University of Alberta

Boreal Plains Peatlands: Characterization, Plant Diversity, Biogeography, and Impacts from Logging

by

David Alexander Locky ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy

in

Environmental Biology and Ecology

Department of Biological Sciences

Edmonton, Alberta

Fall 2005

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ABSTRACT

This thesis examines peatland ecology under the following chapters: (2) The vegetational ecology of black spruce swamps, fens, and bogs in southern boreal Manitoba, Canada, (3) Plant diversity and rarity in the southern boreal peatlands of Manitoba, (4) Determinants of plant diversity and community change in western boreal wooded rich fens, and (5) Impacts of logging in the southern boreal peatlands of Duck Mountain, Manitoba, Canada. Chapter 2 focuses on a multivariate classification of 94 peatlands. Wooded and open moderate-rich fens are the dominant peatland types, and wooded bogs and open extreme-rich fens are rarer. Black spruce swamps were observed as a distinct peatland type. Bogs are differentiated from the other peatland types based on surface water chemistry, but the distinctions are less strong among the other types. Chapter 3 examines bryophyte and vascular plant species richness and rarity in peatlands from Chapter 2. Total diversity was 299, comprised of 87 bryophytes and 212 vascular plants. The highest diversity was found in wooded moderate-rich fens and black spruce swamps, whereas the lowest diversity was observed in wooded bogs and open extreme-rich fens. Rare plant diversity was greatest in wooded and open moderate-rich fens, and black spruce swamps. Plant richness was associated primarily with surface water chemistry and overstory density. Chapter 4 describes the relationship between plant richness/composition and environmental variables in wooded moderate-rich fens across Alberta, Saskatchewan, and Manitoba. Gamma diversity totaled 273, comprised of 86 bryophytes and 187 vascular plants. Alpha diversity decreased along a westward gradient. Bryophyte diversity was explained by location, and vascular plant diversity was predicted by location, elevation, and overstory density. Chapter 5 describes the impacts of logging on peatlands 1-4 and 9-

12 years post harvest by comparing plots in clear-cut areas with plots in remaining wooded peatlands. Increased water temperature and nutrients were observed in clear-cut plots in the 1-4 year class. Regeneration of *Picea mariana* was unchanged between wooded and clear-cut plots, despite significantly higher numbers of shrub stems, exposed peat, and rutting in clear-cut plots. Vascular plant diversity was greatest in clear-cut plots and bryophyte/lichen diversity was greatest in wooded plots.

ACKNOWLEDGEMENTS

The ideas for this research arose from the vestiges of two different project proposals, weeks of data gathering, exploration and reflection during the initial field season, and brainstorming during committee meetings with Suzanne Bayley, Uldis Silins, and Dale Vitt, who was on the committee for most of the thesis. In particular, Suzanne Bayley provided many creative ideas and the space with which to develop and refine and them. Rolf Vinebrooke is thanked for cheerfully joining the committee on short notice and, with Lee Foote, for offering valuable feedback. Paul Glaser is thanked for his insightful comments and stimulating discourse on peatlands and classification.

Over the course of five years, many individuals contributed to this research project in the field and in the lab. In the field and lab, Daniel Kueffler and Chris Shapka provided unwavering and uncomplaining assistance in waterlogged lands for extended periods of time. Their suggestions helped to streamline and improve field sampling. Rob Martineau also contributed assistance in the field. Patricia Burgess and Roselyn Rudy in the University of Alberta Limnology lab provided high quality services whenever called upon. In the lab, Trevor Burgers assisted with peat analyses.

This project was greatly improved through ideas generated and feedback provided during spirited discussions with and reviews of the thesis chapters by various individuals. Markus Thormann supplied many hours of critical reviewing of much of the thesis and offered the support of a mentor. Ellen Macdonald and her students and workers welcomed me into their lab meetings and provided much insight and feedback with respect to data analyses and results. In particular Richard Caners and Joyce Gould spent much time discussing concepts of diversity, multivariate data analyses, and reviewing of my manuscripts. René Belland provided much insight and feedback with data analyses and interpretation of results. Members of the Bayley and Vitt labs, and other Biological Sciences graduate students provided valuable discourse, especially Danielle Cobbaert, Ivor Norlin, Chris Jerde, Agnes Wong, Colleen Prather, and Dave Beilman.

The quickest routes through university administration were revealed with the help of Chesceri Mason, Michelle Green, and Gwen Jewett. Dorothy Fabian and Catherine LaFarge-England provided assistance and unrestricted access to the vascular plant and

cyptogamic herbariums. Bryophyte identification quandaries were solved with the assistance of Martina Krieger, Natalie Cleavitt, and Catherine LaFarge-England.

Logistical, financial, and in-kind support by many individuals and organizations made completion of this project possible and include the following:

- Louisiana-Pacific Canada Ltd., my NSERC Industrial Sponsor and SFMN partner, for monetary, in-kind, and logistical support. In particular, I thank Margaret Donnelly, Donna Grassia, Vern Bauman, Peter Sigurdson, and Barry Wado
- The Mixedwood Forest Society, in particular, Lindy Clubb, Nancy McLellan, and Dan Soprovich for logistical support and accommodations at the Goldeneye Field Station at Wellman Lake, Duck Mountain, Manitoba
- The Sustainable Forest Management Network for generously funding this project from start to finish. Logistical and administrative support was provided by Gillian Binstead, Bruce Maclock, and Bruce Mcnab
- The Natural Sciences and Engineering Research Council of Canada for providing PGS-B and Post-Graduate Industrial Scholarship funding
- The University of Alberta for a Faculty of Science Graduate Entrance Scholarship, Walter H. Johns Graduate Fellowships, Graduate Teaching Assistantships, and a Province of Alberta Graduate Fellowship
- The Canadian Circumpolar Institute for a C/BAR grant.
- Jacques Tardif and France Conciatori from the Centre for Forest Interdisciplinary Research, University of Winnipeg, Manitoba for methodological assistance in tree coring, and France Conciatori for dating all tree cores
- David Walker from the University of Manitoba for valuable discourse on statistical analyses and landscape classification
- Dan Frandsen for access permission and logistical assistance in Prince Alberta National Park, Saskatchewan.

My family and friends were especially supportive throughout the time I spent on this project. And last but foremost, I thank my wife Sarah Wilkinson for her excellent manuscript reviews and unwavering support and love.

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1. PEATLANDS AND EMERGING ISSUES IN BOREAL WESTERN CANADA

The boreal forest of Canada comprises 25% of the world's forests and is one of the largest contiguously forested regions remaining in the world (World Resources Institute 2000). By nature, the boreal forest is complex and dynamic and consequently plays a key role in atmospheric processes and element budgets (Bonan and Shugart 1989). The links between forests and wetlands in the boreal zone are very important, as 30% percent of the boreal region is comprised of wetlands (World Resources Institute 2000). Most of these are peatlands, which are wetlands with at least 40 cm of peat (National Wetlands Working Group 1997). Peatlands can be divided into bogs, fens, and swamps. Bogs receive water and nutrients primarily from atmospheric deposition, whereas fens receive water and nutrients principally from subsurface and surface sources. Both peatland types can be dominated by coniferous trees, coniferous and deciduous shrubs, or graminoid vegetation (National Wetlands Working Group 1997). Peatland swamps in temperate and boreal North America are generally densely forested with conifers and often transitional between uplands and peatlands or water bodies (National Wetlands Working Group 1997, Locky et al. In press).

Many western Canadian boreal fens, *Picea mariana* (Mill.) BSP-dominated swamps, and some bogs are wooded with marketable *Picea mariana*, but timber harvesting is, at this point, limited. This is expected to change because non-peatland timber resources in southern parts of the western boreal region are becoming depleted and peatlands are being logged. In addition to logging pressure, climate change models suggest that peatlands at the southern part of the Boreal Plains in western Canada are likely to be highly sensitive to changes caused by a warming climate (Kettles and Tarnocai 1999). Consequently, it is critical to understand key aspects of western boreal peatlands before successful peatland management initiatives can be developed to address land use and climate change issues. Some aspects of peatlands that require further understanding include floristic and environmental differences among peatland types, plant diversity and rarity among peatland types, biogeographical patterns of plant diversity, composition, and rarity in wooded fens, and the effects of logging peatlands on the plant community and environmental variables.

1.1 WESTERN BOREAL PEATLANDS

Biogeoclimatic variation of wetland types across Canada reduces relevant comparison to wetlands in other regions and necessitates regionally-based studies of flora (Jeglum 1991). In western continental Canada, several studies on floristic diversity and composition have included bogs (Belland and Vitt 1995, Beilman 2001), poor fens (Vitt et al. 1975), and rich fens (Slack et al. 1980, Vitt and Chee 1990), but there is little information on peatlands on the southeastern Boreal Plain Ecozone, including those in the Duck Mountain, Manitoba Ecodistrict (Duck Mountain). Few studies have included both bryophytes/lichens and vascular plants in a range of wooded and non-wooded peatlands (Jeglum 1972, Nicholson 1995, Anderson and Davis 1997). This is particularly true of wooded peatlands in western Canada, especially, black spruce swamps (Jeglum 1972, Jeglum 1973, Nicholson 1995). Additionally, confusion has arisen in conifer swamp terminology, with misapplication to uplands or other peatland types.

1.2 PLANT DIVERSITY, COMPOSITION, AND RARITY

Peatlands are wide-ranging in environmental conditions and are a rich botanical resource (Wheeler 1993). Fens are among the most floristically diverse wetlands, often with rare bryophytes and vascular plants (Wheeler 1993, Bedford and Godwin 2003). Diversity and rarity is variable by specific fen types. In western boreal Canada, the greatest bryophyte diversity has been found in moderate-rich fens (Vitt and Chee 1990), extreme-rich fens (Vitt et al. 1995), and wooded moderate-rich fens (Vitt et al. 2003). Diversity of rare bryophytes in Canada's western continental peatlands is found to be greatest in wooded moderate-rich fens, 'swamp' (Vitt et al. 2003), and extreme-rich fens (Vitt et al. 1995). Less is known of vascular plant diversity in boreal peatlands (Jeglum 1972), particularly in black spruce swamps. Rare vascular plants have been described in New York rich fens (Johnson and Leopold 1994), but not in western boreal peatlands in Canada.

Declines in species richness along latitudinal, elevational, and moisture gradients occur in continental regions (Begon et al. 1986, Tivy 1993). These gradients are often surrogates for other more elemental variables and are interrelated, making exact causal agents difficult to discern. This is true when examining plant species richness, as plant communities are inherently variable and important environmental variables operate simultaneously (Glaser 1992). Hypothesis testing using latitude, elevation, and moisture can be problematic and controversial (Willig et al. 2003, Rahbek 2005), and selecting sites with well-defined boundaries and relative uniformity, such as islands, is one solution (Williamson 1981, Brown and Gibson 1983, Glaser 1992). Alternatively, discretely bounded terrestrial ecosystems with consistent physical, chemical, and floristic properties, such as peatlands, also make appropriate study sites (Glaser 1992). Patterns of plant community composition and diversity in peatlands have usually been examined across regions through comparison of different peatland types (Vitt and Chee 1990, Anderson and Davis 1997, Vitt et al. 1995, Locky et al. In press). There have been few studies that have examined plant community composition and diversity in peatlands of one type at the regional scale other than in bogs (Glaser 1992, Bielman 2001).

1.3 PEATLANDS AND LOGGING

Wooded peatlands in Canada's boreal forest often have marketable *Picea mariana* (Mill.) BSP and *Larix laricina* (Du Roi) K. Koch that are harvested primarily for pulpwood. Harvesting this timber is relatively common in the eastern boreal region (Jeglum 1991), but is limited in the western boreal region. This is expected to change in southern regions of the western boreal forest, as timber resources are becoming increasingly depleted and peatlands are beginning to be logged. For example, in the Boreal Plains Ecozone, less than 17% of the remaining forest is intact and contiguous (Lee et al. 2003).

Logging is arguably the greatest current disturbance factor in the boreal landscape. Compared to natural disturbances, such as fire and natural tree fall, clear-cutting differs in several ecological respects. This includes increases in water table depth (Dubé et al. 1995), release of nutrients (Knighton and Stiegler 1980), and loss of biomass in a uniform pattern (Franklin et al. 2000). Peatlands are particularly susceptible to peat disturbance, including rutting, compaction, and erosion (Groot 1987, review in Nugent et al. 2003). Bare peat is exposed, limiting plant growth (Brumelis and Carleton 1989), and nutrient-rich microsites are created that favour fast-growing weed species (Groot 1987). Regeneration of *Picea mariana* on clear-cut peatlands is not usually considered a problem (Jeglum 1987), but other aspects of the plant community may be affected negatively (Brumelis and Carelton 1988, 1989). One of the most significant potential changes is the long-term continuity of hardwood species after harvest (Neiring and Goodwin 1974, Brumelis and Carleton 1988, 1989). The expansion of dense thickets (e.g., *Alnus, Salix, Rubus* spp.) by regeneration and invasion on logged black spruce sites is associated with the most nutrient-rich sites (Brumelis and Carleton 1988, 1989). Fens may be more susceptible to released nutrients that result from clear-cutting than bogs because of significantly higher water yields (Knighton and Stiegler 1980). Clear-cuts on fens may also result in alteration of bryophyte and vascular plant community composition and loss of diversity (Hannerz and Hånell 1997). Clear-cuts cause the most significant change to vascular plant communities (Hannerz and Hånell 1993, Bergstedt and Milberg 2001), which can lead to difficulties in site renewal (Hannerz and Hånell 1993). Bryophytes, particularly hepatics, may show compositional changes in response to the severity of harvest impacts to forest floors (Fenton et al. 2003). The effects of forest harvest on peatlands have been studied primarily in the eastern boreal region of Canada (Brumelis and Carleton 1988, 1989, Jeglum 1991, Trettin et al. 1997). Studies of peatland logging in the western boreal region have generally been limited to the physical impacts of drainage (Silins and Rothwell 1998, 1999) and impacts on tree growth (Macdonald and Yin 1999). The effects of logging on the plant community and other site conditions in peatlands in the western boreal region of Canada have not yet been studied.

1.4 RESEARCH ISSUES ADDRESSSED

1. Chapter 2, *The vegetational ecology of black spruce swamps, fens, and bogs in southern boreal Manitoba, Canada,* supplements and broadens our knowledge of the vegetational ecology of western boreal peatlands by determining floristic and environmental differences among the types of peatlands that comprise Duck Mountain, and clarifies conifer swamp terminology. The specific objectives were to classify the peatland types, identify typical indicator plants, illustrate typical environmental conditions of the surface waters and peat, characterize the forest cover, and determine any relationship between the environmental factors and the vegetation community. The discriminating characteristics of black spruce swamp

require highlighting and swamp terminology requires clarification. This chapter has been accepted as a manuscript for publication in the September 2005 issue of *Wetlands* by D.A. Locky, S.E. Bayley, and D.H. Vitt.

2. Chapter 3, *Plant diversity, composition, and rarity in the southern boreal peatlands of Manitoba, Canada* examines bryophyte and vascular plant species richness, percent occurrences, and rarity among wooded bogs, black spruce swamps, wooded moderate-rich fens, open moderate-rich fens, and open extreme-rich fens at Duck Mountain, Manitoba using the same sites as in Chapter 2. Environmental variables are examined, as well as associations between plant species richness and rarity, and plant species richness and environmental variables.
3. Chapter 4, *Regional scale biogeography: determinants of plant diversity and community change in Boreal Plains wooded rich fens* further examines plant diversity patterns in wooded fens along a longitudinal transect, and to a lesser extent latitudinal transect, across the Boreal Plains Ecozone (Alberta, Saskatchewan, and Manitoba). Specifically, the objectives were to examine plant diversity indices and rarity by bryophyte taxa and vascular plant life forms among the three locations, and explore interactions between plant diversity patterns and environmental variables such as latitude, longitude, elevation, precipitation, and surface water chemistry, and peat physical variables.
4. Chapter 5, *Impacts of logging in the southern boreal peatlands of Manitoba, Canada* compares plant diversity and community attributes, along with site environmental variables between wooded peatland remnants and clear-cut portions of the same peatland, 1-4 and 9-12 years since harvest. Components that are examined include characteristic indicator species, diversity indices, percent cover, and environmental variables such as logging debris, site disturbance parameters, surface water chemistry, and peat physical variables.

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2. THE VEGETATIONAL ECOLOGY OF BLACK SPRUCE SWAMPS, FENS, AND BOGS IN SOUTHERN BOREAL MANITOBA, CANADA

2.1 INTRODUCTION

The boreal forest of Canada is one of the largest contiguously forested regions remaining in the world, comprising 25% of the world's forests (World Resources Institute 2000). The links between forests and wetlands in the boreal zone are very important, as 30% percent of the region is comprised of wetlands (World Resources Institute 2000). Most of these are peatlands, which are wetlands with at least 40 cm of peat (National Wetlands Working Group 1997). Many western boreal peatlands are wooded with *Picea mariana* (Mill.) BSP, but timber harvesting is, at this point, limited. This is expected to change since timber resources in southern parts of the western boreal region are becoming increasingly depleted and peatlands are beginning to be logged; currently, less than 17% of the boreal plains ecozone remains as intact contiguous forest (Lee et al. 2003). In addition to this pressure, climate change models suggest that peatlands at the southern part of the boreal plain in western Canada are likely to be highly sensitive to disturbance due to climate change (Kettles and Tarnocai 1999).

Regional-based studies of peatland flora are important because comparison to other regions may not be relevant due to the biogeoclimatic variation of wetland types across Canada (Jeglum 1991). While there have been several studies on the western continental peatlands of Canada, including bogs (Belland and Vitt 1995, Beilman 2001), poor fens (Vitt et al. 1975), and rich fens (Slack et al. 1980, Vitt and Chee 1990), there is little information on peatlands on the southeastern boreal plain, including those at Duck Mountain, Manitoba. Few studies have included both bryophytes/lichens and vascular plants in a range of wooded and non-wooded peatlands (Jeglum 1972, Nicholson 1995, Anderson and Davis 1997). This is especially true of wooded peatlands in western Canada, and in particular, black spruce swamps (Jeglum 1972, Jeglum 1973, Nicholson 1995). In addition, there has been some confusion in conifer swamp terminology, with some peatlands and uplands being misidentified as conifer swamp.

The purpose of this research at Duck Mountain, Manitoba was to supplement and broaden the knowledge of the vegetational ecology of western boreal peatlands by including sites at the southeastern edge of the boreal plain. The specific goals were to (1) classify the peatland types, (2) describe the typical indicator plants in the peatlands, (3) illustrate the typical environmental conditions of the surface waters and peat and characterize the forest cover, (4) investigate the relationship between the environmental factors and the peatland vegetation community, and (5) highlight discriminating characteristics of black spruce swamp and clarify swamp terminology.

2.2 MATERIALS AND METHODS

Study region

Duck Mountain is located on the boreal plain of western Canada (Ecological Stratification Working Group 1995) and is one in a series of highlands on the prairie that straddle southern Manitoba and Saskatchewan. Approximately 70 km from north to south and 60 km from east to west (51° 15' - 52° 00' N, 100° 35' - 102° 35' E) (Figure 2.1), the base geologic feature of Duck Mountain is the erosion-resistant Riding Mountain shale layer that is overlain by glacially deposited clay, gravel, sand, and boulders. The glacial drift depth is variable, up to 260 m deep, and has produced hummocky moraine throughout much of the region (Klassen 1979), with lakes, rivers, and wetlands. The vegetation is typical of the boreal mixed-wood region (Ecological Stratification Working Group 1995), with the dominant conifers as *Picea mariana*, *Picea glauca* (Moench) Voss, *Pinus banksiana* Lamb., and *Larix laricina* (Du Roi) K. Koch, and the dominant deciduous trees as *Populus balsamifera* L., *Populus tremuloides* Michx., and *Betula papyrifera* Marsh.

The orographic effect of land masses on the prairies has been known to increase precipitation over 100 mm per year (Hogg 1994). While there are no precipitation records for Duck Mountain, the approximate 500-m increase in elevation above the surrounding prairie (810 m amsl) suggests that Duck Mountain likely receives a significant amount of orographic precipitation; Swan River (336 m amsl) is just north of Duck Mountain and has a total mean annual precipitation of 419 mm (1959-2000) (Environment Canada 2000).

Duck Mountain lies in the South Mid-boreal Wetland Region of Manitoba where wetlands make up 22% of the area (Halsey et al. 1997a) and peatlands are at the southern limit of their distribution (Halsey et al. 1997b).

Site selection and vegetation surveys

Ninety-nine peatlands were selected based on sufficient geographic coverage of the region and reasonable access (Appendix A). Sites had to have peat depths of at least 40 cm, based on the definition of a peatland in Canada (National Wetlands Working Group 1997), and have areas of homogeneous vegetation areas based on Ivanov's (1981) concept of peatland microtope. Microtopes are areas with no clear boundaries within, are principally defined by vegetation, and include smaller elements such as hummocks and hollows.

Plant community surveys were completed June 15 – September 15, 2000 using a time-bounded floristic habitat sampling that combines species richness with frequency/cover (abundance). This method is useful in capturing a large number of species in a large number of sites in a relatively short period of time (Newmaster 2000, Newmaster et al. 2005). Sites were surveyed for vascular plants, bryophytes, and three common *Cladina* (reindeer) lichen species within a three hour limit. Three hours was found to be adequate time in which no new species were found (sites ranged in size between 0.1 - 8.9 ha). Species were assigned a 1-4 occurrence/cover value that was adapted from the 1-3 occurrence scale of Vitt et al. (1995a): (1) Rare – present less than five times (≤1%); (2) Few – found a few times (~2-10% cover); (3) Common – found regularly but did not dominate the community (~11-74% cover); and (4) Abundant – dominated the community (~75-100% cover). Scientific names for vascular plants follow the Plant Element List from the Alberta Natural Heritage Information Centre (2002) and Scoggan (1978-1979). True mosses follow Anderson et al. (1990), *Sphagnum* follows Anderson (1990), hepatics follow Stötler and Crandall- Stötler (1977), and lichens follow Esslinger and Egan (1995).

Environmental variables

In-situ pH, specific conductance (adjusted for temperature and hydrogen ions), and water temperature measurements were taken once at each site. Measurements were taken in open pools, depressions in the substrate, or in excavated wells (20 – 80 cm). Water samples were collected and packed in ice, and the same day, one 500-ml sample was filtered with Whatman® GF/F glass microfibre filters and one 500-ml sample was left unfiltered. Both samples were frozen for later chemical analysis at the Limnology Laboratory at the University of Alberta of total phosphorus (TP), soluble reactive phosphorus (SRP), nitrate ($N0_2^- + N0_3^-$), ammonium, (NH_4^+), total nitrogen (TN), sodium (Na^+), potassium (K^+), calcium (Ca^{2+}), magnesium (Mg^{2+}), iron (Fe^+), sulphate (SO_4^{2-}), chloride (Cl^-), and dissolved organic carbon (DOC) following methods used in Vitt et al. (1995b). pH (< 5.5) and specific conductance values were adjusted by subtracting the effect of hydrogen ions per Sjörs (1952). Means for pH were calculated using hydrogen ions and then reconverted to pH for display and discussion. Water-table depth was estimated at the water sample location and placed in one of three groups: (1) 0 – 10 cm, (2) 11 – 20 cm, and (3) 21 cm or greater. Mean peat depth was determined with a 3-m metal probe from the center to the outer boundaries of each site. A soil core 5.2-cm diameter x 5.0-cm long was extracted from each site near the water sampling locations 15 cm below the surface and bagged, labelled, and frozen the same day. From these cores, I determined bulk density and organic C and inorganic C content using the loss on ignition method (Dean 1974). Carbon to nitrogen (C:N) analyses of the peat core were performed using a Carlo-Erba NA 1500 Carbon/Nitrogen Elemental analyzer at the University of Alberta Soils Laboratory. To characterize the peatland forests, I used the point-centered quarter (PCQ) method and measured tree height, tree diameter at breast height (dbh), and percent overstory density (Spherical Crown Concave Densiometer), and calculated trees/ha (Cottam and Curtis 1956). Survey criteria included trees ≥5 cm dbh within 7.5-m distance from the quadrat center. Many peatlands were small (< 1.0 ha) or non-linear in shape and limited the PCQ transect length to 45 m. Site areas were calculated using ARC/INFO.

Data analyses

Outliers in the community data and environmental data sets were identified using outlier analysis in PC ORD v. 4.25 (McCune and Mefford 1999), and five sites were removed from the analyses to improve the classification (99 sites to 94 sites). Collection of corticolous bryophytes was incomplete, and most of those species were left out of the analyses. Plant species with less than five occurrences were removed from the community dataset to improve the ordinations, as rare species are not useful for site classifications (McCune and Grace 2002). The non-normal environmental data were monotonic square root transformed and then relativized by general relativization to account for unequal variable units (McCune and Grace 2002). I used the Sørensen distance measure for all multivariate data analyses requiring distance measures because of its robustness in quantifying compositional distance (Faith et al. 1987).

Peatland Classification and Indicator Species. Cluster analysis using flexible beta grouping linkage (-0.25) was used to classify the total species community data (McCune and Grace 2002) into peatland types. Cluster dendrogram pruning at the most informative level was determined quantitatively using Indicator Species Analysis (ISA) (Dufrêne and Legendre 1997), Multiple Response Permutation Procedure (MRPP) (McCune and Grace 2002), and ecological considerations. By consistently pruning the dendrogram to lower levels, I determined which peatland types had the closest floristic affinities.

ISA calculates indicator species values by multiplying the relative abundance of each species in a specific group by the relative frequency of the species' occurrence in that group. A Monte Carlo simulation test with 1000 randomized runs, where samples are randomly assigned to types, was used to determine the significance ($P \leq 0.05$) of the indicator values (Dufrêne and Legendre 1997, McCune and Mefford 1999). The percent relative frequency and significance level for each species generated by the simulation test can be listed for each peatland type, indicating the likelihood of finding each species in each peatland type. High species indicator values and perfect membership within types are often difficult to achieve; to enhance the descriptions, I reported significant species also found abundantly in other types, as well as selected non-significant species that were relatively restricted to a type.

MRPP is the non-parametric analogue of Discriminant Function Analysis but without many of the associated assumptions. It was used for the multivariate test of the null hypothesis of no significant difference among samples of *a priori* (cluster analysis) groups (McCune and Mefford 1999).

To explore structure in the community data and verify the cluster analysis groups, a non-metric multidimensional scaling (NMS) ordination was performed using the community data, selecting the autopilot function with the slow and thorough analysis and varimax rotation option. Varimax rotation is an eigenvalue-based method that orients the axes through clusters of sample units and variables, with the result that both high and low correlations of the individual variables are emphasized (McCune and Grace 2002). A random starting configuration number was used for Monte Carlo tests with 1000 randomized runs completed. The proportion of variance represented by the ordination axes was determined using after-the-fact r^2 correlations between the distances in the ordination space and the original space (McCune and Mefford 1999). The NMS solution was compared with a solution derived from detrended correspondence analysis (DCA) to assess concordance between different methods for the community data (McCune and Grace 2002).

The wetlands were then classified based primarily on concepts from the Canadian Wetland Classification System, a three-level hierarchical classification (National Wetlands Working Group 1997). The coarsest level is class (bog, fen, swamp, marsh, shallow water wetland), followed by form (surface morphology, surface pattern, water type, and underlying mineral soil morphology), and then type (general physiognomy of the vegetation cover without reference to species). I could not apply all three levels of the classification to each cluster group, as that level of detail is best applied to individual sites. Thus, cluster groups were named by peatland class (e.g., bog, fen) and, where appropriate, given a form (e.g., shore) or type (e.g., shrub, wooded) that best depicted collective aspects of sites in the cluster group. Because fens have unique attributes related to fen plant indicator species and water chemistry derived from ground water (e.g., pH, alkalinity), fens were given a wetland class modifier based on Sjörs' (1952) concept of fen indicator species, which includes rich, and specifically, moderate-rich and extreme-rich. These fen modifiers have been used extensively in western Canada (Chee and Vitt

1989, Vitt et al. 1995a,b, Vitt et al. 2003). In addition, the term 'conifer swamp' (*sensu* National Wetlands Working Group 1997) was replaced with black spruce swamp to contrast this peatland type with eastern white cedar, *Thuja occidentalis* L.-dominated swamps in the eastern boreal region.

Environmental Variables. Two pH outliers (4.2 and 4.9) were removed from the water chemistry calculations in the open-wooded moderate-rich fen type to characterize the pH of this peatland type more accurately. Missing values of peat bulk density, organic C, and inorganic C for three sites in other types were replaced by averaging the values from other sites within the respective types. Most of the water chemistry and peat variables had skewed, non-normal distributions that could not be transformed, and Kruskal-Wallis H non-parametric tests were used to determine differences in ranks of environmental variables among the peatland types. To help assess the ecological importance of the observed differences among the eight peatland types (non-parametric *post hoc* tests were not available), 95% confidence interval plots were used, which are useful in displaying effect size measures and associated measures of precision, in addition to P values (Di Stefano 2003). Forest mensuration variables were normally distributed, and one-way Analysis of Variance (ANOVA) was used to determine differences between the means of the peatland types, with Tukey HSD *post hoc* tests to reveal specific type differences. All univariate analyses were completed using SPSS v. 11.5 (SPSS Inc. 2003).

Environmental Variables and Vegetation Communities. The relationship between environmental variables and vegetation communities has often been explored using direct methods of ordination, such as Canonical Correspondence Analysis. These methods are subject to noisy or irrelevant environmental variables, and therefore indirect methods, such as NMS, are preferred, as they maintain community structure (McCune 1997); passive overlays of environmental variables were used to deduce vegetation-environment relationships (McCune and Grace 2002). Joint plot overlays of environmental variables significantly correlated (Spearman's rank correlations) to the NMS site scores for axes one and two were used to produce overlay vectors. To assess concordance with different methods, principal components analysis (PCA) was also performed with the environmental variables, using a correlation coefficients cross-products matrix and broken stick eigenvalues to determine the number of axes worth interpreting (Jackson 1993). All multivariate analyses and data transformations were completed using PC-ORD v. 4.25 (McCune and Mefford 1999).

2.3 RESULTS

Most of the peatlands surveyed were found in low-lying basins, surrounded by uplands. A total of 302 plant species were identified, comprised of 87 bryophytes, three reindeer lichens, and 212 vascular plants (See species list in Appendix B).

Peatland classification and indicator species

Eight peatland types were recognized in the cluster analysis, including wooded bog, black spruce swamp, wooded moderate-rich fen, open-wooded moderate-rich fen, open shrub moderate-rich fen, open moderate-rich fen/marsh, open shore moderate-rich fen, and open extreme-rich fen (Figure 2.2). The MRPP test produced significant results (A-value = 0.233, $P \leq 0.001$), indicating high within-group homogeneity (McCune and Mefford 1999). The NMS ordination of the community data resulted in a relatively stable, two-dimensional solution with a high but acceptable final stress of 16.17 (Kruskal 1964) and final instability of 0.00481. The proportion of variation represented by ordination axes was 90%, comprised of 71% on axis one and 18% on axis two. Distinct patterns formed by overlaying the peatland types derived from cluster analysis on the ordination diagram and concordance with the DCA ordination (results not shown) confirmed that robust and useful solutions were found (Figure 2.3).

Pronounced calciphiles were found in sites in all eight peatland types, including *Sphagnum warnstorfii, Campylium stellatum,* and *Tomenthypnum nitens* (Table 2.1). Peatland type descriptions and indicator species (in order of importance values and significance) follow below.

Wooded Bog. These sites comprised 8% of the 94 peatlands and were isolated in basins within conifer forest or located adjacent to wooded moderate-rich fens. Characterizing plant indicator species included *Dicranum polysetum*, *Rubus chamaemorus*, *Sphagnum magellanicum*, *Cladina mitis*, *Gaultheria hispidula*, *Dicranum undulatum*, *Cladina rangiferina*, *Oxycoccus microcarpus, Vaccinium myrtilloides, Ledum groenlandicum,* *Picea mariana,* and *Sphagnum angustifolium* (Table 2.1).

Black Spruce Swamp. Seventeen percent of the 94 peatlands and 27% of the 60 wooded peatlands were classified as black spruce swamps. Most sites were located along gentle slopes on drainages associated with lakes or streams. This peatland type had more mesic species commonly found in upland boreal mixed wood sites than any of the other types. Significant indicator plants that were found on hummocks and drier areas included *Equisetum sylvaticum, Petasites frigidus* var. *palmatus, Cornus canadensis, Linnaea borealis, Rosa acicularis, Moneses uniflora, Geocaulon lividum, Orthillia secunda, Equisetum arvense, Listera cordata,* and *Mertensia paniculata,* and nearly continuous carpets of *Pleurozium schreberi* and *Hylocomium splendens* (Table 1). Significant indicator species found in hollows and pools included *Rhizomnium pseudopunctatum, Rhizomnium gracile,* and *Plagiochila porelloides.* Many species with affinities to rich fens were also found. When the cluster analysis was pruned into a seven-type solution, black spruce swamp coalesced with wooded moderate-rich fen. This suggests that the vegetation affinities are close between these two types (see also Figure 2.3).

Wooded Moderate-rich Fen. This peatland type comprised the same number of sites as black spruce swamp (17% of all peatlands). Significant plant indicators included *Mitella nuda, Amerorchis rotundifolia, Rhamnus alnifolia, Thuidium recognitum, Caltha palustris, Galium triflorum, Carex disperma, Ribes hudsonianum, Carex leptalea, Hypnum lindbergii, Equisetum scorpoides, Platanthera obtusata, Cinclidium stygium, Viola* spp., and *Sphagnum warnstorfii,* among others (Table 2.1).

Open-wooded Moderate-rich Fen. Twenty-one percent of all peatlands were of this type. One significant plant indicator, *Spiranthes romanzoffiana*, was restricted here, and *Empetrum nigrum* was also found in black spruce swamp (Table 2.1). Other significant plant indicators included *Sphagnum fuscum, Polytrichum strictum, Salix myrtillifolia, Tomenthypnum nitens, Larix laricina, Maianthemum trifolium,* and *Platanthera hyperborea.* A number of extreme-rich fen indicator species were found (*Scorpidium scorpioides, Limprichtia revolvens,* and *Triglochin maritimum*), usually in small springs with *Carex limosa* and sometimes with marl precipitate.

Open Shrubby Moderate-rich Fen. Sites in the open shrubby moderate-rich fen peatland type tended to have a large number of tall shrubs and occasional pockets of open water with aquatic species. These sites comprised 10% of the surveyed sites and were in riparian areas adjacent to lakes and streams where sites may have been affected by beaver activity. There were many strong plant indicator species in this type, including *Mentha arvense, Ranunculus scleratus* (restricted to this type), *Climacium dendroides, Sium suave, Glyceria striata, Salix planifolia, Salix discolor, Lycopus uniflorus, Cicuta bulbifera, Campanula aparanoides, Ribes oxycanthoides, Polygonum amphibium* var. *emersum, Carex lacustris, Potentilla norvegica,* and *Rumex orbiculatus,* among others. Few bryophytes were indicator species, despite a large pool of bryophytes being found within the peatland type (Table 2.1).

Open Moderate-rich Fen/Marsh. This peatland type comprised 7.5% of the sites surveyed. It was the most difficult type to classify due to the diverse species assemblage that included drier habitat grasses and emergent aquatics (Table 2.1). There was a lack of bryophyte indicator species despite a variety of species being found throughout the sites. Shrubs were present but did not dominate any site, and trees were rare. All sites except one were isolated from open water, and most were in discrete, often oval, basins surrounded by mixed wood upland forests. Sites were generally topographically higher compared to other peatlands and would be considered isolated depressional wetlands.

Open Shore Moderate-rich Fen. Most of the open shore moderate-rich fens were associated with lake or creek edges and were either floating mats or anchored to the mineral substrate. They comprised 12% of the surveyed sites. There were few strong plant indicator species in this type, with most species having high frequencies in other peatland types, as well. Indicator species included *Helodium blandowii, Vaccinium vitis-idaea, Andromeda polifolia, Carex magellanica, Equisetum fluviatile, Calliergon giganteum, Carex tenuifolia,* and *Aulocomnium palustre.* Rich fen floristic elements were also found in this type, including *Limprichtia revolvens, Salix pedicellaris,* and *Campylium stellatum.* In addition, some extreme-rich fen indicator plants were found, including *Triglochin maritmum* and *Scorpidium scorpioides.*

Open Extreme-rich Fen. All seven of the open extreme-rich fen sites (7.5% of sites) were isolated from adjacent water bodies, except one that was a floating shoreline mat. No significant indicators species were restricted to this type, but significant species with extreme-rich fen affinities included *Utricularia intermedia, Triglochin maritimum,* *Scorpidium scorpioides*, *Carex limosa* (also found in poor fens), *Salix pedicellaris*, *Limprichtia revolvens*, *Eriophorum gracile*, and *Campylium stellatum* (Table 2.1). Significant indicators arguably not relegated to extreme-rich fens included *Menyanthes trifoliata*, *Carex lasiocarpa*, and *Carex aquatilis*.

Environmental variables

There were significant differences among the peatland types for all forest mensuration variables except the number of trees per hectare (Table 2.2). Overstory density was significantly greater ($F = 8.406$, df = 3, 45, $P < 0.001$) in black spruce swamp compared to open wooded moderate-rich fen and wooded bog, and in wooded moderate-rich fen compared to open-wooded moderate-rich fen. The same pattern was evident with tree height ($F = 10.349$, df = 3, 45, $P < 0.001$). Tree diameter at breast height was significantly greater ($F = 5.754$, df = 3, 45, $P = 0.002$) in black spruce swamp compared with open-wooded moderate-rich fen, and in wooded moderate-rich fen compared with open-wooded moderate-rich fen.

All environmental variables except water table, area, and Na^+ were significantly different among the peatland types (Figure 2.4). In general, the peatlands were relatively small, averaging 1.8 ± 2.0 ha (mean and standard deviation), but ranged between 0.1 and 8.9 ha (Figure 2.4). The smallest, least variable types were open moderate-rich fen/marsh (0.6 ± 0.6 ha) and black spruce swamp (1.6 ± 1.2 ha). Wooded bog, open shore moderate-rich fen, and open extreme-rich fen had the deepest peat, whereas the shallowest peat was in black spruce swamp and open shrub moderate-rich fen. Wooded bog had the highest peat organic C content and C:N ratio and lowest peat inorganic C content. Peat inorganic C content was highest in the wooded fen types.

Water temperatures were lower in wooded peatland types than open types, except for open moderate-rich fen/marsh, where temperatures were more similar to the wooded fens (Figure 2.4). The median pH over all peatland types was 6.8. The lowest mean pH was in wooded bog (3.8 ± 0.3) with a range of 3.6 to 4.7. Based on pH, alkalinity, Ca^{2+}, and Mg^{2+}, the majority of sites were rich fens; when the peatland sites are plotted by pH, the distribution is weighted towards rich fens (data not shown but easily seen in Figure 2.4). Of the fen peatland types, open moderate-rich fen/marsh had the lowest mean pH

(5.4 ± 0.4), and the highest pH was in wooded moderate-rich fen (6.9 ± 0.5) and open shrubby moderate-rich fen (7.0 ± 0.5). pH was most variable in black spruce swamp (5.6 – 7.9) and open shore moderate-rich fen (5.3 – 7.4).

Patterns of specific conductance, Ca^{2+}, Mg^{2+}, and alkalinity of surface water were similar to those seen in pH plots for the peatland types (Figure 2.4). Overall, other than a distinction between bogs and fens in pH and cations, surface-water chemistry did not discriminate among the peatland types. However, there was a general trend of similarity for some constituents between wooded bog and open moderate-rich fen/marsh compared to the other peatland types. This included greater Fe^{+}, DOC, and NH_4^{+}, and lower Ca^{2+}, Mg^{2+}, and alkalinity. Overall, most nutrients were of highest concentrations in the open moderate-rich fen/marsh (Figure 2.4).

Environmental variables and vegetation communities

The PCA ordination of environmental variables resulted in weak results, with no axes worth interpreting (i.e., the broken stick eigenvalues were larger than the axes eigenvalues) (Jackson 1993) and poor discrimination among the peatland types in the ordination diagram (not shown). The joint plot overlay of environmental variables with the NMS ordination of community data revealed a strong physiognomic gradient of wooded-open sites along axis one, and a similar, weaker gradient along axis two (Figure 2.3). The most strongly associated variables along axis one were all forest mensuration variables (represented by percent overstory density: range = 7 to 80%) and peat C:N (13.5 to 67.1), which were oriented towards black spruce swamps and wooded moderate-rich fens, and surface-water temperature (3 to 20 °C), which was associated the open peatland types (Figure 2.3). Along axis two, the most strongly associated variables were peat bulk density (0.19 to 0.64 g/cc) and surface-water Ca^{2+} (1.8 to 111.4 mg/L) and specific conductance (0 to 989 μS/cm), which were oriented towards wooded moderate-rich fens, and peat depth (0.4 to ≥ 3.0 m), organic C (54 to 98%), and area (0.1 to 8.9 ha), which were associated with the open peatland types.

2.4 DISCUSSION

Peatland classification and indicator species

Most of the peatlands surveyed at Duck Mountain were basin peatlands, sites in low areas constrained by uplands (*sensu* National Wetlands Working Group 1988), which reflects the glaciated nature of the region. *Sphagnum warnstorfii, Campylium stellatum,* and *Tomenthypnum nitens* characterize moderate-rich fens (Malmer 1986, Chee and Vitt 1989) and were found in all Duck Mountain peatland types. The occurrence of these species is probably related to the basic soils and base-rich waters emanating from deep sedimentary glacial tills, which in turn probably result from large amounts of orographic precipitation. The most common peatland types at Duck Mountain were rich fens, and when the sites are plotted by pH, the distribution is weighted more strongly towards rich fens than bogs. This distribution is different from that seen in other western boreal areas, where the occurrence of peatlands on the landscape, as plotted by pH, is more evenly split between bogs/poor fens and rich fens (Vitt 2000). With respect to discrimination among peatland types, the ordination diagram shows the wooded peatland types with the most overlap, which has also been noted in vegetation ordinations in northwestern Ontario peatlands (Kenkel 1987).

Wooded Bog. None of the indicator species in this peatland type were restricted to bogs, something recognized long ago by Du Rietz (1949). The species assemblage of Duck Mountain wooded bogs was similar to other western Canadian boreal bogs (Belland and Vitt 1995, Beilman 2001) and '*Picea mariana/Ledum groenlandicum/Sphagnum fuscum* muskeg' (Jeglum 1972). While *Sphagnum riparium*, a bog-poor fen species, had its highest fidelity in Duck Mountain bogs, there was no *Sphagnum jensenii* H. Lindberg, a common bog carpet collapse scar species (Vitt and Slack 1984, Beilman 2001). This suggests the absence of permafrost in Duck Mountain bogs.

Black Spruce Swamp. Coniferous swamps have been considered a minor component (0.19%) of the Duck Mountain landscape (Halsey et al. 1997a). However, this is somewhat misleading in that, although small in area, black spruce-dominated conifer swamp is a relatively common component of Duck Mountain peatlands (17%). Given the paucity of quantitative data on black spruce swamps in western North America, these sites may be more common than previously reported. The Canadian Wetland

Classification System (National Wetlands Working Group 1997) describes these as peatland margin swamps, located between upland and other peatland. Conifer swamps have been found in association with gentle slopes adjacent to lakes (Zoltai et al. 1988) and with comparatively small sites on the edges of peatland complexes (Jeglum 1991). These factors suggest that black spruce swamps could be easily overlooked.

Wooded Moderate-rich Fens. There are few studies on the total flora of wooded moderate-rich fens in western Canada. However, the total species assemblage at Duck Mountain sites bore similarities to sites classified as "black spruce swamp" in Saskatchewan (Jeglum 1972, 1973), and the bryophyte flora was very similar to that in wooded moderate-rich fens in Alberta (Vitt et al. 1995b, Vitt et al. 2003). *Rhamnus alnifolia* was found as a common understory species in Duck Mountain wooded moderate-rich fens. While it is common east of Manitoba (Zoltai et al. 1988) in horizontal fens, fens that occupy broad, ill-defined depressions (National Wetlands Working Group 1997), it is less common in peatlands west of Manitoba (Locky, unpublished data).

Open Moderate-rich Fens. Floristically, open moderate-rich fen/marshes were similar to open fens in Elk Island National Park, Alberta (Nicholson 1995), and a broad-leaved sedge fen in Saskatchewan (Jeglum 1972). Although floristically similar to some meadow marshes (Zoltai et al. 1988), these sites have formed significant amounts of peat and are considered peatlands (Bayley and Mewhort 2004).

Open Extreme-rich Fen. The species assemblage in open extreme-rich fens was generally similar to that in other western continental sites (Slack et al. 1980, Vitt and Chee 1990). In particular, the extreme-rich fen indicators *Scorpidium scorpioides* and *Limprichtia revolvens*, and the fen indicators, *Triglochin maritimum* and *Carex limosa*, have been found in western Alberta minerotrophically rich patterned fens (Slack et al. 1980). *Tofieldia glutinosa* (Michx.) Pers. was a common fen indicator species in central Alberta open extreme-rich fens (Vitt and Chee 1990) but was found only once in an open-wooded moderate-rich fen at Duck Mountain (data not shown).

Environmental variables

Other than a distinct division between bog and fen/swamp, clear differences between the peatland types at Duck Mountain based on water chemistry were not seen, and no clear nutrient patterns among the peatland types were observed. Substantial overlap in pH and Ca^{2+} among peatland types (Sjörs 1952, Sjörs and Gunnarsson 2002) and other chemical constituents among fens (Glaser et al. 1990, Vitt and Chee 1990) have been noted. In addition, nutrients are variable with depth and season, often obscuring distinctions among peatland types (Vitt et al. 1995b).

The open moderate-rich fen/marsh sites were more similar by surface-water and peat chemistry to wooded bogs than other more similarly vegetated open moderate-rich fens. The flow of water in depressional isolated wetlands is typically upward due to evapotranspiration (Winter 1989), and surface waters may have low specific conductance (Keely and Zedler 1998, Podniesinski and Leopold 1998) and low salinity levels (Driver and Peden 1977), conditions similar to Duck Mountain sites. Duck Mountain sites also had low mean pH (5.4), which suggests poor fen water chemistry (c.f. Vitt et al. 1995b, Nicholson et al. 1996). However, *Sphagnum* cover was low, indicator mosses few, and the vascular plants intolerant of low pH (Table 2.1), indicating that low pH may be either a temporary (i.e., seasonal) or recent condition. pH can decrease with depth up to 1.0 pH increment (Vitt et al. 1995b, Tahvanainen and Tuomaala 2004) and high DOC concentration and organic-acid-metal binding can occur in soils with low pH, leading to comparatively higher concentrations of Fe^{++} (Vitt et al. 1995b). Open-moderate-rich fen/marsh sites had higher mean surface-water N and P concentration and lower peat C:N than the other peatland types. This may be the effect of aeration associated with summer water-table drawdowns that result in increased P and N in peatland surface waters (Devito and Dillon 1993).

Environmental variables and vegetation communities

The most significant variables associated with compositional variation in community data in this study were overstory density, peat C:N, depth, bulk density, organic C, surface-water temperature, specific conductance, Ca^{2+}, and size of area (Figure 2.3). Overstory density has been associated with influencing distributions of peatland vascular plants in Maine (Anderson and Davis 1997) and bryophytes in Alberta (Vitt and Slack 1984), whereas soil physical characteristics have been found related to peatland plant species in northern Ontario (Jeglum and He 1995). As observed in my study, bulk density is greater in sites with woody peat (i.e., wooded sites) than sites with moss peat (i.e., open sites) (Moore and Bellamy 1974). Specific conductance, Ca^{2+}, and Mg^{2+} have been observed as significant environmental factors in structuring vegetation in northeastern Ontario forested wetlands (Jeglum and He 1995) and Maine peatlands (Anderson and Davis 1997). However, while the pH-alkalinity gradient has been a significant determinant in structuring plant communities in some peatlands (Vitt and Chee 1990, Vitt et al. 1995b, Anderson and Davis 1997), it was less important in my study. The use of one water sample per site, sampled over three months, and assembled into three classes probably reduced the sensitivity of the analyses; water-table depth has been found to as been an important explanatory variable for patterns of vegetation in peatlands in some studies (Vitt and Slack 1984, Glaser et al. 1990, Anderson and Davis 1997). Environmental variables can form complex gradients in ecosystems (Kenkel 1987) and variable results among studies can be expected.

Boreal wooded swamps: Comparisons and contrasts in terminology

Although 'swamp' usually refers to fens with forest cover in the English-language peatland literature, the term has been used loosely and widely (Charman 2002). This is not entirely unexpected where terminology crosses borders and disciplines.

Europe. In Russia, wetlands with 'minimal' peat depth are considered 'swamp', and sites with deeper peat depths are considered 'mires' (Ivanov 1981). In Fennoscandia, 'boreal swamp forest' or 'swamp forest' are common terms used to describe wooded peatlands (Eurola et al. 1984, Hörnberg et al. 1998). However, the latter term also refers to tropical swamp forests that are unlike boreal swamps (Koponen et al. 2003). In Sweden, 'swamp forests' are described as forested ecosystems (peatlands) with *Picea abies* (L.) H. Karst. at least 3 m in height, more than 30% tree canopy cover, and an understory dominated by hydrophilous species (Økland et al. 2001). These sites are also located at the 'mire margin' but would not be directly comparable with boreal black spruce swamp; the more open canopies and higher species richness suggest affinities with western boreal wooded moderate-rich fens (Vitt et al 2003, Locky unpub. data). However, swamp forests and black spruce swamp are similar from the perspective of sharing floristic elements of both uplands and peatlands (Korpela and Reinikainen 1996). Finnish spruce mires appear more similar to Duck Mountain black spruce swamps than Swedish swamp forests by peat depth, overstory density, and flora. Many of the common indicator species are the same or have analogs to those in Canadian black spruce swamps (Eurola et al. 1984) (c.f. Table 1).

North America. The term 'swamp' is not used in the U.S. wetland classification system, where wooded wetlands are referred to as shrub-scrub or forested, and conifer-dominated wetlands are called needle-leaved evergreen wetlands (Cowardin et al. 1979). In Canada, wetlands wooded with trees or shrubs are called swamps, with conifer-dominated wetlands referred to as conifer swamps (National Wetlands Working Group 1997). In Canada's boreal region, conifer swamps can be differentiated based on the dominant tree species. In the southern part of the eastern boreal region *Thuja occidentalis* dominates (Schwintzer 1981, Kenkel 1987, Zoltai et al. 1988, Jeglum 1991), while *Picea mariana* (with some *Larix laricina*) dominate sites in west (Jeglum 1991) and other sites in the east (Zoltai et al. 1988). *Abies balsamea* (L.) P. Mill. is sometimes a component in both eastern (Kenkel 1987) and western boreal regions (this study). *Thuja occidentalis*-dominated systems generally occur in places with circumneutral, base-rich waters and have many species with upland affinities (Schwintzer 1981). *Picea mariana*-dominated conifer swamp also has species with upland affinities but can vary greatly in pH and 'trophic level' (i.e., nutrient regime) (Jeglum 1991, National Wetlands Working Group 1997). Jeglum (1991) listed five different 'trophic' classes of conifer swamp ranging from pH 5.2 to 6.8 in the Northern Clay section of northeastern Ontario, which is similar to Duck Mountain sites with pH 5.6 to 7.9. Boreal conifer swamp in eastern boreal Canada is considered more comparable to genuine forested types in Fennoscandia, which are somewhat drier and with higher hummocks, compared to fens. Treed fens are, to some extent, wetter and comparable to sparsely forested types of Fennoscandian peatlands (Jeglum 1991); these criteria are also applicable to western boreal wooded peatlands.

Western Canada. At Elk Island National Park, Alberta, peatlands with *Picea glauca-Picea mariana-Larix laricina* associations had floristic affinities with peatland margin conifer swamps in eastern temperate Canada (Nicholson 1995). "Moist forest class black spruce stands" with shallow peat located upslope from peatland types at Candle Lake

Saskatchewan (Jeglum 1972) suggest conifer swamp. These sites were similar to Duck Mountain black spruce swamps with respect to forest mensuration variables and floristics.

Forested wetlands have been delineated as swamps based on more closed canopies in Ontario (Jeglum 1991) and Manitoba (Halsey et al. 1997a), with the latter having sites with >70% cover of *Picea mariana* and *Larix laricina*. In Duck Mountain black spruce swamps, mean percent overstory density was 68%, the largest trees of all the peatland types, and *Larix laricina* was present in 50% relative abundance. The maximum tree height at these sites is 14.7 m, which is similar to a conifer swamp in Pointe du Bois, Manitoba (Zoltai et al. 1988).

Peat depths in Duck Mountain black spruce swamps were generally the shallowest (mean 90 cm, range 40 to 200 cm) compared to the other peatland types. This has been seen in "black spruce moist forest" in Saskatchewan (Jeglum 1972) and conifer swamps in northeastern Ontario (Jeglum 1991). Organic accumulation in some conifer swamps is generally limited; feather mosses, as the dominant bryophytes, decompose faster than *Sphagnum* and therefore accumulate comparatively less peat (Camill et al. 2001).

Black spruce swamp sometimes grades into wooded bog (National Wetlands Working Group 1997), but most Duck Mountain black spruce swamps are more similar to, and associated with, wooded moderate-rich fens. This is similar to Saskatchewan treed fens, which tend to cluster closer to conifer swamp than wooded bog in ordinations (Jeglum 1973). The association may have more to do with the dominant peatland types on the landscape; eastern boreal sites are primarily influenced by the base-poor Canadian Shield, with more bogs on the landscape, whereas western boreal plain sites are influenced by sedimentary deposits, with more fens on the landscape. The distinction between moderate-rich fens and some black spruce swamps can be difficult, as many swamps have plants with rich fen affinities. Jeglum (1991) found that conifer swamp (*Picea mariana*-dominated, with some *Thuja occidentalis*) in northeastern Ontario had comparatively high mean pH and associated vegetation, and he attributed this to supplementary base cations from sub-surface waters flowing down from adjacent uplands. The hummock tops and sides, and hollows and pools species assemblages in

Duck Mountain black spruce swamps are similar to these eastern boreal sites (c.f. Jeglum 1991) and also some Canadian shield sites (Zoltai et al. 1988). However, care must be taken in comparing the flora of specific peatland types between regions; detailed vegetation studies of peatlands are often only relevant to areas where the data are collected due to biogeoclimatic variation in wetland vegetation in Canada (Jeglum 1991). The term 'black spruce swamp' has not always accurately conveyed the true meaning of conifer swamp in North America. Because of floristic similarities with fens, 'black spruce swamp' has been applied to wooded fens (Jeglum 1972, Jeglum 1973, Charman 2002). Alternatively, because black spruce swamps also share floristic affinities with upland woodlands (Klinka et al. 2002), they have been referred to as black spruce moist forest (Jeglum 1972) and black spruce upland (McLaughlin et al. 1996). In the western boreal region of Canada, conifer swamp is frequently defined as being black spruce-dominated (Zoltai et al. 1988). The term, 'black spruce swamp' then accurately reflects the western (and eastern) boreal association of *Picea mariana* conifer swamp, while separating these from eastern boreal *Thuja occidentalis* conifer swamps, which generally occur only in the lower eastern boreal region (e.g., Schwintzer 1981, Kenkel 1987). I feel that this is an important distinction and that the refinement of peatland terminology is an ongoing and worthwhile endeavor (c.f. Schwintzer 1981, Bayley and Mewhort 2004).

2.5 CONCLUSIONS

Duck Mountain peatlands are primarily wooded moderate-rich fens, with bogs and extreme-rich fens much rarer in this survey. Black spruce swamp is a distinct peatland type at Duck Mountain and may be underreported in the boreal plain of western Canada. These peatlands are often found on gentle slopes adjacent to water bodies and are characterized by the tallest and largest trees, greatest percent overstory density, shallower relative peat depths, and smaller relative area. The species assemblage is closest to wooded moderate-rich fen, but with large abundances of indicator species often found in mesic non-peatland sites.

Duck Mountain peatlands are similar floristically to other boreal peatlands. Chemically, there is a distinction between bogs and fens, but much overlap exists among fens and swamps. Open fens that were in isolated depressions in topographically high areas had typical moderate-rich fen vegetation but surface-water chemistry and certain elements of peat that are more similar to wooded bogs. This may be attributed to the effects of fluctuating water levels.

The environmental variables most strongly associated with Duck Mountain peatland community data included forest mensuration data, peat physical variables, some cations and anions, and surface-water temperature.

There has been little published quantitative information on wooded peatlands, especially black spruce-dominated swamps in western Canada. The terms 'swamp' and 'conifer swamp' have been inconsistently used in the past. Conifer swamp with peat at least 40 cm and dominated by *Picea mariana* in the boreal region of North America should be referred to as black spruce swamp to avoid confusion with *Thuja occidentalis*-dominated swamps found in the eastern boreal region and *Picea mariana*-dominated uplands found throughout the boreal region.

2.6 LITERATURE CITED

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Table 2.1. Two-way table of indicator plants for peatland types at Duck Mountain, Manitboa, with indicator values, significance (bold type denotes P ≤ 0.05), and % relative frequencies. From Indicator Species Analysis (Dufrêne and Legendre 1997). Peatland types derived from cluster analysis; see text for details.

Peatland Type	Species	Indicator Value	P Value	% Relative Frequency							
				I	II	III	IV	V	VI	VII	VIII
I - Wooded Bog	*Dicranum polysetum* Sw.	**44.7**	**0.001**	88	50	19	15	0	0	0	0
	Sphagnum magellanicum Brid.	**40.2**	**0.001**	100	38	25	45	0	14	27	0
	Cladina mitis (Sandst.) Hustich	**34.0**	**0.003**	75	6	31	35	0	0	18	0
	Rubus chamaemorus L.	**33.1**	**0.001**	100	81	38	65	0	0	18	0
	Gaultheria hispidula (L.) Muhl. *ex* Bigelow	**29.3**	**0.003**	88	63	56	55	0	0	0	0
	Dicranum undulatum Brid.	**28.9**	**0.007**	63	25	13	35	0	0	0	0
	Cladina rangiferina (L.) Nyl.	**27.5**	**0.003**	75	38	19	55	0	0	18	0
	Hylocomium splendens (Hedw.) Schimp. *in* B.S.G.	**23.4**	**0.001**	100	100	94	85	22	0	27	0
	Vaccinium myrtilloides Michx.	**20.8**	**0.035**	63	56	38	20	11	0	0	0
	Sphagnum angustifolium (C. Jens. *ex* Russ.) C. Jens. *in* Tolf	18.9	0.070	75	56	44	70	11	14	27	0
	Sanionia uncinatus (Hedw.) Loeske var *uncinata*	16.8	0.100	63	50	25	45	0	14	36	0
	Sphagnum capillifolium (Ehrh.) Hedw.	16.7	0.122	75	75	50	40	33	0	64	0
	Sphagnum riparium Ångstr.	10.0	0.261	25	0	0	5	0	14	18	0
	Pohlia nutans (Hedw.) Lindb.	9.3	0.361	25	13	19	0	11	0	0	0
II - Black Spruce Swamp	*Equisetum sylvaticum* L.	**44.6**	**0.001**	25	88	25	20	0	14	0	0
	Cornus canadensis L.	**36.4**	**0.001**	0	81	75	25	0	0	0	0
	Moneses uniflora (L.) Gray	**35.6**	**0.001**	0	63	31	5	11	0	0	0
	Petasites frigidus var. *palmatus* (Ait.) Cronq.	**35.0**	**0.002**	0	69	31	15	11	0	9	0
	Linnaea borealis L.	**33.0**	**0.002**	25	81	44	30	11	0	9	0
	Rosa acicularis Lindl.	**30.8**	**0.001**	0	50	31	0	0	0	0	0
	Rhizomnium pseudopunctatum (Bruch & Schimp.) T. Kop.	**29.7**	**0.004**	25	88	44	25	44	14	18	0
	Ptilium crista-castrensis (Hedw.) De Not.	**29.1**	**0.001**	75	100	69	80	11	0	9	0
	Geocaulon lividum (Richards.) Fern.	**27.4**	**0.006**	0	50	31	10	0	0	0	0
	Orthilia secunda (L.) House	**27.1**	**0.002**	13	75	50	50	11	0	9	0
	Rhizomnium gracile T. Kop.	**26.1**	**0.005**	25	88	50	65	33	0	18	14
	Pleurozium schreberi (Brid.) Mitt.	**23.7**	**0.001**	88	100	94	85	11	0	45	0
	Equisetum arvense L.	**21.6**	**0.034**	13	75	44	50	56	14	9	0
	Listera cordata (L.) R. Br. *ex* Ait. f.	**21.3**	**0.026**	0	44	31	15	0	0	0	0
	Ranunculus lapponicus L.	**20.0**	**0.023**	0	50	44	20	11	0	0	0
	Epilobium angustifolium L.	**19.0**	**0.049**	0	56	50	15	22	14	9	0
	Plagiochila porelloides (Torrey *ex* Nees) Lindenb.	**18.9**	**0.042**	13	44	25	20	0	0	0	0
	Mertensia paniculata (Ait.) G. Don	**18.0**	**0.037**	0	44	31	0	22	0	9	0
	Ribes triste Pallas	16.9	0.058	0	44	38	10	22	0	0	0
	Carex vaginata Tausch	14.8	0.091	0	31	19	5	11	0	0	0
	Cladina stellaris (Opiz) Brodo	10.9	0.160	13	25	0	20	0	0	0	0
	Aralia nudicaulus L.	9.7	0.309	0	19	13	5	0	0	0	0
	Riccardia multifida (L.) S. Gray var. *multifida*	8.5	0.333	13	19	0	10	0	0	0	0
	Hypnum pratense (Rabenh.) W. Koch *ex* Spruce	13.3	0.393	25	69	50	60	44	14	64	29

Peatland Type	Species	Indicator Value	P Value	% Relative Frequency							
				I	II	III	IV	V	VI	VII	VIII
III - Wooded Moderate-rich Fen	*Mitella nuda* L.	38.7	0.001	0	81	100	55	22	0	0	0
	Amerchis rotundifolia (Banks *ex* Pursh) Hulten	38.4	0.001	0	6	56	20	0	0	0	0
	Thuidium recognitum (Hedw.) Lindb.	32.7	0.002	13	25	75	25	11	14	9	0
	Equisetum scirpoides Michx.	28.2	0.003	13	75	81	65	0	0	0	0
	Caltha palustris L.	27.5	0.001	0	50	94	45	67	0	64	0
	Rhamnus alnifolia L'Her.	26.2	0.005	0	56	75	30	44	0	9	0
	Hypnum lindbergii Mitt.	26.0	0.005	0	44	88	40	44	14	36	29
	Galium triflorum Michx.	26.0	0.010	0	19	44	0	11	0	0	0
	Ribes hudsonianum Richards.	25.1	0.019	0	38	56	10	22	0	0	0
	Carex disperma Dewey	24.7	0.001	63	81	94	55	44	0	18	0
	Platanthera obtusata (Banks *ex* Pursh) Lindl.	22.4	0.015	25	50	56	10	0	0	0	0
	Oxycoccus microcarpus Turcz.	22.2	0.001	100	88	100	95	22	0	45	0
	Carex leptalea Wahlenb.	22.1	0.010	13	50	75	65	33	0	18	0
	Pyrola asarifolia Michx.	21.7	0.021	13	13	56	35	11	0	18	0
	Cinclidium stygium Sw. *in* Schrad.	20.9	0.012	13	19	88	55	67	43	55	29
	Ledum groenlandicum Oeder	20.1	0.001	100	100	100	95	33	0	55	14
	Viola spp.	19.2	0.033	0	6	50	0	22	0	9	43
	Sphagnum warnstorfii Russ.	18.8	0.001	63	75	100	90	56	14	91	43
	Lonicera caerulea var. *villosa* (Michx.)	18.4	0.052	0	13	50	20	44	0	9	0
	Aulacomnium palustre (Hedw.) Schwaegr.	15.4	0.001	88	94	100	95	89	43	100	43
	Bryum pseudotriquetrum (Hedw.) Gaertn. et al.	15.2	0.005	63	81	100	95	78	57	100	86
	Carex gynocrates Wormsk. ex Drej.	19.0	0.055	13	56	75	70	22	0	45	14
	Abies balsamea (L.) P. Mill.	14.5	0.099	13	19	31	5	0	0	0	0
	Salix maccaliana Rowlee	13.2	0.114	13	0	31	5	11	0	0	14
	Plagiomnium ellipticum (Brid.) T. Kop.	17.2	0.130	0	81	94	80	89	71	82	14
	Trientata borealis Raf.	11.2	0.186	0	13	19	0	0	0	0	0
	Equisetum pratense Ehrh.	10.8	0.206	0	19	25	5	0	0	9	0
	Tomenthypnum falcifolium (Ren. *ex* Nichols) Tuom. *in* Ahti & Fagers	11.1	0.231	13	6	31	20	0	0	18	0
	Rubus pubescens Raf.	15.8	0.236	13	69	75	60	56	29	55	0
	Carex interior Bailey	11.0	0.274	13	6	31	30	0	0	9	0
	Rubus arcticus L.	10.9	0.321	13	19	44	25	33	0	27	14
	Plagiomnium medium (Bruch & Schimp. *in* B.S.G.) T. Kop. var. *medium*	7.8	0.511	0	6	25	5	11	14	18	0
	Marchantia polymorpha L.	7.8	0.530	13	6	25	0	22	0	0	14
	Ptilidium pulcherrimum (G. Web.) Hampe	4.5	0.690	13	0	13	10	0	0	0	0
	Deschampsia caespitosa (L.) Beauv.	5.4	0.765	13	13	19	10	11	0	0	0
IV - Open-wooded Moderate-rich Fen	*Spiranthes romanzoffiana* Cham.	40.0	0.001	0	0	0	40	0	0	0	0
	Empetrum nigrum L.	31.8	0.001	0	19	0	45	0	0	0	0
	Sphagnum fuscum (Schimp.) Klinggr.	23.6	0.002	88	75	38	95	0	0	73	14
	Polytrichum strictum Brid.	23.5	0.001	75	63	63	95	11	0	64	14
	Vaccinium vitis-idaea L.	21.7	0.001	75	56	88	100	0	14	100	29
	Maianthemum trifolium (L.) Sloboda	21.4	0.001	63	100	94	100	33	0	64	14
	Salix myrtillifolia Anderss.	20.4	0.021	0	25	44	65	56	0	18	0
	Tomenthypnum nitens (Hedw.) Loeske	19.7	0.001	25	88	81	100	22	43	91	57
	Platanthera hyperborea (L.) Lindl.	19.1	0.050	0	69	44	70	22	14	9	29
	Picea mariana (P. Mill.) B.S.P.	17.5	0.001	100	100	100	100	56	14	73	29
	Mylia anomala (Hook.) S. Gray	16.7	0.039	13	0	0	25	0	0	0	0
	Cephalozia connivens (Dicks.) Lindb. var. *connivens*	16.4	0.075	13	13	0	30	0	0	0	0
	Campylium stellatum (Hedw.) C. Jens. var. *stellatum*	18.7	0.085	13	50	81	90	22	29	64	86
	Lophozia rutheana (Limpr.) M.A. Howe	14.7	0.090	13	13	6	30	0	0	0	0
	Larix laricina (Du Roi) K. Koch	17.5	0.128	88	50	94	95	44	43	73	29
	Meesia longiseta Hedw.	11.3	0.208	0	0	6	20	0	0	9	0
	Calypogeia sphagnicola (H. Arnell et J. Perss.) Warnst. *et* Loeske	10.3	0.250	13	0	6	20	0	0	0	0
	Drosera rotundifolia L.	11.9	0.258	38	0	6	40	0	14	36	0
	Pinus banksiana Lamb.	10.5	0.316	0	25	13	30	0	0	18	0
	Populus balsamifera L.	9.2	0.346	0	13	0	20	11	0	0	0
	Platydictya jungermannioides (Brid.) Crum	5.8	0.555	0	0	13	15	11	0	0	0
	Meesia uliginosa Hedw.	5.3	0.642	0	6	13	15	0	0	9	0

Peatland Type	Species	Indicator Value	P Value	% Relative Frequency I	II	III	IV	V	VI	VII	VIII
V - Open Shrubby Moderate-rich Fen	*Mentha arvensis* L.	65.7	0.001	0	0	0	0	78	14	0	0
	Ranunculus scleratus L.	55.6	0.001	0	0	0	0	56	0	0	0
	Climacium dendroides (Hedw.) Web. & Mohr	37.1	0.001	0	19	56	5	100	29	18	43
	Sium suave Walt.	36.7	0.001	0	0	0	0	56	29	0	0
	Salix planifolia Pursh	35.4	0.001	13	6	31	30	100	43	45	14
	Glyceria striata (Lam.) A.S. Hitchc.	30.5	0.001	0	19	31	15	67	14	0	0
	Salix discolor Muhl.	30.0	0.001	0	25	13	65	100	57	45	29
	Potentilla norvegica L.	29.5	0.005	0	0	6	0	56	29	0	14
	Cicuta bulbifera L.	29.4	0.008	0	0	6	5	89	43	55	71
	Ribes oxycanthoides L.	27.0	0.004	0	6	13	10	44	0	0	0
	Lycopus uniflorus Michx.	26.6	0.006	0	6	6	5	56	29	0	14
	Campanula aparanoides Pursh	26.4	0.003	0	0	13	5	67	29	27	29
	Galium palustre L.	26.0	0.012	0	0	13	10	44	0	9	0
	Rumex orbiculatus Gray	25.6	0.007	0	0	0	10	33	0	0	0
	Polygonum amphibium var. *emersum* Michx.	25.2	0.005	0	0	25	15	78	43	36	43
	Geum rivale L.	24.2	0.010	0	6	6	0	33	0	0	0
	Carex cannescens L.	23.2	0.016	25	6	19	5	67	29	27	14
	Carex lacustris Willd.	22.8	0.014	0	0	19	0	56	29	18	14
	Calamagrostis stricta ssp. *inexpansa* (Gray) C.W. Greene	20.6	0.016	0	0	0	10	44	0	27	14
	Rubus idaeus L.	19.0	0.043	0	6	19	0	33	0	0	0
	Sagittaria spp.	17.9	0.028	0	0	0	0	33	14	0	14
	Galium labradoricum (Wieg.) Wieg.	17.0	0.081	0	0	31	25	56	14	27	29
	Drepanocladus aduncus (Hedw.) Warnst. var. *aduncus*	17.5	0.115	50	44	75	35	100	100	82	86
	Stellaria longifolia Muhl. ex Willd.	16.2	0.125	13	0	38	15	56	29	27	14
	Alnus incana (L.) Moench	16.9	0.148	13	69	75	40	78	14	55	14
	Fragria virginiana Duchesne	11.7	0.198	13	25	0	15	33	0	9	0
	Populus tremuloides Michx.	11.4	0.210	0	6	0	15	22	0	0	0
	Ranunculus gmelii DC.	10.3	0.211	0	0	6	5	22	14	0	0
	Leptobryum pyriforme (Hedw.) Wils.	11.0	0.224	0	6	6	10	22	0	0	0
	Lysimachia thrysifolia L.	9.9	0.482	0	0	31	10	44	43	27	43
	Brachythecium mildeanum (Schimp.) Schimp. ex Milde.	12.2	0.803	25	69	69	70	78	57	73	57
VI - Open Moderate-rich Fen/Marsh	*Bidens cernua* L.	42.2	0.002	0	0	0	0	11	57	9	0
	Agrostis scabra Willd.	39.5	0.001	0	0	6	10	33	86	36	14
	Galium trifidum L.	36.7	0.001	0	6	38	5	44	100	36	43
	Carex utriculata Boott	35.6	0.001	0	0	6	10	11	86	36	57
	Scutellaria gallericulata L.	35.2	0.001	13	0	6	10	89	100	9	57
	Epilobium leptophyllum Raf.	28.6	0.005	0	6	13	5	22	71	18	43
	Rumex occidentalis S. Wats.	26.1	0.007	0	0	0	0	44	57	9	14
	Carex atherodes Spreng.	23.2	0.019	0	0	0	5	22	43	9	0
	Poa palustris L.	16.7	0.053	0	25	0	15	0	43	27	0
	Calamagrostis canadensis (Michx.) Beauv.	16.4	0.092	0	19	19	25	56	57	9	14
	Aster puniceus (L.) A.& D. L've	15.2	0.103	0	13	6	10	22	43	27	0
	Calla palustris L.	12.6	0.149	0	0	0	5	22	29	9	0
	Eriophorum vaginatum L.	10.6	0.259	25	0	0	5	0	29	18	0
	Calliergon stramineum (Brid.) Kindb.	9.0	0.345	0	19	0	5	11	29	27	0
	Epilobium ciliatum Raf.	4.8	0.540	0	13	6	0	0	14	9	0
VII - Open Shore Moderate-rich Fen	*Helodium blandowii* (Web. & Mohr) Warnst. var. *blandowii*	22.3	0.012	0	38	75	30	33	43	82	0
	Comarum palustris L.	21.7	0.031	0	19	38	45	89	86	100	86
	Carex magellanica Lam.	21.3	0.016	38	38	44	60	11	14	82	29
	Calliergon giganteum (Schimp.) Kindb.	18.3	0.005	38	50	88	80	78	29	100	86
	Equisetum fluviatile L.	18.5	0.064	13	13	50	35	56	43	82	71
	Hamatocaulis vernicosus (Mitt.) Hedenäs	17.7	0.077	0	13	19	25	0	14	55	43
	Warnstorfia exannulata (Schimp. *in* B.S.G.) Loeske var. *exannulata*	16.7	0.078	13	13	6	10	11	29	55	43
	Salix candida Fluegge ex Willd.	17.0	0.087	13	13	69	70	89	71	91	71
	Paludella squarrosa (Hedw.) Brid.	13.0	0.093	0	0	25	5	0	0	27	0
	Kalmia polifolia Wangenh.	14.2	0.096	25	0	0	0	0	0	27	0
	Andromeda polifolia L.	16.9	0.099	50	31	63	40	0	14	73	43
	Carex tenuifolia Wahlenb.	14.8	0.117	38	31	31	35	11	0	55	0
	Parnassia palustris L.	11.2	0.285	0	0	6	25	22	0	36	29
	Taraxacum officinale G.H. Weber ex Wiggers	7.9	0.316	0	13	0	0	11	0	18	0
	Salix bebbiana Sarg.	11.0	0.353	0	25	31	25	33	0	45	29
	Epilobium palustre L.	9.9	0.445	0	6	25	30	44	43	45	14
	Meesia triquetra (Richt.) Ångstr.	6.2	0.556	0	6	0	15	0	0	18	14
	Eriophorum viridi-carinatum (Engelm.) Fern.	5.0	0.755	13	0	6	15	0	0	18	14
	Petasites sagittatus (Banks ex Pursh) Gray	8.2	0.880	13	31	44	45	44	29	45	0

Peatland Type	Species	Indicator Value	P Value	% Relative Frequency							
				I	II	III	IV	V	VI	VII	VIII
VIII - Open Extreme-rich Fen	*Utricularia intermedia* Hayne	46.7	0.001	0	0	0	10	44	14	45	100
	Triglochin maritimum L.	42.2	0.001	0	0	6	25	0	0	18	71
	Scorpidium scorpioides (Hedw.) Limpr.	40.2	0.001	0	0	0	15	0	0	9	57
	Carex limosa L.	28.9	0.003	0	0	0	5	0	14	36	57
	Eriophorum gracile W.D.J. Koch	26.8	0.009	0	0	0	5	11	57	45	71
	Carex lasiocarpa Ehrh.	25.0	0.010	0	0	0	20	44	71	73	86
	Salix pedicellaris Pursh	23.6	0.016	25	38	38	50	11	71	91	100
	Typha latifolia L.	23.0	0.014	0	0	0	0	33	71	45	71
	Carex chordorhiza Ehrh. *ex* L. f.	23.0	0.019	0	0	13	15	11	57	55	71
	Carex aquatilis Wahlenb.	21.5	0.014	13	31	38	80	89	43	73	100
	Menyanthes trifoliata L.	21.0	0.021	13	6	38	40	11	0	64	71
	Limprichtia revolvens (Sw.) Loeske.	20.6	0.018	13	6	13	45	11	14	0	57
	Betula pumila L.	18.5	0.003	25	63	88	80	67	29	91	100
	Carex diandra Schrank	19.0	0.079	0	0	25	70	67	57	82	86
	Calliergonella cuspidata (Hedw.) Loeske	13.8	0.139	0	0	0	5	11	14	0	29
	Salix pyrifolia Anderss.	10.1	0.399	25	0	25	10	0	43	36	43
	Pohlia wahlenbergii (Web & Mohr) Andrews	4.9	0.564	0	6	0	10	11	0	0	14
	Calliergon richardsonii (Mitt.) Kindb. *in* Wamst.	6.9	0.595	13	25	19	15	0	0	18	29
	Salix serissima (Bailey) Fern.	6.6	0.690	25	13	6	15	22	14	0	29
	Pentaphylloides floribunda (Pursh) A. Love	4.0	0.740	0	6	6	10	0	14	0	14

Table 2.2. Means and ranges of forest mensuration variables for four wooded peatland types at Duck Mountain, Manitoba. Numbers in parentheses refer to number of sites surveyed for forest mensuration variables. Tree dbh refers to tree diameter measured at breast height and MRF refers to moderate-rich fen. Means of adjacent peatland types followed by the same letter are significantly different based on Tukey's *post hoc* tests ($P \leq 0.05$).

n =	8 (8)	16 (16)	16 (14)	20 (11)
Peatland group	Wooded Bog	Black spruce Swamp	Wooded MRF	Open-wooded MRF
Tree height (m)	7.1 (5.3 - 10.8)^{a}	9.7 (5.7 - 14.7)^{ab}	8.2 (5.3 -12.1)^{c}	5.9 (3.8 - 8.5)^{bc}
Tree dbh (cm)	10.5 (8.5 - 14.9)	12.6 (9.0 - 20.3)^{b}	12.2 (8.1 - 17.1)^{c}	9.0 (7.0 - 12.5)^{bc}
Overstory density (%)	53 (20 - 79)^{a}	68 (55 - 80)^{ab}	61 (41 - 77)^{c}	44 (7 - 61)^{bc}
Trees/ha	2001 (869 - 3150)	2656 (791 - 5427)	2687 (893 - 5108)	2116 (1186 - 3557)

Figure 2.1. Location of Duck Mountain Ecoregion in the Province of Manitoba, Canada.

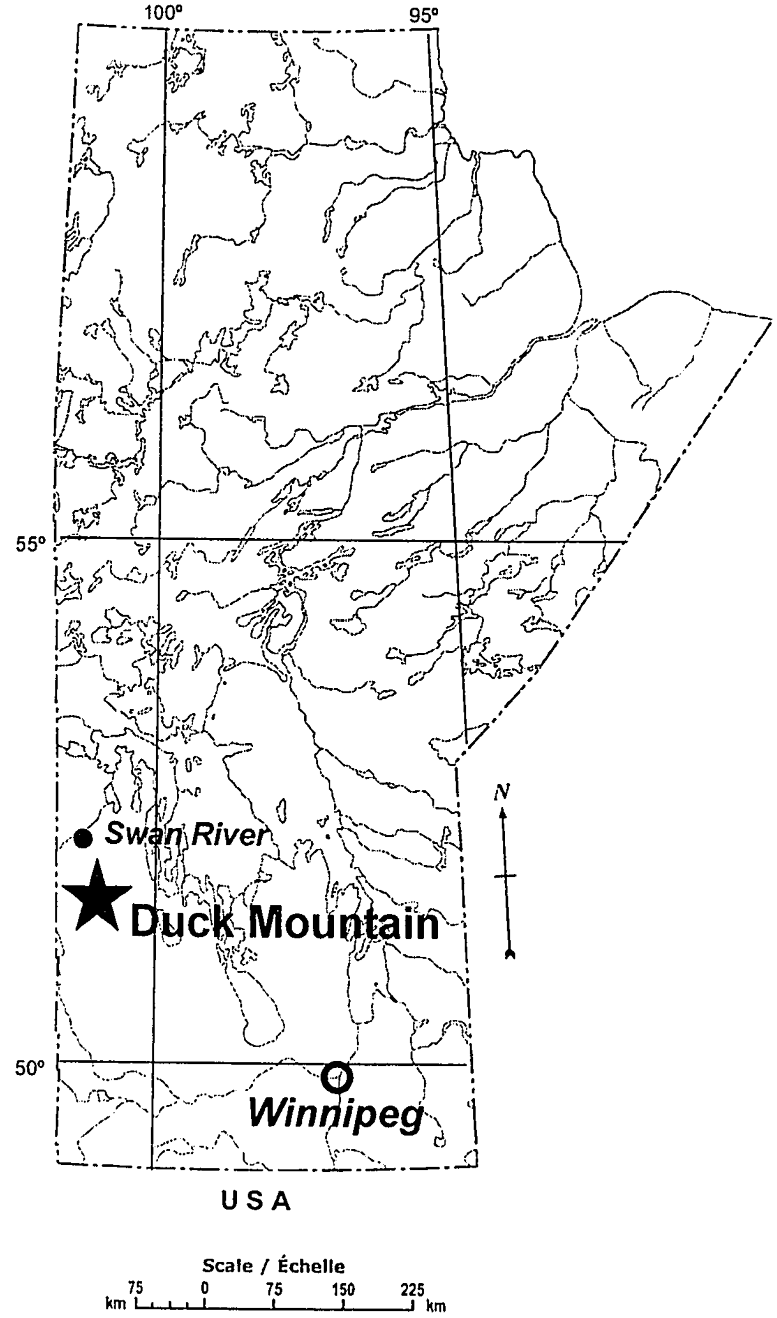


Figure 2.2. Eight peatland types from Duck Mountain, Manitoba derived from cluster analysis. See text for details. MRF refers to moderate-rich fen and ERF refers to extreme-rich fen.

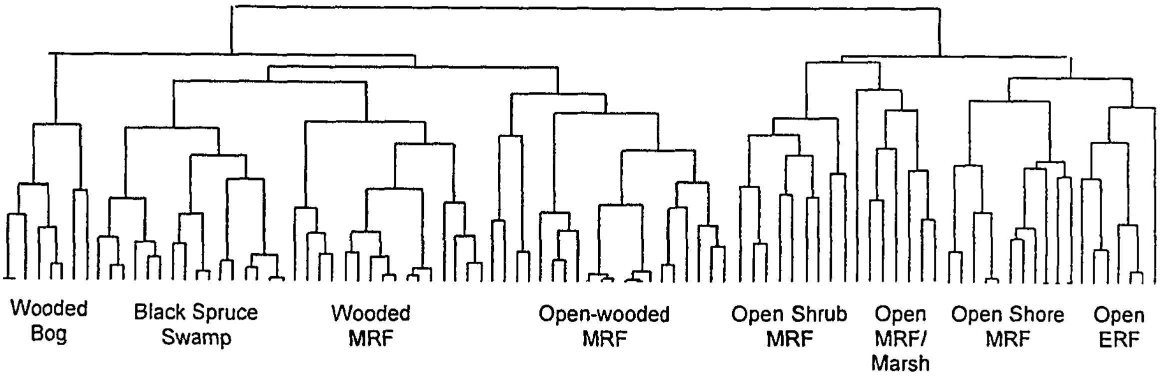


Figure 2.3. Ordination of bryophytes/lichens and vascular plant species in Duck Mountain, Manitoba peatlands. Peatland types were derived from cluster analysis. Inset plot shows environmental variables significantly correlated to the ordination site scores and overlain as vectors. Overstory density represents all forest mensuration variables, Ca^{2+} (calcium) represents magnesium and alkalinity from surface water, and specific conductance is from surface water. MRF denotes moderate-rich fen and ERF denotes extreme-rich fen.

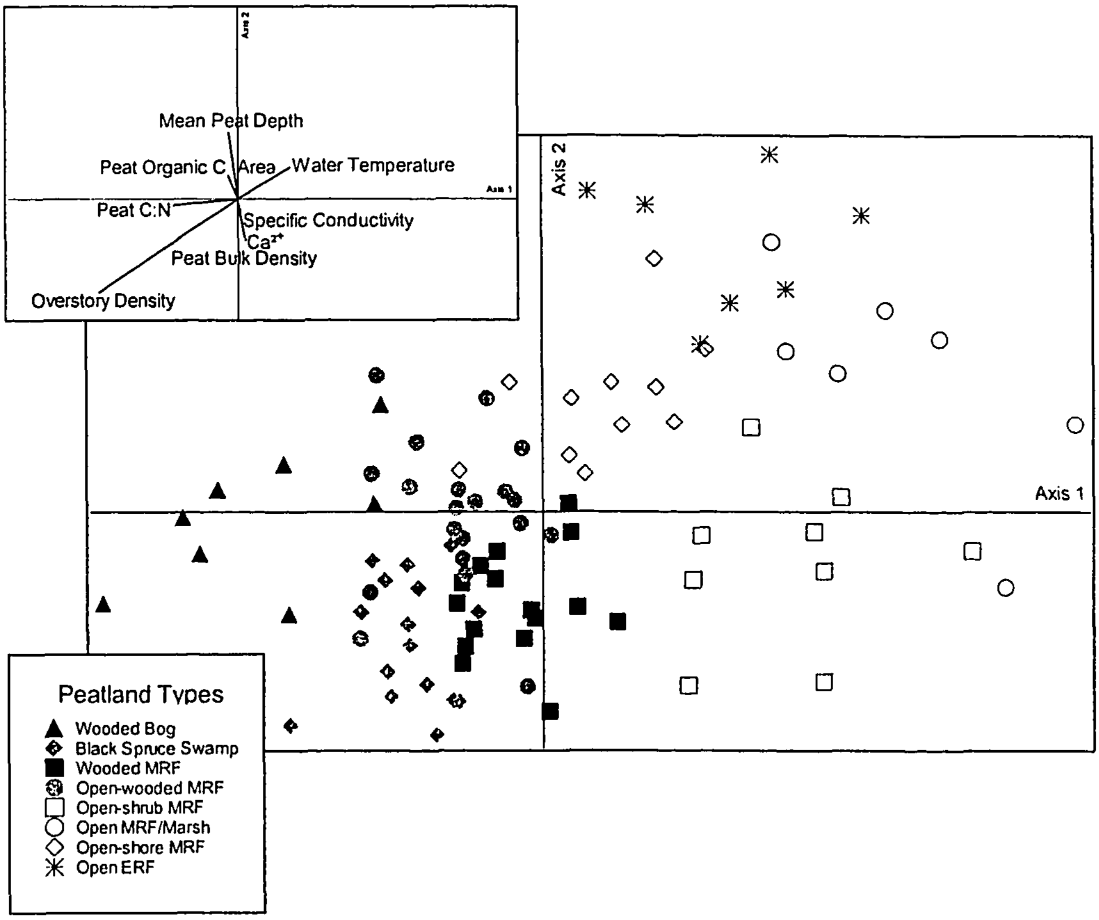
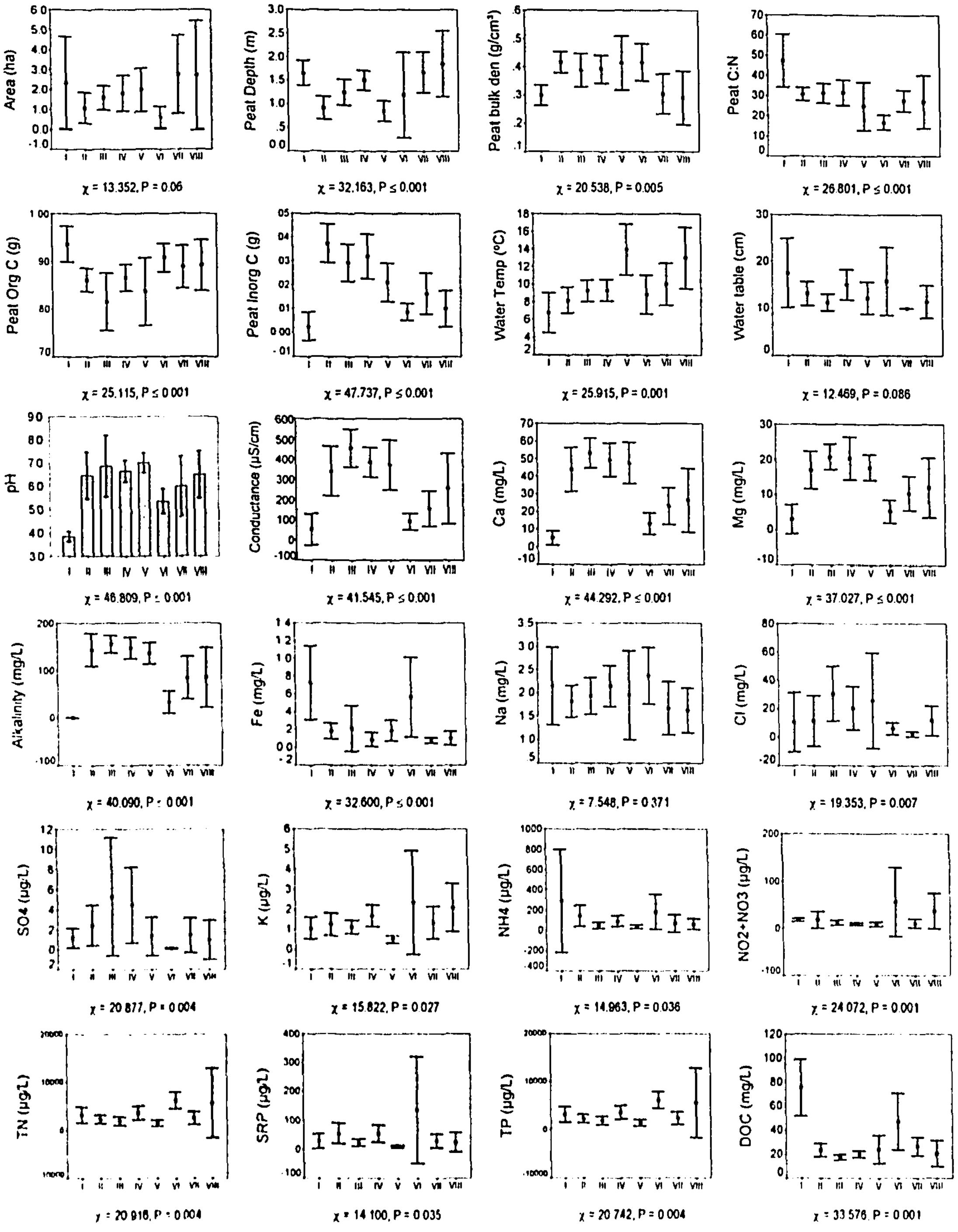


Figure 2.4. Distributions of selected environmental variables from eight peatland types at Duck Mountain, Manitoba with Krukall Wallis H test statistics, and 95% confidence interval error bars that show approximate significant differences among groups (see text). I = wooded bog, II = black spruce swamp, III = wooded moderate-rich fen, IV = open-wooded moderate-rich fen, V = open shrub moderate-rich fen, VI = open moderate-rich fen/marsh, VII = open shore moderate-rich fen, and VIII = open extreme-rich fen.



3 PLANT DIVERSITY, COMPOSITION, AND RARITY IN THE SOUTHERN BOREAL PEATLANDS OF MANITOBA, CANADA

3.1 INTRODUCTION

Diversity and rarity are important components in determining the value of natural habitats (Magurran 2004). While there are numerous uncommon or diminishing habitats that require attention from the perspective of biodiversity conservation, habitats that are more common also require consideration. These include peatlands (Crins 1997), wetlands with at least 40 cm of peat. Peatlands are the dominant wetland type in Canada and can be divided into bogs, fens, and swamps. Whereas bogs receive water and nutrients principally from atmospheric deposition, fens receive water and nutrients primarily from subsurface and surface sources. Both peatland types can be dominated by coniferous trees, coniferous and deciduous shrubs, or graminoid vegetation (National Wetlands Working Group 1997). In North America, peatland swamps are densely forested with conifers and often located on slopes in the transition between uplands and peatlands or water bodies (National Wetlands Working Group 1997, Locky et al. In press).

While peatlands have been considered specific habitat types by some, environmental conditions within are often heterogeneous and the botanical diversity high (Wheeler 1993). Fens have been found to be among the most floristically diverse wetlands, containing uncommon and rare bryophytes and vascular plants (Wheeler 1993, Bedford and Godwin 2003). However, diversity and rarity is variable by specific fen types and there is little consensus on which types have the greatest diversity. For example, in the western boreal region, bryophyte diversity was found to be highest in moderate-rich fens (Vitt and Chee 1990), extreme-rich fens (Vitt et al. 1995), and wooded moderate-rich fens (Vitt et al. 2003), whereas rare bryophyte diversity was found to be greatest in wooded moderate-rich fens, 'swamp' (Vitt et al. 2003), and extreme-rich fens (Vitt et al. 1995). Less is known of vascular plant diversity in boreal peatlands (Jeglum 1972), particularly in black spruce swamps. In addition, while vascular plant rarity has been described in New York rich fens (Johnson and Leopold 1994), little is known of rare vascular plants in western boreal peatlands in Canada.

Species composition is also an important aspect of biodiversity (Debinsky and Humphrey 1997). Functional aspects of plant biodiversity, i.e., species composition, can be examined by determining the relative occurrences of plant taxa or life forms. This is effectively an inference of abundance, and can often reveal aspects of the environmental conditions of the habitat. For example, in boreal Canada, chamaephytes, short or prostrate plants, are often associated with habitats most exposed to extreme environmental conditions and geophytes, plants with renewal buds beneath the ground, are associated with thick, 'nutrient-rich' (i.e., mineral-rich), organic soils (Charest et al 2000). Bryophyte taxa have been examined among peatland types (Vitt et al. 1995), compared with vascular plants as a group in bogs (Bielman 2001), and vascular plant life forms have been used to differentiate different boreal habitats, including bogs from fens, in Newfoundland (Charest et al. 2000). However, no comparisons have been made of bryophyte taxa and vascular plant life forms among a suite of peatland types.

The factors controlling species richness in vegetation communities are complex (Keddy and Fraser 1999). In peatlands, bryophyte richness has been associated with the pH – alkalinity gradient and shade (Vitt et al. 1990, Anderson et al. 1995), and vascular plant richness has been related to pH, alkalinity, base cations, proximity to mineral substrate, percent overstory for the lower strata (Anderson and Davis 1997), and nutrients (Vitt et al. 1990). The diversity of plants in peatlands has been correlated to the richness of rare vascular plants (Wheeler 1988, Moore et al. 1989, Johnson and Leopold 1994) and rare bryophytes (Vitt et al. 2003). However, not all species rich sites have a high diversity of rare plants (Johnson and Leopold 1994, Vitt et al. 2003).

Understanding plant biodiversity in boreal peatlands is important, particularly in the southern Boreal Plains Ecozone where industrial development is intense (Lee et al. 2003), and where peatlands are considered to be highly sensitive to disturbance due to climate change (Kettles and Tarnocai 1999). I compared bryophyte and vascular plant species richness, percent occurrences, and rarity among wooded bogs, black spruce swamps, wooded moderate-rich fens, open moderate-rich fens, and open extreme-rich fens at Duck Mountain, Manitoba, Canada to answer the following questions: (1) How does the diversity and occurrences of bryophyte taxa and vascular plant life forms compare among peatland types?, (2) How does rare bryophyte and vascular plant richness differ among peatland types?, and (3) Are plant species richness and rarity associated with each other, and is richness related to environmental variables?

Study region

The Duck Mountain Ecodistrict in Manitoba is one of a series of highlands that rises above the prairie across Manitoba and Saskatchewan on Canada's Boreal Plains Ecozone (Ecological Stratification Working Group 1995). The region is approximately 70 km from north to south and 60 km from east to west (51° 15' – 52° 00' N, 100° 35' – 102° 35' E) (Figure 3.1). Glacially deposited clay, gravel, sand, and boulders cover the erosion-resistant Riding Mountain shale to produce a hummocky landscape (Klassen 1979). Lakes, rivers, and wetlands intersperse the region and the vegetation is typical of the boreal mixed-wood region (Ecological Stratification Working Group 1995). The dominant conifers are *Picea mariana* (Mill.) BSP, *Picea glauca* (Moench) Voss, *Pinus banksiana* Lamb., and *Larix laricina* (Du Roi) K. Koch, and the dominant deciduous trees are *Populus balsamifera* L., *Populus tremuloides* Michx., and *Betula papyrifera* Marsh.

Duck Mountain lies in the South Mid-boreal Wetland Region of Manitoba and approximately 22% of the area is covered by wetlands that are mostly peatlands (Halsey et al. 1997). These peatlands are at the southern limit of peatland distribution for the boreal forest (Ecological Stratification Working Group 1995).

The climate on the Boreal Plains Ecozone is humid continental, with a mean annual precipitation of 430 mm, ranging from 250 to 660 mm (Klassen 1979). The orographic effect of land masses in western Canada has been known to increase precipitation by over 100 mm per year in localized areas (Hogg 1994). Using calculations based on Hogg (1994), I estimated that Duck Mountain (810 m amsl) receives 668.6 mm of precipitation per year, 37% more precipitation than at adjacent Swan River, which is approximately 379 m lower in elevation.

3.2 MATERIALS AND METHODS

Peatland sites

For this study, the eight peatland types classified using cluster analysis, ordination, and environmental variables from 94 sites at Duck Mountain, Manitoba (Locky et al. In press, Appendix A) were collapsed into five peatland types as follows: wooded bogs, black spruce swamps, wooded moderate-rich fens, open moderate-rich fens, and open extreme-rich fens. Descriptive statistics from the environmental variables were calculated based on the five peatland types (Table 3.1). Details of the classification methodology, environmental sampling protocols, and associated statistical analyses can be found in Locky et al. (In press).

Wooded bogs are comprised of varying densities of *Picea mariana* overstory and an understory dominated by bryophytes, especially *Sphagnum* and feather mosses. Black spruce swamps are densely forested with *Picea mariana* (Table 3.1), and are often found on gentle grades above other peatland types and/or adjacent to water courses or lakes. Wooded moderate-rich fens are comprised of sites with open and closed canopies of *Picea mariana* and *Larix laricina*, with diverse understories of bryophytes and vascular plants. Open moderate-rich fens are associated with the edges of lakes or streams and vary from shrubby to herb-dominated. Open extreme-rich fens are mostly isolated from adjacent open waters, and with few shrubs or trees, instead dominated by *Carex* spp. and brown mosses. Most open extreme-rich fen sites also have *Scorpidium scorpioides* (Hedw.) Limpr. and marl deposits suggesting highly alkaline conditions.

Duck Mountain peatlands are generally small, averaging 1.8 ha in size and ranging 0.1 to 8.9 ha (Table 3.1). Of the three wooded peatland types, black spruce swamps have the highest mean tree height (mean = 9.7 m, range = 5.7 – 14.7 m) (χ = 13.219, df = 2, ≤ 0.001) and overstory density (67.6%, 54.9 – 80.1%) (χ = 12.524, df = 2, P = 0.002). Of all the peatland types, black spruce swamps have the lowest mean peat depth (0.9 m, 0.4 – 2.0 m) (χ = 18.161, df = 2, P = 0.001) and wooded bogs have the lowest mean pH (3.8, 3.6 – 4.7) (χ = 29.851, df = 2, ≤ 0.001), specific conductance (51.3 µS/cm^{-1}, 0.0 – 275.4 µS/cm^{-1}) (χ = 29.741, ≤ 0.001), Ca^{2+} (5.0 mg/L, 1.8 – 15.8 mg/L) (χ = 33.473, df = 2, ≤ 0.001) and alkalinity (0.2 mg/L, 0.0 – 1.2 mg/L) (χ = 33.401, df = 2, P ≤ 0.001). Wooded bogs also have the lowest mean surface water temperature (6.8 °C, 3.0

– 11.6 °C) ($\chi = 19.297$, df = 2, $P \leq 0.001$). There is much overlap of environmental variables among the fens and black spruce swamps.

Plant diversity surveys

Each peatland site was methodically surveyed for bryophytes and vascular plants over a three-hour time period, which was found to be an adequate period in which no new species were found. A time-bounded floristic habitat sampling method was used to capture a high number of plant species over a large number of sites based on Newmaster (2000) (Newmaster et al. 2005). I assigned a 1 to 4 occurrence scale to species adapted from Vitt et al. (1995): (1) Rare – present less than five times (≤1%); (2) Few – found a few times (~2-10% cover); (3) Common – found regularly but did not dominate the community (~11-74% cover); and (4) Abundant – dominated the community (~75-100% cover). Due to logistical constraints, collection of corticolous bryophytes was incomplete and most species were not included in the analyses. Surveys were completed from June 15 to September 15, 2000. Scientific names for vascular plants follow the Plant Element List from the Alberta Natural Heritage Information Centre (2002) where possible and Scoggan (1978-1979) for others. True mosses follow Anderson et al. (1990), *Sphagnum* follows Anderson (1990), and hepatics follow Stotler and Crandall-Stotler (1977).

Data analysis

Plant diversity

In this paper, diversity refers to species richness. "Second order" jackknife estimates of total diversity were calculated for total, bryophyte, and vascular plant diversity using PC-ORD v. 4.25 (McCune and Mefford 1999). Gamma, alpha, and beta diversities were determined for each of the five peatland types following the concepts of Whittaker (1972, 1977). Gamma diversity is the total species richness calculated over all peatland sites at Duck Mountain (landscape diversity) and alpha diversity is the total number of species observed in each peatland type (richness). Mean alpha diversity is the average number of species per site by peatland type and mean gamma diversity is the average number of species per site at Duck Mountain. Beta diversity is a measure of among-site variability in species composition, independent of site position on spatial or environmental gradients. It is useful as an index of unstructured heterogeneity in species composition, and is appropriate when underlying gradients are unknown (Vellend 2001). Beta diversity was calculated following Whittaker's (1972) adjusted beta diversity to compensate for unequal sample sizes as $b = S_t/S_m$, where S_t = total species among samples at N_{min} (minimum sample size among types) and S_m = alpha diversity of each type. The species area curve function in PC-ORD v. 4.25 (McCune and Mefford 1999) was used to determine the number of species at (S_t) at N_{min}, which is also the adjusted alpha diversity per peatland type.

Species richness data was assessed for normality and homogeneity of variances before a one-way analysis of variance (ANOVA) was used to determine differences in mean bryophyte and vascular plant alpha diversity among peatland types. Tukey HSD post hoc tests were used to reveal group differences. All univariate analyses were completed using SPSS v. 11.5 (SPSS Inc. 2003).

The number of sites surveyed per peatland type ranged from seven to 36, and Cole's curves for rarefaction estimates of mean species richness were used to standardize and compare the different data sets (Gotelli and Colewell 2001). These analyses were completed using total, bryophyte, and vascular plant species data sets for all peatland types at the lowest sample size, i.e., n = 7, using EstimateS v. 6.0 (Colewell 2001). I also discuss total richness at the full sample sizes and support these numbers with comparative floristics. Comparative floristics is the inference of richness based on comparisons with other similar areas (Palmer 1995) and is used to avoid loss of information inherent in rarefaction (Melo et al. 2003).

Species composition

Abundance estimates may be difficult to obtain when species richness is high (i.e., approximately 100 species). Species abundance can be inferred by using presence-absence data to determine frequency of occurrences in a large number of sites (Debinsky and Humphrey 1997, Charest et al. 2000). Following this reasoning, the relative frequency of life forms or taxa in sampling areas can be calculated by division of observed species occurrences in sampling stations by the total number of sampling stations (see Charest et al. 2000), in this case, by peatland type. Patterns of diversity can be modelled using species richness of ecologically-defined species groups (Cox and Larson 1993, Bruun et al. 2003). Comparison of diversity patterns by ecologically-defined groups is particularly useful when comparing bryophytes and vascular plants (Lee and La Roi 1979, Cox and Larson 1993). Therefore, I examined plant functional diversity (abundances) using species occurrences of bryophyte taxa and vascular plant life forms. Bryophyte taxa included true mosses (excludes *Sphagnum*), *Sphagnum*, and hepatics. Vascular plant life forms are a useful first-approximation for functional-type subdivisions despite being considered a crude division of plant functional types (Lavorel et al. 1997). Life forms were derived from Scoggan (1978-1979) following Raunkiaer's (1934) classification of the position and seasonality of the perennating buds or rejuvenating organs as follows:

Phanerophytes: trees and tall shrubs > 2 m
Nanophanerophytes: shrubs < 2 m
Chamaephytes: short or prostrate plants; buds not above 25 cm from soil surface
Hemicryptophytes: renewal buds at soil surface
Geophytes: renewal buds underground (rhizomes, tubers, corms, bulbs)
Helophytes: plants submersed in mud
Hydrophytes: plants submersed or floating
Therophytes (annuals): renewal buds protected by seed

Chara spp., aquatic macroscopic green algae, were occasionally found in Duck Mountain peatlands and were grouped with the hydrophyte vascular plant life form for convenience.

Bog – rich fen gradient

For comparisons of plant diversity, occurrences, and rarity, the peatland types found at Duck Mountain were arranged along a modified bog – rich fen gradient based on the concepts of Du Rietz (1949), Sjörs (1952), and Vitt et al. (1995) as follows: wooded bogs, black spruce swamps, wooded moderate-rich fens, open moderate-rich fens, and open extreme-rich fens. Du Rietz (1949) observed that Scandinavian fens could be grouped based on floristic species composition and vegetation structure. Fens with a large number or high cover of plant species with high fidelity to particular site conditions, i.e., rich in fen indicator species, were termed "rich" fens, and those with few fen indicator species were termed "poor" fens. Richness in fen indicator species is not analogous to total species richness or chemical conditions (Vitt et al. 1995). Sjörs (1952) recognized that peatlands rich in fen indicator species had comparatively higher surface water pH and specific conductance compared to peatlands poor in fen indicator species; division into moderate-rich and extreme-rich could be based on these indicators. In contrast, bogs have no fen indicator species or species exclusive to bog conditions. Typical rich fen indicator species include calciphiles such as *Scorpidium scorpioides, Tomenthypnum nitens* (Hedw.) Loeske, *Triglochin maritimum,* and *Tofieldia glutinosa* (Michx.) Pers. Although the division of fens into rich and poor (e.g., Du Rietz 1949, Sjörs 1952) is widely accepted today, clear distinctions among fen types cannot always be reliably made based on surface water chemistry (Sjörs and Gunnarsson 2002). This overlap is evident in Duck Mountain peatlands where only wooded bog separates distinctly from the other peatland types (Locky et al In press). While no poor fens were found in the surveys, some open moderate-rich sites had atypically low pH values due to processes related to seasonally lowered water tables (Locky et al. In press) (Table 3.1). For these reasons, the arrangement of the five peatland types, wooded bog, black spruce swamp, wooded moderate-rich fen, open moderate-rich fen, and open extreme-rich fen, along a peatland gradient is based primarily on number and cover of fen indicator species, not surface water chemistry. Additionally, black spruce swamps were not included in the original fen indicator species-water chemistry gradient (Sjörs 1952). Because black spruce swamps are sometimes found in association with wooded bogs (National Wetlands Working Group 1997, Locky et al. In press), but are similar floristically to wooded moderate-rich fens (Locky et al. In press), they were placed between wooded bog and wooded moderate-rich fen in the modified bog – rich fen gradient developed in the present study.

Community similarity

Sørensen's coefficient of community similarity was calculated for paired peatland types to determine shared species amongst the peatland types. This measure is the most robust of the qualitative (presence-absence) diversity measures (Magurran 2004). Separate analyses were performed on bryophyte taxa and vascular plant life forms.

Plant rarity

Rare species occurrences were determined by plant taxa and life forms for all five peatland types. Since there are no provincial rarity rankings for bryophytes in Manitoba, species were defined as locally rare based on one to two occurrences following Vitt and Belland (1997) and Vitt et al. (2003). For comparison with bryophytes, locally rare occurrences of vascular plants were determined using the same criteria. Locally rare plants were further separated into upland, mineral wetland, and peatland species, and their distributional importance within the Duck Mountain Ecodistrict determined. In addition, vascular plants were defined as provincially rare based on Manitoba S rankings: S1 (very rare) for plants with 1 to 5 occurrences; S2 (rare) for plants with 6 to 20 occurrences; S3 (uncommon) for plants with 21 to 100 occurrences; S4 (widespread/abundant) for plants with > 100 occurrences, and; S5 for plants with secure abundance and distribution within the province (Manitoba Conservation 2003). S1 to S3 plants were considered rare in the analyses.

Associations

Spearman's rank correlations were used to reveal associations between bryophyte and vascular plant species richness and environmental variables. The relationship was investigated for all sites and by peatland types. Because of multicollinearity among the forest mensuration variables and among some surface water variables, overstory density was used to represent all other mensurative variables and specific conductance was used to represent cations in the surface water.

Linear regressions were used to model bryophyte richness by vascular plant richness, and conducted on bryophyte taxa and vascular plant life forms by peatland type to determine if species richness was a function of area (log transformed for normality). This was verified by using sequence bar graphs of species richness and area (smallest to largest) for bryophytes and vascular plants, and when appropriate, taxa and life forms, by all peatlands and peatland type (data not shown).

3.3 RESULTS

Plant diversity

Gamma and alpha diversity

Gamma diversity in Duck Mountain peatlands was 299 plant species, comprised of 87 bryophytes and 212 vascular plants (Table 3.2) (See species list in Appendix B). Wooded moderate-rich fens had the highest alpha diversity for bryophytes (78) and vascular plants (164). Wooded bogs had the fewest vascular plants (54), whereas open extreme-rich fens had the fewest bryophytes (26). At the site level, bryophyte diversity was roughly similar among peatland types, but wooded moderate-rich fens and black spruce swamps had much higher vascular plant diversity (data not shown).

Second order jackknife estimates of alpha diversity indicated that species richness was well captured for bryophytes (93), and relatively well captured for vascular (256) and total plant species (349). Calculation of Coles 'rarefaction' curves for each peatland type (to control for uneven sampling effort) indicated that no undersampling of plants occurred in any peatland type except for bryophytes in open moderate-rich fens at the level of n = 8 (wooded bog) and n = 16 (black spruce swamp). Overall, sites within peatland types were homogenous based on the location of the species accumulation curve at or above the Cole's 'rarefaction' curve (Colewell 2001) (data not shown).

Of the gamma diversity observed at Duck Mountain, wooded moderate-rich fens captured the greatest percent of total (81%), bryophyte (90%), and vascular plant diversity (77%). Wooded bogs and open extreme-rich fens comprised the lowest total diversity (32%, 30%), with the former containing more bryophytes (47% compared with 30%), and the latter with more vascular plants (37% compared with 26%). The percent of total gamma diversity in open moderate-rich fens was much lower than wooded moderate-rich fens for bryophytes (54%) and total diversity (73%), but similar for vascular plants (75%).

Mean alpha diversity

There were significant differences in mean alpha diversity among peatland types for total species ($F = 18.619$, df = 4, 89, $P \leq 0.001$), bryophytes ($F = 19.101$, df = 4, 89, $P \leq 0.001$), and vascular plants ($F = 13.730$, df = 4, 89, $P \leq 0.001$) (Table 3.2). Wooded moderate-rich fens had significantly higher mean alpha diversity than all other peatland types, except black spruce swamps, for total species (mean = 59.0) and bryophytes (22.2), and significantly higher mean vascular plant alpha diversity (36.8) than wooded bog and extreme-rich fen sites. Open extreme-rich fen sites had the lowest mean alpha diversity of bryophytes (10.4) and wooded bogs had the lowest mean alpha diversity of vascular plants (16.4) (Figure 3.2). Examination of mean alpha (and gamma) diversity along the wooded bog – rich fen gradient revealed unimodal distributions for bryophytes and vascular plants (Figure 3.2). The pattern is attributed primarily to changes in richness of true mosses, phanerophytes (trees and tall shrubs > 2 m), nanophanerophytes (shrubs < 2 m), hemicryptophytes (renewal buds at soil surface), and geophytes (renewal bud underground) (Table 3.3).

Beta diversity

Adjusted beta diversity, the variation in plant composition among sites adjusted for *n*, was greater for vascular plants than bryophytes for each peatland type (Table 3.2). Bryophyte compositional change was most pronounced in wooded bogs and open fens, whereas vascular plant compositional change was greatest in wooded bogs and open moderate-rich fens. Variation in bryophyte and vascular plant composition was lowest in black spruce swamps.

Species composition

By number of occurrences (abundance), true mosses and hemicryptophytes were observed more times than any taxa or life form over all peatlands (Table 3.3). Along the wooded bog – rich fen gradient, percent occurrences of true mosses increased and *Sphagnum* occurrences decreased (Figure 3.3). Hepatic occurrences were similar among the wooded peatland types and between the open peatland types. Percent occurrences of phanerophytes and nanophanerophytes decreased along the wooded bog – open extreme-rich fen gradient, and chamaephytes (short or prostrate plants) were most prevalent in wooded bogs and least prevalent in the open fen types. Geophytes and hemicryptophytes had relatively similar occurrences in all peatland types (~63%), except wooded bogs, where occurrences were lowest (45%). Most of the helophyte (submersed in mud) and hydrophyte (floating or submerged) occurrences were observed in open extreme-rich fens, particularly the helophyte *Typha latifolia* L., and the hydrophyte *Utricularia intermedia* Hayne. However, species diversity was highest in open moderate-rich fens, and comprised primarily of helophytes such as *Lysimachia thrysifolia* L., *Polygonum amphibium* var. *emersum* Michx., and *Typha latifolia* L., and hydrophytes such as *Utricularia intermedia.*

Community similarity

The Sørensen coefficients of similarity indicated that the bryophyte assemblage was more similar between peatland types than the vascular plant assemblage. Wooded moderate-rich fens were most similar to black spruce swamps and open moderate-rich fens in terms of bryophytes (0.78, 0.78), and vascular plants (0.71, 0.75). Wooded bogs were most similar to black spruce swamps and wooded moderate-rich fens in terms of bryophytes (0.69, 0.67). The bryophyte assemblage was least similar between open extreme-rich fens and wooded moderate-rich fens (0.48) and wooded bogs (0.51). The vascular plant assemblage was least similar between wooded bogs and open moderate-rich fens (0.41), open extreme-rich fens (0.42) and wooded moderate-rich fens (0.46), and between open extreme-rich fens and black spruce swamps (0.36), wooded moderate-rich fens (0.46), and open moderate-rich fens (0.54).

Plant rarity

Twenty-four bryophyte species (28% of total bryophyte species) were observed one to two times and are considered locally rare species (Table 3.4). Thirteen species were true mosses (54% of rare bryophyte species), seven were hepatics (29%), and four were *Sphagnum* (16%). Forty percent of the rare true mosses are from the family Amblystegiaceae. Of these rare bryophytes, *Dicranum acutifolium* (Lindb. & Arnell) C. Jens. *Ex* Weinm., *Oncophorus wahlenbergii* Brid., and *Rhytidiadelphus triquetrus* (Hedw.) Warnst. are commonly found in uplands (Crum and Anderson 1981).

Fifty-three vascular plant species (25% of total vascular plants) were observed one to two times and considered locally rare species in Duck Mountain peatlands (Table 3.4). Most vascular plant species were comprised of hemicryptophytes (40% of locally rare vascular plants) and geophytes (28%), followed by hydrophytes (11%), phanerophytes (9%), nanophanerophytes (6%), helophytes (4%), and therophytes (2%). Of these, 45% are considered common upland plants occasionally found in peatlands. The remaining 55% are wetland/aquatic species comprised of 30% peatland and 15% mineral wetland species, most of which are common in Manitoba. *Chamaedaphne calyculata* (L.) Moench, found once in a wooded bog, and *Sarracenia purpurea* L., found once in a wooded moderate-rich fen, are uncommon at Duck Mountain and would be considered rare species in the region, although not elsewhere (Table 3.4). *Betula neoalaskana* Sarg., found once in an open moderate-rich fen, is near the southern edge of its North American range and is potentially uncommon at Duck Mountain. Additionally, *Tofieldia glutinosa* (Michx.) Pers. was observed adjacent to a marl pool once in a wooded moderate-rich fen and is relatively uncommon at Duck Mountain due to its requirement of alkaline conditions for establishment; it is often found in extreme-rich fens (Vitt and Chee 1990).

The 53 locally rare vascular plants were observed 63 times in total. Of these occurrences, 26 (41%) were found in open moderate-rich fens, followed by 21 (33%) in wooded moderate-rich fens, 8 (13%) in black spruce swamps, 6 (10%) in open extreme-rich fens, and 2 (3%) were observed in wooded bogs.

At the provincial level, four of the 53 (8%) locally rare vascular plants were provincially rare species (S1-S3) (Table 3.4). Three of the four species were orchids, including *Arethusa bulbosa* L. (S2), *Liparis loeselii* L. Rich. (S3), and *Platanthera orbiculata* (Pursh) Lindl. (S3). The fourth species was the sedge, *Carex pauciflora* Lightf. (S3). If species found over two times are included, two more provincially rare species are listed: *Listera borealis* Morong (S2) and *Coralhiza striata* Lindl. (S3). All provincially rare vascular plants are geophytes, except *Liparis loeselii*, which is a hemicryptophyte, and all of these rare plants are found primarily in peatlands or wet upland conditions, except *Corlhiza striata*, which has upland affinities. Although not included in the data, *Malaxis paludosa* (L.) Sw. (S1), a very rare species in Manitoba, was found once in a wooded moderate-rich fen during related work.

By peatland type, three provincially rare vascular plant species each (50%) were found in black spruce swamps and wooded moderate-rich fens, and two species (33%) were observed in open moderate-rich fens (Table 3.4).

Associations

Vascular plant richness predicted bryophyte species richness ($R^2 = 0.138$, F = 14.784, df = 1, 92, $P \leq 0.001$) and moss species richness ($R^2 = 0.232$, df = 1, 92, F = 27.719, $P \leq 0.001$) over all peatland sites, and was correlated to moss species richness in wooded bogs (0.903, $P = 0.002$) and open moderate-rich fens (0.419, $P = 0.030$). Total plant species richness was related to locally rare bryophytes (0.250, $P = 0.015$) and total rare species (locally rare bryophytes, and vascular plants, and provincially rare vascular plants) (0.237, $P = 0.022$). There was also a positive relationship between vascular plant richness and total rare species richness (includes locally rare bryophytes and provincially rare vascular plants) (0.341, $P = 0.001$).

Linear regressions and ranked area sequence graphs demonstrated no relationship between peatland area and species richness, except for a weak, positive relationship between area and bryophyte richness in wooded bogs. There were positive correlations between bryophyte richness and percent overstory density over the combined peatland sites and by specific peatland type, in wooded moderate-rich fens. Vascular plant richness was positively associated with shallower water table depths over all peatland sites and in wooded moderate-rich fens (Table 3.5). Bryophyte and vascular plant richness was positively correlated to surface water pH, specific conductance, and Ca^{2+} over all peatlands, while vascular plant richness and pH were positively correlated in open moderate-rich fens, and bryophyte richness and specific conductance negatively correlated in wooded bogs. While peat depth was associated with vascular plant richness over all peatland sites, a negative association was observed with bryophytes in open moderate-rich fens.

3.4 DISCUSSION

Diversity at Duck Mountain compared with other boreal regions

Bryophyte gamma diversity in Duck Mountain, Manitoba is lower than Alberta boreal peatlands and may be related to the sampling of fewer upland and corticolous species (c.f. Vitt et al. 2003), and/or sampling in a smaller geographic region (c.f. Vitt et al. 1995). However, mean alpha diversity of bryophytes at Duck Mountain peatlands is similar to that found in peatlands in central Alberta (Vitt et al. 2003). Vascular plant gamma diversity is similar to that found in central Saskatchewan peatlands, where alpha diversity was highest in wooded fens, lower in open peatlands, and lowest in bogs (Jeglum 1972).

Duck Mountain wooded bog alpha diversity is similar to that found collectively in non-permafrost and permafrost bogs by Beilman (2001), and mean alpha bryophyte diversity is similar to that in other western continental bogs (Beilman 2001, Vitt et al. 2003). Vascular plant alpha diversity and mean alpha diversity are higher in Duck Mountain bogs than other western boreal bogs (Beilman 2001), and similar to that found in southern boreal continental bogs in eastern North America (Glaser et al. 1990). This may be related to lower latitudes and a larger species pool, as Duck Mountain is at the southeastern edge of the western Boreal Plains Ecozone. A positive correlation was found between site size and bryophyte richness in wooded bogs. However, only eight sites were surveyed and a larger sample size may be needed to verify the significance of this relationship. Glaser et al. (1990) found no relationship between eastern North American raised bog size and vascular species richness and related this to the characteristic microtopography and habitat assemblage that is consistently repeated during bog development.

Alpha diversity in open moderate-rich fens at Duck Mountain was higher than in other western boreal sites for bryophytes (Vitt et al. 2003) and vascular plants (Jeglum 1972), but mean vascular plant diversity in wooded fens was similar to sites in Saskatchewan (Jeglum 1972).

Beta diversity (compositional change) of vascular plants is higher than that of bryophytes in all Duck Mountain peatland types, and is similar to observations by Ingerpuu et al. (2001) in peatlands (and uplands). This contrasts with Beilman (2001), who found beta diversity of bryophytes higher than vascular plants for localized permafrost bogs in the western boreal region; there were no permafrost features in Duck Mountain bogs. Bryophyte species richness has been found to be more variable among fens than bogs (Vitt et al. 1995, Anderson and Davis 1997), and among fens, extreme-rich fens have been found to be the most variable in terms of bryophyte diversity (Vitt et al. 1995). The bryophyte, vascular plant, and combined plant communities were most variable in open moderate-rich fens at Duck Mountain (Table 3.2); these sites were visibly among the most varied, with some sites shrub-dominated, and others sedge-dominated, and most with few bryophytes and bearing similarities to marshes (Locky et al. In press). Bayley and Mewhort (2004) found that open moderate-rich fens in central Alberta varied considerably based on vegetation, and that some marshes had deep deposits of peat.

Diversity and environmental variable relationships

Significant correlations were found between the richness of bryophytes and vascular plants, similar to Glaser et al. (1990) and Ingerpuu et al. (2001) in peatlands. Vitt et al. (2003) found that at the site level bryophyte diversity was no different between fens and bogs. My results were somewhat similar for bryophytes among the peatland types, but vascular plant richness at the site level was much higher in wooded and open fens and black spruce swamps compared to wooded bogs.

Contrary to Vitt et al. (1995), and similar to my results, Vitt and Chee (1990) observed that moderate-rich fens in Alberta had greater species diversity than extreme-rich fens, and attributed this to moderate-rich fens having floristic elements from both extreme-rich and poor fens, in addition to, or because of, higher nutrient status and greater chemical variability. While linear increases in species richness along the minerotrophic peatland gradient (i.e., bogs to rich fens) have been observed for all plants (Schwintzer 1981, Anderson and Davis 1997) and bryophytes (Vitt et al. 1995), unimodal distributions of species richness along a pH/Ca^{2+} gradient have been noted for vascular plants (Glaser et al. 1990, Johnson and Leopold 1994, Chytrý et al. 2003). Bryophyte alpha diversity was not found to be uniform over the bog – rich fen gradient as in Vitt et al. (1995), nor was it uniform for vascular plants. Inconsistencies between studies of species distributions exist for a number of reasons. Sites may be classified based on different criteria (Anderson and Davis 1997), or the selection of wetlands or gradients for comparison may vary among studies. For example, the downward trend of a unimodal distribution may not be observed if the full range of peatlands along a minerotrophic gradient, i.e., extreme-rich fens, is not surveyed (Johnson and Leopold 1994). In addition, the method of measuring the gradient may affect the results.

High species diversity

The unimodal distribution of richness in Duck Mountain peatlands along the bog – rich fen gradient appears related to a number of factors. Wooded and open moderate-rich fens and black spruce swamps have the greatest diversity of Duck Mountain peatland types, and mean alpha diversity, especially of bryophytes, is greatest in wooded moderate-rich fens. Wooded and open fens and black spruce swamps are comparable in that they have similar occurrences of phanerophytes (trees and tall shrubs > 2 m) (although few are tree sized in open moderate-rich fens), nanophanerophytes (shrubs < 2 m), and chamaephytes (short or prostrate plants) (Figure 3.3), and similar moderate levels of pH and alkalinity (Table 3.1). The occurrence of woody species in peatlands has been shown to positively affect species richness (Scwintzer 1981). Trees provide habitats for widespread upland species, and the wet depressions at the tree bases (Vitt et al. 1995, Vitt et al. 2003) and adjacent open lawns create additional habitat diversity for more open peatland species (Vitt et al. 2003). Shrubs (and chamaephytes) are known to be important hummock-forming components in peatlands, and interact with *Sphagnum* in a positive feedback loop, creating more microhabitats (Malmer et al. 1992) and increased species richness (Johnson and Leopold 1994). This can significantly affect species richness in both raised bogs (Glaser 1992) and rich fens (Johnson and Leopold 1994).

Overstory density was positively related to bryophyte richness in Duck Mountain peatlands, particularly in wooded moderate-rich fens, and has been found to be an important determinant of diversity for bryophytes (Schwintzer 1981, Vitt et al 1995, Anderson and Davis 1997, Pharo et al. 1999, Vitt et al. 2003) and vascular plants (Schwintzer 1981, Glaser 1992, Anderson and Davis 1997). Tree canopies potentially influence lower strata by increasing habitat heterogeneity through light quality alteration, wind protection, evapotranspiration augmentation, water table height reduction, and precipitation and aerosols interception, which may change the water chemistry (Anderson and Davis 1997). The close-canopied Duck Mountain black spruce swamps have lower alpha diversity than the more open canopied wooded moderate-rich fens. This suggests that there are critical points where diversity is reduced with increasing overstory density; canopy gaps in wooded rich fens have been associated with higher vascular plant diversity (Anderson and Leopold 2002), and undisturbed spruce swamp forests are less diverse than similar forests characterized by moderate levels of disturbance (Hörnberg et al. 1998).

Low species diversity

The lowest plant diversity in Duck Mountain peatlands was observed in wooded bogs and open extreme-rich fens. Bogs are considered unsaturated by vascular plants (Lindholm 1980) due to the hostile environment caused by low pH, low nutrients (Malmer 1986), low mean water table (Økland 1990), and potential for overgrowth by *Sphagnum* (Backéus 1985). Low pH can create plant toxicity related to elevated levels of Fe^{3+} (Vitousek and Hooper 1993), increasing NH_4^+, and decreasing $N0_2^- + N0_3^-$ (Sharpley 1991), leading to decreased plant diversity in tussock tundra (van der Welle et al. 2003). Conversely, high pH, as observed in extreme-rich fens, can also lead to plant toxicity, with increases in pH reducing vascular plant richness in saline meadows (Rey Benyas and Scheiner 1993, Gough et al. 1994), and is purported to reduce vascular plant richness in rich fens (Chytrý et al. 2003). Vitt et al. (1995) have suggested that "site harshness" (which can include extremes of pH and water table depth), in both poor fens and extreme-rich fens is a factor in determining richness. pH and mineral concentrations differed little between Duck Mountain open extreme-rich and moderate-rich fens, reflecting the variability in these variables observed among rich fens (Malmer 1986, Sjörs and Gunnarsson 2002). However, the presence of marl and fen indicator species with high fidelity to sites with high pH and mineral concentrations in Duck Mountain open extreme-rich fens confirms that highly minerotrophic conditions exist there (Locky et al. In press).

Bryophyte and vascular plant diversity was related to pH over combined sites. However, the association is driven primarily by the relationship in open moderate-rich fens (n = 27), the peatland type with the greatest range in pH. An association between bryophyte richness and pH over many peatland types was found by Vitt et al. (1995), but not by Vitt et al. (2003). The patterns observed between richness and pH in Duck Mountain peatlands was similar for richness and Ca^{2+} and specific conductance. The strong negative correlation between specific conductance and vascular plant richness in Duck Mountain wooded bogs is similar to Glaser (1992).

The negative association between peat depth and vascular plant richness over all peatland sites was concomitant with a decrease in vascular plant richness with increasing depth to water table, especially in wooded moderate-rich fens (Table 3.5). However, peat depth was positively associated with bryophyte richness in open moderate-rich fens, and probably reflects shallower sites with marsh-like elements and low diversity; some of these sites are characterized by few bryophyte species and may be developing into marshes as a result of beaver activity. Open rich fens often have higher mean water table levels, which discourages trees and tall shrubs and may discourage bryophytes. For example, open peatlands and flarks within string fens had the lowest bryophyte diversity in central Alberta peatlands (Vitt et al. 2003). Water table depth has been positively associated with bryophyte richness (Anderson et al. 1997) and vascular plant richness (Johnson and Leopold 1994). At Duck Mountain, helophyte (submerged in mud) and hydrophyte (floating or submerged) occurrences were greatest in open extreme-rich fens, although species richness was greatest in open moderate-rich fens.

Species composition in peatland types

Brown mosses commonly dominate minerotrophic peatlands and *Sphagnum* dominates oligotrophic peatlands (Vitt et al. 1995). Brown mosses, mostly from the Amblystegiaceae family, comprised the greatest number of species occurrences for all plants, and probably reflects the minerogenous water sources at Duck Mountain. Percent occurrences of true mosses increased steadily along the bog – rich fen gradient, but with an almost perfect unimodal richness distribution. Conversely, while *Sphagnum* percent occurrences decrease along the gradient, species richness remains similar among the peatland types until diversity drops markedly in extreme-rich fens. This contrasts with Vitt et al. 1995, who observed similar *Sphagnum* diversity among bogs and moderate-rich and extreme-rich fens. In that study, poor fens had the greatest *Sphagnum* alpha diversity. The number of species of true mosses and hepatics in Duck Mountain wooded bogs were similar to that found in continental bogs and peat plateaus primarily in Alberta by Vitt et al. (1995).

Most of the vascular plant diversity in Duck Mountain peatlands was comprised of hemicryptophytes (renewal buds at soil surface) and geophytes (renewal buds below surface), which is similar to peatlands in Tera Nova National Park, Newfoundland (TNNP) (Charest et al. 2000). In that study, hemicryptophytes were associated with more open, wet habitats; at Duck Mountain, the greatest occurrences were in wooded peatlands. Geophyte occurrences at Duck Mountain were lowest in wooded bogs, similar to that in TNNP peatlands where geophytes were associated more strongly with fens and other 'nutrient' (mineral) -rich sites (Charest et al. 2000). Occurrences of chamaephytes, helophytes, and hydrophytes in Duck Mountain peatlands were also similar to that in TNNP peatlands, but with more occurrences of phanerophytes and almost half a many occurrences of nanophanerophytes (averaged over all peatland types). Whereas many of the nanophanerophytes in TNNP peatlands were evergreen, mostly from family Ericaceae (Charest et al. 2000), most were deciduous shrubs in Duck Mountain peatlands, although *Ledum groenlandicum* was commonly found (Locky et al. In press). As well, nanophanerophytes were most strongly associated with chamaephytes and 'boggy habitats' (Charest et al. 2000) in TNNP, where it would be expected that bogs would be the dominant peatland type (National Wetlands Working Group 1988); fens are the dominant peatland type at Duck Mountain. Chamaephytes, comprised primarily of ericaceous shrubs, occurred two to four times more often in wooded bogs than any other peatland type at Duck Mountain. This is similar to bogs in TNNP, where chamaephytes were associated with dry habitats, in particular hummocks that are exposed to wind, sun drought, and 'nutrient-poor' (i.e., mineral-poor) conditions (Charest et al. 2000). Ericaceous shrubs are well-adapted to extreme environmental conditions, as they are evergreen, sclerophyllous, good translocaters of nutrients before leaf abscission, have high nutrient use efficiency, root-shoot ratio, and tolerance to high manganese, shade and poor nutrients (Bonan 1992). The higher percentage of chamaephyte occurrences in Duck Mountain bogs also reflects the significantly lower vascular plant diversity there, with occurrences of five of only six chamaephyte species. Helophytes are adapted to nutrient-rich, wet habitats, like geophytes (Wetzel 1988), and were found in most open extreme-rich fens. Hydrophytes, particularly the insectivorous *Utricularia intermedia,* were found in all open extreme-rich fens. *Utricularia* spp. are adapted to low levels of nutrients (Wetzel 1988), in addition to rapid decreases in light availability, currents, and water turbidity (Dawson 1988). Compared to other boreal habitats, peatlands are relatively stable, and there were few therophytes (renewed buds protected by seed), species adapted to disturbances, in peatlands at Duck Mountain, and none in TNNP peatlands (Charest et al. 2000). The three therophyte species observed at Duck Mountain all were observed in open moderate-rich fens. Of the peatland types, open fens are most susceptible to disturbance-adapted species in boreal ecosystems (Rose and Hermanutz 2004).

Plant rarity and peatland types

A significant relationship between species-rich wetlands and rare vascular plants was observed, similar to other studies (Wheeler 1988, Moore et al. 1989, Johnson and Leopold 1994). However, no relationship between species-rich wetlands and locally rare bryophytes was observed as in Vitt et al. (2003). Most locally rare bryophytes at Duck Mountain were found in wooded moderate-rich fens, similar to Vitt et al. (2003). Vitt et al. (1995) found more rare bryophytes in extreme-rich fens than moderate-rich fens. However, in that study, wooded and non-wooded categories were not used, and only open extreme-rich fens were encountered at Duck Mountain. While locally rare bryophytes were comprised primarily of true mosses and hepatics at Duck Mountain, hepatics and *Sphagnum* comprised most rare bryophytes in central Alberta peatlands (Vitt et al. 2003).

Until this study, vascular plant rarity had not yet been determined in western continental peatlands in Canada. At Duck Mountain, locally rare vascular plants occurrences were greatest in open and wooded moderate-rich fens and black spruce swamps. Most of these species were common upland species with no conservation concerns found generally in Manitoba (Manitoba Conservation 2003). However, at the Ecodistrict level, others may be of concern because they are generally uncommon at

Duck Mountain because they are at the edge of their range or their preferred habitat is not common. *Chamaedaphne calyculata* was found in a wooded bog, *Sarracenia purpurea* and *Betula neoalaskana* in wooded moderate-rich fens, and *Tofieldia glutinosa* was observed near a marl pool in a wooded moderate-rich fen; wooded bogs (low pH) and extreme-rich fen conditions (with marl pools and high pH) are uncommon habitats at Duck Mountain (Locky et al. In press).

Reasons for rare species occurrences are complex. Rare environments and environmental conditions may lead to rare species (Crins 1997), but habitat heterogeneity is also a contributing factor. Peatlands with woody vegetation are more likely to have greater species richness and more rare bryophytes than open stands due to increased habitat complexity (Vitt et al. 1995, Vitt et al. 2003). However, rare vascular plant diversity has also been associated with canopy gaps in New York forested wetlands (Anderson and Leopold 2002).

3.5 CONCLUSIONS

Duck Mountain peatlands have similar diversity patterns as other western boreal peatlands. Wooded moderate-rich fens, black spruce swamps, and open moderate-rich fens are among the most common wetland types on the southwestern Boreal Plains landscape, but contain the greatest plant diversity and number and occurrences of rare plants. In contrast, wooded bogs and open extreme-rich fens are rare on the landscape, but contain some locally rare and potentially regionally important species. Diversity and rare plant occurrences follow a unimodal distribution over a bog – rich fen gradient. Reasons for this pattern are complex, but high diversity appears to be related to high habitat heterogeneity and moderate environmental variables, such as pH and alkalinity, in wooded moderate-rich fens and black spruce swamps, and low diversity appears related to environmental extremes, e.g., pH and alkalinity, in bogs and extreme-rich fens. Patterns of bryophyte taxa and vascular plant life forms were distinct between bogs and fens, but were characteristically different along the bog – rich fen gradient. High diversity and rarity of plants, and rarity of some peatland types, coupled with the relatively small sizes of Duck Mountain peatlands and potential impacts from logging and climate change, suggests that peatlands are important from a conservation perspective in the western boreal region.

Acknowledgements

I gratefully acknowledge the funding and technical support from the Sustainable Forest Management Network, Edmonton, Alberta. Louisiana-Pacific Canada Ltd., Swan River, Manitoba, especially Margaret Donnelly and Donna Grassia, are thanked for providing technical and in-kind support. Funding was also graciously provided by the Canadian Circumpolar Institute with a C/BAR grant to DAL. Sarah Wilkinson, Markus Thormann, and Joyce Gould provided valuable feedback regarding this manuscript, and Dan Kueffler assisted with field work.

3.6 LITERATURE CITED

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Table 3.1. Means (ranges) for environmental variables of the five peatland types at Duck Mountain, Manitoba.

n =	8 (8)*	16 (16)*	36 (25)*	27	7	94 (49)*
Peatland type	Wooded Bog	Sb Swamp	Wooded MRF	Open MRF	Open ERF	All Peatlands
Tree height (m)	7.1	9.7	7.2	N/A	N/A	8.3
	(5.3 - 10.8)	(5.7 - 14.7)	(3.8 - 12.1)			(3.8 - 14.7)
Tree dbh (cm)	10.5	12.6	10.8	N/A	N/A	11.3
	(8.5 - 14.9)	(9.0 - 20.3)	(7.0 - 17.1)			(7.0 - 20.3)
Overstory density (%)	52.8	67.6	53.2	N/A	N/A	57.8
	(20.2 - 7904)	(54.9 - 80.1)	(6.9 - 76.8)			(6.9 - 80.1)
Trees/ha	2001.0	2656	2436.0	N/A	N/A	2437
	(869 - 3150)	(791 - 5427)	(894 - 5108)			(7917 - 5427)
Area (ha)	2.3	1.1	1.7	1.9	2.7	1.8
	(0.3 - 8.3)	(0.1 - 5.9)	(0.2 - 7.4)	(0.1 - 8.5)	(0.6 - 8.9)	(0.1 - 8.9)
Mean peat depth (m)	1.7	0.9	1.4	1.3	1.9	1.3
	(1.1 - 2.2)	(0.4 - 2.0)	(0.7 - 2.6)	(0.5 - 3.0+)	(0.9 - 3.0+)	(0.4 - 3.0+)
Water Temperature (°C)	6.8	8.2	9.3	11.0	13.0	9.6
	(3.0 - 11.6)	(5.0 - 16.5)	(3.5 - 13.5)	(3.8 - 19.5)	(8.0 - 17.0)	(3.0 19.5)
**Water table (cm)	17.5	13.1	13.3	12.2	11.4	13.2
	(10.0 - 30.0)	(10.0 - 20.0)	(10.0 - 30.0)	(10.0 - 30.0)	(10.0 - 20.0)	(10.0 - 30.0)
pH	3.8	6.5	6.7	5.8	6.5	4.9
	(3.6 -4.7)	(5.6 - 7.9)	(6.0 - 7.9)	(4.7 - 8.2)	(6.2 - 7.5)	(3.6 - 8.2)
pH (median)	3.8	6.7	7.3	6.6	6.6	6.8
Conductivity (μS/cm^{-1})	51.3	339.9	417.9	210.1	255.1	293.6
	(0.0 - 275.4)	(30.6 - 988.5)	(151.3 - 782.0)	(15.1 - 606.0)	(51.4 - 622.5)	(0.0 - 988.5)
Ca^{2+} (mg/L)	5.0	43.9	51.2	28.6	26.5	36.7
	(1.8 - 15.8)	(7.5 - 95.5)	(17.7 - 111.4)	(3.4 - 72.4)	(6.4 - 64.6)	(1.8 - 111.4)
Alkalinity (mg/L)	0.2	143.6	151.4	88.1	84.7	110.9
	(0.0 - 1.2)	(12.2 - 223.7)	(67.6 - 225.2)	(2.5 - 199.7)	(18.6 - 217.5)	(0.0 - 225.2)

* Number of sites surveyed for forest mensuration variables

** Water table values based on three mean measures, 10 cm (0 - 10 cm), 20 cm (11 - 20 cm), and 30 cm (> 21 cm

Sb = Black Spruce, MRF = moderate-rich fen, ERF = extreme-rich fen

Table 3.2. Diversity indices for A) total plant species, B) bryophytes, and C) vascular plants by peatland type at Duck Mountain, Manitoba. Values in the last row (Total) beneath the alpha diversity columns are Gamma diversity.

A. Total plants

						Diversity		
Peatland Type	n =	Max	Min	SD	P≤ 0.05*	Alpha	Mean Alpha	Adj. Beta**
Wooded bog	8	47	16	10.3	a	95	32.3	2.9
Sb Swamp	16	73	38	10.2	a b	157	53.4	2.4
Wooded MRF	36	73	39	8.6	a c	242	59.0	2.6
Open MRF	27	68	25	11.8	a c d	218	47.4	3.0
Open ERF	7	44	25	7.7	b c d	90	34.7	2.7
Total	94	73	16	13.2	.	299	50.6	-

B. Bryophytes

						Diversity		
Peatland Type	n =	Max	Min	SD	P≤ 0.05*	Alpha	Mean Alpha	Adj. Beta**
Wooded bog	8	21	7	4.8	a	41	15.9	2.7
Sb Swamp	16	27	14	3.6	b	55	20.4	2.3
Wooded MRF	36	31	14	4.1	a c	78	22.2	2.4
Open MRF	27	27	1	5.9	b c	56	13.7	2.8
Open ERF	7	14	4	3.5	b c	26	10.4	2.7
Total	94	31	1	6.2		87	18.0	-

C. Vascular plants

						Diversity		
Peatland Type	n =	Max	Min	SD	P≤ 0.05*	Alpha	Mean Alpha	Adj. Beta**
Wooded bog	8	26	9	6.5	a	54	16.4	3.1
Sb Swamp	16	51	22	8.9	a	102	33.0	2.4
Wooded MRF	36	53	23	7.2	a c	164	36.8	2.7
Open MRF	27	51	20	8.3	a	162	33.7	3.1
Open ERF	7	31	17	6.1	c	64	24.3	2.6
Total	94	53	9	9.6		212	32.6	-

* Mean alpha diversity of adjacent peatland types followed by the same letter are significantly different based on Tukey's post hoc tests ($P \leq 0.05$).

** Beta diversity adjusted to n = 7 using species area curves to account for unequal sample sizes

SD: standard deviation; Alpha: mean site diversity;

MRF: moderate-rich fen; Sb: black spruce; ERF: extreme-rich fen

Table 3.3. Species richness and occurrences of plant taxa and life forms in five peatland types at Duck Mountain, Manitoba. MRF = moderate-rich fen, Sb = black spruce, ERF = extreme-rich fen. Occur. refers to occurrences, or the number of times species were observed at each site, i.e., presence-absence, tabulated by bryophyte taxa and vascular plant life forms. Percent of total taxa refers to percent to total bryophyte taxa, or percent of total vascular plant life forms.

n =	8	16	36	27	7	94	% of	% of	No. of	% of
Taxa/Life forms	Wooded Bog	Sb Swamp	Wooded MRF	Open MRF	Open ERF	Total	taxa	ttl taxa	occur.	occur.
Bryophytes	41	55	78	56	26	87	100.0	31.1	1773	100.0
Hepatics	8	7	17	3	1	17	18.9	5.9	89	5.0
True Mosses	25	40	51	43	23	57	63.2	19.7	1361	76.8
Sphagnum	8	8	10	10	2	13	14.7	4.6	265	14.9
Vascular plants	54	102	164	162	64	212	100.0	69.5	3063	100.0
Phanerophytes	7	13	20	18	8	22	10.4	7.2	375	12.2
Nanophanerophytes	8	15	20	18	6	22	10.4	7.2	443	14.5
Chamaephytes	5	6	6	4	2	6	2.8	2.0	245	8.0
Hemicrpytophytes	19	42	71	69	24	87	41.0	28.5	1100	35.9
Geophytes	15	26	41	32	18	54	25.5	17.7	769	25.1
Helophytes	0	0	3	8	4	8	3.8	2.6	80	2.6
Hydrophytes	0	0	2	10	2	10	4.7	3.3	38	1.2
Therophytes	0	0	1	3	0	3	1.4	1.0	13	0.4
Total Plants	95	157	242	218	90	299	100.0	100.0	4836	100.0

Table 3.4. Rare plant species occurrences by plant taxa/life form, family, and peatland type at Duck Mountain, Manitoba. There were 53 locally rare vascular plants observed, but most of these were common species occasionally found in peatlands. I list only locally rare vascular plant species that are provincially significant or appear regionally important. Rarity Criteria: L = locally rare (1-2 occurrences); P = provincially significant (S1 - S3). See text for details.

Rarity		Taxa/Life Form	Family	Species	Occurrences by Peatland Type				
L	P				WBOG	SBSW	WMRF	OMRF	OERF
•		Hepatic	Aneuraceae	*Aneura pinguis* (L.) Dum.			1		
•				*Riccia canaliculata* Hoffm.		1	1		
•			Cephaloziaceae	*Cephalozia bicuspidata* (L.) Dum. subsp. *bicuspidata*			1		
•				*Cephalozia lunulifolia* (Dum.) Dum.			1		
•			Conocephalaceae	*Conocephalum conicum* (L.) Lindb.			1	1	
•			Jungermaniaceae	*Lophozia ventricosa* (Dicks.) Dum. var. *ventricosa*			1	1	
•			Pallaviciniaceae	*Moerckia hibernica* (Hook.) Gott.			2		
•		True Moss	Amblystegiacae	*Calliergon richardsonii* (Mitt.) Kindb. *in* Warnst.		1			
•				*Calliergon trifarium* (Web. & Mohr) Kindb.					1
•				*Campylium hispidulum* (Brid.) Mitt.				1	
•				*Campylium radicale* (P. Beauv.) Grout		1			
•				*Palustriella commutatum* (Brid.) Ochyra			1	1	
•			Brachytheciaceae	*Brachythecium starkei* (Brid.) Schimp. *In* B.S.G.			1		
•			Catoscopiaceae	*Catoscopium nigritum* (Hedw.) Brid.			1	1	
•			Dicranaceae	*Dicranum acutifolium* (Lindb. & H. Arnell) C. Jens. *ex* Weinm.*	1				
•				*Oncophorus wahlenbergii* Brid.*				1	
•			Rhytidiaceae	*Rhytidiadelphus triquetrus* (Hedw.) Warnst.*		1	1		
•			Splachnaceae	*Sphlachnum sphaericum* Hedw.			1		
•				*Splachnum luteum* Hedw. Var. *luteum* var. *melanocaulon* Wahlenb.			2		
•				*Splachnum rubrum* Hedw.			2		
•		*Sphagnum*	Sphagnaceae	*Sphagnum centrale* C. Jens. *in* Arnell & C. Jens.		2			
•				*Sphagnum girgensohnii* Russ.		1	1		
•				*Sphagnum squarrosum* Crome				2	
•				*Sphagnum subsecundum* Nees *in* Sturm var. *subsecundum* var. *andrusii* Crum				1	
•		Phanerophyte	Betulatceae	*Betula neoalaskana* Sarg. (S5)				1	
•		Nanophanerophyte	Ericaceae	*Chamaedaphne calyculata* (L.) Moench (S5)	1				
•		Hemicryptophyte	Sarraceniaceae	*Sarracenia purpurea* L. (S5)			1		
•			Tofieldiaceae	*Tofieldia glutinosa* (Michx.) Pers. (S5)			1		
•	•	Geophyte	Cyperaceae	*Carex pauciflora* Lightf. (S3)				1	
•	•	Hemicryptophyte	Orchidaceae	*Liparis loeselii* L. Rich. (S3)			1		
•	•	Geophyte		*Arethusa bulbosa* L. (S2)				1	
•	•			*Platanthera orbiculata* (Pursh) Lindl. (S3)		1			
	•			*Coralhiza striata* Lindl. (S3)*		2	1		
	•			*Listera borealis* Morong (S2)		1	1		

Table 3.5. Spearman's rank correlations between plant species richness and environmental variables over all peatlands and by peatland type at Duck Mountain, Manitoba, Canada. Significance levels: ** ≤ 0.001, * ≤ 0.01.

Peatland Types	Environmental Variables	Bryophytes	Vascular Plants
All Peatlands (n = 94)	Overstory Density	0.387**	0.051
	Mean Peat Depth	0.043	-0.211*
	Water Table	-0.057	-0.232*
	pH	0.296**	0.371**
	Specific Conductance	0.240**	0.375**
	Ca^{2+}	0.270**	0.399**
Wooded Bog (n = 8)	Area	0.735*	0.398
	Specific Conductance	-0.600	-0.727*
Wooded Moderate-rich Fen (n = 36)	Overstory Density	0.332*	0.066
	Water Table	-0.302	-0.432**
Open Moderate-rich Fen (n = 27)	Peat Depth	0.620**	-0.011
	pH	0.170	0.481*

Figure 3.1. Location of Duck Mountain Ecoregion in the Province of Manitoba, Canada.

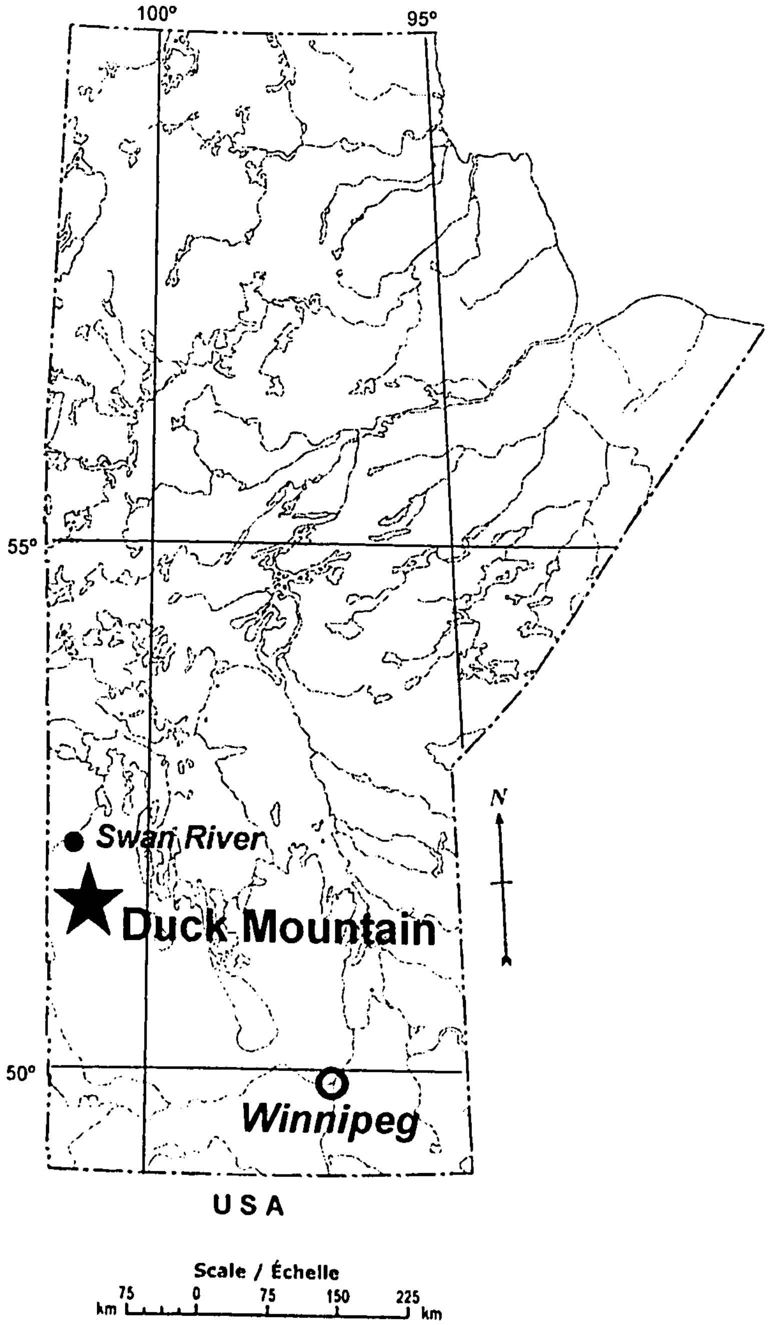


Figure 3.2. Mean species richness and 95% confidence intervals of bryophytes and plants in peatlands at Duck Mountain, Manitoba. W = wooded, Sb – black spruce, MRF = moderate-rich fen, O = open, ERF = extreme-rich fen. Peatland types arranged along a fen indicator species gradient, i.e., bog to extreme-rich fen (see text for details).

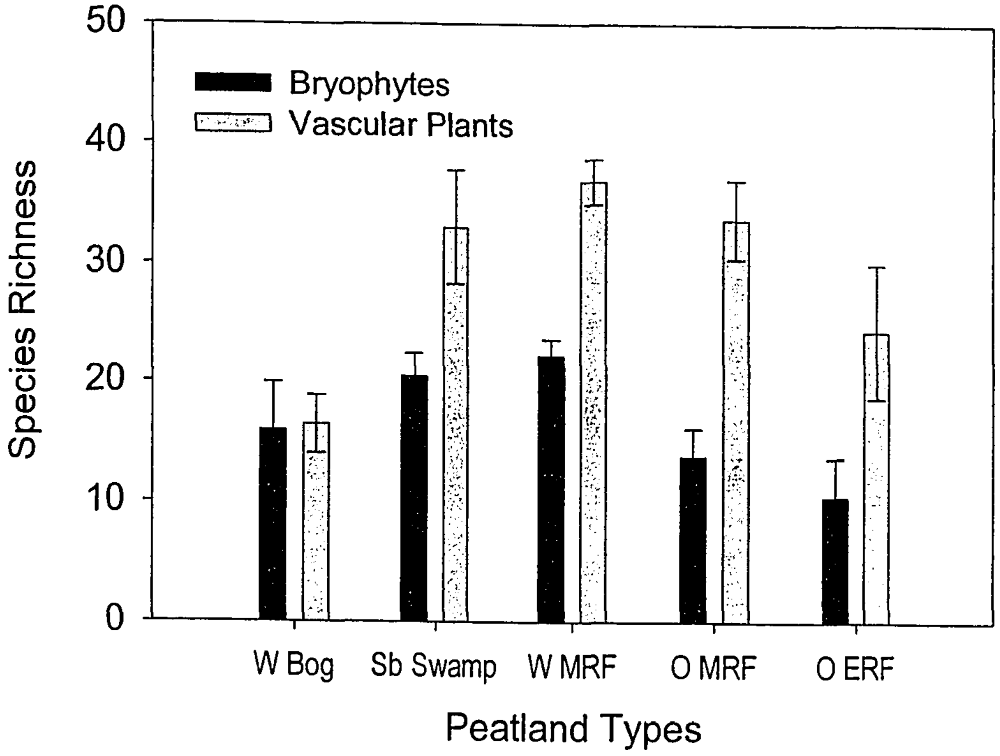
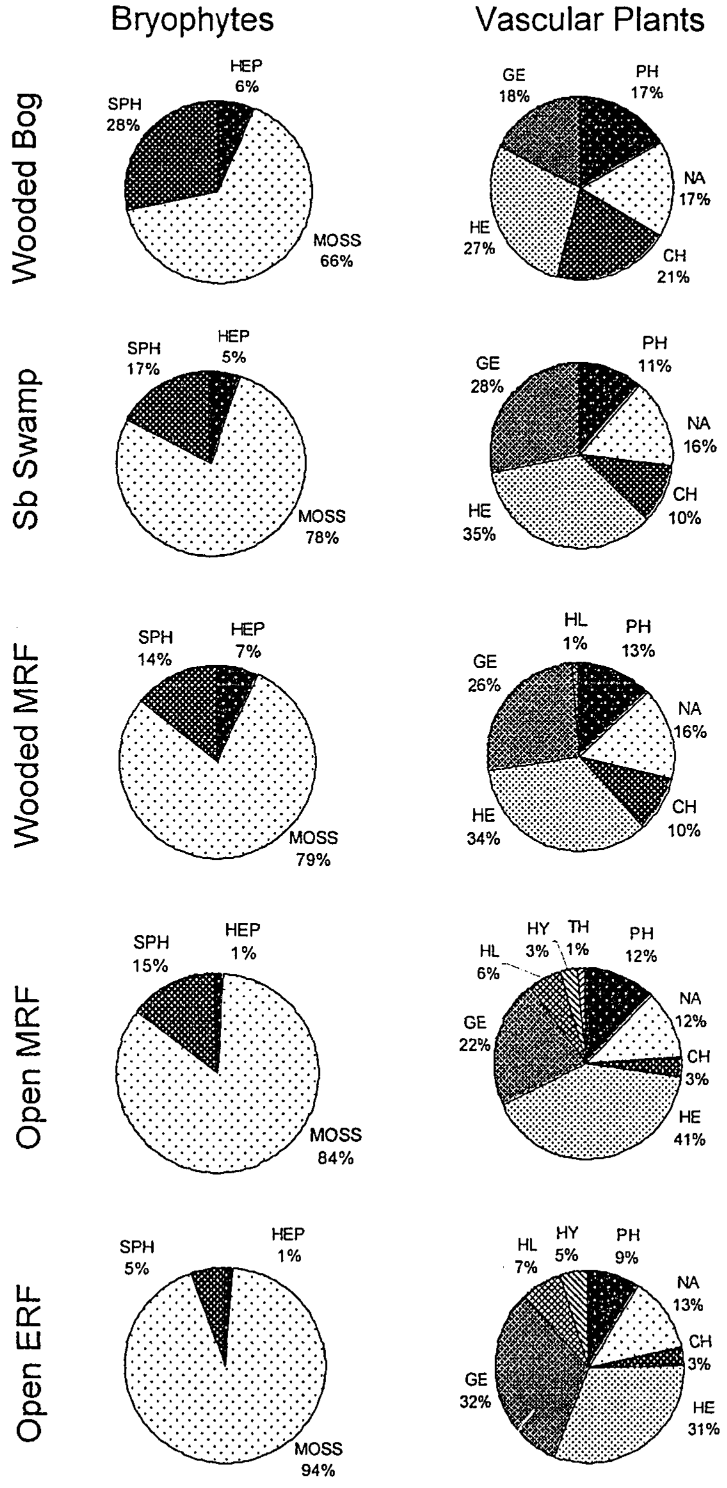


Figure 3.3. Percent occurrences of bryophyte taxa and vascular plant life forms in peatlands. Life forms with less than 1% occurences were removed from the graphs. HEP – Hepatics, SPH – *Sphagnum*, Moss – True Mosses, PH – Phanerophytes, NA – Nanophanerophytes, CH – Chamaephytes, GE – Geophytes, HE – Hemicryptophytes, HY – Hydrophytes, HL – Helophytes, and T – Therophytes.



4. DETERMINANTS OF PLANT DIVERSITY AND COMMUNITY CHANGE IN WESTERN BOREAL WOODED RICH FENS

4.1 INTRODUCTION

Declines in species richness along latitudinal, elevational, and moisture gradients have been commonly observed in continental regions (Begon et al. 1986, Tivy 1993). Species richness has been related to equilibrium effects influenced by gradients of harshness of weather, landscape heterogeneity, area, productivity, biological interactions and historical factors such as habitat age or earlier perturbations (Begon et al. 1986, Tivy 1993). The exact causal agents are difficult to discern because these gradients are often surrogates for other more elemental variables and are commonly interrelated. In particular, plant communities are inherently variable and multiple environmental variables operate simultaneously (Williamson 1981, Glaser 1992). Consequently, testing hypotheses using these variables can be problematic and controversial because of confounding results (Willig et al. 2003, Rahbek 2005). One solution is to select sites with well-defined boundaries and relative uniformity of habitat for measurement (Williamson 1981, Brown and Gibson 1983, Glaser 1992). Islands have traditionally been used for this purpose, but terrestrial ecosystems with consistent physical, chemical, and floristic properties that are discretely bounded are also appropriate, such as raised bogs (Glaser 1992), a type of peatland. Other peatland types can also be described as discretely bounded and relatively consistent in physical, chemical, and floristic attributes (Sjörs 1952, Vitt and Chee 1990, Locky et al. In press).

Peatlands are wetlands with at least 40 cm of peat and are comprised of bogs, fens, and swamps. Bogs receive water and nutrients principally from atmospheric deposition, whereas fens receive water and nutrients primarily from subsurface and surface sources. Both bogs and fens can be dominated by coniferous trees, coniferous and deciduous shrubs, or graminoids (National Wetlands Working Group 1997). Peatland swamps are densely forested with conifers and often found down slope between uplands and other peatlands or water bodies. Groundwater and surface water movement is characteristic of fens and contributes to making this peatland type one of the most variable in terms of water chemistry, floristic composition, and vegetation physiognamy

(National Wetlands Working Group 1997, Locky et al. In press). Fens with a large number of plant species (or a few with high dominance) with high fidelity to particular site conditions, i.e., rich in fen indicator species, are termed "rich" fens (Du Rietz 1949). Richness in fen indicator species is not analogous to total species richness or chemical conditions (Vitt et al. 1995), but peatlands rich in fen indicator species generally have comparatively higher surface water pH, alkalinity, and specific conductance compared to peatlands poor in fen indicator species. Rich fens can be further divided into moderate-rich and extreme-rich fens based on these indicators (Sjörs 1952).

Examination of richness patterns at the regional scale is useful because the source pools of colonizing plants have a greater likelihood of similarity at either end of the sampled region, and the vegetation communities and structure will more likely display homogeneity. This is particularly significant, given that the effects of local and regional scale factors can veil or intensify latitudinal patterns of species richness at a larger scale, e.g., over temperate and tropical gradients (Gotelli and Ellison 2002). Recently, the use of Ecoregions, areas of recurring patterns of interacting biotic and abiotic features (Olson et al. 2001, Bailey 2005) has gained interest as a means of defining biogeographic units suitable for biodiversity conservation (Wikramanayake et al. 2001). Studies or plants species richness and community composition in peatland have not yet been made within an Ecoregion, but been examined over regions of varying size usually through comparison of different peatland types (Vitt and Chee 1990, Anderson et al. 1995, Vitt et al. 1995a, Locky et al. In press). Few studies have examined patterns of plant community composition or diversity within a region using one type of peatland other than bogs (Glaser 1992, Bielman 2001).

Localized permafrost dynamics increase total plant diversity in western continental bogs. In particular, bryophytes respond most strongly to environmental gradients and exhibit greater beta diversity (species turnover) than vascular plants across bog landforms (Beilman 2001). In the eastern North American boreal region, vascular plant richness is most strongly related to mean annual precipitation, annual freezing degree-days, mean annual temperature, the number of wet-to-dry habitats, and some surface water cations in raised bogs (Glaser 1992). The relationship of vascular plant richness and latitude is complex, with decreases in the Maritime region and increases in the continental region. The addition of temperate species explains the pattern in the Maritime region, and higher occurrences of bog pools and mud bottoms in the north accounts for higher diversity in the continental region. Additionally, vascular plant richness decreases with longitude along a coastal to continental transect, and is attributed to climatic factors (Glaser 1992).

The purpose of this study is to examine patterns of plant diversity, community composition, and species rarity in wooded moderate-rich fens in three locations along a longitudinal and a latitudinal transect in the Boreal Plains Ecozone of western Canada. Specifically, are there any differences in alpha and beta diversity and plant rarity among the three locations? Does composition of the bryophyte taxa and vascular plant life forms change across the landscape? Is there any interaction between aspects of the plant community and regional scale variables such as latitude, longitude, elevation, and precipitation, and local scale variables such as surface water chemistry and physical components of the peat?

4.2 MATERIALS AND METHODS

Study region and site selection

The Boreal Plains Ecozone stretches from the Peace River country in British Columbia to the northwest and southeast corners of Manitoba within the Western Boreal Forest (Figure 4.1). The climate is strongly influenced by its continental location, with mean annual temperature between -2° and 1°C, and mean annual precipitation ranging from 300 mm in northern Alberta to 625 mm in southwest Manitoba (Ecological Stratification Working Group 2005).

Wooded moderate-rich fens are a widespread component of peatlands in Canada's western boreal forest, often have the greatest plant diversity and numbers of rare species (Vitt et al. 2003, Chapter 3), and are commonly forested with marketable size trees (Locky et al. In press). Three locations with wooded peatlands were chosen in the Boreal Plains Ecozone: Utikuma Lake, Alberta, Prince Albert National Park area, Saskatchewan, and Duck Mountain, Manitoba (Figure 4.1). These three locations span approximately four and a half degrees of latitude (550 km) and seven degrees of longitude (1000 km) (Table 4.4.1). All three locations are situated within the Mid-Boreal Uplands Ecoregion, while Prince Albert National Park also comprises part of the Boreal Transition Ecoregion. Cretaceous shales underlie the landscape, which is covered by kettled to dissected, deep, loamy to clayey-textured glacial till, lacustrine deposits, and coarse, fluvoglacial deposits (Ecological Stratification Working Group 2005). The vegetation is comprised of mixed-wood forest of medium to tall stands of trembling aspen (*Populus tremuloides* Michx.) and balsam poplar (*Populus balsamifera* L.), and in later successional stages, white and black spruce (*Picea glauca* (Moench) Voss, *P. mariana* (P. Mill.) B.S.P.), and balsam fir (*Abies balsamea* (L.) P. Mill.). Tamarack (*Larix laricina* (Du Roi) K. Koch) is found in peatlands. Precipitation records for 40 years (1963 – 2002) for each of the three study locations were obtained from Natural Resources Canada, Canadian Forestry Service. Mean annual precipitation was determined to be 404.6 mm at Utikuma Lake, Alberta and 449.9 mm at Prince Albert National Park, Saskatchewan (Table 4.1). There are no weather stations at Duck Mountain, so precipitation values were extrapolated from data at nearby Swan River, MB, following Hogg (1994). Swan River is approximately 379 m lower in elevation than the mean elevation of the Duck Mountain sites. I calculated a 26.1 mm increase per year (May – September) per 100 m increase of elevation. This gave a mean estimate of 668.6 mm per year, or approximately 37% more precipitation at Duck Mountain than Swan River.

Growing degree days >5° C per year number 1237 days at Utikuma Lake, 1455 days at Prince Albert National Park, and 1590 days at Swan River, Manitoba, which is adjacent to Duck Mountain. I was unable to estimate growing degree days for the Duck Mountain sites. Additionally, mean annual temperatures could not be adjusted for elevational differences at Duck Mountain, so quantitative comparisons were not made. However, mean annual temperature values do not appear different among the three regions.

The criteria for choosing individual wooded rich fen stands in these locations included sites with trees ≥ 5 cm diameter at breast height (dbh) within 7.5 m radius from a quadrat centre (following Locky et al. In press), presence of rich fen indicator species such as *Tomenthypnum nitens* (Hedw.) Loeske, presence of *Larix laricina* (Du Roi) K. Koch, and surface water pH of at least 6.0. Data were collected from 26 sites in Alberta and 29 sites in Saskatchewan from 15 June to 15 August 15, 2002, and 25 sites in

Manitoba 15 June to 31 August 2000 (Manitoba sites from Locky et al. In press). A Garmin® GPS 12 portable global positioning system unit was used to determine latitude, longitude (Appendix A), and elevation at each site.

Areal extents were only available for Duck Mountain sites, which had a mean size of 1.8 ha, range of 0.2 to 5.1 ha, and standard deviation of 1.4 ha. The topography is similar across the Mid-Boreal Uplands Ecoregion and peatlands are often found discretely among uplands, and I assumed that the wooded rich fens at Utikuma Lake and Prince Albert National Park were relatively similar in size. Additionally, previous research has shown that area is not related to species richness in fens (Chapter 3).

Wooded moderate-rich fens were physically similar among the three locations, but some differences were noted. While Duck Mountain sites appeared to have the lushest vegetation, Utikuma Lake sites tended to be the driest, often with large sections of dessicated and bleached *Tomenthynum nitens* that crumbled and collapsed when traversed (possibly a temporary state). Sites were dominated by *Picea mariana* (P. Mill.) B.S.P. over the three locations. However, a number of sites in the Prince Albert National Park area had comparatively higher cover of *Larix laricina*, with two sites almost completely dominated by this species.

Plant diversity surveys

Each site was surveyed systematically for bryophytes and vascular plants using a time-bounded floristic habitat sampling method to capture a large number of plant species in a relatively short period of time based on Newmaster (2000) (Newmaster et al. 2005). The surveys were limited to a three-hour time period, which was found to be an adequate period in which no new species were found. I assigned a 1 to 4 occurrence scale to species adapted from Vitt et al. (1995a): (1) Rare – present less than five times (≤1%); (2) Few – found a few times (~2-10% cover); (3) Common – found regularly but did not dominate the community (~11-74% cover); and (4) Abundant – dominated the community (~75-100% cover). Habitats within sites were sampled consistently, but collection of corticolous bryophytes was incomplete and most species from that group were not included in the analyses. Scientific names for vascular plants follow the Plant Element List from the Alberta Natural Heritage Information Centre (2002) where possible, and Scoggan (1978-1979) for others, true mosses follow Anderson et al. (1990), *Sphagnum* follows Anderson (1990), and hepatics follow Stötler and Crandall-Stötler (1977).

Environmental variables

I collected measurements of pH, specific conductance (adjusted for temperature and hydrogen ions), and water temperature at each site. Measurements were taken in open pools, depressions in the substrate, or in excavated wells 20 – 80 cm deep. Water samples were collected for analysis of total phosphorus (TP), soluble reactive phosphorus (SRP), nitrate ($N0_2^- + N0_3^-$), ammonium (NH_4^+), total nitrogen (TN), sodium (Na^+), potassium (K^+), calcium (Ca^{2+}), magnesium (Mg^{2+}), iron (Fe^+), sulphate (SO_4^{2-}), chloride (Cl^-), and dissolved organic carbon (DOC) following methods used in Vitt et al. (1995b). pH (< 5.5) and specific conductance values were adjusted by subtracting the effect of hydrogen ions per Sjörs (1952). Means for pH were calculated using hydrogen ions and then reconverted to pH for display and discussion. Depth to water table, mean peat depth, peat C:N, bulk density, organic C, and inorganic C were determined following methods in Locky et al. (In press). The forests on the peatlands were characterized by the point centred quarter (PCQ) method, tree height, tree diameter at breast height (dbh), and percent overstory density (Spherical Crown Concave Densiometer), and trees/ha calculated following methods in Locky et al. (In press).

Data analysis

Bryophyte taxa and vascular plant life forms

The ability to predict species richness by using environmental variables is tempered by the large differences in habitat preferences and autoecology among species (Bruun et al. 2003). This is particularly true when comparing the response of bryophytes to vascular plants (Lee and La Roi 1979, Cox and Larson 1993). Thus, modelling species richness of ecologically defined groups of species can help elucidate patterns of diversity and their causes (Cox and Larson 1993, Pausus and Austin 2001, Bruun et al. 2003). Species composition was examined by bryophyte taxa and vascular plant life forms. Bryophyte taxa include true mosses (excludes *Sphagnum*), *Sphagnum*, and hepatics.

Vascular plant life forms are sometimes considered a crude division of plant functional types, but are a useful first-approximation for functional-type subdivisions (Lavorel et al. 1997). I used life form designations from Scoggan (1978-1979), following Raunkiaer's (1934) classification of the position and seasonality of the perennating buds or rejuvenating organs as follows:

Phanerophytes: trees and tall shrubs > 2 m
Nanophanerophytes: shrubs < 2 m
Chamaephytes: short or prostrate plants; buds not above 25 cm from soil surface
Hemicryptophytes: renewal buds at soil surface
Geophytes: renewal buds underground (rhizomes, tubers, corms, bulbs)
Helophytes: plants submersed in mud
Hydrophytes: plants submersed or floating
Therophytes (annuals): renewal buds protected by seed

Plant diversity

Gamma, alpha, and beta diversities were determined following the concepts of Whittaker (1972, 1977). Gamma diversity is the total species richness of wooded moderate-rich fens sampled in the Boreal Plains Ecozone (regional diversity). Alpha diversity is a measure of species richness by location, i.e., Alberta, Saskatchewan, and Manitoba (local diversity). Mean gamma diversity is the mean number of species per site across the Boreal Plains Ecozone, and mean alpha diversity is the mean number of species per site by location. Beta diversity is a measure of among-site variability in species composition (species turnover), independent of site position on spatial or environmental gradients. It is useful as an index of unstructured heterogeneity in species composition, and is appropriate when underlying gradients are unknown (Vellend 2001).

Species richness data was assessed for normality and homogeneity of variances before one-way Analysis of Variance (ANOVA) was used to determine differences in mean alpha diversity of bryophyte taxa (bryophytes, true mosses, hepatics) and vascular plant life forms (phanerophytes, nanophanerophytes, chamaephytes, hemicryptophytes, geophytes) among locations. Tukey HSD post hoc tests were used to reveal group (location) differences. Taxa and life form data that deviated from normality and homogeneity of variances had group differences determined with Kruskall-Wallis H-tests and comparison of group means with 95% confidence interval plots, which are useful in displaying effect size measures and associated measures of precision, in addition to *P* values (Di Stefano 2003). All univariate analyses were completed using SPSS v. 11.5 (SPSS Inc. 2003).

Community similarity

Sørensen's coefficient of community similarity was calculated for paired locations to determine the number of shared species between locations, as this measure is among the most robust of the qualitative (presence-absence) diversity measures (Magurran 2004). Separate analyses were performed on bryophyte taxa and vascular plant life forms.

Plant rarity and uniqueness

Rare species were calculated by plant taxa and life forms. There are no provincial rarity rankings for bryophytes in Manitoba and Saskatchewan and species were defined as locally rare based on 1 to 2 occurrences following Vitt and Belland (1997) and Vitt et al. (2003). For comparison with bryophytes, I determined locally based occurrences of vascular plants using the same criteria. Locally rare vascular plants were further separated into upland, mineral soil wetland, and peatland species. In addition, vascular plants were defined as provincially rare based on S rankings in Alberta (Alberta Heritage Information Centre 2005), Saskatchewan (Province of Saskatchewan 2005), and Manitoba (Province of Manitoba 2005): S1, rare, for plants with 1 to 5 occurrences; S2, rare, for plants with 6 to 20 occurrences; S3, uncommon, for plants with 21 to 100 occurrences; S4, widespread/ abundant, for plants with > 100 occurrences, and; S5, for plants with secure abundance and distribution within the province. S1 to S3 plants were considered as rare in the analyses. Species unique to each province were determined and geographical ranges of those species established using the provincial species lists.

Community composition

To explore structure in the plant community data, non-metric multidimensional scaling (NMS) ordinations were performed on the bryophyte and vascular plant community data, selecting the autopilot function with the slow and thorough analysis. Monte Carlo tests with 1000 randomized runs were completed using a random starting configuration number. After-the-fact r^2 correlations between the distances in the ordination space and the original space were used to determine the proportion of variance represented by the ordination axes (McCune and Mefford 1999). The NMS solution was compared with a solution derived from detrended correspondence analysis (DCA) to assess concordance between different methods for the community data (McCune and Grace 2002).

Plant species with less than five occurrences were removed from the community dataset to improve the ordinations as rare species are not useful for site classifications (McCune and Grace 2002). In addition to using raw data, square root transformation and general relativization, and Beals smoothing were applied to the data to obtain the clearest and most statistically significant ordination. While all of these analyses resulted in relatively similar visual outcomes, I chose to report results of the Beals smoothing function because Beals smoothing function reduces noise in heterogenous data sets by enhancing the strongest patterns within the data (Beals 1984, McCune 1997). These ordinations had the highest stability, lowest stresses, and most distinct ordination diagram patterns, but care was taken not to 'over interpret' the diagrams because of the enhanced patterns that result from Beals smoothing. The Sørensen distance measure was used for all ordinations because of its robustness in quantifying compositional distance (Faith et al. 1987).

Environmental variables

ANOVAs were used to determine differences among the means of normally distributed (raw or transformed) environmental variables from the three study locations. Tukey HSD post hoc tests were used to reveal specific group differences. For environmental variables with non-normal distributions that could not be transformed, Kruskal-Wallis H non-parametric tests were used to determine differences in ranks among the three locations. To help assess the ecological importance of the observed differences among the three locations, I used 95% confidence interval plots (Di Stefano 2003). Latitude and longitude were converted to northing and easting values to produce continuous values suitable for statistical analyses.

Diversity and environmental variable relationships

Direct methods of ordination, such as Canonical Correspondence Analysis have often been used to explore the relationship between environmental variables and the vegetation community. However, these methods are subject to noisy or irrelevant environmental variables, and therefore indirect methods, such as NMS ordination, are useful as they maintain community structure (McCune 1997). Passive joint plot overlays of environmental variables were employed to deduce vegetation-environment relationships (McCune and Grace 2002) using the PC-ORD defaults of r^2 cutoff of 0.200 and 100% vector length on all ordination diagrams (McCune and Mefford 1999).

Diversity-environment relationships were also determined with multiple linear regressions using forward and stepwise selection procedures for variable selection. Bryophyte and vascular plant species richness were modelled using co-variables chosen from NMS ordinations with environmental variable biplots and Monte Carlo permutation tests. Precipitation, northing, and easting were all highly correlated, so easting was used to represent these variables in the multiple regressions. pH, Ca^{2+}, and alkalinity were highly correlated, and alkalinity was used to represent these variables. To account for nonlinear effects and for visual comparisons, scatterplots using quadratic functions of each predictor that was significant in the multiple regressions were produced (Currie 1991). All multivariate analyses and data transformations were completed with PC-ORD v. 4.25 (McCune and Mefford 1999), except for the multivariate regressions, which were completed using SPSS v. 11.5.

To adjust for the effect of percent overstory density and alkalinity on differences in species richness among locations, I used an Analysis of Covariance (ANCOVA) with overstory density and alkalinity as co-variables. Latitude, longitude, and elevation could not be used as co-variables in ANCOVAs, as the means of these variables differed significantly by location and were correlated to location (Quinn and Keough 2004).

To account for the effect of latitude and longitude on the community data, distance-based redundancy analysis (db-RDA) with Sorenson's distance measure was used with latitude and longitude as covariables, individually and combined. This method is useful for analyzing data sets with detrended correspondence analysis gradient lengths well below 4.0 (McCune and Grace 2002); the gradient length for the bryophyte data set was 1.477 and for the vascular plant data set, 2.100. The environment variables used were chosen from correlations with the major NMS axes and included precipitation, surface water alkalinity (correlated with specific conductance, pH, and Ca^{2+}) and temperature, percent overstory density, and peat organic C (correlated with peat inorganic C and bulk density). db-RDAs were completed using CANOCO v. 4.5 (ter Braak and Šmilauer 2002).

4.3 RESULTS

Plant diversity

Gamma and alpha diversity

Gamma diversity in the wooded moderate-rich fens surveyed across the Boreal Plains Ecozone was 273 species, comprised of 86 bryophytes and 187 vascular plants (Table 4.2) (See species list in Appendix B). Alpha diversity followed a decreasing east to west gradient (Manitoba - Saskatchewan - Alberta) of diversity for total plant species (223, 195, 171) and vascular plants (149, 135, 100), and a U-shaped distribution for bryophytes (74, 60, 71). By taxa and life forms, the U-shaped distribution was generally observed for hepatics, true mosses, and *Sphagnum*, and the east to west trend of decreasing diversity followed for hemicryptophytes (buds at soil surface) and geophytes (buds underground).

Mean alpha diversity of total plant and vascular plant species richness was significantly higher overall in Saskatchewan ($F = 17.345$, df = 2, 77, $P \leq 0.001$), and higher in Manitoba compared with Alberta ($F = 36.188$, df = 2, 77, $P \leq 0.001$) (Table 4.2). When broken down into vascular plant life forms, the mean alpha diversity pattern was attributed primarily to hemicryptophytes ($F = 22.290$, df = 2, 77, $P \leq 0.001$) and geophytes ($F = 29.680$, df = 2, 77, $P \leq 0.001$). Mean nanophanerophyte (shrubs < 2 m) alpha diversity was significantly higher in Saskatchewan than Alberta ($\chi = 17.067$, df =

2, $P \leq 0.001$). Mean bryophyte alpha diversity was significantly higher overall in Alberta, and marginally higher in Saskatchewan than Manitoba ($F = 12.291$, df = 2, 77, $P \leq 0.001$). When examined by bryophyte taxa, the mean alpha bryophyte diversity pattern was attributed primarily to hepatics ($F = 33.167$, df = 2, 77, $P \leq 0.001$), whereas mean alpha diversity of *Sphagnum* was higher in Saskatchewan than Manitoba ($\chi = 6.744$, df = 2, $P = 0.034$).

Beta diversity and variability

Beta diversity, the variation in plant composition among sites, was higher for vascular plants than bryophytes at each location (Table 4.3). Compositional change of both bryophytes and vascular plants was highest in Manitoba. The standard deviation of bryophyte diversity was similar at all three locations, but the standard deviation for vascular plant diversity was highest in Saskatchewan.

Community similarity

Sørensen coefficients of similarity for pairwise comparisons are reported in the following order: Alberta-Saskatchewan, Alberta-Manitoba, Saskatchewan-Manitoba. The bryophyte assemblage was similar across the Boreal Plains locations (0.85, 0.83, 0.82), with a similar pattern for true mosses (0.88, 0.89, 0.87). The vascular plant assemblage was more similar between sites in Alberta and Saskatchewan (0.74) and Saskatchewan and Manitoba (0.75), than between Alberta and Manitoba (0.66). The assemblages of hepatics (0.86, 0.70, 0.69), phanerophytes (trees and shrubs > 2 m) (0.86, 0.70, 0.69), and nanophanerophytes (0.90, 0.80, 0.84) were most similar between Alberta and Saskatchewan, whereas Saskatchewan and Manitoba sites had the most similar assemblages of chamaephytes (0.91, 0.91, 1.00), helophytes (submersed in mud) (0.00, 0.00, 0.89), and hydrophytes (submersed or floating) (N/A, 0.00, 1.00). The *Sphagnum* assemblage was most similar between Alberta and Manitoba (0.71, 0.89, 0.71).

Plant rarity and uniqueness

Locally rare species

Twenty-one bryophytes (21% of the total bryophyte assemblage) were observed one to two times and are considered locally rare species (Table 4.4A). Eleven species were true mosses (53% of locally rare bryophytes), seven were hepatics (33%), and three were *Sphagnum* (15%). Of the rare bryophytes, *Dicranum acutifolium* (Lindb. & Arnell) C. Jens. *ex* Weinm., *Plagiomnium cuspidatum* (Hedw.) T. Kop., and *Rhytidiadelphus triquetrus* (Hedw.) Warnst. are commonly found in uplands (Crum and Anderson 1981).

Sixty-four vascular plants (34% of the total vascular plant assemblage) were observed one to two times and considered locally rare species in wooded moderate-rich fens in this study (Table 4.4A). The community assemblage was comprised of hemicryptophytes (30% of locally rare vascular plants) and geophytes (20%). Of the locally rare vascular plants, 47% are considered common upland plants. The remaining 53% are wetland/aquatic species comprised of 23% peatland and 30% mineral soil wetland/peatland species; most of these are common across the western boreal region. By location, wooded moderate-rich fens in Duck Mountain had 67% of the locally rare species, whereas 26% were found in Prince Albert National Park, and 20% were found at Utikuma Lake.

Provincially rare species

Of those plants in which provincial rarity information was available, a total of ten S1-S3 plants were observed in wooded rich fens across Alberta, Saskatchewan, and Manitoba (Table 4.4B). Of these, five were hemicryptophytes, four were geophytes, and one was a nanophanerophyte. By location, five were found in Alberta, three in Saskatchewan, and two in Manitoba.

Unique species

Species unique to wooded moderate-rich fens by location decreased in richness from Manitoba (50 species), to Saskatchewan (19), and Alberta (16) (Table 4.5). Of the unique species observed in Manitoba, *Carex siccata* Dewey, *Galium palustre* L., and

Liparis loeselii (L.) Rich. *ex.* Lindley were not listed as part of Alberta's flora (Alberta Natural Heritage Information Centre 2005).

Community composition

The NMS ordinations of community data resulted in stable, low stress (Kruskal 1964) three-dimensional solutions for both bryophytes (stress = 9.82709, final instability = 0.00001, iterations = 196) and vascular plants (stress = 6.99123, final instability = 0.00001, iterations = 76). For bryophytes, the proportion of variation represented by ordination axes was 94%, comprised of 23% on axis one, 57% on axis two, and 15% on axis 3. For vascular plants, the proportion of variation represented by ordination axes was 97%, comprised of 29% on axis one, 57% on axis two, and 11% on axis 3. Distinct patterns formed by overlaying the wooded fen locations as symbols on the ordination diagram and concordance with the DCA ordinations (results not shown) confirmed that robust and useful solutions were found for both ordinations (Figure 4.2). Sites formed remarkably distinct groups, with some overlap evident between provinces: Saskatchewan and Alberta sites overlapped in the bryophyte ordination (axes 2 x 3), and; Saskatchewan and Manitoba (axes 1 x 2), and Alberta and Manitoba (axes 2 x 3) overlapped in the vascular plant ordination.

Environmental variables

All three study locations were significantly different based on latitude (F = 10457.402, df = 2, 77, $P \leq 0.001$), longitude (χ = 70.125, df = 2, $P \leq 0.001$), and elevation (χ = 60.528, df = 2, $P \leq 0.001$) (Table 4.1). Mean precipitation 1963--2002 at Duck Mountain, MB (668.6 mm) was significantly higher (F = 84.055, df = 2, 77, $P \leq$ 0.001) than at Prince Alberta National Park, SK (449.4 mm) and Utikuma Lake, AB (404.6). Mean percent overstory density of the peatland forest was highest in Manitoba (F = 8.831, df = 2, 77, $P \leq 0.001$), and the mean number of trees/ha was higher in Saskatchewan than Manitoba (F = 3.398, df = 2, 77, P = 0.039). Compared to Alberta, peat depth was greater in Manitoba (χ = 7.610, df = 2, P = 0.022). Mean peat C:N was significantly different among all three locations, with a distinct east to west gradient of decreasing values (χ = 15.234, df = 2, $P \leq 0.001$). Peat bulk density and surface water temperature followed the same general pattern, with the former significantly lowest in Alberta ($F = 8.471$, df = 2, 77, $P \leq 0.001$), and the latter significantly lower in Alberta than Manitoba ($\chi = 47.852$, df = 2, $P \leq 0.001$). Peat organic C was greater in Manitoba than in Alberta ($F = 4.094$, df = 2, 77, $P = 0.020$) and Saskatchewan peat inorganic C was greater than in Manitoba peat ($F = 4.325$, df = 2, 77, $P = 0.017$). In terms of water chemistry, wooded moderate-rich fens in Saskatchewan had higher mean pH ($F = 3.591$, df = 2, 77, $P = 0.032$) than in Alberta, and Manitoba had higher specific conductance than Alberta ($\chi = 8.396$, $P = 0.015$). Alkalinity was lowest in Alberta sites ($\chi = 20.788$, df = 2, $P \leq 0.001$). Differences in nutrient concentrations across the Boreal Plains sites were minor, with only mean TP found to be significantly higher in Alberta sites ($\chi = 6.1756$, df = 2, $P = 0.046$).

Community composition, species richness, and environmental variables

The joint plot overlays of environmental variables with the ordination of bryophyte and vascular plant community data indicated that the most strongly associated variables were location (latitude and longitude), precipitation, elevation, and surface water temperature. In both ordinations, precipitation, surface water temperature, and elevation were oriented towards Manitoba sites, and location was oriented towards Alberta sites (Figure 4.2). The vascular plant ordination had a greater number of environmental variables than the bryophyte ordination. These included peat bulk density and percent overstory density, oriented towards Manitoba sites, and pH, alkalinity, and specific conductance, oriented primarily towards Saskatchewan sites.

The forward and stepwise multiple regressions chose the same model for both bryophyte and vascular plant species richness. For bryophytes, the only significant predictor variable was longitude ($R^2 = 0.233$, $F = 23.732$, df = 1, 78, $P \leq 0.001$) (Table 4.6). The relationship was more robust for vascular plant richness, with the same optimal predictive model chosen by both regression methods and including longitude, elevation, and percent overstory density ($R^2 = 0.506$, $F = 25.942$, df = 3, 76, $P \leq 0.001$). For both multiple regressions, latitude and precipitation would also be considered significant variables due to the strong collinearity among them. These results are supported, for the most part, by the weak, but significant relationships between richness and individual environmental variables in scatterplots with fitted quadratic regression lines and linear regression statistics (Figure 4.3). While some of the significant relationships appear relatively linear, e.g., bryophyte richness by latitude, longitude, and precipitation, and vascular plant richness by overstory density, most of the relationships emerge as non-linear, usually hump- or U-shaped.

The results of ANCOVAs to determine the response of species richness and the covariables, percent overstory density and surface water alkalinity, among the three locations indicated that the effect was not significant for bryophytes ($F = 0.696$, df = 2, 77, $P = 0.502$; $F = 0.019$, df = 2, 77, $P = 0.981$) or vascular plants ($F = 2.793$, df = 2, 77, $P = 0.068$; $F = 0.614$, df = 2, 77, $P = 0.544$).

Distance-based redundancy analyses used to account for the effect of latitude and longitude on the community data revealed that the environmental variables (elevation, precipitation, surface water alkalinity and temperature, percent overstory density, and peat organic C) explained a comparatively higher proportion of the variation in the data, especially for vascular plants (Table 4.7). By covariables, longitude explained slightly more variation in the vascular plant data set (8.4%) compared to latitude (7.9%). The pattern was opposite for bryophytes with longitude accounting for 8.2% of variation, and latitude accounting for 9.3%. When latitude and longitude were combined as covariables, the percent of variation explained was slightly higher for vascular plants. The total amount of variation accounted for by all environmental variables was higher for vascular plants (29.6%) compared to bryophytes (24.0%).

4.4 DISCUSSION

Latitudinal and altitudinal (i.e., elevation) gradients are surrogates for various environmental variables and are often interrelated. This makes tests using latitude and altitude problematic and potentially controversial (Willig et al. 2003, Rahbek 2005). Selection of well-defined sites with discrete boundaries, such as raised bogs (Glaser 1992) and wooded moderate-rich fens (this study) is one potential solution to this problem. Raised bogs were noted as relatively uniform with specific areas related to the wet-to-dry gradient and acidity and low Ca^{2+}, which represent important controls on species composition (Glaser 1992). While wooded moderate-rich fens have relatively distinct boundaries and homogenous vegetation, they are comparatively more variable than bogs with respect to surface water chemistry (Sjörs and Gunnarsson 2002, Locky et al. In press) and peat physical characteristics (Locky et al. In press), in addition to the wet-to-dry gradient (Vitt et al 1995b). The inherent variability within wooded moderate-rich fens may be manifested in the generally weak relationship between species richness and environmental variables, and the low total variance of the community data explained by the environmental variables (24 – 30%). Nonetheless, a number of relationships illustrate factors affecting both species diversity and community composition.

Climatic factors

Latitude

Generally, decreases in vascular plant diversity in North America are related to increasing latitude (Qian 1998). I observed that with increasing latitude (550 km), bryophyte richness increased and vascular plant richness decreased in wooded moderate-rich fens. A similar trend was observed with bryophytes and vascular plants over 800 km of talus slopes in south-central Ontario (Cox and Larson 1993), and for vascular plants in Maritime raised bogs (Glaser 1992). The relationship between latitude and diversity is one of the fundamental unsolved problems in community ecology (Morin 1999), although a number of factors have been used to describe the association. The decrease in vascular plant richness with latitude has been attributed to environmental energy, the decreasing amount of energy available (e.g., annual potential evapotranspiration) with increasing latitude (Currie 1991). While coarse scale studies, e.g., tropical to temperate regions, have shown evidence of environmental energy (Hutchinson 1959, Brown 1981, Turner et al. 1987), similar environmental energy effects have also been noted at finer scales, e.g., region (Kelly et al. 1992, Cox and Larson 1993). Growing degree days > 5°C (GDD) (or mean annual temperature) is an important component of the environmental energy concept (Currie 1991). GDDs were not associated with vascular plant species richness in raised bogs in eastern North America (Glaser 1992), but decreases in GDD with latitude have been noted in reducing vascular plant diversity in talus slopes along the Niagara Peninsula (Cox and Larson 1993). It is likely that GDD are a contributing factor to decreasing vascular plant diversity with latitude in the present study. Although it is difficult to determine the exact number of GDD at Duck Mountain due to the elevational effect, there is a relatively distinct gradients across the studied locations: Utikuma Lake, Alberta = 1237 days, Prince Albert National Park, Saskatchewan = 1455 days, and Swan River, Manitoba (adjacent to Duck Mountain) = 1590 days.

Increasing bryophyte richness with latitude cannot be easily explained using environmental energy. Taxonomic bias, particularly in North America, has lead to misapplication of ecological, morphological, and physiological perspectives of vascular plants as models for the effects of stress and marginal habitats (Keddy 1989). This is not applicable to organisms tied more closely to their immediate substrate, such as lichens and bryophytes (Cox and Larson 1993). Regions apparently depauperate in vascular plants due to harsh environmental conditions, such as arctic ecosystems, can have high bryophyte diversity (Fahselt and Maycock 1992).

The bryophyte and vascular plant ordinations and similarity and uniqueness analyses illustrate relatively discrete differences in sites among the three locations. However, the bryophyte assemblage was found to be more similar across the Boreal Plains Ecozone than the vascular plant assemblage. Nicholson and Gignac (1995) observed that most bryophytes have relatively long climatic and geographic ranges along north-south gradients spanning five ecoclimatic regions in the MacKenzie River Basin.

Longitude

While latitude has been considered the strongest explanatory variable in describing vascular plant richness, longitude has not (Grytnes et al. 1999). In the present study the richness of bryophytes increased and vascular plants decreased with longitude. Glaser (1992) observed a similar phenomenon for vascular plants in raised bogs along a gradient from Maritime to continental regions. The pattern was explained to be potentially related to the effect of climate, with Maritime sites having a more temperate climate, more precipitation, and concomitant southern outlier species. Longitude was also highly correlated with precipitation and annual freezing days. The present study examined diversity in sites only within the Boreal Plains Ecozone, a continental region. However, based on 40 years of precipitation data, patterns due to orographic precipitation were significantly different within this region, creating a steeper gradient possibly similar to that observed when examining sites over more than one ecological region (e.g., Glaser 1992).

Precipitation

Alpha diversity was highest at Duck Mountain where precipitation was consistently associated with those sites in the ordinations, and mean annual precipitation was significantly higher than at Utikuma Lake and Prince Albert National Park. Climate modeling for the last century has shown that at Duck Mountain, climate warming and changes in precipitation have had no significant impacts on summer drought severity (Girardin et al. 2004). In the simple linear ordinations, precipitation was negatively associated with bryophyte species richness. However, there was no association with vascular plant species richness, despite precipitation being highly correlated with latitude in the forward and stepwise multiple regression models. In addition to annual freezing degree days, mean annual precipitation is among the strongest predictive variables in determining vascular plant richness in eastern North American raised bogs across a sharp climatic gradient of regions. The same effect was not observed within a continental region from Minnesota to Manitoba (Glaser 1992).

Elevation

No relationship was observed between bryophyte species richness or community composition and elevation. This is not surprising, as Slack (1977) found no clear relationship between bryophyte richness and elevation over a range of 500 to 1500 m asl in the Adirondacks, NY; the elevational range in the present study was 500 to 800 m asl. Elevation was correlated to vascular plant richness and was a strong vector in the vascular plant species ordination. Lee and La Roi (1979) suggest that bryophytes have wider tolerances to elevation-correlated factors, as they found that vascular plants have higher beta diversity than bryophytes along elevational gradients. Vascular plant richness responses to altitude have been variable and complex, often unimodal and in different directions (Grytnes 2003). The beta diversity of bryophytes has been found to be greater along moisture gradients than elevational gradients, while vascular plant beta diversity is similar. However, beta diversities of bryophytes and vascular plants are similar along complex moisture gradients (Lee and LaRoi 1979).

Floristics, surface water chemistry, and habitat heterogeneity

Alpha diversity of most vascular plant life forms was greatest in Manitoba (Table 4.2). This suggests floristic elements from eastern Canada are included in the Manitoba flora, as sites there were the most eastern and southern. Glaser (1992) observed that Maritime eastern raised bogs were more species-rich than continental sites, in part due to proximity to a species pool from a more temperature region (due to climatic factors). However, in the present study, overlap from eastern and southern species pools seems unlikely to be a significant contributing factor to the greater total diversity found in Manitoba sites. Athough most of the unique species were found in Manitoba, only three species would not be found in Alberta, and no species found in Alberta or Saskatchewan would not potentially be found in Manitoba (Table 4.5). In addition, mean alpha diversity was significantly higher for most vascular plant life forms in Saskatchewan. This may in part be related to the Prince Albert National Park area being comprised of the Boreal Transition Ecoregion, a thin band that separates the Mid-Boreal Upland Ecoregion from that of the Parkland Ecoregion, and access to a greater species pool; the Manitoba and Alberta sites are completely within the Mid-Boreal Upland Ecoregion. In addition, higher alpha diversity may be related to the *Larix laricina*-dominated sites that were observed in Saskatchewan, but not Alberta or Manitoba. Further research on *Larix laricina*-dominated fens across the western boreal region may lead to new conclusions on diversity and rarity compared to *Picea mariana*-dominated fens.

Alpha diversity of all vascular plant life forms was lowest in Alberta sites which, although not statistically significant, had the lowest depth to water table. Glaser (1992) observed that bogs subjected to substantial water table drawdowns due to drought were the most floristically impoverished. The Utikuma Lake sites have been undergoing drought-like conditions in the early 2000's (Whitehouse and Bayley 2005). Although comparative studies are not available, this drought may have contributed to comparatively lower vascular plant richness than was observed pre-drought.

Each of the three areas surveyed appears to have unique community assemblages. The ordinations showed a distinct separation by province of the vascular plant species and bryophyte data. When data is collected over a relatively small area, the distribution patterns of plant species, as elucidated by multivariate ordinations, can be successfully explained by ecological processes, particularly edaphic patterns (Økland 1988, Wassen and Barendregt 1992). This does not hold true when data are collected over a larger area (e.g., continental). Multivariate ordinations of compositional data from large areas have revealed that distributional patterns may be associated primarily with processes of speciation, extinction, immigration, and adaptation. Qian et al. (1998) use the example of two alpine tundra sites with similar ecological conditions, but with no shared species owing to separate locations in the high latitudes of the northern and southern hemispheres. That similarity between sites for most groups of organisms decreases with distance, irrespective of changes in habitat and even in the absence of habitat specialists, is predicted by community theory (Hubbell 2001). In continental areas, the composition of bryophytes in two locations is generally more similar than that of vascular plants, as bryophytes colonize and spread faster on bare ground after glacial retreat (Qian et al. 1998). Evidence suggests that vascular plants, especially woody forms, may not yet have reached pre-glacial equilibria (Delcourt and Delcourt 1987).

Along a geographic gradient across British Columbia and Alberta, Gignac and Vitt (1990) established that *Sphagnum* species groups and peatland stand dispersal were determined largely by climate and surface water chemistry, in particular specific conductance and cations. Local habitat factors such as shade and relative height to water table have little effect on *Sphagnum,* as a range of these requirements are often found somewhere within individual peatland stands, irrespective of climate. Over a smaller scale in northern areas, climatic factors (allogenic) are related to specific landforms, which in turn influence shade and dryness (autogenic) in individual bogs. It is shade and dryness which largely control bryophyte vegetation patterns, primarily through successional changes related to thermokarst activity (Belland and Vitt 1995).

Climate, along with degree of minerotrophy, was a primary influence in determining bryophyte distributions in western Canada (Gignac et al. 1991). Some mosses have growth that is variable over their boreal ranges and related to broad climatic patterns (e.g., drought tolerant mosses like *Hylocomium splendens* (Hedw.) Schimp. *in* B.S.G.), whereas other mosses have constant growth across their boreal range (e.g., less-tolerant *Polytricum strictum* Brid.) (Vitt 1990). In bogs over the eastern North American region, vascular plant species richness was related to annual freezing degree-days, mean annual temperature, the number of wet-to-dry habitats, and surface water magnesium and sodium (Glaser 1992).

Surface water alkalinity and percent overstory density were observed to have the same effects irrespective of location sampled in the present study. The linear regressions demonstrated a positive, but somewhat unimodal association between these variables and vascular plant species richness. Vascular plant richness has been associated with alkaline sites compared with acidic sites in Sweden (Bruun et al. 2003). Glaser (1992) has suggested that the flora of bogs is related to controls based on low pH, low Ca^{2+}, and increased solubility and toxicity of metals which limit the availability of nutrients (Begon et al. 1986, Fitter and Hay 1987). There is no such limitation in moderate-rich fens.

Habitat heterogeneity is one of the most important factors associated with the diversity of bryophytes (Vitt et al. 1995, Vitt et al. 2003) and vascular plants (Chapter 3). Bryophyte richness was significantly correlated with forest cover and sites with the greatest number of microhabitats (Vanderpoorten and Engels 2003), and localized permafrost dynamics in bogs in western Canada (Beilman 2001). Glaser (1992) found that diversity increased with latitude in a continental interior zone, and attributed this to more bog pools and mud-bottomed habitat in the north.

Peatland age

Climate and history can be important aspects of describing plant diversity patterns (Grytnes et al. 1999). Vascular plant richness has been related to age in Maritime bogs and has been attributed to greater time for populations to adapt to local conditions and increasing heterogeneity of the peat surface with age (Glaser 1992). No clear patterns were observed in the present study, but while peatlands in the Utikuma Lake area are the oldest (ca 6000 - 8000 YBP) (Zoltai and Vitt 1990) and have the greatest mean bryophyte diversity, sites in the Duck Mountain area are the youngest (ca 2000 -- 4000 YBP) (Zoltai and Vitt 1990) and have the greatest total, vascular plant, and bryophyte species alpha diversity.

Beta diversity

Vascular plant beta diversity was observed to be higher than bryophyte beta diversity at all three locations, and was highest for bryophytes and vascular plants in Manitoba sites. Beilman (2001) reported that bryophytes exhibited greater beta diversity than vascular plants, and responded more strongly to long environmental gradients in continental permafrost bogs. Lee and LaRoi (1979) found that bryophyte and vascular plant beta diversity was similar along moisture gradients, but quite different along elevational gradients.

Rare plants

Research has shown that, in western Canada, locally rare bryophytes are most numerous in wooded moderate-rich fens (Vitt et al. 2003, Chapter 3) and black spruce swamps (Chapter 3), and locally and provincially rare vascular plant species are greatest in wooded moderate-rich fens and black spruce swamps (Chapter 3). One might expect similar patterns of diversity in similar ecosystems across a geographic region, and perhaps few differences in provincially rare vascular plant species abundance. However, locally rare plants exhibited a distinct east to west gradient in decreasing abundance for vascular plants and total plants (Table 4.4). This pattern is similar to alpha diversity (Table 4.4), and is probably related to similar factors discussed above, although the literature shows conflicting results. For example, with bryophytes, peatland sites that are species-rich often have more rare species, but rare species are not always found in species-rich sites (Vitt et al. 2003). Additionally, peatlands with woody vegetation are more likely to have more rare bryophytes than open stands due to increased habitat complexity (Vitt et al. 1995, Vitt et al. 2003, Chapter 3), with a similar response for vascular plants (Chapter 3), but rare vascular plant diversity has also been associated with canopy gaps in forested wetlands (Anderson and Leopold 2002).

4.5 CONCLUSIONS

Few studies have examined patterns of plant diversity, composition, and rarity in specific peatland types across a similar landscape unit (Glaser 1992, Beilman 2001) or Ecoregion. The present study has shown that patterns of plant species diversity, composition, and rarity are complex in wooded moderate-rich fens across the Boreal Plains Ecoregion. The total variation explained in the community data is relatively low. While most of that variation is ascribed to environmental variables, yet a significant component is attributed to latitude and longitude. Alpha diversity is greatest in Manitoba, and decreases in a longitudinal trend through Saskatchewan and Alberta. This may be related, in part, to differences in growing degree days and the influence of orographic precipitation at Duck Mountain, Manitoba. However, mean alpha diversity is significantly greater in Saskatchewan for total and vascular plant species diversity, and greater in Alberta for bryophyte species diversity. High mean diversity in Saskatchewan may be explained by the significantly lower overall elevation, a larger species pool (adjacency to the Boreal Transition Ecoregion), and, compared to Alberta, higher surface water pH, alkalinity, and specific conductance. In Alberta, high mean alpha bryophyte diversity may be related to site age, but it is likely that other factors are at play. Exact causal agents of diversity changes can be challenging to extract from latitude, longitude, and other climatic gradients, as these gradients are often surrogates for more elemental variables that are commonly interrelated (Williamson 1981, Glaser 1992). Further research is required in homogeneous communities with well-defined boundaries (Williamson 1981, Brown and Gibson 1983), such as peatlands (Glaser 1992), to confidently test hypotheses using regional and local scale environmental variables. Because ecoregions are increasingly being used as a framework for conservation planning, tests of their boundaries are required to determine their validity from the perspective of different organisms (Magnusson 2004). Utilizing different sets of ecoregions based on relevance to major taxonomic groups or processes may be more appropriate from a conservation perspective; few organisms have ranges restricted to ecoregion boundaries (McDonald et al. 2005). Comparing floristic diversity and composition in peatlands in other Boreal Plains Ecoregions or with ecoregions in other Boreal and Subarctic Ecozones would contribute to this goal.

Acknowledgements

The author graciously acknowledges funding and technical support from the Sustainable Forest Management Network, Edmonton, Alberta. Louisiana-Pacific Canada Ltd., Swan River, Manitoba, especially Margaret Donnelly and Donna Grassia, are thanked for providing technical and in-kind support. Dan Frandsen is thanked for access permission and logistical assistance in Prince Alberta National Park. Funding was also graciously provided by the Canadian Circumpolar Institute with a C/BAR grant to DAL. Ted Hogg from Natural Resources Canada, Canadian Forestry Service is thanked for providing custom weather data for the western boreal research sites. Joyce Gould, René Belland, and Chris Jerde supplied valuable discourse on statistical analyses. Sarah Wilkinson and Chris Jerde provided constructive feedback regarding this manuscript. Dan Kueffler and Chris Shapka assisted with field work.

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Table 4.1. Means (ranges) for environmental variables in wooded rich fens at Utikuma Lake, AB, Prince Albert, SK, and Duck Mountain, Manitoba. Mean values followed by the same letter are statistically significantly different based on ANOVAs and post-hoc tests or Kruskall-Wallis tests with 95% confidence interval plots. See text for details. dbh = diameter at breast height, conductivity = surface water specific conductance.

Location	Utikuma Lake, AB		Prince Albert, SK		Duck Mountain, MB		All
n =	26		29		25		80
Wetland Region	High Boreal		Mid Boreal		Mid Boreal		Boreal
Latitude	6224904	a	5976864	ab	5733649	ab	5981473
	(6203430 - 6252577)		(5962549 - 6002270)		(5711099 - 5750337)		(5711099 - 6252577)
Longitude	591008	a	434880	ab	366981	ab	464403
	(572741 - 603991)		(420284 - 441019)		(359672 - 374960)		(359762 - 603991)
Elevation (m)	641	a	564	ab	714	ab	636
	(558 - 688)		(495 - 601)		(671 - 745)		(495 - 745)
Precip. 1963 - 2002 (mm)	404.6	a	449.4	b	668.6[1]	ab	507.5[1]
	(263.2 - 564.4)		(264.0 - 771.9)		(417.5 - 917.1)[1]		(263.2 - 917.1)[1]
Tree height (m)	6.9		7.2		7.2		7.1
	(4.1 - 11.1)		(4.3 - 10.6)		(3.8 - 12.1)		(3.8 - 12.1)
Tree dbh (cm)	9.7		9.3		10.8		9.9
	(6.4 - 16.5)		(6.3 - 13.7)		(7.0 - 17.1)		(6.3 - 17.1)
Overstory density (%)	38	a	43	b	53	ab	45
	(22 - 59)		(16 - 65)		(7 - 77)		(7 - 77)
Trees/ha	2545		3260	b	2436	b	2770
	(1288 - 5835)		(1220 - 7347)		(894 - 5108)		(894 - 7347)
Mean peat depth (m)	1.0	a	0.9		1.4	a	1.3
	(0.3 - 1.8)		(0.7 - 2.6)		(0.7 - 2.9)		(0.3 - 2.9)
Peat bulk density (g/cm^3)	0.26	a	0.34	a	0.37	a	0.32
	(0.10 - 0.42)		(0.13 - 0.54)		(0.22 - 0.64)		(0.10 - 0.64)
Peat organic C (g)	0.89	a	0.87		0.84	a	0.87
	(0.71 - 0.94)		(0.75 - 0.92)		(0.54 - 0.92)		(0.54 - 0.94)
Peat inorganic C (g)	0.04		0.05	b	0.03	b	0.04
	(0.00 - 0.14)		(0.01 - 0.14)		(0.00 - 0.06)		(0.00 - 0.14)
Peat C:N	24	a	25	ab	33	b	27
	(16 - 42)		(14 - 49)		(18 - 58)		(14 - 58)
Water table (cm)	15.0		11.9		7.8		11.6
	(0.0 - 55.0)		(0.0 - 40.0)		(0.0 - 20.0)		(0.0 - 55.0)
Water Temperature (°C)	1.8	a	3.4		9.3	a	4.7
	(0.0 - 5.5)		(0.0 - 10.5)		(6.0 - 13.0)		(0.0 - 13.0)
pH	6.7	a	6.8	a	6.9		6.8
	(6.2 - 8.0)		(6.1 - 8.0)		(6.1 - 7.9)		(6.1 - 8.0)
pH (median)	6.8		7.3		7.2		7.1
Conductivity ($\mu S/cm^{-1}$)	300.7	a	397.9		419.1	a	372.9
	(37.0 - 1080.4)		(78.8 - 718.0)		(151.3 - 782.0)		(37.0 - 1080.4)
Ca^{2+} (mg/L)	41.2		43.4		50.9		45.1
	(4.8 - 142.8)		(10.2 - 68.7)		(17.7 - 82.4)		(4.8 - 142.8)
Alkalinity (mg/L)	76.5	a	142.9	a	158.7	a	126.3
	(16.2 - 232.2)		(38.0 - 230.8)		(67.6 - 225.2)		(16.2 - 232.2)
TP (mg/L)	291.7	a	200.8	a	174.3		221.7
	(52.5 - 824.2)		(95.4 - 458.2)		(10.4 - 649.0)		(10.4 - 824.2)

Table 4.2. Alpha and gamma diversity for bryophytes, vascular plants and total plants in wooded moderate-rich fens at Utikuma Lake, AB, Prince Albert National Park, SK, and Duck Mountain, MB. Mean values followed by the same letter are statistically significantly different using ANOVA, and for helophytes and hydrophytes, Kruskall-Wallis mean rank tests. See text for *P*-values.

Taxa/Life-form	Western Boreal Location										
	Alberta			Saskatchewan			Manitoba			All	
	Alpha	(Mean)		Alpha	(Mean)		Alpha	(Mean)		Gamma	(Mean)
Bryophytes	71	(28.3)	a	60	(25.5)	a	74	(23.0)	a	86	(25.6)
Hepatics	20	(5.6)	a	15	(4.1)	ab	17	(1.7)	ab	24	(3.9)
True Mosses	42	(18.7)		40	(17.4)		48	(18.0)		52	(18.0)
Sphagnum	9	(4.0)		5	(4.0)	b	9	(3.2)	b	10	(3.7)
Vascular plants	100	(29.3)	a	135	(44.4)	ab	149	(36.9)	ab	187	(37.1)
Phanerophytes	15	(4.8)		20	(5.4)		19	(5.1)		27	(5.1)
Nanophanerophytes	14	(3.7)	a	15	(5.6)	a	16	(4.7)		18	(4.7)
Chamaephytes	5	(2.4)	a	6	(3.0)	ab	6	(3.8)	ab	6	(3.1)
Hemicryptophytes	43	(10.0)	a	57	(17.2)	ab	64	(13.0)	ab	83	(13.5)
Geophytes	23	(8.3)	a	34	(13.0)	ab	39	(9.7)	b	47	(10.4)
Helophytes	0	(0.0)	a	3	(0.3)	a	2	(0.4)	a	3	(0.3)
Hydrophytes	0	(0.0)	a	0	(0.0)	b	3	(0.2)	ab	3	(0.1)
Total plant species	171	(57.5)	a	195	(69.9)	ab	223	(59.9)	b	273	(62.7)

Table 4.3. Maximum (Max), minimum (Min), standard deviation (SD), and beta diversity (Beta) for A) total plant species, B) bryophytes, and C) vascular plants in wooded moderate-rich fens at Utikuma Lake, AB, Prince Albert National Park, SK, and Duck Mountain, MB, Canada.

A. Total plant species

	n =	Max	Min	SD	Beta
Utikuma Lake, AB	26	78	40	7.2	3.0
Prince Albert, SK	29	91	46	10.5	2.8
Duck Mountain, MB	25	77	39	6.0	3.7
Total	80	95	33	9.8	4.4

B. Bryophytes

	n =	Max	Min	SD	Beta
Utikuma Lake, AB	26	37	21	4.1	2.5
Prince Albert, SK	29	33	19	3.5	2.4
Duck Mountain, MB	25	31	14	3.9	3.2
Total	80	37	14	4.3	3.4

C. Vascular Plants

	n =	Max	Min	SD	Beta
Utikuma Lake, AB	26	41	19	5.7	3.4
Prince Albert, SK	29	58	27	8.2	3.0
Duck Mountain, MB	25	46	25	5.2	4.0
Total	80	58	19	9.0	5.0

Table 4.4. Locally rare bryophytes and vascular plants (A), and provincially rare vascular plants (B) in wooded moderate-rich fens at Utikuma Lake, AB, Prince Albert National Park, SK, and Duck Mountain, MB.

A. Locally rare bryophytes and vascular plants

Taxa/Life-form	Location			
	AB	SK	MB	Total
Bryophytes	8	2	15	21
Hepatics	2	0	5	7
True Mosses	4	2	7	11
Sphagnum	2	0	3	3
Vascular Plants	9	20	42	64
Phanerophytes	1	1	5	7
Nanophanerophytes	0	0	2	2
Hemicryptophytes	7	11	19	31
Geophytes	1	7	13	20
Helophytes	0	1	0	1
Hydrophytes	0	0	3	3
Total Plants	17	22	57	85

B. Provincially rare vascular plants

Life-form	Location			
	AB	SK	MB	All
Nanophanerophytes	*Lonicera caerulea* (S3)			1
Hemicryptophytes	*Galium labradoricum* (S3)	*Campanula aparanoides* (S2S3)	*Liparis loeselii* (S2)	5
	Carex prairieae (S3)			
	Carex tennuifolia (S3S4)			
Geophytes	*Cypripedium acaule* (S3)	*Platanthera dilatata* (S2)	*Listera borealis* (S2)	4
		Malaxis monophylla (S1S2)		
Total Plants	5	3	2	10

Table 4.5. Unique plant species in wooded moderate-rich fens in the Boreal Plains Ecozone, Canada. Provincially rare species (S1-S3) are indicated and species not found in Alberta are noted with an asterisk.

Taxa/Life-form	Location		
	Utikuma Lake, Alberta	Prince Albert National Park, Saskatchewan	Duck Mountain, Manitoba
True Mosses	*Calliergon trifarium* (Web. & Mohr) Kindb. *Ceratodon purpureus* (Hedw.) Brid. var. *purpureus* *Plagiomnium cuspidatum* (Hedw.) T. Kop.	*Dicranum acutifolium* (Lindb. & H. Arnell) C. Jens. *ex* Weinm.	*Catoscopium nigritum* (Hedw.) Brid. *Meesia longiseta* Hedw. *Platydictya jugermanniodes* (Brid.) Crum *Rhytidiadelphus triquetrus* (Hedw.) Warnst. *Sphlachnum sphaericum* Hedw. *Splachnum luteum* Hedw. Var. *luteum* var. *melanocaulon* Wahlenb.
Sphagnum	*Sphagnum teres* (Schimp.) Ångstr. *in* Hartm.		*Sphagnum rubellum* Wils.
Hepatics	*Cladopodiella fluitans* E. Joerg. *Gymnoclea inflata* (Huds.) Dum. var. *inflata* *Tritomaria quinquedentata* (Huds.) Buch var. *quinquedentata*		*Cephalozia bicuspidata* (L.) Dum. subsp. *bicuspidata* *Conocephalum conicum* (L.) Lindb. *Riccardia multifida* (L.) S. Gray var. *multifida* *Riccia canaliculata* Hoffm.
Phanerophytes	*Viburnum edule* (Michx.) Raf.		*Alnus viridis* ssp *crispa* (Ait.) Turrill *Cornus stolonifera* Michx. *Corylus cornuta* Marsh. *Populus tremuloides* Michx. *Salix exigua* Nutt. *Salix maccaliana* Rowlee
Nanophanerophytes			*Lonicera oblongifolia* (Goldie) Hook. *Vaccinium angustifolium* Ait.
Hemicryptophytes	*Agrostis scabra* Willd. *Bromus ciliatus* L. *Castilleja raupii* Pennell *Cicuta maculata* L. *Galium labradoricum* (Wieg.) Wieg. *Solidago canadensis* L. *Stellaria calycantha* (Ledeb.) Bong.	*Aster borealis* (Torr. & Gray) A. & D. L"ve *Aster ciliolatus* (Lindl.) A & D. L"ve *Campanula rotundifolia* L. *Carex bebbii* Olney *ex* Fern. *Cicuta bulbifera* L. *Geum allepicum* Jacq. *Glyceria borealis* (Nash) Batchelder *Rumex aquaticus* S. Wats. *Sium suave* Walt. *Taraxacum officianale* G.H. Weber *ex* Wiggers *Tofieldia glutinosa* (Michx.) Pers.	*Carex retrorsa* Schwein. *Carex siccata* Dewey* *Chrysosplenium tetrandrum* (Lund) Th. Fries *Cinna latifolia* (Trev. *ex* Goepp.) Griseb. *Deschampsia caespitosa* (L.) Beauv. *Dryopteris carthusiana* (Vill.) H.P. Fuchs *Epilobium palustre* L. *Galium palustre* L.* *Geum rivale* L. *Glyceria pulchera* (Nash) K. Schum. *Liparis loeselii* (L.) Rich. *ex* Lindley* (S3?) *Luzula parviflora* (Ehrh.) Desv. *Lycopus uniflorus* Michx. *Potentilla norvegica* L. *Rubus idaeus* L. *Rumex orbiculatus* Gray *Sanicula marilandica* L.
Geophytes	*Elymus* spp.	*Carex atherodes* Spreng. *Eriophorum angustifolium* Honckeny *Maianthemum canadense* Desf. *Malaxis monophyllos* (L.) Sw. (S1/S2) *Monotropa uniflora* L. *Scirpus acutus* Muhl. *ex* Bigelow	*Actaea rubra* (Ait.) Willd. *Botrychium virginianum* (L.) Sw. *Carex lacustris* Willd. *Carex lasiocarpa* Ehrh. *Carex trisperma* Dewey *Corallhiza maculata* (Raf.) Raf. *Equisetum variegatum* Schleich. *ex* F. Weber & D.M.H. Mohr *Eriophorum gracile* W.D.J. Koch *Listera borealis* Morong (S2) *Scirpus hudsonianus* (Michx.) Fern. *Urtica dioica* L.
Helophytes		*Typha latifolia* L.	
Hydrophytes			*Potamogeton* spp. *Ranunculus gmelinii* DC *Utricularia intermedia* Hayne

Table 4.6. Total R^2 of multiple regression models of bryophyte and vascular plant species richness and environmental variables. Forward and stepwise methods were used with identical results.

Variables Included	R^2	F	P
Bryophytes			
Easting	0.233	23.732	≤ 0.001
Vascular Plants			
Easting	0.216	21.543	≤ 0.001
Easting + Elevation	0.487	35.251	≤ 0.001
Easting + Elevation + Overstory Density	0.506	25.942	≤ 0.001

Table 4.7. Percent of variance explained in the bryophyte and vascular plant community data with latitude and longitude used as covariables, individually and combined, in distance-based redundancy analyses. Other environmental variables include elevation, precipitation, surface water alkalinity and temperature, percent overstory density, and peat organic C.

Environmental Variables	Bryophytes			Vascular Plants		
Latitude	9.3	-	-	7.9	-	-
Longitude	-	8.2	-	-	8.4	-
Latitude and Longitude	-	-	11.8	-	-	12.2
Other Environmental Variables	14.7	15.8	12.1	21.7	21.2	17.5
Total Variance Explained	24.0	24.0	23.9	29.6	29.6	29.7
Total Variance Unexplained	76.0	76.0	76.1	70.4	70.4	70.3

Figure 4.1. Western boreal forest Ecozones. Study site locations at Utikuma Lake, Alberta, Prince Albert National Park (NP), Saskatchewan, and Duck Mountain, Manitoba are within the Boreal Plains Ecozone. Image adapted from map provided by Ducks Unlimited Canada, Western Boreal Office.

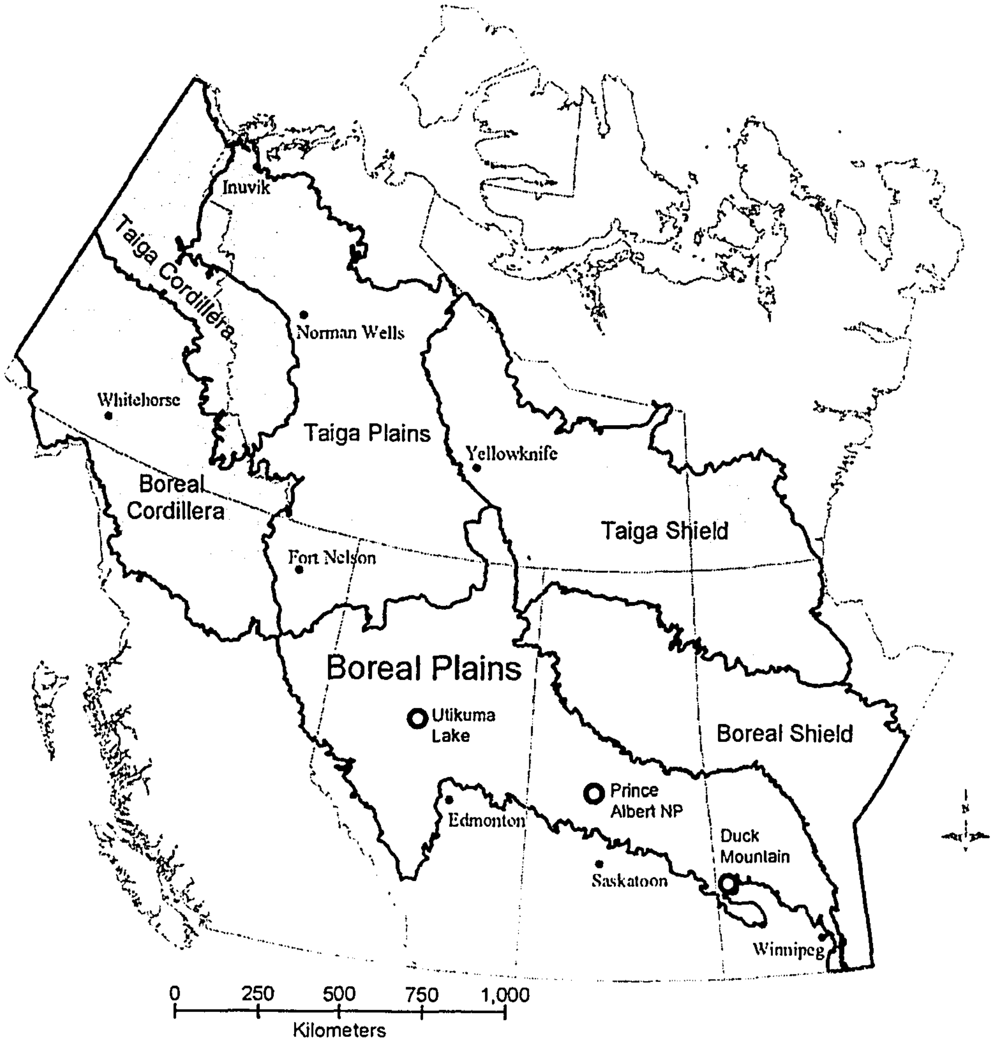


Figure 4.2. Ordinations of (A) bryophytes and (B) vascular plants in wooded moderate-rich fens at Utikuma Lake, Alberta (AB), Prince Albert National Park, Saskatchewan (SK), and Duck Mountain, Manitoba (MB). Selected environmental variables overlain the ordination surface: North = latitude, East = longitude; Elev = elevation; Precip = precipitation; OSD = forest overstory density; °C = surface water temperature; SC = specific conductance, Alk = alkalinity, and; Peat BD = peat bulk density.

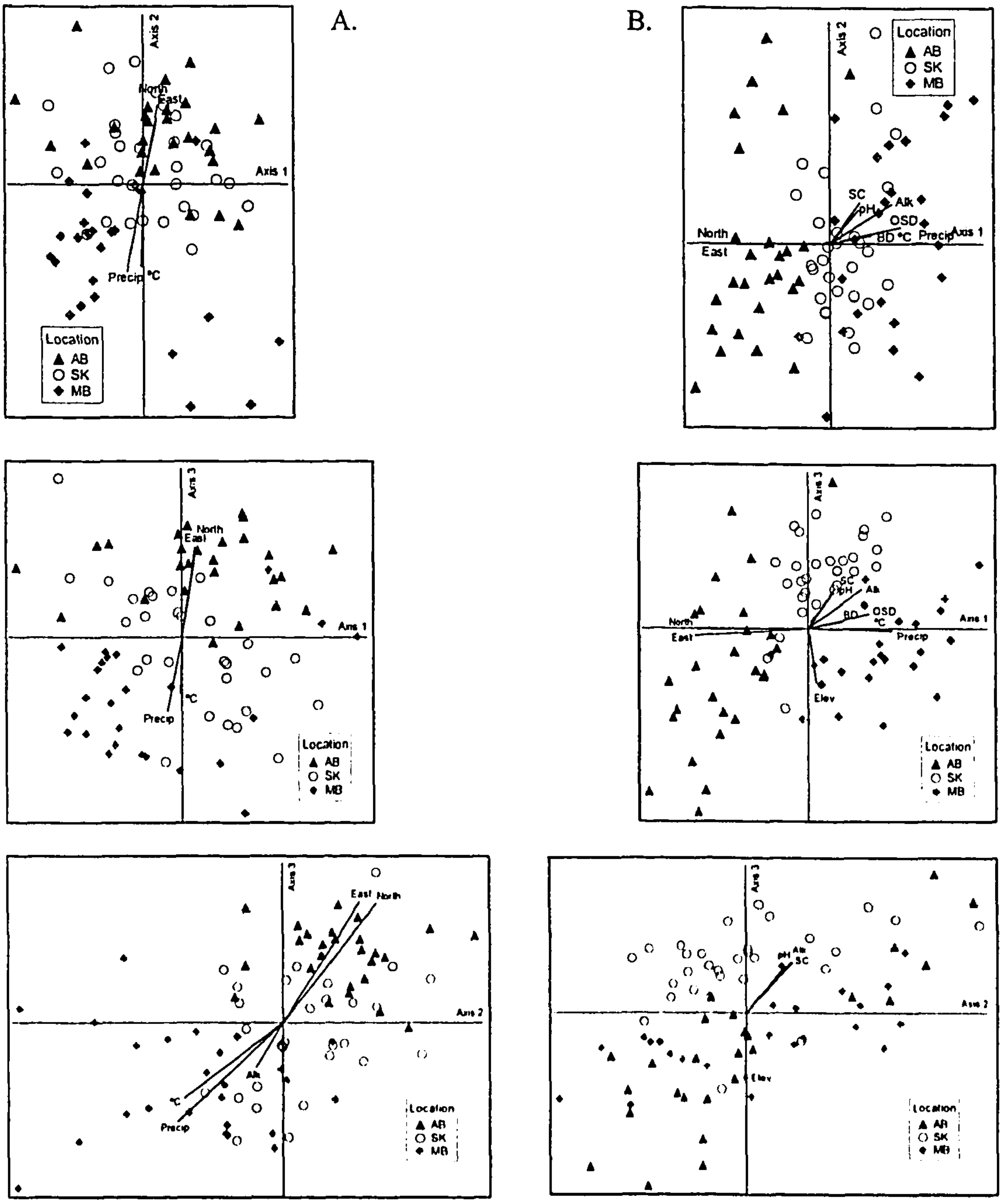
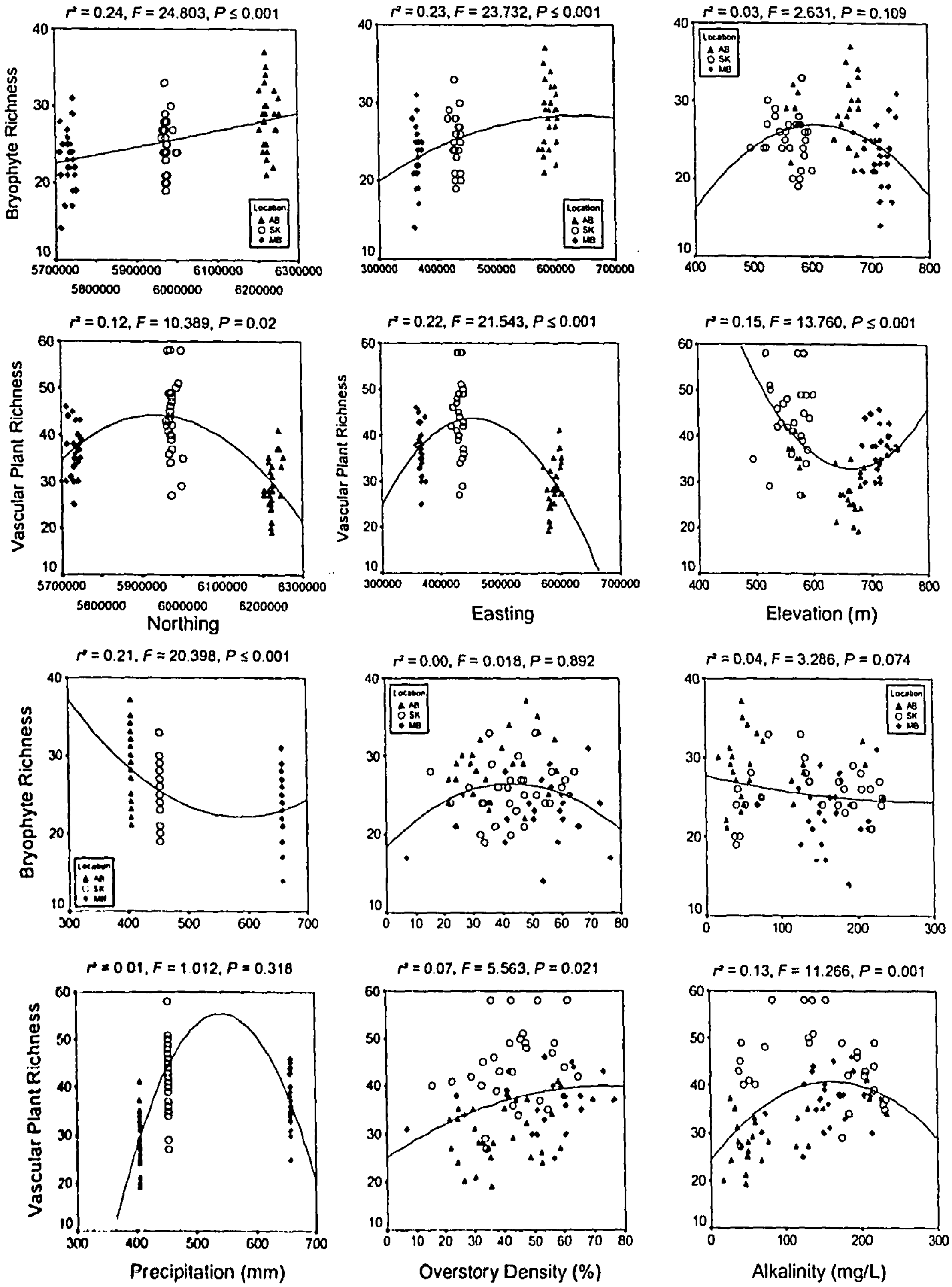


Figure 4.3. Scatter plots of bryophyte and vascular plant richness and selected environmental variables at Utikuma Lake, Alberta (AB), Prince Albert National Park, Saskatchewan (SK), and Duck Mountain, Manitoba (MB). Fitted quadratic regression lines and linear regression statistics are included.



5. IMPACTS OF LOGGING IN THE SOUTHERN BOREAL PEATLANDS OF MANITOBA, CANADA

5.1 INTRODUCTION

Approximately 30% percent of the world's boreal region is comprised of wetlands (World Resources Institute 2000), most of which are peatlands, wetlands with at least 40 cm of peat (National Wetlands Working Group 1997). In North America, peatlands are comprised of bogs, fens, and swamps. Bogs are ombrogenous and receive water and nutrients primarily from atmospheric deposition, while fens receive water and nutrients principally from subsurface and surface water. Both types can be dominated coniferous trees, coniferous and deciduous shrubs, or graminoids (National Wetlands Working Group 1997). In North America, peatland swamps have dense forests of conifers, and are often down slope and transitional between uplands and peatlands or water bodies (National Wetlands Working Group 1997, Locky et al. In press).

Recent studies in Canada's western boreal region have shown that the greatest diversity and rarity of bryophytes is found in wooded peatlands, in particular wooded moderate-rich fens (Vitt et al. 2003, Locky unpublished), and black spruce swamps (Locky unpublished). Additionally, vascular plant diversity and rarity have also been found to be highest in wooded moderate-rich fens and black spruce swamps (Locky unpublished). Many wooded peatlands have marketable *Picea mariana* (Mill.) BSP and *Larix laricina* (Du Roi) K. Koch that are harvested primarily as high quality pulpwood. In Canada, harvesting timber on peatlands is relatively common in the eastern boreal region (Jeglum 1991), but is limited in the western boreal region. This is expected to change since timber resources in southern parts of the western boreal region are becoming increasingly depleted and peatlands are beginning to be logged. Currently, less than 17% of the boreal plains ecozone remains as intact contiguous forest (Lee et al. 2003).

Compared to natural disturbances, such as fire and natural tree fall in mature forests, clear-cutting differs in several ecological respects, including increases in water table depth (Dubé et al. 1995), release of nutrients (Knighton and Stiegler 1980), and loss of biomass in a uniform pattern (Franklin et al. 2000). Peatlands with harvestable timber are particularly susceptible to the disturbance of the peat substrate, including rutting, compaction, and erosion (Groot 1987, review in Nugent et al. 2003). This in turn affects plant species composition; the process of logging can lead to the creation of bare peat where few plants will grow (Brumelis and Carleton 1989) and nutrient-rich microsites that favour fast-growing weed species (Groot 1987). Regeneration of *Picea mariana* on clear-cut peatlands is not usually considered a problem (Jeglum 1987), but other aspects of the plant community may be affected (Brumelis and Carelton 1988, 1989). In post-harvest peatland sites, regeneration is generally dependent on portions of the understory taxa (aboveground genets, belowground parts, and seed bank) rather than seed rain from adjacent areas. The presence of understory taxa (including bryophytes) is important and may affect the successional direction of the site post-harvest (Taylor et al. 1987). Most seedbeds in the boreal forest are dominated by bryophytes which may either facilitate or hinder seedling survival (Hörnberg et al. 1997).

Potential changes on post-harvest sites include long-term continuity of woody species after harvest (Neiring and Goodwin 1974, Brumelis and Carleton 1988, 1989). Often the expansion of dense thickets (e.g., *Alnus, Salix, Rubus*) by regeneration and invasion on logged black spruce sites is associated with the most nutrient-rich sites (Brumelis and Carleton 1988, 1989). Compared to bogs, fens may be more susceptible to released nutrients from clear-cutting due to significantly higher water yields (Knighton and Stiegler 1980). On these sites, clear-cuts may result in loss of diversity and alteration of community composition of vascular plants and bryophytes (Hannerz and Hånell 1997). Harvest intensity affects plant communities in different ways and clear-cuts cause the most significant change to vascular plant communities, increased plant cover and changes in species composition (Hannerz and Hånell 1993, Bergstedt and Milberg 2001), which can lead to difficulties in site renewal, including significant losses of the original tree biodiversity (Hannerz and Hånell 1993). Communities of bryophytes, particularly hepatics, may show compositional changes in response to the severity of harvest impacts to forest floors (Fenton et al. 2003).

Studies on the effects of forest harvest on peatlands have been primarily restricted to the eastern boreal region of Canada (Brumelis and Carleton 1988, 1989, Jeglum 1991, Trettin et al. 1997). Research on forestry on peatlands in the western boreal region has been limited to the physical impacts of drainage (Silins and Rothwell 1998, 1999) and tree growth (Macdonald and Yin 1999). Thus, the impacts of logging peatlands on the plant community and site conditions in the western boreal region of Canada have not yet been studied. This is especially important, given that the western boreal region, particularly the boreal plain, receives significantly lower precipitation than the eastern boreal region.

In this chapter I compare various aspects of the plant community and site environmental variables between wooded peatland remnants and clear-cut portions of the same peatland 1-4 and 9-12 years since harvest. The specific objectives were to describe trends in: (1) the plant community (characteristic indicator species, species richness, diversity, cover, similarity indices, composition, vegetation physiognamy, number of regenerating tree stems, number of shrub stems), and (2) environmental variables (site physical variables, surface water chemistry, peat physical variables).

5.2 MATERIALS AND METHODS

Study region and site description

Duck Mountain is approximately 70 km from north to south and 60 km from east to west (51° 15' - 52° 00' N, 100° 35' - 102° 35' E), and one of a series of highlands that rises above the prairie in Manitoba and Saskatchewan on Canada's Boreal Plain (Ecological Stratification Working Group 1995). The hummocky landscape is produced by deep deposits of glacial clay, gravel, sand, and boulders over the erosion-resistant shale bedrock (Klassen 1979), and lakes, rivers, and wetlands are interspersed throughout the region. The vegetation is typical of the Boreal Mixed-wood Region (Manitoba Natural Resources 1997). The Boreal Plain climate in Manitoba is humid continental, with a mean annual precipitation of 430 mm, ranging between 250 and 660 mm (Klassen 1979). In localized areas on the prairies, the orographic effect of land masses has been known to increase precipitation by over 100 mm per year (Hogg 1994). Riding Mountain National Park (50° 43' N, 99° 33' W) (756 m amsl) is 35 km south of Duck Mountain and receives 111 mm more precipitation per year than the adjacent plain (Hogg 1994). Using methods from Hogg (1994), I estimated that Duck Mountain (810 m amsl) receives 668.6

mm of precipitation per year. This is 37% more precipitation than at adjacent Swan River, which is approximately 379 m lower in elevation.

Duck Mountain is within the South Mid-boreal Wetland Region and approximately 22% of the area is covered by wetlands. Most of these wetlands are peatlands (Halsey et al. 1997). Because these peatlands are at the southern limit of peatland distribution for the Boreal Plain (Ecological Stratification Working Group 1995), they are likely to be highly sensitive to disturbance due to climate change (Kettles and Tarnocai 1999). In addition, as timber resources in upland areas of the south-western Boreal Plain come under increased pressure (Lee et al. 2003), some peatlands within the region are being logged.

Thirty-five wooded peatland stands were located in stands that had been clear-cut in winter using feller-bunchers (location coordinates in Appendix A). These sites were primarily wooded moderate-rich fens, with some gradating to black spruce swamps, and one wooded bog site, per the classification in Locky et al. (In press). Duck Mountain peatlands are relatively small and isolated due to the rolling topography of the area (Locky et al. In press). Consequently, most of the clear-cuts were relatively small and estimated to be less than 2 ha in size. The sizes of the remaining wooded portions were variable, but relatively small. The clear-cuts ranged in age between 1 and 12 years since harvest, but two clear-cut age classes emerged: 1-4 years and 9-12 years. Divided this way there were 20 1-4 year class sites and 15 9-12 year class sites. Paired surveys were conducted, with one plot in the clear-cut portion and one plot in the remaining wooded portion at each of these sites.

Plant diversity surveys

One 5-m radius plot (78.5 m^2) was placed in a representative area of each clear-cut and wooded site. Plots were located at least 10 m away from the edge of the clear-cut to avoid edge effects. Each plot was surveyed for bryophytes, three common *Cladina* (reindeer) lichens, and vascular plants. Habitats within plots were sampled consistently, but collection of corticolous bryophytes was incomplete and most species from that group were not included in the analyses. Total percent cover was estimated for the bryophyte/lichen layer, herbaceous layer, shrub layer, and tree layer. In addition, a 10 m transect across the plot perpendicular to the forest edge was used to determine cover of vegetation physiognomic layers (shrub, herb, ground). The number of shrub stems and spruce seedlings/young trees were counted in each plot, including stems resulting from *Picea mariana* layering. There are difficulties in separating seedling and juvenile *Picea mariana* from *Picea glauca* (Moench) Voss, so these species were grouped. Surveys were completed between 15 June and 15 September, 2001 and 2002. Nomenclature for vascular plants follows the Plant Element List from the Alberta Natural Heritage Information Centre (2002) where possible and Scoggan (1978-1979) for others, true mosses follow Anderson et al. (1990), *Sphagnum* follows Anderson (1990), hepatics follow Stötler and Crandall-Stötler (1977), and lichens follow Esslinger and Egan (1995).

Environmental variables

Specific conductance (adjusted for temperature and hydrogen ions), pH, and water temperature measurements were taken at one location at each site in open pools, depressions in the substrate, or in excavated wells (20 – 80 cm). The collected water samples were packed in ice, and the same day, one 500 ml sample was filtered with Whatman® GF/F glass microfibre filters and one 500 ml sample was left unfiltered. Samples were frozen for later chemical analysis at the Limnology Laboratory at the University of Alberta of total phosphorus (TP), soluble reactive phosphorus (SRP), nitrate ($N0_2^- + N0_3^-$), ammonium, (NH_4^+), total nitrogen (TN), sodium (Na^+), potassium (K^+), calcium (Ca^{2+}), magnesium (Mg^{2+}), iron (Fe^+), sulphate (SO_4^{2-}), chloride (Cl^-), and dissolved organic carbon (DOC) following Vitt et al. (1995). pH (< 5.5) and specific conductance values were adjusted by subtracting the effect of hydrogen ions following Sjörs (1952). Means for pH were calculated using hydrogen ions and then were reconverted to pH for display and discussion. Water table depths were measured at each water sampling station, and nearby a soil core 5.2 cm diameter x 5.0 cm long was extracted 15 cm below the surface, and bagged, labelled, and frozen the same day. From these cores, bulk density, organic C, and inorganic C content were determined using the loss on ignition method (Dean 1974). A Carlo-Erba NA 1500 Carbon/Nitrogen Elemental analyzer was used to determine peat carbon to nitrogen (C:N) at the University of Alberta Soils Laboratory. Mean peat depth was determined with a 3 m metal probe from the centre to the outer boundaries of each site. I used the point centred quarter (PCQ) method to characterize the peatland forests, and measured tree height, tree diameter at breast height (dbh), and percent overstory density (Spherical Crown Concave Densiometer), and calculated tree density by trees/ha (Cottam and Curtis 1956). The survey criteria included trees ≥ 5 cm dbh within 7.5 m distance from the quadrat centre. Some peatlands were small (< 1.0 ha) or non-linear in shape and limited the PCQ transect length to 45 m. Surveyed trees were also cored with a 5 mm increment borer and the cores aged by France Conciatori from the Centre for Forest Interdisciplinary Research, University of Winnipeg, Manitoba.

Peatlands that have been logged are prone to 'watering-up' or higher water tables, during the growing season due to reduced transpiration and interception (Heikurainen 1967, Dubé et al. 1995). To determine oxygen restrictions to rooting in the peat due to 'watering up', the depth of the aerated zone was measured using 6 to 10 steel welding rods inserted into the peat of each of the paired plots in early summer. Measurements were made of various oxidation layers following Carnell and Anderson (1986), and were measured approximately four and eight weeks after installation for the following effects: bright steel (abundant oxygen), orange-brown (scarcely abundant oxygen), black (previously anaerobic), and matte grey (no oxygen).

In clear-cut plots, physical damage from mechanized logging was assessed by measuring degree of rutting, coarse woody debris (i.e., logs > 7.5 cm), fine woody debris, exposed peat, and exposed mineral soil with a 0 – 3 cover scale: 0 = none; 1 = < 25%, 2 = 26 - 50%, and 3 = > 50%.

Data analysis

Most of the water chemistry and peat variables and some categories of species diversity and cover data had skewed, non-normal distributions that could not be transformed. Kruskal-Wallis H non-parametric tests for groups of two (or more) were used to determine differences in ranks of these variables between wooded and clear-cut pairs of the 1-4 and the 9-12 year class plots. Kruskal-Wallis H tests were also used to determine differences in the same variables but between the 1-4 year and 9-12 year class clear-cut plots. Species data was analyzed by species richness of total, bryophyte/lichen, vascular plant, and bryophyte taxa and vascular plant life forms (see below). To help assess the ecological importance of the observed differences in selected variables between the paired wooded and clear-cut plots, 95% confidence interval plots, which are useful in displaying effect size measures and associated measures of precision, were used in addition to reporting P values (Di Stefano 2003). All univariate analyses were completed using SPSS v. 11.5 (SPSS Inc. 2003).

Community composition

Community composition was examined by determining species occurrences and diversity of bryophyte/lichen taxa and vascular plant life forms. Bryophytes were split into true mosses (excludes *Sphagnum*), hepatics, and *Sphagnum,* and vascular plants were split into Raunkiaer's (1934) vascular plant life form divisions, a classification based on the position and seasonality of the perennating buds or rejuvenating organs following Scoggan (1978-1979) as follows (See species list in Appendix B):

Phanerophytes: trees and tall shrubs > 2 m
Nanophanerophytes: shrubs < 2 m
Chamaephytes: short or prostrate plants; buds not above 25 cm from soil surface
Hemicryptophytes: renewal buds at soil surface
Geophytes: renewal buds underground (rhizomes, tubers, corms, bulbs)
Helophytes: plants submersed in mud
Hydrophytes: plants submersed or floating
Therophytes (annuals): renewal buds protected by seed

Phanerophytes were further classified as Raunkiaer's (1934) mesophanerophytes (trees) and microphanerophytes (tall shrubs) for the percent occurrences analyses (see below).

Indicator species

Indicator species analysis (ISA) (Dufrêne and Legendre 1997) was used to determine significant indicator species for the wooded plots and clear-cut plots. The wooded plots were combined as there were no significant differences in any variables measured between 1-4 year and 9-12 year class plots. Thus, ISA was calculated for three groups: wooded plots, 1-4 year class clear-cut plots, and 9-12 year class clear-cut plots. ISA calculates indicator species values by multiplying the relative abundance of each species in a specific group by the relative frequency of the species' occurrence in that group. A Monte Carlo simulation test with 1000 randomized runs, where samples are randomly assigned to types, was used to determine the significance ($P \leq 0.05$) of the indicator values (Dufrêne and Legendre 1997, McCune and Mefford 1999). The significance level and percent relative frequency for each species generated by the simulation test can be listed for each group, indicating the likelihood of finding each species in each group. To test the significance of the wooded, 1-4 year clear-cut, and 9-12 year clear-cut group indicator species, Multiple Response Permutation Procedure (MRPP), a non-parametric analogue of Discriminant Function Analysis, but without many of the associated assumptions was used (McCune and Mefford 1999, McCune and Grace 2002).

Community similarity

Sørensen's coefficient of community similarity was calculated for pairs of wooded and clear-cut plots for 1-4 and 9-12 year age classes to determine shared species. Sørensen's measure is the most robust of the qualitative (presence-absence) diversity measures (Magurran 2004). Separate analyses were performed on bryophyte/lichen taxa and vascular plant life forms.

Plant community and environmental variables

To explore structure in the plant community data, non-metric multidimensional scaling (NMS) ordination was employed. Plant species with a 'trace' percent occurrence were converted to 0.25 % for the NMS ordination. The autopilot function with the slow and thorough analysis and varimax rotation option was selected. Varimax rotation is an eigenvalue-based method that orients the axes through clusters of sample units and variables, emphasizing both high and low correlations of the individual variables (McCune and Grace 2002). A random starting configuration number was used for Monte

Carlo tests with 1000 randomized runs. The proportion of variance represented by the ordination axes were determined using after-the-fact r^2 correlations between the distances in the ordination space and the original space (McCune and Mefford 1999).

Direct methods of ordination, such as Canonical Correspondence Analysis, have been used to explore the relationship between environmental variables and vegetation communities, but can be strongly influenced by extraneous environmental variables. Therefore, NMS, an indirect method employed in order to maintain community structure (McCune 1997), was used to deduce vegetation-environment relationships using joint plot overlays of environmental variables (McCune and Grace 2002). The environmental variables included degree of rutting, coarse and fine woody debris cover, exposed peat, exposed mineral soil, water table depth and temperature, peat depth, number of pools, and hummock-hollow height were used to determine differences between the 1-4 and 9-12 year class clear-cuts. All multivariate analyses and data transformations were completed using PC-ORD v. 4.25 (McCune and Mefford 1999).

5.3 RESULTS

The wooded portions of the peatlands of both age classes were the control sites and characterized as having a mean tree height of 10.3 m (range: 9.4 – 11.1 m), mean diameter at breast height of 12.3 cm (11.4 – 13.3 cm), mean percent overstory density of 42% (37 – 47%), and mean tree density of 2322 trees/ha (1965 – 2678 trees/ha). The mean age of the forest, as measured in the plots, was 110 years (65 – 245 years). There were no differences in these or any other variables measured between from either the 1-4 year and 9-12 year classes of wooded control plots.

Indicator species

Based on MRPP, there were significant differences between the indicator species in the wooded and the 1-4 year clear-cut plots (A-value = 0.134, $P \leq 0.001$), and wooded and 9-12 year clear-cut plots (A-value = 0.148, $P \leq 0.001$), but not between the clear-cut groups. The wooded control plots had the strongest suite of indicator species (by importance value) of the three groups tested (Table 5.1). These plots were characterized by *Picea mariana* trees and shrubs, *Larix laricina* trees, *Ledum groenlandicum,* *Vaccinium vitis-idaea,* and *Rubus chamaemorus.* The wooded group was also strongly distinguished by bryophytes, including *Pleurozium schreberi, Hylocomium splendens, Ptilium crista-castrensis* (primarily in wooded plots), *Rhizomnium gracile, Dicranum undulatum, Sphagnum warnstorfii* and *S. fuscum*, and three hepatic species. The lichen *Cladina rangiferina* was commonly found, and there were few hemicryptophyte (renewal buds at soils surface) or geophyte (renewal buds underground) indicator species.

Clear-cut plots in the 1-4 year class had the fewest indicator species, and were characterized by two true mosses, *Polytrichum strictum* and *Funaria hygrometrica*, shrub-sized *Betula papyrifera* and *Pinus banksiana*, hemicryptophytes such as *Calamagrostis canadensis, Rubus pubescens,* and *Taraxacum officinale*, and the geophyte, *Carex vaginata* (Table 5.1).

Clear-cut plots in the 9-12 year category had the greatest number of significant indicator species of the three groups, and were characterized by upland phanerophytes (trees and tall shrubs > 2 m) such as *Populus balsamifera* and *P. tremuloides,* shrub-sized *Larix laricina,* various *Salix* spp., a large number of hemicryptophytes, including many grasses, and the geophytes *Carex aquatilus* and *Petasites frigidus* var. *palmatus* (Table 5.1).

Plant community change

Diversity

Total plant diversity was approximately 30% higher in clear-cut plots compared to wooded plots in both age classes (Table 5.2). There were 74 species found in clear-cut plots that were not found in wooded plots (1-4 year class = 51 species; 9-12 year class = 55 species), and 25 species found in wooded plots not found in clear-cut plots (1-4 year class = 15 species; 9-12 year class = 20 species). Total mean species richness (SR) was also significantly higher in clear-cut plots in the 1-4 (χ = 6.486, df = 1, P = 0.011) and 9-12 year age classes (χ = 12.596, df = 1, $P \leq 0.001$). However, wooded plots had significantly higher mean SR for bryophytes/lichens in comparisons with both age classes (χ = 5.706, df = 1, P = 0.017; χ = 6.652, df = 1, P = 0.010), whereas vascular plant SR was significantly higher in clear-cut plots of age both age classes (χ = 11.635, df = 1, P = 0.001; χ = 21.040, df = 1, $P \leq 0.001$) (Table 5.2, Fig. 5.1A). Significantly higher bryophyte/lichen SR in wooded plots was attributed to *Sphagnum* ($\chi = 6.040$, df = 1, $P = 0.014$), hepatics ($\chi = 18.646$, df = 1, $P \leq 0.001$), and lichens ($\chi = 5.732$, df = 1, $P = 0.017$) in 1-4 year class plots, and hepatics ($\chi = 8.629$, df = 1, $P = 0.003$) and lichens ($\chi = 4.737$, df = 1, $P = 0.030$) in 9-12 year class plots. Of the vascular plant life forms, significantly higher SR in 1-4 year class clear-cut plots was comprised of phanerophytes ($\chi = 15.098$, df = 1, $P \leq 0.001$) and hemicryptophytes ($\chi = 19.723$, df = 1, $P \leq 0.001$); mean chamaephyte (short or prostrate plants) SR was higher in wooded plots of the 1-4 year age class ($\chi = 10.474$, df = 1, $P = 0.001$). Increases in vascular plant SR in the 9-12 year class clear-cut plots were attributed to phanerophytes ($\chi = 20.228$, df = 1, $P \leq 0.001$), nanophanerophytes (shrubs < 2 m) ($\chi = 8.702$, df = 1, $P = 0.003$), and hemicryptophytes ($\chi = 20.711$, df = 1, $P \leq 0.001$).

Mean diversity as measured by Simpson's diversity index was significantly higher in clear-cut plots for vascular plants in both the 1-4 ($\chi = 6.329$, df = 1, $P = 0.012$) and 9-12 ($\chi = 4.047$, df = 1, $P = 0.044$) year classes, whereas evenness was significantly higher for both bryophytes/lichens ($\chi = 4.339$, df = 1, $P = 0.037$; $\chi = 5.691$, df = 1, $P = 0.017$) and vascular plants in clear-cut plots of both age classes ($\chi = 5.165$, df = 1, $P = 0.023$; $\chi = 4.132$, df = 1, $P = 0.042$).

The number of regenerating tree stems was significantly higher in clear-cut plots of both age classes for *Larix laricina* ($\chi = 6.927$, df = 1, $P \leq 0.001$; $\chi = 9.566$, df = 1, $P = 0.002$), and in the 1-4 year class of clear-cut plots for *Pinus banksiana* ($\chi = 8.181$, df = 1, $P = 0.004$) (Figure 5.2). There was no difference in the number of *Picea* spp. tree stems between wooded and clear-cut plots of both age classes. Plot vegetation physiognamy (along the 10 m transect) was significantly higher in wooded plots of both age classes for the ground layer ($\chi = 29.971$, df = 1, $P \leq 0.001$; $\chi = 23.254$, df = 1, $P \leq 0.001$), and in 9-12 year class clear-cut plots, significantly higher for the shrub layer ($\chi = 8.574$, df = 1, $P = 0.003$), and marginally higher for the herb layer ($\chi = 3.809$, $P = 0.051$). Noteworthy, is the discovery of *Malaxis paludosa* (L.) Sw., an S1 species (rare throughout its range) (Manitoba Conservation 2003), near a wooded plot.

In comparing clear-cut plots of both age classes, there was significantly higher richness in 9-12 year class plots for total species ($\chi = 4.714$, df = 1, $P = 0.030$), total vascular plants ($\chi = 4.780$, df = 1, $P = 0.029$), and hemicryptophytes ($\chi = 4.578$, df = 1, $P = 0.032$).

Percent Cover

Mean percent cover (cover) was significantly higher for bryophytes/lichens in wooded plots of 1-4 year (96% vs. 55%: $\chi = 20.438$, df = 1, $P \leq 0.001$) and 9-12 year (96% vs. 56%: $\chi = 16.514$, df = 1, $P \leq 0.001$) classes, but higher for vascular plants in wooded plots of the 1-4 year class (131% vs. 83%: $\chi = 8.776$, df = 1, $P = 0.003$) (Fig. 5.1B). Of the bryophytes/lichens, significantly greater mean cover in the wooded plots was attributed to true mosses (64% vs. 40%: $\chi = 7.767$, df = 1, $P = 0.005$), *Sphagnum* (27% vs. 7%: $\chi = 15.933$, df = 1, $P \leq 0.001$), and lichens (4.0% vs. 0.3%: $\chi = 11.061$, df = 1, $P = 0.001$) for 1-4 year class plots, and true mosses (64% vs. 32%: $\chi = 11.995$, df = 1, $P = 0.001$) and *Sphagnum* (31% vs. 15%: $\chi = 4.234$, df = 1, $P = 0.040$) for 9-12 year class plots. True mosses and *Sphagnum* in the clear-cut plots appeared dessicated, discoloured, and stressed, particularly in the 1-4 year class. *Sphagnum* was rarely dry, but plants were often discoloured black or white, with the capitula very densely packed. Although not considerably different in mean hepatic cover, both age classes of clear-cut plots contained robust patches of *Marchantia polymorpha* L, primarily in ruts, compared with wooded plots. Higher vascular plant cover for wooded plots was comprised of phanerophytes (61% vs. 14%: $\chi = 24.529$, df = 1, $P \leq 0.001$), nanophanerophytes (39% vs. 15%: $\chi = 21.266$, df = 1, $P \leq 0.001$), and chamaephytes (2.6% vs. 0.7%: $\chi = 8.110$, df = 1, $P = 0.004$) in 1-4 year class plots. While there were no significant differences in total mean vascular plant cover in 9-12 year class plots, by life forms there was significantly higher cover of phanerophytes (54% vs. 26%: $\chi = 12.003$, df = 1, $P = 0.001$) and nanophanerophytes (37% vs. 10%: $\chi = 7.347$, df = 1, $P = 0.007$) in wooded plots. Hemicryptophyte cover was significantly higher in both 1-4 and 9-12 year class clear-cut plots (16% vs. 39%: $\chi = 8.147$, df = 1, $P = 0.004$; 17% vs. 56%: $\chi = 17.903$, df = 1, $P \leq 0.001$).

In comparing clear-cut plots of both age classes, 9-12 year class plots had significantly higher cover of vascular plants ($\chi = 5.370$, df = 1, $P = 0.020$), *Sphagnum* (χ

$= 4.551$, df = 1, $P = 0.033$), phanerophytes ($\chi = 5.152$, df = 1, $P = 0.023$), and nanophanerophytes ($\chi = 4.398$, df = 1, $P = 0.036$).

Community similarity

Community similarity between wooded and clear-cut plots in 1-4 and 9-12 year age classes, as indicated by Sørenson's index, was higher for bryophytes/lichens (0.51, 0.56) than vascular plants (0.32, 0.29). Bryophyte taxa were less similar in the 1-4 year age class plots than the 9-12 year age class plots (true mosses: 0.58, 0.62; *Sphagnum*: 0.61, 0.66; hepatics: 0.09, 0.20), whereas the opposite was observed for lichens (0.28, 0.24). All vascular plant life forms were more similar in 1-4 year age class plots than 9-12 year class plots (phanerophytes: 0.28, 0.17; nanophanerophytes: 0.50, 0.42; chamaephytes: 0.56, 0.55; hemicryptophytes 0.16, 0.14), except geophytes (0.28, 0.37).

Community composition

Percent occurrences (occurrences) of bryophyte/lichen taxa and vascular plant life forms were virtually identical in wooded plots from the 1-4 and 9-12 year classes, and results are discussed using a single wooded category and two clear-cut classes (Fig. 5.3).

There were lower occurrences of lichens (50%) and hepatics (53%) in the clear-cut plots of both age classes than wooded plots, whereas moss occurrences were greater (~19%) in clear-cut plots (Fig. 5.3). *Sphagnum* occurrences were similar across the wooded and clear-cut plots.

Occurrences of hemicryptophytes were 43% greater between clear-cut than wooded plots of both age classes, whereas chamaephyte and geophyte occurrences were 60% and 36% less, respectively (Fig. 5.3). While phanerophyte occurrences appeared to be similar between the wooded and clear-cut classes, subdividing phanerophytes revealed that mesophanerophytes (trees) were ~80% less in cut plots, and microphanerophytes (tall shrubs) were ~26% greater in cut plots. Nanophanerophyte occurrences were ~12% less in clear-cut plots than wooded plots.

Environmental variables

Compared to wooded plots, hummock to hollow heights were significantly lower in clear-cut plots of both 1-4 ($\chi = 25.758$, df = 1, $P \leq 0.001$) and 9-12 year ($\chi = 20.280$, df = 1, $P \leq 0.001$) classes, and mean peat depth was significantly lower in 9-12 year class plots ($\chi = 4.315$, df = 1, $P = 0.035$) (Fig. 5.2). Clear-cut plots in the 1-4 year class had significantly higher NH_4^+ ($\chi = 13.140$, df = 1, $P \leq 0.001$), $NO_2^- + NO_3^-$ ($\chi = 9.566$, df = 1, $P = 0.002$), SRP ($\chi = 11.617$, df = 1, $P = 0.001$), and surface water temperature ($\chi = 12.660$, df = 1, $P \leq 0.001$). Peat bulk density was marginally significantly higher in 1-4 year class clear-cut plots ($\chi = 3.689$, df = 1, $P = 0.055$). No significant differences were observed in the oxidation patterns of the steel rods placed in peat between wooded and clear-cut plots.

Between clear-cut plots, regeneration of *Picea* spp. and *Larix laricina* was significantly higher in 9-12 year class plots ($\chi = 8.810$, df = 1, $P = 0.003$; $\chi = 3.832$, df = 1, $P = 0.050$). Plots that were 1-4 years old had significantly higher NH_4^+ ($\chi = 7.656$, df = 1, $P = 0.006$), $NO_2^- + NO_3^-$ ($\chi = 4.989$, df = 1, $P = 0.026$), and SRP ($\chi = 10.240$, df = 1, $P = 0.001$), while water table depth was significantly lower in 9-12 year class plots ($\chi = 3.542$, df = 1, $P = 0.060$).

Plant community and environmental variables

The NMS ordination of community data resulted in a stable two dimensional solution with a high, but acceptable final stress of 17.2 (Kruskall 1964), and final instability of 0.00015 at 400 iterations. The proportion of variation represented by the ordination axes was 76%, and comprised of 52% on axis one and 23% on axis two. A clear separation between wooded and clear-cut plots was evident in the ordination diagram (Fig. 5.4). However, clear-cut plots of both age classes were not clearly separated in the ordination space. Vegetation physiognamy of ground cover and hummock to hollow heights were the only environmental variables that were associated with the wooded plots in the ordination diagram joint plot overlays. Exposed peat, surface water temperature, coarse and fine woody debris, and the vegetation physiognamy of shrubs and herbs were associated with clear-cut plots, but did not discriminate between the two. The near monoculture of *Typha latifolia* L. in one site with elevated water table is obvious in the upper right hand corner of the main and inset ordination diagrams.

5.4 DISCUSSION

Plant community trends

Abrupt changes in species composition after peatland clear-cutting were illustrated by the significantly different suites of indicator species between the wooded and clear-cut plots. Understory succession in *Picea mariana* stands is strongly linked to stages in tree growth (Taylor et al. 1987), and it is not surprising that the suite of indicator species in the 1-4 and 9-12 year class clear-cut plots were not significantly different; the difference in age between these plots is not great. However, the two clear-cut plot classes were different by individual species and taxa/life forms. 1-4 year class plots had the fewest and least strong indicator species, and were characterized by pioneer mosses, such as *Funaria hygrometrica,* (Ross-Davis and Frego 2002) and *Polytrichum strictum*, the latter which commonly invades milled peatlands (Groeneveld and Rochefort 2005). Plots in the 9-12 year class were obviously more advanced in succession than the 1-4 year class plots, with many *Salix* spp., invading upland trees, grasses, and geophytes (renewal buds below ground), including *Taraxacum officinale. Taraxum officinale* was found to be among the most widespread alien species in disturbed boreal ecosystems in Gros Morne National Park (Rose and Hermanutz 2004), and change of grass cover is significantly enhanced with logging pressure in boreal forests (Peltzer et al. 2000, Bergstedt and Milber 2001). The incidence of various species of *Salix,* in some cases in large patches, and significantly higher richness and cover of phanerophytes (trees and tall shrubs > 2 m) and nanophanerophytes (shrubs < 2 m) in 9-12 year class clear-cut plots suggests the formation of stable communities of shrubs. Long-term continuity of woody species after disturbance can seriously impede the growth of pre-disturbance species (Neiring and Goodwin 1974, Brumelis and Carleton 1988, 1989). The expansion of dense thickets of shrubs (e.g. *Alnus rugosa, Salix* spp.) by regeneration on logged black spruce sites is often associated with nutrient-rich (i.e., mineral-rich) sites (Brumelis and Carleton 1989).

Hepatic cover was unchanged between wooded and clear-cut plots, but species richness and composition did change. Vigorous patches of *Marchantia polymorpha* that often filled whole ruts were observed, similar to that found by Brumelis and Carleton (1988). Hepatic composition changes with intensity of forest floor disturbance (Fenton et al. 2003), and hepatics are more sensitive to drought than true mosses (Moen and Jonsson 2003).

Bryophyte richness and cover were significantly less in clear-cut plots. Bryophytes react more rapidly to microenvironment changes than vascular plants (Slack 1990), and seem to respond more negatively to forestry related perturbations, such as clear-cuts, in peatlands (Deans et al. 2003). Moss cover has been found to be significantly reduced after clear-cutting (Hannerz and Hånell 1997), and dying mosses release space for the germination of plant seedlings (Pykälä 2004). While moss occurrences increased in clear-cut plots of both age classes, this was more a reflection of fewer occurrences of hepatics and lichens, as percent cover of all bryophytes was significantly less in clear-cut plots. Much of the moss cover in the Duck Mountain peatlands is comprised of feather mosses, which eventually die due to high irradiance and drought stress (Brumelis and Carleton 1988). Although isolated patches of feather mosses have a high probability of surviving catastrophes (Ross-Davis and Frego 2002), the loss of mosses means that the successional phases associated with post-fire forest development and canopy-thinning dynamic are altered (Taylor et al. 1987). Early successional mosses, particularly acrocarpous species, e.g., *Ceratodon, Polytrichum*, commonly replace later succession species, primarily pleurocarpous species, e.g., *Pleurozium shreberi* and *Hylocomium splendens*, in clear-cut peatlands (Hannerz and Hånell 1997). Peatland and upland forest species, such as *Dicranum polysetum* and *Pleurozium shreberi,* which were strong wooded plot indicator species, favour dry conditions (Laine and Vanha-Majamaa 1992). *Sphagnum* occurrences were similar across all wooded and clear-cut plots, but richness and cover were significantly lower in clear-cut plots. Contrary to Roy et al. (2000), *Sphagnum* in Duck Mountain clear-cut plots appeared stressed. *Sphagnum* mosses are poor pioneer species or substrate stabilizers in peatlands (Rochefort 2000) and peat can blow away. If *Polytrichum strictum* becomes established in a disturbed peatland, it can lead to enhanced growth of conifers, various woody species, (Groeneveld and Rochefort

2005) and *Sphagnum* (Filion and Morin 1996). *Sphagnum,* in turn, increases receptivity of the seedbed for *Picea mariana* seed rain (Groot and Adams 1994). Moss establishment, in turn, is also dependent on post-logging tree recruitment, and feather mosses will not return until the reestablishment of evergreen trees (Brumelis and Carleton 1988, 1989).

The removal of overstory trees increases light availability and decreases competition of tree saplings (Grubb 1994), and also helps to explain increased vascular plant richness in Duck Mountain peatland clear-cuts. Pykälä (2004) observed that mean and total vascular plant richness almost doubled in < 2 year old scarified clear-cuts than mature forests, and clear-cut and mature forests were distinctly separated in multivariate analyses in the present study. Also observed were several dozen non-forest species in the clear-cuts. These plants are assumed to have come from a long-term persistent species pool, or were wind-dispersed (Pykälä 2004). As many of the new species are not common peatland plants, and unlikely in the seed bank, these species were most likely dispersed by wind from adjacent upland clear-cuts or along logging roads where they are also commonly found.

For vascular plants, the shift in species composition to increased hemicryptophytes (renewal buds at soil surface) in 9-12 year class clear-cut plots was also reflected in significantly higher species richness. Vascular plant diversity is considered highest in the earliest stages of succession (Zobel 1989, Pitkänen 2000). The increases are probably related to increased light, which can also increase the biomass of herbs after three to five years (Kardell and Eriksson 1983). Increases in phanerophyte and nanophanerophyte richness and cover, particularly a shift to more microphanerophytes (tall shrubs) in 9-12 year class clear-cuts, is similar to Roy et al. (2000), who observed pronounced invasions of *Populus tremuloides* and *Betula papyrifera* in forested wetland clear-cuts.

All of the phanerophytes and nanophanerophytes that dominated 9-12 year class clear-cuts at Duck Mountain were native species commonly found in peatlands, which sometimes dominate open shrubby fens (Locky et al. In press). *Pinus banksiana*, which is commonly found in peatlands as an incidental species (National Wetlands Working Group 1988), invaded clear-cut plots of the 1-4 year class, but were virtually absent in the

9-12 year class plots. This species may have been out-competed by *Larix laricina*, which had germinated in great numbers in both clear-cut plot age classes, but particularly in 9-12 year class plots (Fig. 4). *Larix laricina* is a strong competitor in open peatlands compared to other conifers; Macdonald and Yin (1999) observed that *Larix laricina* out-competed *Picea mariana* after the drainage of a peatland.

Bryophyte and vascular plant diversity and evenness, as measured by Simpson's indexes, were slightly higher in clear-cuts of both age classes, contrary to Hannerz and Hånell (1997). The increased diversity and evenness in clear-cuts may be the result the original suite of peatland flora remaining, (with reduction of dominance of some plants, e.g., feather mosses) and new, 'non-peatland' species originating as a result of disturbance.

Logging disturbances in peatlands may negatively affect rare species that lack a persistent seed bank and that require sheltered habitats (Elofsson and Gustafsson 2000), or have specific germination requirements, such as orchids (Kevan et al. 1993). One *Malaxis paludosa*, a S1 species was found in a wooded site plot, but other rare orchids (and sedges) have been found in wooded moderate-rich fens and black spruce swamps at Duck Mountain (Chapter 3).

Patterns in environmental variables

Hummock heights were significantly lower in both clear-cut age classes. Loss of hummocks also means loss of microhabitats, and increased microhabitats have been directly related to increased bryophyte richness and rarity (Vitt et al. 1995, Vitt et al. 2003), and conifer regeneration in peatlands (Hörnberg et al. 1997). Hummocks comprised 35% of the forest floor of a Swedish peatland, but contributed almost 50% of the *Picea abies* regeneration (Hörnberg et al. 1997). Although hummock development is complex and depends on a number of factors, including the species pool (van der Molen and Hoekstra 1988) and environmental conditions (Belyea and Clymo 1998), increased *Sphagnum* cover in 9-12 year class over 1-4 year class plots suggests that hummocks are beginning to reform.

I observed a significant, but apparently temporary (only in 1-4 year class clear-cut plots) flush of various forms of nitrogen and phosphorus, concomitant with higher water temperatures in clear-cut plots. This may be related to the marginally higher bulk density observed in 1-4 year class clear-cuts, which may be evidence of compaction; peat compaction can increase bulk density and the capacity to retain water (Price 1997). The increased nutrients may also be related to aeration or peat oxidation associated with summer water table drawdowns that result in increased P and N in peatland surface waters (Devito and Dillon 1993) or the decomposition of woody debris.

In general, water table increases are proportional to the amount of wood cut on peatlands (Heikurainen 1967). No water table rises were observed in the clear-cut plots compared to the wooded plots that were studied. This is similar to Groot (1998) who found water table increases only under the most intense harvest conditions, and contrary to Dubé et al. (1995), who found substantial water table increases (e.g., 20 cm) in their 120 m x 80 m peatland clear-cuts. Statistically significantly lower water tables in 9-12 year class clear-cut plots compared to 1-4 year class clear cut plots may have resulted from environmental effects; in peatlands with saturated soil profiles, water tables can drop due to increased soil radiation and wind speed in the clear-cut area (Verry 1980, Dubé et al. 1995). The significantly reduced peat depths in 9-12 year class clear-cuts may also be related to the peat physically abrading and blowing away due to long-term exposure. Bare peat is prone to high surface temperatures and drought, which also inhibits plant establishment and growth (Brumelis and Carleton 1989).

5.5 CONCLUSIONS

Clear-cutting wooded peatlands at Duck Mountain results in significant changes in plant richness, cover, and community composition. These changes may ultimately alter the successional trajectory of the site, depending on the severity of site disturbance. Advance growth of *Picea mariana* appears to be protected, but there is evidence of establishment of stable shrub communities of *Salix* and *Alnus*, change in species composition to hemicryptophytes, such as grasses, ruderals such as *Marchantia polymorpha*, and in particularly wet disturbances in the peat, *Typha latifolia*. Minimization of site disturbance should be a priority when clear-cutting peatlands (Brumelis and Carleton 1989). Dubé et al. (1995) propose that watering up can be reduced with the use of low pressure wide-tired skidders and harvesting on frozen soils to prevent rutting and ponding of water, and retention of advanced regeneration.

The rolling topography at Duck Mountain often leads to peatlands developing spatially independent of each other. Further fragmentation due to clear-cut logging may have longer-term implications on the plant community. While adult plants can survive at one scale, deriving nutrients and other resources at the microsite level, reproductive success of these plants often occurs at a much broader scale, including pollen interception from distant plants for successful outcrossing, and pollinator movement in the surrounding landscape (Kollmann 2000).

Boreal wooded fens and swamps often have the greatest diversity and rarity in bryophytes (Vitt et al. 2003, Locky, unpublished) and vascular plants (Locky, unpublished) and require some conservation consideration. The portion of the peatland left unharvested, i.e., ecosystem remnant, could help to determine the natural vegetation (Allen and Wilson 1991), provide a propagule source through the soil (Brown and Bedford 1997), or allow general ecosystem conservation (Webb and Vermaat 1990). Older forest stands often contain the greatest diversity of uncommon vascular plants, and retention of live trees and heavy shrubs is beneficial to the flora (Elofsson and Gustafsson 2000).

This study is a preliminary investigation into the impacts of logging on peatlands in the western boreal region. Further research over an extended period is required to determine how long impacts to peatlands will persist into the future. Peatland logging in Canada's western boreal region will continue to increase and it is important to understand the vegetation dynamics in these sites.

Acknowledgements

Funding and technical support from the Sustainable Forest Management Network, Edmonton, Alberta for this project was greatly appreciated. I thank Louisiana-Pacific Canada Ltd., Swan River, Manitoba, especially Margaret Donnelly, Donna Grassia, Peter Sigurdson, and Barry Waito for providing technical and in-kind support. A C/BAR grant to DAL provided by the Canadian Circumpolar Institute was appreciated. Jacques Tardif and France Conciatori from the Centre for Forest Interdisciplinary Research, University of Winnipeg, Manitoba are thanked for methodological assistance in tree coring, and all tree cores were dated by France Conciatori. Sarah Wilkinson and Richard Caners provided valuable feedback regarding this manuscript.

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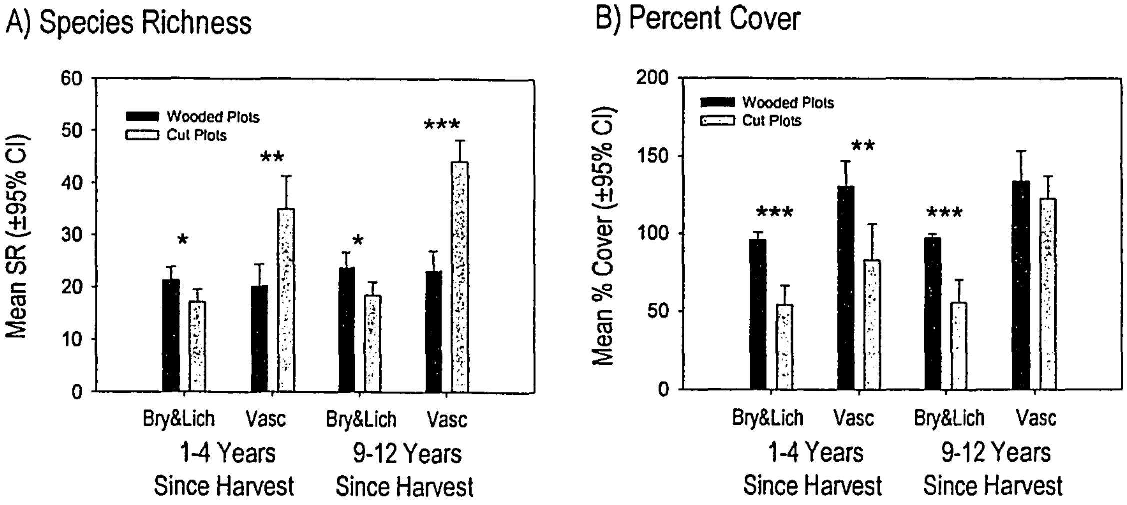
Table 5.1. Two-way table of characteristic indicator species from Duck Mountain, Manitoba wooded sites (wooded) and clear-cut sites 1-4 (CC 1-4) and 9-12 (CC 9-12) years old before surveys. Importance values, significance ($P \leq 0.05$), and relative type frequencies (% fidelity to treatment) from Indicator Species Analysis (Dufrêne and Legendre 1997). Bolded numbers highlight the category in which characteristic indicator species are significant. Wooded sites were treated as one control group in the analysis (see text for details). Moss = true moss, Spha = *Sphagnum*, Pha = phanerophyte, Nan = nanophanerophyte, Cha = chamaephyte, Hem = hemicryptophyte, Geo = geophyte.

Treatment	Indicator Species	Taxa/	% Relative Frequency			Importance	*P*
		Life Form	Wooded	CC 1-4	CC 9-12	Value	Value
Wooded (control)	*Picea mariana* (P. Mill.) B.S.P.	Pha	**97**	20	13	96.0	0.001
	Hylocomium splendens (Hedw.) Schimp. *in* B.S.G.	Moss	**100**	50	67	90.8	0.001
	Pleurozium schreberi (Brid.) Mitt.	Moss	**100**	80	93	81.2	0.001
	Ptilium crista-castrensis (Hedw.) De Not.	Moss	**89**	40	33	79.5	0.001
	Ledum groenlandicum Oeder	Nan	**97**	90	87	79.0	0.001
	Vaccinium vitis-idaea L.	Cha	**94**	85	80	73.5	0.004
	Ptilidium pulcherrimum (G.Web.) Hampe	Hepatic	**94**	20	27	71.7	0.001
	Picea mariana (P. Mill.) B.S.P. shrub-size	Pha	**80**	35	73	66.6	0.001
	Maianthemum trifolium (L.) Sloboda	Geo	**83**	70	53	61.2	0.006
	Cladina rangiferina (L.) Nyl.	Lichen	**66**	30	20	57.1	0.002
	Sphagnum warnstorfii Russ.	Spha	**86**	50	73	55.7	0.003
	Sphagnum fuscum (Schimp.) Klinggr.	Spha	**74**	50	47	51.4	0.006
	Rubus chamaemorus L.	Hem	**51**	30	33	48.6	0.003
	Larix laricina (Du Roi) K. Koch	Pha	**49**	5	13	47.7	0.001
	Carex gynocrates Wormsk. ex Drej.	Geo	**69**	50	53	47.3	0.007
	Rhizomnium gracile T. Kop.	Moss	**60**	10	13	43.2	0.003
	Lepidozia reptans (L.) Dum.	Hepatic	**51**	15	0	39.8	0.003
	Dicranum undulatum Brid.	Moss	**66**	30	13	39.6	0.002
	Calypogeia sphagnicola (H. Arnell et J. Perss.) Warnst. et Loeske	Hepatic	**46**	5	13	32.6	0.005
1 - 4 Years Since Harvest	*Polytrichum strictum* Brid.	Moss	77	**95**	93	56.3	0.012
	Taraxacum officinale G.H. Weber ex Wiggers	Hem	3	**75**	60	52.9	0.008
	Calamagrostis canadensis (Michx.) Beauv.	Hem	26	**70**	60	50.0	0.013
	Carex vaginata Tausch	Geo	31	**70**	67	45.0	0.004
	Rubus pubescens Raf.	Hem	23	**45**	20	41.4	0.012
	Betula papyrifera Marsh. shrub-size	Pha	0	**45**	20	39.4	0.001
	Funaria hygrometrica Hedw.	Moss	0	**45**	27	28.3	0.012
	Pinus banksiana Lamb. shrub-size	Pha	0	**35**	13	25.3	0.006
9 - 12 Years Since Harvest	*Rubus idaeus* L.	Hem	0	75	**87**	69.1	0.001
	Bromus ciliatus L.	Hem	0	25	**80**	66.8	0.001
	Achillea millefolium L.	Hem	0	10	**67**	64.6	0.001
	Populus tremuloides Michx. shrub-size	Pha	0	65	**93**	63.2	0.002
	Rubus arcticus L.	Hem	29	40	**80**	62.0	0.001
	Epilobium angustifolium L.	Hem	6	80	**80**	60.3	0.001
	Larix laricina (Du Roi) K. Koch shrub-size	Pha	31	50	**87**	57.3	0.001
	Fragria virginiana Duchesne	Hem	3	50	**87**	53.1	0.001
	Salix bebbiana Sarg.	Pha	14	75	**87**	52.9	0.001
	Salix planifolia Pursh	Pha	11	45	**67**	51.6	0.001
	Deschampsia caespitosa (L.) Beauv.	Hem	3	30	**73**	50.6	0.001
	Carex aquatilus Wahlenb.	Geo	63	45	**67**	49.6	0.005
	Populus balsamifera L. shrub-sized	Pha	3	45	**80**	47.3	0.004
	Petasites frigidus var. *palmatus* (Ait.) Cronq.	Geo	3	30	**60**	46.4	0.002
	Poa palustris L.	Hem	11	55	**67**	41.5	0.009
	Mertensia paniculata (Ait.) G. Don	Hem	0	45	**53**	41.2	0.003
	Agrostis scabra Willd.	Hem	3	50	**53**	39.4	0.010
	Salix serissima (Bailey) Fern.	Pha	3	15	**40**	37.7	0.001
	Aster ciliolatus (Lindl.) A. & D. L"ve	Hem	3	20	**53**	32.2	0.013
	Utica dioica L.	Geo	0	35	**53**	32.2	0.006
	Geum allepicum Jacq.	Hem	0	5	**27**	26.1	0.012
	Galium trifidum L.	Hem	9	5	**33**	23.7	0.012
	Ribes oxyanthoides L.	Nan	0	5	**27**	22.5	0.007

Table 5.2. Total (mean) species richness in wooded and clear-cut plots in peatland sites 1-4 years and 9-12 years since harvest at Duck Mountain, Manitoba. Kruskall-Wallis H test statistics significance levels indicate differences between mean richness: *** ≤ 0.001, ** ≤ 0.01, * ≤ 0.05. See text for significance values.

	1 - 4 Years				9 - 12 Years			
Taxa or Life Form	Wooded		Clear-cut		Wooded		Clear-cut	
	n = 20		n = 20		n = 15		n = 15	
Total Species	135	(41.6)	183	(52.2) *	149	(46.9)	184	(62.7) ***
Bryophytes and Lichens	51	(21.4) **	50	(17.2)	54	(23.7) *	51	(18.5)
True Mosses	30	(13.1)	33	(13.2)	32	(15.8)	34	(13.7)
Sphagnum	4	(2.9) *	5	(2.0)	5	(3.1)	6	(2.7)
Hepatics	14	(4.2) ***	9	(1.5)	14	(3.5) **	8	(1.7)
Lichens	3	(1.3) *	3	(0.5)	3	(1.3) *	3	(0.5)
Vascular Plants	84	(20.2)	133	(35.1) ***	95	(23.2)	133	(44.2) ***
Phanerophytes	12	(3.1)	17	(6.6) ***	13	(4.0)	17	(8.3) ***
Nanophanerophytes	11	(2.8)	15	(3.3)	10	(2.7)	15	(4.4) **
Chamaephytes	6	(2.9) **	4	(1.8)	6	(2.4)	6	(2.1)
Hemicryptophytes	32	(5.7)	68	(16.6) ***	39	(7.2)	66	(21.5) ***
Geophytes	22	(5.9)	27	(6.7)	25	(6.8)	25	(7.5)
Helophytes	1	(0.1)	1	(0.2)	1	(0.1)	3	(0.3)
Therophytes	0	(0.1)	1	(0.1)	1	(0.1)	1	(0.1)

Figure 5.1. Mean species richness (A) and percent cover (B) of bryophytes and lichens and vascular plants between wooded and clear-cut (cut) plots in peatland sites 1-4 years and 9-12 years since harvest at Duck Mountain, Manitoba. Kruskall-Wallis H test statistics significance levels: *** ≤ 0.001, ** ≤ 0.01, * ≤ 0.05. Bry&Lich = Bryophytes and Reindeer Lichens, Vasc = Vascular Plants, SR = Species Richness, % = Percent Cover.



A) Species Richness

B) Percent Cover

Figure 5.2. Distributions of selected statistically significantly different biotic, physical, and environmental variables between wooded (black) and clear-cut (gray) plots in peatland sites 1-4 years and 9-12 years since harvest at Duck Mountain, Manitoba with 95% confidence interval error bars. Kruskall-Wallis H test statistics significance levels: *** ≤ 0.001, ** ≤ 0.01, * ≤ 0.05. See text for significance values. Veg Phys = Vegetation Physiognamy, SRP = Soluble Reactive Phosphorus. Vegetation physiognamy displayed in cm, but discussed in percent in text.

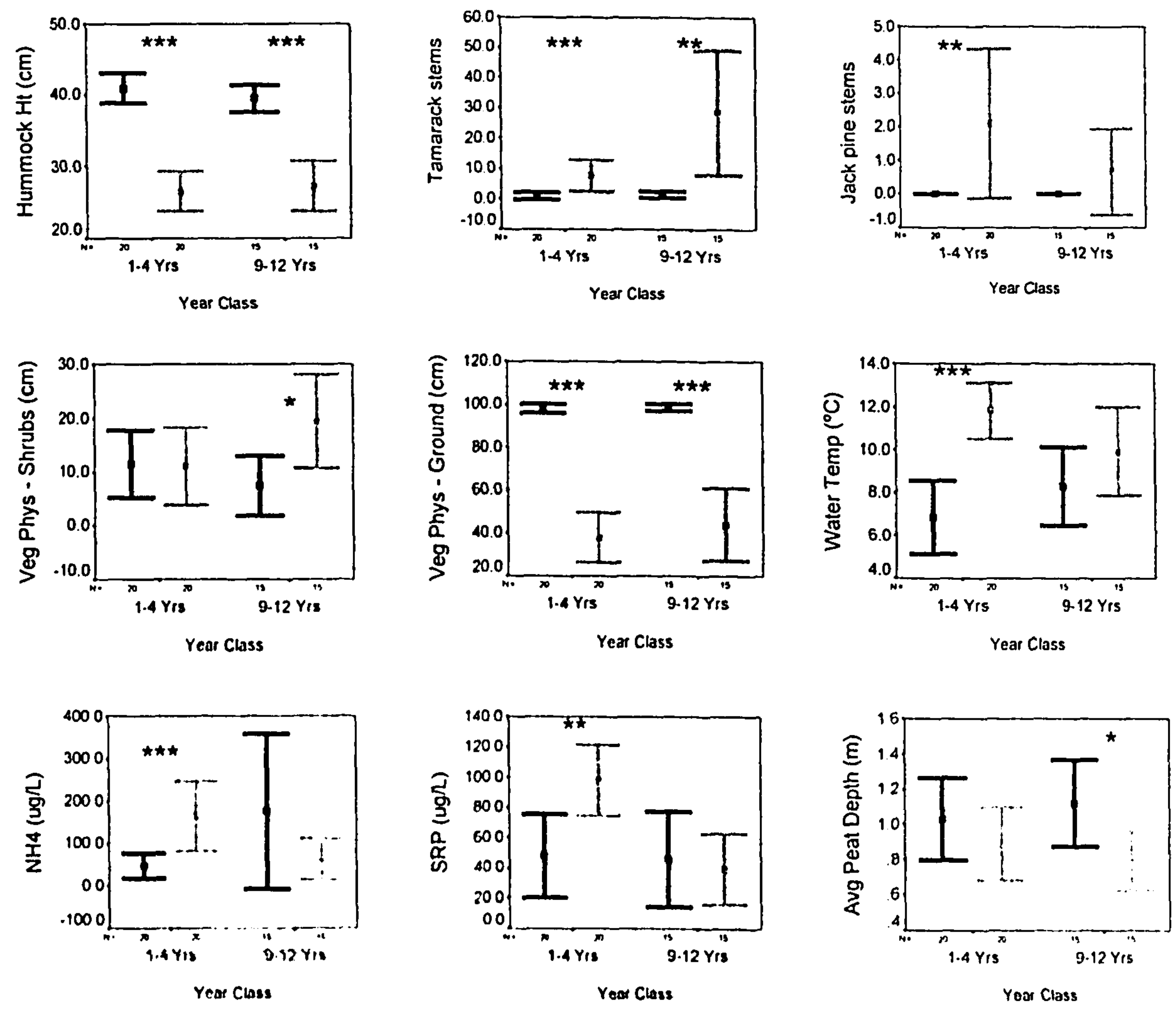


Figure 5.3. Percent occurrences of bryophyte and lichen taxa and vascular plant life forms between control wooded plots and clear-cut plots 1-4 years and 9-12 years since harvest. Mosses = true mosses, Pha = phanerophytes, Nan = nanophanerophytes, Cha = chamaephytes, Hem = hemicryptophytes, Geo = geophytes, Hel = helophytes, and The = therophytes. Phanerophyte total percent is displayed with subdivision into (a) mesophanerophytes (trees) and (b) microphanerophytes (tall shrubs).

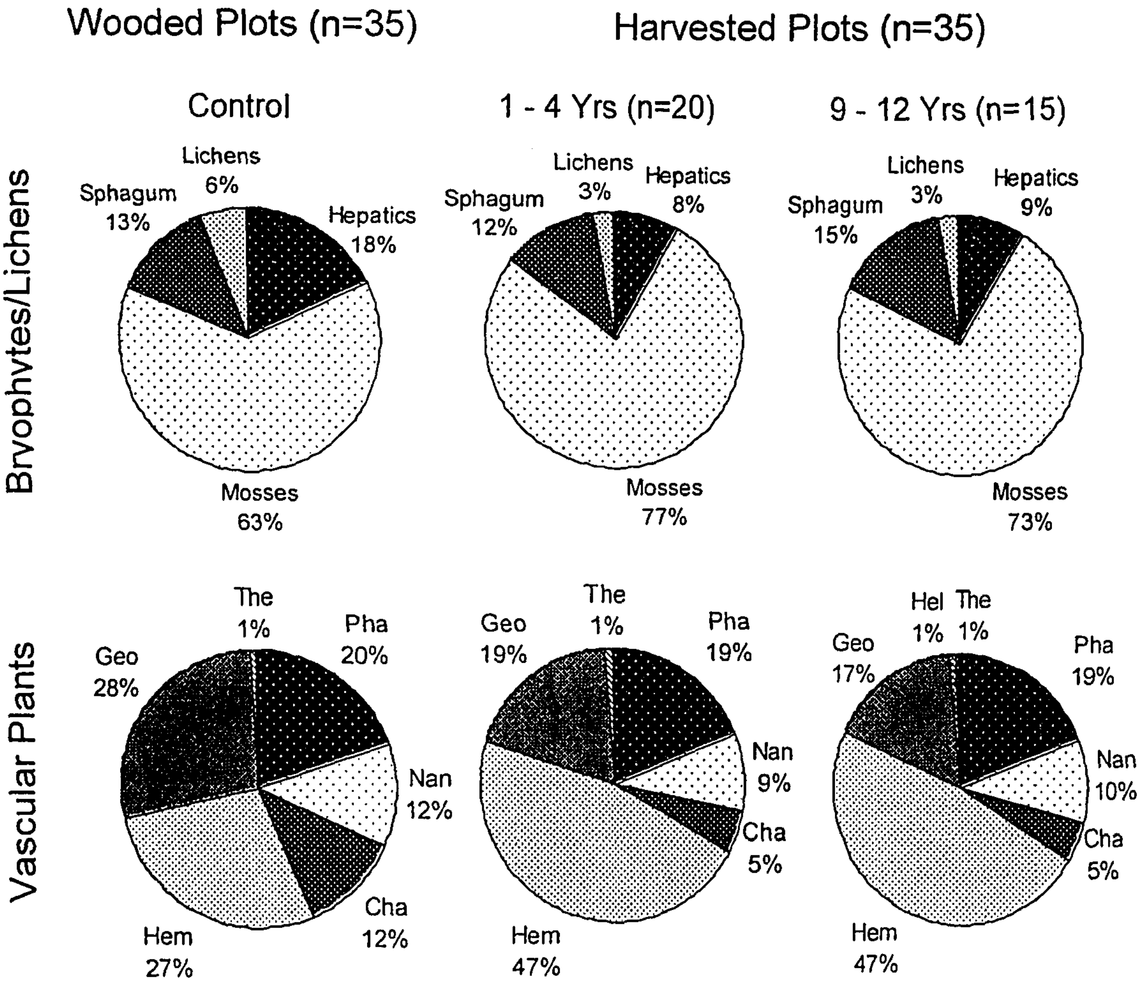
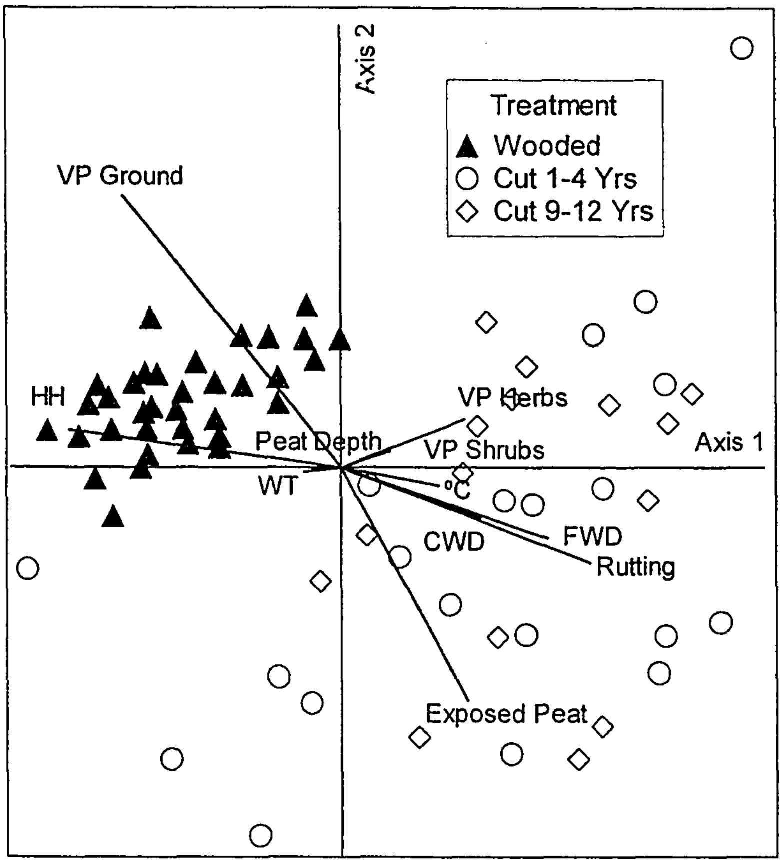


Figure 5.4. Varimax rotation NMS ordination of species data with wooded and 1-4 year and 9-12 year clear-cut class sites at Duck Mountain, MB are indicated. Vectors are passive environmental variable overlays. VP = Vegetation Physiognomy, HH = Hummock – Hollow Height, WT = Water Table, CWD = Coarse Woody Debris, FWD = Fine Woody Debris, °C = Water Temperature.



6. SYNTHESIS

This thesis examines a number of different aspects of peatland ecology that are emerging issues in Canada's western boreal forest, including wetland classification, plant diversity and rarity at different scales, and impacts from logging. Together, these results present a more complete picture of western boreal peatlands which can facilitate development of effective policy and mitigation initiatives related to industrial land use and potential climate warming in the boreal region.

6.1 ARE BLACK SPRUCE SWAMPS DISTINCT ENTITIES?

Few studies have described black spruce swamps (Zoltai et al. 1988, Jeglum 1991, National Wetlands Working Group 1997), and Locky et al. (In press) have shown that these peatlands can be differentiated from bogs and fens based on a number of characteristics. These include location on gentle slopes adjacent to water bodies, taller and larger trees, greater percent overstory density, shallower relative peat depths, and smaller relative area. The plant species assemblage in black spruce swamps is most similar to wooded moderate-rich fens, but there is an abundance of fen indicator species often found in mesic non-peatland sites. As with previous research (Jeglum 1991), black spruce peatlands were found to have surface waters and peat that are highly variable.

Terminology in wetland research is constantly being refined (Schwintzer 1981, Mewhort and Bayley 2004). Conifer swamp with peat at least 40 cm and dominated by *Picea mariana* in the North American boreal region should be referred to as black spruce swamp for clarity when comparing with *Thuja occidentalis*-dominated swamps in the eastern boreal region (Kenkel 1987) and *Picea mariana*-dominated uplands found throughout the boreal region (Klinka et al. 2002). *Larix laricina*-dominated peatlands with a relatively high percent overstory density (>60%) are occasionally found within the Boreal Plains Ecozone (Chapter 4). Further investigations into these sites should take place to determine whether they would be included as conifer swamps as some workers have proposed, or if they are better classified as wooded moderate-rich fens.

6.2 PLANT DIVERSITY, COMPOSITION, AND RARITY AT DIFFERENT SCALES

This research supported evidence that wooded moderate-rich fens are among the most species-rich in bryophytes (Vitt et al. 1995, Vitt et al. 2003), and illustrated similarly high diversity in black spruce swamps (Chapter 3). Little research has been done on vascular plant species diversity in peatlands, and it was observed that diversity patterns were similar to bryophyte diversity. Bryophyte diversity has been shown to be greatest in both extreme-rich fens (Vitt et al. 1995) and moderate-rich fens (Vitt and Chee 1990). These discrepancies suggest that further work is required to either refine classification terms, or survey additional sites. The best comparisons of diversity will be among sites that are most similar (e.g., Chapter 4). Chapter 3 illustrated a unimodal distribution of species richness, and to a lesser degree, rare species occurrences over a bog – rich fen gradient. Reasons for this pattern are complex, but high diversity appears to be related to high habitat heterogeneity (Vitt et al. 1995, Vitt et al. 2003) and moderate values of some environmental variables, such as pH and alkalinity (Chytrý et al. 2003) in wooded moderate-rich fens and black spruce swamps. Low diversity appears related to environmental extremes, e.g., pH and alkalinity (Chytrý et al. 2003), and related low nutrients (Malmer 1986) and plant toxicity (Rey Benyas and Scheiner 1993, Vitousek and Hooper 1993) in bogs and extreme-rich fens. The patterns revealed in my research provide corroborating evidence for these hypotheses, but more fine-scale study designs are required in order to determine causal relations between environmental variables and plant diversity and composition. A first step would include a study design utilizing a large number of 0.5 m x 0.5 m plots for surveys of plant diversity, cover and environmental variables (e.g., Cox and Larson 1993, Nekola 2004, Mancera et al. 2005). This is particularly true for bryophytes, as the relationships between environmental variables and plant diversity and floristic composition were strongest for vascular plants (Chapters 2, 3, and 4).

From Locky et al. (In press) it is evident that wooded moderate-rich fens are among the commonest peatland types at Duck Mountain, which confirms findings in other western boreal region locations (Zoltai et al. 1988, Vitt et al. 2003, Chapter 4). When examining plant diversity in wooded moderate-rich fens across the Boreal Plains Ecozone, the patterns vary by location depending on which diversity components are examined (Chapter 4). Floristic attributes explain, in part, the greater total diversity (alpha) in Manitoba sites, but climatic considerations related to location including growing degree days, elevation, and local orographic precipitation are also important. Significantly higher mean vascular plant richness (mean alpha diversity) in Saskatchewan may be related to lower elevation, inclusion of another Ecoregion (i.e., species pool), and, compared to Alberta, higher surface water pH and alkalinity. These characteristics may in turn be related to the *Larix laricina*-dominated sites that were observed in Saskatchewan, but not Alberta or Manitoba. More research on *Larix laricina*-dominated fens across the western boreal region may lead to further conclusions on diversity and rarity compared to *Picea mariana*-dominated fens. Alberta sites are the oldest and this may be a factor in the greater mean bryophyte diversity observed there. However, further research into more climatic and historical perspectives of plant species richness (e.g., Grytnes et al. 1999) would increase the resolution of regional plant diversity patterns. The use of ecoregions (and ecozones) is becoming increasingly important in conservation planning (Magnusson 2004). Comparisons of diversity and other measures among ecoregions is an important test of the validity of ecoregion boundaries. However, it is essential to also understand that the distributional ranges of the organisms of interest, as many types of organisms will not follow closely ecoregion boundaries (Magnusson 2004).

This research not only found that wooded moderate-rich fens, compared to other peatland types, have the greatest number of rare locally-rare bryophytes, confirming other studies (Vitt et al. 2003), but that locally and provincially rare vascular plant diversity is also highest in this peatland type (Chapter 3). Locally rare plants were found to be most numerous in black spruce swamps, and also quite high in open moderate-rich fens. This is contrary to other studies which have shown extreme-rich fens to contain the greatest rare species diversity (Vitt et al. 1995). The same recommendations outlined for future diversity studies (above) are given for forthcoming rare species research to provide more comparable results.

6.3 HOW DOES LOGGING AFFECT PEATLANDS?

Logging will most likely continue to place more pressures on western boreal peatlands, especially those in regions such as the Boreal Plains Ecozone where upland wood supplies are diminishing (Lee et al. 2003). Wooded moderate-rich fens, black spruce swamps, and some wooded bogs have marketable timber (Locky et al. In press), and wooded moderate-rich fens and black spruce swamps are among the most species-rich and contain the most rare species (Vitt et al. 2003, Chapter 3). What are the repercussions of logging on these peatlands? The present study demonstrated that increased surface water temperature and nutrient levels post-harvest do not appear to be permanent at Duck Mountain sites, and that advance regeneration of *Picea mariana* was unchanged (Chapter 5), the latter which is not uncommon (Jeglum 1987). Plant species diversity and cover has been shown to increase with disturbance for vascular plants (Pykälä 2004), and decrease for bryophytes (Fenton and Frego 2004), and was demonstrated in my research. The suite of species will change with disturbance intensity, and may include formation of stable shrub communities, expansion of ruderals sometimes found in peatlands, such as *Marchantia polymorpha* and *Typha latifolia,* and introduction of non-peatland graminoids and herbs. It is unclear how permanent these changes are to the logged peatlands at Duck Mountain. This research was preliminary in scope and encompasses the early successional period post-harvest in a peatland. Further work is required to determine more specific impacts to peatlands as a result of forest harvest, and longer-term studies are required to determine the permanence of site-level changes on post-harvest peatlands. The moisture regime in western boreal peatlands is much less than those in the eastern boreal region, where most of the effects of peatland logging have been investigated. It is important to continue research into impacts to peatlands in the western boreal region, as they experience continual pressure from industry and are potentially impacted from global warming.

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APPENDIX A. SITES SURVEYED WITH EASTING AND NORTHING COORDINATES LISTED BY CHAPTER

Site #	Map	Easting	Northing	Location	Chapter
T1	14U	367841	5742699	Duck Mountain, MB	2, 3
T2	14U	364013	5730458		
O3	14U	368089	5724571		
T5	14U	375225	5718980		
O6A	14U	384407	5722294		
O7A	14U	366624	5720341		
O7B	14U	367829	5726764		
T8A	14U	364550	5750337		
O9	14U	364636	5752904		
O10A	14U	367212	5736899		
T10B	Missing				
O11	14U	365353	5733960		
O12	14U	367924	5722425		
T13	14U	361133	5713621		
T14	14U	369053	5740203		
O15	14U	364194	5714923		
O16	14U	349816	5716169		
O17	14U	369054	5739291		
T18	14U	366824	5745756		
T19	14U	374960	5711099		
O20	14U	381737	5691730		
O21	14U	381491	5703421		
T22	14U	367953	5743401		
O23	14U	364766	5753481		
O24	14U	369084	5739165		
T25	14U	367384	5744723		
O27	14U	365895	5728311		
O28	14U	365980	5728197		
O29	14U	366050	5728031		
T30	14U	365364	5748210		
T31	14U	366819	5735924		
O32	14U	366877	5735911		
O33	14U	366962	5735891		
O34	14U	366810	5735468		
O35	14U	366734	5735494		
O36	14U	363693	5731623		
T37	14U	365934	5747250		
T38	14U	369512	5731232		
O39	14U	369477	5731226		
O40	14U	363783	5731586		

Site #	Map	Easting	Northing	Location	Chapter
O41	14U	368159	5724517	Duck Mountain, MB	2, 3
T42	14U	368703	5723365		
T43	14U	360456	5713645		
T44	14U	360362	5713548		
O45	Missing				
T46	14U	365270	5748440		
T47	14U	362686	5755306		
T48	14U	359672	5713729		
O49	14U	352164	5716523		
T50	14U	367349	5731602		
T51	14U	369380	5731437		
O52	14U	368805	5731814		
T53	Missing				
T55	14U	366675	5731506		
T56	14U	373875	5740064		
T57	14U	373921	5740051		
T58	14U	373899	5740104		
T59	14U	367899	5737313		
T60	14U	367840	5737218		
O61	14U	367647	5731619		
T62	14U	368025	5743290		
O63	14U	368085	5743259		
O64	14U	368721	5745787		
O65	14U	366648	5720355		
T66A	14U	370926	5747535		
T66B	14U	370944	5747505		
T67	14U	368197	5744741		
T68A	14U	369747	5730472		
O68B	14U	369733	5730453		
O69	14U	368427	5731925		
T70	14U	367914	5731938		
T71	14U	367941	5731977		
T72	14U	368000	5731691		
T73A	14U	368108	5745452		
T73B	14U	368033	5745436		
O73C	14U	368000	5745505		
T74A	14U	366275	5731432		
O74B	14U	366316	5731369		
T75	14U	366283	5731559		
O76A	14U	374375	5718541		
O76B	Missing				
T77	14U	374419	5718515		
T78A	14U	365982	5731373		

Site #	Map	Easting	Northing	Location	Chapter
O78B	14U	365958	5731320	Duck Mountain, MB	2, 3
T79	14U	365896	5731108		
O80	14U	363246	5714009		
T81	14U	350606	5716136		
T82	14U	350844	5716127		
O83	14U	361867	5713628		
O84	14U	368640	5723523		
O85	14U	366433	5735140		
O86	14U	368366	5739146		
T87A	14U	368304	5739026		
T87B	14U	368341	5739025		
T1	14U	367841	5742699	Duck Mountain, MB	4
T2	14U	364013	5730458		
T13	14U	361133	5713621		
T18	14U	366824	5745756		
T19	14U	374960	5711099		
T25	14U	367384	5744723		
T30	14U	365364	5748210		
T42	14U	368703	5723365		
T43	14U	360456	5713645		
T46	14U	365270	5748440		
T48	14U	359672	5713729		
T50	14U	367349	5731602		
T51	14U	369380	5731437		
T55	14U	366675	5731506		
T59	14U	367899	5737313		
T60	14U	367840	5737218		
T62	14U	368025	5743290		
T67	14U	368197	5744741		
T70	14U	367914	5731938		
T72	14U	368000	5731691		
T73B	14U	368033	5745436		
T74A	14U	366275	5731432		
T77	14U	374419	5718515		
T87B	14U	368341	5739025		
T8A	14U	364550	5750337		
PA1	13U	438872	5967949	Prince Albert National Park, SK area	
PA10	13U	432145	5974320		
PA11	13U	432194	5974594		
PA12	13U	431521	5974306		
PA13	13U	440172	5969963		
PA14	13U	440879	5973413		
PA15	13U	440995	5976829		
PA16	13U	441019	5977893		
PA17	13U	440200	5988681		

Site #	Map	Easting	Northing	Location	Chapter
PA18	13U	428634	5968436	Prince Albert National Park, SK area	4
PA19	13U	440620	5963130		
PA2	13U	434606	5971334		
PA20	13U	440934	5962549		
PA21	13U	422108	5973847		
PA22	13U	420284	5976852		
PA23	13U	440778	5970916		
PA24	13U	438002	5993548		
PA25	13U	437957	5999025		
PA26	13U	437873	6000584		
PA27	13U	437556	6002270		
PA28	13U	430348	5976494		
PA29	13U	430498	5976965		
PA3	13U	433714	5973144		
PA4	13U	433769	5973210		
PA5	13U	433363	5973366		
PA6	13U	433244	5973603		
PA7	13U	433533	5973492		
PA8	13U	432837	5974103		
PA9	13U	432851	5974249		
U1	11V	583690	6218966	Utikuma Lake, AB	
U2	11V	584722	6218439		
U3	11V	584154	6218661		
U4	11V	582420	6219762		
U5	11V	582186	6220376		
U6	11V	581604	6220276		
U7	11V	580935	6220667		
U8	11V	579995	6221511		
U9	11V	578946	6222163		
U10	11V	572741	6223463		
U11	11V	602465	6252577		
U12	11V	602498	6252171		
U13	11V	601385	6246908		
U14	11V	601537	6244420		
U15	11V	600369	6242969		
U16	11V	600383	6241699		
U17	11U	593154	6203430		
U18	11U	591388	6203607		
U19	11V	602975	6214240		
U20	11V	588434	6213987		
U21	11V	589004	6213430		
U22	11V	588973	6213331		
U23	11V	593550	6222009		
U24	11V	593499	6222638		
U25	11V	603991	6216996		
U26	11V	601203	6238813		

Site #	Map	Easting	Northing	Location	Chapter
P1	14U	366684	5731578	Duck Mountain, MB	5
P2	14U	375733	5707509	- coordinates refer to wooded	
P3	14U	363804	5753399	portion of peatland	
P4	14U	363846	5753490		
P5	14U	374894	5707477		
P6	14U	363854	5754409		
P7	14U	364108	5754500		
P8	14U	364272	5753791		
P9	14U	364122	5753474		
P10	14U	368856	5730801		
P11	14U	368754	5730960		
P12a	14U	368507	5731913		
P12b	14U	368622	5731912		
P13	14U	369371	5731475		
P14	14U	370266	5731372		
P17	14U	366719	5731386		
P18	14U	383023	5706554		
P22	14U	368931	5732242		
P23	14U	368449	5730754		
P24	14U	368822	5732076		
P25	14U	368930	5730767		
P31	14U	365126	5730574		
P32	14U	365326	5730995		
P33	14U	365348	5731269		
P34	14U	365446	5730974		
P37	14U	365251	5730799		
P40	14U	357271	5712413		
P41	14U	357193	5712712		
P42	14U	357214	5712622		
P43	14U	358400	5712617		
P44	14U	358346	5712547		
P45	14U	359355	5713070		
P46	14U	359320	5713088		
P47	14U	359076	5712644		
P48	14U	359128	5712674		
P49	14U	366520	5731743		

APPENDIX B. BRYOPHYTE, LICHEN, AND VASCULAR PLANT SPECIES WITH AUTHORITIES AND TAXA/LIFE FORM DESIGNATIONS LISTED BY CHAPTER

Taxa/Life-form	Scientific Name and Authority	Ch 2	Ch 3	Ch 4	Ch 5
Bryophytes and Lichens					
True Mosses	*Aulacomnium palustre* (Hedw.) Schwaegr.	*	*	*	*
	Brachythecium mildeanum (Schimp.) Schimp. *ex* Milde.	*	*	*	*
	Brachythecium rivulare Schimp. *in* B.S.G.	*	*	*	*
	Brachythecium starkei (Bridw.)	*	*		
	Brachythecium turgidum (Hartm.) Kindb.				*
	Brachthecium velutinum (Hedw.)	*	*		
	Bryum pseudotriquetrum (Hedw.) Gaertn. et al.	*	*	*	*
	Calliergon giganteum (Schimp.) Kindb.	*	*	*	*
	Calliergon richardsonii (Mitt.) Kindb. *in* Warnst.	*	*	*	*
	Calliergon stramineum (Brid.) Kindb.	*	*	*	*
	Calliergon trifarium (Web. & Mohr) Kindb.	*	*	*	
	Calliergonella cuspidata (Hedw.) Loeske	*	*	*	
	Campylium hispidulum (Brid.) Mitt.	*	*		
	Campylium radicale (P. Beauv.) Grout	*	*		
	Campylium stellatum (Hedw.) C. Jens. var. *stellatum*	*	*	*	*
	Catoscopium nigritum (Hedw.) Brid.	*	*	*	
	Ceratodon purpureus (Hedw.) Brid. var. *purpureus*			*	*
	Cinclidium stygium Sw. *in* Schrad.	*	*	*	*
	Climacium dendroides (Hedw.) Web. & Mohr	*	*	*	*
	Cratoneuron commutatum ((Brid.) G. Roth	*	*		
	Dicranum acutifolium (Lindb. & H. Arnell) C. Jens. *ex* Weinm.	*	*	*	
	Dicranum polysetum Sw.	*	*	*	*
	Dicranum undulatum Brid.	*	*	*	*
	Drepanocladus aduncus (Hedw.) Warnst. var. *aduncus*	*	*	*	*
	Hamatocaulis vernicosus (Mitt.) Hedenäs	*	*	*	*
	Helodium blandowii (Web. & Mohr) Warnst. var. *blandowii*	*	*	*	*
	Hylocomium splendens (Hedw.) Schimp. *in* B.S.G.	*	*	*	*
	Hypnum lindbergii Mitt.	*	*	*	*
	Hypnum pratense (Rabenh.) W. Koch *ex* Spruce	*	*	*	*
	Leptobryum pyriforme (Hedw.) Wils.	*	*	*	*
	Limprichtia revolvens (Sw.) Loeske.	*	*	*	*
	Meesia longiseta Hedw.	*	*	*	
	Meesia triquetra (Richt.) Åongstr.	*	*	*	
	Meesia uliginosa Hedw.	*	*	*	
	Myurela julacea (Schwaegr.) Schimp *in* B.S.G.	*	*	*	*
	Oncophorus wahlenbergii var. *compactus* (Bruch & Schimp. *in* B.S.G.) Braithw.	*	*		
	Paludella squarrosa (Hedw.) Brid.	*	*	*	
	Plagiomnium cuspidatum (Hedw.) T. Kop.			*	
	Plagiomnium ellipticum (Brid.) T. Kop.	*	*	*	*
	Plagiomnium medium (Bruch and Schimp. *in* B.S.G.) T. Kop. var. *medium*	*	*	*	*
	Platydictya jugermanniodes (Brid.) Crum	*	*	*	
	Pleurozium schreberi (Brid.) Mitt.	*	*	*	*
	Pohlia nutans (Hedw.) Lindb.	*	*	*	*
	Pohlia wahlenbergii (Web. & Mohr) Andrews	*	*	*	*
	Polytrichum strictum Brid.	*	*	*	*
	Ptilium crista-castrensis (Hedw.) De Not.	*	*	*	*
	Rhizomnium gracile T. Kop.	*	*	*	*
	Rhizomnium pseudopunctatum (Bruch & Schimp.) T. Kop.	*	*	*	*
	Rhytidiadelphus triquetrus (Hedw.) Warnst.	*	*	*	
	Sanionia uncinata (Hedw.) Loeske var. *uncinata*	*	*	*	*
	Scorpidium scorpioides (Hedw.) Limpr.	*	*	*	*

Taxa/Life-form	Scientific Name and Authority	Ch 2	Ch 3	Ch 4	Ch 5
Bryophytes and Lichens					
True Mosses	*Sphlachnum sphaericum* Hedw.	*	*	*	
	Splachnum luteum Hedw. Var. *luteum* var. *melanocaulon* Wahlenb.	*	*	*	
	Splachnum rubrum Hedw.	*	*	*	
	Thuidium delicatulum (Hedw.) Schimp. *in* B.S.G.	*	*	*	*
	Thuidium recognitum (Hedw.) Lindb.	*	*	*	*
	Tomenthypnum falcifolium (Ren. ex Nichols) Tuom. *in* Ahti & Fagers	*	*	*	*
	Tomenthypnum nitens (Hedw.) Loeske	*	*	*	*
	Warnstorfia exannulata (Schimp. *in* B.S.G.) Loeske var. *exannulata*	*	*	*	*
Sphagnum	*Sphagnum angustifolium* (C. Jens. *ex* Russ.) C. Jens. *in* Tolf	*	*	*	*
	Sphagnum capillifolium (Ehrh.) Hedw.	*	*	*	*
	Sphagnum centrale C. Jens. *in* Arnell & C. Jens.	*	*		
	Sphagnum fuscum (Schimp.) Klinggr.	*	*	*	*
	Sphagnum girgensohnii Russ.	*	*	*	
	Sphagnum magellanicum Brid.	*	*	*	*
	Sphagnum riparium Ångstr.	*	*	*	
	Sphagnum rubellum Wils.	*	*	*	
	Sphagnum squarrosum Crome	*	*		*
	Sphagnum subsecundum Nees *in* Sturm var. *subsecundum* var. *andrusii* Crum	*	*		
	Sphagnum teres (Schimp.) Ångstr. *in* Hartm.	*	*	*	
	Sphagnum warnstorfii Russ.	*	*	*	*
	Sphagnum wulfianum Girg.	*	*	*	
Hepatics	*Aneura pinguis* (L.) Dum.	*	*	*	
	Blepharostoma trichophyllum (L.) Dum. subsp. *trichophyllum*	*	*	*	*
	Calypogeia sphagnicola (H.Arnell *ex* J.Perss.) Warnst. *ex* Loeske	*	*	*	*
	Cephalozia bicuspidata (L.) Dum. subsp. *bicuspidata*	*	*	*	*
	Cephalozia connivens (Dicks.) Lindb. var. *connivens*	*	*	*	*
	Cephalozia lunulifolia (Dum.) Dum.			*	*
	Cephalozia pleniceps (Aust.) Lindb. var. *pleniceps*			*	
	Chiloscyphus pallescens (Ehrh. *ex* Hoffm.) Dum. var. *pallescens*			*	
	Cladopodiella fluitans E. Joerg.			*	
	Conocephalum conicum (L.) Lindb.	*	*	*	
	Geocalyx graviolans (Schrad.) Nees			*	*
	Gymnoclea inflata (Huds.) Dum. var. *inflata*			*	
	Lepidozia reptans (L.) Dum.	*	*	*	*
	Lophozia rutheana (Limpr.) M.A. Howe	*	*	*	*
	Lophozia ventricosa (Dicks.) Dum. var. *ventricosa*	*	*	*	*
	Marchantia polymorpha L.	*	*	*	*
	Moerckia hibernica (Hook.) Gott.	*	*	*	*
	Mylia anomala (Hook.) S. Gray	*	*	*	*
	Plagiochila porelloides (Torrey *ex* Nees) Lindenb.	*	*	*	*
	Ptilidium pulcherrimum (G.Web.) Hampe	*	*	*	*
	Riccardia latifrons (Lindb.) Lindb.			*	*
	Riccardia multifida (L.) S. Gray var. *multifida*	*	*	*	
	Riccia canaliculata Hoffm.	*	*	*	
	Tritomaria quinquedentata (Huds.) Buch var. *quinquedentata*			*	
Lichens	*Cladina mitis* (Sandst.) Hustich	*			*
	Cladina rangiferina (L.) Nyl.	*			*
	Cladina stellaris (Opiz) Brodo	*			*

Taxa/Life-form	Scientific Name and Authority	Ch 2	Ch 3	Ch 4	Ch 5
Vascular plants					
Phanerophytes	*Abies balsamea* (L.) P. Mill.	•	•	•	•
Meso-	*Betula neoalaskana* Sarg.	•	•	•	
(Trees)	*Betula papyrifera* Marsh.	•	•	•	•
	Larix laricina (Du Roi) K. Koch	•	•	•	•
	Picea glauca (Moench) Voss	•	•	•	•
	Picea mariana (P. Mill.) B.S.P.	•	•	•	•
	Pinus banksiana Lamb.	•	•	•	•
	Populus balsamifera L.	•	•	•	•
	Populus tremuloides Michx.	•	•	•	•
Micro-	*Alnus incana* (L.) Moench	•	•	•	•
(Tall Shrubs > 2 m)	*Alnus viridis* ssp *crispa* (Ait.) Turrill	•	•	•	•
	Amelanchiar alnifolia (Nutt.) Nutt. *ex* M. Roemer	•	•	•	
	Betula occidentalis Hook.	•	•	•	•
	Betula pumila L.	•	•	•	•
	Cornus stolonifera Michx.	•	•	•	
	Corylus cornuta Marsh.	•	•	•	
	Lonicera dioica L.	•	•	•	•
	Salix bebbiana Sarg.	•	•	•	•
	Salix discolor Muhl.	•	•	•	•
	Salix eriocephala Michx.	•	•		
	Salix exigua Nutt.	•	•	•	•
	Salix lucida Muhl.			•	
	Salix maccaliana Rowlee	•	•	•	
	Salix planifolia Pursh	•	•	•	•
	Salix pseudomonticola Ball	•	•	•	•
	Salix pyrifolia Anderss.	•	•	•	
	Salix serissima (Bailey) Fern.	•	•	•	•
	*Viburnum edule (*Michx.) Raf.			•	•
Nanophanerophytes	*Chaemadaphne calyculata* (L.) Moench	•	•	•	
(Shrubs < 2 m)	*Kalmia polifolia* Wangenh.	•	•		•
	Ledum groenlandicum Oeder	•	•	•	•
	Lonicera caerulea var. *villosa* (Michx)	•	•	•	•
	Lonicera oblongifolia (Goldie) Hook.	•	•	•	
	Pentaphylloides floribunda (Pursh) A. Love	•	•	•	•
	Rhamnus alnifolia L'Her.	•	•	•	•
	Ribes americanum P. Mill.			•	•
	Ribes hudsonianum Richards.	•	•	•	•
	Ribes lacustre (Pers.) Poir.	•	•	•	•
	Ribes oxycanthoides L.	•	•	•	•
	Ribes triste Pallas	•	•	•	•
	Rosa acicularis Lindl.	•	•	•	•
	Salix candida Fluegge *ex* Willd.	•	•	•	•
	Salix myrtillifolia Anderss.	•	•	•	•
	Salix pedicellaris Pursh	•	•	•	•
	Sheperdia canadensis (L.) Nutt.	•	•	•	
	Vaccinium angustifolium Ait	•	•	•	•
	Vaccinium myrtilloides Michx.	•	•	•	•
Chamaephytes	*Andromeda polifolia* L.	•	•	•	•
(Short or prostrate	*Empetrum nigrum* L.	•	•	•	•
plants)	*Gaultheria hispidula* (L.) Muhl. *ex* Bigelow	•	•	•	•
	Linnaea borealis L.	•	•	•	•
	Oxycoccus microcarpus Turcz.	•	•	•	•
	Vaccinium vitis-idaea L.	•	•	•	•

Taxa/Life-form	Scientific Name and Authority	Ch 2	Ch 3	Ch 4	Ch 5
Vascular plants					
Hemicryptophytes (Renewal buds at soil surface)	*Agropyron trachycaulum* (Link) Malte				*
	Agrostis scabra Willd.	*	*	*	*
	Aquillea millefolium L.	*	*	*	*
	Aralia nudicaulus L.	*	*	*	*
	Aster borealis (Torr. & Gray) A. & D. L˝ve	*	*	*	*
	Aster ciliolatus (Lindl.) A.& D. L˝ve			*	*
	Aster hesperius (Gray) Nesom				*
	Aster puniceus (L.) A.& D. L˝ve	*	*	*	*
	Aster umbellatus (P. Mill.) Nees	*	*		*
	Bromus ciliatus L.	*	*		*
	Calamagrostis canadensis (Michx.) Beauv.	*	*	*	*
	Calamagrostis stricta ssp. *inexpansa* (Gray) C.W. Greene	*	*	*	*
	Caltha palustris L.	*	*	*	*
	Campanula aparanoides Pursh	*	*	*	
	Campanula rotundifolia L.	*	*	*	*
	Carex aenea Fern.				*
	Carex bebbii Olney *ex* Fern.	*	*	*	*
	Carex brunescens (Pers.) Poir.	*	*		*
	Carex cannescens L.	*	*	*	*
	Carex capillaris L.			*	
	Carex chordorhiza Ehrh. *ex* L. f.	*	*	*	
	Carex concinna R. Br.	*	*		*
	Carex dewyana Schw.				*
	Carex diandra Schrank	*	*	*	*
	Carex disperma Dewey	*	*	*	*
	Carex interior Bailey	*	*	*	*
	Carex leptalea Wahlenb.	*	*	*	*
	Carex prairieae Dewey *ex* Wood			*	*
	Carex retrorsa Schwein.			*	
	Carex siccata Dewey			*	*
	Carex tenuifolia Wahlenb.	*	*	*	*
	Castilleja raupii Pennell			*	
	Chrysosplenium tetrandrum (Lund) Th. Fries	*	*	*	*
	Cicuta bulbifera L.	*	*	*	*
	Cicuta maculata L.			*	
	Cinna latifolia (Trev. *ex* Goepp.) Griseb.	*	*	*	*
	Cirsium arvense (L.) Scop.				*
	Cornus canadensis L.	*	*	*	*
	Deschampsia caespitosa (L.) Beauv.	*	*	*	*
	Drosera rotundifolia L.	*	*	*	*
	Dryopteris carthusiana (Vill.) H.P. Fuchs	*	*	*	*
	Epilobium angustifolium L.	*	*	*	*
	Epilobium ciliatum Raf.	*	*	*	*
	Epilobium leptophyllum Raf.	*	*	*	*
	Epilobium palustre L.	*	*	*	*
	Eriophorum vaginatum L.	*	*	*	*
	Fragria virginiana Duchesne	*	*	*	*
	Galium boreale L.	*	*	*	*
	Galium labradoricum (Wieg.) Wieg.	*	*	*	
	Galium palustre L.	*	*	*	
	Galium trifidum L.	*	*	*	*
	Galium triflorum Michx.	*	*	*	*
	Geum allepicum Jacq.	*	*	*	*
	Geum macrophyllum Willd.				*
	Geum rivale L.	*	*	*	*
	Geum triflorum Pursh				*

Taxa/Life-form	Scientific Name and Authority	Ch 2	Ch 3	Ch 4	Ch 5
Vascular plants					
Hemicryptophytes (Renewal buds at soil surface)	*Glyceria borealis* (Nash) Batchelder	*	*	*	*
	Glyceria grandis S. Wats.	*	*		
	Glyceria pulchera (Nash) K. Schum.	*	*	*	
	Glyceria striata (Lam.) A.S. Hitchc.	*	*	*	*
	Goodyera repens (L.) R. Br. *ex* Ait. f.	*	*	*	*
	Hedysarum boreal Nutt.				*
	Hieracium umbellatum L.				*
	Hordeum jubatum L.			*	*
	Liparis loeselii (L.) Rich. *ex* Lindley	*	*	*	
	Luzulu parviflora (Ehrh.) Desv.	*	*	*	*
	Lycopus uniflorus Michx.	*	*	*	
	Mentha arvensis L.	*	*		*
	Mertensia paniculata (Ait.) G. Don	*	*	*	*
	Mitella nuda L.	*	*	*	*
	Moneses uniflora (L.) Gray	*	*	*	*
	Muhlenbergia glomerata (Willd.) Trin.	*	*	*	
	Orthilia secunda (L.) House	*	*	*	*
	Parnassia palustris L.	*	*	*	*
	Pedicularis groenlandica Retz.			*	
	Pedicularis labradorica Wirsing			*	
	Phleum pratense L.				*
	Poa palustris L.	*	*	*	*
	Potentilla norvegica L.	*	*	*	*
	Pyrola asarifolia Michx.	*	*	*	*
	Ranunculus lapponicus L.	*	*	*	*
	Rubus arcticus L.	*	*	*	*
	Rubus chamaemorus L.	*	*	*	*
	Rubus idaeus L.	*	*	*	*
	Rubus pubescens Raf.	*	*	*	*
	Rumex crispus L.	*	*		*
	Rumex aquaticus S. Wats.	*	*	*	*
	Rumex orbiculatus Gray	*	*	*	*
	Sanicula marilandica L.	*	*	*	
	Saracenia purpurea L.	*	*	*	
	Scheuchzeria palustris L.	*	*		
	Schizachne purpurascens (Torr.) Swallen				*
	Scirpus cespitosus L.	*	*		
	Scutellaria gallericulata L.	*	*	*	*
	Sencio eremophilus Richards.				*
	Senecio pauperculatus Michx.	*	*	*	*
	Sium suave Walt.	*	*	*	*
	Solidago canadensis L.	*	*	*	*
	Solidago spathulata DC.				*
	Stellaria calycantha (Ledeb.) Bong.	*	*	*	*
	Stellaria crassifolia Ehrh.				*
	Stellaria longifolia Muhl. *ex* Willd.	*	*	*	*
	Taraxacum officinale G.H. Weber *ex* Wiggers	*	*	*	*
	Thalictrum venulosum Trel.	*	*		*
	Tofieldia glutinosa (Michx.) Pers.	*	*	*	
	Triglochin maritimum L.	*	*	*	
	Veronica americana Schwein. *ex* Benth.	*	*		*
	Veronica scutellaria L.				*
	Vicia americana Muhl. *ex* Willd.	*	*		*
	Viola spp.	*	*	*	*

Taxa/Life-form	Scientific Name and Authority	Ch 2	Ch 3	Ch 4	Ch 5
Vascular plants					
Geophytes (Renewal buds below soil surface)	*Actaea rubra* (Ait.) Willd.	*	*	*	
	Amerorchis rotundifolia Banks	*	*	*	
	Anemone canadense L.	*	*		
	Arethusa bulbosa L.	*	*		
	Botrychium virginianum (L.) Sw.	*	*	*	
	Carex aquatilus Wahlenb.	*	*	*	*
	Carex atherodes Spreng.	*	*	*	
	Carex aurea Nutt.	*	*	*	*
	Carex gynocrates Wormsk. *ex* Drej.	*	*	*	*
	Carex lacustris Willd.	*	*	*	*
	Carex lanuginosa Michx.	*	*		
	Carex lasiocarpa Ehrh.	*	*	*	
	Carex limosa L.	*	*	*	
	Carex magellanica Lam.	*	*	*	*
	Carex norvegica Retz.				*
	Carex pauciflora Lightf.	*	*		
	Carex sartwellii Dewey				*
	Carex trisperma Dewey	*	*	*	*
	Carex utriculata Boott	*	*	*	*
	Carex vaginata Tausch	*	*	*	*
	Comarum palustris L.	*	*	*	
	Coralhiza maculata (Raf.) Raf.	*	*	*	
	Coralhiza striata Lindl.	*	*		
	Coralhiza trifida Chatelain	*	*	*	*
	Cypripedium acaule Ait.	*	*	*	
	Eleocharis palustris (L.) Roemer & J.A. Schultes	*	*		
	Elymus innovatus Beal			*	*
	Equisetum arvense L.	*	*	*	*
	Equisetum fluviatile L.	*	*	*	*
	Equisetum pratense Ehrh.	*	*	*	*
	Equisetum scorpoides Michx.	*	*	*	*
	Equisetum sylvaticum L.	*	*	*	*
	Equisetum variegatum Schleich. *ex* F. Weber & D.M.H. Mohr	*	*	*	
	Eriophorum angustifolium Honckeny	*	*	*	*
	Eriophorum chamissonis C.A. Mey.	*	*		
	Eriophorum gracile W.D.J. Koch	*	*	*	
	Eriophorum viridi-carinatum (Engelm.) Fern.	*	*	*	
	Geocaulon lividum (Richards.) Fern.	*	*	*	*
	Juncus balticus Willd.	*	*	*	
	Lactuca tartarica (L.) C.A. Mey.				*
	Lathyrus ochroleucus Hook.				*
	Listera borealis Morong	*	*	*	*
	Listera cordata (L.) R. Br. *ex* Ait. f.	*	*	*	*
	Maianthemum canadense Desf.	*	*	*	*
	Maianthemum trifolium (L.) Sloboda	*	*	*	*
	Malaxis monophyllos (L.) Sw.			*	
	Malaxus paludosa (L.) Sw.				*
	Menyanthes trifoliata L.	*	*	*	*
	Monotropa uniflora L.	*	*	*	*
	Petasites frigidus var *palmatus* (Ait.) Cronq.	*	*	*	*
	Petasites sagittatus (Banks *ex* Pursh) Gray	*	*	*	*
	Platanthera dilitata (Pursh) Lindl. *ex* Beck	*	*	*	*
	Platanthera hyperborea (L.) Lindl.	*	*	*	*
	Platanthera obtusata (Banks *ex* Pursh) Lindl.	*	*	*	*
	Platanthera orbiculata (Pursh) Lindl.	*	*		*

Taxa/Life-form	Scientific Name and Authority	Ch 2	Ch 3	Ch 4	Ch 5
Vascular plants					
Geophytes (Renewal buds below soil surface)	*Scirpus acutus* Muhl. *ex* Bigelow	*	*	*	
	Scirpus hudsonianus (Michx.) Fern.	*	*	*	
	Scirpus validus ssp. *validus* (Vahl) A. & D. Love	*	*		
	Scirpus microcarpus Pers.	*	*		
	Sonchus arvensis L.	*	*		*
	Spiranthes romanzoffianum Cham.	*	*	*	*
	Trientata borealis Raf.	*	*	*	
	Utica dioica L.	*	*	*	*
	Valeriana dioica L.				*
Helophytes (Plants submersed in mud)	*Calla palustris* L.	*	*		*
	Hippuris vulgaris L.	*	*		
	Lysimachia thrysifolia L.	*	*	*	
	Nuphar lutea ssp. *variagata* (Dur.) E.O. Beal	*	*		
	Polygonum amphibium L.	*	*		
	Polygonum amphibium var. *emersum* Michx.	*	*	*	*
	Sagittaria spp.	*	*		
	Typha latifolia L.	*	*	*	*
Hydrophytes (Plants submersed or floating)	*Chara* spp. (aquatic green algae)	*	*		
	Lemna minor L.	*	*		
	Myriophyllum spp.	*	*		
	Potamogeton spp.	*	*	*	
	Ranunculus gmelii DC.	*	*	*	
	Ranunculus longirostris	*	*		
	Sparganium americanum	*	*		
	Sparganium fluctuans (Morong) B.L. Robins.	*	*		
	Utricularia intermedia Hayne	*	*	*	
	Utricularia vulgaris L.	*	*		
Therophytes (Renewal buds protected by seed)	*Bidens cernua* L.	*	*		*
	Impatiens capensis Meerb.	*	*		
	Ranunculus scleratus L.	*	*		

Vascular plants divided into Raunkiaer's (1934) life form divisions, a classification based on the position and seasonality of the perennating buds or rejuvenating organs following Scoggan (1978-1979). Nomenclature for true mosses follows Anderson et al. (1990), *Sphagnum* follows Anderson (1990), hepatics follow Stötler and Crandall-Stötler (1977), and lichens follow Esslinger and Egan (1995). Vascular plant species nomenclature follows the Plant Element List from the Alberta Natural Heritage Information Centre (2002) where possible and Scoggan (1978-1979) for others. Ch = Chapter