University of Alberta

Classification, diversity, and production of Alberta's boreal peatlands during a drought

by

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Chapter 1 – General Introduction

Peatlands are important ecosystems in boreal Alberta, occupying ~103 000 km^2 (16%) of the landscape (Vitt et al. 2000). They provide habitat for a variety of wildlife such as moose, caribou and waterfowl, and contain a diverse range of bryophyte and vascular species. Peatlands also supply important ecosystem services for human society such as water storage, improving water quality through filtration, and carbon retention from the atmosphere (Gorham 1990). Where there are peatlands, floodwaters are retained and less carbon is contributed to global warming (Gorham 1990). If peatlands are altered by human disturbance, the ecosystem processes they support will be greatly changed. In order to assess how sensitive peatlands may be to human disturbance it is important to understand how peatlands function naturally across the landscape.

This study examined the plant communities in the bogs, fens, and marshes of Alberta's mid-boreal region. Past Alberta peatland studies have concentrated in the aspen parkland, low-boreal region, and high-boreal region (i.e. Horton et al. 1979; Chee and Vitt 1989; Nicholson 1995; Vitt et al. 2003; Bayley and Mewhort 2004). The climate (i.e. precipitation, growing degree days) of the mid-boreal region is dissimilar from other boreal regions and this is reflected in the different wetland community types found in each region (Ecoregions Working Group 1989; National Wetlands Working Group 1997).

Climate, topographical position and parent material all affect the type, distribution and biodiversity of plant communities present in any given community. Precipitation rates, aridity, and temperature control how much water is available while topography (hummocky/ flat) and parent material (sand/ gravel/ clay) determine how much and how long water is held in a watershed. Three landforms, outwash plain, moraine, and clay-till plain, each with its own topography and parent material, are present the mid-boreal region. In the outwash plain a sand/ gravel substrate connects peatlands to the regional water table, while a silt/ clay substrate in both the moraine and clay-till plain allow only shallow groundwater connections (Ferone and Devito 2004). The outwash plain and clay-till plain have a flat topography, whereas a hilly terrain characterizes the moraine (Paulen et al. 2003, 2004). Due to the differences in parent material and topography amongst the three landforms, the distance between the water table and the peatland varies. This can affect the amount of water available to each plant community type, especially under drought conditions.

This research focused on peatlands surrounding shallow ponds located in part of Alberta's mid-boreal region. There were three overall objectives; first, to determine whether these peatland-pond complexes were common on the landscape. Second, to classify and describe the peatland community types (species composition, diversity, environmental variables). And third, to document herb and moss production in these peatland communities during a known drought period.

Peatland communities were classified, as first described by DuRietz (1949), by the number of vegetation indicator species (vascular and bryophyte) and verified by examining environmental parameters (pH and water depth). In this study, marsh, fen, and bog plant communities surrounded the shallow ponds.

The Canadian Classification system (National Wetlands Working Group 1997) separated these three communities based on the location of the water table relative to the surface, the accumulation of peat, the presence of bryophytes, and the concentration of nutrients in the surface water. Marshes have water tables at or above the surface, no significant accumulation of peat, lack bryophytes and have high cation concentrations in surface water. Fens differ from marshes, by the accumulation of peat (≥ 40 cm), and a dominant layer of brown mosses. However, Bayley and Mewhort (2004) found that their Alberta marsh sites had peat depths of ~ 1 metre and could be classified as peatlands. The Canadian classification system separates bogs from both marshes and fens, by being precipitation fed, low water tables, and by a dominant layer of moss.

Beyond classifying and describing the peatland communities, I also measured herb and moss production (as peak August biomass) in marshes, fens, and bogs during one of the driest years on record. Past studies have shown that biomass of moss and herbs decreases with both the lowering of the water table, and lower precipitation rates (Szumigalski and Bayley 1997, Thormann and Bayley 1998). Precipitation is the key factor determining the rate and pattern of peat formation as it affects accumulation vs. decomposition levels (Hilbert et al. 2000; Moore 2002). Peat accumulation is the result of slow decomposition, due to anaerobic conditions and a cool climate/ short growing season, not high production rates (Clymo 1984; Vitt 1990). This study was the first to document peatland production during a known drought.

In Chapter 2, through helicopter surveys it was observed that peatland-pond complexes were found around ponds <200 ha, so digital maps from Canada's national topographical database were placed into a GIS to determine if ponds of this size were common in the study area. Next, the peatlands were classified using Cluster Analysis and non-metric multidimensional scaling based on presence/ absence of bryophyte, herb, graminoid, shrub, and tree species. For each community (marsh, fen, and bog) the chemistry of the surface water and aerobic peat layer was determined. A species list for each community was generated with the dominant and rare species noted. Total (vascular and non-vascular), vascular, and bryophyte species richness was calculated for each community and for the entire study area. As well, the number of species found in each community (similarity index) was determined. The diversity and species composition of each community was compared to past Alberta studies of marshes, fens and bogs with similarities and peculiarities noted.

In Chapter 3, herb production in marshes and fens and *Sphagnum* moss production in treed fens and bogs was determined. Herbs were cut to ground level at the peak biomass (mid August), dried, and weighed and Clymo's (1970) crank wire method was used for *Sphagnum* production. Production values were compared between sites, communities and landforms; and also with past Alberta studies. In the year following the drought production (as peak biomass) was measured again to compare a year of low precipitation with one of normal precipitation levels. A wetland drought cycle was proposed for the marsh and fen communities, similar to that of van der Valk and Davis (1978), with a low water wetland and a flooded wetland phase observed. Production in both the marsh and fen is expected to be lowest during the low water phase and highest in the flooded phase of the cycle. A vegetation transition occurs between the two phases; where under increasing water levels marsh annuals are replaced by perennials, and fen vegetation changes from dominance of forbs and grasses to dominance of sedges.

In Chapter 4, a brief concluding discussion of the major results is summarized.

REFERENCES

Bayley, S.E., and Mewhort, R.L. 2004. Plant community structure and functional differences between marshes and fens in the southern boreal region of Alberta, Canada. Wetlands 24: 277-294.

Chee, W.L., and Vitt, D.H. 1989. The Vegetation, Surface-Water Chemistry and Peat Chemistry of Moderate-Rich Fens in Central Alberta, Canada. Wetlands 9: 227-261.

Clymo, R.S. 1970. The growth of *Sphagnum*: Methods of measurement. The Journal of Ecology 58: 13-49.

Clymo, R.S. 1984. The Limits to Peat Bog Growth. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 303: 605-54.

Du Rietz, G.E. 1949. Huvudenheter och huvudgränser i svensk myrvegetation. Svensk Botanisk Tidskrift 43: 274-309.

Ecoregions Working Group. 1989. Ecoclimatic Regions of Canada, First Approximation. Minister of Supply and Services Canada, Ottawa. 118 pp.

Ferone, J.M., and Devito, K.J. 2004. Shallow Groundwater-Surface Water Interactions in Pond-Peatland Complexes Along a Boreal Plains Topographic Gradient. Journal of Hydrology 292: 75-95.

Gorham, E. 1990. Biotic impoverishment in northern peatlands. *In* The Earth in transition: patterns and processes of Biotic Impoverishment. *Edited by* G.M. Woodwell. Cambridge University Press, Cambridge, England. pp. 65-98.

Hilbert, D.W., Roulet, N., and Moore, T. 2000. Modelling and Analysis of Peatlands as Dynamical Systems. Journal of Ecology 88: 230-242.

Horton, D.G., Vitt, D.H., and Slack, N.G. 1979. Habitats of Circumboreal-Subarctic Sphagna .1. Quantitative-Analysis and Review of Species in the Caribou Mountains, Northern Alberta. Canadian Journal of Botany 57: 2283-2317.

Moore, P.D. 2002. The Future of Cool Temperate Bogs. Environmental Conservation 29: 3-20.

National Wetlands Working Group. 1997. The Canadian Wetland Classification System. 2nd ed. Wetlands Research Centre, Waterloo. 68 pp.

Nicholson, B.J. 1995. The Wetlands of Elk Island National-Park - Vegetation Classification, Water Chemistry, and Hydrotopographic Relationships. Wetlands 15: 119-133.

Paulen, R.C., Fenton, M.M., and Pawlowicz, J.G. 2003. Surficial Geology of the Peerless Highlands Area (NTS 84B/NE), scale 1:100,000. Alberta Energy and Utilities Board, EUB/AGS Map 267.

Paulen, R.C., Pawlowicz, J.G., and Fenton, M.M. 2004. Surficial Geology of the Utikuma Area (NTS 83O/ NW), scale 1:100,000. Alberta Energy and Utilities Board, EUB/AGS Map 312.

Szumigalski, A.R., and Bayley, S.E. 1997. Net aboveground primary production along a peatland gradient in central Alberta in relation to environmental factors. Ecoscience 4: 385-393.

Thormann, M.N., Bayley, S.E., and Szumigalski, A.R. 1998. Effects of Hydrologic Changes on Aboveground Production and Surface Water Chemistry in Two Boreal Peatlands in Alberta: Implications for Global Warming. Hydrobiologia 362: 171-183.

van der Valk, A.G., and Davis, C.B. 1978. The role of seed banks in the vegetation dynamics of prairie glacial marshes. Ecology 59: 322-335.

Vitt, D.H. 1990. Growth and Production Dynamics of Boreal Mosses Over Climatic, Chemical and Topographic Gradients. Botanical Journal of the Linnean Society 104: 35-59.

Vitt, D.H., Halsey, L.A., Bray, J., and Kinser, A. 2003. Patterns of Bryophyte Richness in a Complex Boreal Landscape: Identifying Key Habitats at McClelland Lake Wetland. Bryologist 106: 372-382.

Vitt, D.H., Halsey, L.A., Thormann, M.N., and Martin, T. 2000. Peatland Inventory of Alberta Phase 1: Overview of peatland resources in the natural regions and subregions of the province. Sustainable Forest Management Network, Edmonton. 117 pp.

Chapter 2 - Classification and biodiversity of boreal peatland communities surrounding wetland ponds in North-Central Alberta

INTRODUCTION

The ecological and hydrological processes controlling plant communities of peatlands surrounding shallow ponds in a region of mid-boreal Alberta are relatively unknown. Past Alberta peatland studies have focused on the aspen parkland and low and high boreal regions (Horton et al. 1979; Slack et al. 1980; Chee and Vitt 1989; Nicholson 1995). Topography, mineral substrate and regional climate differ within each of these regions (Ecoregions Working Group 1989), and each of these factors has been shown to control the distribution of particular peatland types and their underlying gradients (Gignac and Vitt 1990; Vitt 1994; Halsey et al. 1997).

In part of mid-boreal Alberta, several communities (marsh, fen, bog) surround shallow ponds, with the peatlands ending at the upland slopes. North American studies have measured the important environmental gradients, compiled species lists, and calculated the diversity of each of these communities. Few studies have examined how water levels and nutrient content vary across the peatland complexes from the pond edge to the upland boundary and how these differences affect plant community composition, distribution and biodiversity within peatlands. Furthermore, there has been no research to examine whether the composition, distribution, and biodiversity of peatland plant communities vary in different landforms, which in this region are clay-till plains, outwash plains and moraines. The research presented here documents how water levels, surface water chemistry, peat chemistry, peat depth, and floristics differ between adjacent communities across the marsh-bog community gradient and between landforms.

Classification of peatlands

Peatland classification first began in Sweden where DuRietz (1949) separated peatland types based on the number of vegetation indicator species. *Sphagnum* dominated peatlands (poor fens and bogs) had the least number of species and were classified as species "poor". Brown moss dominated peatlands had many species and were classified as species "rich". Sjors (1950, 1963) related the poor and rich classes to a pH, conductivity, calcium, and magnesium gradient, controlled by ombrotrophic (precipitation fed) and minerotrophic (groundwater fed) conditions. Water temperature also differs between peatland types with bogs lower than all others, due to the insulating value of *Sphagnum* (Vitt and Chee 1990). All of the above factors increase along the ombrotrophic to minerotrophic gradient resulting in *Sphagnum* dominating under ombrotrophic conditions (bog) and brown mosses dominating under minerotrophic conditions (moderate rich fen, extreme rich fen). Vegetation, chemistry, and hydrology all play an important role in separating out peatlands into different community types.

Factors that affect peatland distribution

The distribution of peatland communities on the landscape is a function of both allogenic (regional climate, substrate quality, landscape topography) and autogenic (oligotrophy, acidification, ombrotrophy) factors (Vitt 1994). In western Canada, peatland distribution is controlled by climate, environmental gradients, ombrotrophic to mesotrophic, wet to dry, mire margin to mire expanse, and open to shaded areas (Malmer 1986; Gignac and Vitt 1994; Zoltai and Vitt 1995). Most peatlands in this region receive both precipitation and groundwater input and hence most peatlands are various types of fens (Vitt et al. 2000). Peatland initiation (in early-mid Holocene) occurred because of changes in regional climate, from warm and dry to cool and wet. Initiation, early development and maintenance of the original fen were controlled by allogenic factors (Vitt and Kuhry 1992). Autogenic factors derived from increasing peat depth likely caused the change from the original fen to bog communities in some regions (Nicholson and Vitt 1990). Generally, peatlands occur where precipitation exceeds evapotranspiration, with annual precipitation greater than 500mm and mean annual temperatures between 2 °C and 24 °C (Vitt 1994).

Western Canada peatlands

The Canadian wetland classification system recognizes five wetland types, shallow water wetlands, marshes, swamps, fens, and bogs (National Wetlands Working Group 1997). The latter three are considered peatlands, with a minimum of 40 cm of peat underneath the surface. In western Canada marshes can also be considered peatlands, based on peat depth (Bayley and Mewhort 2004). The study area is in Alberta's North-central mid-boreal region, below the discontinuous permafrost zone, where fens and continental bogs are present. Patterned fens, and peatlands characteristic of permafrost influences (peat plateaus, collapse scars, internal lawns) are absent from this region. Moderate rich fens dominate continental western Alberta, with bogs occupying a smaller portion of the landscape (Vitt et al. 2000).

Past studies have visually demarked a poor or moderate rich fen around a pond, and examined the species composition and environmental gradients underlying the peatland type (Slack et al. 1980; Vitt and Chee 1990). This research was the first study to document the entire range of peatland communities around wetland ponds, and delineate the similarities/ differences in both species composition and environmental gradients as they change from peatlands at a pond edge to the upland boundary. Vitt and Slack (1975) described communities (mostly Canadian Shield communities) around ponds in northern Michigan, but did not compare environmental gradients (i.e. pH) or species composition/ diversity between adjacent communities.

RESEARCH OBJECTIVES

This research was conducted to determine the composition and diversity of the communities found in peatlands that surround some mid-boreal plain ponds and to describe the surface water and peat chemistry for each community. Specific research objectives were:

1. To determine if peatlands surrounding shallow ponds are common in the study area; and whether pond size differs between landform types (outwash plain, moraine, clay-till plain);

2. To classify the peatlands that surround shallow ponds into communities and characterize each plant community by surface water chemistry, depth to water table and peat chemistry;
3. To determine the species composition, and richness of each plant community; examine species similarity between adjacent communities and differences in diversity in the three landform types;
4. To ascertain if the surface elevation (peat surface), mineral substrate and/or peat depth varies significantly throughout these plant communities, between study sites or landform types.

Isolated ponds surrounded by peatlands are numerous on the landscape of the Canadian Shield (Vogwill 1978; National Wetlands Working Group 1988). Helicopter surveys and remote sensing suggested that peatlands surround most wetland ponds in our study area of the mid-boreal region. Based on field observations it was apparent that there was a series of rings of different plant communities (marsh, open fen, treed fen, treed bog) surrounding these ponds and that these vegetation communities varied around the different ponds. All of the community types were found in the three landform types, but not at each of the study sites.

APPROACH AND EXPERIMENTAL DESIGN

Twelve study sites (ponds with surrounding peatland communities) were selected where there was a maximum number of plant community types observed (i.e. marsh, open fen, and treed fen) and at locations where there were only one or two communities observed (i.e. marsh, and open fen). At each site four transects (10 metres wide) were laid out along each cardinal direction. If in any particular direction there was an inflow/outflow, a transect was placed in this area so as to document the total range of plant communities surrounding boreal ponds. Based on preliminary knowledge from other researchers in the Utikuma study area, four ponds were selected from each of the three landforms so that it could be determined if landform type affected the plant communities present. In 2004 the Alberta Geological Survey completed the surficial geology maps (Paulen et al. 2003; Paulen et al. 2004) for the study area and it was discovered that only two of the four clay-till ponds belonged in this category, the other two ponds were part of the moraine landform. Ultimately, there were four ponds in the outwash plain, six in the moraine, and two in the clay-till plain.

Study area/sites

This study was conducted in the mid-boreal ecoclimatic region, in the boreal plain of north-central Alberta (56° 52′N, 115° 27′ W) (Ecoregions Working Group 1989) (Figure 2-1). This region is comprised of three upland community types – pure Aspen (*Populus tremuloides* Michx.) stands, mixed Aspen and White Spruce (*Picea glauca* (Moench) Voss) stands, and Jack Pine (*Pinus banksiana* Lamb.) forests (Achuff 1994). Jack Pine forests are restricted to the outwash plain landform while mixed aspen and white spruce forests are found throughout the three landform types (outwash plain, moraine, clay-till plain).

Peatlands in the study area are located on three different landforms, with bogs, fens and marshes found in each landform (Figure 2-1). The landforms (outwash plain, moraine, clay-till plain) are distinguished by their parent material and topography (Ferone and Devito 2004). Moraines and clay-till plains share similar material (clay, sand, silt) but are distinguished by rolling hummock topography in the moraine while the clay-till plain have a flat topography. Outwash plains are comprised of glaciofluvial deposits (sand and gravel) (Paulen et al. 2003; Paulen et al. 2004). The range of topographic positions over the entire study is small (600-700 metres above mean sea level), with highest topographic position in the outwash plain and lowest in the clay-till plain (Vogwill 1978).

Due to the differences in parent material and topography amongst the three landforms, the distance between the groundwater and the peatland varies. This can affect the amount of water available to each community type, especially under drought conditions. The peatlands and ponds in the outwash plain are the least susceptible to drought conditions, as ponds across the landform are hydrologically connected to each other by the surficial geology (Devito pers. comm.). The moraine and clay-till plain are both fed by shallow groundwater flow paths (Ferone and Devito 2004), in which flow can greatly decrease in times of drought. The rate of decrease is dependent both on the length of the shallow groundwater flow path and the pond shoreline to pond area ratio (Ferone and Devito 2004). In the moraine there are short flow paths and large pond shoreline to pond area ratios, which causes quick increases or declines in the pond water level under wet or drought conditions (Ferone and Devito 2004). Due to a flat topography the clay-till plain has long flow paths and smaller pond shoreline to pond area ratios (Ferone and Devito 2004). In times of drought, water declines are gradual throughout the growing season. In the 2002 field season, summer precipitation levels were at a low for the region and as a result two moraine study ponds with small pond shoreline to pond area ratios dried up while ponds in the clay-till plain decreased in depth but did not disappear entirely. Since there are clearly differences in groundwater hydrology in the landforms (Devito pers. comm.) I wanted to determine if the vegetation communities also differed.

The study area's average mean annual temperature is 2.7°C, with highest mean daily temperatures in July (22.7°C) and lowest in January (-22.8°C). The area receives approximately 420 mm of rain yearly with largest accumulations in June and July. Potential evapotranspiration rates slightly exceed precipitation, on average, and this is reflected in the negative climate moisture index (-4.2 cm). Climate data is based on the 30-year average (1970-2000) from a dataset, created by Ted Hogg of the Canadian Forestry Service, from the Red Earth, Peace River and Fort McMurray Environment Canada weather stations.

METHODS

Frequency of peatland-pond complexes on the landscape

In the study area shallow ponds (<200 ha) were observed, through helicopter surveys, to be surrounded by peatlands. Topographical and surficial geology maps were used in a GIS to analyse if <200 ha ponds are common in the study area. The number of ponds in each landform and the average area of each pond were calculated by overlaying digital map layers from Natural Resources Canada's National Topographic Data Base for sections 84B3, 84B4, 83O13 and 83O14 of the National Topographic System (1:50,000) with Alberta's surficial geology map of 84B southeast and 83O northwest (1:100,000) (Paulen et al. 2003; Paulen et al. 2004). The map was then edited to only include the research area (west and east most ponds) and every pond was assigned a landform position. The area (ha) of each wetland pond was calculated and the range and mean pond area for each landform determined. Water bodies over 200 hectares (22 in total) were not used in this analysis as previous surveys showed that these do not usually have peatlands surrounding them.

Classification and diversity of communities

In 2002 a percent cover study using the Daubenmire cover class system (Daubenmire 1959) was completed using four height classes (moss, herb, shrub, and tree) with $1m^2$ quadrats for moss and herb, $2m^2$ for shrubs and $5\ m^2$ for trees. Four 10 metre wide transects (N, S, E, W) were run in each of the study sites, from the pond edge to the upland boundary and a restricted random sampling method adopted. In a restricted random sampling design quadrats are placed within in each observed community using a random numbers table, with no quadrats placed in the transition zone between each community. Based on visual observations I thought that four communities would result from the classification; marsh, open fen, treed fen and occasionally treed bog community were observed. Species area curves were used in each community (i.e. marsh, open fen, treed fen/ bog) along a transect to ensure that the maximum number of species for that community was recorded.

Herbs, grasses, sedges, shrubs, trees, mosses, liverworts, and lichens were identified. Species were identified in the field, where possible, and the remainder brought back for identification/ verification in the University of Alberta herbaria (vascular, cryptogamic). In 2003, non-vascular species were collected from the same transects and quadrats from the bottom of trees, sides of hummocks, within mats, etc. and identified to ensure that a greater percentage of the total non-vascular species was represented. Vascular species were identified according to Moss (1983), mosses followed Crum (1981), hepatics by Stotler and Crandall-Stotler (1977) and lichens by Esslinger and Egan (1995).

A presence/ absence matrix was used to classify the peatland communities in Cluster Analysis (Sørenson-distance measure, flexible beta-group linkage) and the communities were ordinated by Non-metric Multidimensional Scaling (NMDS) with the Sørenson-distance measure (Kruskal 1964; Wishart 1969). Beals smoothing and relativization by maximum were used to normalize the data set. Rare sites (8 quadrats) but not rare species (88 species) were kept in the ordination, as this helped to explain the second axis. Multiple-response permutation procedures (MRPP), with the Sørenson-distance measure and n/ (sum) n for distance weighting, were then used to assess the strength of separation between each community (Mielke 1984). Indicator species analysis (with 1000 randomizations) was then applied to determine which species were strong indicators for each community (Dufrêne and Legendre 1997). Cluster analysis, NMDS, and MRPP were all calculated in PC-ORD 4.0 (McCune and Mefford 1999).

Alpha, beta and gamma diversity were calculated (rare species included) within each community. Alpha diversity (average species richness per quadrat), Whittaker's (1972) beta diversity (total number of species per community/ alpha diversity) and species similarity between adjacent communities using the Sorenson's similarity index were also completed for all species (Whittaker 1972). The total number of species in each community (gamma diversity) was calculated. Sorenson's similarity coefficient was used instead of Whittaker's Beta (Bw) or Wilson and Shmida's (Bt) to analyse the change in species along the wet to dry gradient (Whittaker 1972; Wilson and Shmida, 1984; Magurran 1988; Vellend 2001). In addition, diversity in each community between landforms was analyzed with Sorenson's similarity index.

Environmental variables

Environmental parameters were also measured in August 2002 and included depth to water table, oxic/ anoxic boundary (Bridgham et al., 1991), surface water anion/ cation concentrations and peat cores (taken in the oxic layer, 10-20 cm below surface). To measure water table depth, PVC wells were placed at every site, at each transect, one per community type (0.5m in marsh and fen, 1.0 m in treed peatlands). Depth to water table was measured monthly, where possible. Drought conditions persisted throughout the 2002 growing season, thus if the water table exceeded one metre below the surface it was recorded as having no water at 1 metre depth. Iron rods, that were used to measure the oxic/ anoxic boundary, were placed at the same locations as the PVC wells at the beginning of June and removed in late August and the rust level relative to the peat surface recorded. Surface water samples were collected in acid washed Nalgene bottles and refrigerated until analyzed. Temperature and pH were measured in the field.

Water samples were analyzed at the University of Alberta Limnology Laboratory for Ca, Mg, Na, K, NO_2, NO_3, NH_4, alkalinity, pH, and conductivity. The Perkin Elmer 3300 Atomic Absorption Spectrometer was used for cations, the Control Equipment Corporation 4440 Elemental Analyzer for nitrogen, the Mettler DL21 Titrator with Mettler ST20 sample for alkalinity and pH, and the Radiometer/Copenhagen model CDM 83 meter for conductivity. Due to the drought, water samples were usually collected only once from each quadrat. Only results from August are presented here, as water from the most quadrats was collected at this time.

In late August 2002 peat cores (~177 cm^3) were taken from the marsh, open fen, and treed peatland communities (two cores per community) at six sites (two outwash plain, 3 moraine, and 1 clay-till plain). Cores were extracted from the acrotelm (below the growing moss layer and no greater than 30 cm beneath the surface) and analyzed for bulk density using the Loss on Ignition method (Dean 1974). In the University of Alberta Earth Science Soils Laboratory %C and %N was calculated using the methods of Tabatabai and Bremner (1991), and %P as per Bremner and Mulvaney (1982).

Slope and elevation of peatland communities

In 2003, peat depth and slope of the mineral substrate from pond edge to upland boundary were analyzed across eight transects (with 1-3 transects per site), representing three sites from the outwash plain and three from the moraine landform. To ensure that the range of variation in slope and elevation were measured, in each landform at least one transect was a short distance (<50 metre) to the upland boundary and another > 50 metres to the upland. At each site a laser level was placed at the centre of the transect, approximately half way between the pond edge and the upland boundary. A sight line was cleared and the surface level of the peat recorded at a minimum of three points for each community zone (marsh, open fen, treed peatland). At each sample point the depth of the peat to the mineral substrate was found, using a peat corer. Feeling where peat ends and clay/ sand material begins along the corer verified the nature of the substrate. Statistical tests determined if there were significant differences in peat depth, surface and mineral elevation between community types or sites.

All statistical analyses (ANOVA, Kruskal Wallis tests) on water chemistry, peat chemistry, diversity, elevation, and peat depth data were performed on SPSS 11.5 for Windows (SPSS Inc. 2002). Statistical results were considered significant when $p \geq 0.05$.

RESULTS

Frequency of these peatland communities on the landscape

Within the 71 175 ha study area (Figure 2-1) there 505 ponds, that averaged 5.2 ha (s = 0.81) in size, the majority of which were surrounded by peatland communities. The study area size is less than 1% of the total area of the mid-boreal region. The ponds located on the clay-till plain were 15.8 ha (s = 4.2) in size and mean pond sizes were smaller in both the outwash plain and moraine at 5.0 ha (s = 1.6) and 4.7 ha (s = 1.0) respectively. Pond perimeter in the clay-till plain was 1268.8 m (s = 293.8) while pond perimeter in the outwash plain and moraine were similar, with 640 m (s = 106.6) in the outwash plain and 804 m (s =

118.7) in the moraine. However, for all ponds in the study area neither pond area or perimeter length was statistically significantly different with landform, despite visual observations of larger ponds in the clay-till plain. See Appendix 1 for pond area of each study site.

Classification of communities

A total of five peatland communities were identified in the classification, which were eventually named a marsh, wet open fen, dry open fen, treed fen and a bog community (Figure 2-2). The classification of the communities produced a low percent chaining in Cluster Analysis (0.71 %) as well as low stress and instability (7.13 and 0.00054 respectively) in NMDS. An MRPP analysis showed that the five communities are distinctly unique ($T=-103$, $A=0.5$, $p \leq 0.000$). Figure 2-3 is a conceptual diagram showing the location of the communities in relation to the pond edge; however, not all communities were present in any of the 12 sites studied.

According to the ordination, the five communities were located along a moisture gradient and a non-vegetated to vegetated gradient (Figure 2-4). The x-axis of the ordination showed that the communities followed a wet to dry gradient. The wettest community (marsh) was found at the pond edge on the left side of the ordination while the driest community (bog) is often furthest away from the pond and found at the right side of the ordination. This was supported by mean depth to water table measurements (Table 2-1) and wet and dry bryophyte species indicators (Slack et al. 1980) for each community. The water table was closest to the surface in the marsh community (5.7 cm below) and furthest from the surface in the bog (42.4 cm below). The wet open fen, dry open fen and treed fen had mean water table depths of approximately 20 cm below the surface. A Kruskal-Wallis test showed that differences in water table depth between groups were significant at 0.011.

The second gradient (y axis) was from non-vegetated to highly vegetated. The bottom of the ordination had marsh quadrats consisting mostly of bare peat and few species (<5-25% total plant cover), followed by mostly vegetated marsh quadrats. The top of the ordination had fully vegetated quadrats that consisted of the remaining four communities.

In addition to the wet to dry and non-vegetated to vegetated gradients, water and peat chemistry variables further defined the five communities (Tables 2-1 & 2-2). Percent nitrogen and carbon/ nitrogen ratios in the peat differed significantly with higher nitrogen values in the marsh and C/ N ratios increasing significantly from the marsh to the open fen to the treed peatland communities (KW=0.000 & 0.001). This was supported by significantly higher NH_4 values found in the marsh and open fen surface waters (KW=0.035). Water temperatures decreased along the marsh to bog gradient, with significantly higher values in the marsh than the all other communities, except the wet open fen, which shared a similar temperature with the marsh (KW=0.001). The amount of organic carbon, carbonate and the bulk density of the peat did not differ between the five communities.

Contrary to literature, surface water chemistry (alkalinity, conductivity, calcium, magnesium, sodium) did not decrease along the marsh-bog gradient

(Malmer 1986; Vitt et al. 1995). All of these variables were highest in the marsh and lowest in the treed fen. The lowest values were not observed in the bog because the water taken was likely groundwater not surface water, as it was collected from pits up to 1 metre deep (as water did not collect in PVC wells). Vitt et al. (1995) have shown that groundwater chemistry below a bog has significantly higher pH values than peat pore water in a bog.

Community structure

The communities were identified based on the presence of indicator species and on pH and depth to water (surface or water from shallow pits). The marsh community was dynamic, species emerged (as was the case in 2002) when the water levels dropped and bare peat was exposed along the pond edge. In both the moraine and the clay-till plain, declining pond water levels exposed the bare pond margin and a marsh community quickly established itself. Pond levels remained relatively stable in the outwash plain landform; the pond margin was not exposed, so marsh fringes were only found in a few areas where the pond receded. The marsh community was dominated by species that are commonly found in marshes (Bayley and Mewhort 2004), such as *Senecio congestus (R. Br.) DC)*, *Typha latifolia* L., *Epilobium leptophyllum* Raf, *Bidens cernua* L., *Sium suave* Walt., and *Sparganium eurycarpum* Michx. (Appendix 2). Lewis et al. (1928) describes a parkland pond (Lily Lake, AB) with similar dominant marsh species (*T. latifola and S. eurycarpum).*

The two open fen communities had similar depths to water table, but were separated along the moisture gradient by species as the dry open fen contained more shrub and grass species (Table 2-3). The wet open fen was dominated by *Drepanocladus aduncus* (Hedw.) Warnst., *Menyanthes trifoliata* L., and *Carex diandra* Schrank. The dry open fen had species found in drier conditions, such as *Amblystegium serpens* (Hedw.) Schimp., *Stellaria longifolia* Muhl., and *Calamagrostis sticta* (Timm) Koeler. The dry open fen also had more low shrubs (i.e. *Betula pumila* L. var. *glandulifera* Regel, *Rubus idaeus* L., *Salix* spp.) than the wet open fen; however indicator species analysis did not list any of the shrubs as indicators of the dry open fen community (Appendix 3).

Typically, a pond had either a wet open fen community or a dry open fen community (~40% of transects). Occasionally, a dry open fen was mixed amongst the wet open fen (~30% of transects). Rarely was the dry open fen community a transitional zone between the wet open fen and the treed fen (<20% of transects).

The treed fen community was distinguished from the wet and dry open fen by the presence of *Salix* spp, birch (*Betula pumila* var. *glandulifera, B. papyrifera Marsh.*), *Larix laricina (DuRoi) K. Koch* and *Tomenthypnum nitens (Hedw.) Loeske*.

The wet open fen, dry open fen and treed fen fall under moderate rich fen communities based on water chemistry (Szumigalski and Bayley 1996), high cation content and species composition, (Vitt and Slack 1975; Vitt et al. 1975; Vitt et al. 1995). The surface water pH (~6.0) was indicative of fens (4.8-6.8) rather than bogs (3.5-4.5) (Table 2-1). All of our fens were dominated by brown mosses (Family Amblystegiaceae as well as *Tomenthypnum nitens* and

Aulacommium palustre (Hedw.) Schawaegr.)) (Vitt and Belland 1995). See Appendix 3 for indicator species (Dufrêne and Legendre 1997) of each community.

The bog community was dominated by *Sphagnum* (*Sphagnum angustifolium* (Russ.) C. Jens., *S. fuscum* (Schimp.) Klinggr.) or *Pleurozium schreberi* (Brid.) Mitt. and covered with shrubs and trees (*Ledum groenlandicum* Oeder, *Picea mariana* (Mill.) BSP, *Vaccinium vitis-idaea* L. ssp. minus (Lodd.) Hult.). Lichens were also prominent. *Rubus chamaemorus* L. and *Smilacina trifolia* (L.) Desf. were the only dominant herbs. Together these species all indicated a bog community (Sjors 1963). *S. magellanicum* Brid. was rare in our bogs, and it is thought that its dominance decreases northward (Moss 1953).

Species richness and diversity of the peatland communities

In the peatland communities a total of 139 species were found, 70 vascular and 69 non-vascular species (Table 2-3). The marsh, wet open fen and dry open fen were dominated by vascular species. The open fen (wet and dry) contained more sedge and moss species than the marsh community. Over half of the species in the treed fen and bog were non-vascular species. Lichens were found almost exclusively in the treed fen and bog, on tree bark and deadfall, with only one lichen species in the dry open fen. The treed fen differed from the bog as it contained more herbs, grasses and *Carex* species. The bog had no grasses, no *Carex* species with *Eriophorum vaginatum* L. ssp. *vaginatum* the sole sedge species and *Smilacina trifolia* the dominant herb.

Total community diversity (gamma) was lowest in the marsh (26 species), and highest in the treed fen (86 species). The wet open fen had the second lowest number of species (48) while the dry open fen and the bog had a similar number of species, 62 and 68 respectively (Table 2-3). The marsh although only delineated as one community in Cluster analysis was observed to been found in two forms, an annual mudflat marsh (26 species, n=24) and a reed/sedge marsh (10 species, n=6) where no mudflat was exposed at the pond edge.

Alpha diversity was lowest in the marsh (7.9 species) and increased in numbers from the wet to dry gradient with highest alpha diversity in the treed fen (25.8 species) (Table 2-4). Alpha diversity differed between the observed two marsh types with 5.2 species seen in the annual mudflat marsh and only 2.8 in the reed/sedge marsh. The bog had the second highest alpha diversity (23.9 species). The wet open fen and dry open fen had 14.1, and 18.2 species respectively. Kruskal Wallis tests were used to compare alpha diversity between total species, vascular species and non-vascular species, and significant results were found in each case (KW = 0.000, 0.02, and 0.000 respectively). For both total species and non-vascular species the marsh, wet open fen and dry open fen had lower alpha diversity than the treed fen and the bog. Alpha diversity of vascular species was significantly lower in the marsh than the treed fen and the bog. Beta diversity was low across all communities; quadrats within each community were homogeneous (Table 2-4).

The five peatland communities had few species in common. When examining adjacent communities, the marsh and dry open fen shared the least number of species (0.2) and the wet and dry open fen had the most species in common (0.3) (Table 2-5). Other similarity values included 0.2 for the marsh and wet open fen, 0.2 for the wet open fen and treed fen, 0.3 for both the dry open fen and treed fen and the treed fen and bog. The marsh and bog represent the wettest and driest communities, and not surprisingly they were dissimilar (0). The two marsh communities (annual mudflat and reed/sedge) had the highest similarity value (0.56) having half of the species in common.

All five communities were found in each of the three landforms. For any given community the species list was not identical between the outwash plain, moraine, and clay-till plain. When comparing any community between landforms, approximately half of the species were held in common. For all three landform comparisons (outwash plain vs. moraine, moraine vs. clay-till plain, outwash vs. clay-till plain) marsh beta diversity values were 0.4, wet open fen were 0.5, dry open fen ranged from 0.4-0.5, treed fen were 0.6, and bog ranged from 0.6-0.7.

Slope and elevation across peatland communities from pond edge to upland boundary

The variability in peat depth, the peat surface elevation, and the mineral slope below the peat were measured across the peatland communities. Comparisons between all five communities could not be made for surface slope, mineral slope or peat depth as there were more communities delineated from cluster analysis than were visually observed in the field. Due to small sample sizes peat depth in the open peatland communities (marsh, wet open fen, dry open fen) was compared to treed peatland communities (treed fen and bog). At most sites the peat thickness decreased from the pond edge to upland boundary. In the two transects with large peatland expanses (>1 km) the peat adjacent to the upland boundary was not sampled and peat depths across the peatland were relatively constant.

Peat depth was significantly higher (KW =0.000) in open communities (marsh and wet/dry open fens) than treed communities (treed fen and bog). Mean peat depth was deeper in the marsh (0.82 m, s = 1.1, n=3) and open fen (wet/ dry) (1.74 m, s = 0.9, n=53) communities than in the treed fen and bog communities (combined 0.8 m, s = 0.8, n=77). The open fen (wet/ dry) had significantly deeper peat than the treed peatland communities.

In the marsh/ open fen and the treed peatland communities, peat depth differed significantly by site (KW=0.000). In the marsh/ open fen peat depth ranged from a high of 3.0 m (s = 0.2) to a low of 1.1 m (s = 0.2). In the treed peatland communities, peat depth varied ranging from a high of 2.7 m (s = 0.2) to a low of 0.28 m (s = 0.03).

Differences in peat depth were seen between landforms with open fen peat depth greater in the outwash plain at 2.1m (s= 0.2) than in the moraine at 1.5 m (s = 0.2) and clay-till plain at 1.5 m (s = 0.2) landform (KW= 0.034). However, peat depth in the treed fen and bog communities did not differ significantly between landforms.

At sites where open fen met a bog community, a noticeable ledge (change in surface elevation) was always present. This ledge (mean rise/ run = 0.7 m) was present at three sites (M (43) and M (111), and O (208)). This ledge did not occur at the boundary between an open fen and treed fen community, there was no noticeable change in surface elevation. There was also no significant change in surface elevation between the marsh and the open fen communities. To assess whether mineral substrate plays a role in the change in communities along the pond to upland edge, the mineral slope between adjacent communities was calculated and compared. There was no significant difference in the range or mean slope of the mineral substrate between communities, and a mineral substrate ledge was not found at any of the community boundaries.

DISCUSSION

Classification of communities: Moisture controls distribution and composition of vegetation communities

Past studies have shown that the acidity-alkalinity gradient is the most useful tool for discerning peatland types (Vitt and Chee 1990; Vitt et al. 1995). In this study, pH and alkalinity did not differ significantly with peatland type, partially due to the fact that most of the communities were fens and due to difficulty in obtaining surface water samples during a drought. Other parameters such as potassium, nitrogen and phosphorus have been shown to fluctuate seasonally or yearly and cannot be used to characterize peatland types (Vitt et al. 1995).

Fens in my study area cannot be distinguished by calcium and pH levels, but are thought, as seen by Slack et al. (1980), to be controlled by water levels and degree of shading. Water levels were similar in both open fens, although this may be a reflection of sampling frequency and water depth may actually be lower in the dry open fen. The wet and dry open fen communities were differentiated by an increase in shade cover in the dry open fen. The treed fen had greater shade and distance to water than the open fen communities.

The dominant bryophyte species offer further support that the communities in this study follow a wet-dry gradient. A wet to dry gradient of moderate rich bryophyte species was described by Slack et al. (1980) with brown mosses as wet species, to hollow (wet) *Sphagnum* species, to hummock (dry) *Sphagnum* species. In my study, the three fen communities followed this wet-dry bryophyte gradient. In the wet open fen the indicator wet brown mosses were not *Drepanocladus revolvens* (Swartz) Warnstorf but *D. aduncus* and *Amblystegium serpens*. In the middle of the gradient was *Tomenthypnum nitens* and this species was first seen in the dry open fen. *S. fuscum*, the driest species in the bryophyte gradient, was the dominant moss in the bog. A bryophyte wet to dry gradient also exists for Alberta's poor fens and bogs (Vitt et al. 1975) with our bog community containing species in the drier part of the gradient (*S. angustifolium*, *S. magellanicum*, *S. fuscum* and *A. palustre*). *Tomenthypnum falcifolium* (Ren. ex Nickols) Tuom., the driest bryophyte indicator was not found at any of the sites.

Community structure

Marshes that form a fringe around ponds have only been previously studied by Moss (1953) in the mid-boreal region, although marshes in other ecoclimates (aspen parkland, low-boreal) have been studied (Nicholson 1995; Bayley and Mewhort 2004). Common to all Alberta marshes are *Carex aquatilis*

Wahlenb., *Carex lasiocarpa* Ehrh. ssp. *americana* D. Löve & Bernard , *Galium trifidum* L., *Hordeum jubatum* L., *Menyanthes trifoliata, Potentilla palustris* (L.) Scop., *Sium suave, Scutellaria galericulata* L., and *Typha latifolia. Drepanocladus aduncus* and *Amblystegium serpens* were the mosses found in my marsh sites, whereas in the aspen parkland Nicholson (1995) found both *Drepanocladus aduncus* and *D. aduncus* var. *polycarpus* (Voit) G. Rothand in the low-boreal region. Bayley and Mewhort (2004) did not find any mosses in their marshes.

Marshes surrounding these mid-boreal ponds differ from both the aspen parkland and the low-boreal marshes in that they were dominated by *Bidens cernua, Senecio congestus* as well as *Typha latifolia* (which is found in all regions). However, these mid-boreal region marshes are new communities, formed in 2002 when the pond margins were exposed. In 2003 the annual communities disappeared in ponds where water levels rose, or began to blend into the neighbouring open fen community. A decrease in marsh species due to increased water levels was also seen in experimental marsh studies at Delta Marsh in Manitoba, Canada (van der Valk 1994).

The open wet moderate rich fen (MRF) community in my mid-boreal study shared many species in common with open fens studied in Alberta's foothills (Slack et al. 1980), the aspen parkland (Nicholson 1995) and the low-boreal region (Chee and Vitt 1989; Bayley and Mewhort 2004). The aspen parkland region (Nicholson 1995) shared many species in common with my study including *Carex lasiocarpa,* C. *aquatilis, Calamagrostis stricta, C. canadensis*

(Michx.) Beauv., *Menyanthes trifoliata*, *Potentilla palustris*, *Salix* spp. as well as mosses *Calliergon giganteum* (Schimp.) Kindb., *Drepanocladus vernicosus* (Mitten) Warnstorf, and *Tomenthypnum nitens*. Similarly, the low-boreal region (Chee and Vitt 1989) shared many species in common with my mid-boreal region study including *Bryum pseudotriquetrum* (Hedw.) Gaertn. *et al*, *Brachythecium* spp., *Drepanocladus aduncus, Potentilla palustris*, *Salix* spp., and *Triglochin maritima* L..

In my mid-boreal study the dominant sedge in the open wet MRF was *Carex diandra*, and this species was also dominant in past parkland and low-boreal region studies (Lewis et al. 1928; Chee and Vitt 1989; Nicholson 1995). In past studies of the aspen parkland, low-boreal region, and foothills Carex *aquatilis*, *C. lasiocarpa,* and/ or *C. limosa* L. were the dominant open fen species (Slack et al. 1980; Nicholson 1995; Bayley and Mewhort 2004). Based on the results of this study and past open fen studies *Carex diandra* appears to be the dominant sedge from the aspen parkland to the mid-boreal region, whereas *C. lasiocarpa* dominates only in the aspen parkland and low-boreal region, and *Carex limosa* is prominent primarily in the foothills.

The open dry MRF shared species in common with Nicholson's (1995) swamp communities including *Agrostis scabra* Willd., *Calamagrostis canadensis*, *Carex aquatilis*, *Galium trifidum*, *Potentilla palustris*, *Rubus* arcticus *ssp. Acaulis* (Michx.) Focke., *Rumex crispus* L., *Scutellaria galericulata,* and *Stellaria longifolia*. Both communities also had *Picea mariana*, *Larix laricina* and *Salix* spp. in low cover. *Aulacomnium palustre*, *Brachythecium* spp., *Marchantia* *polymorpha* L., and *Pleurozium schreberi* were bryophytes found in both communities.

In the moderate rich treed fen community of this study *Picea mariana* and *Larix laricina* were the mature trees with shrubs *Ledum groenlandicum, Chamaedaphne calyculata* (L.) Moench, and hummock mosses *Sphagnum capillifolium* (Ehrh.) Hedw., *S. fuscum, Aulacomnium palustre,* and *Pohlia nutans* (Hedw.) Lindb.. These species were also seen in moderate rich treed fens in past studies from northern Michigan (Vitt and Slack 1975), Alberta's aspen parkland (Nicholson 1995), and the low-boreal region of Alberta (Szumigalski and Bayley 1996). Canopy cover in my study was most similar to the low-boreal region, with sparse *Larix laricina* canopy cover and shrub cover dominated by *Betula pumila* var. *glandulifera* (Szumigalski and Bayley 1996). The wooded rich fens studied in the low-boreal region were dominated by *Tomenthypnum nitens*, whereas in my study either brown mosses or Sphagnum species can dominate groundcover.

In my study all bogs were dominated by both *Sphagnum* (instead of brown mosses) and ericaceous shrubs, had few herbs, and were usually treed with *P. mariana* or a mix of *P. mariana* and *L. laricina.* My bog community was similar to the wooded non-permafrost bogs without internal lawns described by Halsey et al. (1997) as they were dominated by *S. fuscum*, *S. capillifolium* and *S. angustifolium* with lichens comprising less than 50% of the groundcover. In Alberta, *Sphagnum* dominated poor fen and bog communities had been described in the aspen parkland, Mariana Lakes, Swan Hills and low-boreal region (Vitt et al. 1975; Nicholson 1995; Szumigalski and Bayley 1996).

Species richness and diversity: Within and between communities

Marshes had the lowest species richness, as fluctuating water levels prevented the permanent establishment of the marsh community. Marshes in the mid-boreal region appeared to follow the drought cycle of prairie pothole wetlands; during drought mudflats were exposed and annuals germinated, increasing water levels in following years inundates these species and the annual marsh community disappears (van der Valk and Davis 1978). Species richness was highest in the treed fen community.

Diversity in peatlands is typically compared between community types using total species (vascular plus bryophytes) or the number of bryophyte species present. I found that treed fen communities had the highest bryophyte and total (vascular + non-vascular) diversity of all peatland types. Treed fens had high diversity because they had more microhabitats (hummocks, hollows, pools, tree bases) where water levels and amount of shade differed (Karolin and Bliss 1984). One continental western Canada peatland study (Vitt and Belland 1995) showed that extreme rich fens had a higher diversity than moderate rich fens, but this may be due to their inclusion of northwestern Ontario study sites, which had eastern Canada climate patterns and were located on the Canadian Shield, not the Boreal Plain. A later study on a northeast Alberta peatland by Vitt et al. (2003) found that moderate rich treed fens were more diverse than extreme rich fens. Logically, moderate rich fens should have the greatest diversity as they contain species from poor and extreme rich fens, whereas extreme rich fens only share moderate rich fen species.

Mean bryophyte alpha diversity in my mid-boreal region peatlands was lower than the diversity measured in a northeastern Alberta peatland complex (Vitt et al. 2003) for all community types. The low values may reflect the absence of peat plateaus, collapse scars, internal lawns and patterned fens from our study, which focused on the vegetation surrounding ponds. Although bryophyte alpha diversity values were low, the total number of bryophytes in our treed fen (33) and bog (29) were similar to the numbers, (treed fen 35; bog, 36) found by Vitt and Belland (1995) for continental western Canada. Total species (vascular and non-vascular) in our treed fen (86) were similar to those found by Slack et al. (1980) for rich fens (96 species) and our bog total species numbers (68) agreed with Vitt et al. (1975) for poor fens (66 species).

Rare species in the peatland communities

Some of the species found in the communities are listed as rare (rank S1, S2 or S3) in Alberta (Vujnovic 2002). These species include herbs *Barbarea orthoceras* Ledeb., *Epilobium leptophyllum*, and *Lysimachia thrysiflora* L.; liverwort- *Lophozia incisa* (Schrad.) Dum. var *incisa* var. *inermis* K. Müll and mosses; *Bryum algovicum* C. Mull., *Bryum pallens* Swartz, *Calliergon richardsonii* (Mitten) Kindberg, *Plagiomnium medium* (Bruch & Schimp.) T. Kop., *Pohlia sphagnicola* (B.S.G.) Brotherus, *Rhizomnium pseudopunctatum* ((Bruch & Schimp.) T. Kop., *Sphagnum contortum* Schultz, *Sphagnum russowii* Warnst., *Sphagnum subsecundum* Nees, and *Tetraplodon angustatus* (Hedw.) Bruch & Schimp.. Vitt et al. (2003) also conducted a bryophyte diversity study in the mid-boreal region and also found that *Calliergon richardsonii*, *Lophozia* *incisa,* and *Tetraplodon angustatus* were rare species for the region. Two of the rare Alberta species, *Epilobium leptophyllum* and *Sphagnum russowii,* were common in the study area.

CONCLUSIONS

Peatland communities surrounding boreal ponds were common occurrences on the mid-boreal Alberta landscape. Five peatland communities were present, marsh, wet open fen, dry open fen, treed fen and bog. The communities were distributed across a wet/dry gradient (pond edge/upland edge) and the marsh community was less vegetated (during the 2002 drought) than the other four communities, as the surface exposed for plant growth is controlled by pond levels. All of the three fen types (wet open, dry open, treed) fall within the moderate-rich fen category, with pH around 6.0 and water table depths ranging from 20-45 cm below the surface. Species richness was highest in the treed fen, as microhabitats (hummocks, hollows, and pools) abound. The marsh community had the lowest species richness, possibly a result of unstable conditions created by fluctuating pond water levels. The adjacent communities (wet open and dry open fen) shared the most species in common, which explains why these communities were not distinguished from field observations. Peat depth was significantly deeper in the open than the treed peatland communities. Between an open community and the bog, a peat ledge is present; this was not found between an open community and the treed fen. Future work is needed to conduct a detailed water and peat chemistry profile for the bog community during wet conditions, to determine how these mid-boreal peatlands surrounding shallow ponds formed (terrestrialization, paludification) and to assess their stability in the future with global warming.

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REFERENCES

Achuff, P.L. 1994. Natural regions, subregions and natural history themes of Alberta. Alberta Environmental Protection, Edmonton, AB. 72 pp.

Bayley, S.E., and Mewhort, R.L. 2004. Plant community structure and functional differences between marshes and fens in the southern boreal region of Alberta, Canada. Wetlands 24: 277-294.

Bremner, J.M., and Mulvaney, C.S. 1982. Nitrogen total and total P. *In* Methods of Soil Analysis. Second Edition. *Edited by* A.L. R.H. Miller, and D.R. Keeney. American Society of Agronomy: Soil Science Society of America, Madison. pp. 595-599.

Bridgham, S.D., Faulkner, S.P., and Richardson, C.J. 1991. Steel Rod Oxidation as a Hydrologic Indicator in Wetland Soils. Soil Science Society of America Journal 55: 856-862.

Chee, W.L., and Vitt, D.H. 1989. The Vegetation, Surface-Water Chemistry and Peat Chemistry of Moderate-Rich Fens in Central Alberta, Canada. Wetlands 9: 227-261.

Crum, H.A. 1981. Mosses of Eastern North America Volume 1 & 2. Columbia University Press, New York. 1328 pp.

Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Scientist 33: 43-64.

Dean, W.E. 1974. Determination of Carbonate and Organic-Matter in Calcareous Sediments and Sedimentary-Rocks by Loss on Ignition - Comparison With Other Methods. Journal of Sedimentary Petrology 44: 242-248.

Devito, K.J. 2004. Personal communication.

Du Rietz, G.E. 1949. Huvudenheter och huvudgränser i svensk myrvegetation. Svensk Botanisk Tidskrift 43: 274-309.

Dufrêne, M., and Legendre, P. 1997. Species Assemblages and Indicator Species: the Need for a Flexible Asymmetrical Approach. Ecological Monographs 67: 345-366.

Ecoregions Working Group. 1989. Ecoclimatic Regions of Canada, First Approximation. Minister of Supply and Services Canada, Ottawa. 118 pp.

Esslinger, T.L., and Egan, R.S. 1995. A Sixth Checklist of the Lichen-Forming, Lichenicolous, and Allied Fungi of the Continental United States and Canada. Bryologist 98: 467-549.

Ferone, J.M., and Devito, K.J. 2004. Shallow Groundwater-Surface Water Interactions in Pond-Peatland Complexes Along a Boreal Plains Topographic Gradient. Journal of Hydrology 292: 75-95.

Gignac, L.D., and Vitt, D.H. 1990. Habitat limitations of *Sphagnum* along climatic, chemical, and physical gradients in mires of western Canada. The Bryologist 93: 7-22.

Gignac, L.D., and Vitt, D.H. 1994. Responses of northern peatlands to climate change: effects on bryophytes. Journal of the Hattori Botanical Laboratory 75: 119-132.

Halsey, L., Vitt, D.H., and Zoltai, S.C. 1997. Climatic and Physiographic Controls on Wetland Type and Distribution in Manitoba, Canada. Wetlands 17: 243-262.

Horton, D.G., Vitt, D.H., and Slack, N.G. 1979. Habitats of Circumboreal-Subarctic Sphagna .1. Quantitative-Analysis and Review of Species in the Caribou Mountains, Northern Alberta. Canadian Journal of Botany 57: 2283-2317.

Karlin, E.F., and Bliss, L.C. 1984. Variation in Substrate Chemistry Along Microtopographical and Water-Chemistry Gradients in Peatlands. Canadian Journal of Botany 62: 142-153.

Kruskal, J.B. 1964. Nonmetric Multidimensional-Scaling - a Numerical-Method. Psychometrika 29: 115-129.

Lewis, F.J., Dowding, E.S., and Moss, E.H. 1928. The Vegetation of Alberta: II, The Swamp, Moor and Bog Forest Vegetation. The Journal of Ecology 16: 19-70.

Magurran, A.E. 1988. Ecological diversity and its measurement. Princeton University Press, New Jersey. 179 pp.

Malmer, N. 1986. Vegetational Gradients in Relation to Environmental-Conditions in Northwestern European Mires. Canadian Journal of Botany 64: 375-383.

McCune, B., and Mefford, M.J. 1999. PC-ORD. Multivariate analysis of ecological data Version 4 [computer program], MjM Software Design, Gleneden Beach, Oregon.

Mielke, P.W. Jr. 1984. Meteorological applications of permutation techniques based on distance functions. *In* Handbook of Statistics. *Edited by*

P.R. Krishnaiah and P.K. Sen. Elsevier Science Publishers, Amsterdam. pp. 813-830.

Moss, E.H. 1953. Marsh and bog vegetation in northwestern Alberta. Canadian Journal of Botany 31: 448-470.

Moss, E.H. 1983. Flora of Alberta: a manual of flowering plants, conifers, ferns and fern allies found growing without cultivation in the province of Alberta, Canada. University of Toronto Press, Toronto. 687 pp.

National Wetlands Working Group. 1988. Wetlands of Canada. Ecological Land Classification Series. No. 24. Sustainable Development Branch, Environment Canada, Ottawa, Ontario, and Polyscience Publications Inc., Montreal, Quebec. 452 pp.

National Wetlands Working Group. 1997. The Canadian Wetland Classification System. 2nd ed. Wetlands Research Centre, Waterloo. 68 pp.

Nicholson, B.J. 1995. The Wetlands of Elk Island National-Park - Vegetation Classification, Water Chemistry, and Hydrotopographic Relationships. Wetlands 15: 119-133.

Nicholson, B.J., and Vitt, D.H. 1994. Wetland development at Elk Island National Park, Alberta, Canada. Journal of Paleolimnology 12: 19-34.

Paulen, R.C., Fenton, M.M., and Pawlowicz, J.G. 2003. Surficial Geology of the Peerless Highlands Area (NTS 84B/NE), scale 1:100,000. Alberta Energy and Utilities Board, EUB/AGS Map 267.

Paulen, R.C., Pawlowicz, J.G., and Fenton, M.M. 2004. Surficial Geology of the Utikuma Area (NTS 83O/ NW), scale 1:100,000. Alberta Energy and Utilities Board, EUB/AGS Map 312.

Sjors, H. 1950. On the Relation Between Vegetation and Electrolytes in North Swedish Mire Waters. Oikos 2: 241-258.

Sjörs, H. 1963. Bogs and fens on Attawapiskat River, Northern Ontario. National Museum of Canada Bulletin, 186: 45-133.

Slack, N.G., Vitt, D.H., and Horton, D.G. 1980. Vegetation Gradients of Minerotrophically Rich Fens in Western Alberta. Canadian Journal of Botany 58: 330-350.

SPSS Inc. 2002. SPSS 11.5.0. Chicago.

Stotler, R., and Crandall-Stotler, B. 1977. A Checklist of the Liverworts and Hornworts of North America. The Bryologist 80: 405-428.

Szumigalski, A.R., and Bayley, S.E. 1996. Net Above-Ground Primary Production Along a Bog-Rich Fen Gradient in Central Alberta, Canada. Wetlands 16: 467-476.

Tabatabai, M.A., and Bremner, J.M. 1991. Automated instruments for determination of total carbon, nitrogen, and sulphur in soils by combustion techniques. *In* Soil analysis. *Edited by* K.A Smith. Marcel Dekker, New York. pp. 261-286.

van der Valk, A.G. 1994. Effects of Prolonged Flooding on the Distribution and Biomass of Emergent Species Along a Fresh-Water Wetland Coenocline. Vegetatio 110: 185-196.

van der Valk, A.G., and Davis, C.B. 1989. The role of seed banks in the vegetation dynamics of prairie glacial marshes. Ecology 59: 322-335.

Vellend, M. 2001. Do Commonly Used Indices of Beta-Diversity Measure Species Turnover? Journal of Vegetation Science 12: 545-552.

Vitt, D.H. 1994. An Overview of Factors that Influence the Development of Canadian Peatlands. Memoirs of the Entomological Society of Canada 169: 7-20.

Vitt, D.H., and Belland, R.J. 1995. The bryophytes of peatlands in continental western Canada. Fragmenta Floristica Et Geobotanica 40: 339-348.

Vitt, D.H., and Chee, W.L. 1990. The Relationships of Vegetation to Surface-Water Chemistry and Peat Chemistry in Fens of Alberta, Canada. Vegetatio 89: 87-106.

Vitt, D.H., and Kurhy, P. 1992. Changes in moss-dominated wetland ecosystems. *In* Bryophytes and Lichens in a Changing Environment. *Edited by* J.W. Bates and A.M. Farmer. Oxford University Press, Oxford. pp. 178-210.

Vitt, D.H., and Slack, N.G. 1975. Analysis of Vegetation of *Sphagnum*-Dominated Kettle-Hole Bogs in Relation to Environmental Gradients. Canadian Journal of Botany 53: 332-359.

Vitt, D.H., Achuff, P., and Andrus, R.E. 1975. Vegetation and Chemical Properties of Patterned Fens in Swan Hills, North Central Alberta. Canadian Journal of Botany 53: 2776-2795.

Vitt, D.H., Li, Y.H., and Belland, R.J. 1995. Patterns of Bryophyte Diversity in Peatlands of Continental Western Canada. Bryologist 98: 218-227.

Vitt, D.H., Halsey, L.A., Thormann, M.N., and Martin, T. 2000. Peatland

Inventory of Alberta Phase 1: Overview of peatland resources in the natural regions and subregions of the province. Sustainable Forest Management Network, Edmonton. 117 pp.

Vitt, D.H., Halsey, L.A., Bray, J., and Kinser, A. 2003. Patterns of Bryophyte Richness in a Complex Boreal Landscape: Identifying Key Habitats at McClelland Lake Wetland. Bryologist 106: 372-382.

Vogwill, R.I.J. 1978. Hydrogeology of the Lesser Slave Lake Area, Alberta. Report 77-1. Alberta Research Council, Edmonton. 30 pp.

Vujnovic, K., and Gould, J. 2002. Alberta Natural Heritage Information Centre Tracking and Watch Lists - Vascular Plants, Mosses, Liverworts and Hornworts. Alberta Community Development, Parks and Protected Areas Division, Edmonton. 36 pp.

Whittaker, R.H. 1972. Evolution and measurement of species diversity. Taxon 21: 213-251.

Wilson, M.V., and Shmida, A. 1984. Measuring Beta Diversity With Presence Absence Data. Journal of Ecology 72: 1055-1064.

Wishart, D. 1969. An Algorithm for Hierarchical Classifications. Biometrics 25: 165-170.

Zoltai, S.C., and Vitt, D.H. 1995. Canadian Wetlands - Environmental Gradients and Classification. Vegetatio 118: 131-137.

Table 2-1. Standing surface water or water from pits in peat in August 2002 (mean values with standard deviation in brackets)

Variable	Marsh	Wet open fen	Dry open fen	Treed fen	Bog*
pH	6.3 (0.3)	6.2 (0.2)	6.3 (0.4)	6.0 (0.7)	6.0 (0.8)
Alkalinity (mg/L)	133.7 (82.5)	190.5 (127.5)	89.3 (75.2)	102.4 (126)	93.3 (96.9)
Conductivity (uS/cm)	N/A	472.7 (144.9)	174.4 (168.8)	203.3 (263.3)	41.1 (0, n=1)
Temperature °C	13.5 (3.7)	9.8 (0.3)	5.5 (3.7)	4.3 (2.5)	4.9 (3.3)
Calcium (mg/L)	34.3 (23.2)	26.8 (9.0)	23.6 (15.3)	19.8 (20.8)	21.5 (19.8)
Magnesium (mg/L)	7.9 (1.2)	5.1 (0.7)	5.3 (1.8)	3.1 (0.8)	5.3 (1.8)
Sodium (mg/L)	3.2 (0.6)	1.7 (0.6)	1.9 (0.6)	1.5 (0.4)	2.9 (0.5)
Ammonium (ug/L)	1499.8 (1492.3)	1539.7 (1671.7)	1539 (1457)	410.8 (324.3)	511.5 (554.7)
Nitrite/Nitrate (ug/L)	80.7 (275.8)	20.5 (32.5)	88.3 (166.2)	4.6 (2.4)	37.6 (77.8)
Depth to water table (cm)	5.7 (4.8)	22.9 (30.1)	20.1 (13.9)	25.3 (18.5)	42.4 (26.7)

* likely taken from groundwater, most pits >50 cm to over 1 metre in some sites

Table 2-2. Peat chemistry from peatlands in August 2002 (mean values with standard error in brackets)

Variable	Marsh	Wet/ dry open fen	Treed fen/ bog
Bulk density (cm^3)	0.07 (0.04)	0.06 (0.03)	0.04 (0.02)
%Organic Carbon (LOI)	92.5 (1.1)	93.2 (4.1)	93.6 (4.5)
% Carbonate (LOI)	0.5 (0.2)	1.4 (2)	1.1 (1.4)
%C	50.9 (0.6)	50 (1.0)	48.4 (1.9)
%N	3.3 (0.5)	2.8 (0.4)	1.8 (0.6)
C/N	15.8 (2.5)	18.4 (2.8)	30.3 (12.4)
%P	0.15 (0.001)	0.14 (0.01)	0.11 (0.1)
Peat depth (m)	1.8 (1.1)	1.7 (0.9)	0.9 (0.8)

Table 2-3. Numbers of species in each vegetation form for the five peatland communities

Vegetation form	Marsh	Wet open fen	Dry open fen	Treed fen	Bog
grass	2	4	3	5	0
herb	19	22	21	19	8
sedge	2	7	6	3	1
shrub/tree	0	2	6	12	13
lichen	0	0	1	10	11
hepatic	1	2	4	4	6
true moss	2	11	21	33	29
TOTAL	**26**	**48**	**62**	**86**	**68**
Vascular	23	35	36	39	22
Non-vascular	3	13	26	47	46

***Table 2-4.* Alpha (by site) and Beta (Bw) diversity for the five peatland communities**

Diversity Indices	Marsh	Wet open fen	Dry open fen	Treed fen	Bog
Alpha - all	7.9	14.1	18.2	25.8	23.9
Alpha - bryophytes	1.0	3.5	5.9	11.5	10.5
Beta-all	2.3	2.4	2.4	2.3	1.8
Beta-bryophytes	2	2.7	3.2	2.2	2.3
n	30	42	54	53	61

Table 2-5. Measure of the species similarity (Sorenson similarity coefficient) between the five peatland communities

Communities	Marsh	Wet open fen	Dry open fen	Treed fen	Bog
Marsh	1.0	-	-	-	-
Wet open fen	0.2	1.0	-	-	-
Dry open fen	0.2	0.3	1.0	-	-
Treed fen	0.1	0.2	0.3	1.0	-
Bog	0.0	0.1	0.1	0.3	1.0

Note: Sorenson Index (0=dissimilar, 1=identical)

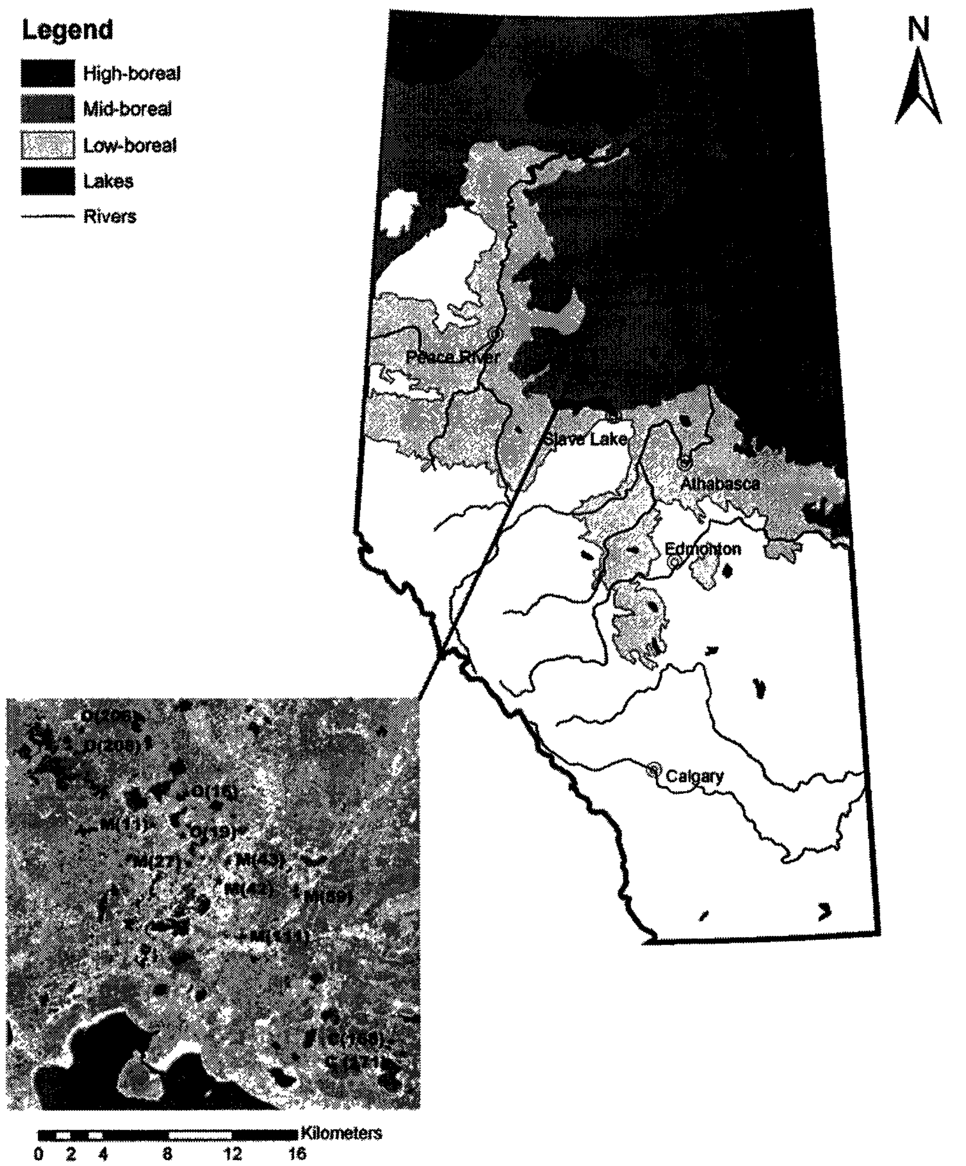

Figure 2-1. Map of Alberta with Landsat 7 2002/05/06 image of study site inset (situated above Utikuma Lake, AB) showing the location of the twelve study sites (C=Clay till plain, M=Moraine, and O=Outwash plain)

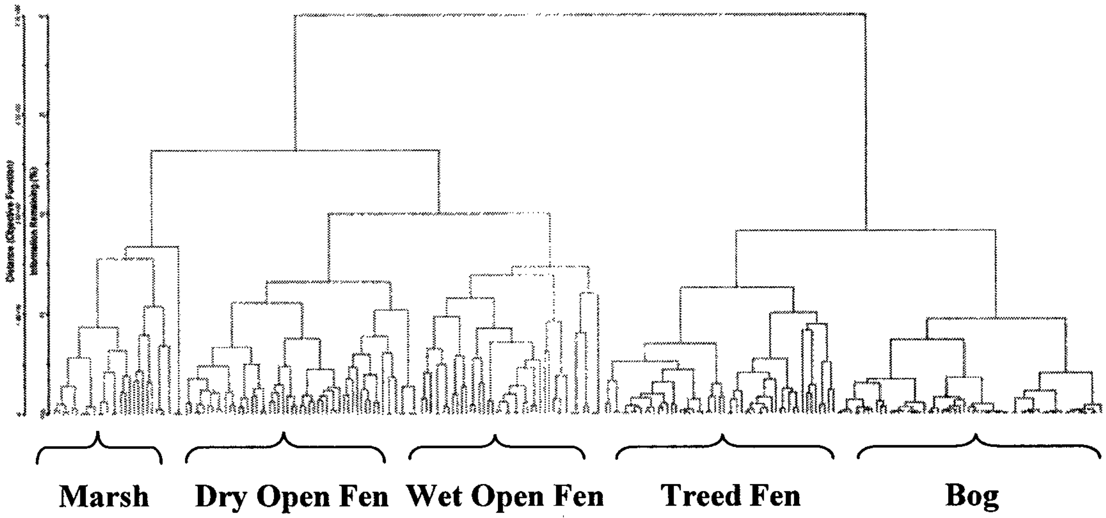

Figure 2-2. Cluster Analysis (using Sørenson-distance measure, flexible beta-group linkage), dendrogram of the five plant communities (T= -103, A = 0.5, p = 0.000)

Figure 2-3. Conceptual diagram illustrating the distribution of the five peatland communities surrounding the mid-boreal region shallow ponds

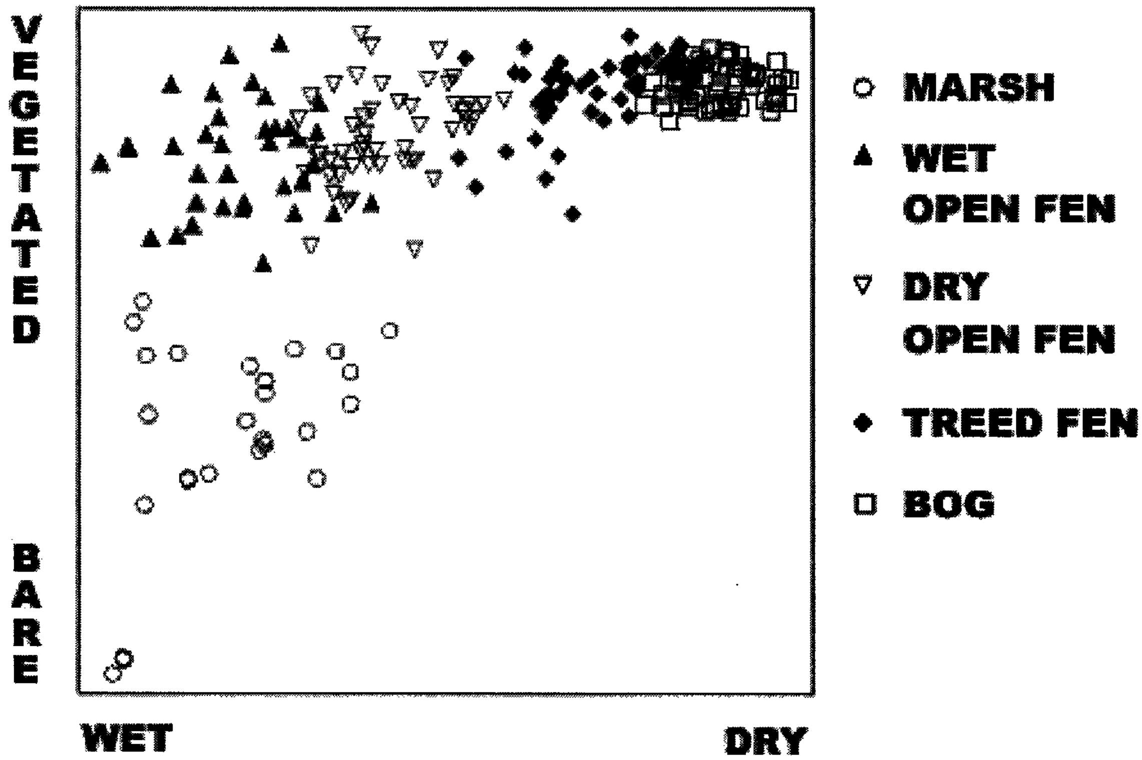

Figure 2-4. Non-metric multidimensional scaling of quadrats, with axis 1 representing a wet to dry gradient and axis two a bare to vegetated gradient

Chapter 3 – Production in Boreal Alberta peatlands during the driest year on record

INTRODUCTION

Peatlands typically occur where precipitation exceeds potential evapotranspiration. In Alberta this area begins at the boundary between the Aspen parkland and western boreal forest (Hogg 1994). In the western boreal forest, higher latitudes coupled with the shelter of trees provides a lower mean monthly temperature than seen in the Aspen parkland. This is why the majority of the over one hundred thousand square kilometres of peatlands that exist in Alberta, can be found in the western boreal forest (Vitt et al. 2000). A low mean temperature and adequate precipitation enable peatlands to establish and accumulate peat (Clymo 1984). In fact, precipitation is the vital factor determining the rate and pattern of peat formation in cool temperate bogs as it affects accumulation vs. decomposition levels (Hilbert et al. 2000; Moore 2002). For northern peatlands, peat accumulation is the result of slow decomposition, due to anaerobic conditions and a cool climate/ short growing season, rather than high production rates (Clymo 1984; Vitt 1990).

Several North American studies have measured production of individual moss and vascular species (Bray et al. 1959; Reader and Stewart 1972; Bartsch and Moore 1985; Moore 1989a) and vascular species. Studies in North America have also estimated moss production in treed fens or bogs and herb production in marshes and fens (Auclair et al. 1976; Klopatek and Stearns 1978; Grigal et al.

1985; Wieder et al. 1989; Rochefort et al. 1990; Szumigalski and Bayley 1996; Thormann and Bayley 1997; Bayley and Mewhort 2004). Correlations between production and latitude (Bernard and Gorham 1978), number of growing degree days (Droste 1984), highest monthly temperature (Gorham 1974), surface water chemistry (Auclair et al. 1976; Bartsch and Moore 1985; Backeus 1990) and water levels (Forrest and Smith 1975; Damman 1978; Backeus 1988; Moore 1989b; Szumigalski and Bayley 1996) have been found. Alberta production studies have examined the differences in marsh and fen production (Bayley and Mewhort 2004) and how production changes along the bog-marsh gradient due to differences in water chemistry, water depth and climatic variables (Szumigalski and Bayley 1996; Thormann and Bayley 1997 and 1998).

While peatlands are initiated in cool wet climates where precipitation exceed evapotranspiration; they can persist for many years after conditions have changed (Ferone and Devito 2004). Drought conditions may develop in western peatlands, either due to higher annual temperatures (which increases potential evapotranspiration rates) or by decreased precipitation. In 2002, most of Alberta experienced a severe meteorological drought, precipitation was less than evapotranspiration. Total precipitation levels were some of the lowest ever recorded (1961-2003). The effect of such a severe drought on the productivity of herbs and mosses has not been studied in western boreal peatlands.

The effect of drought on peatland production may also differ with landscape position (landforms), as topographical relief and mineral substrate has a significant effect on the volume, direction and retention of water in each peatland

(Mitsch and Gosselink 2000). In Alberta, the landforms types were created from retreating glaciers, leaving outwash plain, moraine and clay-till deposits. The amount of water absorbed and retained in peatlands of each landform differs (Ferone and Devito 2004), and the position of the water table (relative to the surface) directly affects the production of aboveground herb vegetation (Thormann et al. 1998). Differences in hydrology, due to landform, may cause differences in peatland production during times of drought.

RESEARCH OBJECTIVES

The purpose of this study was to quantify moss and herb production during and after a drought for several peatlands in Alberta's Western Boreal Forest. The main objectives of this research were to:

1. Compare climate data for Alberta's low-boreal region, where past production studies have been completed, and mid-boreal region (this study area) to determine if climate differs between the regions. For the mid-boreal region, determine the severity of the 2002 drought;
2. Estimate 2002 production (as peak August biomass) of *Sphagnum* hummock moss in a treed fen/bog, and 2002 and 2003 herb production in a marsh and an open fen and determine whether production differs between communities, study sites, and/ or landform positions;
3. Quantitatively compare dry (2002) and wet (2003) production of herbs in marsh and open fen;

4. Compare moss and herb production in the low boreal region to my mid-boreal region.

METHODS

Study area/sites

This study was conducted in the sub-humid ecoclimatic region, in the mid-boreal plain of north-central Alberta (56° 52′N, 115° 27′ W) (Ecoregions Working Group 1989) (See Figure 2-1). This region is comprised of boreal forest and peatlands surrounding small to large shallow ponds (<200 ha). Marsh, open fen, treed fen and/ or treed bog plant communities were found adjacent to the wetland ponds in this region (Chapter 2).

The study area's average mean annual temperature is 2.7°C, with highest mean daily temperatures in July (22.7°C) and lowest in January (-22.8°C). The area receives approximately 420 mm of rain yearly with largest accumulations in June and July. Potential evapotranspiration rates slightly exceed precipitation, on average, and this is reflected in the negative average climate moisture index (-4.2 cm). Climate data is based on the 30-year average (1971-2000) from a dataset created from the Red Earth, Peace River, and Fort McMurray Environment Canada weather stations. A description of how the climate dataset was assembled is described in the methods under the heading "Compiling Climate Data".

The peatlands of Alberta's mid-boreal region are located in three different landforms, with bogs, fens and marshes found in each landform. The landforms (clay-till plain, moraine, and outwash plain) are distinguished by their parent material and topography (Ferone and Devito 2004). Moraines and clay-till plains share similar material (clay, sand, silt) but are distinguished by gently rolling hummock topography in the moraine and flat topography in the clay-till plain. Outwash plains are comprised of glaciofluvial deposits (sand and gravel) (Paulen et al. 2003; Paulen et al. 2004). The range of topographic position over the entire study is small (600-700 metres above mean sea level), with highest topographic position in the outwash plain and lowest in the clay-till plain (Vogwill 1978).

Due to the differences in parent material and topography amongst the three landforms, the distance between the groundwater and the peatland varies. This can affect the amount of water available to each community type, especially under drought conditions. In the outwash plain the water table is high, and the surficial substrate (sand and gravel) acts as a large aquifer, resulting in highly connected peatland-pond complexes throughout the landform (Devito pers. comm.). The moraine and clay-till plain are both fed by shallow groundwater flow paths (Ferone and Devito 2004), in which flow can greatly decrease in times of drought. The rate of decrease is dependent both on the length of the shallow groundwater flow path and the pond shoreline to pond area ratio (Ferone and Devito 2004). In the moraine there are short flow paths and large pond shoreline to pond area ratios, which cause rapid increases or decreases in the pond levels under normal or drought conditions respectively (Ferone and Devito 2004). Due to its flat topography, the clay-till plain has both long shallow groundwater flow paths and a small pond shoreline to pond area ratio (Ferone and Devito 2004). In times of drought, water declines in the clay-till plain are gradual throughout the growing season, whereas moraine ponds quickly decrease. In order to break the hydrologic connectivity of the outwash plain ponds, a drought would need to be severe and long lasting. However, if such a drought did occur it would take a long time for groundwater connections to re-establish on the outwash plain (Devito pers. comm.).

Compiling climate data

Climate data from 1971-2003 from weather stations operated by Environment Canada was compiled for our study area in the mid-boreal region (Red Earth, AB) and for the low-boreal region (Athabasca, AB) where production studies were conducted in the past.

Red Earth Alberta is the closest weather station to our study area (<50 km), but it only operates during summer months, with some summer months missing across several years (1970-1972, 1974-1982 and 1991-1995). Using the data available from Red Earth and data from two secondary weather stations with full twelve-month data sets (Peace River, Fort McMurray), a complete twelve-month data set for Red Earth was created. To calculate both for missing maximum and minimum temperature values, the deviation between each value at both stations was found for any given month/ year. With this information the offset temperature value was calculated for the missing data (i.e. missing value is 2°C higher than that seen on the same day at the secondary station). For missing total precipitation values, the mean precipitation ratio was calculated for each month/ year where both stations had data, and then the ratio was used to calculate missing total precipitation values. For full details on interpolation methods see Hogg (1994). All climate data (minimum/ maximum temperature, total precipitation, and a climate moisture index) for this study was provided by Ted Hogg of the Canadian Forestry Service Edmonton.

Several drought indicators are used in forestry, agriculture and climate research (Hogg 1997). The most common methods are to calculate the deviation in total precipitation from the 30-year normal (1971-2000) or from the long term average (date length set by researcher). The Climatic Moisture Index (CMI) (Hogg 1994) has also been used as it accounts for precipitation, temperature, potential evapotranspiration rates, and aridity. The CMI (cm) is an indication of how wet or dry a given area is in a year. This study used the 30-year normal and CMI index to determine whether 2002 was a meteorological drought year, and if so, how it compared to years in the past.

Sampling design

In 2002 six ponds (sites) surrounded by peatlands (marsh, open fen, treed fen, bog) were selected, with six production plots at each site. Herb and moss production sites were not identical, as ponds surrounded by *Sphagnum* hummocks (treed fen, bog communities) did not always contain marsh or open fen communities. Two sites per landform (subsurface substrate) were chosen for each production study. The sites were labelled by their landform type (C – clay-till plain, M – moraine, O – outwash plain) followed by the pond number. The study sites were as follows; moss production was carried out at treed fen and bog communities of sites C (168), C (171), M (27), M (43), O (16), and O (208). Herb production (peak biomass) was measured in the marsh and open fen communities of sites C (171), M (27), M (42), M (59), O (16), and O (208). In

2003 herb production in the marsh and open fen was conducted at site C (171), M (27), M (42), M (118), O (1), and O (206); a moss production study was not carried out in 2003. A 2003 survey of the surficial geology by the Alberta Geological Survey revealed that pond 59, originally classified as clay-till plain, fell within the moraine. In 2003 marsh and herb production was measured at sites C (171), M (27), M (42), M (118), O (1) and O (206). Sites C (171), M (27), and M (42) overlap with the 2002 production study. Moss production was not measured in 2003.

The marsh community consisted of two different species assemblages based on the water depth at the pond edge (Chapter 2). At the water's edge there was either a mudflat community comprised of *Senecio congestus* (R. Br.) DC. and *Bidens cernua* L., as observed at sites C (171), M (42) and M (59) or, a shallow marsh community of *Typha latifolia* L., and *Carex aquatilis* Wahlenb., found at sites M (27) and O (16). A marsh community was absent from site O (208).

The open and treed fen communities were moderate rich fens, as determined by species indicators and environmental variables (Chapter 2). The open fen was dominated by *Carex diandra* Schrank, *Calamagrostis sticta* (Timm) Koeler, *Menyanthes trifolia* L., *Stellaria longifolia* Muhl., *Drepanocladus aduncus* (Hedw.) Warnst. and *Amblystegium serpens* (Hedw.) Schimp.. Dominant species in the treed fen included *Betula pumila* var. *glandulifera* Regel, *Salix* spp., *Larix laricina* (DuRoi) K. Koch and mosses *Aulacomnium palustre* (Hedw.) Schawaegr., and *Tomenthypnum nitens* (Hedw.) Loeske. The pH was 6.2 in the open fen and 6.0 in the treed fen; the water table was ~20 cm below the surface in the open fen and ~25 cm below in the treed fen. Open fen communities were found at every site except C (168) and M (43). Treed fen communities, where moss production was measured, were found at sites M (27) and O (16).

Bog communities were characterized by *Picea mariana* (Mill.) BSP, *Vaccinium vitis-idaea* L. ssp. minus (Lodd.) Hult., *Ledum groenlandicum* Oeder, *Rubus chamaemorus* L., and non-vasculars *Cladonia rangerifina* (L.) F.H. Wigg, *Pleurozium schreberi* (Brid.) Mitt., *Polytrichum strictum* Brid., and *Sphagnum fuscum* (Schimp.) Klinggr. The water chemistry was taken during a drought, and water samples were likely taken from the groundwater, not the peat pore water. As a result the pH is ~6.0, out of normal range for a bog. These communities were called bogs based on the above named indicator species. Moss production was measured in bog communities at sites C (168), C (171), M (43), and O (208).

Production

Sphagnum hummock moss production was measured with the crank wire method of Clymo (1970). Six circular crank wire plots, twelve wires per plot, were installed in six study sites in early July 2002 and an initial measurement taken. Ideally, it is best to take the initial height for each crank wire in May when moss growth first begins, but the peat was frozen earlier and the wires could not be installed. In the 2002 season, total precipitation in May and June was low (23.9 vs. 42.52 mm 30 year normal) and it was thought that bryophytes did not grow significantly between May and early July. A final measurement was taken at the end of September. At this time two cores per site were taken, one per *Sphagnum* species, or if only one species present, two cores were taken of that species. Production was determined for three *Sphagnum* species (*S. capillifolium* (Ehrh.) Hedw., *S. fuscum*, and *S. russowii* Warnst.), not all of which were found at each site, but all three were found in both treed fens and bogs.

In the laboratory the number of moss stems per core was counted, and the volume of the peat core determined. As well, the top three centimetres of each core was removed (less the capitulum), dried in a 60°C oven for three days and then weighed to the nearest 0.01 gram. Clymo's (1970) capitulum correction method was not used. Moss biomass for each moss species at each site was determined by multiplying the weight of 1 cm of one plant by the average growth to determine the weight that one plant gained in 2002. This value was then multiplied by the number of plants in 1 m^2 to obtain biomass in one year in grams per m^2. Bulk density (g/cm^3), the weight per volume of peat, was determined by extracting 1cm from the peat core, subsequently dried and then weighed. The final weight was extrapolated to a cubic centimetre volume.

In this study production of herb species refers to peak annual biomass (mid-August) and does not account for biomass lost throughout the growing season due to herbivory, senescence, or decomposition, so production may be underestimated. Aboveground herb production data was collected in early to mid August 2002 in both marsh and open fen communities. Four 10 metre wide transects (N, S, E, W) were run in each of the study sites, from the pond edge to the upland boundary and a restricted random sampling method adopted. In a restricted random sampling design quadrats were placed within in each observed community using a random numbers table, with no quadrats placed in the transition zone between each community. Three quadrats (0.25 m x 0.25 m) per plant community (marsh, open fen) were harvested in each transect for a total of twelve herb production samples per plant community per study site. In the laboratory the samples were dried at 60°C. After drying the dead and live material was separated, and the live material further divided into flowering herbs and grasses/ sedges, weighed and biomass recorded.

Statistical analyses

Moss biomass and growth were compared to each factor (landform, site, and moss species). Production by each moss species was not compared against landform, plant communities or study sites, as each individual species production has a wide within-year range of natural variability, which would skew any comparisons of other factors (Wallen et al. 1988). Herb production in the marsh and open fen was compared between landforms, sites and each community.

Kruskal Wallis and Mann-Whitney tests were used as log transformations and/ or removing outliers did not give the data a normal distribution or equal variances. All statistical analyses were performed in SPSS 11.5 (SPSS Inc. 2002).

RESULTS

Climate differences in Alberta's low and mid-boreal forest regions

Total annual precipitation levels and the climate moisture index value indicate that 2002 was a severe drought year in the mid-boreal region (Figures 3-1 & 3-2). Precipitation was very low, only 132 mm during the summer growing season, compared to 258 mm for the 30 year average. Snowmelt does not recharge pore water in the peatlands (Ferone and Devito 2004), thus summer precipitation is important to plant growth. Total annual precipitation was only 287 mm; 136 mm lower than the 30-year average for the mid-boreal region. The lack of precipitation was the major contributor to the low climate moisture index of -20.1. Mean and maximum monthly temperatures were within normal ranges. Low precipitation and CMI values were also observed in the mid-boreal region in 1981, 1995 and 1998. From 1961-2003 droughts occurred in 68% of the years in the mid-boreal region but only in 35% of the years in the low-boreal region. While drought frequently occurs in the mid-boreal region, its impact on the plant (moss and herb) productivity of peatlands in this region is unknown.

There are significant climatic differences within Alberta's boreal forest. The mid-boreal region (this study area) is drier and cooler than the low-boreal region (Athabasca - location of past plant production studies) (Table 3-1). Alberta's mid-boreal region has a 30-year negative moisture balance, the climate moisture index (CMI) -4.2 cm, whereas the low-boreal region has a positive moisture average (CMI 5.9 cm). The CMI value is a reflection of low precipitation inputs, not high potential evapotranspiration rates. The 30-year average total precipitation is only 423 (mm) in the mid-boreal region and 504 (mm) in total precipitation in the low-boreal region. Mean daily temperatures are lower in the mid-boreal region (1.3 °C) than the low-boreal region (2.1 °C).

Plant production in Alberta peatlands

Moss Production

During the 2002 drought moss production was negligible (4.8 $g{\bullet}m^{-2}{\bullet}year^{-1}$), due to low moss growth (0.32 mm, s = 0.2). Moss growth (length) is directly related to the amount of time the moss is wet (Vitt 1990), and in 2002 hummock mosses were often dry due to low precipitation levels. Moss production during wet years, had not been previously measured for the mid-boreal region.

Moss growth (cm) and production ($g \cdot m^2 \cdot year$) did not differ between the treed fen and bog communities but was significantly different between sites (KW=0.006, KW=0.002) due to the dominant *Sphagnum* species present at each site. Site C (171) had higher production than M (27) and M (43) (Table 3-2). Highest moss growth was observed at sites C (171), O (16), and O (208), with lowest growth at site C (168). An examination of individual moss species growth may explain why there were differences between sites. *Sphagnum fuscum* had significantly lower mean moss growth (0.1, s = 0.1) than *S. capillifolium* (0.4, s = 0.2), and *S. russowii* (0.5, s = 0.2) (KW=0.001). *S. fuscum* dominated sites C (168), M (27) and M (43) had low moss growth and production, whereas *S. capillifolium* and *S. russowii* dominated sites C (171), O (16), and O (208) had higher moss growth and production. Moss growth and production in treed fens may also be responding lowered groundwater tables as a result of several years of low precipitation levels.

Moss growth and production differed between landforms (KW=0.007, KW=0.01) with a lower production in the moraine (1.9 $g \cdot m^{-2} \cdot year^{-1}$, s = 1.4) than both the outwash plain (1.9 $g \cdot m^{-2} \cdot year^{-1}$, s = 2.8) and the clay-till plain (1.9 $g \cdot m^{-2} \cdot year^{-1}$, s = 4.53) (Table 3-3). Moss growth was also lowest in the moraine (0.2 mm, s = 0.1), followed by the outwash plain (0.49 mm, s = 0.2), then the clay-till plain (0.3 mm, s = 0.3).

Herb Production

During the 2002, drought marsh and open fen herb production were 357 $g{\bullet}m^{-2}{\bullet}year^{-1}$ and 142 $g{\bullet}m^{-2}{\bullet}year^{-1}$, with peak production in the marsh significantly higher than the open fen (MW=0.000). In 2003, the drought was over (precipitation exceeded potential evapotranspiration) yet herb production in marshes surrounding boreal ponds was the lowest ever measured in Alberta. Marsh herb production was significantly lower in 2003 than in 2002 (Mann W= 0.000), with marsh herb production at 176 $g{\bullet}m^{-2}{\bullet}year^{-1}$ (s = 66). 2003 open fen herb production, at 158 $g{\bullet}m^{-2}{\bullet}year^{-1}$ (s = 120), was similar to the previous year (Table 3-4).

The 2002 study showed significant differences in marsh and fen herb production between sites. Marsh production during the drought differed between sites, with significantly higher values (KW=0.001) at site O (16) (788 $g{\bullet}m^{-2}{\bullet}year^{-1}$, S.D. 57.2) than C (171) (256 $g{\bullet}m^{-2}{\bullet}year^{-1}$, S.D. 155), M (42) (280 $g{\bullet}m^{-2}{\bullet}year^{-1}$, s = 121), or M (59) (200 $g{\bullet}m^{-2}{\bullet}year^{-1}$, s = 141). Production at M (27) (576.5 $g{\bullet}m^{-2}{\bullet}year^{-1}$, s = 310) was significantly higher than C (171), M (42), and M (59). A difference in marsh production between sites is due to plant species composition. The shallow marshes (dominated by cattails and water sedge) were high production sites, while the mudflat marsh (comprising nodding beggar ticks and marsh ragwort) are low production sites. See Chapter 2 for full descriptions of the two marsh communities.

Open fen herb production was lowest at site M (59) (79 $g{\bullet}m^{-2}{\bullet}year^{-1}$), where it is thought that water levels fluctuate greatly year-to-year. Bands of dead cattails in the open fen zone mark one past pond/ marsh edge, showing that water levels in this pond had decreased over the previous 5 years. The bands of standing dead cattails in the open fen decrease establishment of open fen sedges and overall potential production levels through shading. Highest open fen herb production was observed at O (16) (173 $g{\bullet}m^{-2}{\bullet}year^{-1}$), then M (42) and O (208) (both 162 $g{\bullet}m^{-2}{\bullet}year^{-1}$), next is M (27) (144 $g{\bullet}m^{-2}{\bullet}year^{-1}$) and C (171) (98 $g{\bullet}m^{-2}{\bullet}year^{-1}$). Marsh and open fen herb production did not differ significantly across the three-landform types. See Appendix 5 for raw herb production data.

DISCUSSION

Moss production

Both *Sphagnum* and brown mosses are tolerant of drought to some extent; in dry conditions they lay inactive, growing only in wet conditions (Vitt 1990). The physiology of *Sphagnum* enables it to avoid drought (Wallen et al. 1988; Vitt 1990). Hummock *Sphagnum* species were chosen for this study because they are more drought resistant than hollow species due to their fine leaves and a high degree of capillarity and water retention (Clymo 1973). This study showed that after five years of drought conditions *Sphagnum* moss growth was negligible, despite measurement of only hummock species. At some sites *Sphagnum* hummocks were visibly desiccated (brittle and black or white in colour).

Moss production in the mid-boreal region was compared to production in the low-boreal region (Szumigalski and Bayley 1996; Thormann and Bayley 1997), as no previous data exists for the mid-boreal region. 2002 *Sphagnum* production in bog communities was only 5 $g{\bullet}m^{-2}{\bullet}year^{-1}$compared to 55 $g{\bullet}m^{-2}{\bullet}year^{-}$

^{1}and 212 $g \cdot m^{-2} \cdot year^{-1}$recorded by Szumigalski and Bayley (1996) and Thormann and Bayley (1997). *Sphagnum* production in treed fen's in 2002 was only 4 $g \cdot m^{-2} \cdot year^{-1}$versus 142 $g \cdot m^{-2} \cdot year^{-1}$ recorded by Szumigalski and Bayley (1996). Production in this 2002 study may be underestimated as measurements began in July and because only hummock species were measured and hollow species were excluded.

The timing and amount of precipitation are key factors in moss production (Backeus 1988; Moore 1989a). Backeus (1988) found that the amount of precipitation received in June and August most affected moss growth. In this study June and August precipitation levels were only 39.9% and 39.8 % of the normal 30-year value (Table 3-1), suggesting that moss production observed was lower than what would be found in a non-drought year.

The differences in production between the landforms can be explained by the dominant *Sphagnum* species. The two moraine sites (M (27) and M (43)) were *S. fuscum* dominated, whereas the outwash plain sites were dominated by *S. capillifolium*. In the clay-till plain *S. fuscum* dominated site C (168) but C (171) was dominated by *S. russowii*. See Appendices 4a & 4b for moss production raw data.

In this study marsh production (2002, 2003) was higher than in the fen, which is consistent with the results of Thormann and Bayley (1997) who found that production increased along the bog-fen-marsh gradient. Herb production in the marsh was higher than the fen for several reasons, first constant high nutrient supply (nitrogen and phosphorus) from the wet/ dry/ rewetting cycles (Auclair et al. 1976; Klopatek and Stearns 1978; Thormann and Bayley 1997); second, *Typha latifolia* had high biomass values and was only found in the marsh (Jervis 1969; Klopatek and Stearns 1978); third, high leaf area index for marsh species (Jervis 1969); and fourth there were more rhizomatous species in the marsh that provided energy and nutrient storage for early and rapid growth (Auclair et al. 1976).

There were similarities and differences in marsh and fen production from past Alberta studies in the low-boreal region (Table 3-5). Marsh production surrounding small mid-boreal ponds was similar to riverine marshes but smaller than production in clay-till plain marshes (Thormann and Bayley 1997; Bayley and Mewhort 2004). Open fen herb production was similar to a floating sedge fen but lower than observed in the clay-till plain sedge fen and (riverine) sedge fen (Szumigalski and Bayley 1996; Thormann and Bayley 1997; Bayley and Mewhort 2004).

Although herb production (marsh, open fen) was measured in the most severe year of the drought (2002), the lowest production was found in the marsh the following year (2003), while fen production was low in both years. Marsh production was lower in 2003 because in many sites the species composition changed in mid-summer when increasing water levels began to flood out the annuals allowing perennials (*Typha,* sedges, and grasses) to establish. The incoming perennials did not have enough time to reach their peak biomass by the end of the growing season, so that at the time of collection annuals were dying out and perennials were shorter than if they had the entire season to grow. Although 2003 was a normal precipitation year, and water levels began to rise in many sites, it is thought that open fen herb production was low in both 2002 and 2003 because the vegetation was responding to the low water storage conditions created by the five-year drought. Drought conditions existed, not just in 2002, but also from 1998-2002; total precipitation levels and climate moisture index levels for this time frame were low (Figures 3-1 & 3-2). Staff gauge data for sites C (171), M (27) and M (42) show that pond and water table levels decreased steadily from 2001-2003. So, although total precipitation levels returned to 30 year normal values in 2003, there was not enough precipitation to replenish depleted water storage in the pond and subsurface. Spring and summer precipitation levels are the most important contributor to the hydrology of peatland - pond complexes in the Boreal Plain (Ferone and Devito 2004), and continual low precipitation values may threaten the productivity of peatlands surrounding these shallow ponds.

Wet-dry wetland cycle for peatland-pond complexes in mid-boreal Alberta

Marshes and fens surrounding mid-boreal region ponds appear to follow a wet-dry cycle that is determined by precipitation, the vegetation cycle and some of the same characteristics as those described by van der Valk and Davis (1978) for prairie glacial marshes. In mid-boreal Alberta, precipitation inputs are the major contributor to the hydrology of the peatland – pond complexes (Ferone and Devito 2004). Changes in vegetation composition and production were noticed between a low precipitation year (2002) and a normal precipitation year (2003) in the marshes. It is proposed that the marshes and open fens surrounding ponds in boreal Alberta follow a two-phase cycle: low water wetland, and flooded wetland (Figure 3-3 & Figure 3-4).

The low water wetland phase was observed in 2002 and the flooded wetland phase in 2003. In 2002 water levels in the peatland – pond complexes were very low, due to five years of below average total precipitation. Low water levels exposed a mudflat area between the water's edge and the open fen. Annuals *Bidens cernua* L. and *Senecio congestus* (R. Br.) DC. germinated and thrived in the mudflat community. During this time water levels in the marsh were below or just at the surface. The open fen was dominated by forbs and grasses, and likely a result of the water table being greater than 10 cm below the surface (beyond the reach of many root systems). The following year water levels increased slightly, due to more precipitation in the summer months than past years. As a result, the mudflat zone was flooded out in most ponds, and a small cattail/ sedge fringe (marsh) emerged. With continual years of normal to above average total precipitation it is expected that water levels will remain above the surface, promoting the success of rushes, cattails, and sedges in the marsh community. In the flooded wetland phase the water level in the open fen was observed to be closer to the surface (< 10 cm below) to just above the surface. Under wetter conditions sedges, not grasses and forbs were observed to be the dominant vegetation in the open fen. The marsh and open fen flooded wetland phase was observed at some sites in 2003.

The two wetland phases represent low and high water levels and it is expected that both marsh and fen production will differ significantly between the two phases, with highest production in both communities in the flooded wetland phase. In the flooded wetland phase standing surface water is suitable for a marsh comprised of dense stands of cattails, rushes and sedges (Harris and Marshall 1963), with high production rates reflected by large *Typha* stands. Fen production is also expected to be highest at the flooded wetland phase as water will be within reach of roots, and at a suitable level for high production of sedge species. Past studies have shown that herb production increases when the water levels are close to or at the surface (Richardson 1978; Lieffers and Shay 1982; Bayley et al. 1985; and Thormann and Bayley 1997). Future research by the author, using a 2002-2004 data set will determine if production is significantly higher for both marsh and fen communities in the flooded wetland phase.

The boreal wetland cycle proposed here differs from the prairie pothole marsh cycle seen by van der Valk and Davis (1978). In this boreal study, changes in species composition were observed in both marsh and fens as a result of drought and flooding. Only two (dry and flooded) of the four phases (dry, regenerating, degenerating, flooded) described for prairie pothole wetlands were seen in this boreal study. In the boreal's dry wetland phase the ponds shrunk, exposing a mudflat fringe where annuals soon germinated. In the prairie pothole dry wetland phase the pond disappears entirely and annuals occupy the pond bed. A regenerating or degenerating phase, if present in the boreal, was short lived as insects, disease, or muskrat activity (feeding and lodge building) were not observed. In the flooded phase of both the boreal and prairie pothole wetlands, a small fringe of emergents surrounds the lakes. For the boreal, the change in the frequency of floating and submerged aquatic vegetation was not collected, however both types of vegetation were not observed in the dry wetland phase but present beyond the emergent fringe in the flooded wetland phase. For prairie pothole wetlands, floating and submerged aquatic vegetation frequency was absent in the dry phase, highest in the regenerating and degenerating phases and lower in the flooded wetland phase.

CONCLUSIONS

Peatlands that surround Alberta's boreal ponds follow a wet to dry cycle. In 2002 and 2003 a low water and a flooded water wetland were found. Production levels are expected to be highest for both marsh and fen communities during the flooded water wetland phase. A vegetation transition was observed for both communities as a site moved from the low water to a flooded wetland phase. In the marsh annuals were replaced by perennials, and in the open fen, dominance switched from forbs and grasses to mainly sedges. The length of time a given site remains at a particular phase likely depends on both the precipitation and groundwater inputs and the water storage capacity of the peat and mineral substrate. Drought causes low growth in these peatlands as regional groundwater flows are disconnected, and precipitation inputs are the major hydrological drive in these systems. Future climate scenarios predict warmer and drier conditions for Alberta's boreal (Nicholson et al. 1997) which may prove detrimental in maintaining the wetlands of Alberta's boreal ponds.

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REFERENCES

Auclair, A.N.D., Bouchard, A., and Pajaczkowski, J. 1976. Productivity Relations in a Carex-Dominated Ecosystem. Oecologia 26: 9-31.

Backeus, I. 1988. Weather variables as predictors of Sphagnum growth on a bog. Holarctic ecology 11: 146-150.

Backeus, I. 1990. Production and Depth Distribution of Fine Roots in a Boreal Open Bog. Annales Botanici Fennici 27: 261-265.

Bartsch, I., and Moore, T.R. 1985. A preliminary investigation of primary production and decomposition in four peatlands near Schefferville, Québec. Canadian Journal of Botany 63: 1241-1248.

Bayley, S.E., and Mewhort, R.L. 2004. Plant community structure and functional differences between marshes and fens in the southern boreal region of Alberta, Canada. Wetlands 24: 277-294.

Bayley, S.E., Zoltek J., Hermann, A.J., Dolan, T.J., and Tortora, L. 1985. Experimental Manipulation of Nutrients and Water in a Fresh-Water Marsh - Effects on Biomass, Decomposition, and Nutrient Accumulation. Limnology and Oceanography 30: 500-512.

Bernard, J.M., and Gorham, E. 1978. Life history aspects of primary production in sedge wetlands. *In* Freshwater wetlands: ecological processes and management potential. *Edited by* R.E. Good, D.F. Whigham, and R.L. Simpson. Academic Press, New York. pp. 39-51.

Bray, J.R., Lawrence, D.B., and Pearson, L.C. 1959. Primary production in some Minnesota terrestrial communities for 1957. Oikos 10: 38-49.

Clymo, R.S. 1970. The growth of *Sphagnum*: Methods of measurement. The Journal of Ecology 58: 13-49.

Clymo, R.S. 1973. Growth of *Sphagnum* - Some Effects of Environment. Journal of Ecology 61: 849-869.

Clymo, R.S. 1984. The Limits to Peat Bog Growth. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 303: 605-54.

Damman, A.W.H. 1978. Distribution and movement of elements in ombrotrophic peat bogs. Oikos 30: 480-495.

Devito, K.J. 2004. Personal communication.

Droste, M. 1984. Above Ground Standing Crop and Production of Carex-Gracilis Curt in a Fen. Archiv Fur Hydrobiologie 100: 533-538.

Ecoregions Working Group. 1989. Ecoclimatic Regions of Canada, First Approximation. Minister of Supply and Services Canada, Ottawa. 118 pp.

Ferone, J.M., and Devito, K.J. 2004. Shallow Groundwater-Surface Water Interactions in Pond-Peatland Complexes Along a Boreal Plains Topographic Gradient. Journal of Hydrology 292: 75-95.

Forrest, G.I., and Smith, R.A.H. 1975. Productivity of a Range of Blanket Bog Vegetation Types in Northern Pennines. Journal of Ecology 63: 173-202.

Gorham, E. 1974. Relationship Between Standing Crop in Sedge Meadows and Summer Temperature. Journal of Ecology 62: 487-491.

Grigal, D.F., Buttleman, C.G., and Kernick, L.K. 1985. Biomass and productivity of the woody strata of forested bogs in northern Minnesota. Canadian Journal of Botany 63: 2416-2424.

Harris, S.W., and Marshall, W.H. 1963. Ecology of Water-Level Manipulations on a Northern Marsh. Ecology 44: 331-343.

Hilbert, D.W., Roulet, N., and Moore, T. 2000. Modelling and Analysis of Peatlands as Dynamical Systems. Journal of Ecology 88: 230-242.

Hogg, E.H. 1994. Climate and the southern limit of the western Canadian boreal forest. Canadian Journal of Forest Research 24: 1835-1845.

Hogg, E.H. 1997. Temporal Scaling of Moisture and the Forest-Grassland Boundary in Western Canada. Agricultural and Forest Meteorology 84: 115-122.

Jervis, R.A. 1969. Primary production in the freshwater marsh of Troy meadows, New Jersey. Bulletin of the Torrey Botanical Club 96: 209-231.

Klopatek, J.M., and Stearns, F.W. 1978. Primary productivity of emergent macrophytes in a Wisconsin freshwater productivity ecosystem. American Midland Naturalist 100: 320-332.

Lieffers, V.J., and Shay, J.M. 1981. The effects of water level on growth and reproduction of Scirpus maritimus var. paludosus on the Canadian prairies. Canadian Journal of Botany 59: 118-121.

Mitsch, W.J., and Gosselink, J.G. 2000. Wetlands. 3rd ed. John Wiley & Sons, New York. 920 pp.

Moore, P.D. 2002. The Future of Cool Temperate Bogs. Environmental Conservation 29: 3-20.

Moore, T.R. 1989a. Growth and net production of *Sphagnum* at five fen sites, subarctic eastern Canada. Canadian Journal of Botany 67: 1203-1207.

Moore, T.R. 1989b. Plant production, decomposition, and carbon efflux in a subarctic patterned fen. Arctic and Alpine Research 21: 156-162.

Nicholson, B.J., Gignac, L.D., Bayley, S.E., and Vitt, D.H. 1997. Vegetation responses to global warming: Interactions between boreal forest wetlands and regional hydrology. *In* Mackenzie Basin Impact Study (MBIS). *Edited by* S.J. Cohen. Environment Canada, University of British Columbia, Vancouver. pp. 125-45.

Paulen, R.C., Fenton, M.M., and Pawlowicz, J.G. 2003. Surficial Geology of the Peerless Highlands Area (NTS 84B/NE), scale 1:100,000. Alberta Energy and Utilities Board, EUB/AGS Map 267.

Paulen, R.C., Pawlowicz, J.G., and Fenton, M.M. 2004. Surficial Geology of the Utikuma Area (NTS 83O/ NW), scale 1:100,000. Alberta Energy and Utilities Board, EUB/AGS Map 312.

Reader, R.J., and Stewart, J.M. 1972. The relationship between primary production and accumulation fore a peatland in southeastern Manitoba. Ecology 53: 1024-1037.

Richardson, C.J., Tilton, D.L., Kadlec, J.A., Charmie, J.P.M., and Wentz, D.L. 1978. Nutrient dynamics of northern wetland systems. *In* Freshwater wetlands: ecological processes and management potential. *Edited by* R.E. Good, D.F.Whigham, D.F., and R.L. Simpson. Academic Press, New York. pp. 217-41.

Rochefort, L., Vitt, D.H., and Bayley, S.E. 1990. Growth, Production, and Decomposition Dynamics of *Sphagnum* Under Natural and Experimentally Acidified Conditions. Ecology 71: 1986-2000.

SPSS Inc. 2002. SPSS 11.5.0. Chicago.

Szumigalski, A.R., and Bayley, S.E. 1996. Net Above-Ground Primary Production Along a Bog-Rich Fen Gradient in Central Alberta, Canada. Wetlands 16: 467-476.

Thormann, M.N., and Bayley, S.E. 1997. Decomposition Along a Moderate-Rich Fen-Marsh Peatland Gradient in Boreal Alberta, Canada. Wetlands 17: 123-37.

Thormann, M.N., Bayley, S.E., and Szumigalski, A.R. 1998. Effects of Hydrologic Changes on Aboveground Production and Surface Water Chemistry in Two Boreal Peatlands in Alberta: Implications for Global Warming. Hydrobiologia 362: 171-183.

van der Valk, A.G., and Davis, C.B. 1978. The role of seed banks in the vegetation dynamics of prairie glacial marshes. Ecology 59: 322-335.

Vitt, D.H. 1990. Growth and Production Dynamics of Boreal Mosses Over Climatic, Chemical and Topographic Gradients. Botanical Journal of the Linnean Society 104: 35-59.

Vitt, D.H., Halsey, L.A., Thormann, M.N., and Martin, T. 2000. Peatland Inventory of Alberta Phase 1: Overview of peatland resources in the natural regions and subregions of the province. Sustainable Forest Management Network, Edmonton. 117 pp.

Vogwill, R.I.J. 1978. Hydrology of the Lesser Slave Lake Area, Alberta. Report 77-1. Alberta Research Council, Edmonton. 30 pp.

Wallen, B., Falkengrengrerup, U., and Malmer, N. 1988. Biomass, Productivity and Relative Rate of Photosynthesis of *Sphagnum* at Different Water Levels on a South Swedish Peat Bog. Holarctic Ecology 11: 70-76.

Wieder, R.K., Yavitt, J.B., Lang, G.E., and Bennett, C.A. 1989. Aboveground net primary production at big run bog, West Virginia. Castanea 54: 209-216.

Table 3-1. Climate data for Alberta's low-boreal region (Athabasca, AB) and mid-boreal region (Red Earth, AB) regions (standard deviation in brackets)

Year	Min./Max. Temperature (°C)	Mean Daily Temp. (°C)	Total Precip. (mm)	Total Summer Precip. (May-Aug.) (mm)	CMI (cm)	
2002	-5.7/7.1	0.7	287 (22)	132 (27)	-20.1	Mid-boreal
2003	-5.2/7.3	1.1	416 (30)	266 (32)	4.7	
30 yr avg.	**-5.3/7.8**	**1.3**	**423 (87)**	**258 (75)**	**-4.2**	
2002	-4.0/7.2	1.6	339 (24)	175 (31)	-10.7	Low-boreal
2003	-3.0/7.5	1.9	491 (39)	309 (51)	6.1	
30 yr avg.	**-3.5/7.6**	**2.1**	**504 (87)**	**307 (68)**	**5.9**	

Table 3-2. Moss growth (cm) and production ($g \cdot m^{-2} \cdot year^{-1}$) by site (standard deviation in brackets)

Site	Growth (cm)	Production ($g \cdot m^{-2} \cdot year^{-1}$)
C (168)	0.1 (0.1)	3.3 (4.1)
C (171)	0.5 (0.1)	8.8 (3.2)
M (27)	0.5 (0.04)	2.3 (1.9)
M (43)	0.5 (0.2)	1.5 (0.5)
O (16)	0.2 (0.1)	6.3 (3.0)
O (208)	0.2 (0.0)	6.1 (2.8)

Table 3-3. Differences in moss production ($g \bullet m^{-2} \bullet year^{-1}$) between landforms for both moderate rich treed fen and bog communities (standard deviation in brackets)

Landform	Community Moderate Rich Treed Fen	Bog	Combined
Clay-till plain	N/A	6.0 (4.5)	6.0 (4.5)
Moraine	2.3 (1.9)	1.5 (0.5)	1.9 (1.4)
Outwash	6.3 (3.0)	6.1 (2.8)	6.2 (2.8)

Table 3-4. Differences in herb production ($g \cdot m^{-2} \cdot year^{-1}$) for the marsh and moderate rich open fen between 2002 and 2003 for three sites (standard deviation in brackets)

	Community			
	Marsh		**Moderate Rich Open Fen**	
Site	**2002**	**2003**	**2002**	**2003**
C (171)	256 (155)	124 (56)	98 (3)	304 (91)
M (27)	577 (310)	166 (52)	144 (92)	87 (47)
M (42)	280 (121)	217 (62)	162 (144)	84 (27)
Average	374 (255)	176 (66)	147 (113)	158 (120)

Table 3-5. Herb production values ($g \cdot m^{-2} \cdot year^{-1}$) in Alberta's marsh and open fen communities

Wetland Type	Herb production	Reference
Marsh 1	757	Thormann and Bayley (1997)
Marsh 1	1092, 818	Bayley and Mewhort (2004)
Marsh 2	743	Bayley and Mewhort (2004)
Riverine Marsh	323	Thormann and Bayley (1997)
Riverine Marsh 2	328, 87	Bayley and Mewhort (2004)
Marsh	357, 52	This Study
Floating Sedge Fen	148	Thormann and Bayley (1997)
Floating Sedge Fen	135, 178	Bayley and Mewhort (2004)
Sedge Fen	163	Szumigalski and Bayley (1996)
Sedge Fen	190	Thormann and Bayley (1997)
(Riverine) Sedge Fen	409	Thormann and Bayley (1997)
Sedge Fen	312, 344	Bayley and Mewhort (2004)
Open Fen	142, 31	This Study

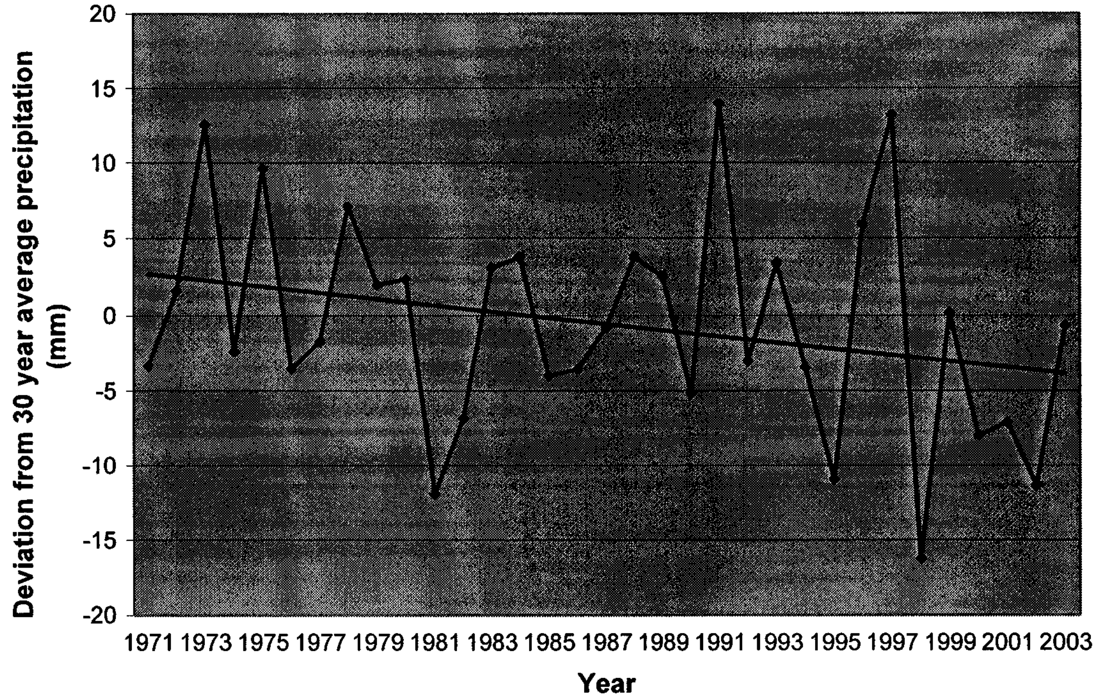

Figure 3-1. Deviation from 30-year average (1971-2000) precipitation (mm) for Alberta's mid-boreal region (Red Earth, AB)

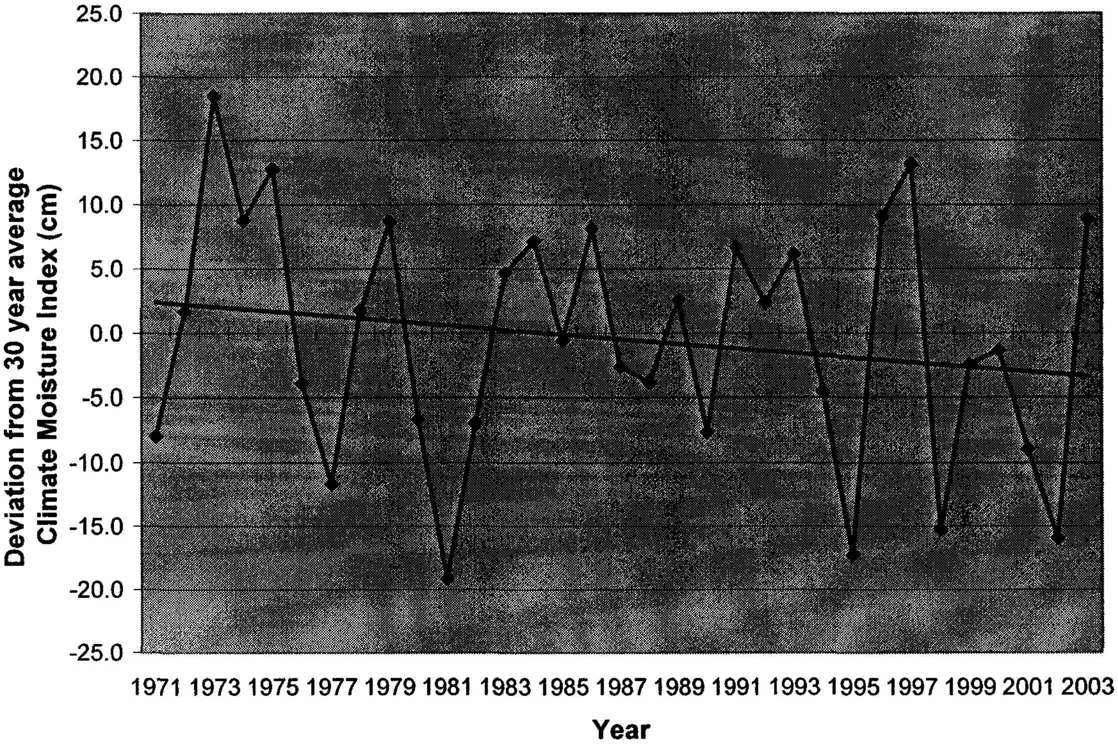

Figure 3-2. Deviation from 30-year average (1971-2000) Climate Moisture Index (cm) for Alberta's mid-boreal region (Red Earth, AB)

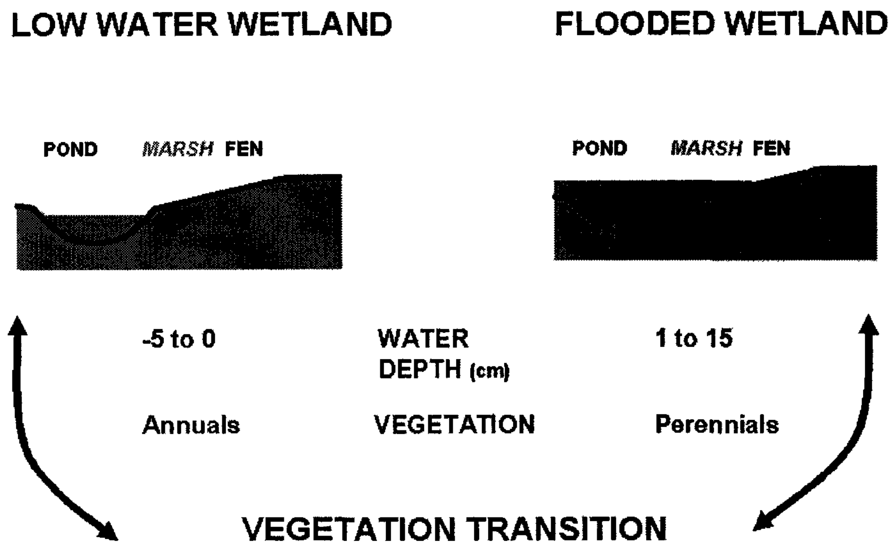

Figure 3-3. Marshes in the boreal wetland cycle

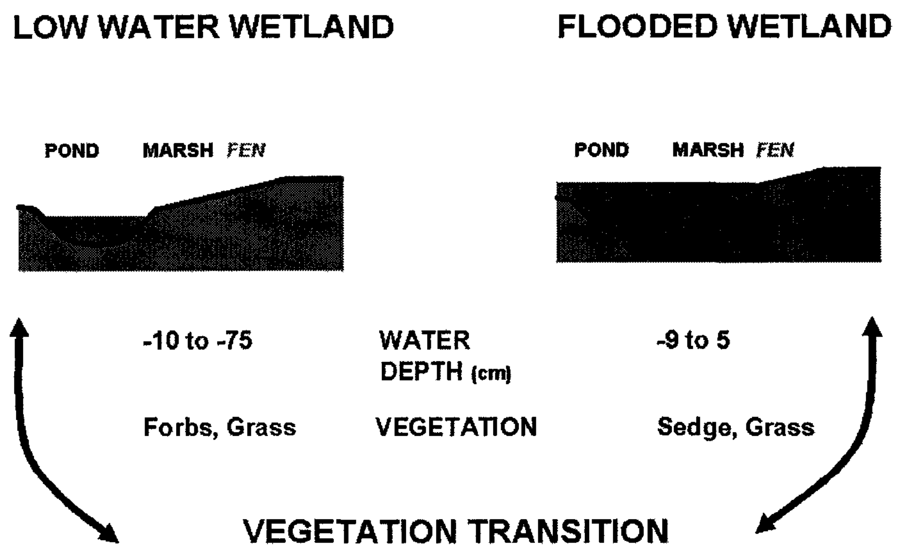

Figure 3-4. Open fens in the boreal wetland cycle

Chapter 4 – Conclusions

Peatlands surrounding shallow ponds were common and found in three different landforms (outwash plain, moraine, clay-till plain). Pond area and perimeter was larger in the clay-till plain than the other landforms, but these numbers were not statistically significant. Around the ponds, five peatland communities were classified; marsh, wet open fen, dry open fen, treed fen, and bog. These communities were separated across both a wet to dry gradient and a non-vegetated to vegetated gradient. The species composition of each community was distinct (MRPP, Sorenson's similarity index) and indicator vascular and bryophyte species were found in each community. The pH was similar between the communities but water depth, water temperature, peat depth, and peat C/ N ratios differed between open and treed peatland communities. Generally, the peat was deep at the pond edge and shallow at the upland boundary. Both total species (vascular and bryophyte) and bryophyte species alpha and gamma diversity were highest in the treed fen and lowest in the marsh community. Between-community diversity was low; communities shared few species in common. Some communities had rare Alberta herb and bryophyte species.

The production study was conducted in the final year of a five-year drought. Sphagnum moss production (4.8 $g{\bullet}m^{-2}{\bullet}year^{-1}$) was negligible, whereas herb production in the marsh (357 $g{\bullet}m^{-2}{\bullet}year^{-1}$) and open fen (142 $g{\bullet}m^{-2}{\bullet}year^{-1}$) herb communities were similar to past studies during non-drought years. Moss production was lowest at sites with *Sphagnum fuscum* (Schimp.) Klinggr., while herb production was lowest in marshes dominated by mudflat annual species.

Herb production was significantly lower in the marsh (176 $g \cdot m^{-2} \cdot year^{-1}$) the year following the drought but open fen (158 $g \cdot m^{-2} \cdot year^{-1}$) was similar. Peatland communities were found in three landforms (outwash plain, moraine, clay-till plain), and moss and herb production differed amongst landforms. It was expected that each landform, based on parent material and hydrologic connectivity, would have a different response and recovery time to drought conditions. A wet-dry wetland plant community cycle was proposed for Alberta's boreal region; a low water wetland and a flooded wetland phase were observed.

In this research there were three general objectives; to determine whether these peatland - pond complexes in my study area of the mid-boreal region were common, to classify and describe the peatland community types, and to document herb and moss production during a known drought. This was one of the first studies to classify, describe the floristics and diversity of peatland plant communities surrounding ponds, and to determine the underlying environmental conditions (water table and peat depth, surface water and peat chemistry) surrounding these shallow ponds in Alberta's mid-boreal region. This research documented the baseline information for these undisturbed peatland -complexes, and can be used for comparison over time under changing conditions (anthropogenic disturbance, climate warming). As well, this was one of the first peatland production studies to provide herb and moss production rates during a severe drought. Finally, in this study a wet-dry wetland cycle was proposed for the marsh and fen communities, with a low water wetland and a flooded wetland phase present, each phase differing in water levels and vegetation community structure.

Appendix 1. Pond area (hectares) for each study site

Site	Area (ha)
O (11)	0.73
O (16)	36.79
O (206)	12.58
O (208)	2.86
M (111)	6.64
M (19)	2.09
M (27)	5.95
M (42)	1.34
M (43)	1.34
M (59)	26.46
C (168)	11.47
C (171)	9.55

Appendix 2. Species list, by guild, for the five plant communities

SPECIES	COMMUNITIES				
VASCULAR	Marsh	Wet open fen	Dry open fen	Treed fen	Bog
GRASS					
Agrostis scabra Willd.	X	X	X	X	
Calamagrostis canadensis (Michx.) Beauv.		X	X	X	
Calamagrostis sticta (Timm) Koeler		X	X	X	
Deschampsia cespitosa (L.) Beauv.				X	
Hordeum jubatum L.	X				
Poa palustris L.		X			
Schizachne purpurascens (Torr.) Swallen				X	
HERB					
Alopecurus aequalis Sobel.	X				
Barbarea orthoceras Ledeb.	X				
Bidens cernua L.	X				
Calla palustris L.	X	X	X		
Caltha palustris L.		X	X	X	
Cicuta bulbifera L.			X	X	
Cicuta maculata L. var. *angustifolia* Hook		X	X	X	
Epilobium angustifolium L.		X	X	X	
Epilobium leptophyllum Raf.	X	X	X	X	
Equisetum arvense L.	X	X	X	X	X
Equisetum hyemale L.		X	X	X	
Equisteum scirpoides Michx.					X
Fragaria virginiana Duchesne					X
Galium boreale L.	X	X	X		
Galium trifidum L.	X	X	X	X	
Geum rivale L.		X	X	X	
Listera cordata (L.) R. Br.				X	
Lysimachia thyrsiflora L		X	X		
Menyanthes trifoliata L.	X	X	X		
Petasites saggitatus (Pursh) A. Gray				X	
Polygonum lapathifolium L.	X				
Potentilla norvegica L.	X				
Potentilla palustris (L.) Scop.	X	X	X	X	
Rubus arcticus ssp. acaulis (Michx.) Focke.		X	X		X
Rubus chamaemorus L.				X	X
Rumex crispus L.	X	X	X	X	
Scutellaria galericulata L.	X	X	X	X	
Senecio congestus (R. Br.) DC.	X				
Sium suave Walt.	X	X			
Smilacina trifolia (L.) Desf.				X	X
Sparganium eurycarpum Engelm.	X				
Spiranthes romazoffiana Cham. & Schlecht.					X

SPECIES	COMMUNITIES				
VASCULAR	Marsh	Wet open fen	Dry open fen	Treed fen	Bog
HERB c'ont					
Stellaria longifolia Muhl.		X	X	X	
Trifolium hybridum L.		X			
Triglochin maritima L.		X	X		
Typha latifolia L	X	X	X		
Urtica dioica L. ssp. *gracilis* (Ait.) Selander	X	X	X	X	
Viola nephrophylla Greene				X	X
SEDGE					
Carex aquatilis Wahlenb.	X	X	X		
Carex brunnescens (Pers.) Poir. ?		X	X	X	
Carex capillaris L.		X			
Carex chordorrhiza		X			
Carex diandra Schrank		X	X	X	
Carex disperma Dewey			X		
Carex lasiocarpa Ehrh. ssp. americana D. Löve & Bernard	X	X	X		
Carex limosa L.				X	
Carex utriculata Boott		X	X		
Eriophorum vaginatum L. ssp. *vaginatum*					X
SHRUB/TREE					
Alnus tenuifolia Nutt.				X	X
Betula papyrifera Marsh.			X	X	X
Betula pumila L.				X	X
Betula pumila L. var. *glandulifera* Regel			X	X	X
Chamaedaphne calyculata (L.) Moench				X	X
Empetrum nigrum L.					X
Larix laricina (DuRoi) K. Koch			X	X	X
Ledum groenlandicum Oeder				X	X
Oxycoccus microcarpus Turcz.				X	X
Picea glauca (Moench) Voss				X	
Picea mariana (Mill.) BSP			X	X	X
Rubus idaeus L.		X	X		
Salix spp.		X	X	X	X
Vaccinium myrtilloides Michx.					X
Vaccinium vitis-idaea L. ssp. minus (Lodd.) Hult.				X	X
NON-VASCULAR					
LICHEN					
Bryoria fuscescens (Gyelnik) Brodo & D. Hawksw. Syns.				X	
Cladonia botrytes (K.Hagen) Willd.					X
Cladonia chlorophaea (Flörke ex Summerf.) Sprengel				X	X
Cladonia coniocrea (Flörke) Sprengel				X	X
Cladonia mitis Sandst.					X
Cladonia rangerifina (L.) F.H. Wigg.					X

SPECIES **NON-VASCULAR**	**COMMUNITIES** **Marsh**	**Wet open fen**	**Dry open fen**	**Treed fen**	**Bog**
Cladonia stellaris (Opiz) Pouzar & Vzda					X
Icmadophila ericetorum (L.) Zahlbr.					X
Parmelia sulcata Taylor				X	X
Peltigera neopolydactyla (Gyelnik) Gyelnik				X	
Ramalina dilacerata (Hoffm.) Hoffm. Syn.: Fistulariella minuscula				X	
Ramalina pollinaria (Westr.) Ach.				X	
Usnea lapponica Vainio					X
Vulpicida pinastri (Scop.) J.-E.Mattsson & M. J. Lai.				X	X
Xanthomendoza fallax (Hepp) Sochting, Karnefelt & S. Kondr.			X	X	X
LIVERWORT					
Jamesoniella autumnalis (D.C.) Steph. var. *autumnalis*			X	X	X
Lepidozia reptans (L.) Dum.					
Lophozia incisa (Schrad.) Dum. var *incisa* var. *inermis* K. Müll					X
Lophozia ventricosa (Dicks.) Dum. var. *ventricosa*		X	X	X	X
Marchantia polymorpha L.	X	X	X		
Mylia anomala (Hook.) S. Gray				X	X
Ptilidium ciliare (L.) Hampe					X
Ptilidium pulcherrimum (G.Web.) Hampe			X	X	
Amblystegium riparium (Hedw.) Schimp.			X	X	X
Amblystegium serpens (Hedw.) Schimp.	X	X	X	X	X
Aulacomnium palustre (Hedw.) Schawaegr.			X	X	X
Brachythecium spp.			X	X	
Bryum algovicum C. Mull		X	X		
Bryum pallens Swartz			X		
Bryum pseudotriquetrum (Hedw.) Gaertn. *et al*.		X	X		X
Calliergon giganteum (Schimp.) Kindb.		X		X	
Calliergon richardsonii (Mitten) Kindberg		X		X	
Calliergon stramineum (Dickson ex Bridel) Kindberg		X		X	X
Campylium stellatum (Hedw.) C. Jens.			X		
Climacium dendroides (Hedw.) Web. & Mohr.				X	
Dicranum flagellare Hedw.					X
Dicranum fuscescens Turn.				X	X
Dicranum polysetum Sw.					X
Dicranum undulatum Brid.				X	X
Drepanocladus aduncus (Hedw.) Warnst.	X	X	X	X	
Drepanocladus revolvens (Swartz) Warnstorf			X	X	
Drepanocladus uncinatus (Hedwig) Warnstorf			X	X	X
Drepanocladus vernicosus (Mitten) Warnstorf		X		X	
Helodium blandowii (Web. & Mohr.) Warnst.			X	X	X
Hylocomium brevistore (Bridel) Schimp.					X
Hylocomium splendens (Hedw.) Schimp.				X	X

SPECIES	COMMUNITIES				
NON-VASCULAR	**Marsh**	**Wet open fen**	**Dry open fen**	**Treed fen**	**Bog**
Leptobryum pyriforme (Hedwig) Wilson			X	X	
Plagiomnium cuspidatum (Hedw.) T. Kop.			X	X	
Plagiomnium medium (Bruch & Schimp.) T. Kop.					X
Pleurozium schreberi (Brid.) Mitt.			X	X	X
Pohlia nutans (Hedw.) Lindb.			X	X	X
Pohlia sphagnicola (B.S.G.) Brotherus		X		X	X
Polystrichum strictum Brid.				X	X
Ptilium crista-castrensis (Hedw.) De Not.					X
Rhizomnium pseudopunctatum (Bruch & Schimp.) T. Kop.				X	
Rhizomnium punctatum (Hedw.) T. Kop.			X	X	
Sphagnum angustifolium (Russ.) C. Jens.			X	X	X
Sphagnum capillifolium (Ehrh.) Hedw.				X	X
Sphagnum capillifolium var. tenellum (Schimp.)					X
Sphagnum contortum Schultz				X	X
Sphagnum fimbriatum Wils.				X	
Sphagnum fuscum (Schimp.) Klinggr.				X	X
Sphagnum magellanicum Brid.					X
Sphagnum russowii Warnst.			X	X	X
Sphagnum squarrosum Crome		X	X	X	
Sphagnum subsecundum Nees					X
Sphagnum teres (Schimp.) Angstr.			X	X	
Tetraplodon angustatus (Hedw.) Bruch & Schimp.					X
Tomenthypnum nitens (Hedw.) Loeske		X		X	X

Appendix 3. Indicator species for each community (1=marsh, 2=wet open fen, 3=dry open fen, 4=treed fen, 5=bog; Obs. IV = Observed Indicator Value)

		Relative frequency of each species in each group						
Species	**Community**	**1**	**2**	**3**	**4**	**5**	**Obs. IV**	**P**
Senecio congestus	1	57	0	0	0	0	56.7	0.001
Typha latifolia	1	73	12	11	0	0	55.8	0.001
Bidens cernua	1	53	0	0	0	0	53.3	0.001
Epilobium leptophyllum	1	63	14	13	4	2	41.8	0.001
Sium suave	1	20	2	0	0	0	17.9	0.001
Sparganium eurycarpum	1	13	0	0	0	0	13.3	0.001
Agrostis scabra	1	30	14	17	9	0	12.8	0.005
Rumex crispus	1	27	17	11	4	0	12.2	0.006
Barbarea orthoceras	1	10	0	0	0	0	10.0	0.002
Drepanocladus aduncus	2	20	55	24	9	0	27.7	0.001
Menyanthes trifoliata	2	7	31	4	0	0	23.2	0.001
Carex diandra	2	0	38	31	6	0	19.3	0.001
Carex utriculata	2	0	19	6	0	0	14.7	0.001
Stellaria longifolia	3	0	29	48	6	2	27.6	0.001
Amblystegium serpens	3	3	31	50	13	7	24.0	0.001
Calamagrostis stricta	3	0	17	24	9	2	11.2	0.011
Pseudomnium cuspidatum	3	0	0	15	11	0	8.4	0.011
Aulacomnium palustre	4	0	0	7	75	38	47.2	0.001
Betula pumila var. glandulifera	4	0	0	19	57	20	33.8	0.001
Salix spp.	4	0	19	76	79	52	27.7	0.001
Larix laricina	4	0	0	4	45	33	25.1	0.001
Tomenthypnum nitens	4	0	2	0	26	2	22.9	0.001
Betula papyrifera	4	0	0	13	40	25	20.3	0.001
Potentilla palustris	4	0	29	46	47	7	17.3	0.005
Calliergon stramineum	4	0	2	0	19	5	13.6	0.003
Sphagnum russowii	4	0	0	2	21	16	11.0	0.004
Sphagnum teres	4	0	0	2	11	0	9.7	0.001
Helodium blandowii	4	0	0	2	9	2	6.9	0.01
Picea mariana	5	0	0	2	23	87	67.8	0.001
Vaccinium vitis-idaea	5	0	0	0	11	77	67.2	0.001
Rubus chamaemorus	5	0	0	0	2	64	62.1	0.001
Ledum groenlandicum	5	0	0	0	43	89	59.4	0.001
Pleurozium schreberi	5	0	0	4	8	61	51.2	0.001
Cladonia rangerifina	5	0	0	0	0	33	32.8	0.001
Chamaedaphne calyculata	5	0	0	0	15	43	31.5	0.001
Polytrichum strictum	5	0	0	0	17	39	27.5	0.001
Xanthomendoza fallax	5	0	0	2	9	34	25.9	0.001
Sphagnum fuscum	5	0	0	0	17	34	23.1	0.001
Usnea lapponica	5	0	0	0	17	33	21.6	0.001
Parmelia sulcata	5	0	0	0	21	34	21.5	0.001
Smilacina trifolia	5	0	0	0	34	36	18.6	0.001

Oxycoccus microcarpus	5	0	0	0	17	28	17.3	0.001

		Relative frequency of each species in each group						
Species	**Community**	**1**	**2**	**3**	**4**	**51**	**Obs. IV**	**P**
Sphagnum angustifolium	5	0	0	4	21	30	16.1	0.001
Cladonia chlorophaea	5	0	0	0	2	15	13.1	0.001
Eriophorum vaginatum	5	0	0	0	0	10	9.8	0.006
Hylocomnium splendens	5	0	0	0	6	13	9.2	0.006
Sphagnum magellanicum	5	0	0	0	0	7	6.6	0.014

Appendix 4a. Moss production (biomass, bulk density) raw matrix

Site	Transect	Moss species	Landform	Biomass g/m^2	Bulk density g/cm^3
1	1	1	1	6.88	0.01
1	2	1	1	4.41	0.01
1	3	1	1	2.15	0.01
1	4	1	1	9.03	0.01
1	5	1	1	10.10	0.01
1	6	1	1	5.16	0.01
2	3	1	1	7.14	0.01
2	4	1	1	7.71	0.01
2	5	1	1	7.37	0.01
2	1	3	1	8.63	0.01
2	2	3	1	1.11	0.01
2	6	3	1	4.46	0.01
3	2	1	2	1.86	0.01
3	4	1	2	3.24	0.01
3	5	1	2	5.59	0.01
3	1	2	2	0.55	0.01
3	3	2	2	1.01	0.01
3	6	2	2	1.46	0.01
4	1	2	2	1.68	0.01
4	2	2	2	0.94	0.01
4	3	2	2	1.16	0.01
4	4	2	2	2.13	0.01
4	5	2	2	1.61	0.01
5	1	2	3	10.98	0.03
5	2	2	3	1.50	0.03
5	3	2	3	3.95	0.03
5	4	2	3	3.11	0.03
5	5	2	3	0.00	0.03
5	6	2	3	0.00	0.03
6	5	1	3	6.42	0.03
6	1	3	3	14.26	0.03
6	2	3	3	8.70	0.03
6	3	3	3	9.71	0.03
6	4	3	3	8.42	0.03
6	6	3	3	5.00	0.03

Appendix 4b. Legend for moss production matrix

Code	Site	Code	Moss Species	Code	Landform
1	O (16)	1	*Sphagnum capillifolium*	1	Outwash Plain
2	O (208)	2	*Sphagnum fuscum*	2	Moraine
3	M (27)	3	*Sphagnum russowii*	3	Clay-till Plain
4	M (43)				
5	C (168)				
6	C (171)				

Appendix 5a. Herb production raw matrix (where quadrats p1eq1=pond 1, emergent, quadrat 1; 16neq1 = pond 16, north transect, emergent, quadrat 1)

Quadrat	Site	Community	Year	Landform	Biomass g/m^2
p1eq1	1	1	3	1	190
p1eq2	1	1	3	1	225
p1eq3	1	1	3	1	190
p1eq4	1	1	3	1	223
p1eq5	1	1	3	1	187
p1eq6	1	1	3	1	164
p1eq7	1	1	3	1	111
p1eq8	1	1	3	1	226
p1eq9	1	1	3	1	118
p1eq10	1	1	3	1	236
p1fq1	1	2	3	1	120
p1fq2	1	2	3	1	262
p1fq3	1	2	3	1	102
p1fq4	1	2	3	1	86
p1fq5	1	2	3	1	54
p1fq6	1	2	3	1	84
p1fq7	1	2	3	1	107
p1fq8	1	2	3	1	56
p1fq9	1	2	3	1	148
p1fq10	1	2	3	1	91
16ne1	2	1	2	1	810
16ne2	2	1	2	1	831
16ne3	2	1	2	1	723
16nf1	2	2	2	1	228
16nf2	2	2	2	1	86
16nf3	2	2	2	1	166
16sf1	2	2	2	1	8
16sf2	2	2	2	1	300
16sf3	2	2	2	1	363
16ef1	2	2	2	1	255
16ef2	2	2	2	1	159
16ef3	2	2	2	1	115
16wf1	2	2	2	1	137
16wf2	2	2	2	1	120
16wf3	2	2	2	1	136

Quadrat	Site	Community	Year	Landform	Biomass g/m^2
p206eq1	3	1	3	1	357
p206eq2	3	1	3	1	447
p206eq3	3	1	3	1	259
p206eq4	3	1	3	1	319
p206eq5	3	1	3	1	320
p206eq6	3	1	3	1	449
p206eq7	3	1	3	1	196
p206eq8	3	1	3	1	137
p206eq9	3	1	3	1	286
p206eq10	3	1	3	1	335
p206fq1	3	2	3	1	47
p206fq2	3	2	3	1	33
p206fq3	3	2	3	1	29
p206fq4	3	2	3	1	35
p206fq5	3	2	3	1	96
p206fq6	3	2	3	1	76
p206fq7	3	2	3	1	31
p206fq8	3	2	3	1	23
p206fq9	3	2	3	1	36
p206fq10	3	2	3	1	41
208ef1	4	2	2	1	137
208ef2	4	2	2	1	242
208ef3	4	2	2	1	143
208nf1	4	2	2	1	104
208nf2	4	2	2	1	122
208nf3	4	2	2	1	240
208sf1	4	2	2	1	266
208sf2	4	2	2	1	115
208sf3	4	2	2	1	112
208wf1	4	2	2	1	66
208wf2	4	2	2	1	256
208wf3	4	2	2	1	138
27ee1	5	1	2	2	23
27ee2	5	1	2	2	445
27ee3	5	1	2	2	499
27ne1	5	1	2	2	314
27ne2	5	1	2	2	1077
27ne3	5	1	2	2	1044
27se1	5	1	2	2	358
27se2	5	1	2	2	549
27se3	5	1	2	2	701

Quadrat	Site	Community	Year	Landform	Biomass g/m^2
27we1	5	1	2	2	432
27we2	5	1	2	2	576
27we3	5	1	2	2	900
p27eq1	5	1	3	2	214
p27eq2	5	1	3	2	81
p27eq3	5	1	3	2	124
p27eq4	5	1	3	2	151
p27eq5	5	1	3	2	145
p27eq6	5	1	3	2	170
p27eq7	5	1	3	2	196
p27eq8	5	1	3	2	208
p27eq9	5	1	3	2	254
p27eq10	5	1	3	2	122
27ef1	5	2	2	2	113
27ef2	5	2	2	2	300
27ef3	5	2	2	2	240
27nf1	5	2	2	2	51
27nf2	5	2	2	2	110
27nf3	5	2	2	2	52
27sf1	5	2	2	2	95
27sf2	5	2	2	2	80
27sf3	5	2	2	2	232
27wf1	5	2	2	2	54
27wf2	5	2	2	2	275
27wf3	5	2	2	2	124
p27fq1	5	2	3	2	59
p27fq2	5	2	3	2	61
p27fq3	5	2	3	2	57
p27fq4	5	2	3	2	42
p27fq5	5	2	3	2	137
p27fq6	5	2	3	2	91
p27fq7	5	2	3	2	189
p27fq8	5	2	3	2	39
p27fq9	5	2	3	2	97
p27fq10	5	2	3	2	100
42ee1	6	1	2	2	521
42ee2	6	1	2	2	273
42ee3	6	1	2	2	240
42ne1	6	1	2	2	382
42ne2	6	1	2	2	112
42ne3	6	1	2	2	89

Quadrat	Site	Community	Year	Landform	Biomass g/m^2
42se1	6	1	2	2	226
42se2	6	1	2	2	180
42se3	6	1	2	2	291
42we1	6	1	2	2	332
42we2	6	1	2	2	364
42we3	6	1	2	2	346
p42eq1	6	1	3	2	163
p42eq2	6	1	3	2	187
p42eq3	6	1	3	2	305
p42eq4	6	1	3	2	233
p42eq5	6	1	3	2	244
p42eq6	6	1	3	2	179
p42eq7	6	1	3	2	199
p42eq8	6	1	3	2	260
p42eq9	6	1	3	2	106
p42eq10	6	1	3	2	293
42ef1	6	2	2	2	319
42ef2	6	2	2	2	325
42ef3	6	2	2	2	80
42nf1	6	2	2	2	43
42nf2	6	2	2	2	447
42nf3	6	2	2	2	145
42sf1	6	2	2	2	129
42sf2	6	2	2	2	278
42sf3	6	2	2	2	78
42wf1	6	2	2	2	12
42wf2	6	2	2	2	0
42wf3	6	2	2	2	91
p42fq1	6	2	3	2	64
p42fq2	6	2	3	2	63
p42fq3	6	2	3	2	60
p42fq4	6	2	3	2	81
p42fq5	6	2	3	2	89
p42fq6	6	2	3	2	144
p42fq7	6	2	3	2	74
p42fq8	6	2	3	2	108
p42fq9	6	2	3	2	57
p42fq10	6	2	3	2	102
59ee1	7	1	2	2	186
59ee2	7	1	2	2	273
59ee3	7	1	2	2	286

Quadrat	Site	Community	Year	Landform	Biomass g/m^2
59ne1	7	1	2	2	454
59ne2	7	1	2	2	317
59ne3	7	1	2	2	190
59se1	7	1	2	2	53
59se2	7	1	2	2	65
59se3	7	1	2	2	59
59we1	7	1	2	2	79
59we2	7	1	2	2	381
59we3	7	1	2	2	54
59ef1	7	2	2	2	78
59ef2	7	2	2	2	107
59ef3	7	2	2	2	136
59nf1	7	2	2	2	46
59nf2	7	2	2	2	56
59nf3	7	2	2	2	51
59sf1	7	2	2	2	26
59sf2	7	2	2	2	224
59sf3	7	2	2	2	38
59wf1	7	2	2	2	33
59wf2	7	2	2	2	87
59wf3	7	2	2	2	62
p118eq1	8	1	3	3	150
p118eq2	8	1	3	3	246
p118eq3	8	1	3	3	172
p118eq4	8	1	3	3	135
p118eq5	8	1	3	3	282
p118eq6	8	1	3	3	143
p118eq7	8	1	3	3	190
p118eq8	8	1	3	3	147
p118eq9	8	1	3	3	270
p118eq10	8	1	3	3	300
p118fq1	8	2	3	3	152
p118fq2	8	2	3	3	182
p118fq3	8	2	3	3	155
p118fq4	8	2	3	3	154
p118fq5	8	2	3	3	211
p118fq6	8	2	3	3	49
p118fq7	8	2	3	3	33
p118fq8	8	2	3	3	18
p118fq9	8	2	3	3	57
p118fq10	8	2	3	3	40

Quadrat	Site	Community	Year	Landform	Biomass g/m^2
171ee1	9	1	2	3	370
171ee2	9	1	2	3	447
171ee3	9	1	2	3	364
171ne1	9	1	2	3	96
171ne2	9	1	2	3	137
171ne3	9	1	2	3	183
171se1	9	1	2	3	162
171se1	9	1	2	3	406
171se2	9	1	2	3	75
171se2	9	1	2	3	472
171se3	9	1	2	3	102
p171eq1	9	1	3	3	166
p171eq2	9	1	3	3	215
p171eq3	9	1	3	3	86
p171eq4	9	1	3	3	70
p171eq5	9	1	3	3	88
p171eq6	9	1	3	3	122
171nf1	9	2	2	3	98
171nf2	9	2	2	3	94
171nf3	9	2	2	3	101
p171fq1	9	2	3	3	269
p171fq2	9	2	3	3	222
p171fq3	9	2	3	3	237
p171fq4	9	2	3	3	328
p171fq5	9	2	3	3	426
p171fq6	9	2	3	3	242
p171fq7	9	2	3	3	270
p171fq8	9	2	3	3	356
p171fq9	9	2	3	3	479
p171fq10	9	2	3	3	209

Appendix 5b. Legend for herb production matrix

Code	Site	Code	Community	Code	Year	Code	Landform
1	O (1)	1	Marsh	2	2002	1	Outwash Plain
2	O (16)	2	Open Fen	3	2003	2	Moraine
3	O (206)					3	Clay-till Plain
4	O (208)						
5	M (27)						
6	M (42)						
7	M (59)						
8	C (118)						
9	C (171)						