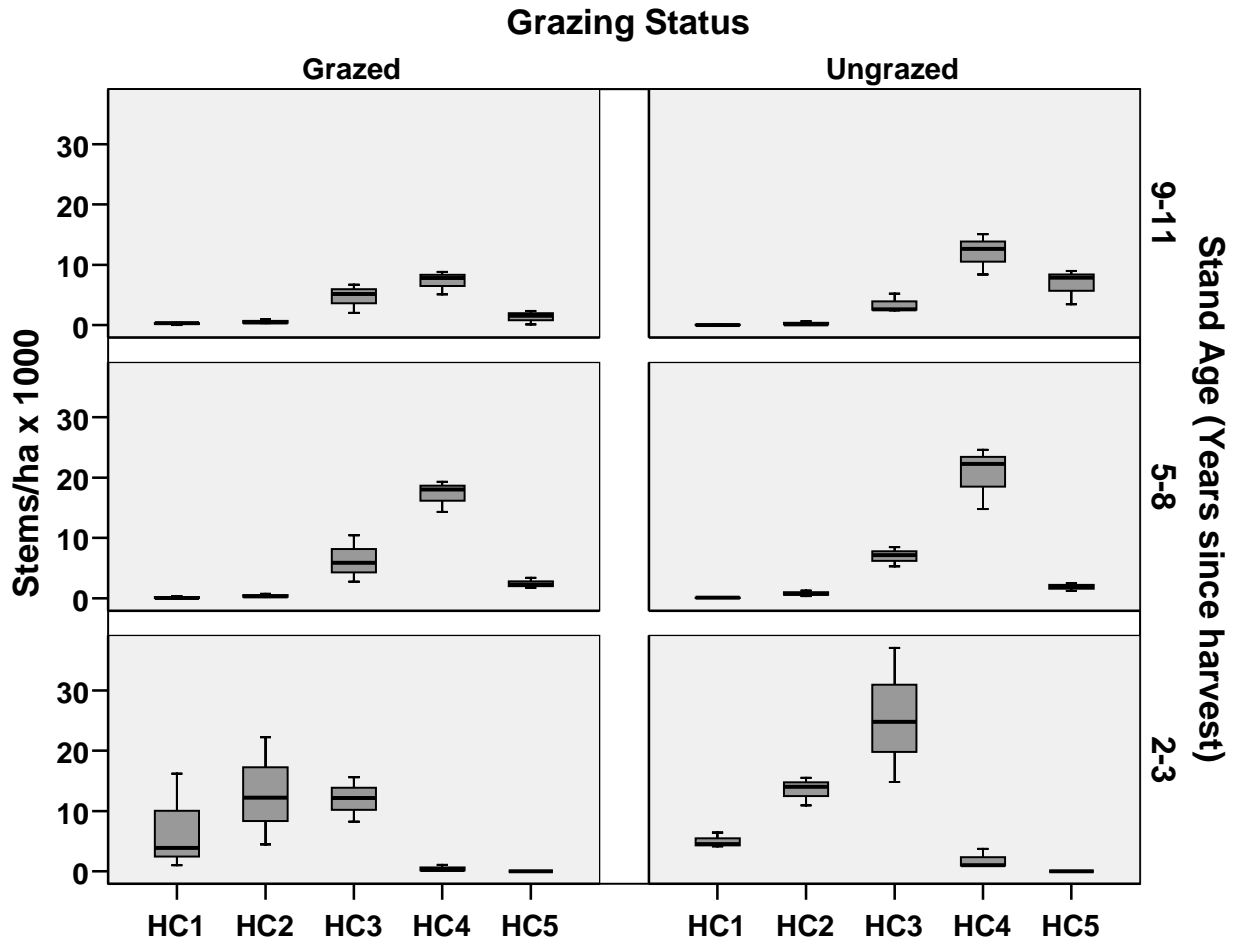
**Table 2-3:** Contrast table of mean stem densities (stems ha<sup>-1</sup>) and standard deviations (in brackets) for all commercial species (aspen, balsam poplar, and white birch) between grazing treatments within each stand age class.

	<b>+HC1</b>		<b>HC2</b>		<b>HC3</b>		<b>HC4</b>		<b>HC5</b>		<b>Total</b>	
9-11UG <sup>1</sup>	45.4	(38.41)	292.0	(312.51)	3444.1	(1549.31)	12055.5	(3374.98)	<b>*6774.1</b>	(2901.09)	22611.0	(4004.20)
9-11G	238.8	(177.02)	585.5	(358.00)	4650.9	(2366.78)	7253.7	(1906.78)	<b>*1349.7</b>	(1148.48)	14078.5	(2675.84)
5-8UG	140.5	(194.92)	412.3	(288.83)	6347.6	(3874.07)	17206.0	(2582.44)	2465.4	(817.33)	26571.9	(5417.54)
5-8G	92.8	(53.81)	782.8	(439.43)	6968.3	(1603.45)	20544.7	(5120.64)	1880.5	(629.59)	30269.2	(4629.26)
2-3UG	5038.9	(1233.33)	13500.1	(2324.24)	<b>*25562.7</b>	(11129.92)	<b>*1882.6</b>	(1586.70)	5.1	(8.86)	45989.4	(14973.28)
2-3G	7028.9	(8054.34)	12998.8	(8910.63)	<b>*12001.2</b>	(3685.64)	<b>*470.6</b>	(552.77)	0.0	(0.00)	32499.5	(20031.44)

Note: <sup>1</sup> 9-11 = Years since harvest, UG – Ungrazed and G – Grazing. All bolded results indicated significant differences at  $P < 0.1$ . +HC refers to height class.



**Figure 2-2:** Boxplots of total stems  $\text{ha}^{-1}$  of all commercial tree species (aspen, balsam poplar, and white birch). Uncoloured boxes represent the grazed sites, and shaded boxes represent the ungrazed sites.

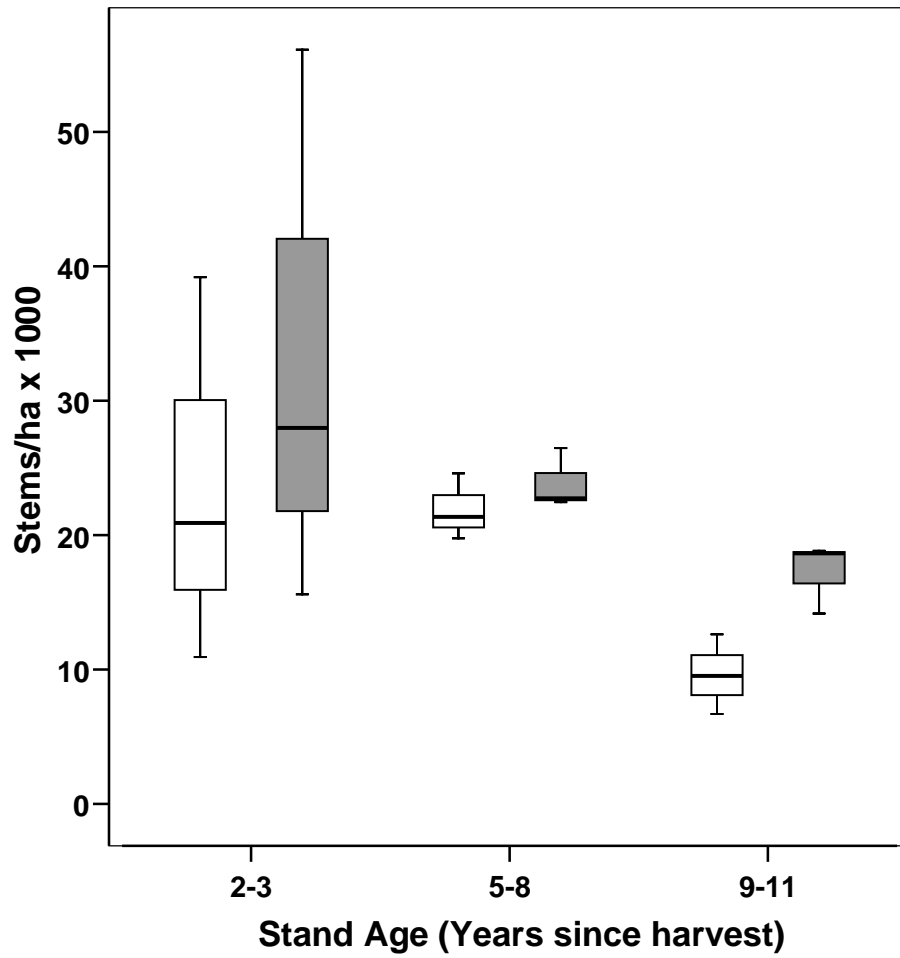


**Figure 2-3:** Boxplots of stems  $\text{ha}^{-1}$  of all commercial tree species (aspen, balsam poplar, and white birch).

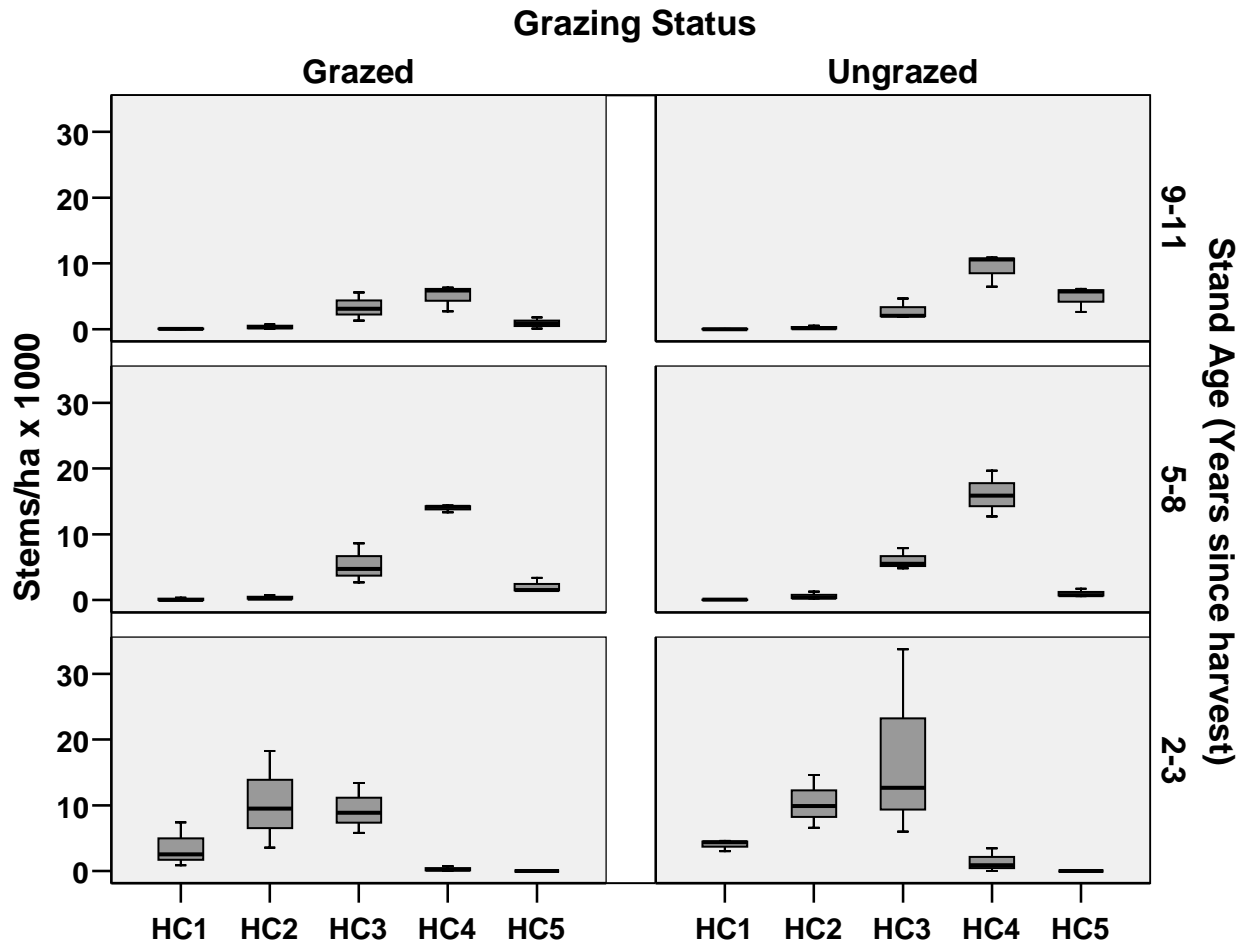
**Table 2-4:** Contrast table of mean stem densities (stems ha<sup>-1</sup>) and standard deviations (in brackets) for aspen between grazing treatments within each stand age class.

	<b>+HC1</b>		<b>HC2</b>		<b>HC3</b>		<b>HC4</b>		<b>HC5</b>		<b>Total</b>	
9-11UG <sup>1</sup>	5.3	(9.11)	236.5	(232.67)	2841.7	(1560.53)	9254.0	(2569.71)	<b>*4829.6</b>	(1934.21)	<b>*17167.3</b>	(2722.06)
9-11G	39.8	(42.01)	344.0	(360.67)	3338.7	(2134.75)	4976.9	(1976.09)	<b>*900.3</b>	(835.37)	<b>*9599.8</b>	(2962.75)
5-8UG	<b>*66.5</b>	(49.33)	608.8	(540.49)	6108.	(1659.45)	16170.5	(3392.11)	1018.0	(596.82)	23971.8	(2182.98)
5-8G	<b>*127.4</b>	(191.31)	365.6	(326.64)	5312.0	(3014.08)	13989.6	(521.16)	2069.7	(1119.72)	21864.2	(2501.54)
2-3UG	3647.4	(977.91)	9622.5	(4629.33)	16661.6	(15110.02)	1396.6	(1792.63)	5.1	(8.86)	31333.1	(22271.28)
2-3G	3447.9	(3316.35)	10006.1	(7299.56)	8926.7	(3873.56)	291.6	(339.37)	0.0	(0.00)	22672.4	(14237.87)

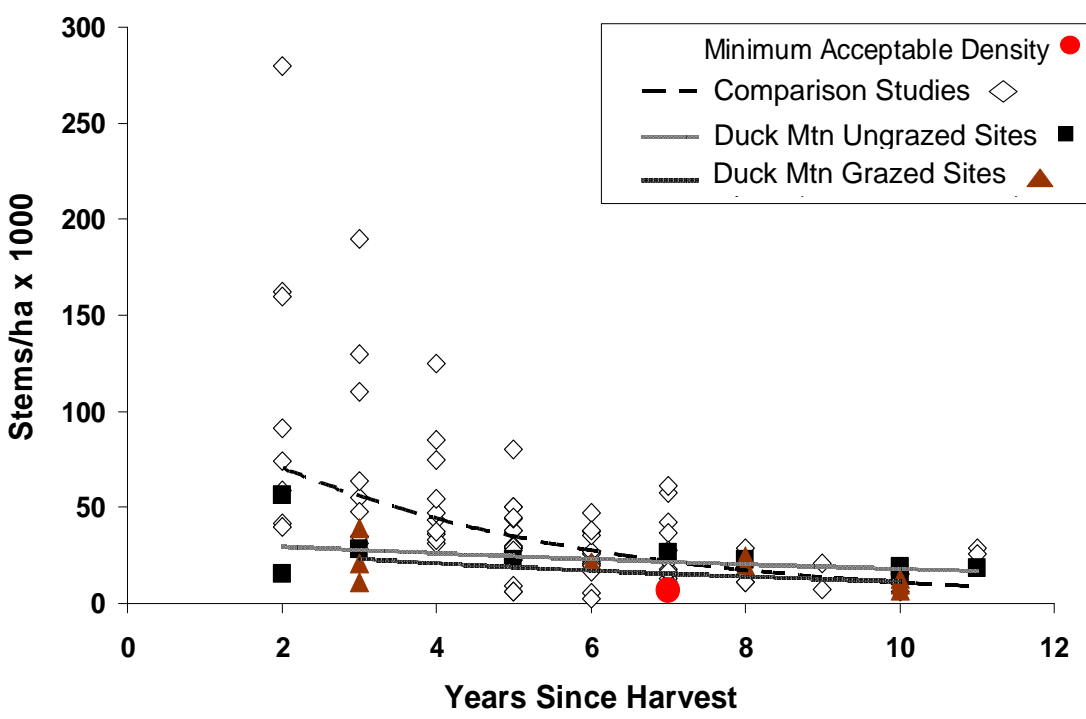
Note: <sup>1</sup> 9-11 = Years since harvest, UG – Ungrazed and G – Grazing. All bolded results indicated significant differences at  $P < 0.1$ . +HC refers to height class.



**Figure 2-4:** Boxplots of total stems  $\text{ha}^{-1}$  of aspen within each treatment. Uncoloured boxes represent grazed sites, and shaded boxes represent the ungrazed sites.



**Figure 2-5:** Boxplots of stems  $\text{ha}^{-1}$  of aspen of each height class within each treatment.



**Figure 2-6:** A comparison of stand density of aspen stems amongst naturally regenerating clear-cut stands from multiple comparison studies ( $y = 113.000^{18\exp-0.2367x}$ ,  $r^2 = 0.35$ ), and the grazed ( $y = 31.000^{501\exp-0.0987x}$ ,  $r^2 = 0.31$ ) and ungrazed stands ( $y = 33.758^{\exp-0.0611x}$ ,  $r^2 = 0.29$ ) from this study.



**Table 2-5:** Mean health indices and standard deviations (in brackets) for aspen. Values with different letters indicate significant differences (Mann-Whitney U test,  $P \leq 0.1$ ).

Treatment	Vigour		Crown Dieback		Defoliation		MD1		MD2		Chlorosis		Necrosis	
9-11UG	0.21	(0.057)	0.29	(0.018)a	0.27	(0.021)	0.22	(0.007)	0.21	(0.009)	0.25	(0.003)	0.30	(0.023)
9-11G	0.29	(0.144)	0.34	(0.003)cd	0.27	(0.019)	0.33	(0.125)	0.28	(0.118)	0.26	(0.013)	0.33	(0.017)
5-8UG	0.30	(0.015)	0.33	(0.095)abc	0.32	(0.121)	0.37	(0.215)	0.31	(0.168)	0.27	(0.018)	0.27	(0.008)
5-8G	0.25	(0.099)	0.34	(0.063)ad	0.29	(0.016)	0.43	(0.115)	0.38	(0.137)	0.29	(0.040)	0.31	(0.053)
2-3UG	0.19	(0.015)	0.41	(0.028)e	0.31	(0.022)	0.44	(0.005)	0.34	(0.122)	0.30	(0.030)	0.33	(0.023)
2-3G	0.27	(0.136)	0.30	(0.055)b	0.27	(0.011)	0.32	(0.095)	0.27	(0.118)	0.26	(0.014)	0.31	(0.029)

Note: Abbreviation definitions are as follows: MD1 – Mechanical damage to the stem, MD2 – Mechanical damage to the root collar.

**Table 2-6:** Mean health indices and standard deviations (in brackets) for balsam poplar. Values with different letters indicate significant differences (Mann-Whitney U test,  $P \leq 0.1$ ).

Treatment	Vigour		Crown Dieback		Defoliation		MD1		MD2		Chlorosis		Necrosis	
9-11UG	0.42	(0.018)	0.25	(0.000)	0.25	(0.000)	0.29	(0.059)	0.23	(0.023)	0.26	(0.011)	0.25	(0.000)a
9-11G	0.36	(0.188)	0.31	(0.064)	0.25	(0.005)	0.26	(0.016)	0.28	(0.108)	0.26	(0.009)	0.40	(0.110)cd
5-8UG	0.14	(0.149)	0.25	(0.000)	0.25	(0.006)	0.31	(0.079)	0.27	(0.118)	0.27	(0.018)	0.28	(0.023)ab
5-8G	0.32	(0.138)	0.27	(0.034)	0.27	(0.016)	0.34	(0.163)	0.30	(0.127)	0.31	(0.086)	0.43	(0.091)d
2-3UG	0.19	(0.047)	0.26	(0.015)	0.27	(0.010)	0.41	(0.011)	0.41	(0.002)	0.34	(0.062)	0.31	(0.043)bc
2-3G	0.22	(0.071)	0.28	(0.030)	0.29	(0.047)	0.50	(0.100)	0.44	(0.026)	0.31	(0.044)	0.30	(0.032)bc

Note: Abbreviation definitions are as follows: MD1 – Mechanical damage to the stem, MD2 – Mechanical damage to the root collar.

**Table 2-7:** Mean pest indices and standard deviations (in brackets) for aspen. Values with different letters indicate significant differences (Mann-Whitney U test,  $P \leq 0.1$ ).

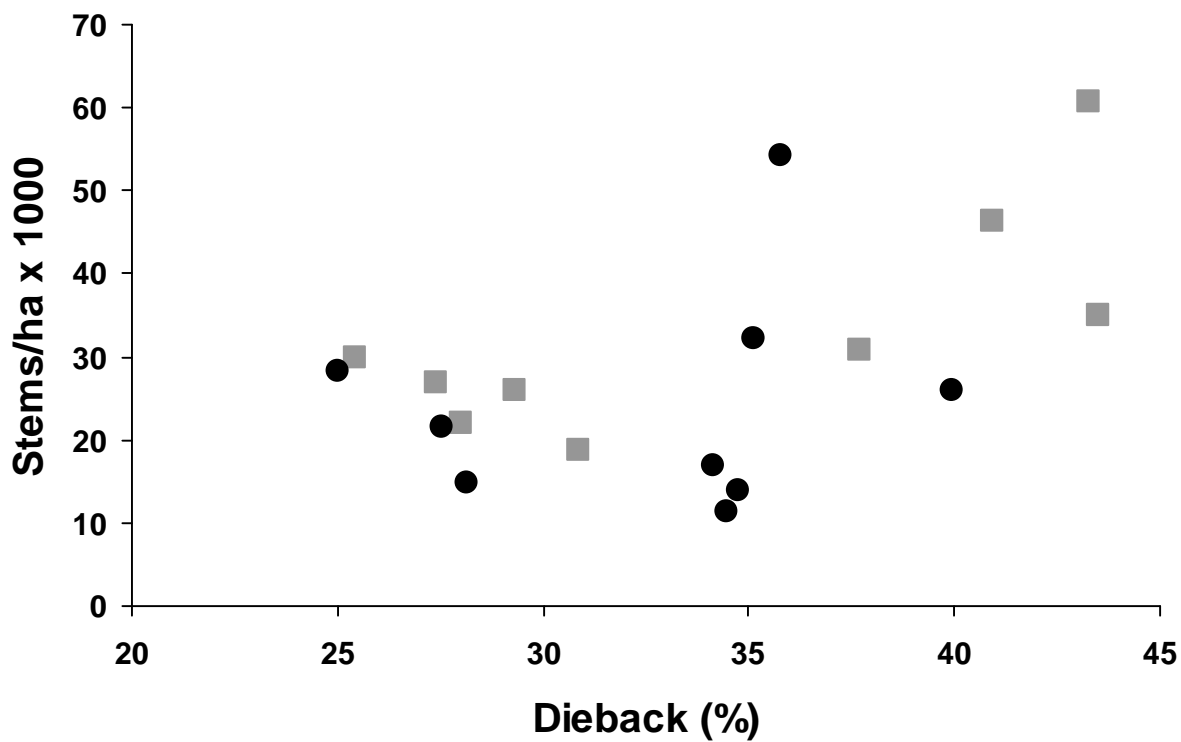
Treatment	Roll	Mine	Def	Skel	Gall	Suc	LR	CA	SR	LS
9-11UG	0.03 (0.038)	0.01 (0.005)	0.00 (0.005)	0.98 (0.019)	0.15 (0.063)	0.33 (0.187)	0.00 (0.000)a	0.76 (0.085)	0.28 (0.153)	0.00 (0.005)b
9-11G	0.07 (0.066)	0.27 (0.307)	0.84 (0.153)	0.99 (0.021)	0.02 (0.018)	0.63 (0.543)	0.65 (0.224)c	0.63 (0.409)	0.47 (0.181)	0.95 (0.038)c
5-8UG	0.07 (0.060)	0.36 (0.462)	0.12 (0.186)	0.74 (0.315)	0.25 (0.205)	0.27 (0.222)	0.20 (0.285)bc	0.50 (0.437)	0.03 (0.029)	0.37 (0.301)a
5-8G	0.01 (0.011)	0.18 (0.214)	0.43 (0.433)	0.76 (0.390)	0.08 (0.084)	0.56 (0.467)	0.27 (0.456)abc	0.43 (0.325)	0.30 (0.309)	0.80 (0.212)c
2-3UG	0.00 (0.000)	0.01 (0.004)	0.00 (0.008)	0.54 (0.131)	0.03 (0.003)	0.15 (0.034)	0.05 (0.076)ab	0.00 (0.000)	0.00 (0.000)	0.21 (0.173)a
2-3G	0.00 (0.000)	0.02 (0.024)	0.02 (0.015)	0.50 (0.109)	0.02 (0.012)	0.10 (0.028)	0.01 (0.018)ab	0.01 (0.009)	0.00 (0.000)	0.19 (0.044)a

Note: Heading definitions are as follows: Roll – leaf rolling insects, Mine – leaf mining insects, Def – defoliating insects, Skel – skeletonizing insects, Gall – gall forming insects, Suc – leaf sucking insects, LR – leaf rust, CA – Canker, SR – stem rust, and LS – leaf spots.

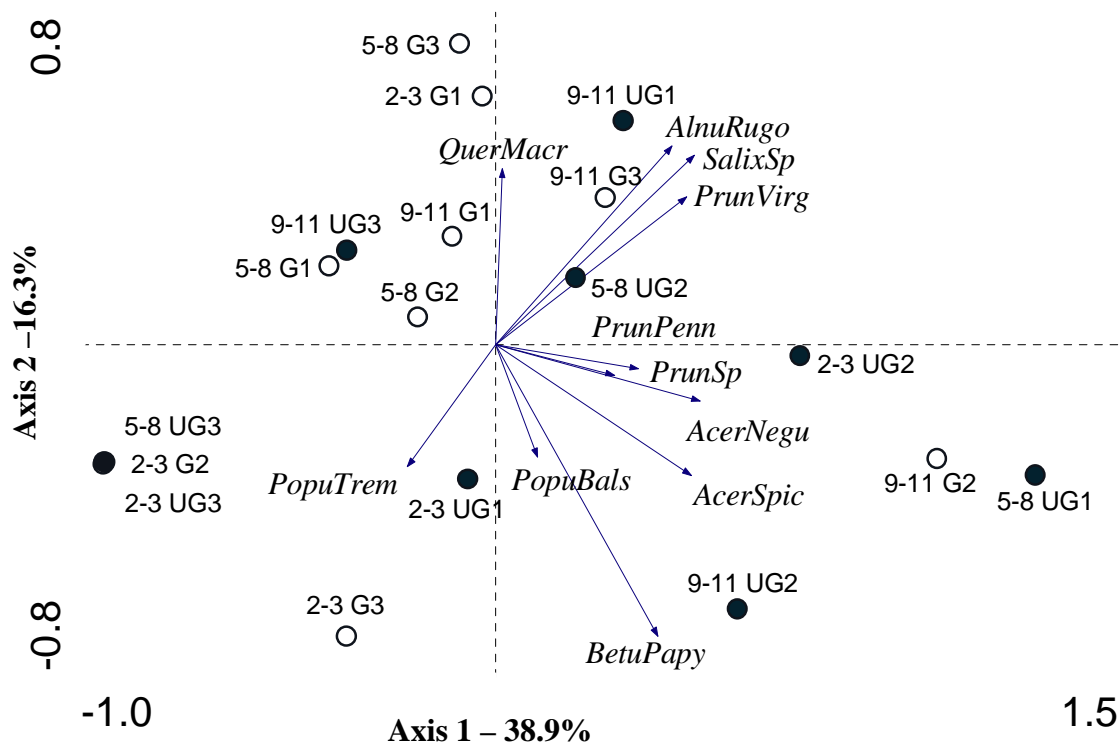
**Table 2-8:** Mean pest indices and standard deviations (in brackets) for balsam poplar. Values with different letters indicate significant differences (Mann-Whitney U test,  $P \leq 0.1$ ).

Treatment	Roll	Mine	Def	Skel	Gall	Suc	LR	CA	SR	LS
9-11UG	0.05 (0.082)a	0.02 (0.043)ab	0.00 (0.000)	0.85 (0.076)b	0.13 (0.023)b	0.32 (0.364)	0.02 (0.041)	0.77 (0.136)c	0.35 (0.176)ab	0.00 (0.000)a
9-11G	0.43 (0.135)b	0.26 (0.245)b	0.81 (0.178)	0.99 (0.019)b	0.02 (0.018)a	0.51 (0.488)	0.31 (0.323)	0.48 (0.222)bc	0.29 (0.073)b	0.86 (0.061)b
5-8UG	0.03 (0.046)a	0.07 (0.115)ab	0.26 (0.336)	0.72 (0.477)ab	0.00 (0.000)a	0.16 (0.147)	0.04 (0.069)	0.34 (0.358)ab	0.00 (0.000)a	0.73 (0.385)b
5-8G	0.01 (0.025)a	0.03 (0.042)ab	0.48 (0.486)	0.66 (0.470)ab	0.02 (0.034)a	0.53 (0.383)	0.34 (0.465)	0.30 (0.309)ab	0.21 (0.182)a	0.88 (0.110)b
2-3UG	0.00 (0.000)a	0.00 (0.005)a	0.00 (0.000)	0.39 (0.132)a	0.00 (0.000)a	0.13 (0.115)	0.00 (0.000)	0.00 (0.000)a	0.00 (0.000)a	0.77 (0.086)b
2-3G	0.00 (0.000)a	0.02 (0.020)ab	0.02 (0.004)	0.26 (0.085)a	0.01 (0.009)a	0.14 (0.013)	0.00 (0.000)	0.00 (0.000)a	0.00 (0.000)a	0.75 (0.158)b

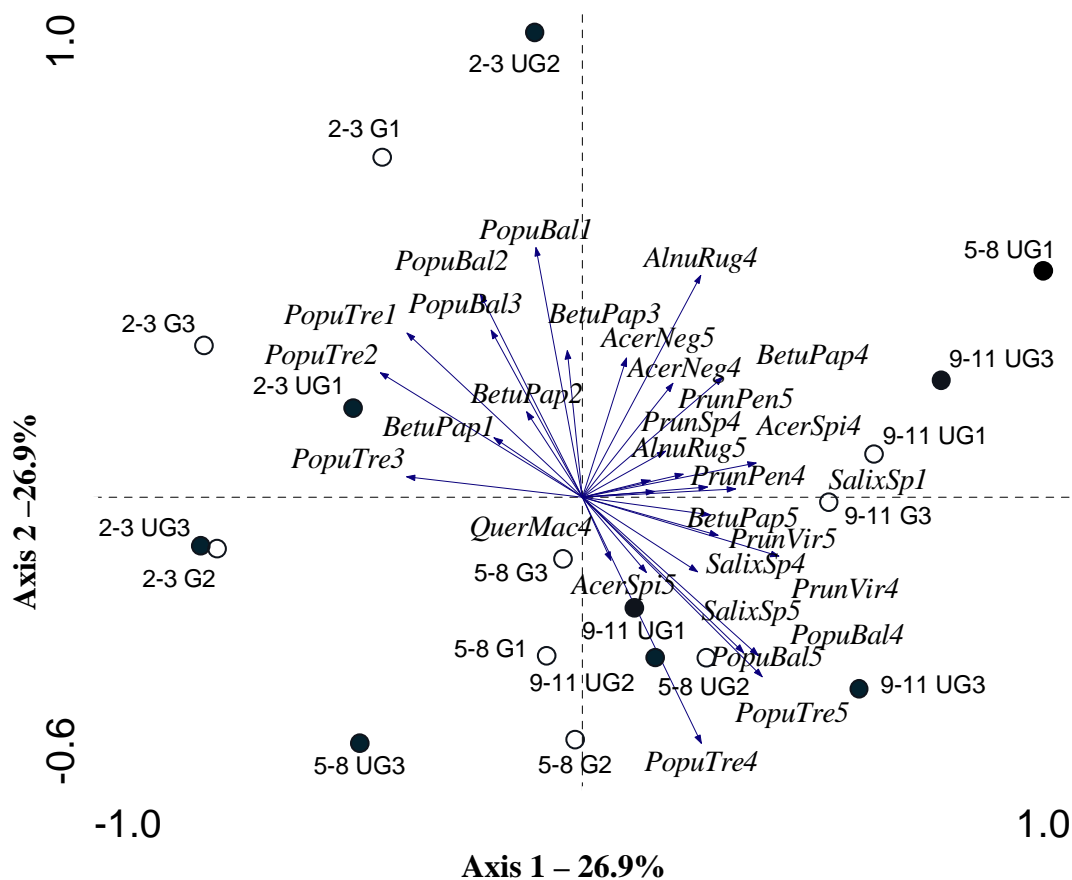
Note: Heading definitions are as follows: Roll – leaf rolling insects, Mine – leaf mining insects, Def – defoliating insects, Skel – skeletonizing insects, Gall – gall forming insects, Suc – leaf sucking insects, LR – leaf rust, CA – Canker, SR – stem rust, and LS – leaf spots.



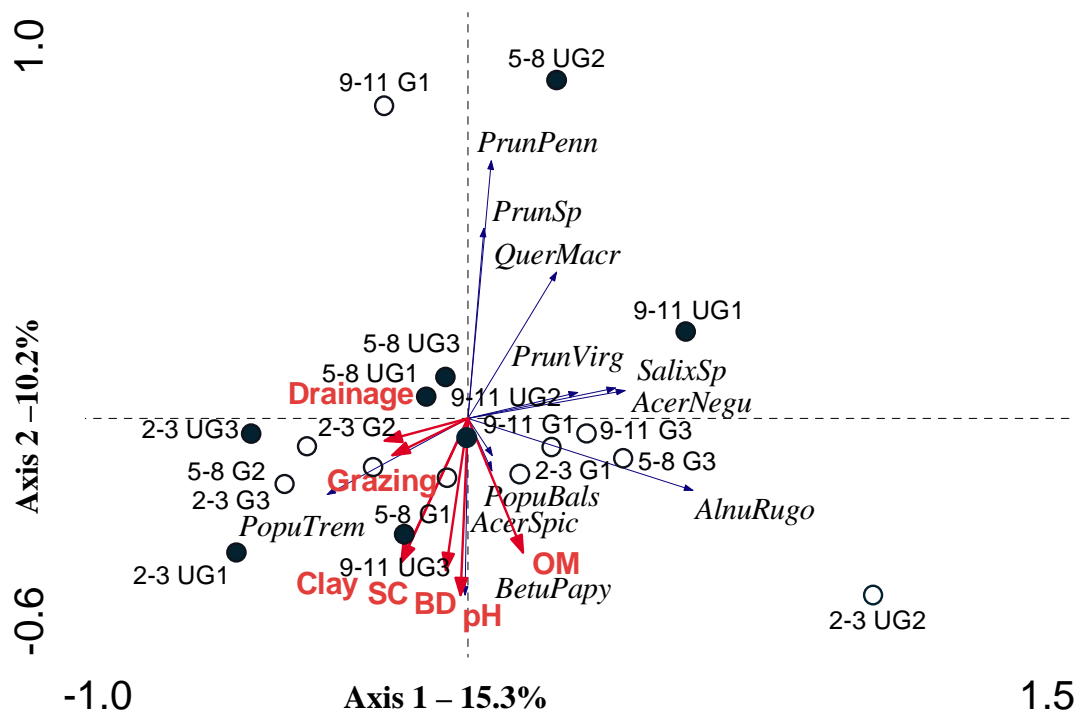
**Figure 2-7:** Scatter plot of crown dieback (%) and stem density (stems ha<sup>-1</sup>) of aspen in all plots (n = 18). Grey squares represent ungrazed stand, and black circles represent grazed stands.



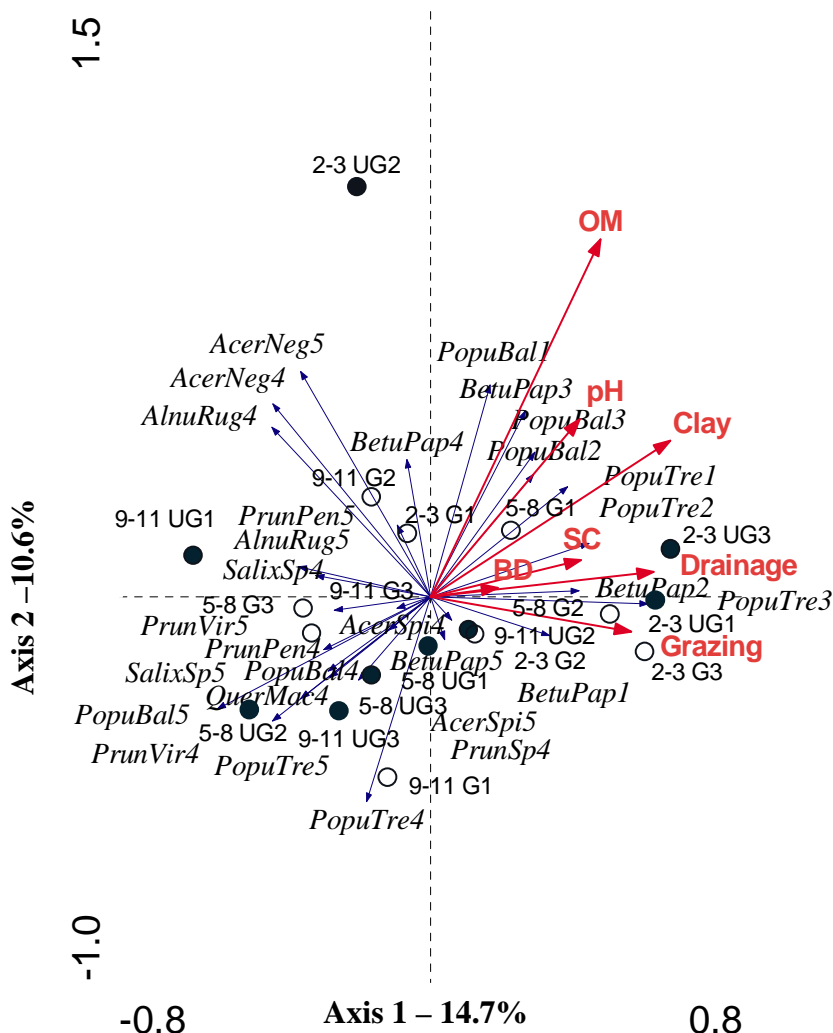
**Figure 2-8:** Total stem density for each tree species observed – PCA Ordination diagram with plots (O) and species by height class (arrows). Uncoloured circles represent grazed plots and coloured circles represent ungrazed plots. Tree species are: *AcerNegu* = *Acer negundo*, *AcerSpic* = *Acer spicatum*, *AlnuRugo* = *Alnus rugosa*, *BetuPapy* = *Betula papyrifera*, *PopuBals* = *Populus balsamifera*, *PopuTrem* = *Populus tremuloides*, *PrunPenn* = *Prunus pennsylvanica*, *PrunSp* = *Prunus* spp., *PrunVirg* = *Prunus virginiana*, *QuerMacr* = *Quercus macrocarpa*, *SalixSp* = *Salix* spp.



**Figure 2-9:** Individual height classes of all tree species observed – PCA Ordination diagram with plots (O) and species by height class (arrows). Uncoloured circles represent grazed plots and coloured circles represent ungrazed plots. Species height classes 1 - 5. Tree species are: AcerNeg = *Acer negundo*, AcerSpi = *Acer spicatum*, AlnuRug = *Alnus rugosa*, BetuPap = *Betula papyrifera*, PopuBal = *Populus balsamifera*, PopuTre = *Populus tremuloides*, PrunPen = *Prunus pennsylvanica*, PrunSp = *Prunus* spp., PrunVir = *Prunus virginiana*, QuerMac = *Quercus macrocarpa*, SalixSp = *Salix* spp. Note: for display purposes, height classes 1-3 for all non-commercial species were suppressed.



**Figure 2-10:** Total stem density for each tree species observed – RDA Ordination diagram with plots (O), species by height class (thin arrows) and environmental variables (thick arrows). Uncoloured circles represent grazed plots and coloured circles represent ungrazed plots. Tree species are: *AcerNegu* = *Acer negundo*, *AcerSpic* = *Acer spicatum*, *AlnuRugo* = *Alnus rugosa*, *BetuPapy* = *Betula papyrifera*, *PopuBals* = *Populus balsamifera*, *PopuTrem* = *Populus tremuloides*, *PrunPenn* = *Prunus pennsylvanica*, *PrunSp* = *Prunus* spp., *PrunVirg* = *Prunus virginiana*, *QuerMacr* = *Quercus macrocarpa*, *SalixSp* = *Salix* spp. Environmental variables are: Drainage = drainage class, OM – organic matter content, Clay – clay fraction, pH, SC – soil compaction, BD – bulk density and Grazing – grazing pressure.



**Figure 2-11:** Individual height classes of all tree species observed – RDA Ordination diagram with plots (O), species by height class (thin arrows) and environmental variables (thick arrows). Uncoloured circles represent grazed plots and coloured circles represent ungrazed plots. Species height classes 1-5. Tree species are: AcerNeg = *Acer negundo*, AcerSpi = *Acer spicatum*, AlnuRug = *Alnus rugosa*, BetuPap = *Betula papyrifera*, PopuBal = *Populus balsamifera*, PopuTre = *Populus tremuloides*, PrunPen = *Prunus pennsylvanica*, PrunSp = *Prunus* spp., PrunVir = *Prunus virginiana*, QuerMac = *Quercus macrocarpa*, SalixSp = *Salix* spp. Environmental variables are: Drainage = drainage class, OM – organic matter content, Clay – clay fraction, pH, SC – soil compaction, BD – bulk density and Grazing – grazing pressure.

**Table 2-9:** Results of RDA partial ordination of stem totals.

Source of variation	Sum of Canonical Values
Environment	0.361
Grazing	0.035
Shared environment and grazing	0.018
Unexplained variation	0.586
Total	1.000

Note:  $P > 0.1$  for all of these values.

**Table 2-10:** Results of RDA partial ordination of pseudospecies.

Source of variation	Sum of Canonical Values
Environment	0.368
Grazing	0.043
Shared environment and grazing	0.017
Unexplained variation	0.589
Total	1.000

Note:  $P > 0.1$  for all of these values. In addition, total variation may exceed 1.00 because of rounding errors.



## 2.5. Discussion

### 2.5.1. Tree Density

The presence of cattle in regenerating aspen stands appeared to cause a reduction in average stem height and a noticeable reduction in stem density (Figure 2-2 and Figure 2-4). Although, grazing intensity was not correlated with stem density of aspen or pooled commercial species, the presence of cattle was found to affect stem density of the pooled commercial hardwood stems as observed in the ANOVA (Figure 2-2). Planned comparisons revealed that height reductions were concentrated in grazed 9-11 year-old stands. Note, that although box plots suggest an overall reduction in aspen stem density, a difference may not have been detected statistically due to low power of sample size (i.e., each grazing-stand age combinations had only three replicates).

Although cattle grazing affected stem density, all stands in our study met or exceeded the minimum stem density required for seven year-old hardwood stands in Province of Manitoba stocking guidelines (Manitoba Conservation 2001, Figure 2-6). Aspen stem density in the Duck Mountain region at six to seven years post harvest was comparable to aspen stem densities in other studies with similar ages. This observation suggests that long term grazing below to slightly above recommended stocking levels did not affect the ability of stands to regenerate to adequate commercial stem densities in the sites under investigation.

Figure 2-6 also supports the general finding that aspen stands converge on a common density approximately six to seven years after disturbance irrespective of the range of initial stem densities present (Peterson and Peterson 1992, Bokalo *et al.* 2007).

Other studies have also shown that aspen can regenerate to adequate levels in the presence of cattle (Dockrill *et al.* 2004, Krzic *et al.* 2004). It should be noted, however, that in these studies the grazing period was both shorter and less variable than in my study (i.e., 0.5-2.0 months in Dockrill *et al.* 2004, Krzic *et al.* 2004 versus 1.5-9.5 months in any given year of my study).

Several of the grazed stands had cattle stocking levels exceeding that recommended by Manitoba Agriculture for the individual land parcel. Recommended grazing capacity of individual land parcels were exceeded on average 1.49 AUM ha<sup>-1</sup>, with only three of the nine grazed sites exceeding recommended grazing capacity by more than 0.45 AUM ha<sup>-1</sup>. Additionally, there was no correlation between grazing pressure and stem density. Furthermore, cattle in most sites had additional access to surrounding pasture and were provided with supplements to the available graze (e.g., hay, oats, etc.). It was therefore likely that sufficient forage was available in aspen stands and the surrounding pasture to sustain the cattle on their preferred sources of forage and to discourage them from switching their diet from grasses and forbs towards aspen on a long term basis (Fitzgerald *et al.* 1986). There was one stand that did appear to be in decline (2-3G3) where grazing pressure greatly exceeded recommended levels, although, this observation was made two years after the sampling of the stand. In regard to the reduced height of the aspen stems in grazed stands, some browsing of aspen is likely to occur even when the preferred source of forage is available for cattle (Hilton and Bailey 1974). For this reason, a deferral of cattle grazing after harvest is often recommended to allow aspen to reach a height where cattle cannot reach the leading stem (Sampson 1919, Dockrill 2001). In the Duck Mountain study

however, there was no grazing deferral in eight of the nine grazed stands, and a one year deferral in the remaining stand (9-11 G3).

### 2.5.2. Tree Health

Crown dieback may be a precursor to serious stem mortality during the self-thinning of aspen stands (Graham *et al.* 1963). In my study, the incidence of crown dieback was positively correlated with a stem density in all harvested stands ( $r = 0.52$ ,  $P = 0.028$ , Figure 2-7). Greater self thinning would be expected in stands with higher stem densities because, as stems increase in size, intraspecific competition increases. This will lead to increased competition for light, nutrients, and water, and as a result reduce availability, leading to a decline in the health of subordinate stems, and to their eventual death (Krasny and Johnson 1992).

It should be noted that health indices in balsam poplar appeared to respond more often to stand age and grazing treatments than those of aspen. Though the indices did not indicate biologically significant differences in treatments due to the lack of any observable pattern, they highlighted the increased susceptibility of balsam poplar to environmental stressors compared to aspen (Haeussler and Coates 1986).

Although the incidence of pests was sometimes greater in grazed plots, cattle grazing did not decrease overall tree vigour, thus higher pest susceptibility could not be linked to reduced tree vigour (Christiansen *et al.* 1987, Frey *et al.* 2004). It should be noted that almost all trees had some sign of injury or stress, which can be expected in recently harvested regenerating aspen stands (Millers 1972). While most trees in the heath index survey were given a value representing low vigour (i.e., vigour category 2- tree is showing signs of stress, but likely to recover), leading to a low site vigour value for aspen and balsam

poplar, this finding may not have been biologically significant in terms of increased mortality. Perhaps a lack of differentiation between typical signs of stress and signs that will not lead to mortality but have consequences to stem health may lead to a bias in the reporting of health conditions in aspen and balsam poplar. It should also be noted that there are no studies that assess the impacts of cattle grazing on the health of juvenile aspen. Furthermore, an extensive literature review revealed only one study dealing with the general health and incidence of pests in young aspen stands (Perala 1984). This study detailed the incidence of pest and disease in a harvest origin regenerating aspen stand from one to seven years post-harvest. It was concluded that although there was a high incidence of pests and disease on young aspen stems, they did not have a significant impact on aspen mortality, intraspecific competition has a much greater influence on aspen mortality than pests and disease.

### 2.5.3. Environmental Variables

Grazing pressure did not affect bulk density or soil compaction. This finding may be attributed to cattle having only localized impacts on soil properties in well used cow paths (personal observation). These results are similar to those of Krzic *et al.* (2003), who found similar bulk densities in ten-year-old grazed plots and ungrazed exclosures in a regenerating aspen stand in British Columbia. Krzic *et al.* (2003) reported soil bulk densities at depths of 0-7.5 cm and 7.5-15.0 cm of  $1.42 \pm 0.20 \text{ g/cm}^3$ , and  $1.60 \pm 0.13 \text{ g/cm}^3$  in ungrazed treatments compared to  $1.38 \pm 0.21 \text{ g/cm}^3$  and  $1.50 \pm 0.17 \text{ g/cm}^3$  in grazed treatments.

Other studies have found a higher amount of compaction in soils within areas that were grazed by cattle (Ferrero 1991, Bezkorowajnyj *et al.* 1993). Bezkorowajnyj *et al.* (1993) conducted a grazing experiment in Grand Valley, Ontario involving seedlings of

hybrid poplar (*Populus* spp.) and tree species native to the region. Cattle density in experimental enclosures ranged from 2-5 animals per 315 m<sup>2</sup> plot for 3-7 day intervals. Levels of soil compaction were significantly higher in the grazed areas (1700 kPa) than in ungrazed areas (1480 kPa). Differences in levels of soil compaction found by Bezkorowajnyj *et al.* (1993) may be attributable to presence of higher cattle densities than in my study, and the colder climate found in western Manitoba that will ameliorate soil compaction through expansion of water during the freezing process (Gatto 1997, Environment Canada 2008)

The average soil compaction threshold that impedes root penetration in a range of species (e.g., cereal crops; and trees such as *Pinus contorta* var. *latifolia*) is believed to be approximately 2500 kPa (Ball and O'Sullivan 1982, Busscher *et al.* 1986, Brady and Weil 2002., pg 211, Blouin *et al.* 2008). This level of soil compaction was not found in any of the sites surveyed in the Duck Mountain area, and therefore it is unlikely that growth limiting levels of compaction were reached in any of the sampled stands. It can be concluded that amount of soil compaction caused by cattle in this study was unlikely to substantially limit aspen and balsam poplar growth.

It should be noted that in the harvested areas where cattle were put to graze, they often had access to adjacent cleared pasture. Cattle movements in this study had to be estimated, as it was impossible to accurately determine the amount of time cattle spent in the harvested areas. Therefore, cattle stocking levels reported in this study may not accurately reflect the actual grazing pressures experienced by the regenerating aspen stands surveyed in this study. Future studies should document the actual grazing time in both the regenerating

aspen stand and adjacent pasture, possibly through the use of exclosures to ensure or prevent cattle presence in the harvested areas.

#### *2.5.4. Conclusion*

The presence of grazing cattle appeared to produce a general reduction in commercial hardwood stem density among all stands, and a lead to reduction in stem height of 9-11 year-old stands regenerating in Aspen Parkland of western Manitoba. Density and height of regenerating aspen stems was also reduced in older stands. Despite the lower commercial stem densities in grazed aspen stands, all sites met the minimum hardwood stocking levels recommended by Manitoba Provincial Guidelines. Moreover, it appears the harvested stands surveyed in this study may regenerate to adequate levels at rotation age providing cattle ranchers do not greatly exceed cattle stocking guidelines recommended by Manitoba Agriculture.

## Chapter 3 - Grazing Effects on Aspen Understory

### 3.1. Introduction

Aspen stands are a productive source of forage for wildlife and livestock. Mature aspen stands are able to produce more than 2000 kg ha<sup>-1</sup> of palatable forage each year, which is significantly more than a coniferous forest, but less productive than a typical grassland (Reynolds 1969). In addition, the aspen canopy provides shade to grazing animals and protection to the understory plants during times of drought (Powell and Bork 2007). When grassland vegetation is adversely affected by drought conditions, cattle, if given the opportunity, spend more time grazing in adjacent aspen stands (Hilton and Bailey 1972).

Cattle put out to graze in areas of mixed pasture and aspen woodland during the early to mid summer preferentially graze pasture grasses (Fitzgerald *et al.* 1986). Aspen stems become increasingly browsed later in the summer as the abundance of desired forage decreases (Fitzgerald and Bailey 1984, Fitzgerald *et al.* 1986).

Livestock grazing in aspen stands can cause considerable mechanical and physiological stress to aspen stems when managed improperly (Ellison and Houston 1958, Willoughby and Lane 2004). Aspen understories are sensitive to disturbance, and grazing may change the composition of understory vegetation communities if cattle selectively graze more palatable species. Trampling by cattle may alter understory species composition in aspen stands as well (Weatherill 1969, DeByle 1985). As a result of cattle grazing and movements, the community composition may shift over time to less palatable plant species and the resulting soil disturbance may foster the proliferation of invasive species (Houston 1954, Kay and Bartos 2000, Willoughby and Lane 2004).

Intense grazing of the herbaceous understory layer also has the potential to reduce the amount of organic matter in the soil (Naeth *et al.* 1991). With little or no grazing in the understory, dead plant matter decomposes slowly, leaving a layer rich in organic matter on top of the soil. However, constant large-scale removal of live plant matter through herbivory, followed by digestion and excretion converts the plant material directly to nutrients preventing accumulation of organic matter (Floate 1970). Decreasing soil organic matter content can decrease site productivity and cause degradation of soil quality (Pimentel *et al.* 1995, Jurgensen *et al.* 1997, Brady and Weil 2002, pg 28).

Repeated travel by cattle may cause localized compaction and increased bulk density in soil (Lull 1959, Ferrero 1991, Bezkorowajnyj *et al.* 1993). As soil bulk density increases, the proportion of macropores in the soil decreases, impeding infiltration of water (Lull 1959, Rauzi and Hanson 1966, Patric and Helvey 1986, Abdelmagid *et al.* 1987, Wood *et al.* 1989, Greenwood and McKenzie 2001, Sharrow 2007). Reduced pore space decreases oxygen concentration in the soil, allowing carbon dioxide concentrations from root and microbial respiration to increase, which may increase soil denitrification rates leading to a decrease in plant available nitrogen (Greacen and Sands 1980, Bezkorowajnyj *et al.* 1993, Sharrow 2007).

The impact of cattle grazing on forest understory plants has rarely been studied in conjunction with the impacts of logging on the same area of land.

### *3.1.1. Aspen Harvest and Agricultural Land*

Louisiana Pacific Canada Limited (LP) opened an oriented strand board (OSB) mill in Minitonas, Manitoba in 1995 to expand the usage of under used aspen fibre in the region.



Louisiana Pacific obtains fibre from both crown agricultural and forestry coded land parcels in western Manitoba. A considerable amount of LP's harvesting activities are carried out on agricultural crown land that is also used for livestock grazing. Moreover, it is common for the cattle of local agricultural crown land leaseholders to graze freshly harvested stands due to their open nature and high levels of palatable forage in the regenerating understory. Louisiana Pacific foresters and forestry staff in the Manitoba government are concerned that grazing in recently harvested crown agricultural areas may reduce aspen density and result soil compaction.

### *3.1.2. Objectives*

The purpose of this study was to investigate the impact of livestock grazing on understory plant communities in post harvest regenerating aspen stands. The objectives were: 1) Assess impact of cattle grazing on species diversity and composition of herbaceous and shrub species in a chronosequence of post-harvest aspen stands, and 2) Explore the influence of local site factors on understory species composition and diversity in grazed and ungrazed sites of the chronosequence.

## **3.2. Methods**

### *3.2.1 Study Area and Site Selection*

Reference section 2.2.1.

### *3.2.2. Data collection*

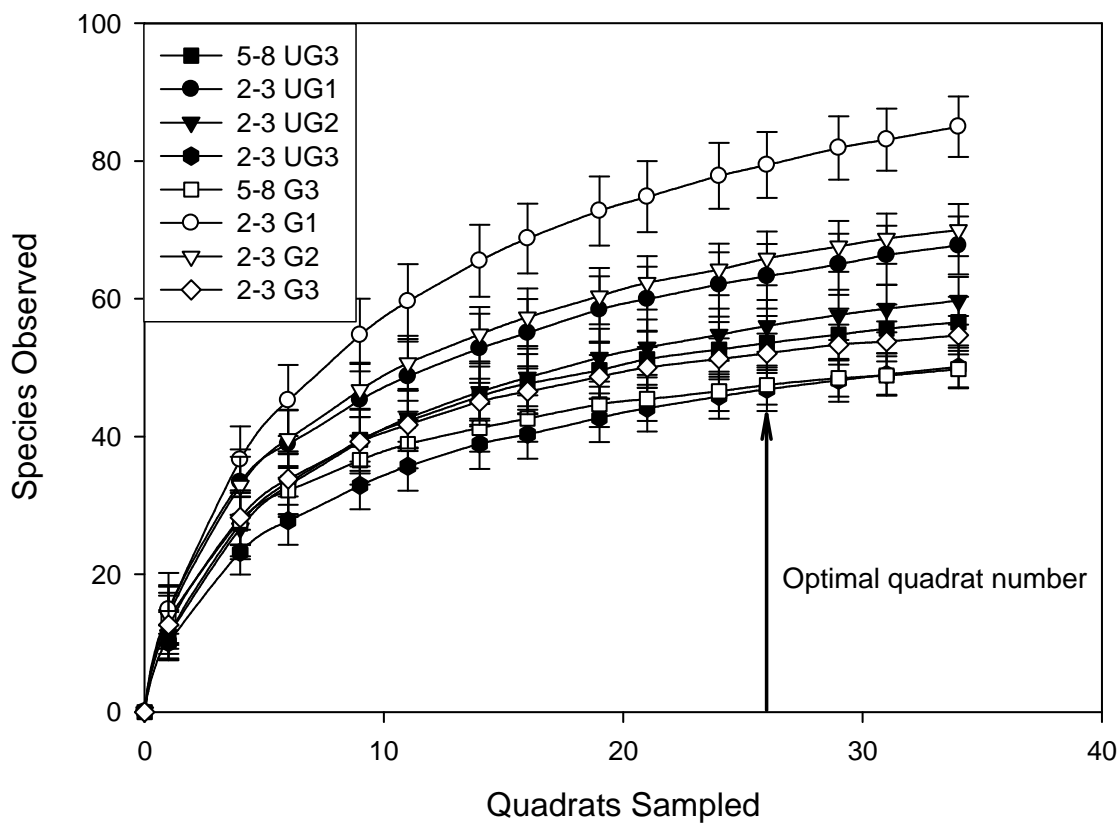
For details of plot establishment reference section 2.2.2.

### *Plant Species Diversity*

All plants less than 2 m in height in the understory were sampled using a 1 x 1 m quadrat placed randomly within each 24.6 m<sup>2</sup> subplot (n=36/plot). Shrubs were considered

plants with a permanent woody stem (note: woody species that were classified as commercial and non-commercial tree regeneration in Chapter 2, where not recorded as shrubs, or counted in the quadrats), and herbs were those with non-permanent herbaceous stems. The percent cover of all understory plants was estimated for each species observed in a 1 x 1 m quadrat. The majority of plants were identified to the species level with the exception of *Salix* spp. and graminoids, which were identified to genus, or, in a few cases, the family level. There were instances where individuals that could only be identified to the genus level, and belonged to a genus where individuals were identified to the species level. In this situation, the unidentified and identified species were analyzed separately, and the unidentified species were classified as *Genus spp.*

In 2006, 1 x 1 m quadrats were placed in each of the 36 understory subplots of eight plots (5-8 UG3, 2-3 UG1, 2-3 UG2, 2-3 UG3, 5-8 G3, 2-3 G1, 2-3 G2, and 2-3 G3). Species accumulation curves were calculated for these plots to assess the probability that 36 quadrats were adequate for sampling the majority of the species present in the understory. Accumulation curves were constructed using Ecosim Version 7.72 (Acquired Intelligence Inc. & Kesey-Bear, Jericho, VT). Results showed that curves neared the asymptote at approximately 26 sample quadrats, where a minimum of 90% of species found within each plot were sampled (Figure 3-1). During subsequent sampling, because of time constraints, sampling was reduced to 26 randomly selected 1 x 1 m vegetation quadrats within each plot.



**Figure 3-1:** Species accumulation curves of all species in the first eight plots sampled (5-8 UG3, 2-3 UG1, 2-3 UG2, 2-3 UG3, 5-8 G3, 2-3 G1, 2-3 G2, and 2-3 G3). The arrow indicates the 26<sup>th</sup> vegetation plot sampled in each site, where a minimum 90% of all species sampled in 36 quadrats within each site were included.

### 3.2.3. Grazing Pressure

Reference section 2.2.5.

### 3.2.4. Soil Compaction

Reference section 2.2.5.

### 3.2.5. Soil Characteristics

Reference section 2.2.6.

### 3.2.6 Coarse Woody Debris

Reference section 2.2.7.

### *3.3. Data Analysis*

#### *3.3.1. Plant Species Diversity.*

##### *Diversity Indices*

Herbaceous and shrub species were placed in separate data sets to analyze the alpha ( $\alpha$ ) and beta ( $\beta$ ) diversity in the stands. Alpha diversity was measured using species richness, Shannon's  $H'$ , Shannon's Evenness, and Simpson's Reciprocal Index (Magurran 2004). Jaccard's Qualitative Similarity Index, which uses presence/absence of species observed within the two sites being compared was used to measure beta diversity. Species abundance data of alpha diversity indices were calculated according to number of quadrats observed within a plot. All diversity indices were calculated according to the methods outlined in Magurran (2004). The alpha diversity indices for each site were compared using two-way analysis of variance (ANOVA) with the critical type I error rate set to  $\alpha = 0.1$ , for the rejection of the null hypotheses that grazing and age had no influence on the on the species diversity indices. If any main effect was significant, Tukey's test was used to test for differences between means.

##### *Indicator Species Analysis*

Indicator species analysis (ISA) (Defrêne and Legendre 1997) was used to determine the identity of herbaceous or shrub species characteristic of particular stand age-grazing status combinations. This analysis produces indicator values (IV) for each species equal to the number of treatments in the mensurational groups. The indicator value is calculated using the following equation adopted from Defrêne and Legendre (1997):

$$\text{INDVAL}_{ij} = A_{ij} \times B_{ij} \times 100 \quad \text{Equation 5}$$

where,  $A_{ij}$  = relative frequency of species  $i$  in group  $j$ , and  $B_{ij}$  = relative abundance of species  $i$  in group  $j$ . The significance of each indicator was determined using a Monte-Carlo randomization test with 4999 permutations. Each permutation was a random allocation of species relative abundance and frequency data among site categories (grazed/ungrazed or stand age class) from which a new indicator value is calculated. The probability of type I error was based on the proportion of times that the randomized indicator values for species  $i$  exceeds the indicator values calculated from original data (Defrêne and Legendre 1997, McCune and Mefford 1999). The analysis was done with PC-ORD Version 5.0 for Windows (MJM Software Design, 2005).

#### *Rarefaction Analysis*

The frequency with which a given species is encountered varies by site. For this reason unequal numbers of species may be sampled among sites even when sampling effort is the same (Magurran 2004). To standardize the accumulation of species observations according to species density, a technique called rarefaction was employed. Species richness from all sites was standardized to the number of observations made in the site (i.e., any occurrence of a species in a subplot counted as one occurrence) with the smallest sample size among all sites ( $N$ ) (Magurran 2004). A rarefaction curve was then created through random selection of species from different numbers of individuals from the total species pool in each site, to a maximum of  $N$  observations, and by averaging the number of species observed in 1000 permutations (Gotelli and Colwell 2001). EcoSim Version 7.72 was used to calculate the rarefaction curves (Acquired Intelligence Inc. & Kesey-Bear, Jericho, VT).

The rarefied species richness for each site as calculated at N observations for each site and then compared between sites using ANOVA in SPSS 14.0 (SPSS Inc, 2005).

### *Cluster Analysis*

A hierarchical cluster analysis was used to group sites based on their similarity of species composition and abundance. The site values of each species and abundance were translated into Bray-Curtis space, where they were plotted relative to each other according to the proportion of species not shared between sites. The sites were then “clustered” using the Ward’s linkage method (McCune and Grace 2002, pp 46-48 and 92). Ward’s linkage method clusters sites based on minimum error sum of squares. Error sum of squares is defined as sum of the squares of distances between individual points within a cluster and the centroid within that particular cluster (McCune and Grace 2002, pg 92). The cluster analysis was conducted using PC-ORD Version 5.0 for Windows (MJM Software Design, 2005).

### *Site Proximity*

Similarity of species composition between sites is often a function of distance between areas sampled (Gilbert and Lechowicz 2004). Under these conditions autocorrelation may produce inflated real type I error rates in statistical tests (Legendre and Legendre 1998, pp 8-17). In this study inter-site distance varied considerably due to the lack of suitable sites within a narrow range of distance. Therefore, this test was employed to determine if the inter-site distances created a bias in the site differences found amongst the species assemblages. Tests for autocorrelation such as the Mantel’s Test are able to determine if distance between sites affects species composition and abundance (McCune and Mefford 1999). The test is calculated using two dissimilarity matrices, such as species presence and inter-site distance, to determine the effect distance has on species composition.

Mantel's statistic is a correlation coefficient calculated from inter-site species distance using a standard distance matrix, such as Bray-Curtis space and inter-site geographical distance (McCune and Mefford 1999). The Mantel's statistic for each site is taken as the empirical data for comparison against subsequent permutations (Legendre and Legendre 1998). To arrive at a type I error rate, the rows and columns of one of the matrices are permuted repeatedly at random, preserving the relative cell addresses (Legendre and Legendre 1998). The probability of type I error is based on the proportion of permuted Mantel's statistics that equal or exceed the Mantel's statistic calculated from the original data (McCune and Mefford 1999). Mantel's Test is calculated using the following equation:

$$r_m = \frac{1}{d-1} \sum_{i=1}^{n-1} \sum_{j=i+1}^n \left( \frac{x_{ij} - \bar{x}}{s_x} \right) \left( \frac{y_{ij} - \bar{y}}{s_y} \right) \quad \text{Equation 6}$$

where,  $n$  = total number of distances in within matrix Y, the distance matrix (excluding where  $j = i$ ),  $y$  = values from matrix Y,  $x$  = values from matrix X,  $i$  and  $j$  are column and row indices,  $s_x$  and  $s_y$  are standard deviations for matrices X and Y (Legendre and Fortin 1989). Mantel's Test was calculated using PC-ORD version 5.0 (McCune and Mefford 1999).

### 3.3.2. Soil Moisture Correction

Reference section 2.3.3.

### 3.3.3. Multivariate Analysis

Species diversity data for herbaceous and shrub species were analyzed separately because grazing pressure and the soil variables will affect each stratum differently (i.e., herbs vs. shrubs). A Detrended Correspondence Analysis (DCA) was used to assess the gradient length (in standard deviations) of the primary ordination axes. This procedure is commonly used to provide a criterion for choosing between multivariate techniques that

presuppose either linear or univariate responses to underlying environmental gradients (Jongman *et al.* 1995, pp 106-108). As a rule of thumb, if the variation encompassed by an axis is not much more than 2.0 standard deviations, the underlying responses of the variables being analyzed are assumed to be roughly linear (Jongman *et al.* 1995, pg 154). Gradient lengths were between 1.058 and 2.086, therefore Principle Components Analysis (PCA) and Redundancy Analysis (RDA) were used to assess species-site relationships (ter Braak and Smilauer 2002). The environmental variables used in the RDAs were soil drainage class, organic matter content, clay fraction, pH, soil compaction, bulk density, and grazing pressure. The statistical significance of the first ordination axis and of all axes pooled together ( $P \leq 0.1$ ) was tested using 9999 Monte Carlo permutation tests under the reduced model (ter Braak and Smilauer 2002). Stepwise analysis of environmental variables was carried out within the RDA to determine the individual effect each environmental variable had on species distribution. Ordination analysis was carried out using CANOCO 4.5 for Windows (ter Braak and Smilauer 2002), and species data were transformed [ $x' = \log_{10}(x+1)$ ] using the log transformation option in CANOCO.

### **3.4. Results**

#### *3.4.1. Diversity Indices and Rarefaction*

Alpha diversity indices for herbaceous species were unaffected by either time since harvest or grazing ( $P > 0.1$ , Table 3-1). Mean herb species richness was  $41.2 \pm 9.4$  in ungrazed sites, and  $44.4 \pm 13.0$  in grazed sites. Shrub diversity was also similar between harvest years and grazing treatments. Mean shrub species richness was  $11.8 \pm 1.6$  in ungrazed stands and  $13.1 \pm 3.1$  in grazed stands (Table 3-2).



Shannon's Evenness for shrubs was lower in 9-11 year-old grazed stands than the other stands, indicating a less proportionate distribution of species than in the other stand ages (Table 2-1). No significant difference in Shannon's Evenness was found amongst treatments for herbaceous species.

**Rarefied species richness indices of herbaceous and shrub species was similar in all stand age/grazing treatment combinations ( $P > 0.10$ , Figure 3-2 –Figure 3-5). Although differences in rarefied species richness were apparent from rarefaction curves, these differences were not significant ( Figure 3-2 – Figure 3-5).**

Jaccard's Similarity Index varied considerably between pairs of sites although there were no clear trends or associations based on stand age or grazing status (Table 3-3, Table 3-4). Sites shared an average of 47.8% of their herbaceous, and 36.3% of their shrub species (Species similarity ranged from 29% to 81%). The average herbaceous species similarity of all sites (47.2%) did not differ greatly from either grazed stands (48.4%) or ungrazed stands (48.5%). Average Jaccard's Similarity values for shrub species were almost equal when sites were separated by grazing treatment: 36.1% between grazed stands, 37.4% between ungrazed stands and 36.0% between grazed and ungrazed stands.

#### 3.4.2. Cluster Analysis and Mantel's Test

Five out of the six of the 5-8 and 9-11 year old ungrazed stands formed clusters in the 50-100% similarity range (Figure 3-6). The 2-3 year-old grazed stands were clustered separately from both the 5-8 and 9-11 year-old grazed stands (Figure 3-6). Furthermore, with the exception of 5-8 UG3, the 2-3 year-old stands were quite dissimilar from the other older sites (Figure 3-6). Two sites that had a relatively similar species composition, 2-3 UG2 and 2-3 UG3 were the most dissimilar from others sampled in this study (Figure 3-6).

Based on the cluster analysis, the majority of sites within 12 km of each other shared more than 75% of herbaceous species (Figure 3-6, Figure 3-7, Appendix 1). Average site

distance was 62.8 km, with a maximum distance of 143.8 km and a minimum distance of 0.1 km. A Mantel's test to explore the relationship between geographical distance (sites were placed in one of seven distance classes) and species composition influence of distance between sites on herbaceous species composition, showed that species composition and abundance of sites less than 2.5 km apart were positively autocorrelated ( $r_m = 0.31$ ,  $P < 0.001$ , Figure 3-7). Conversely, sites that were between 112.5 km and 137.5 km apart, species exhibited negative autocorrelation ( $r_m = -0.53$ ,  $P < 0.001$  and  $r_m = -0.24$ ,  $P = 0.007$ , respectively, Figure 3-7).

For shrubs, time since harvest appeared to have some influence on the linkages between sites, where five out of six stands in the 9-11 stand age class were completely dissimilar from the 2-3 year-old stands according to the cluster dendrogram, this may be more reflective of similar abundances of species shared between sites than simply number of species shared (Figure 3-9). Proximity, grazing class or treatment did not appear to have a significant influence on linkages between sites (Figure 3-9).

### 3.4.3. Indicator Species Analysis

Of the 188 species included in the indicator species analysis, 27 were associated with a specific treatment or main effect. Of these, 23 were herbs and four were shrubs (Tables 3-5 to 3-9). *Geum macrophyllum* (IV = 66.7,  $P = 0.011$ ) and *Plantago major* (IV = 66.7,  $P = 0.012$ ) were indicators of grazed sites, and *Mertensia paniculata* (IV = 73.1,  $P = 0.007$ ), and *Disporum trachycarpum* (IV = 56.6,  $P = 0.026$ ) were associated with ungrazed sites (Table 3-5).

Most herbaceous indicator species were associated with a particular stand age class. For instance, *Cirsium spp.* (IV = 61.6,  $P = 0.029$ ) and *Viola canadensis* (IV = 62.2,  $P =$

0.039) were indicators of 9-11 year-old stands (Table 3-6). There were 14 indicators of the 2-3 year-old age class; *Equisetum pretense* (IV = 96.4,  $P < 0.001$ ) and *Lactuca tatarica* (IV = 95.7,  $P < 0.001$ ) had the highest indicator values. There were no indicator species were found for the 5-8 year-old stands (Table 3-6).

Six species were indicative of a particular stand age/grazing class combination (Table 3-7). *Mertensia paniculata* (IV = 32.9,  $P = 0.003$ ), and *Cirsium spp.* (IV = 56.5,  $P = 0.045$ ) were indicators in the ungrazed 9-11 year-old stands. The only indicator in the ungrazed 5-8 year-old stands was *Pyrola asarifolia* (IV = 55.0,  $P = 0.042$ ). A total of five indicator species were found in the ungrazed 2-3 year-old stands, they were *Equisetum pretense* (IV = 66.7,  $P = 0.008$ ), *Equisetum arvense* (IV = 61.0,  $P = 0.009$ ), *Galium triflorum* (IV = 37.9,  $P = 0.016$ ), *Erigeron philadelphicus* (IV = 80.8,  $P = 0.022$ ), and *Sonchus arvensis* (IV = 50.0,  $P = 0.030$ ). The 9-11 year-old, grazed stands had only one indicator; *Senecio pauperculus* (IV = 100.0,  $P = 0.008$ ). In the 2-3 year-old, grazed stands, the three indicator species were *Petasites spp.* (IV = 73.3,  $P = 0.005$ ), *Cirsium arvense* (IV = 40.3,  $P = 0.013$ ), and *Mitella nuda* (IV = 50.8,  $P = 0.016$ ).

No shrubs species were found to be indicators for any grazing/stand age class combination ( $P > 0.05$ ). *Lonicera oblongifolia* (IV = 55.6,  $P = 0.030$ ) was the only shrub grazing indicator significantly associated with grazed plots (Table 3-8). Among the shrub species, *Symphoricarpos albus* (IV = 67.8,  $P = 0.006$ ) and *Ribes hirtellum* (IV = 55.6,  $P = 0.027$ ) were indicative of 9-11 year-old stands (Table 3-9). *Cornus stolonifera* (IV = 50.2,  $P = 0.040$ ) was an indicator of 2-3 year-old stands.

#### 3.4.4. Principle Components Analysis

In the PCA ordination of herbaceous species, the first two axes (PCA-1 and PCA-2) explained 32.7% of the variation in the species abundance (Figure 3-10). The first axis represented a gradient of time since harvest, with 2-3 year-old stands on the right side of the axis, and the 5-8 and 9-11 year-old stands on the left side of the axis. While the second axis separated 5-8 and 9-11 year-old grazed stands from the 5-8 and 9-11 year-old ungrazed stands with the ungrazed sites being on the bottom of the second axis. No pattern was observed in the species positioning in the PCA according to stand age, presence of grazing or environmental gradient (according to the environmental conditions of the sites). The two sites displayed distally from the main sites clusters (2-3UG1 and 2-3UG2) were also located an average distance of 87.8 km away from the other sites, whereas the average inter-site distance was 62.8 km (Figure 3-10). Four of the six sites in the youngest stand age class (2-3 G1, 2-3 G2, 2-3 G3 and 2-3 UG1) were closely located geographically with an average inter-site distance of 13.9 km, and were also located proximally to each other in the ordination.

In the PCA ordination of shrubs species, the first two axes (PCA-1 and PCA-2) explained 33.5% of the variation in the species abundance (Figure 3-11). Within the ordination, there was no apparent separation of sites based on stand age or grazing in PCA-1 or PCA-2.

#### *3.4.5. Redundancy Analysis*

In the RDA ordination of herbaceous species with soil variables and grazing pressure as the environmental variables, the first two axes explained 20.4% of the variation in the species data (Figure 3-12). Within the triplot there was no clear delineation of grazed and ungrazed plots regardless of time since harvest. Neither the first axis (RDA-1) nor the

pooled axes were statistically significant (Monte Carlo test,  $P > 0.1$ ). Since the influence of grazing pressure and soil variables were not significant they were only shown for exploratory purposes. Poorly drained soils appeared to be associated with plants that required higher soil moisture contents, such as *Equisetum hymale*, *Equisetum pratense*, *Cornus canadensis*, *Galium trifidum*, *Epilobium angustifolium*, and *Sonchus arvensis* (Chambers *et al.* 1996)

In the RDA of shrub species 22.9% of the total variance explained was in the first two axes (Figure 3-13). The first RDA axis (RDA-1) was not statistically significant (Monte Carlo test,  $P > 0.1$ ), although the pooled axes returned a Monte Carlo of  $P = 0.045$ . However, stepwise analysis of environmental variables within the RDA failed to reveal any variable that contributed significantly to species variance in the species-environmental space. With the exception of stand age class, where there was a subtle transition between younger and older stands along RDA-1, there was no obvious separation of sites or species based on environmental variables, proximity between sites, and grazing class. Grazing pressure was negatively associated with poor drainage, high clay content, and high pH, none of which were closely associated with soil compaction, bulk density or organic matter content. Some species commonly found on wet soils (i.e., *Rubus pubescens*, *Ribes lacustre*, *Ribes triste*, and *Vaccinium myrtilloides*) were positively associated with poor site drainage. *Viburnum rafinesquianum* and *Viburnum acerifolia* were associated with better drained soils. It should also be noted that *Viburnum acerifolia* is also commonly associated with acidic soil, which is evident in the ordination.

**Table 3-1:** Mean alpha diversity indices and standard deviations (in brackets) for herbaceous species (n = 3 for all treatments).

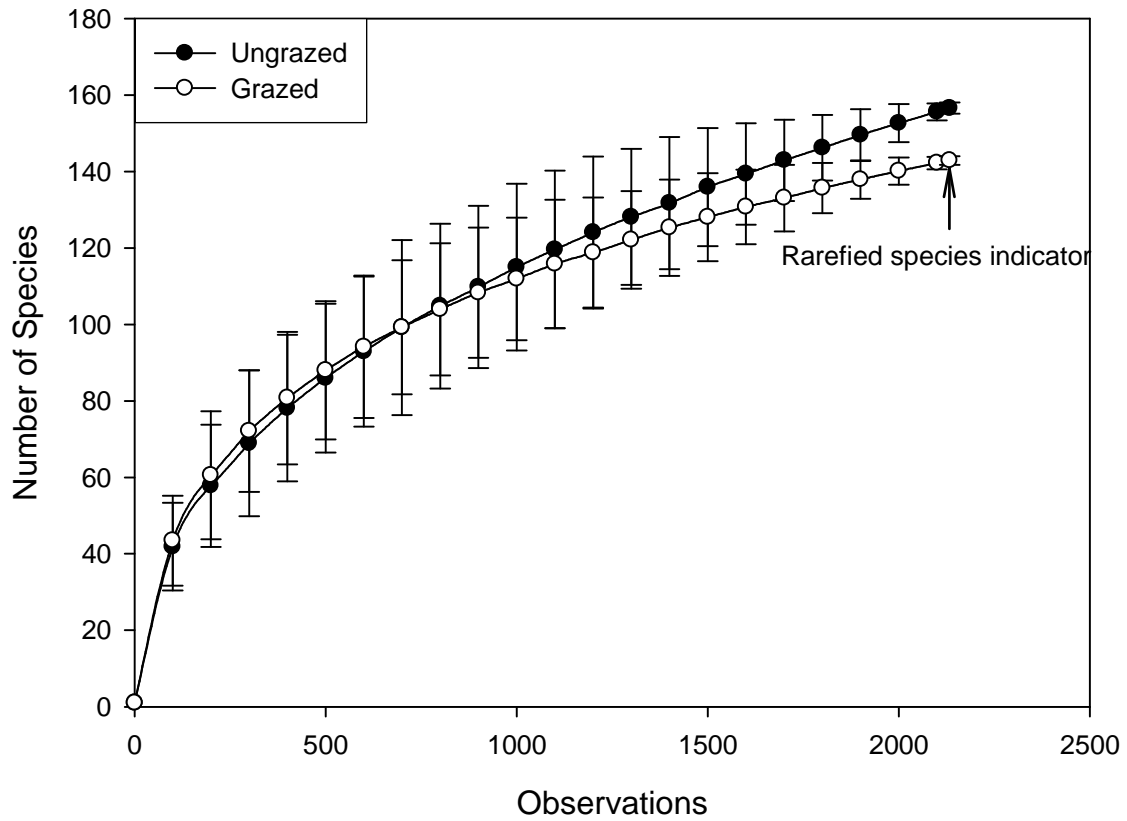
Treatment	R	H	E	1/D
9-11UG	38.3 (9.29)	3.2 (0.23)	0.88 (0.012)	21.6 (5.07)
9-11G	39.3 (8.14)	3.2 (0.23)	0.89 (0.021)	22.1 (4.47)
5-8UG	37.3 (8.08)	3.2 (0.12)	0.89 (0.006)	19.8 (4.17)
5-8G	37.0 (8.00)	3.1 (0.27)	0.85 (0.029)	17.3 (4.10)
2-3UG	48.0 (10.00)	3.3 (0.25)	0.86 (0.021)	22.6 (5.83)
2-3G	57.0 (13.53)	3.5 (0.20)	0.88 (0.010)	27.2 (4.65)

Note: Definitions of abbreviations are as follows: R – Species Richness, H – Shannon’s  $H'$ , E – Shannon’s Evenness, and 1/D – Reciprocal Simpson Index.

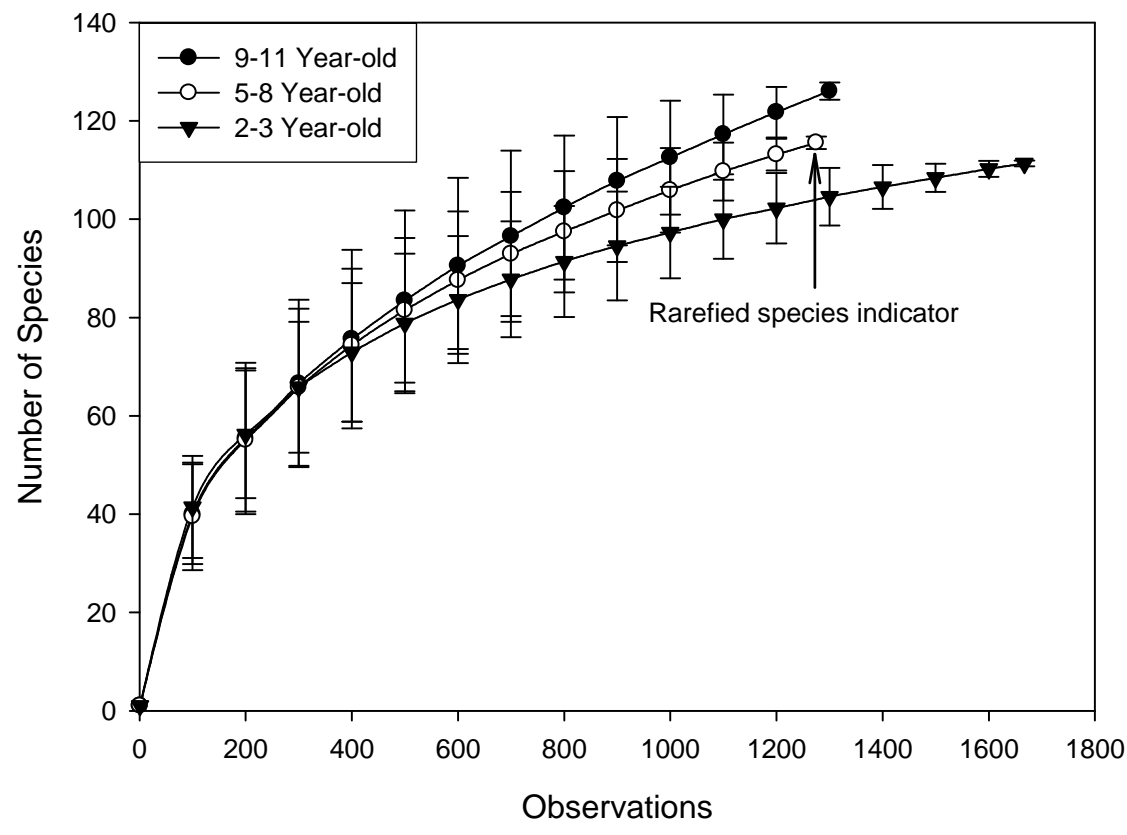
**Table 3-2:** Mean alpha diversity indices and standard deviations (in brackets) for shrub species (n = 3 for all treatments).

Treatment	R	H	E	1/D
9-11UG	13.0 (2.00)	2.1 (0.14)	0.83 (0.015)a	7.9 (1.47)
9-11G	14.3 (1.53)	2.2 (0.11)	0.84 (0.029)a	7.9 (0.84)
5-8UG	11.7 (0.58)	2.1 (0.14)	0.84 (0.038)a	6.9 (0.88)
5-8G	11.3 (1.53)	2.0 (0.07)	0.84 (0.021)a	6.8 (0.20)
2-3UG	10.7 (1.53)	1.7 (0.18)	0.71 (0.047)b	4.4 (0.54)
2-311G	13.7 (5.13)	2.1 (0.42)	0.82 (0.025)a	7.4 (2.53)

Note: Definitions of abbreviations are as follows: R – Species Richness, H – Shannon’s  $H'$ , E – Shannon’s Evenness, and 1/D – Reciprocal Simpson Index.

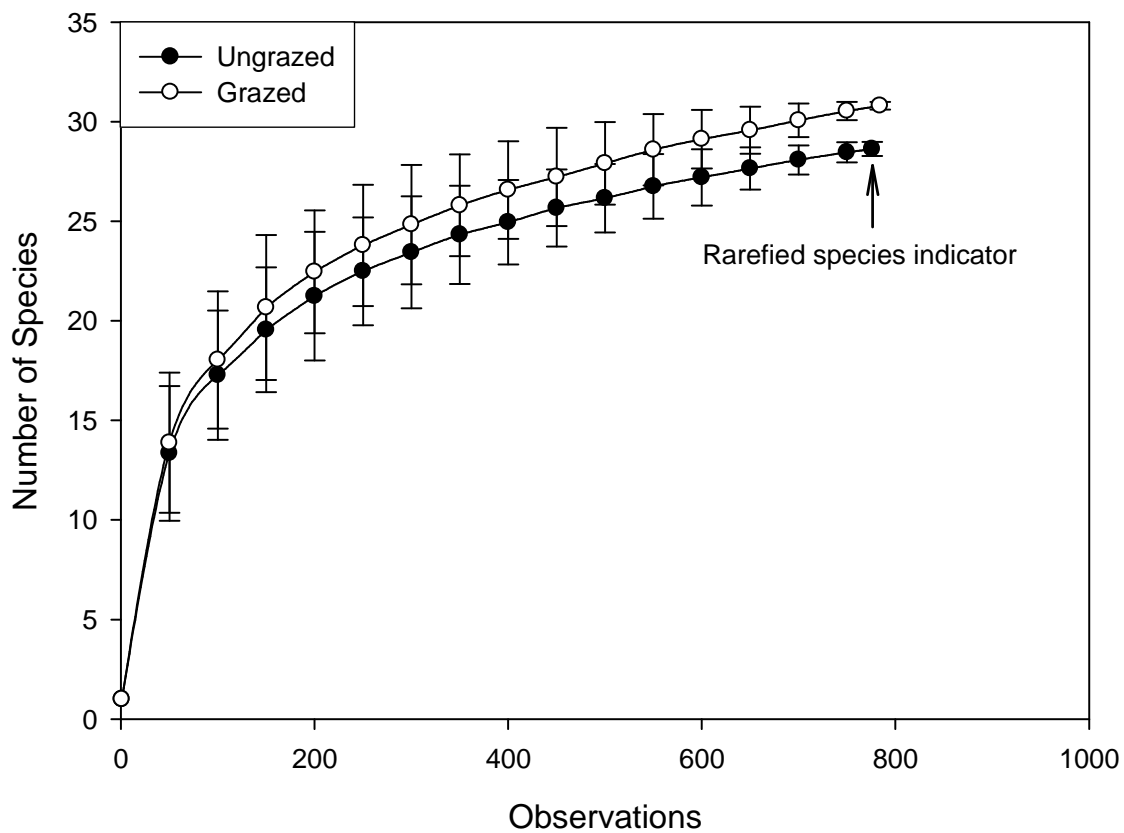


**Figure 3-2:** Rarefaction curve of the number of herbaceous species found in grazed and ungrazed sites. Error bars are  $\pm$  standard deviation. The rarefied species indicator at 2133 individual observations: ungrazed – 156.57 and grazed – 142.90. Differences between grazed and ungrazed plots were not significant ( $F_{1,16}=1.30$ ,  $P = 0.301$ ).

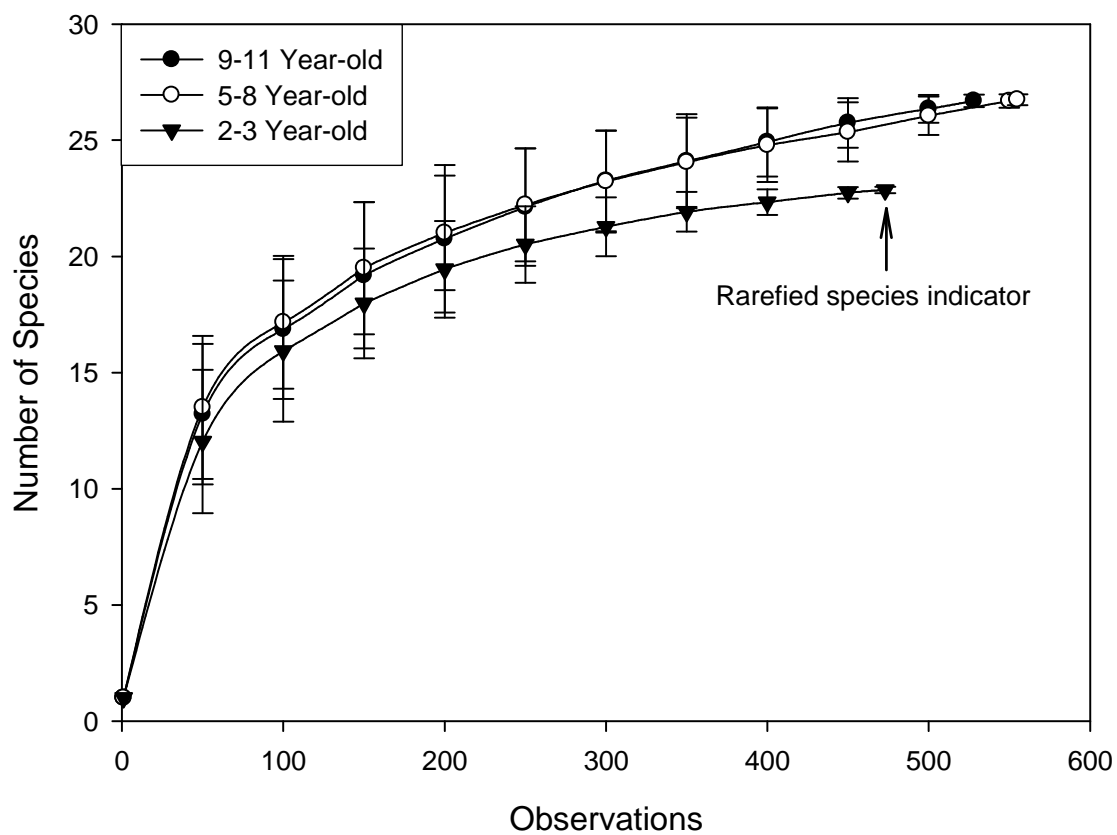


**Figure 3-3:** Rarefaction curve of the number of herbaceous species found in each stand age. Error bars are  $\pm$  standard deviation. The rarefied species indicator at 1275 individual observations: 9-11 year-old stands – 125.05, 5-8 year-old stands – 115.63, and 2-3 year-old stands – 103.92. Differences between stand ages were not significant ( $F_{2,15} = 0.02$ ,  $P = 0.896$ ).





**Figure 3-4:** Rarefaction curve of the number of shrub species found in grazed and ungrazed sites. Error bars are  $\pm$  standard deviation. The rarefied species indicator designates 776 individual observations: ungrazed – 26.01 and grazed – 25.67. Differences between grazed and ungrazed plots were not significant ( $F_{1,16} = 0.95$ ,  $P = 0.409$ )



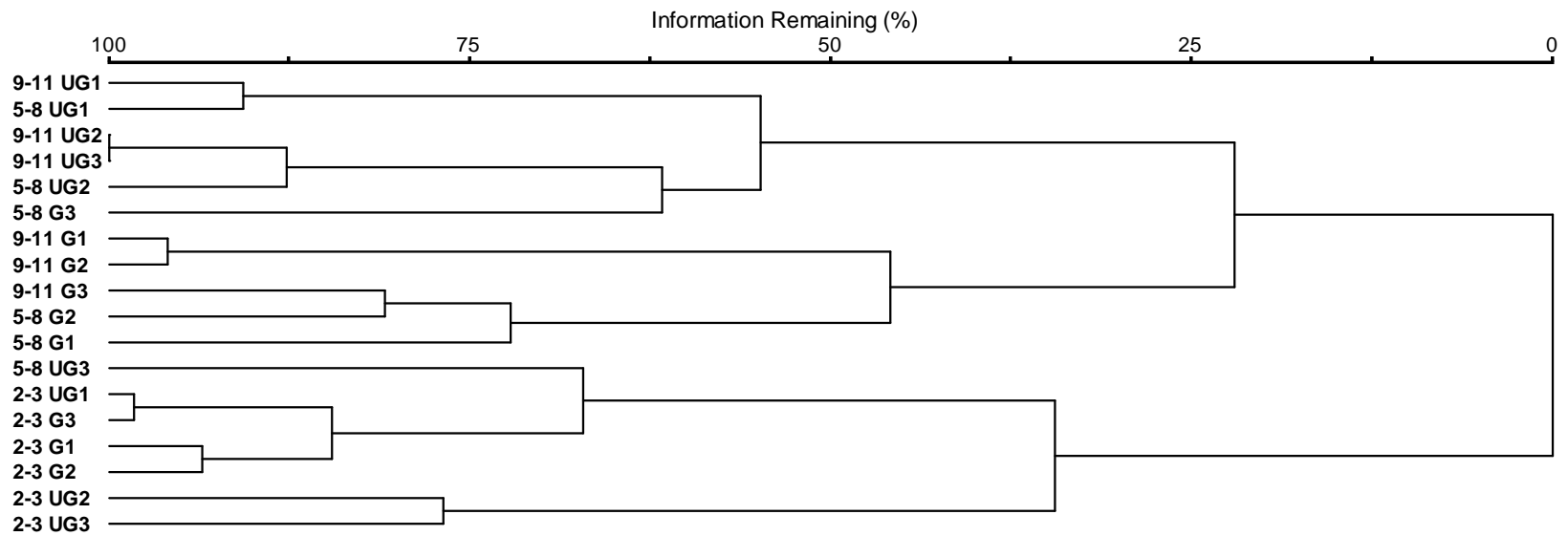
**Figure 3-5:** Rarefaction curve of the number of shrub species found in each stand age. Error bars are  $\pm$  standard deviation. The rarefied species indicator designates 473 individual observations: 9-11 year-old stands – 26.02, 5-8 year-old stands – 25.68, and 2-3 year-old stands – 22.85. Differences between stand ages were not significant ( $F_{2,15} = 1.40$ ,  $P = 0.254$ ).

**Table 3-3:** Jaccard's Similarity Matrix (% Similarity) for herbs for all sites. Similarity ranges from 0-1, 0 being completely dissimilar and 1 being completely similar.

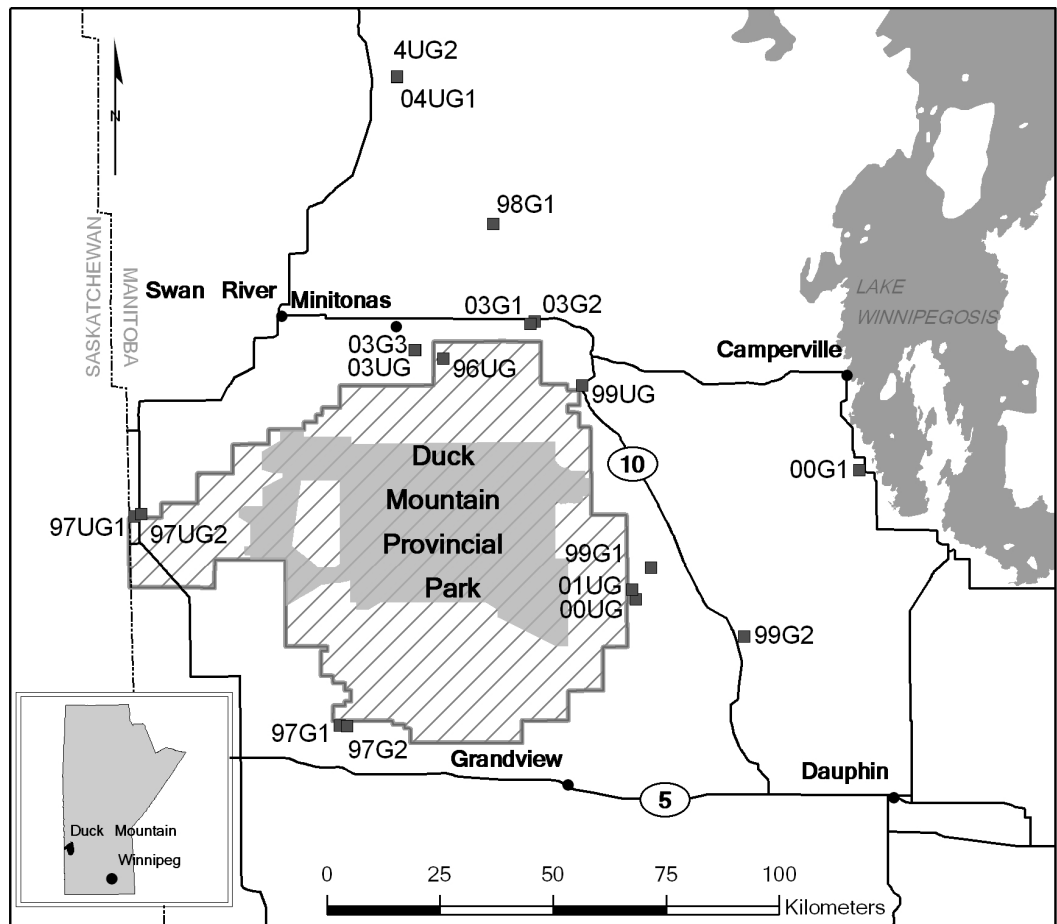
Plot	9-11UG1	2	3	5-8UG1	2	3	2-3UG1	2	3	9-11G1	2	3	5-8G1	2	3	2-3G1	2	
<b>9-11UG1</b>																		
<b>2</b>	0.44																	
<b>3</b>	0.71	0.56																
<b>5-8UG1</b>	0.44	0.69	0.56															
<b>2</b>	0.44	0.59	0.47	0.50														
<b>3</b>	0.40	0.39	0.53	0.47	0.38													
<b>2-3UG1</b>	0.40	0.67	0.53	0.57	0.57	0.54												
<b>2</b>	0.44	0.42	0.47	0.33	0.33	0.57	0.47											
<b>3</b>	0.38	0.53	0.41	0.35	0.35	0.40	0.62	0.53										
<b>9-11G1</b>	0.53	0.58	0.47	0.50	0.50	0.32	0.56	0.35	0.53									
<b>2</b>	0.56	0.53	0.50	0.44	0.44	0.33	0.50	0.44	0.47	0.81								
<b>3</b>	0.41	0.65	0.53	0.79	0.56	0.44	0.64	0.32	0.41	0.56	0.50							
<b>5-8G1</b>	0.41	0.56	0.53	0.67	0.39	0.35	0.53	0.32	0.41	0.56	0.42	0.63						
<b>2</b>	0.40	0.67	0.53	0.69	0.57	0.54	0.67	0.38	0.50	0.47	0.50	0.77	0.53					
<b>3</b>	0.29	0.37	0.33	0.44	0.44	0.50	0.50	0.35	0.29	0.44	0.39	0.41	0.41	0.40				
<b>2-3G1</b>	0.36	0.48	0.39	0.35	0.41	0.45	0.53	0.55	0.50	0.55	0.50	0.39	0.33	0.38	0.43			
<b>2</b>	0.44	0.58	0.47	0.50	0.42	0.47	0.67	0.42	0.44	0.58	0.53	0.56	0.47	0.56	0.44	0.70		
<b>3</b>	0.36	0.44	0.40	0.43	0.54	0.38	0.64	0.33	0.36	0.44	0.38	0.40	0.40	0.38	0.46	0.35	0.44	

**Table 3-4:** Jaccard's Similarity Matrix (% Similarity) of shrubs for all sites. Similarity ranges from 0-1, 0 being completely dissimilar and 1 being completely similar.

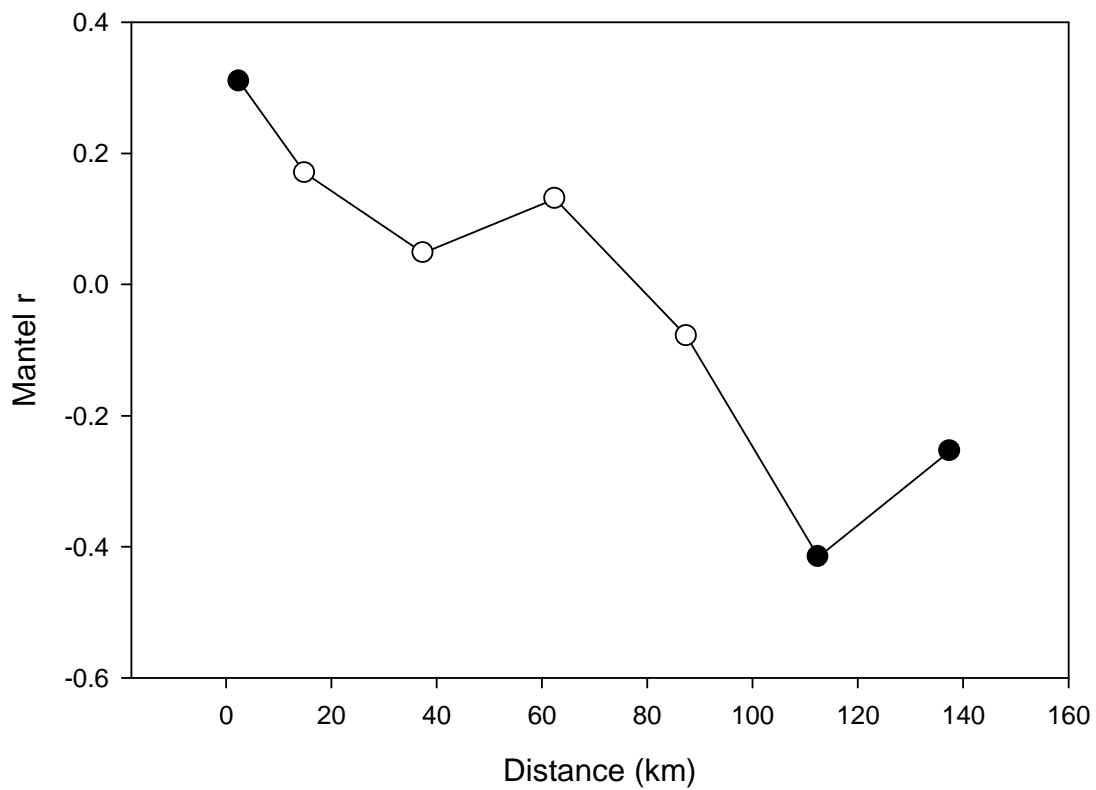
Plots	9-11UG1	2	3	5-8UG1	2	3	2-3UG1	2	3	9-11G1	2	3	5-8G1	2	3	2-3G1	2	
<b>9-11UG1</b>																		
<b>2</b>	0.43																	
<b>3</b>	0.40	0.53																
<b>5-8UG1</b>	0.47	0.53	0.43															
<b>2</b>	0.43	0.48	0.58	0.47														
<b>3</b>	0.38	0.31	0.34	0.35	0.48													
<b>2-3UG1</b>	0.35	0.28	0.32	0.33	0.35	0.37												
<b>2</b>	0.35	0.32	0.25	0.37	0.27	0.30	0.34											
<b>3</b>	0.34	0.25	0.28	0.38	0.28	0.31	0.41	0.39										
<b>9-11G1</b>	0.39	0.40	0.36	0.45	0.45	0.37	0.35	0.32	0.29									
<b>2</b>	0.28	0.29	0.30	0.40	0.36	0.34	0.23	0.24	0.25	0.41								
<b>3</b>	0.44	0.40	0.39	0.47	0.43	0.37	0.37	0.32	0.35	0.62	0.36							
<b>5-8G1</b>	0.45	0.41	0.35	0.51	0.38	0.30	0.34	0.35	0.36	0.54	0.30	0.47						
<b>2</b>	0.26	0.26	0.30	0.29	0.33	0.29	0.28	0.22	0.25	0.29	0.21	0.29	0.23					
<b>3</b>	0.34	0.31	0.35	0.39	0.33	0.34	0.38	0.23	0.30	0.25	0.27	0.32	0.28	0.20				
<b>2-3G1</b>	0.38	0.30	0.30	0.35	0.36	0.34	0.48	0.39	0.31	0.41	0.25	0.38	0.35	0.27	0.30			
<b>2</b>	0.38	0.32	0.33	0.36	0.36	0.36	0.52	0.41	0.40	0.39	0.25	0.38	0.36	0.29	0.33	0.46		
<b>3</b>	0.43	0.37	0.38	0.44	0.47	0.45	0.57	0.40	0.48	0.50	0.33	0.48	0.39	0.33	0.45	0.51	0.54	



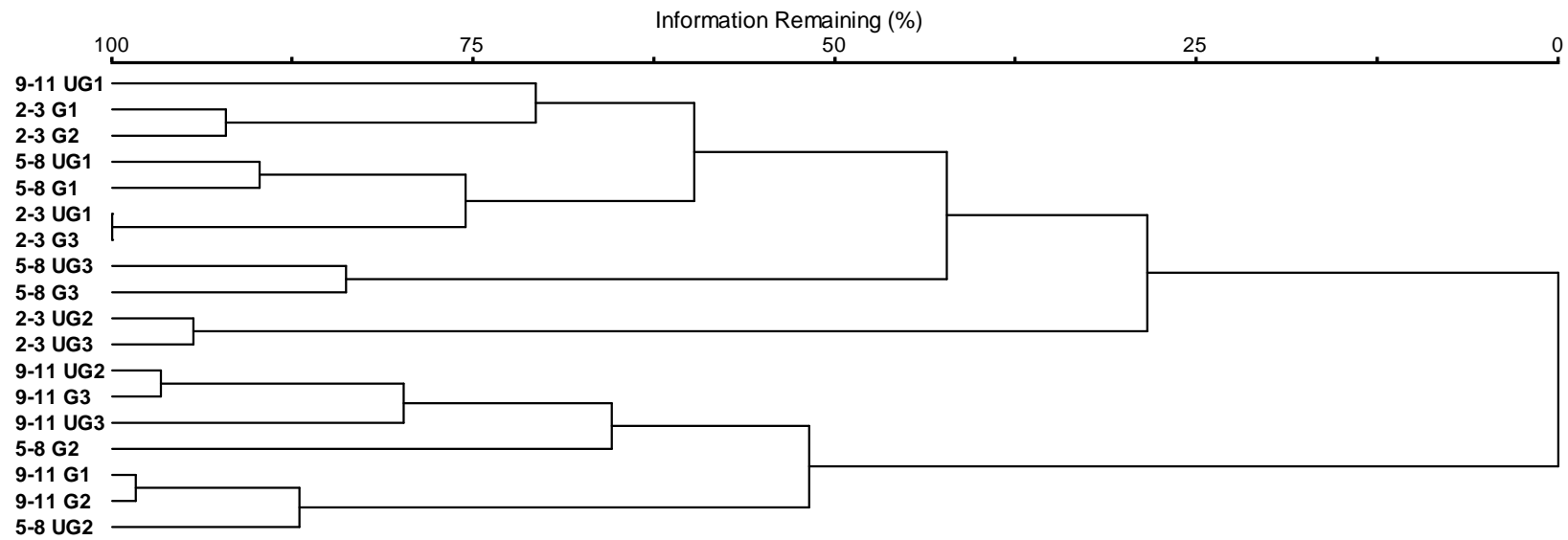
**Figure 3-6:** Ward method dendrogram of each site using herbaceous species data.



**Figure 3-7:** Distribution of study sites in the Duck Mountain area. Map prepared by Tim Davis, University of Manitoba 2009).



**Figure 3-8:** Correlogram of Mantel's Test, relating species composition data to inter-site geographical distances. Points filled in black indicate a significant correlation of species composition and inter-site distance.



**Figure 3-9:** Ward method dendrogram of each site using shrub species data.



**Table 3-5:** Herbaceous indicator species by grazing treatment.

Species	Common Name	Treatment	Indicator Value	p value
<i>Mertensia paniculata</i>	Northern bluebell / Tall lungwort	Ungrazed	73.1	0.007
<i>Disporum trachycarpum</i>	Fairybells	Ungrazed	56.6	0.026
<i>Geum macrophyllum</i>	Large-leaved avens	Grazed	66.7	0.011
<i>Plantago major</i>	Common plantain	Grazed	66.7	0.012

**Table 3-6:** Herbaceous indicator species by stand age.

Species	Common Name	Stand Age (years)	Indicator Value	p value
<i>Viola canadensis</i>	Canada violet	9-11	62.2	0.039
<i>Cirsium spp</i>	Thistles	9-11	61.6	0.029
<i>Equisetum pratense</i>	Meadow horsetail	2-3	96.4	<0.001
<i>Lactuca tatarica</i>	Common blue lettuce	2-3	95.7	<0.001
<i>Equisetum arvense</i>	Common horsetail	2-3	94.9	<0.001
<i>Mitella nuda</i>	Bishop's cap / Miterwort	2-3	78.7	<0.001
<i>Sonchus arvensis</i>	Perennial sow thistle	2-3	78.6	<0.001
<i>Petasites spp</i>	Coltsfoot	2-3	77.8	0.005
<i>Viola nephrophylla</i>	Bog violet	2-3	76.5	0.002
<i>Mentha arvensis</i>	Wild mint	2-3	71.4	0.015
<i>Erigeron philadelphicus</i>	Philadelphia fleabane	2-3	66.7	0.016
<i>Galium triflorum</i>	Fragrant bedstraw	2-3	66.5	<0.001
<i>Aster puniceus</i>	Purple stemmed aster	2-3	65.7	0.012
<i>Solidago spp</i>	Goldenrods	2-3	59.3	0.036
<i>Stachys palustris</i>	Marsh hedgenettle	2-3	55.6	0.020
<i>Taraxacum officinale</i>	Common dandelion	2-3	45.3	0.046

Note: *Cirsium* spp. refers to individuals that could only be identified to the genus level

**Table 3-7:** Herbaceous indicator species by grazing and stand age combinations.

Species	Common Name	Treatment (Years)	Indicator Value	p value
<i>Cirsium spp.</i>	Thistles	9-11 UG	56.5	0.045
<i>Mertensia paniculata</i>	Northern bluebell / Tall lungwort	9-11 UG	32.9	0.003
<i>Pyrola asarifolia</i>	Pink wintergreen	5-8 UG	55.0	0.042
<i>Erigeron philadelphicus</i>	Philadelphia fleabane	2-3 UG	80.0	0.022
<i>Equisetum pratense</i>	Meadow horsetail	2-3 UG	66.7	0.008
<i>Equisetum arvense</i>	Common horsetail	2-3 UG	61.0	0.009
<i>Sonchus arvensis</i>	Perennial sow thistle	2-3 UG	50.0	0.030
<i>Galium triflorum</i>	Fragrant bedstraw	2-3 UG	37.9	0.016
<i>Senecio pauperculus</i>	Balsam Groundsel	9-11 G	100.0	0.008
<i>Petasites spp</i>	Coltsfoot	2-3 G	73.3	0.005
<i>Mitella nuda</i>	Bishop's cap / Miterwort	2-3 G	50.8	0.016
<i>Cirsium arvense</i>	Canada thistle	2-3 G	40.3	0.013

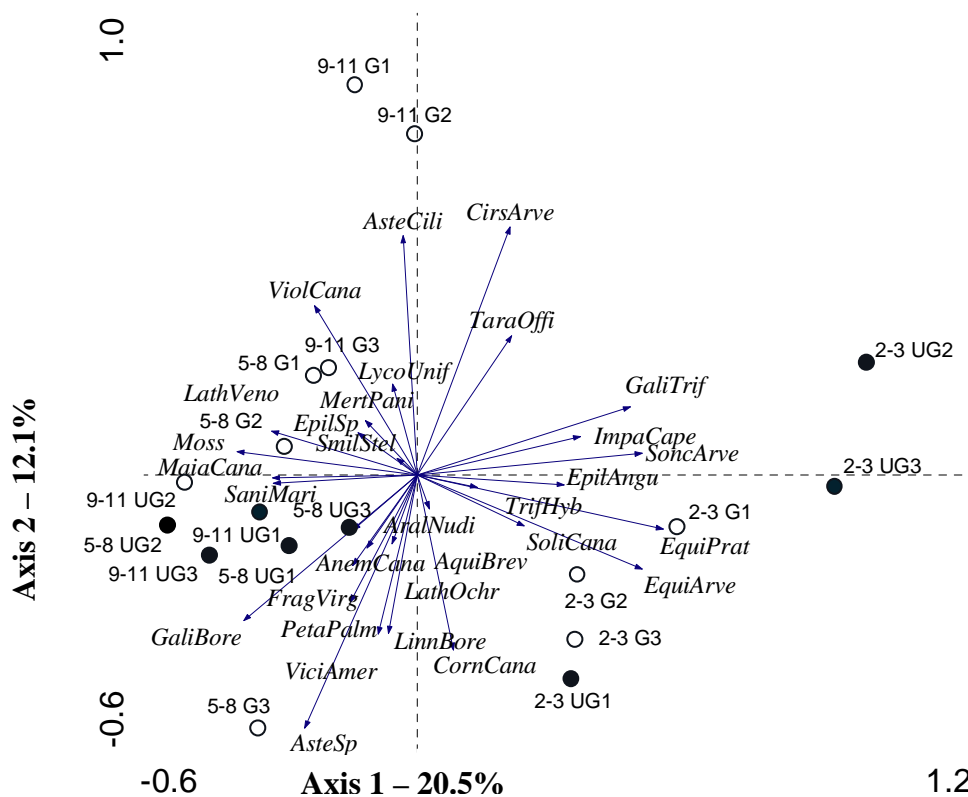
Note: *Cirsium spp.* refers to individuals that could only be identified to the genus level.

**Table 3-8:** Shrub indicator species by grazing treatment.

Species	Common Name	Treatment	Indicator Value	p value
<i>Lonicera oblongifolia</i>	Swamp fly honeysuckle	Grazed	55.6	0.003

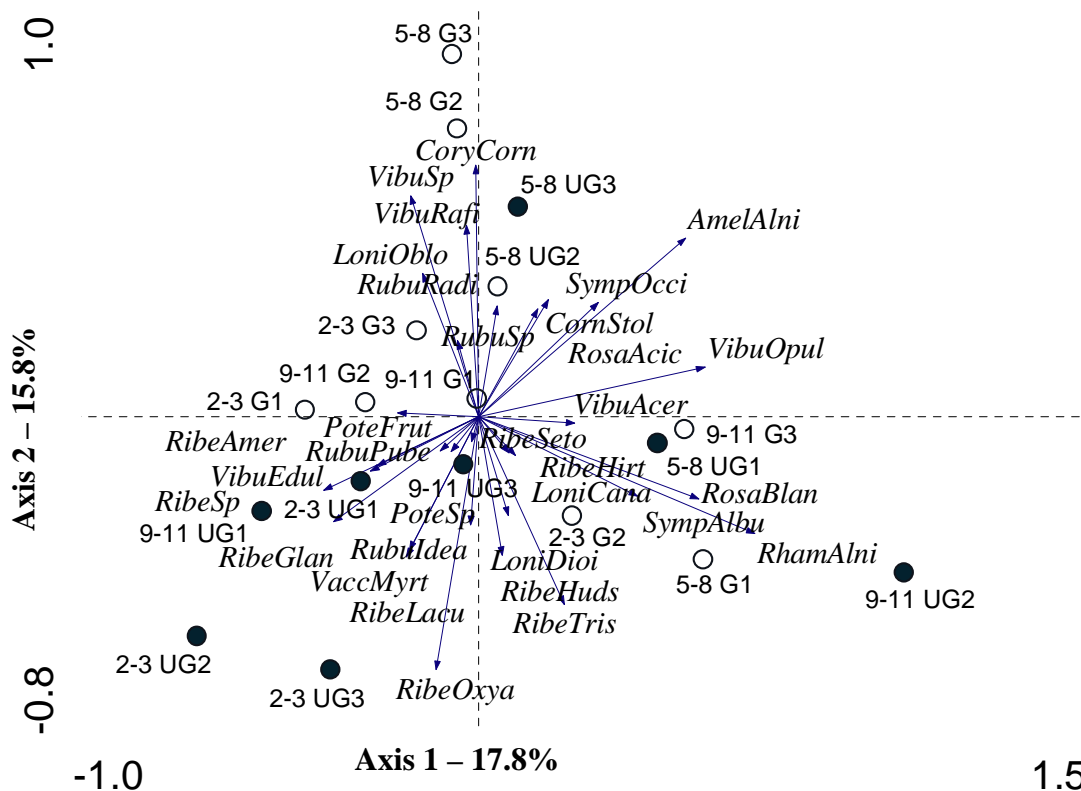
**Table 3-9:** Shrub indicator species by stand age.

Species	Common Name	Stand Age (Years)	Indicator Value	p value
<i>Symphoricarpos albus</i>	Snowberry	9-11	67.8	0.006
<i>Ribes hirtellum</i>	Smooth Gooseberry	9-11	55.6	0.027
<i>Cornus stolonifera</i>	Red-osier dogwood	2-3	50.2	0.040

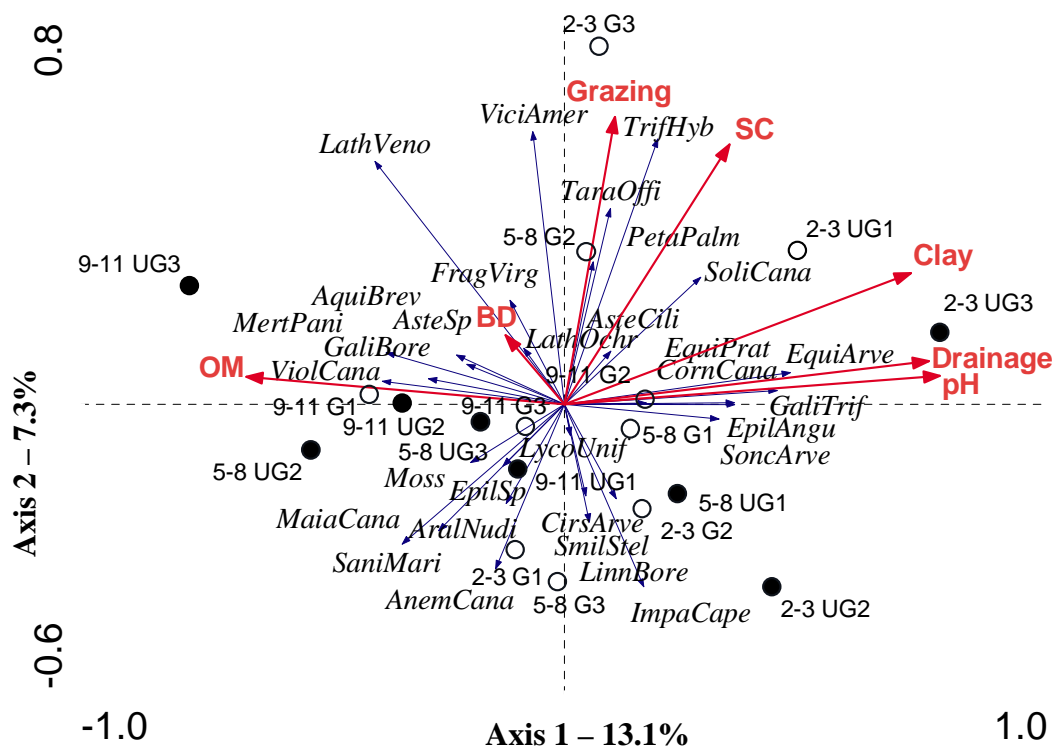


**Figure 3-10:** Herbaceous species observed amongst all sites – PCA Ordination diagram with plots (O) and species (arrows). Uncoloured circles represent grazed plots and coloured circles represent ungrazed plots. For display purposes only species with a greater than 5% average abundance displayed. Herbaceous species are: AgriGryp – *Agrimonia gryposepala*, AnemCana - *Anemone canadensis*, AquiBrev - *Aquilegia brevistyla*, AralNudi - *Aralia nudicaulis*, AsteCili - *Aster ciliolatus*, AsteSp - *Aster* spp, CirsArve - *Cirsium arvense*, CornCana - *Cornus canadensis*, EpilAngu - *Epilobium angustifolium*, EpilSp - *Epilobium* spp, EquiArve - *Equisetum arvense*, EquiPrat - *Equisetum pratense*, FragVirg - *Fragaria virginiana*, GaliBore - *Galium boreale*, GaliTrif - *Galium triflorum*, ImpaCape - *Impatiens capensis*, LathOchr - *Lathyrus ochroleucus*, LathVeno - *Lathyrus venosus*, LinnBore - *Linnaea borealis*, LycoUnif - *Lycopus uniflorus*, MaiaCana - *Maianthemum canadense*, MertPani - *Mertensia paniculata*, Moss - Moss spp, PetaPalm - *Petasites palmatus*, SaniMari - *Sanicula marilandica*, SmilStel - *Smilacina stellata*, SoliCana - *Solidago canadensis*, SoncArve - *Sonchus arvensis*, TaraOffi - *Taraxacum officinale*, TrifHyb - *Trifolium hybridum*, ViciAmer - *Vicia americana*, and ViolCana - *Viola canadensis*.

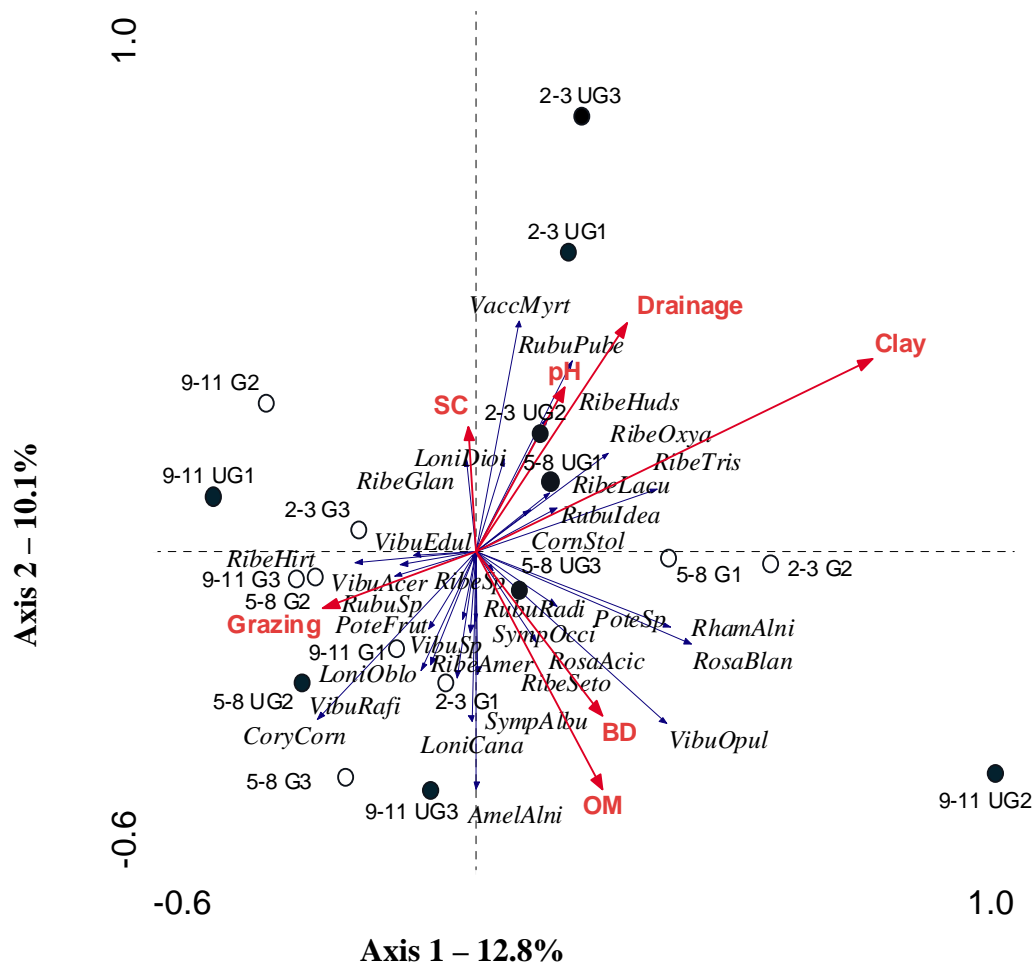
**Note:** Plants that could only be identified to the genus level were labeled as *Genus* sp. These labels only refer to the particular plant, and not others of the same genus.



**Figure 3-11:** Shrub species observed amongst all sites – PCA Ordination diagram with plots (O) and species (arrows). Uncoloured circles represent grazed plots and coloured circles represent ungrazed plots. Shrub species are AmelAlni – *Amelanchier alnifolia*, CornStol – *Cornus stolonifera*, CoryCorn – *Corylus cornuta*, LoniCana – *Lonicera canadensis*, LoniDioi – *Lonicera dioica*, LoniOblo – *Lonicera oblongifolia*, PoteSp – *Potentilla* spp, PoteFrut – *Potentilla fruticosa*, RhamAlni – *Rhamnus alnifolia*, RibeAmer – *Ribes americanum*, RibeGlan – *Ribes glandulosum*, RibeHirt – *Ribes hirtellum*, RibeHuds – *Ribes hudsonianum*, RibeLacu – *Ribes lacustre*, RibeOxya – *Ribes oxyacanthoides*, RibeSeto – *Ribes setosum*, RibeTris – *Ribes triste*, RibeSp – *Ribes* spp, RosaAcic – *Rosa acicularis*, RosaBlan – *Rosa blanda*, RubuIdea – *Rubus ideaus*, RubuPube – *Rubus pubescens*, RubuRadi – *Rubus radicans*, RubuSp – *Rubus* spp, SympAlbu – *Symphoricarpos albus*, SympOcci – *Symphoricarpos occidentalis*, VaccMyrt – *Vaccinium myrtilloides*, VibuAcer – *Viburnum acerifolium*, VibuEdul – *Viburnum edule*, VibuOpul – *Viburnum opulus*, VibuRafi – *Viburnum rafinesquianum*, VibuSp – *Viburnum* spp.



**Figure 3-12:** Herbaceous species observed amongst all sites – RDA Ordination diagram with plots (O), species (blue arrows) and environmental variables (red arrows). Uncoloured circles represent grazed plots and coloured circles represent ungrazed plots. For display purposes only species with a greater than 5% average abundance displayed. Herbaceous species are: AnemCana - *Anemone canadensis*, Aquibrev - *Aquilegia brevistyla*, AralNudi - *Aralia nudicaulis*, AsteCili - *Aster ciliolatus*, AsteSp - *Aster* spp, CirsArve - *Cirsium arvense*, CornCana - *Cornus canadensis*, EpilAngu - *Epilobium angustifolium*, EpilSp - *Epilobium* spp, EquiArve - *Equisetum arvense*, EquiPrat - *Equisetum pratense*, FragVirg - *Fragaria virginiana*, GaliBore - *Galium boreale*, GaliTrif - *Galium triflorum*, ImpaCape - *Impatiens capensis*, LathOchr - *Lathyrus ochroleucus*, LathVeno - *Lathyrus venosus*, LinnBore - *Linnaea borealis*, LycUnif - *Lycopus uniflorus*, MaiaCana - *Maianthemum canadense*, MertPani - *Mertensia paniculata*, Moss - Moss spp, PetaPalm - *Petasites palmatus*, SaniMari - *Sanicula marilandica*, SmilStell - *Smilacina stellata*, SoliCana - *Solidago canadensis*, SoncArve - *Sonchus arvensis*, TaraOffi - *Taraxacum officinale*, TrifHyb - *Trifolium hybridum*, ViciAmer - *Vicia americana*, and ViolCana - *Viola canadensis*. Environmental variables are: Drainage = drainage class, OM – organic matter content, Clay – clay fraction, pH, SC – soil compaction, BD – bulk density and Grazing – grazing pressure.



**Figure 3-13:** Shrub species observed amongst all sites – RDA Ordination diagram with plots (O), species (blue arrows) and environmental variables (red arrows). Uncoloured circles represent grazed plots and coloured circles represent ungrazed plots. Shrub species are AmelAlni – *Amelanchier alnifolia*, CornStol – *Cornus stolonifera*, CoryCorn – *Corylus cornuta*, LoniCana – *Lonicera canadensis*, LoniDioi – *Lonicera dioica*, LoniOblo – *Lonicera oblongifolia*, PoteSp – *Potentilla* spp, PoteFruit – *Potentilla fruticosa*, RhamAlni – *Rhamnus alnifolia*, RibeAmer – *Ribes americanum*, RibeGlan – *Ribes glandulosum*, RibeHirt – *Ribes hirtellum*, RibeHuds – *Ribes hudsonianum*, RibeLacu – *Ribes lacustre*, RibeOxya – *Ribes oxycanthoides*, RibeSeto – *Ribes setosum*, RibeTris – *Ribes triste*, RibeSp – *Ribes* spp, RosaAcic – *Rosa acicularis*, RosaBlan – *Rosa blanda*, RubuIdea – *Rubus ideoaus*, RubuPube – *Rubus pubescens*, RubuRadi – *Rubus radicans*, RubuSp – *Rubus* spp, SympAlbu – *Symphoricarpos albus*, SympOcci – *Symphoricarpos occidentalis*, VaccMyrt – *Vaccinium myrtilloides*, VibuAcer – *Viburnum acerifolium*, VibuEdu – *Viburnum edule*, VibuOpul – *Viburnum opulus*, VibuRafi – *Viburnum rafinesquianum*, VibuSp – *Viburnum* spp. Environmental variables are: Drainage = drainage class, OM – organic matter content, Clay – clay fraction, pH, SC – soil compaction, BD – bulk density and Grazing – grazing pressure.

### 3.5. Discussion

#### 3.5.1. *Effects of Grazing and Harvest Year*

The presence of grazing did not appear to influence the alpha diversity of either herbs or shrubs within the understory of post-harvest aspen stands. Stand age and the presence or absence of grazing appeared to affect landscape (beta) diversity, as indicated in the cluster analysis (Figure 3-10). The species turnover indicated in the cluster analysis likely has its source in different abundances of the species held in common between stands, since no patterns were prevalent in the Jaccard's Similarity Index, which analyzes only presence/absence of shared species and not their abundances (Table 3-3). A study done in British Columbia by Krzic *et al.* (2003), compared species diversity using Shannon's  $H'$  and Simpson's Reciprocal Index, also found no significant differences in  $H'$  and  $1/D$  between grazed and ungrazed plots. Although in their study, species richness was significantly higher in grazed stands. There was little difference in shrub alpha diversity, which may be a function of their greater tolerance of cattle related disturbance and lower levels of shrub species in the study sites.

Herbaceous species composition also varied as a function of distance between sites. This would suggest that the ability of herbaceous species to disperse throughout the study area was hindered by inter-site distances greater than 112.5 km (negative autocorrelation). Dispersal was much more successful at inter-site distances less than 2.5 km (positive autocorrelation). The lack of positive autocorrelation beyond 2.5 km suggests that there is dispersal limitation at work associated with other closely located sites (located greater than 2.5 km apart). Sites located less than 12.5 km from one another shared the highest species composition and abundance, the average Jaccard's Similarity Index for those sites was

54.9% compared to the overall site average of 47.2%. Many plant species shared among pairs of neighboring sites were particular only to those two sites, and were responsible for much of similarity in understory vegetation composition among neighboring sites (i.e., 9-11 G1 and 9-11 G2; and 2-3 G1 and 2-3 G2). Species composition was positively autocorrelated among nearby sites; this may be caused by the inability of plant species to disperse all sites throughout such a wide area. Furthermore, in addition to sites greater than 112.5 km apart being negatively autocorrelated, it should also be noted that sites 2-3 UG2 and 2-3 UG3, had the least in common with the other sites and were located furthest from the other sites, on the northern periphery of the study area. In this study the presence of autocorrelation, unfortunately, could not be avoided as there was only a limited number of sites were available for this study, partially because many of the older harvests were not done on agricultural land. Despite the presence of autocorrelation, differences in species composition between different stand ages, as well as between grazed and ungrazed stands at certain ages were quite prevalent.

Indicator species of 2-3 year-old stands, *Cirsium arvense*, *Sonchus arvensis*, *Equisetum arvense*, and *Taraxacum officinale* are typically found in recently disturbed, open areas (Moore 1975, Cody and Wagner 1981, Lemna and Messersmith 1990, Stewart-Wade *et al.* 2002). Presence of these species ranged from 15% to 77% of quadrats sampled in the six 2-3 year-old stands. Additionally, these species, and most of the indicator species found in the recently disturbed 2-3 year-old stands are often considered weedy species (Royer and Dickinson 1999).

Stand age was one of the main distinguishing factors in the separation of species composition and abundance, which suggests a short term successional gradient in the species



composition. The 2-3 year-old and 5-8/9-11 year-old stands shared the fewest number of species in the cluster analysis and the PCA/RDA ordination biplots and triplots. In fact, of the 16 herbaceous indicator species associated with stand age, and 14 of those were indicative of 2-3 year-old stands (Table 3-6). An explanation for difference in species composition between stand ages may be the difference in the amount of light present in the younger versus older stands. The 5-8 and 9-11 year-old stands had greater crown closure than in the 2-3 year-old stands which may result in a different microclimate in the understory (i.e., greater humidity, and decreased temperature fluctuations, Powell and Bork 2007). For example, in the 5-8 and 9-11 year-old stands *Mertensia paniculata* and *Pyrola asarifolia* were found to be indicator species and also are known to have high moisture requirements (Chambers *et al.* 1996). It would be expected that open 2-3 year-old stands would be drier than 5-8 and 9-11 year-old stands where with greater canopy closure where plants with greater moisture requirements may occur (Powell and Bork 2007, Hart and Chen 2008).

### 3.5.2. Site Factors

Many herbaceous and shrub species did not appear to orient themselves within the two RDAs ordination proximally to environmental eigenvectors according to their environmental requirements (i.e., high moisture requirement). It is likely that the influence of the environmental variables had much less of an impact on species composition in the aspen understory than successional differences between stands. It would likely require considerably more environmental variation between sites to noticeably alter herbaceous and shrub community composition in the understory. The relatively small amount of change in

physical aspects between sites that were spaced up to 143.8 km apart is probably indicative that the physical attributes of many sites were quite similar.

Previous studies have analyzed the effects of soil variables on species diversity and composition in forested stands (Whittaker 1956, Werger *et al.* 1983, Leuschner and Lenzion 2009). Few studies, however, have examined the isolated and interactive effects of cattle grazing and soil variables on species diversity in regenerating stands (Krzic *et al.* 2003).

### 3.5.3. Conclusion

The presence of cattle grazing did not affect levels of plant species alpha diversity in aspen stands after harvest. Composition of both herbaceous and shrub species showed some differences between treatments, most differences could be attributed to inter-site distance or succession rather than a treatment effect. Although, several herbaceous and shrub species were indicative of sites that had post-harvest grazing. It appears that if cattle ranchers utilized site forage levels close to the recommended grazing capacity guidelines set out by Manitoba Agriculture, cattle grazing will not lead to a significant loss or change in plant species diversity within a regenerating aspen stand.

## Chapter 4 - Synopsis

### 4.1. *Aspen Density and Height*

Commercial hardwood stands in the Duck Mountain region of western Manitoba that were grazed after forest harvest generally had shorter and less numerous regenerating stems of commercial species than in ungrazed stands. Also cattle grazing negatively affected overall aspen density and height in 9-11 year-old stands, where overall aspen stem density in grazed stands was significantly less than in ungrazed stands. Despite this decrease in stem density, grazing at the observed livestock stocking levels did not prevent the stands from meeting or exceeding the minimum stem density mandated for seven year-old hardwood stands in Province of Manitoba stocking guidelines (Manitoba Conservation 2001).

Although, since cattle in grazed stands were often able to move freely from pasture to forest, it is unknown if grazing pressure in the aspen stands in forested areas was at reported levels. In addition, both grazed and ungrazed stands from the Duck Mountain area appeared to have a higher average stem density than in the comparison studies after 8 years post-harvest.

Both grazed and ungrazed 2-3 year-old stands had lower stem densities than similarly aged stands surveyed in the comparison studies (Figure 2-6). However, regardless of initial stem density, stands usually converged on a common stem density approximately seven years after harvest (Peterson and Peterson 1992, Bokalo *et al.* 2007). The rate of self-thinning during the first eight years after harvest in the from the comparison studies was much greater than that found in the stands surveyed in the Duck Mountain area. Stem density in the 5-8 and 9-11 year-old stands was comparable to stands of a similar age from the other studies (Pollard 1971, Bella and de Franceschi 1980, Weingartner 1980, Crouch

1981, Crouch 1983, Perala 1984, Bella 1986, Steneker 1976b, Dockrill 2001, DesRochers and Lieffers 2001, Berger et al. 2004).

Regardless of availability of desired forage, cattle will usually browse a portion of aspen stems (Hilton and Bailey 1974). When stands are overgrazed, as was the case in several stands in this study, incidence of browsing can be greatly increased. For this reason, the presence of cattle in a regenerating aspen stand may still depress stem height, and deferral of cattle grazing after harvest is often recommended to allow aspen to reach a height where cattle cannot reach the leading stem (Sampson 1919, Dockrill 2001). In my study, only one site, 9-11 G3 had any grazing deferral, therefore in this context a grazing deferral may not be required.

#### *4.2. Tree Health*

Overall tree vigour, degree of mechanical damage to stem and root collar, and incidence of pests were similar in both grazed and ungrazed stands in this study. Almost all trees used for health assessment had some sign of injury or stress, but this is common attribute of young aspen stems (Millers 1972). Such damage is likely to impair stem survival in the short term. Although, higher incidences of certain pests were found in particular ages of grazed or ungrazed stands, there was no consistent pattern found between stand ages or grazed and ungrazed stands. Comparison of impacts on tree health in this study with other research was not possible due to lack of comparable studies examining the link between cattle grazing and tree condition (Peterson and Peterson 1992).

Crown dieback was the only health variable that showed a consistent pattern across all stand ages and treatments. A higher incidence of crown dieback was correlated with higher stem densities in all harvested stands. A crown dieback in excess 30% of the total

canopy is a common symptom of stems likely to die within one year (Steinman 1998, Brandt *et al.* 2003). Increased stem mortality or a higher incidence of self thinning would be expected in stands with higher stem densities (Brandt *et al.* 2003, Bokalo *et al.* 2007).

#### *4.3. Aspen Regeneration and the Soil Environment*

Neither aspen density nor height were related to soil variables. There were few extreme variables recorded within the soil (i.e., pH, soil drainage class, clay content, etc.) and soil conditions in all sites were well within the natural range tolerated by aspen. Values of all the soil variables sampled were within the typical range of reported for aspen stands in northern habitats. The amount of soil compaction found in this study was below levels that cause substantial aspen and balsam poplar growth reductions (Stone and Elioff 1998, Busscher *et al.* 1986). This finding may be attributed to cattle having only localized impacts on soil properties in well used cow paths. Furthermore, collecting standardized measurements of soil compaction between sites is logistically difficult, for instance accounting for the effects of moisture content on compaction may not always be possible, as was found in this study.

#### *4.4. Grazing and the Aspen Understory*

The presence of cattle grazing did not affect the levels of understory alpha diversity of stands after harvest. Although composition of both herbaceous and shrub species was somewhat different between treatments, succession and inter-site proximity may override treatment effects. For instance, considerably more indicator species were associated with a particular stand age than were associated with either grazed or ungrazed status.

Differences in understory plant species composition between the youngest stands and 5-8 and 9-11 year-old stands may in part be dependant on the amount light present under the

tree canopy (Bartemucci *et al.* 2006). The older stands had considerably greater crown closure, which decreases light and ambient temperature in the understory (Peterson and Peterson 1992, Powell and Bork 2007). In addition, soil moisture which tends to increase as canopy closure increases creating different microclimate conditions in older stands. Furthermore, most of the species that were indicative of 2-3 year-old stands are considered weedy species and would typically be found in recently disturbed, open areas, as was characteristic of the recently harvested sites (Royer and Dickinson 1999).

Spatial analyses revealed that species composition was positively autocorrelated among sites that were closer than 2.5 km to each other. Lack of significant differentiation among species assemblages among stand ages may have highlighted the need to sample much older harvested stands, perhaps because stands used in this study were not old enough to observe differentiation of diversity. As LP only began harvesting in 1995 there were no stands older than 11 years-old in that study area at the time of sampling.

#### *4.5. Conclusion*

Although there was a reduction in stem height and density in aspen stands, it appears that if cattle ranchers are willing to graze cattle near the recommended grazing capacity guidelines set out by Manitoba Agriculture, cattle will not over graze regenerating aspen and other commercial hardwood stems. Stems present in grazed stands are in good health and did not experience an increased incidence of pests and disease than in ungrazed stands. Cattle grazing in these recently harvested stands did not decrease understory plant diversity, although herbaceous species composition did differ between sites.

## Literature Cited

- Abdelmagid, A.H., Schuman, G.E. and Hart, R.H. 1987. Soil Bulk-Density and Water Infiltration as Affected by Grazing Systems. *Journal of Range Management*, 40: 307-309.
- Anderson, N.A., Ostry, M.E. and Anderson, G.W. 1979. Insect wounds as infection sites for *Hypoxylon mammatum* on trembling aspen. *Phytopathology*, 69: 476-479.
- Arthur, R.L. 1983 Cattle preferences for plant communities and forages in the aspen parkland. *Agriculture-Forestry Bulletin, Feeder's Day Report*. University of Alberta, Edmonton, AB. pp. 66-70
- Arthur, R.L. 1984. Plant community and forage preferences of cattle on native aspen parkland range. MSc. thesis. University of Alberta, Edmonton, AB.
- Bagga, D.K. and Smalley, E.B. 1974. The development of hypoxylon canker of *Populus tremuloides*: role of interacting environmental factors. *Phytopathology*, 64: 658-662.
- Bailey, A.W. and Arthur, R.L. 1985. Cattle use of aspen suckers encroaching into native fescue rangeland. University of Alberta. *Agriculture-Forestry Bulletin, Feeder's Day Report*. Edmonton, AB. p. 83-84.
- Bailey, A.W., Irving, B.D. and Fitzgerald, R.D. 1990. Regeneration of Woody Species Following Burning and Grazing in Aspen Parkland. *Journal of Range Management*, 43: 212-215.
- Ball, B.C. and O'Sullivan, M.F. 1982. Soil Strength and Crop Emergence in Direct Drilled and Ploughed Cereal Seedbeds in 7 Field Experiments. *Journal of Soil Science*, 33: 609-622.
- Bartemucci, P., Messier, C. and Canham, C.D. 2006. Overstory influences on light attenuation patterns and understory plant community diversity and composition in southern boreal forests of Quebec. *Canadian Journal of Forest Research*, 36: 2065-2079.
- Bates, P.C., Blinn, C.R. and Alm, A.A. 1993. Harvesting impacts on quaking aspen regeneration in northern Minnesota. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, 23: 2403-2412.
- Beck, J.L. and Peek, J.M. 2005. Diet Composition, Forage Selection, and Potential for Forage Competition Among Elk, Deer, and Livestock on Aspen-Sagebrush Summer Range. *Rangeland Ecology & Management*, 58: 135-147.
- Belanger, R.R., Manion, P.D. and Griffin., D.H. 1989. Amino acid content of water-stressed plantlets of *Populus tremuloides* clones in relation to clonal susceptibility to *Hypoxylon mammatum* in vitro. *Canadian Journal of Botany*, 68: 26-29.

- Bella, I.E. 1986. Logging practices and subsequent development of aspen stands in east-central Saskatchewan Forestry Chronicle, 62: 81-83.
- Bella, I.E. and De Franceschi, J.P. 1980. Biomass productivity of young aspen stands in western Canada. Environment Canada, Canadian Forestry Service, Northern Forestry Research Centre, Edmonton, AB. Information Report NOR-X-219.
- Berger, A.L., Puettmann, K.J. and Host, G.E. 2004. Harvesting impacts on soil and understory vegetation: the influence of season of harvest and within-site disturbance patterns on clear-cut aspen stands in Minnesota. Canadian Journal of Forest Research- Revue Canadienne De Recherche Forestiere, 34: 2159-2168.
- Bezkorowajnyj, P.G., Gordon, A.M. and McBride, R.A. 1993. The Effect of Cattle Foot Traffic on Soil Compaction in a Silvo-Pastoral System. Agroforestry Systems, 21: 1-10.
- Bird, R.D. 1961. Ecology of the aspen parkland of western Canada in relation to land use. Contribution No. 27. Department of Agriculture, Research Branch, Ottawa, Ontario.
- Blouin, V.M., Schmidt, M.G., Bulmer, C.E. and Krzic, M. 2008. Effects of compaction and water content on lodgepole pine seedling growth. Forest Ecology and Management, 255: 2444-2452.
- Bokalo, M., Comeau, P.G. and Titus, S.J. 2007. Early development of tended mixtures of aspen and spruce in western Canadian boreal forests. Forest Ecology and Management, 242: 175-184.
- Boone, R. and Westwood, R. 2006. An assessment of tree health and trace element accumulation near a coal-fired generating station, Manitoba, Canada. Environmental Monitoring and Assessment, 121: 151-172.
- Borcard, D., Legendre, P. and Drapeau, P. 1992. Partialling out the spatial component of ecological variation. Ecology, 73: 1045-1055.
- Brady, N.C. and Weil, R.R. 2002. The nature and properties of soils. 13th Edition. Prentice Hall, Inc., Upper Saddle River, NJ. pg 211.
- Brandt, J.P., Cerezke, H.F., Mallett, K.I., Volney, W.J.A. and Weber, J.D. 2003. Factors affecting trembling aspen (*Populus tremuloides* Michx.) health in the boreal forest of Alberta, Saskatchewan, and Manitoba, Canada. Forest Ecology and Management, 178: 287-300.
- Burt, R. 2004. Soil Survey Laboratory Methods Manual. Soil Survey Investigations Report No. 42. Version 4.0. U. S. Department of Agriculture, Natural Resources Conservation Service. Washington, DC.



- Busscher, W.J., Sojka, R.E. and Doty, C.W. 1986. Residual Effects of Tillage on Coastal-Plain Soil Strength. *Soil Science*, 141: 144-148.
- Cayford, J.H., Hildahl, V., Nairn, L.D. and Wheaton, M.P.H. 1959. Injury to trees from winter drying and frost in Manitoba and Saskatchewan in 1958. *Forestry Chronicle*, 35: 282-290.
- Chambers, B.A., Legasy, K. and Bentley, C.V. 1996. Forest plants of central Ontario. Lone Pine Publishing, Edmonton, AB. 448 p.
- Christiansen, E., Waring, R.H. and Berryman, A.A. 1987. Resistance of Conifers to Bark Beetle Attack - Searching for General Relationships. *Forest Ecology and Management*, 22: 89-106.
- Churchill, G.B., John, H.H., Duncan, D.P. and Hodson, A.C. 1964. Long-term effects of defoliation of aspen by the forest tent caterpillar. *Ecology*, 45: 630-636.
- Cody, W.J. and Wagner, V. 1981. The Biology of Canadian Weeds .49. *Equisetum-arvense* L. *Canadian Journal of Plant Science*, 61: 123-133.
- Crouch, G.L. 1981. Regeneration on aspen clearcuts on north-western Colorado. U. S. Department of Agriculture, Forest Service, Rocky Mountain Forest Range Experiment Station, Fort Collins, CO. Research Note RM-407
- Crouch, G.L. 1983. Aspen regeneration after commercial clearcutting in southwestern Colorado. *Journal of Forestry*, 81: 316-319.
- Crouch, G.L. 1986. Aspen regeneration in 6 to 10 year old clearcuts in southwestern Colorado. U.S. Department of Agriculture, Forestry Service, General Technical Report RM-119.
- Crown Land Classification Committee. 2004. Crown Land Classification Committee Guidelines: Policy and Procedures Manual. Accessed Sept 10, 2008.
- DeByle, N.V. 1964. Detection of Functional Intraclonal Aspen Root Connections by Tracers and Excavation. *Forest Science*, 10: 386-396.
- DeByle, N.V. 1985. Animal Impacts. *In Aspen: ecology and management in the western United States. Edited by N. V. DeByle and R. P. Winokur.* U. S. Department of Agriculture, Forest Service. General Technical Report. Report RM-119.pp. 115-123.
- Defrêne, M. and Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetric approach. *Ecological Monographs*, 67: 345-366.

- DesRochers, A. and Lieffers, V.J. 2001. Root biomass of regenerating aspen (*Populus tremuloides*) stands of different densities in Alberta. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, 31: 1012-1018.
- Dockrill, C. 2001. Effects of cattle and wild ungulate foraging on trembling aspen regeneration in Alberta's Lower Boreal Forest. M.Sc. thesis. University of Alberta, Edmonton, AB
- Dockrill, C.W.M., Bailey, A.W., Blenis, P.V. and King, J.R. 2006. Seasonal variation in resistance of aspen stems to shearing force. *Rangeland Ecology & Management*, 59: 212-215.
- Dockrill, C.W.M., Blenis, P.V., Bailey, A.W. and King, J.R. 2004. Effect of summer cattle grazing on aspen stem injury, mortality and growth. *Forestry Chronicle*, 80: 257-261.
- Donnelly, M. 2003. Ecologically-based forest planning and management for aquatic ecosystems in the Duck Mountains, Manitoba. *Journal of Environmental Engineering and Science*, 2: S35-S40.
- Dray, S., Chessel, D. and Thioulouse, J. 2003. Co-inertia analysis and the linking of ecological data tables. *Ecology*, 84: 3078-3089.
- Drewry, J.J., Cameron, K.C. and Buchan, G.D. 2001. Effect of simulated dairy cow treading on soil physical properties and ryegrass pasture yield. *New Zealand Journal of Agricultural Research*, 44: 181-190.
- Eliasson, L. 1971a. Growth Regulators in *Populus-Tremula* .3. Variation of Auxin and Inhibitor Level in Roots in Relation to Root Sucker Formation. *Physiologia Plantarum*, 25: 118-121.
- Eliasson, L. 1971b. Adverse Effect of Shoot Growth on Root Growth in Rooted Cuttings of Aspen. *Physiologia Plantarum*, 25: 263-268.
- Ellison, L. and Houston, W.R. 1958. Production of herbaceous vegetation in openings and under canopies of western aspen. *Ecology* 39: 337-345.
- Environment Canada. 1996. State of the Environment Infobase, Narrative Descriptions of Terrestrial Ecozones and Ecoregions of Canada, Mixedwood Plains Ecozone. Website accessed August 2009. [http://www.ec.gc.ca/soer-ree/English/Framework/Nardesc/mixpln\\_e.cfm](http://www.ec.gc.ca/soer-ree/English/Framework/Nardesc/mixpln_e.cfm)
- Environment Canada. 2008. Canadian Climate Normals or Averages 1971-2000. Retrieved 20 February 2009 [http://www.climate.weatheroffice.ec.gc.ca/climate\\_normals/index\\_e.html](http://www.climate.weatheroffice.ec.gc.ca/climate_normals/index_e.html)

- Farmer, R.E.J. 1962. Aspen root sucker formation and apical dominance. *Forest Science* 8: 403-410.
- Federer, C.A., Turcotte, D.E. and Smith, C.T. 1993. The organic fraction - bulk density relationship and expression of nutrient content in forest soils. *Canadian Journal of Forest Research* 23: 1026-1032.
- Ferrero, A.F. 1991. Effect of compaction simulating cattle trampling on soil physical characteristics in woodland. *Soil & Tillage Research*, 19: 319-329.
- Fitzgerald, R.D. and Bailey, A.W. 1984. Control of Aspen Regrowth by Grazing with Cattle. *Journal of Range Management*, 37: 156-158.
- Fitzgerald, R.D., Hudson, R.J. and Bailey, A.W. 1986. Grazing Preferences of Cattle in Regenerating Aspen Forest. *Journal of Range Management*, 39: 13-18.
- Floate, M.J.S. 1970. Mineralization of nitrogen and phosphorus from organic materials of plant and animal origin and its significance in nutrient cycle in grazed upland and hill soils. *Journal of the British Grassland Society*, 25: 295-302.
- Forestry Canada. 1988. Canada's Forest Inventory 1986. Forestry Canada. Petawawa National Forestry Institute, Chalk River, ON.
- Frey, B.R., Lieffers, V.J., Hogg, E.H. and Landhausser, S.M. 2004. Predicting landscape patterns of aspen dieback: mechanisms and knowledge gaps. *Canadian Journal of Forest Research*, 34: 1379-1390.
- Frey, B.R., Lieffers, V.J., Landhausser, S.M., Comeau, P.G. and Greenway, K.J. 2003. An analysis of sucker regeneration of trembling aspen. *Canadian Journal of Forest Research*, 33: 1169-1179.
- Gatto, L.W. 1997. Ground freezing effects on soil erosion of army training lands. Part 1: initial test results. U.S. Army Cold Regions Research and Engineering Laboratory, Special Report 97-15.
- Gilbert, B. and Lechowicz, M.J. 2004. Neutrality, niches, and dispersal in a temperate forest understory. *Proceedings of the National Academy of Sciences of the United States of America*, 101: 7651-7656.
- Gotelli, N.J. and Colwell, R.K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, 4: 379-391.
- Graham, S.A. and Harrison, R.P. 1954. Insect attacks and Hypoxylon infections in aspen. *Journal of Forestry*, 52: 741-743.

- Greacen, E.L. and Sands, R. 1980. Compaction of forest soils. A review. *Australian Journal of Soil Research*, 18: 163-189.
- Greenwood, K.L. and McKenzie, B.M. 2001. Grazing effects on soil physical properties and the consequences for pastures: a review. *Australian Journal of Experimental Agriculture*, 41: 1231-1250.
- Gross, H.L. and Basham, J.T. 1981. Diseases of aspen suckers in Northern Ontario. Canadian Forest Service, Information Report O-X-329.
- Haack, R.A. 1996. Will global warming alter paper birch susceptibility to bronze birch borer attack? *In Dynamics of forest herbivory: quest for pattern and principle. Edited by W.J. Mattson, P. Niemela, and M. Rousi.* U.S. Department of Agriculture, Forest Service General Technical Report. NC-183. pp 234-247.
- Haapalla, H., Goltsovab, N., Seppalaa, R., Huttunenc, S., Koukia, J., Lamppuc, J. and Popovichevb, B. 1996. Ecological condition of forests around the eastern part of the Gulf of Finland. *Environmental Pollution*, 91: 253- 265.
- Haeussler, S. and Coates, D. 1986. Autecological characteristics of selected species that compete with conifers in British Columbia: a literature review. Ministry of Forests, Land Management Rep. No. 33, Victoria, B.C.
- Haeussler, S. and Kabzems, R. 2005. Aspen plant community response to organic matter removal and soil compaction. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, 35: 2030-2044.
- Hart, S.A. and Chen, Y.H. 2008. Fire, logging, and overstory affect understory abundance, diversity, and composition in boreal forest. *Ecological Monographs*, 78:123-140.
- Heeney, C.J., Kemperman, J.A. and Brown, G. 1975. A silvicultural guide to the aspen working group in Ontario. OMNR, Forest Management Division. 47 pp. .
- Heitschmidt, R. and Walker, J. 1983. Short Duration Grazing and the Savory Grazing Method in Perspective. *Rangelands*, 5: 147-150.
- Higgins, J.J. 2004. Introduction to Modern Nonparametric Statistics. Brooks/Cole-Thomson Learning, USA. pp 309-314.
- Hildahl, V. and Campbell, A.E. 1975. Forest tent caterpillar in the prairie provinces. Environment Canada, Canadian Forestry Service, Northern Forestry Research Centre, Edmonton, AB. Information Report NOR-X-135.
- Hildahl, V. and Reeks, W.A. 1960. Outbreaks of the forest tent caterpillar, *Malacosoma disstria* Hbn., and their effects of stands of trembling aspen in Manitoba and Saskatchewan. *Canadian Entomologist* 92: 199-209.

- Hilton, J.E. and Bailey, A.W. 1972. Cattle use of a sprayed aspen parkland range *Journal of Range Management*, 25: 257-260.
- Hilton, J.E. and Bailey, A.W. 1974. Forage Production and Utilization in a Sprayed Aspen Forest in Alberta. *Journal of Range Management* 27: 375-380.
- Hinds, T.E. 1972. Insect transmission of *Ceratocystis* species associated with aspen cankers. *Phytopathology*, 62: 221-225.
- Hiratsuka, Y., Gibbard, D., Bakowsky, O. and Maier, G. 1990. Classification and measurement of aspen decay and stain in Alberta. Forestry Canada, Northwest Forestry Centre, Edmonton, AB. Information Report NOR-X-314.
- Hiratsuka, Y. and Zalasky, H. 1993. Frost and other climate-related damage of forest trees in the prairie provinces. Forestry Canada, Northern Forestry Center. Information Report NOR-X-331.
- Hogg, E.H. 1994. Climate and the Southern Limit of the Western Canadian Boreal Forest. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, 24: 1835-1845.
- Hogg, E.H. 1997. Temporal scaling of moisture and the forest-grassland boundary in western Canada. *Agriculture, Forestry and Meteorology*, 84: 115-122.
- Hogg, E.H., Brandt, J.P. and Kochtubajda, B. 2002. Growth and dieback of Aspen forests in northwestern Alberta, Canada, in relation to climate and insects. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, 32: 823-832.
- Hogg, E.H., Brandt, J.P. and Michaellian, M. 2008. Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, 38: 1373-1384.
- Hogg, E.H. and Hurdle, P.A. 1995. The Aspen Parkland in Western Canada - a Dry-Climate Analog for the Future Boreal Forest. *Water Air and Soil Pollution*, 82: 391-400.
- Hogg, E.H. and Schwarz, A.G. 1999. Tree-ring analysis of declining aspen stands in west-central Saskatchewan. Environment Canada, Canadian Forestry Service, Northern Forestry Research Centre, Edmonton, AB. Information Report Information Report NOR-X-359.
- Holechek, J.L., Hilton de Souza, G., Molinar, F. and Galt, D. 1998. Grazing Intensity: Critique and Approach. *Rangelands*, 20: 15-18.
- Holling, C.S. 1988. Temperate forest insect outbreaks, tropical deforestation and migratory birds. *Memoirs of the Entomological Society of Canada*, 21-32.

- Horton, K.W. and Maini, J.S. 1964. Aspen reproduction: its characteristics and control. Canadian Department of Forestry and Rural Development. Forest Research Branch. Research Report. 64-0-12.
- Houston, D.R. 1992. A host-stress-saprogen model for forest dieback-decline diseases. *In* Forest decline concepts. *Edited by* P.D. Manion and D. Lachance. American Phytopathological Society, St Paul, Minnesota. pp 3-25.
- Houston, W.R. 1954. A condition guide for aspen ranges of Utah, Nevada, southern Idaho, and western Wyoming. U.S. Department of Agriculture, Intermountain Forest and Range Experiment Station, Station Paper 32, Ogden, Utah. 17 p.
- Hubbes, M. 1966. Inhibition of *Hypoxylon prunatum* (Klotzsche) Cke. by aspen bark meal and the nature of active extractives. Canadian Journal of Botany 44: 365-386.
- Huffman, R.D., Fajvan, M.A. and Wood, P.B. 1999. Effects of residual overstory on aspen development in Minnesota. Canadian Journal of Forest Research, 29: 284-289.
- Ives, W.G.H. 1981. Environmental factors affecting 21 forest insect defoliators in Manitoba and Saskatchewan 1945-1969. Environment Canada, Canadian Forest Service, Edmonton, AB. Information Report NOR-X-233
- Ives, W.G.H. and Wong, H.R. 1988. Tree and shrub insects of the prairie provinces. Environment Canada, Canadian Forestry Service, Northern Forestry Research Centre, Edmonton, AB. Information Report Information Report NOR-X-292.
- Jongman, R.H., ter Braak, C.J. and van Tongeren, O.F. 1995. Data analysis in community and landscape ecology. Pudoc, Wageningen, the Netherlands.
- Jurgensen, M.F., Harvey, A.E., Graham, R.T., Page-Dumroese, D.S., Tonn, J.R., Larsen, M.J. and Jain, T.B. 1997. Impacts of timber harvesting on soil organic matter, nitrogen, productivity, and health of Inland Northwest forests. Forest Science, 43: 234-251.
- Kabzems, R. and Haeussler, S. 2005. Soil properties, aspen, and white spruce responses 5 years after organic matter removal and compaction treatments. Canadian Journal of Forest Research, 35: 2045-2055.
- Kay, C.E. and Bartos, D.L. 2000. Ungulate herbivory on Utah aspen: Assessment of long-term exclosures. Journal of Range Management, 53: 145-153.
- Kenkel, N.C., Derksen, D.A., Thomas, A.G. and Watson, P.R. 2002. Multivariate analysis in weed science research. Weed Science, 50: 281-292.
- Kimmins, J.P. 1997. Forest ecology. Prentice-Hall, Inc., Upper Saddle River, N.J.

- Krajina, V.J., Klinka, K. and Worrall, J. 1982. Distribution and ecological characteristics of trees and shrubs of British Columbia. Faculty of Forestry, University of British Columbia, Vancouver, BC.
- Krasny, M.E. and Johnson, E.A. 1992. Stand Development in Aspen Clones. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere, 22: 1424-1429.
- Krebill, R.G. 1972. Mortality of aspen on the Gros Vente elk winter range. U.S. Department of Agriculture. Forestry Service, Intermountain Forest and Range Experiment Station. Research Paper INT-129.
- Krzic, M., Bulmer, C.E., Teste, F., Dampier, L. and Rahman, S. 2004. Soil properties influencing compactability of forest soils in British Columbia. Canadian Journal of Soil Science, 84: 219-226.
- Krzic, M., Newman, R.F. and Broersma, K. 2003. Plant species diversity and soil quality in harvested and grazed boreal aspen stands of northeastern British Columbia. Forest Ecology and Management, 182: 315-325.
- Landhausser, S.M. and Lieffers, V.J. 2003. Seasonal changes in carbohydrate reserves in mature northern *Populus tremuloides* clones. Trees-Structure and Function, 17: 471-476.
- Landhausser, S.M., Lieffers, V.J. and Mulak, T. 2006. Effects of soil temperature and time of decapitation on sucker initiation of intact *Populus tremuloides* root systems. Scandinavian Journal of Forest Research, 21: 299-305.
- Landhausser, S.M., Silins, U., Lieffers, V.J. and Liu, W. 2003. Response of *Populus tremuloides*, *Populus balsamifera*, *Betula papyrifera* and *Picea glauca* seedlings to low soil temperature and water-logged soil conditions. Scandinavian Journal of Forest Research, 18: 391-400.
- Lane, C.T. and Willoughby, M.G. 2000. Forage growth of deciduous communities in northern Alberta. 53rd Annual Meeting, Society for Range Management, Boise, ID.
- Legendre, P. and Fortin, M.J. 1989. Spatial Pattern and Ecological Analysis. Vegetatio, 80: 107-138.
- Legendre, P. and Legendre, L. 1998. Numerical ecology, 2nd English edition. Elsevier, Amsterdam.
- Lemna, W.K. and Messersmith, C.G. 1990. The Biology of Canadian Weeds .94. *Sonchus arvensis* L. Canadian Journal of Plant Science, 70: 509-532.

- Leuschner, C. and Lenzion, J. 2009. Air humidity, soil moisture and soil chemistry as determinants of the herb layer composition in European beech forests. *Journal of Vegetation Science*, 20: 288-298.
- Lull, H.W. 1959. Soil compaction on forest and range lands. U. S. Department of Agriculture. Miscellaneous Publication 768.
- MacArthur, R.H. 1965. Patterns of Species Diversity. *Biological Reviews of the Cambridge Philosophical Society*, 40: 510-533.
- Magurran, A.E. 2004. *Measuring Biological Diversity*. Blackwell Publishing Limited, MA.
- Maini, J.S. and Cayford, J.H. 1968. Silvics and ecology of *Populus* in Canada. *In Growth and utilization of poplars in Canada*. Departmental Publication 1205. *Edited by* Maini, J.S., Cayford, J.H. Ottawa, ON, Department of Forestry and Rural Development, Forestry Branch. pp 20-69.
- Maini, J.S. and Horton, K.W. 1964. Influence of temperature and moisture on initiation and initial development of *Populus tremuloides* suckers. Canadian Department of Forestry, Forest Research Branch, Ottawa, ON. Report 64-0-11.
- Maini, J.S. and Horton, K.W. 1966. Vegetative propagation of *Populus* spp.I. Influence of temperature on formation and initial growth of aspen suckers. *Canadian Journal of Botany*, 44: 1183-1189.
- Manitoba Conservation. 2001. Forest Renewal Standards. Forestry Branch, Manitoba Conservation, MB. 8 p. Accessed May 15, 2008 at <http://www.gov.mb.ca/conservation/forestry/forest-renewal/fr-contents.html>.
- Marshall, P.L., Davis, G. and LeMay, W.M. 2000 Using line intersect sampling for coarse woody debris Service, B.C.F. TR-003
- Mattson, W.J. and Addy, N.D. 1975. Phytophagous Insects as Regulators of Forest Primary Production. *Science*, 190: 515-522.
- McCartney, D.H. 1993. History of grazing research in the Aspen Parkland. *Canadian Journal of Animal Science*, 73: 749-763.
- McCune, B. and Grace, J.B. 2002. *Analysis of Ecological Communities*. MjM Software Design, Gleneden Beach, OR.
- McCune, B. and Mefford, M.J. 1999. PC-ORD. Multivariate Analysis of Ecological Data, Version 4. MjM Software Design, Gleneden Beach, Oregon.
- Millers, I. 1972. Injury to young trembling aspen stems. U.S. Department of Agriculture. Forestry Service, Forest Pest Management Report S-72-4.



- Moore, R.J. 1975. Biology of Canadian Weeds .13. *Cirsium-arvense*(L) Scop. Canadian Journal of Plant Science, 55: 1033-1048.
- Mundell, T.L., Landhausser, S.M. and Lieffers, V.J. 2008. Root carbohydrates and aspen regeneration in relation to season of harvest and machine traffic. Forest Ecology and Management, 255: 68-74.
- Naeth, M.A., Bailey, A.W., Pluth, D.J., Chanasyk, D.S. and Hardin, R.T. 1991. Grazing impacts on litter and soil organic-matter in Mixed Prairie and Fescue Grassland ecosystems of Alberta. Journal of Range Management, 44: 7-12.
- Navratil, S. 1991. Regeneration challenges. *In Aspen management for the 21st century. Edited by S. Navratil and P.B. Chapman.* Canadian Forest Service, Poplar Council of Canada, Edmonton, AB. pp. 15-27.
- Nordstrom, L.O. 1984. The ecology and management of forest range in British Columbia: a review and analysis. BC Ministry of Forests, Land Management Report 19, Victoria, BC. 91pp.
- Patric, J.H. and Helvey, J.D. 1986. Some effects of grazing on soil and water in the Eastern Forest. U. S. Department of Agriculture, Forest Service. General Technical Report, NE-115, Washington, DC. 24 pp.
- Peet, R.K. 1974. The measurement of species diversity. Annual Review of Ecology and Systematics 5:285-307.
- Perala, D.A. 1974. Prescribed burning in an aspen-mixed hardwood forest. Canadian Journal of Forest Research-*Revue Canadienne De Recherche Forestiere*, 4: 222-228.
- Perala, D.A. 1984. How Endemic Injuries Affect Early Growth of Aspen Suckers. Canadian Journal of Forest Research-*Revue Canadienne De Recherche Forestiere*, 14: 755-762.
- Perala, D.A. 1990. Quaking aspen (*Populous tremuloides* Michx.). In *Silvics of North America; II. Deciduous. Edited by R.M. Burns and B.H. Honkala.* U.S. Department of Agriculture Handbook. pp. 555-569.
- Perala, D.A. and Russell, J. 1983. Aspen. *In Silvicultural systems of the major forest types of the United States. Compiled by R.M.Burns.* U.S. Department of Agriculture, Agricultural Handbok 445. Washington, DC
- Peterson, E.B. and Peterson, N.M. 1992. Ecology, management, and use of aspen and balsam poplar in the prairie provinces, Canada. Forestry Canada, Northern Forestry Center, Edmonton, AB. Spec.Report 1.
- Pielou, E.C. 1975. Ecology diversity. Wiley, New York.

- Pimentel, D., Harvey, C., Resosudarmo, P., Sinclair, K., Kurz, D., McNair, M., Crist, S., Shpritz, L., Fitton, L., Saffouri, R. and Blair, R. 1995. Environmental and economic costs of soil erosion and conservation benefits. *Science*, 267: 1117-1123.
- Pitt, M.D., Newman, R.F., Youwe, P.L., Wikeem, B.M. and Quinton, D.A. 1998. Using a grazing pressure index to predict cattle damage of regenerating tree seedlings. *Journal of Range Management*, 51: 417-422.
- Pollard, D.F.W. 1971. Mortality and annual changes in distribution of above-ground biomass in an aspen sucker stand. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, 1: 262-266.
- Powell, G.W. and Bork, E.W. 2006. Aspen canopy removal and root trenching effects on understory vegetation. *Forest Ecology and Management*, 230: 79-90.
- Powell, G.W. and Bork, E.W. 2007. Effects of aspen canopy removal and root trenching on understory microenvironment and soil moisture. *Agroforestry Systems*, 70: 113-124.
- Prévost, M. and Pothier, D. 2003. Partial cuts in a trembling aspen-conifer stand: effects on microenvironmental conditions and regeneration dynamics. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, 33: 1-15.
- Quinn, R.O. and Wu., L. 2001. Quaking aspen reproduce from seed after wildfire in the mountains of Southeaster Arizona. pp 369-376. *In* D.W.D. Sheppard, D. Binkley, D.L. Bartos, T.J. Stohlgren, and L.G. Eskaew compilers. Sustaining aspen in western landscapes symposium proceedings. 13th-15th of June 2000. Grand Junction, CO, USA.
- Rauzi, F. and Hanson, C.L. 1966. Water intake and runoff as affected by intensity of grazing. *Journal of Range Management* 19: 351-356.
- Reynolds, H.G. 1969. Aspen grove use by deer, elk, and cattle in south-western coniferous forests. U. S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. Research Note RM-138, 4p.
- Romme, W.H., Turner, M.G., Gardner, R.H., Hargrove, W.W., Tuskan, G.A., Despain, D.G. and Renkin, R.A. 1997. A rare episode of sexual reproduction in Aspen (*Populus tremuloides* Michx) following the 1988 Yellowstone fires. *Natural Areas Journal*, 17: 17-25.
- Royer, F. and Dickinson, R. 1999. Weeds of Canada and the Northern United States. University of Alberta Press, Edmonton, AB and Lone Pine Publishing, Edmonton, AB. pp. 434.
- Sampson, A.R. 1919. Effects of grazing upon aspen reproduction. U. S. Department of Agriculture, Forest Service. Washington, D.C. Bulletin No. 741.

- Schier, G.A. 1972. Apical dominance in multishoot cultures from aspen roots. *Forestry Science*, 18: 147-149.
- Schier, G.A. 1976. Physiological and environmental factors controlling vegetative regeneration of aspen. U.S. Department of Agriculture. Forestry Service, General Technical Report RM-29.
- Schier, G.A. 1981. Physiological research on adventitious shoot development in aspen roots. U.S. Department of Agriculture. Forestry Service, General Technical Report INT-107.
- Schier, G.A., Jones, J.R. and Winokur, R.P. 1985. Vegetative regeneration. *In Aspen: ecology and management in the western United States. Edited by N.V. DeByle and R.P. Winokur.* U.S. Department of Agriculture, Forest Service. General Technical Report RM-119. pp. 29-33.
- Sharrow, S.H. 2007. Soil compaction by grazing livestock in silvopastures as evidenced by changes in soil physical properties. *Agroforestry Systems*, 71: 215-223.
- Shepperd, W. 1990. A Classification of Quaking Aspen in the Central Rocky Mountains Based on Growth and Stand Characteristics. *Western Journal of Applied Forestry*, 5: 69-75.
- Shepperd, W.D. and Engelby, O. 1983. Rocky Mountain aspen. *In Silviculture systems for the major forest types of the United States. Compiled by R.M. Burns.* U.S. Department of Agriculture, Agricultural Handbook 445. pp. 77-79.
- Shepperd, W.D., Reichert, D.R. and Mata, S.A. 2004 Overwinter storage of carbohydrate in aspen. *Transactions of the Western Section of the Wildlife Society*, 40: 45-48.
- Shmida, A. and Wilson, M.V. 1985. Biological Determinants of Species Diversity. *Journal of Biogeography*, 12: 1-20.
- Springfield, H.W. and Reynolds, H.G. 1951. Grazing preferences of cattle for certain reseeding grasses. *Journal of Range Management*, 4: 83-87.
- Stanosz, G.R. and Patton, R.F. 1987. Armillaria root rot in Wisconsin aspen sucker stands. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, 17: 995-1000.
- Steinman, J. 1998. Tracking the health of trees over time on forest health monitoring plots. IUFRO Conference, St. Paul, MN. U.S. Department of Agriculture, Forest Service, North Central Research Station.
- Steneker, G.A. 1974. Factors affecting the suckering of trembling aspen *Forestry Chronicle* 50: 32-34.

- Steneker, G.A. 1976a. Guide to the silvicultural management of trembling aspen in the prairie provinces. Environment Canada, Canadian Forestry Service, Northern Forestry Research Centre, Edmonton, AB. Information Report Information Report NOR-X-164.
- Steneker, G.A. 1976b. Early performance of poplar clones in Manitoba. Environment Canada, Canadian Forestry Service, Northern Forestry Research Centre, Edmonton, AB. Information Report Information Report NOR-X-156.
- Stewart-Wade, S.M., Neumann, S., Collins, L.L. and Boland, G.J. 2002. The Biology of Canadian weeds. 117. *Taraxacum officinale* G. H. Weber ex Wiggers. Canadian Journal of Plant Science, 82: 825-853.
- Stoekeler, J.H. and Macon, J.W. 1956. Regeneration of aspen cutover areas in northern Wisconsin. Journal of Forestry 54: 13-16.
- Stolte, K. 1997. 1996 National Technical Report on Forest Health. U.S. Department of Agriculture. Forest Service. FS-605, p. 47.
- Stone, D.M. and Elioff, J.D. 1998. Soil properties and aspen development five years after compaction and forest floor removal. Canadian Journal of Soil Science, 78: 51-58.
- ter Braak, C.J.F. and Smilauer, P. 2002. CANOCO Reference manual and CanoDraw for Windows User's guide: Software for Canonical Community Ordination (version 4.5). Microcomputer Power, Ithaca, NY, USA.
- Tew, R.K. 1970. Root carbohydrate reserves in vegetative reproduction of aspen. Forest Science 16: 318- 320.
- Tew, R.K., DeByle, N.V. and Schultz, J.D. 1969. Intraclonal root connections among quaking aspen trees. Ecology, 50: 920-921.
- Turner, M.G., Romme, W.H., Reed, R.A. and Tuskan, G.A. 2003. Post-fire aspen seedling recruitment across the Yellowstone (USA) Landscape. Landscape Ecology, 18: 127-140.
- Wan, X.C., Landhausser, S.M., Lieffers, V.J. and Zwiazek, J.J. 2006. Signals controlling root suckering and adventitious shoot formation in aspen (*Populus tremuloides*). Tree Physiology, 26: 681-687.
- Wang, C.G. 2003. Early regeneration and growth dynamics of *Populus tremuloides* suckers in relation to fire severity. Canadian Journal of Forest Research. , 33: 1998-2006.
- Weatherill, R.G. and Keith, L.B. 1969. The effect of livestock grazing on an aspen forest community. Canadian Department of Lands and Forests, Fish and Wildlife Division, Technical Bulletin 1. Ottawa, ON. 31 p.

- Weingartner, D.H. 1980. The effects of scarification on trembling aspen in northern Ontario: a preliminary report. *Forestry Chronicle* 56: 173-175.
- Werger, M.J.A., Louppen, J.M.W. and Eppink, J.H.M. 1983. Species performances and vegetation boundaries along an environmental gradient. *Vegetatio*, 52: 141-150.
- Whittaker, R.H. 1956. Vegetation of the Great Smokey Mountains. *Ecological Monographs*, 21: 2-80.
- Whittaker, R.H. 1977. Evolution of species diversity in land plant communities. *Evolutionary Biology*, 10: 1-67.
- Williams, D.J.M., Parry, D. and Langor, D.W. 1996. Sampling and identification of forest tent caterpillar parasitoids in the prairie provinces. Canadian Forest Service Northwest Region Northern Forestry Center. Information Report NOR-X-345.
- Williams, K.R. 1972. *In* Schier, G.A., Jones, J.R., and Winokur, R.P. 1985. Vegetative regeneration. *In* *Aspen: ecology and management in the western United States*. Edited by N.V. DeByle and R.P. Winokur. U.S. Department of Agriculture. Forest Service General Technical Report RM-119. pp. 29-33.
- Willoughby, M.G. and Lane, C.T.P. 2004. Forage growth and nutrient cycle of aspen forest communities in Alberta's Lower Foothills Subregion. Alberta Sustainable Resource Development, Edmonton, AB. Publication No. T/064.
- Wood, J.C. and Blackburn, W.H. 1989. Infiltration and runoff water quality response to silvicultural and grazing treatments on a longleaf pine forest. *Journal of Range Management*, 42: 378-381.
- Zoladeski, C.A., Wickware, G.M., Delorme, R.J., Sims, R.A. and Corns, I.G.W. 1995. Forest ecosystem classification for Manitoba: field guide. Environment Canada, Canadian Forestry Service, Northwest Region, Northern Forestry Center, Edmonton, AB. Special Report 2.
- Zoltai, S.C., Singh, T. and Apps, M.J. 1991. Aspen in a changing climate. *In* *Aspen Management for the 21st Century*. Proceedings of a Symposium, 20-21 November 1990, Edmonton, AB. *Edited by* S. Navratil and P.B. Chapman. Forestry Canada, Northern Forestry Centre and Poplar Council of Canada, Edmonton, AB.

## Appendix

**Appendix 1:** Descriptions of study sites (UG = Ungrazed, G = Grazed), site coordinates are described in latitude and longitude that are in degree/decimal format.

Site Name	Latitude	Longitude	Age class	Grazing Status	Grazing Capacity (AUM ha-1)
96UG	52.02	100.95	9-11	Ungrazed	
97UG1	51.71	101.55	9-11	Ungrazed	
97UG2	51.71	101.56	9-11	Ungrazed	
97G1	51.29	101.15	9-11	Grazed	0.54
97G2	51.29	101.14	9-11	Grazed	Unknown
98G	52.29	100.85	9-11	Grazed	3.08
99UG	51.97	100.67	5-8	Ungrazed	
00UG	51.54	100.56	5-8	Ungrazed	
01UG	51.56	100.57	5-8	Ungrazed	
99G1	51.47	100.35	5-8	Grazed	1.65
99G2	51.61	100.53	5-8	Grazed	1.98
00G	51.80	100.12	5-8	Grazed	0.29
03UG	52.04	101.00	2-3	Ungrazed	
04UG1	52.58	101.04	2-3	Ungrazed	
04UG2	52.58	101.04	2-3	Ungrazed	
03G1	52.09	100.77	2-3	Grazed	0.37
03G2	52.09	100.77	2-3	Grazed	0.37
03G3	52.04	101.00	2-3	Grazed	1.64

**Appendix 2: Sample Calculations for Partial Ordination**

**Ex.** Environment with grazing as a covariate + Grazing with no covariates = Total explained variation

$$0.367 + 0.054 = 0.421$$

Shared variance was explained by subtracting the results from ordinations of 1 and 3 or 2 and 4.

**Ex.** Environment with grazing as a covariate + Environments with no covariates = Shared variance.

$$0.388 - 0.367 = 0.021$$

**Appendix 3:** Plot averages of environmental variables collected.

Plot	Grazing (AUM)	Drainage	SC (kPa)	BD (g/cm <sup>3</sup> )	OM (g/g)	Clay (%)	pH	CWD (m <sup>3</sup> ha <sup>-1</sup> )
96UG1	0.00	4	762 ± 261	0.62 ± 0.16	0.07 ± 0.05	18 ± 9.1	7.1 ± 0.3	6.6
97UG2	0.00	5	716 ± 280	1.07 ± 0.10	0.06 ± 0.11	35 ± 14.9	5.7 ± 0.5	5.0
97UG3	0.00	5	907 ± 260	1.00 ± 0.17	0.03 ± 0.13	12 ± 9.8	5.8 ± 0.4	9.6
97G1	0.35	6						
97G2	0.74	5	814 ± 374	0.60 ± 0.19	0.18 ± 0.07	17 ± 7.1	7.0 ± 0.4	
98G	0.41	5	933 ± 349	0.92 ± 0.25	0.08 ± 0.62	10 ± 4.5	6.6 ± 0.6	
99UG1	0.00	7	454 ± 124	0.52 ± 0.15	0.08 ± 0.08	16 ± 5.7	7.0 ± 0.1	5.5
00UG2	0.00	5						5.2
01UG3	0.00	6	582 ± 189	0.65 ± 0.27	0.04 ± 0.11	19 ± 6.4	7.0 ± 0.2	130.0
99G1	2.10	6	512 ± 13	0.64 ± 0.21	0.14 ± 0.040	29 ± 6.3	7.1 ± 0.4	6.7
99G2	6.20	5	830 ± 189	0.80 ± 0.29	0.12 ± 0.05	24 ± 8.9	7.1 ± 0.3	7.4
00G	3.38	6	529 ± 237	0.92 ± 0.10	0.07 ± 0.04	5 ± 1.0	7.1 ± 0.3	17.9
03UG1	0.00	6	1119 ± 237	0.80 ± 0.25	0.20 ± 0.07	27 ± 9.4	7.2 ± 0.3	
04UG2	0.00	6	417 ± 112	0.47 ± 0.21	0.36 ± 0.04	20 ± 6.2	6.8 ± 0.7	
04UG3	0.00	7	636 ± 116	0.25 ± 0.19	0.22 ± 0.06	28 ± 6.7	7.0 ± 0.8	
03G1	0.69	5	690 ± 294	0.91 ± 0.29	0.11 ± 0.05	16 ± 3.3	7.2 ± 0.1	17.3
03G2	0.69	5	602 ± 142	0.78 ± 0.25	0.10 ± 0.04	35 ± 1.1	7.2 ± 0.4	
03G3	8.02	6	999 ± 215	0.86 ± 0.10	0.10 ± 0.05	26 ± 5.3	7.5 ± 0.2	6.4

Note: Variables are: Grazing – grazing pressure, Drainage = drainage class, SC – soil compaction, BD – bulk density, OM – organic matter content, Clay – clay fraction, pH, CWD coarse woody debris. All soil variables except drainage class were not collected in plots 00UG and 97G1. Soil variables (excluding drainage class) were collected in the top 20cm of mineral soil.



**Appendix 4:** Planned contrasts of all height classes and total stems of aspen ( $P < 0.1$ ).

		Stand age		df	SS	F	p-value	
HC1	Grazing			1	0.015	0.26	0.875	
	Year-Class			2	23.407	19.98	<b>&lt;0.001</b>	
	Yr x Gr			2	1.125	0.96	0.410	
	Error			12	7.029			
		9-11	UG vs G		1	0.857		0.615
		5-8	UG vs G		1	0.229		<b>&lt;0.001</b>
		2-3	UG vs G		1	0.055		0.945
HC2	Grazing			1	0.058	0.27	0.875	
	Year-Class			2	10.183	23.59	<b>&lt;0.001</b>	
	Yr x Gr			2	0.024	0.06	0.410	
	Error			12	2.590			
		9-11	UG vs G		1	0.005		0.880
		5-8	UG vs G		1	0.071		0.577
		2-3	UG vs G		1	0.006		0.870
HC3	Grazing			1	0.031	0.46	0.509	
	Year-Class			2	1.099	8.33	<b>0.005</b>	
	Yr x Gr			2	0.039	0.29	0.751	
	Error			12	0.792			
		9-11	NG vs G		1	0.002		0.865
		5-8	UG vs G		1	0.013		0.663
		2-3	UG vs G		1	0.054		0.383
HC4	Grazing			1	0.256	0.82	0.383	
	Year-Class			2	10.564	16.95	<b>&lt;0.001</b>	
	Yr x Gr			2	0.081	0.13	0.879	
	Error			12	3.739			
		9-11	UG vs G		1	0.125		0.538
		5-8	UG vs G		1	0.005		0.906
		2-3	UG vs G		1	0.207		0.430
HC5	Grazing			1	0.548	2.92	0.113	
	Year-Class			2	34.654	92.36	<b>&lt;0.001</b>	
	Yr x Gr			2	1.198	3.19	<b>0.077</b>	
	Error			12	2.251			
		9-11	UG vs G		1	1.332		<b>0.021</b>
		5-8	UG vs G		1	0.150		0.390
		2-3	UG vs G		1	0.265		0.257
Total	Grazing			1	0.100	3.31	0.940	
	Year-Class			2	0.303	4.99	<b>0.026</b>	
	Yr x Gr			2	0.038	0.63	0.549	
	Error			12	0.364			
		9-11	UG vs G		1	0.105		<b>0.088</b>
		5-8	UG vs G		1	0.002		0.792
		2-3	UG vs G		1	0.032		0.326

Note: Abbreviation definitions are as follows: Yr – Year, G – Grazing Class, G – Grazing, and UG – Ungrazed. All bolded results indicated significant differences at  $P < 0.1$ .

**Appendix 5:** Planned contrasts of all height classes and total stems of commercial species ( $P < 0.1$ ).

	Stand Age		df	SS	F	p-value	
HC1	Grazing		1	0.004	0.01	0.924	
	Year-Class		2	7.037	15.96	< <b>0.001</b>	
	Yr x Gr		2	0.927	1.05	0.380	
	Error		12	5.292			
		9-11	UG vs G	1	0.610		0.262
		5-8	UG vs G	1	0.307		0.420
		2-3	UG vs G	1	0.013		0.865
HC2	Grazing			0.000	< 0.001	0.955	
	Year-Class			8.789	48.65	< <b>0.001</b>	
	Yr x Gr			0.402	2.22	0.151	
	Error			1.084			
		9-11	UG vs G		0.258		0.117
		5-8	UG vs G		0.130		0.254
		2-3	UG vs G		0.014		0.701
HC3	Grazing		1	0.045	1.03	0.330	
	Year-Class		2	1.338	15.40	< <b>0.001</b>	
	Yr x Gr		2	0.133	1.53	0.255	
	Error		12	0.521			
		9-11	UG vs G	1	0.017		0.538
		5-8	UG vs G	1	0.013		0.592
		2-3	UG vs G	1	0.147		<b>0.090</b>
HC4	Grazing		1	0.521	6.75	<b>0.023</b>	
	Year-Class		2	7.032	45.52	< <b>0.001</b>	
	Yr x Gr		2	0.360	2.33	0.139	
	Error		12	0.927			
		9-11	UG vs G	1	0.072		0.353
		5-8	UG vs G	1	0.007		0.762
		2-3	UG vs G	1	0.802		<b>0.007</b>
HC5	Grazing		1	0.735	3.97	<b>0.070</b>	
	Year-Class		2	39.008	105.33	< <b>0.001</b>	
	Yr x Gr		2	0.822	2.22	0.151	
	Error		12	2.222			
		9-11	UG vs G	1	1.290		<b>0.022</b>
		5-8	UG vs G	1	0.022		0.739
		2-3	UG vs G	1	0.245		0.272
TOTAL	Grazing		1	0.105	5.01	<b>0.045</b>	
	Year-Class		2	0.286	6.79	<b>0.011</b>	
	Yr x Gr		2	0.020	0.47	0.634	
	Error		12	0.252			
		9-11	UG vs G	1	0.064		0.107
		5-8	UG vs G	1	0.005		0.636
		2-3	UG vs G	1	0.056		0.129

Note: Abbreviation definitions are as follows: Yr – Year, G – Grazing Class, G – Grazing, and UG – Ungrazed. All bolded results indicated significant differences at  $P < 0.1$ .