National Library
of Canada

Acquisitions and
Bibliographic Services Branch

395 Wellington Street
Ottawa, Ontario
K1A 0N4

Bibliothèque nationale
du Canada

Direction des acquisitions et
des services bibliographiques

395, rue Wellington
Ottawa (Ontario)
K1A 0N4

Your file Votre référence

Our file Notre référence

NOTICE

The quality of this microform is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us an inferior photocopy.

Reproduction in full or in part of this microform is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30, and subsequent amendments.

AVIS

La qualité de cette microforme dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure [illegible] production.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de qualité inférieure.

La reproduction, même partielle, de cette microforme est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30, et ses amendements subséquents.

Canada

UNIVERSITY OF ALBERTA

Production and decomposition of vegetation along a wetland gradient in Central Alberta

BY

Anthony Ralph Szumigalski ©

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

IN

Plant Ecology

DEPARTMENT OF BOTANY

EDMONTON ALBERTA

SPRING 1995

National Library
of Canada

Acquisitions and
Bibliographic Services Branch

395 Wellington Street
Ottawa, Ontario
K1A 0N4

Bibliothèque nationale
du Canada

Direction des acquisitions et
des services bibliographiques

395, rue Wellington
Ottawa (Ontario)
K1A 0N4

Your file Votre référence

Our file Notre référence

ISBN 0-612-01657-9

Canadä

UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR: Anthony Ralph Szumigalski

TITLE OF THESIS: **Production and decomposition of vegetation along a wetland gradient in Central Alberta**

DEGREE: Master of Science in Plant Ecology

YEAR THIS DEGREE GRANTED: 1995

Anthony Ralph Szumigalski
#9 Connaught Place
Saskatoon, SK

Dec. 20, 1994

UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Production and decomposition of vegetation along a wetland gradient in Central Alberta** submitted by Anthony Ralph Szumigalski in partial fulfillment of the requirements for the degree of **Master of Science** in **Plant Ecology**

S E Bayley
S. E. Bayley

D. H. Vitt
D. H. Vitt

Donald J. Pluth
D. Pluth

Nov. 29, 1994

For my parents Anne and Jan, who were my first source of botanical inspiration

Abstract

The net primary production (NPP), decomposition, changes in C and N and peat accumulation potential of the above ground vegetation of differe[illegible]lands representing the bog-rich fen gradient in central A[illegible]anada were measured during two growing seasons (1991 a[illegible]992). The wetland gradient studied was: bog - poor fen - open moderate-rich fen - wooded moderate-rich fen - sedge fen - extreme-rich fen.

Total above ground NPP increased along the gradient from the bog to wooded moderate-rich fen and then abruptly decreased in the sedge and extreme-rich fens. Average above ground production in the bog (264-297 g/m^2/yr) was lower than values from more southerly North American ombrotrophic systems. The Alberta fens had intermediate values of NPP (214-360 g/m^2/yr) compared to other North American minerotrophic peatlands.

Moss production did not differ significantly between most of the sites and showed greater variation between years. Vascular production and litter fall were highest in the middle of the bog-rich fen gradient. Herb production tended to increase along the gradient and was correlated to water level and pH-related characteristics. Shrub production decreased along the gradient and was negatively correlated to water level and pH-related characteristics. Tree production was a minor component of total NPP in these sites.

Weight loss of the dominant species at the sites was negatively correlated with initial and final C:N ratios and positively correlated with initial and final %N. Rates of decay within sites differed according to litter types with *Carex* > *Betula* > mosses. After one year, weight loss of the standard litter (*Carex lasiocarpa*), used for a cross site comparison, was negatively correlated with water level and pH-related parameters and positively correlated with surface water concentrations of TDP. The sites ranked: poor fen > wooded-rich fen > bog > open-rich fen > sedge fen, in order of greatest to least percent weight loss of the standard after two years.

The peat accumulation potential decreased along the bog-rich fen gradient. The bog had the greatest production to decomposition ratio, while the sedge fen had the lowest ratio. The sedge fen also had the lowest litter accumulation rate, while the bog, poor fen and wooded-rich fen had similar rates.

Acknowledgements

First, I would like to thank my supervisor, Suzanne Bayley, for her valuable advice, support and encouragement throughout this project and helpful editorial comments on the many drafts of this thesis. I am also grateful to Dale Vitt for introducing me to the fascinating world of peatlands and bryophytes and for his timely advice during different stages of my research. Don Pluth also provided many helpful comments and ideas towards this thesis.

I owe special gratitude to my wife, Carla Zelmer, whose constant support, help and understanding are very much appreciated.

I gratefully acknowledge the field and technical assistance provided by Elizabeth Joyce, Suzanne Campeau, Linda Halsey, Markus Thormann, Trevor Coleman, Mathew Nash, André Rahugisha and Joan Montagnes. I would also like to thank Sandi Vitt and Heather Wind-Mulder for computer advice, while Mark Dale and Shawn Urban gave me valuable statistical advice. The use of Randy Currah's computer was very much appreciated. I am also indebted to John Stadt, Jan Volney and Graham Hillman at Forestry Canada for the use of the Digimic machine and Steven's water level recorders. Gertie Hutchinson provided the chemical analyses of the water and vegetation samples, while Barb Nicholson and Dale Vitt suggested the design for the litter traps. The staff at Meanook Biological Research Station made my stay there a pleasant one. This project would not have been possible without the cooperation of Robert Bryant and Dr. Person, who allowed me permission to carry out research at sites on their properties.

This research was supported by an NSERC grant to S.E. Bayley, a Canadian Circumpolar Institute (CCI) bar grant to the author and a STEP grant from Employment and Immigration Canada.

Table of Contents

Chapter Page

List of Tables

List of figures

List of abbreviations and symbols

Sites

ERF - extreme-rich fen
OB - open bog
ORF - open (moderate)-rich fen
PF - poor fen
SF - sedge fen
WB - wooded bog
WRF - wooded (moderate)-rich fen

Ecological measurement terms

dbh - diameter at breast height
Decomp. - decomposition
Diam. sq. - basal diameter squared
GDD - growing degree days
Ht. - height
k' - percent weight loss
NPP - net primary production
Precip. - precipitation
Prod. - production
Temp. - temperature

Chemical terms

C - carbon
C:N - carbon to nitrogen ratio
Ca - calcium
Ca^{2+} - calcium ion
$CaCO_3$ - calcium carbonate
Cl^- - chloride ion
Conduct. - conductivity
DOC - dissolved organic carbon
HCO_3^- - bicarbonate ion
HNO_3 - nitric acid
K - potassium
K^+ - potassium ion
Mg - magnesium
Mg^{2+} - magnesium ion
N - nitrogen
Na - sodium

Na^+ - sodium ion
NH_4^+ - ammonium ion
NO_3^- - nitrate
P - phosphorus
SO_4^{2-} - sulfate
SRP - soluble reactive phosphorus
TDP - total dissolved phosphorus
TP - total phosphorus

Statistical terms

a - y-intercept of a regression line
ANOCOVA - analysis of covariance
ANOVA - analysis of variance
AVE. - average
b - slope of a regression line
n - sample size
n.d. - not determined
n.s. - not significant ($p > 0.05$)
* - $0.05 > p > 0.01$
** - $0.01 > p > 0.001$
*** - $p < 0.001$
p - probability
r - correlation coefficient
r-square - coefficient of determination (r^2)
SE - standard error
Sqrt. - square root
Transf. - transformed
x - independent variable
y - dependent variable

1. INTRODUCTION

Peatlands cover about 20% of Canada's boreal regions and are defined as wetlands that have an accumulated organic matter deposit (peat) greater than 40 cm in depth (National Wetlands Working Group, 1988).

The first major division in peatland classification is between bogs and fens. Bogs are ombrotrophic systems, meaning that they receive nutrient inputs only from precipitation and are isolated from mineral-rich groundwater. Fens are minerotrophic systems that receive nutrients from surface and ground water as well as precipitation. The next major division is among fens, which can be divided into poor and rich fens on the basis of richness of indicator species (*sensu* Du Rietz, 1949) and pH/alkalinity (Sjörs, 1950). Poor fens, like bogs, are *Sphagnum* moss-dominated with few indicator species, while rich fens are brown moss-dominated (*i.e.* mosses from the families Amblystegiaceae and Brachytheciaceae) and contain many indicator species. Rich fens can be divided further. Moderate-rich fens have lower pH values, reduced conductivties, Ca and Mg than extreme-rich fens and have different indicator species (Vitt and Chee, 1990). The number of indicator species and the surface water pH and concentration of base cations (Ca, Mg, Na) generally increase along a gradient from bog to poor fen to rich fen. This same trend does not seem to apply to the amounts of major nutrients N, P (Malmer, 1986, Vitt, 1990) and K (Gorham, 1950; Vitt *et al.*, in press), which have no apparent concentration gradient. However, fens may still receive more nutrients than bogs because of greater water flow (Sparling, 1966; Vitt, 1990).

Peatland systems are important to the global carbon cycle because they sequester large amounts of carbon (Gorham, 1991). Forestry Canada (1992) estimates that peatlands account for 60% of all organic carbon stored in Canada. This accumulation of organic carbon is the result of an imbalance between two processes: net primary production (NPP) and decomposition, with the rate of NPP exceeding the rate of decomposition. Net primary production is the amount of organic matter incorporated by vegetation (gross primary production minus respiration losses) in a defined area over a given period of time, while decomposition is the process by which organic matter is broken down to simpler substances (Chapman, 1976). In this thesis production is used interchangeably with NPP, while decomposition and decay are also considered synonymous.

Peat accumulation in peatlands is believed to be related more to slow rates of decay than rapid production rates (Clymo, 1965; Malmer, 1986; Farrish and Grigal, 1988; Vitt, 1990). However, research measuring the relative rates of total organic matter production and decomposition simultaneously has been limited (Reader and Stewart, 1972; Bartsch and Moore, 1985). Furthermore, there are very few studies relating either of these processes to water levels or other environmental factors (Forrest and Smith, 1975; Farrish and Grigal, 1988; Moore, 1989).

The peat accumulation rates along the bog-rich fen gradient are relatively unknown, although bogs are reported to have greater accumulation rates than fens (Malmer, 1986; National Wetlands Working Group, 1988). However, Reader and Stewart (1972) found that a minerotrophic peatland (lagg) had greater long-term peat accumulation than an ombrotrophic site (muskeg) in Manitoba. Rates of organic matter accumulation can vary greatly between similar sites and between sites within the same geographic area (Gorham, 1982).

The objectives of this thesis were to measure the rates of aerial production and decomposition in different peatlands of central Alberta representing the bog-rich fen gradient, and to relate these processes to hydrology (water levels), water chemistry and climatic factors. Hydrology is important due to its control over the aeration/redox potential of substrates and the transport and availability of nutrients which are important for both production and decomposition. Major nutrients (N, P and K) in the surface water were investigated because they are important in controlling plant growth in wetlands (Reader, 1978) and may influence the activities of decomposers. Decomposition and production may also be strongly influenced by pH and related characteristics (e.g. conductivity, alkalinity, Ca^{2+}). Climatic variables (precipitation and temperature) were examined to help explain some of the differences between years and with other studies.

Chapter two focuses on the production aspects of this thesis. The above ground NPP of the moss, herb, shrub and tree strata was measured in five sites (bog, poor fen, wooded moderate-rich fen, rich sedge fen and extreme-rich fen) for two growing seasons to estimate total production in each. The herb layer included both forbs and graminoids, while the shrub layer included deciduous and evergreen species with above ground woody stems. The tree stratum referred to seedlings as well as large individuals of coniferous species. Production estimates of each layer and total NPP were compared with literature values from similar sites. Total litter fall was also measured over a one year period in the sites. My hypothesis is that total NPP will increase along this bog-rich fen gradient.

Chapter three deals with decomposition. Decomposition rates were measured in the same sites as Chapter two, except the extreme-rich fen was replaced with an open moderate-rich fen. Decomposition was measured as percent weight loss of the litter during a two year period from October 1990 to October 1992. In this section two major questions were asked: 1) does decomposition differ between the dominant native litter types and is this related to substrate quality (N content and C:N ratio); and 2) does decomposition differ between peatlands using one standard litter type (*Carex lasiocarpa*) and is this related to environmental parameters (water levels and chemistry)? I hypothesize that the tissue types with lower C:N ratios and greater percent N will decompose faster because of greater N availability for decomposers. Rates of decomposition, as measured by the common substrate, should also increase across the bog-rich fen gradient because the increasing pH may be more favourable for decomposers.

Chapter four represents a synthesis of Chapters two and three. In the fourth chapter, production data from Chapter two was first used to investigate the relationship between NPP and environmental factors (*i.e.* water levels and chemistry). My hypothesis is that NPP will increase with higher water levels because of more available water and nutrients. Secondly, in Chapter four, the production and decomposition (Chapter three) data were combined to estimate the above ground peat accumulation potential in four sites (bog, poor fen, wooded-rich fen and sedge fen). I hypothesize that the accumulation of peat will decrease along the bog-rich fen gradient because the decomposition rate will increase relative to the rate of production.

In Chapter five (a brief concluding discussion), the major results of Chapters two, three and four were summarized and integrated.

Literature cited

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

Chapman, S. B. 1976. Production ecology and nutrient budgets, pp. 85-155. *In*: S. B. Chapman (ed.). Methods in plant ecology. Blackwell Scientific Publications, London.

Clymo, R. S. 1965. Experiments on breakdown of *Sphagnum* in two bogs. J. Ecol. 53:747-757.

Du Rietz, G. E. 1949. Huvudenheiter och huvugranser i svensk myrvegetation. Svenska botaniska Tidskrift 43:274-309.

Farrish, K. W. and D. F. Grigal. 1988. Decomposition in an ombrotrophic bog and a minerotrophic fen in Minnesota. Soil Sci. 145:353-358.

Forestry Canada. 1992. The state of Canada's forests. 112 pp.

Forrest, G. I. and R. A. H. Smith. 1975. The productivity of a range of blanket bog vegetation types in the Northern Pennines. J. Ecol. 63:173-202.

Gorham, E. 1950. Variation in some chemical conditions along the borders of a *Carex lasiocarpa* fen community. Oikos 2:217-240.

Gorham, E. 1982. Some unsolved problems in peatland ecology. Naturaliste Can. 109:533-541.

Gorham, E. 1991. Northern peatlands: Role in the carbon cycle and probable responses to climatic warming. Ecol. Applic. 1:182-195.

Malmer, N. 1986. Vegetational gradients in relation to environmental conditions in northwestern European mires. Can. J. Bot., 64:375-383.

Moore, T. R. 1989. Plant production, decomposition, and carbon efflux in a subarctic patterned fen. Arc. Alp. Res. 21:156-162.

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

Reader, R. J. 1978. Primary production in northern bog marshes, pp. 53-62. *In* : R. E. Good, D. F. Whigham and R. L. Simpson (eds.). Freshwater wetlands: ecological processes and management potential. Academic Press, New York.

Reader, R. J. and J. M. Stew[illegible] 1972. The relationship between net primary production and accumulation for a peatland in southeastern Manitoba. Ecology 53:1024-1037.

Sjörs, H. 1950. On the relation between vegetation and electrolytes in north Swedish mire waters. Oikos 2:241-258.

Sparling, J. H. 1966. Studies on the relationship between water movement and water chemistry in mires. Can. J. Bot. 44:747-758.

Vitt, D. H. 1990. Growth and production dynamics of boreal mosses over climatic, chemical and topographical gradients. Bot. J. Linn. Soc. 104:35-59.

Vitt, D. H., S. E. Bayley, L. Halsey and T. L. Jin. in press. Seasonal variation in water chemistry over a bog-rich fen gradient in continental western Canada. Can. J. Fish. Aquat. Sci.

Vitt, D. H. and W. L. Chee. 1990. The relationships of vegetation to surface water chemistry and peat chemistry in fens of Alberta, Canada. Vegetatio 89:87-106.

2. NET ABOVE GROUND PRIMARY PRODUCTION ALONG A BOG-RICH FEN GRADIENT IN CENTRAL ALBERTA

Introduction

Peatlands cover approximately 20% of Canada's boreal regions (National Wetlands Working Group, 1988) and are defined as wetlands where organic detritus accumulates at a thickness greater than 30-40 cm (Gorham 1991). Peat accumulates in these systems because the rate of net primary production (NPP) exceeds the rate of decomposition. This study focuses on the first process: net primary production.

There have been a number of studies quantifying above ground vascular and non-vascular peatland production in North America (Reader and Stewart, 1972; Wein and Bliss, 1974; Bartsch and Moore, 1985; Grigal *et al.*, 1985; Wieder *et al.*, 1989) and Europe (Forrest, 1971; Doyle, 1973; Forrest and Smith, 1975; Wielgolaski, 1975; Vasander, 1982; Francez, 1992a). Most of this research has focused on either ombrotrophic or tundra/sub-arctic ecosystems, while few studies of total NPP have been done in southern-boreal minerotrophic systems (Reader and Stewart, 1972; Richardson *et al.*, 1976). Despite the abundance of peatlands in Alberta, production studies in these systems have been scarce and limited to either bryophytes (Busby *et al.*, 1978; Vitt, 1990) or sedges (Gorham and Somers, 1973). The rates of total above ground NPP of bogs and fens in Western Canada are relatively unknown.

In this paper, five different boreal peatlands in central Alberta, Canada were studied during two years (1991 and 1992). These sites (bog, poor fen, wooded-rich fen, sedge fen and extreme-rich fen) represent a vegetational gradient of mire types. This was termed the "poor-rich" gradient by Du Rietz (1949), with the bog at the poor end and the extreme-rich fen representing the rich end of the gradient. Bogs are ombrotrophic systems that receive nutrient inputs only from precipitation, while fens are minerotrophic and receive inputs from surface and/or ground water as well as from precipitation. Progressing from poor to rich, systems change from *Sphagnum* moss-dominated to "brown moss"-dominated and the number of peatland type indicator species increases. Sjörs (1950) related this vegetation gradient to water chemistry and found that pH, reduced conductivity and Ca also increased along the gradient. Concentrations of N and P do not seem to follow this trend (Malmer, 1986); however, nutrient supply may still increase because water movement is greater in fens than bogs (Sparling, 1966).

The major objective of this paper is to document the above ground net primary production of the different strata (moss, herb, shrub and tree) to arrive at an estimate of total above ground production for each of the sites. My hypothesis is that total above ground NPP will increase along the bog-rich fen gradient. The environmental parameters responsible for this gradient were examined in a later paper (Chapter 4).

Study area and site descriptions

Five sites were chosen to represent the range of peatlands present in the central Alberta region. The sites sampled include a bog, poor fen (PF), wooded moderate-rich fen (WRF), open-rich sedge fen (SF) and extreme-rich fen (ERF). The bog and poor fen are located north of Bleak Lake, Alberta at 54° 41' N and 113° 28' W, while the wooded-rich fen (54° 28' N, 113° 17' W) and sedge fen (54° 28' N, 113° 20' W) are located east of Perryvale (Fig 2.1). The extreme-rich fen is located south of Calahoo at 53° 42' N and 113° 57' W.

The climate of the area is characterized by mild summers and cold, snowy winters (Vitt *et al.*, in press). The long-term mean annual temperature (Environment Canada, 1982) is 1.7 °C for the first four sites (average of two weather stations: Meanook and Athabasca 2) and 2.2 °C for the extreme-rich fen (average of four surrounding weather stations). The total mean annual precipitation is about 500 mm for all sites. More detailed climatic data for the growing seasons are in Appendix 1. All the peatlands studied are located within the Boreal Forest Region of Canada (Rowe, 1972). Detailed descriptions of the vegetation and water chemistry are also in Vitt *et al.* (in press) for the first four sites and in Rochefort (1987) for the extreme-rich fen. Moss nomenclature follows Ireland *et al.* (1987) while that of vascular plants follows Moss and Packer (1983). Cover values of the dominant species were estimated in 10 by 10 m plots.

General descriptions of the sites are as follows:

Bog

This site is a large, raised ombrotrophic island within a peatland complex bordered by a poor fen water track. The peat surface is raised about 0.3-0.5 m above the associated water track, and is composed of large, dry hummocks separated by a few wetter hollows. This site can be further divided into an open bog (OB) and wooded bog (WB). The only difference between these sites is that there is a sparse tree layer of small *Picea mariana* (Mill.) BSP. covering about 25% of the wooded bog. The ericaceous shrub stratum of both is dominated by *Ledum groenlandicum* Oeder with a cover value of about 75%. *Vaccinium vitis-idaea* L., *Oxycoccus microcarpus* Turcz., *Andromeda polifolia* L. and *Chamaedaphne calyculata* (L.) Moench are also present. Herbaceous species are rare at the bog with *Smilacina trifolia* (L.) Desf., *Rubus chamaemorus* L. and *Eriophorum vaginatum* L. sparsely distributed throughout. The moss layer is dominated by *Sphagnum fuscum* (Schimp.) Klinggr. with a cover of about 90%. The remainder of this stratum consists mostly of *S. magellanicum* Brid. and *S. angustifolium* (C. Jens. ex Russ.) C. Jens in Tolf, on mid-hummocks and hollows and *Polytrichum strictum* (Brid.) on dry hummocks. The peat depth at the bog averaged 5 m (as determined by steel rod), while the surface water pH ranged from 3.4 to 4.2 (see methods, Chapter 3 or 4).

Poor Fen

This fen is a water track adjacent to the bog island. The poor fen has a hummocky microtopography, but is wetter than the bog, with open water usually present during the ice-free season. This site has a well developed shrub layer of *Betula pumila* L. var. *glandulifera* Regel. (40% cover) and *Salix pedicellaris* Pursh (20%). Dwarf shrubs are also common with *Oxycoccus microcarpus* (15%) and *Andromeda polifolia* (10%) the most common species. The herb layer is dominated by *Smilacina trifolia, Menyanthes trifoliata* L. and *Carex* species [*C. brunescens* (Pers.) Poir., *C. aquatalis* Wahlenb., *C. chordorrhiza* L.f., *C. limosa* L., *C. lasiocarpa* Ehrh., *C. paupercula* Michx. and *C. tenuiflora* Wahlenb.]. The ground layer has a *Sphagnum* cover of about 90% with *S. teres* (Schimp.) Aongstr. ex C. Hartm. and *S. angustifolium* the most common. *Aulacomnium palustre* (Hedw.) Schwaegr. is also abundant covering about 10% of the sample area. The surface water pH varied between 4.3 and 5.2 during the study period and the peat thickness averaged 4 m at this site.

Wooded-Rich Fen

This site forms the grounded, forested fen adjacent to a floating mat fen which surrounds a small open pond. The peat surface consists of large hummocks and wet lawns, with pools of water present during much of the season. This moderate-rich fen has an open tree canopy dominated by *Larix laricina* (Du Roi) K. Koch (25% cover) and some small *Picea mariana* (3%). *Betula pumila var. glandulifera* is the dominant shrub with a cover of 30% followed by

Salix pedicellaris (10-15%). The dwarf shrub layer is also well developed (25%) with *Oxycoccus microcarpus* and *Andromeda polifolia* the most important species. The most abundant herbs are *Menyanthes trifoliata* and *Smilacina trifolia* each with a cover of about 10%. Sedges are also common (10% cover) with *Carex lasiocarpa, C. diandra* Schrank, *C. limosa, C. chordorrhiza* and *C. tenuiflora* the most abundant species. The ground layer is brown moss-dominated with *Tomenthypnum nitens* (Hedw.) Loeske covering about 75% of the study area followed by *Aulacomnium palustre* (10%) and *Sphagnum warnstorfii* Russ. (10%). Peat depth at the wooded-rich fen was about 4.5 m while surface water pH ranged between 5.7 and 6.6.

Sedge Fen

This site is situated in a former north-south drainage channel that presently contains several large bodies of open water, separated by large expanses of sedge-dominated wetlands (Vitt *et al.*, in press). The microtopography is mainly flat with a few isolated, small hummocks constituting less than 5% of the surface. The site was inundated with water for most of 1991, and therefore has characteristics of a marsh, but began to dry out during the 1992 season. Vitt *et al.* (in press) designated this site as an extreme-rich fen and that it is probably transitional between a moderate- and extreme-rich fen. The vascular plant vegetation is almost completely sedge-dominated with *Carex lasiocarpa* and *C. diandra* the two most important species. Other species present include *C. chordorrhiza, C. limosa, C. aquatalis* and *Eriophorum gracile* Koch. The shrub layer is sparse (<5%) with *Salix pedicellaris* and *Betula pumila var. glandulifera* the only two species found. The moss layer is discontinuous covering only about 75% of the surface. *Drepanocladus aduncus* (Hedw.) Warnst. (65%) is the dominant species, forming mats at the bases of sedge plants. *Calliergon giganteum* (Schimp.) Kindb. is also present, growing in wet pools, while *Aulacomnium palustre* is found on some hummocks. The pH of the water ranged between 6.1 and 6.9, while peat thickness was 2-2.5 m.

Extreme-Rich Fen

This spring-fed, open fen consists of strings alternating with flarks and pools of water with marl ($CaCO_3$) mud bottoms. These marl ponds were not included in the study. The extreme-rich fen has a great richness of herbaceous species with the dominant, *Scirpus cespitosus* L., covering about 50% of the study area. The insectivorous *Drosera rotundifolia* L. and *D. anglica* Huds. are also important components (10%). The shrub and tree layers are both sparse. The former is dominated by *Betula pumila var. glandulifera* and *Salix candida* Fluegge ex Willd. and covers only about 5% of the fen. The latter is even less prevalent with the combined cover value of *Picea mariana* and *Larix laricina* only about 2%. The moss layer follows the typical sequence for extreme-rich fens in Western Canada (Vitt 1990). From pools to dry hummock this sequence is: *Scorpidium scorpioides* (Hedw.) Limpr. - *Drepanocladus revolvens* (Sw.) Warnst. - *Campylium stellatum* (Hedw.) C. Jens. - *Tomenthypnum nitens*. Together these species make up 95% of the ground layer with *C. stellatum* (55%) the most important. The site is surrounded by a bog-forest with a closed canopy of *P. mariana* and *L. laricina* and a ground layer dominated by *Pleurozium schreberi* (Brid.) Mitt., *Tomenthypnum nitens* and *Ptilium crista-castrensis*. (Hedw.) De Not. Peat depth was about 2.5 m and surface water pH ranged between 7.8 and 8.4 at the extreme-rich fen.

Methods

Production measurements

Moss

Moss growth was measured by the cranked wire method of Clymo (1970) in all sites except the sedge fen. In early June 1991, two 5 by 50 m (250 m^2) plots were established at each site to determine the growth and production of the dominant moss species. Five randomly placed circular transects of 20 wires placed approximately 5 cm apart were established in each plot for a total of 200 wires per site (in the extreme-rich fen, the wires were only placed on hummocks of *T. nitens* and *S. warnstorfii*). Growth in length was measured during the growing season (defined as early May to mid-October) in 1991 and 1992. Since the wires were established in early June 1991 part of the growing season was missed (May 1 to June 10) that year. Moss growth was measured during approximately this same 6 week period in 1992 to estimate the amount missed in 1991. This is probably a reasonable estimate since most climatic variables (mean daily temperatures, growing degree days and total precipitation) and water levels were similar for the sites during this period in both years.

To convert linear growth increment (cm/yr) to production ($g/m^2/yr$), the mass per unit length per surface area ($g/cm/m^2$) or bulk density is required. To measure bulk density, five surface cores of 85 cm^2 were collected perpendicular to the peat surface in late July or early August 1992 for each of the major moss species per site, except for the extreme-rich fen where only *T. nitens* was collected. The number of stems in each core was counted and the top 3 cm was removed for drying and weighing. For *Sphagnum* mosses the capitula were removed first before measuring the 3 cm with the assumption that capitulum size does not change significantly during the growing season (Rochefort *et al.*, 1990). The stem sections for each core were dried at 60 °C and then weighed to the nearest 0.1 g. All results were then converted to average weight per 1 cm of stem per square meter (g/cm/m^2) of area for each major species. These results multiplied by the yearly length increments (cm/yr) of the species yielded production values (g/m^2/yr).

The actual moss surface area due to microtopography must also be taken into account when estimating moss production (Grigal, 1985; Rochefort *et al.*, 1990). To estimate actual moss surface area per vertically projected area, a 2500 cm^2 quadrat was set up (using wires strung across) into a grid of 25 equal 100 cm^2 squares. This design created 36 evenly spaced grid nodes on the quadrat surface. At the sample area the quadrat was placed at the highest point and then levelled. The distance (cm) of each grid node was then measured from the ground surface. The coordinates of the grid nodes (x,y) and depth (z) to moss surface were used by the computer program MacGridzo to calculate the surface area within the quadrat. A total of 10 randomly placed quadrats were measured in each site except in the extreme-rich fen where only 3 quadrats placed on *T. nitens* hummocks were measured. The average ratio of actual surface area to vertically projected area was then determined for each site. The moss production values estimated above were then multiplied by the appropriate site ratio (correction factor) to arrive at final corrected production (g/m^2/yr) figures.

Although *T. nitens* made up only about 20% of the moss layer at the extreme-rich fen, its production value may still be considered an approximation of total moss production at the site. Vitt (1990) showed the two production values (*T. nitens* and total moss) to be similar over three years in two different extreme-rich fens with *T. nitens* averaging about 96% of the total moss production over that period.

The sedge fen had very few hummock species, therefore the cranked wire method could not be employed at this site. Moss production was determined instead by harvesting the live moss mat in quadrats during two or three sample periods. From each harvested

quadrat a sub-sample of about 20 moss stems was taken and the ratio of the mass of new growth (estimated by colour change) to total biomass of the sub-sample was determined (*cf.* Vitt and Pakarinen, 1977; Vasander, 1982). To estimate total moss production per quadrat this ratio of new growth to total weight was multiplied by the total harvested moss weight per quadrat. The sample period with the highest production was used as an estimate of annual NPP. All samples were oven-dried at 60 °C before weighing.

Herbs and shrubs

These two strata were measured in the same randomly placed 50 cm by 50 cm (0.25 m^2) quadrats in 250 m^2 plots adjacent to those used to measure moss production. Harvest periods were in late June, late July and late August in both years. In 1991 six quadrats were clipped per site per harvest period, while in 1992 the sample size was increased to 10.

All herbaceous material was clipped at the ground level at each harvest period. Samples were sorted into live and dead components and into various taxa. Before weighing, all samples were oven-dried at 60 °C. Two different estimations of herb production were calculated. 1) Minimum seasonal production was calculated by pooling the monthly biomass data if there was no significant difference (one-way ANOVA) in herb biomass between those months for a site. Only the months that had the highest biomass were included. 2) Maximum above ground herb production was also estimated by using only the month (June, July or August) of peak live standing crop. This measurement was used in the determination of total site NPP.

For shrubs, only the non-ericaceous, deciduous new terminal growth (leaves, flowers, new twigs) was harvested during all three sample periods. Within each site there were no significant differences (one-way ANOVA) in non-ericaceous terminal shrub biomass between months. At the final (August) harvest period, all shrub material (deciduous and evergreen species) was clipped at ground level (to be used in the estimation of radial production) and terminal production was measured for all species. Because all three months were similar for deciduous shrub terminal production and since ericaceous terminal production and radial production of the major species were only measured during the August sample period, shrub production was calculated from this month only.

Shrub radial production was only determined for the larger species (*Betula, Salix* and *Ledum*) as the radial increment of dwarf shrubs is believed to be minimal (Vasander, 1982). Radial production was estimated by a modification of the methods of Reader and Stewart (1972). First, the leaves were removed and total stem biomass was determined for the major species in each quadrat. Then the amount of total new terminal stem production for these was weighed. Next, the average age of the shrub species for each quadrat was estimated by counting terminal bud scale scars. Finally, the total shrub stem weight was divided by the average quadrat age to get a mean stem production per year. To arrive at total radial production the amount of new terminal stem production was subtracted from the total. Total shrub production was determined by adding total terminal to total radial production for each quadrat.

To estimate total vascular plant above ground NPP (excluding trees and shrub radial production), the August herb biomass and shrub terminal production from the quadrats were combined. This was used to test for differences in vascular plant production between sites.

Trees

Significantly developed tree canopies were only present in the wooded bog (*P. mariana*) and the wooded moderate-rich fen (*L. laricina, P. mariana*). At the end of the 1992 growing season, two linear plots of 2 m by 50 m (100 m^2) were established at each of these sites. Within the plots each tree was classified as being either large (>1.75 m) or small (<1.75 m). For the large trees the dbh (diameter to the nearest 0.1 mm at approximately 1.3 m) and height (to the nearest 0.1 m)) were measured, while the small trees were measured for basal diameter, height and leader length. About 10 cross-sectional disks were removed at the dbh level from large individual trees representative of a range of sizes from each site for measurement of radial growth increments. Ten small *P. mariana* from the bog and six small *L. laricina* from the forested fen were destructively sampled to construct biomass prediction equations (Table 2.1). These trees were separated into various components (trunk, live branches, dead branches, needles etc.) and dried at 60 °C for 48 hours and weighed to the nearest 0.1 g. Basal disks were then removed from these individuals to be used later for radial growth measurements to construct biomass increment prediction equations. To estimate the biomass of the large trees, regression equations developed by Grigal and Kernik (1984) for *P. mariana* and Lavigne (1982) for *L. laricina* were utilized (Table 2.1).

The biomass increment (production) of the trees was predicted using the simple equation

$$\Delta B = B_2 - B_1$$

where ΔB is the biomass production, B_2 is the biomass at the end of the growing season and B_1 is the biomass at the beginning of the growing season. B_2 and B_1 were estimated using the regression equations in Table 2.1. The diameter (basal or dbh) and height (small trees only) used to estimate B_1 were determined by

$$D_1 = D_2 - 2(I) \text{ and } H_1 = H_2 - L$$

where D_1 and D_2 are the diameters at the beginning and end of the growing season respectively and I is the mean annual radial increment. The radial increments over the previous five years were measured to the nearest 0.01 mm using a Digimic machine and then averaged to get the mean annual increment (I). H_1 and H_2 are the heights at the beginning and end of the growing season respectively, while L represents the leader length.

Regression equations to estimate annual above ground biomass change using current biomass as the independent variable were then developed for each species combining both large and small trees (Table 2.1). These equations were then applied to the sample plots to arrive at total site estimates of biomass production ($g/m^2/yr$). The *P. mariana* equations used in the bog were also applied to this species in the wooded-rich fen. Final site tree NPP values were derived by combining annual biomass production with annual tree litter fall (Grigal *et al.*, 1985).

Litter traps

To estimate litter fall, litter traps were randomly placed in plots adjacent to the other plots within each site at the beginning of the growing season (early May) in 1992. The traps were constructed of circular embroidery hoops with a diameter of 14.5 cm and 1 mm nylon mesh screen on the bottom. Fifty traps were placed in the bog, poor fen and wooded-rich fen while 25 were placed in the sedge and extreme-rich fens. The litter traps were left out for a period of about a year. During this period they were emptied three times: late August/early September 1992, mid-October 1992 and early May

1993. The contents were dried at 60 °C for 48 hours, sorted into various groups and weighed to the nearest 0.001 grams.

Statistical analyses

The moss production was tested using nested ANOVA's (Zar, 1984) with transect nested in plot nested in site. Since the sedge fen was sampled differently it was excluded from this analysis. Differences in moss production between sites were tested separately for 1991 and 1992. To test for differences between years, a paired t-test was done using only the growth period from June to October for both years. In the poor fen there was no significant difference in production between *S. teres* and *S. angustifolium* (t-test, $p > 0.05$) both years and therefore these two sphagna were treated as the same population and their data pooled for the statistical analyses and to calculate total site moss production.

Randomized block-nested ANOVA designs were used to test herb, terminal shrub and vascular plant (excluding trees) production with site and year as the main factors and plot nested within site. Both minimum seasonal herb production and and peak herb biomass were tested. Litter fall was tested by a one-way ANOVA with site as the factor.

To maintain homogeneity of variances and normalcy most of the data were either square root- or log-transformed before the analyses (Zar 1984).

Statistical analyses were performed with SYSTAT version 5.2.1.

Results and discussion

Moss production

Moss growth and production by species

Production of the moss species on an annual basis did not differ significantly between *Sphagnum fuscum*, *S. angustifolium*, *S. teres* or *Tomenthypnum nitens*. The two poor fen species (*S. teres* and *S. angustifolium*) showed the greatest length increments in both years (Table 2.2). This increased growth did not translate into greater production as these two species also had the lowest bulk densities (45 and 43 g/cm/m^2 respectively). Conversely, the hummock species (*S. fuscum* and *T. nitens*) had lower growth rates but were compensated by greater bulk densities. Lindholm and Vasander

(1990) also reported greater length increments for S. *angustifolium* compared to *S. fuscum* in a Finnish mire, but with the latter having a higher bulk density as well. Similar relationships have also been found between other hummock and hollow species (Wieder and Lang, 1983; Wallén *et al.*, 1988; Moore, 1989; Rochefort *et al.*, 1990; Francez, 1992b) and for a single species (*S. magellanicum*) growing on hummocks and hollows at the same site (Forrest and Smith, 1975). The compact, dense growth form of hummock species probably helps to reduce evaporation losses (Moore, 1989) and to increase water transport through capillary movement.

Production of *S. fuscum* in the bog for the two years ranged from 119 to 189 g/m^2/yr (Table 2.2) and was well within the range for this species (7-800 g/m^2/yr) reported in a literature search compiled by Rochefort *et al.* (1990). Compared to similar sites in North America, these Alberta values seem to be intermediate between those recorded in N.W. Ontario (Rochefort *et al.*,1990) for an oligotrophic mire (69-119 g/m^2/yr) and a minerotrophic mire (156-303 g/m^2/yr). However *S. fuscum* production reported by Reader and Stewart (1972) in a S.E. Manitoba bog was only 7-8 g/m^2/yr. This much lower figure may be due to different methods used. Other studies in Eastern North America resulted in higher production of *S. fuscum* than my study. Grigal (1985) measured 300 g/m^2/yr on a raised bog in Minnesota, while Pakarinen and Gorham (1983) cited a figure of 240 g/m^2/yr in N.E. Ontario for a forested bog.

Production of *S. angustifolium* in the poor fen ranged from 95 to 166 g/m^2/yr and was well within the range in the literature (19-1656 g/m^2/yr). My results are comparable to those of a poor fen in N.W. Ontario obtained by Rochefort *et al.* (1990) where *S. angustifolium* production ranged from 97-198 g/m^2/yr. My values appear to be slightly greater than those (29-127 g/m^2/yr) reported from sub-arctic fens in Quebec (Moore 1989).

Measurements of bulk density, growth and production of *S. teres* in the PF were very similar to those of *S. angustifolium* (Table 2.2). Production estimates of *S. teres* were 143 and 101 g/m^2/yr for 1991 and 1992 respectively. No production values were found for this species in the literature.

Studies on the production of the brown moss *Tomenthypnum nitens* are also rare. Production of *T. nitens* in the wooded-rich fen was 170 and 115 g/m^2/yr in 1991 and 1992 respectively. These results are somewhat lower than those obtained by Busby *et al.* (1978) for this species in a similar rich fen in west-central Alberta (190 g/m^2/yr). The range of *T. nitens* production values (95-204 g/m^2/yr) for the extreme-rich fen were greater than those of the wooded-rich fen and from two other boreal extreme-rich fens in Alberta (104-131 g/m^2/yr) reported by Vitt (1990).

Moss production by site

The sedge fen had the lowest moss production (47 g/m^2/yr in 1991 and 38 g/m^2/yr in 1992) of all the sites (Fig. 2.2). The bog, poor fen, wooded-rich fen and extreme-rich fen had values between 147 and 204 in 1991 and 95 to 119 in 1992. There were no significant differences between these four sites, however, there was a significant difference between years ($p < 0.001$). In every site moss production was lower in 1992 ranging from 50% to 80% of the 1991 rates. This trend of large variation between years has also been reported in other studies (Wallén *et al.*, 1988; Moore, 1989; Rochefort *et al.*, 1990 and Francez, 1992b). Others have also shown that moss production may differ minimally between sites. Rochefort *et al.* (1990) reported four year means of total moss production of 141 g/m^2/yr for an oligotrophic site and 132 for a minerotrophic site in Ontario. Bartsch and Moore (1985) also found minimal differences in *Sphagnum* production between three sub-arctic peatland types: poor fen, rich fen and transitional fen. However, Reader and Stewart (1972) found moss production to increase across a wooded bog - open bog - lagg gradient in Manitoba, and Moore (1989) recorded greater moss production in a sub-arctic extreme-rich fen than in nearby rich or poor fens. This contradicts Vitt (1990) who found extreme-rich fens to be similar or slightly less productive than bogs and poor fens.

The average (1991 and 1992) moss production of the bog (154 g/m^2/yr) and PF (123) were quite similar to the four year averages of the oligotrophic (141) and minerotrophic (132) sites of Rochefort *et al.* (1990). The values for my bog and poor fen were, however, greater than those recorded (55 g/m^2/yr) for a Manitoba bog (Reader and Stewart, 1972) and the 70-84 g/m^2/yr for sub-arctic poor fens (Moore, 1989). The moss production of my two *Sphagnum*-dominated sites was much lower than values (320-380) cited for Minnesota bogs (Grigal, 1985).

Total moss production of the wooded-rich fen (115-170 g/m^2/yr) and extreme-rich fen (95-204) showed more variation between years than the two boreal extreme-rich fens of Vitt (1990). In the latter, total production remained fairly constant over three years (125-131 g/m^2/yr). Reader and Stewart (1972) also studied a boreal rich fen (lagg) in S. E. Manitoba. The production (76 g/m^2/yr) for this site was within the low range of values for my Alberta rich fens and similar to the sedge fen estimates (38-47).

My production values represent only approximations of the total moss NPP per site because only the dominant species were measured by cranked wires. However, these figures are probably good estimates of total moss production because the sites had more or less 100% moss cover and in most cases the dominant species had cover values greater than 75%. The production values obtained may be low because the cranked wire method has been shown to underestimate moss production (Grigal, 1985; Wallén *et al.*, 1988).

Herb production

Minimum seasonal herb production (see methods) and peak herb standing crop (maximum production) were both significantly different ($p < 0.01$) between sites (Figs. 2.3 and 2.4). Herb NPP increased along the bog-rich fen gradient with minimum seasonal production values ranging from 7 to 203 g/m^2/yr in the order: sedge fen > extreme-rich fen > wooded-rich fen > poor fen > bog. With the exception of the bog in 1992, peak standing crops were attained in either July or August in 1991 and 1992 (Fig. 2.4). Peak standing crops were greater in 1991 in all sites except the bog. The sedge fen showed the greatest yearly change in maximum above ground biomass dropping from 203 g/m^2 in 1991 to 122 g/m^2 in 1992.

The low values of herbaceous peak standing crop in the bog (8 and 14 g/m^2) are consistent with other studies done on ombrotrophic systems. For example, Grigal *et al.* (1985) recorded herb production values of 14 g/m^2/yr in raised bogs and 22 g/m^2/yr in perched bogs from Minnesota. Herb biomass in Finnish forested bogs was also low with values of 3 g/m^2 reported by Paavilainen (1980) and 30-40 g/m^2 by Vasander (1982).

The results of increased herb production in the minerotrophic sites are also supported by other researchers. Malmer (1986), for example, found graminaceous production in Swedish sites to be greater in both poor and rich fens than in bogs. Herbaceous production measured by Bartsch and Moore (1985) in a number of different sub-arctic fens is also comparable to my results. Their value for a poor fen of 27 g/m^2/yr is somewhat lower than the results of the poor fen in this study (52-55 g/m^2/yr). Total herb production in their rich fens (90-233 g/m^2/yr) appears to be only slightly higher than the rich fens of this study (52-203 g/m^2/yr). Reader and Stewart (1972) also found similar herb production (164 g/m^2/yr) in a Manitoba lagg where the major species were *Carex rostrata* Stokes and *Calamagrostis canadensis* (Michx.) Beauv., while Reiners (1972) recorded a value of 50 g/m^2/yr in a Minnesota marginal fen of neutral pH.

The sedge fen had much lower herbaceous production (122-203 g/m^2/yr) than values reported by Bernard and Gorham (1978) for North American sedge wetlands. These ranged from 340 to 1500 g/m^2/yr for above ground production, however, several of the studies were located at much lower latitudes.

The estimates of above ground herb NPP by the harvest method likely contain errors. Under-estimates will occur due to shoot mortality, different time of peak biomass for different species and herbivory, while over-estimates will occur due to over-wintering green shoots and translocation of material from old to new tissues (Bernard and Gorham, 1978; Reader, 1978; Richardson, 1978; Wheeler and Shaw, 1991).

Shrub production

Shrub above ground production appears to decrease along the bog-rich fen gradient (Fig. 2.5). Total shrub terminal production was highly significant ($p < 0.001$) between sites ranging from 6 to 128 g/m^2/yr. The bog, poor fen and wooded-rich fen had much greater shrub production than the sedge fen and the extreme-rich fen. Shrub terminal production was generally higher in 1992 but this difference was not significant ($p > 0.05$). The estimated radial production of the major shrub species at each site was low compared to the terminal production. This secondary wood growth only accounted for an additional 2-26% (mean of 12%) of the terminal production.

Total (terminal and radial) above ground shrub production (77-97 g/m^2/yr) for the bog in this study was slightly higher than the values of Reader and Stewart (1972) for shrub production in a bog forest (53 g/m^2/yr) but lower than values they obtained for more open peatlands. In a sparsely-treed muskeg and a tree-less bog respectively, they recorded above ground shrub productions of 241 and 308 g/m^2/yr. Grigal *et al.* (1985) also reported higher figures (200 g/m^2/yr) for raised bogs in Minnesota. However, shrub production in their perched bogs averaged only 40, which is somewhat lower than the Alberta bog.

In the minerotrophic sites that had any substantial shrub cover (poor fen and wooded-rich fen) the shrub production ranged from 96 to 152 g/m^2/yr. These values are high compared to similar fens in sub-arctic Quebec (Bartsch and Moore, 1985) where shrub production ranged from 43 to 71 g/m^2/yr. However, my values are not as large as similar peatlands in lower latitudes. For instance, Reader and Stewart (1972) in Manitoba and Richardson *et al.* (1976) in Michigan reported shrub production values of 458 and 338 g/m^2/yr respectively from minerotrophic sites.

The sedge fen and extreme-rich fen had the lowest estimates of above ground shrub production (6-9 g/m^2/yr) in all the sites. These values are comparable to that of a Minnesota marginal fen (7 g/m^2/yr) recorded by Reiners (1972).

The estimates of net above ground shrub production may be low because of losses due to retranslocation, litter fall and herbivory. Ericaceous terminal production could have also been underestimated because current leaves and stems may continue to increase in weight until October (Backéus, 1985), while my harvests were only performed in late August. Estimates of average radial production are most certainly conservative because they do not take into account stem mortality and burial by peat surface (Forrest and Smith, 1975). These values may also be inaccurate because dividing average quadrat weight by age represents a long-term average of radial growth rather than a current estimate (*cf.* Reiners, 1972).

Vascular plant production (excluding trees)

There was a significant difference ($p < 0.05$) in above ground vascular plant (excluding trees) production between sites but there was no significant difference between the two years ($p > 0.05$). The two sites at the ends of the gradient (bog and extreme-rich fen) had the lowest herb and shrub production combined (Fig. 2.6) while the rest of the sites had values that were similar. Production figures ranged from 76 to 211 g/m^2/yr but were less variable than between site comparisons of either herb (Fig. 2.3) or shrub production (Fig. 2.5).

A detailed list of the major taxa that comprise the herb and shrub layers is in Appendices 2 and 3.

Tree production

Total above ground estimated tree production was similar between the wooded bog and wooded-rich fen (Table 2.3). The bog had slightly greater production (54 g/m^2/yr) mainly due to the larger biomass estimates and growth increments of *P. mariana*, while about half of the estimated WRF tree production (44 $g/m^2/yr$) was measured as *L. laricina* leaf litter.

Estimated *P. mariana* above ground biomass (592 g/m^2) and production (54 $g/m^2/yr$) in the wooded bog were similar to biomass (368) and production (58) values measured by Reader and Stewart (1972) for the same species in a Manitoba muskeg. Their bog forest, however, had much greater tree biomass (4186 g/m^2) and production (303 $g/m^2/yr$). Bogs in Minnesota also had larger *P. mariana* growth, where biomass and production averaged 3100 g/m^2 and 100 $g/m^2/yr$ for raised bogs and 10,000 and 310 for perched bogs respectively (Grigal *et al.*, 1985). Estimates of *Pinus Sylvestris* L. biomass (254 g/m^2) and production (23 $g/m^2/yr$) from a raised bog in Finland (Vasander, 1982) were lower than the wooded bog in Alberta.

The wooded bog and wooded-rich fen had very similar tree production values despite being dominated by different species. Tree production estimates from fens are not as common as those from bogs. No production studies on *Larix laricina*-dominated fens could be located in the literature. In Minnesota, tree biomass and production in a *Fraxinus nigra* Marsh. and *Thuja occidentalis* L. - dominated fen were 9800 g/m^2 and 650 $g/m^2/yr$ respectively (Reiners, 1972). These were much higher than the wooded-rich fen where a biomass of 351 and a production of 44 were estimated for the tree layer.

Errors in the estimates of tree biomass and production most likely occurred. The regression equations used to predict biomass of the large trees were developed outside of Alberta and therefore may not provide accurate estimations for the sites. Also, the independent variables (biomass or production) were probably under-estimated from the log-log equations (Table 2.1) when antilog transformed (Baskerville, 1972; Beauchamp and Olson, 1973; Crow and Laidly, 1980). Increments used to develop the production equations represent five year averages so tree production values may not necessarily reflect the current year's growth.

Total production

Total above ground NPP, when averaged for the two years (Fig. 2.7), appears to increase along the gradient from bog to poor fen to wooded-rich fen and then it abruptly drops towards the rich end of the gradient. The wooded moderate-rich fen had the greatest average production (36[illegible] $g/m^2/yr$) followed by the poor fen (310). This supports Vitt ([illegible]90), who suggested that moderate-rich fens have higher nutrient levels than the other mire types and therefore should be more productive. The sedge fen (214 g/m^2/yr) and extreme-rich fen (245) had the lowest values. The average NPP of the bog sites were intermediate with the wooded bog (297 g/m^2/yr) slightly higher than the open bog (264).

Yearly total production values of the bog sites (235-311 g/m^2/yr) were among the lowest reported for North American bogs (Table 2.4). In S.E. Manitoba, Reader and Stewart (1972) recorded total above ground production values of 342 and 371 g/m^2/yr for their muskeg and open bog respectively, while other North American values are much higher (634-1045). There appears to be a trend of increasing above ground NPP with decreasing latitude in North American bogs (Table 2.4).

European total NPP values for ombrotrophic systems are comparable with those from this study. Doyle (1973) measured 175 g/m^2/yr on an Irish blanket bog, while Vasander (1982) recorded a value of 238 for a Finnish raised bog. Forrest and Smith (1975) reported somewhat higher figures for a number of British blanket bogs (285-653 g/m^2/yr).

Estimated yearly above ground production values for the Alberta fens (167-388 g/m^2/yr) are slightly higher than those from the sub-arctic fens (114-335) studied by Bartsch and Moore (1985). Richardson *et al.* (1976), in a Michigan fen, recorded a value (341) that was similar to the wooded-rich fen, however, estimates from North American marginal fens or laggs are two to three times higher (Reader and Stewart, 1972; Reiners, 1972). The trend of increasing NPP with decreasing latitude does not appear to be as strong in fens as bogs in North America (Table 2.4), suggesting the importance of local hydrology on minerotrophic systems in addition to climatic factors.

My least productive fens were the sedge and extreme-rich fens. In Europe, wetlands similar to these have also been reported to have lower standing crops than other nearby fens. For example, Verhoeven *et al.* (1983) and Wheeler and Shaw (1991) found *Carex diandra/C. lasiocarpa/C. rostrata* communities to have low production values (210-250 g/m^2/yr). These are comparable to my *C. lasiocarpa*-dominated sedge fen (167-260). Some extreme-rich fen communities have also been reported to have relatively low production (Boyer and Wheeler, 1989; Wassen *et al.*, 1990; Wheeler and Shaw, 1991). The latter authors reported standing crop increments of only 137 to 170 g/m^2 in "short-fen" vegetation from spring-fed calcareous fens in England and attributed this to low phosphorus availability.

Litter fall

There were significant differences in total litter (Fig. 2.8), shrub litter and tree litter fall between the sites ($p < 0.001$). The wooded-rich fen had the greatest total litter production (65.3 g/m^2/yr) which was similar to that of the poor fen (61.8 g/m^2/yr). The extreme-rich fen and sedge fen had the lowest litter fall (8.1 and 15.3 g/m^2/yr respectively), while the open bog (22.3) and wooded bog (39.9) were intermediate. The wooded-rich fen also had the highest tree litter production (24.7 g/m^2/yr) while the poor fen had the greatest shrub litter production (61.7 g/m^2/yr).

Total combined tree and shrub litter production (Fig. 2.8) was greatest in the poor and wooded-rich fens because these sites had large proportions of deciduous species. Both peatlands had a well-developed shrub layer dominated by *Betula* and *Salix*, while the WRF also had a tree stratum dominated by the deciduous species *L. laricina*. The bog sites had relatively low litter fall despite the presence of well-developed shrub layers in both the OB and WB and a tree layer in the WB. This is because all the non-herbaceous vascular plant species were evergreen and therefore leaf fall was minimal in the bog. The very low litter fall in the extreme-rich and sedge fens was due to the sparseness or lack of tree and shrub layers.

Few studies have been done directly measuring litter fall in peatlands. Grigal *et al.* (1985) reported values of 130 g/m^2/yr for raised and 250 for perched bogs in Minnesota. These results are 3 to 6 times greater than total litter fall measured in the wooded bog (40 g/m^2/yr), however, tree and shrub biomass was also much larger in the Minnesota sites. Forrest and Smith (1975) found that *Calluna vulgaris* (L.) Hull litter fall in blanket bogs from the United Kingdom averaged approximately 90 g/m^2/yr. Reiners (1972) recorded much higher values (412 g/m^2/yr) in a Minnesota fen dominated by deciduous trees. Comparisons between different studies must be made with caution because of the different types and sizes of litter traps that were employed. However, Rytter *et al.* (1989) found no difference in the capture rate between large and small traps.

My traps may have under-estimated litter fall because their shallow design may have allowed some litter to be blown out by strong winds, however, this could have been compensated for by additional litter being blown into the traps. Estimates may also be low as a result of leaching and decomposition of materials in the traps before collection. Litter traps in general under-estimate the true deposition of aerial organic matter in forested ecosystems because they do not account for falling trees which may add considerable amounts of material to the peat (Reiners, 1972, Grigal *et al.*, 1985).

Conclusions

The hypothesis of increasing production along the bog-rich fen gradient was only partially supported by the data. Total above ground NPP increased along the gradient from the bog to wooded moderate-rich fen and then abruptly decreased in the sedge and extreme-rich fens. Above ground production of the bog sites (264-297 g/m^2/yr) was lower than values from other North American ombrotrophic systems. The Alberta fens were intermediate in NPP (214-360 g/m^2/[illegible] compared to other North American minerotrophic [illegible]nds.

Moss pro[illegible]erally showed greater variation between years than sites [illegible]es having similar values except for the sedge fen which [illegible] lower moss NPP than the other sites. Herbaceous produc[illegible] increased along the bog-rich fen gradient while shrub production tended to decrease along the gradient. Tree production was only measurable in two of the sites (bog and wooded-rich fen) and contributed a minimum amount to the total above ground production. Total tree and shrub litter fall followed a similar trend to total NPP and was greatest in the middle of the gradient in the poor and wooded-rich fens and lowest at the rich end in the sedge and extreme-rich fens.

Literature cited

Backéus, I. 1985. Aboveground production and growth dynamics of vascular bog plants in Central Sweden. Acta. Phytogeogr. Suec. 74. 98 pp.

Bartsch, I. and T. R. Moore. 1985. A preliminary investigation of primary production and decomposition in four peatlands near Schefferville, Quebéc. Can. J. Bot. 63:1241-1248.

Baskerville, G. L. 1972. Use of logarithmic regression in the estimation of plant biomass. Can. J. Forest Res. 2:49-53.

Beauchamp, J. J. and J. E. Olson. 1973. Corrections for bias in regression estimates after logarithmic transformation. Ecology 54:1403-1407.

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

Boyer, M. L. H. and B. D. Wheeler. 1989. Vegetation patterns in spring-fed calcareous fens: calcite precipitation and constraints on fertility. J. Ecol. 77:597-609.

Busby, J. R., L. C. Bliss and C. D. Hamilton. 1978. Microclimate control of growth rates and habitats of the boreal forest mosses, *Tomenthypnum nitens* and *Hylocomium splendens*. Ecol. Monogr. 48:95-110.

Clymo, R. S. 1970. The growth of *Sphagnum*: methods of measurement. J. Ecol. 58:13-49.

Crow, T. R. and P. R. Laidly. 1980. Alternative models for estimating woody plant biomass. Can. J. For. Res. 10:367-370.

Doyle, G. J. 1973. Primary production estimates of native blanket bog and meadow vegetation growing on reclaimed peat at Glenamoy, Ireland, pp. 141-151. *In*: L. C. Bliss and F. E. Wielgolaski (eds.). Primary production and production processes. Tundra Biome Steering Committee, Edmonton.

Du Rietz, G. E. 1949. Huvudenheiter och huvugranser i svensk myrvegetation. Svenska botaniska Tidskrift 43:274-309.

Environment Canada. 1982. Canadian climate normals, 1951-1980, temperature and precipitation, prairie provinces. Canadian Climate Program. 429 pp.

Forrest, G. I. 1971. Structure and production of northern Pennine blanket bog vegetation. J. Ecol. 59:453-479.

Forrest, G. I. and R. A. H. Smith. 1975. The productivity of a range of blanket bog vegetation types in the Northern Pennines. J. Ecol. 63:173-202.

Francez, A. J. 1992a. Structure, function and evolution of the ecosystem of a peat bog: Primary production and nitrogen flow in a peat bog in central France. Ann. Bot. Fennici. 29:197-211.

Francez, A. J. 1992b. The growth and primary production of *Sphagnum* in a peat-bog of Monts du Forez (Puy-de-Dome, France). Vie et Milieu 42:21-34.

Gorham, E. 1991. Northern peatlands: Role in the carbon cycle and probable responses to climatic warming. Ecol. Applic. 1:182-195.

Gorham, E. and M. G. Somers. 1973. Seasonal changes in the standing crop of two montane sedges. Can. J. Bot. 51:1097-1108.

Grigal, D. F. 1985. *Sphagnum* production in forested bogs of northern Minnesota. Can. J. Bot. 63:1204-1207.

Grigal, D. F., C. G. Buttleman and L. K. Kernik. 1985. Biomass and productivity of the woody strata of forested bogs in northern Minnesota. Can. J. Bot. 63:2416-2424.

Grigal, D. F. and L. K. Kernik. 1984. Generality of black spruce biomass estimation equations. Can. J. For. Res. 14:468-470.

Ireland, R. R., G. R. Brassard, W. B. Schofield and D. H. Vitt. 1987. Checklist of the mosses of Canada II. Lindbergia 13:1-62.

Lavigne, M. B. 1982. Tree biomass equations for common species of Newfoundland. Can. For. Serv. Nfld. For. Res. Cent. Info. Rep. N-X-213. 40 pp.

Lindholm, T. and H. Vasander. 1990. Production of eight species of *Sphagnum* at Suurisuo mire, southern Finland. Ann. Bot. Fennici. 27:145-157.

Malmer, N. 1986. Vegetational gradients in relation to environmental conditions in northwestern European mires. Can. J. Bot. 64:375-383.

Moore, T. R. 1989. Growth and net production of *Sphagnum* at five fen sites, subarctic eastern Canada. Can. J. Bot. 67:1203-1207.

Moss, E. H. and J. G. Packer. 1983. Flora of Alberta. 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 Poly Science Publications, Inc., Montreal, Québec. 452 pp.

Paavilainen, E. 1980. Effect of fertilization on plant biomass and nutrient cycle on a drained dwarf shrub pine swamp. Commun. Inst. For. Fenn. 98:1-71.

Pakarinen, P. and E. Gorham. 1983. Mineral element composition of *Sphagnum fuscum* peaks collected from Minnesota, Manitoba, and Ontario, pp. 417-429. *In*: Proceedings of the International Symposium on Peat Utilization, Bemidji State University, Bemidji, Minnesota, USA.

Reader, R. J. 1978. Primary production in northern bog marshes, pp. 53-62. *In*: R. E. Good, D. F. Whigham and R. L. Simpson (eds.). Freshwater wetlands: ecological processes and management potential. Academic Press, New York.

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

Reiners, W. A. 1972. Structure and energetics of three Minnesota forests. Ecol. Monogr. 42:71-94.

Richardson, C. J. 1978. Primary productivity values in freshwater wetlands, pp. 131-145. *In*: Wetland functions and values: the state of our understanding. Proceedings of the National Symposium on Wetlands, Lake Beuna Vista, Florida, Nov. 7-10, 1978.

Richardson, C. J., W. A. Wentz, J. P. M. Chamie, J. A. Kadlec and D. L. Tilton. 1976. Plant growth, nutrient assimilation, and decomposition in a central Michigan peatland used for effluent treatment, pp. 77-117. *In*: D. L. Tilton, J. A. Kadlec and C. J. Richardson (eds.). Freshwater wetlands and sewage effluent disposal. Academic Press, New York.

Rochefort, L. 1987. Biological effects of wet acid deposition on peatland bryophytes. Unpublished M. Sc. thesis, University of Alberta, Edmonton. 171 pp.

Rochefort, L., D. H. Vitt and S. E. Bayley. 1990. Growth, production and decomposition dynamics of *Sphagnum* under natural and experimentally acidified conditions. Ecology 71:1986-2000.

Rowe, J. S. 1972. Forest regions of Canada. Dept. of Environment, Canadian Forestry Services Publication 1300, Ottawa, Ontario.

Rytter, L., T. Slapokas and U. Granhall. 1989. Woody biomass and litter production of fertilized grey alder plantations on a low-humified peat bog. For. Ecol. Manage. 28:161-176.

Sjörs, H. 1950. On the relation between vegetation and electrolytes in north Swedish mire waters. Oikos 2:241-258.

Sparling, J. H. 1966. Studies on the relationship between water movement and water chemistry in mires. Can. J. Bot. 44:747-758.

Vasander, H. 1982. Plant biomass and production in virgin, drained and fertilized sites in a raised bog in southern Finland. Ann. Bot. Fennici. 19:103-125.

Verhoeven, J. T. A., S. Van Beek, M. Dekker and W. Storm. 1983. Nutrient dynamics in small mesotrophic fens surrounded by cultivated land: I. Productivity and nutrient uptake by the vegetation in relation to the flow of eutrophicated ground water. Oecologia 60:25-33.

Vitt, D. H. 1990. Growth an production dynamics of boreal mosses over climatic, chemical and topographical gradients. Bot. J. Linn. Soc. 104:35-59.

Vitt, D. H., S. E. Bayley, L. Halsey and T. L. Jin. in press. Seasonal variation in water chemistry over a bog-rich fen gradient in continental western Canada. Can. J. Fish. Aquat. Sci.

Vitt, D. H. and P. Pakarinen. 1977. The bryophyte vegetation, production, and organic components of Truelove Lowland, pp. 225-244. *In*: L. C. Bliss (ed.). Truelove Lowland, Devon Island, Canada: a high arctic ecosystem. Univ. of Alberta Press, Edmonton.

Wallén, B., U. Falkengren-Grerup and N. Malmer. 1988. Biomass, productivity and relative rate of photosynthesis at different water levels on a South Swedish peat bog. Holarc. Ecol. 11:70-76.

Wassen, M. J., A. Barendregt, A. Palczynski, J. T. De Smidt and H. De Mars. 1990. The relationship between fen vegetation gradients, ground water flow and flooding in an undrained valley mire at Biebrza, Poland. J. Ecol. 78:1106-1122.

Wein, R. W. and L. C. Bliss. 1974. Primary production in arctic cotton grass tussock tundra communities. Arctic and Alpine Res. 6:261-274.

Wheeler, B. D. and S. C. Shaw. 1991. Above-ground crop mass and species richness of the principal types of herbaceous rich-fen vegetation of lowland England and Wales. J. Ecol. 79:285-301.

Wieder, R. K. and G. E. Lang. 1983. Net primary production of the dominant bryophytes in a *Sphagnum*-dominated wetland in West Virginia. Bryologist 86:280-286.

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

Wielgolaski, F. E. 1975. Primary production of alpine meadow communities, pp. 121-128. *In*: F.E. Wielgolaski (ed.). Fennoscandian tundra ecosystems. Springer-Verlag, New York.

Zar, J. 1984. Biostatistical analysis. Prentice-Hall, Toronto. 718 pp.

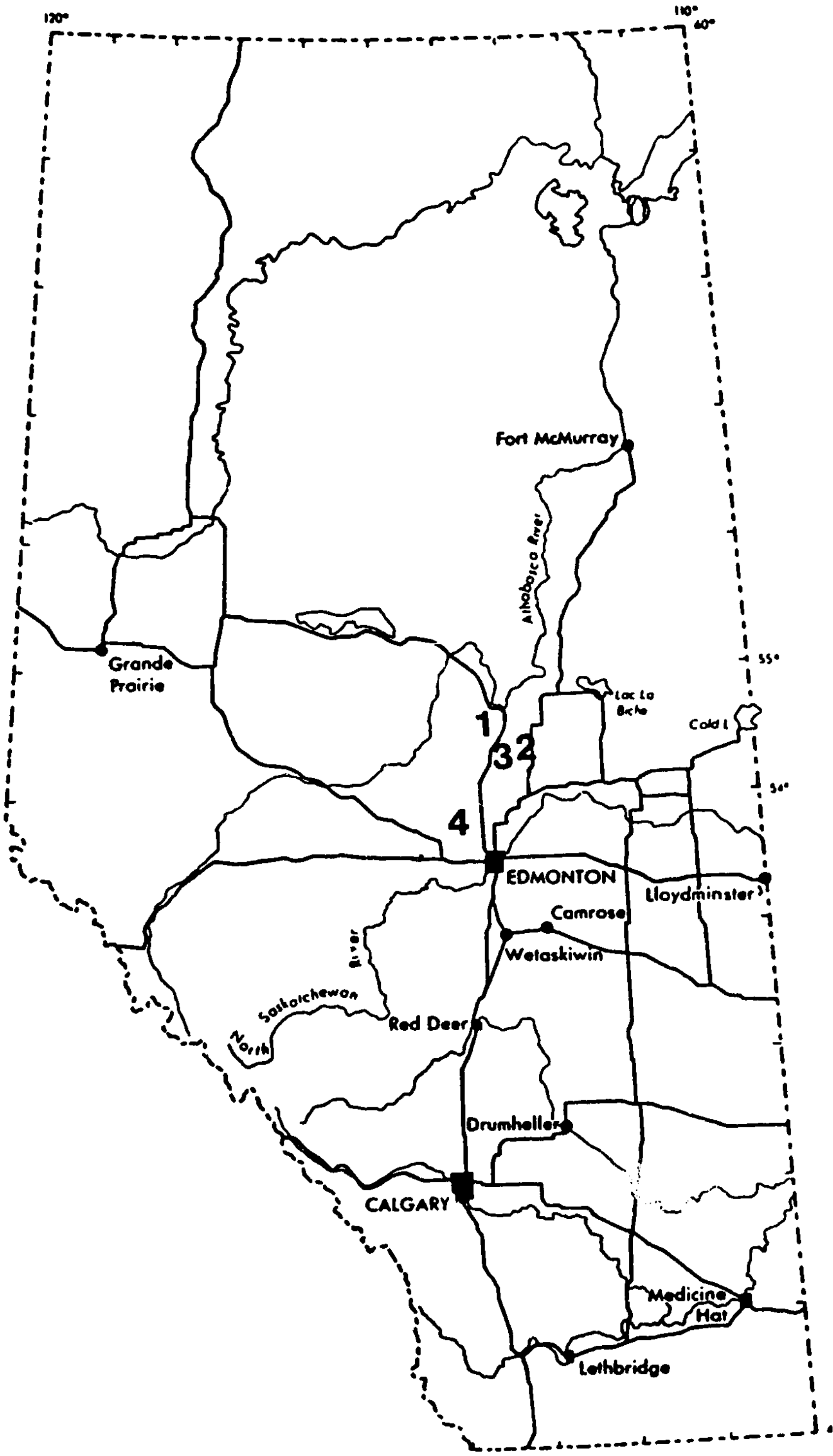


Fig. 2.1. Relative location of the sites in central Alberta (**1** = bog and poor fen, **2** = wooded-rich fen, **3** = sedge fen and **4** = extreme-rich fen).

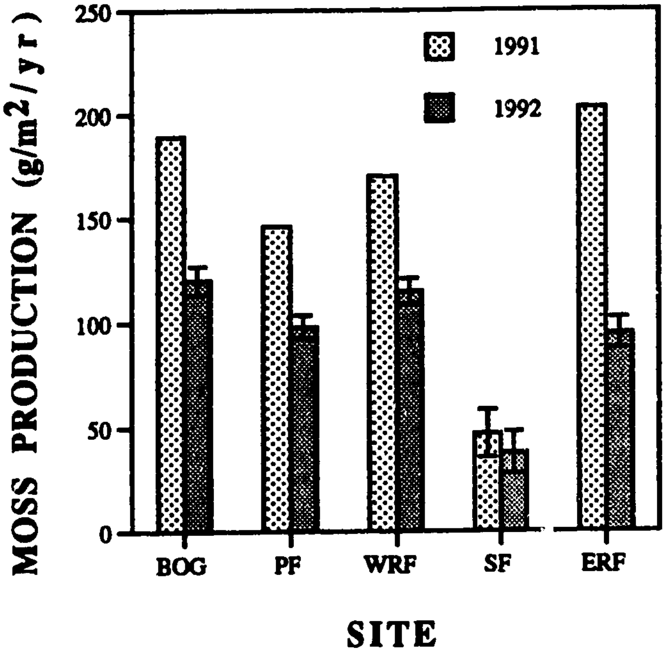


Fig. 2.2: Comparison of moss production (mean +/- SE) assuming 100% cover of ground layer by dominant species at five sites (PF = poor fen, WRF = wooded-rich fen, ERF = extreme-rich fen and SF = sedge fen) in 1991 and 1992. No error bars on 1991 estimated values (see methods).

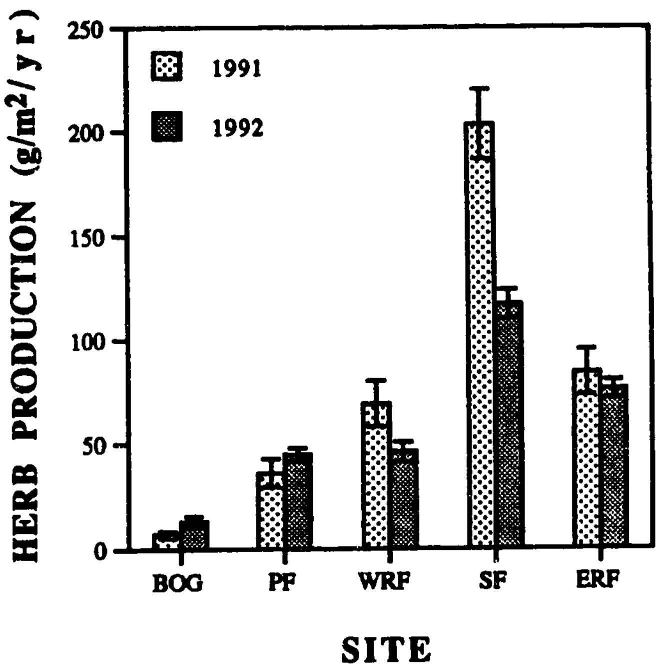
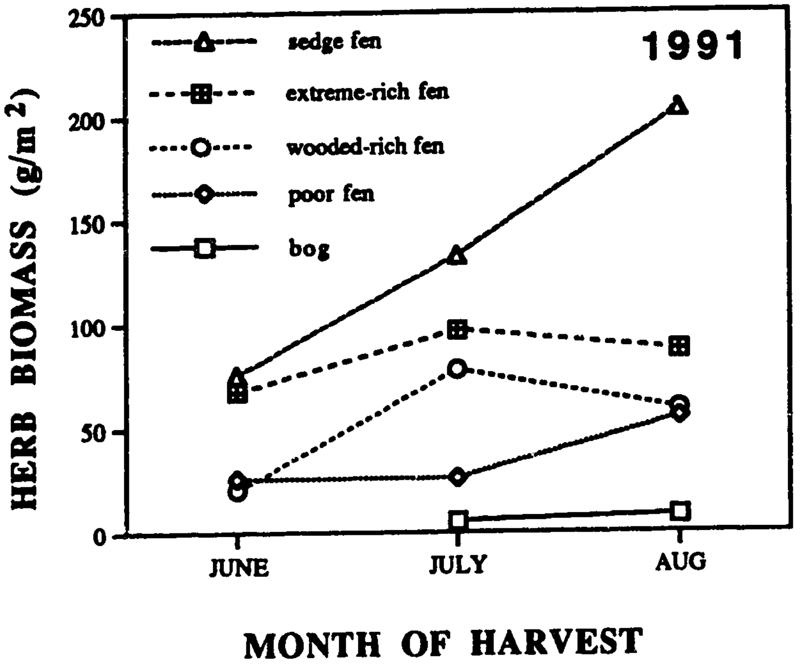


Fig. 2.3: Comparison of minimum seasonal above ground herb production (mean +/- SE) in five sites (PF = poor fen, WRF = wooded-rich fen, SF = sedge fen and ERF = extreme-rich fen) in 1991 and 1992.



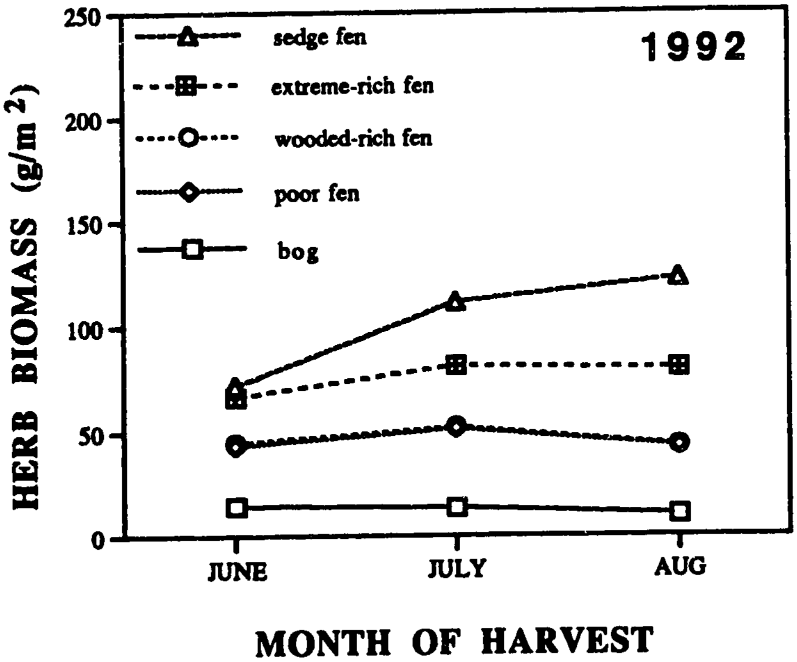


Fig. 2.4: Above ground herbaceous biomass at three monthly harvest periods in five peatlands during the summers of 1991 and 1992.

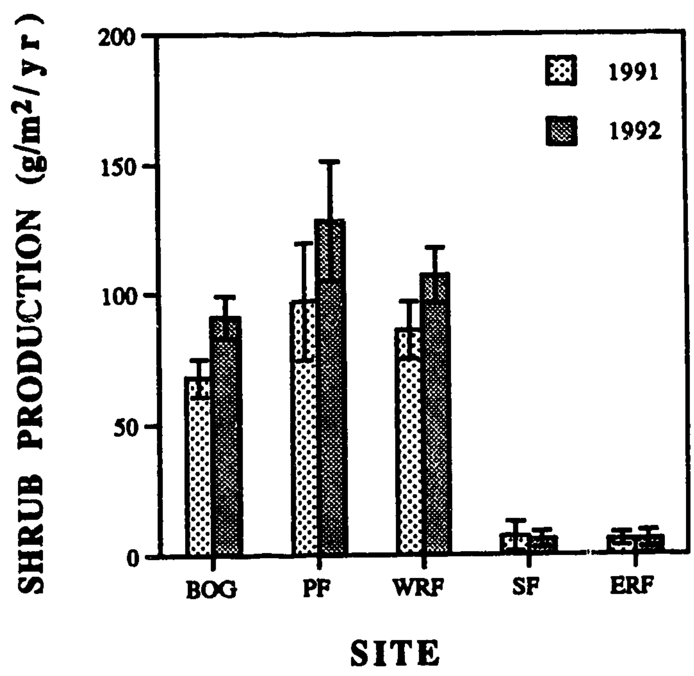


Fig. 2.5: Comparison of above ground terminal shrub production (mean +/- SE) in five sites (PF = poor fen, WRF = wooded-rich fen, SF = sedge fen and ERF = extreme-rich fen) in 1991 and 1992.

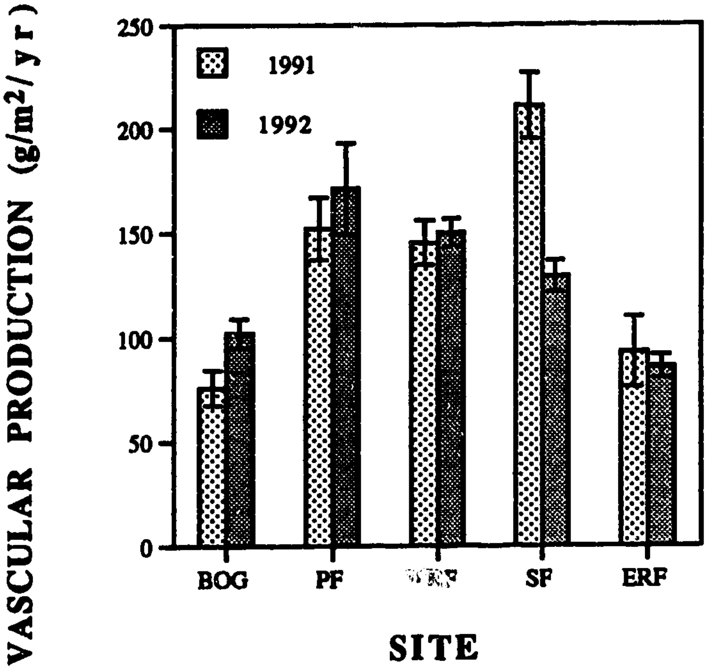


Fig. 2.6: Comparison of above ground vascular plant production (mean +/- SE) in five sites (PF = poor fen, WRF = wooded-rich fen, SF = sedge fen and ERF = extreme-rich fen) in 1991 and 1992. Figures derived from August herb standing crop and terminal shrub production. Shrub radial production and tree production not included.

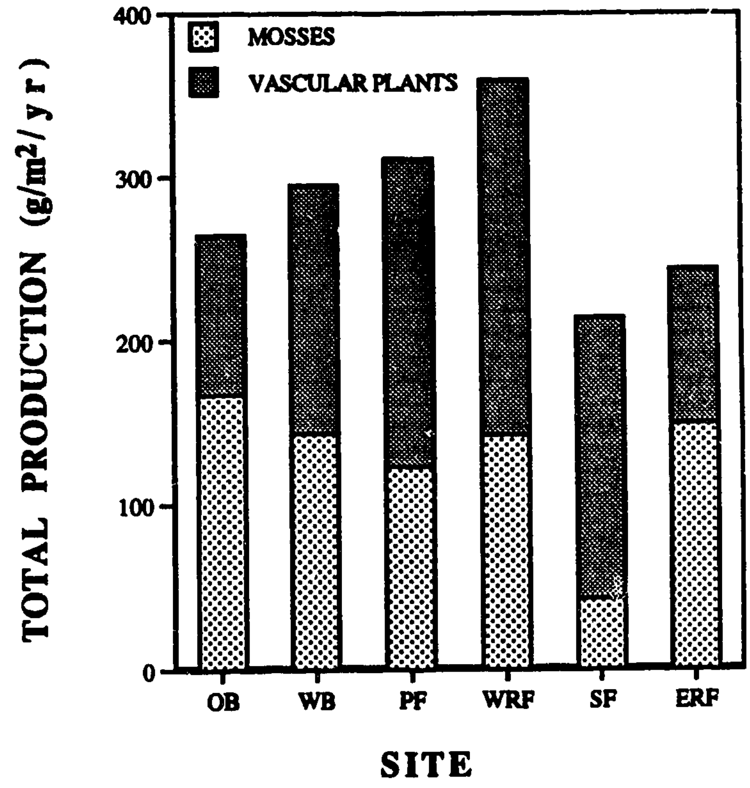


Fig. 2.7: Comparison of total above ground plant production (vascular plants and mosses) in six sites (OB = open bog, WB = wooded bog, PF = poor fen, WRF = wooded-rich fen, SF = sedge fen and ERF = extreme-rich fen). Bars represent averages of 1991 and 1992, except estimated tree production (where applicable) which is based on the average of five year growth increments.

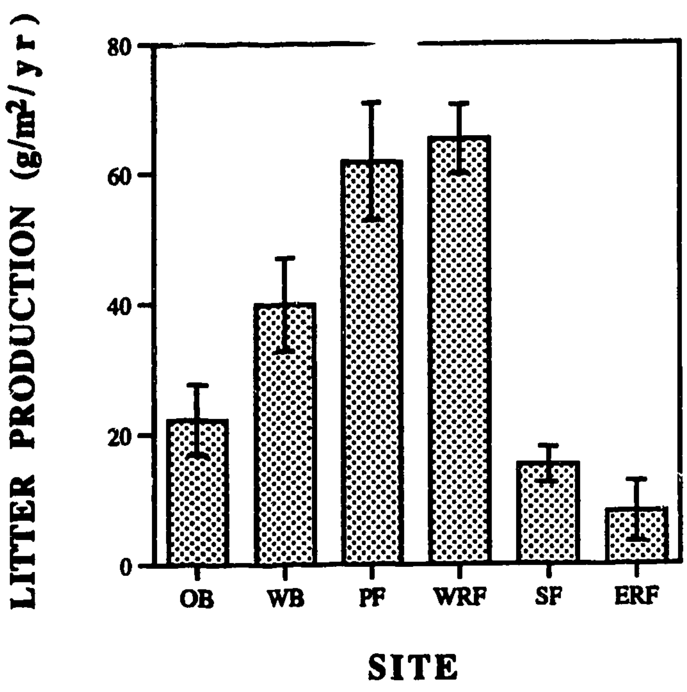


Fig. 2.8: Comparison of total shrub and tree litter production (mean +/- SE) in six sites (OB = open bog, WB = wooded bog, PF = poor fen, WRF = wooded-rich fen, SF = sedge fen and ERF = extreme-rich fen) during the period of May 1992 to May 1993.

Table 2.1: Regression equations used to estimate above ground tree biomass and production. Equations follow the general format: $y = a + bx$, where y is the dependent variable, x is the independent variable and a and b are the y-intercept and slope respectively. The sample size of trees used to construct the equation is *n* and *r-square* is the coefficient of determination.

Species	Tree size	y	a	b	x	n	r-square	Source
Picea mariana	small	Biomass	38.091	36.500	(Diam. sq.) ht.	10	0.990	This study
Larix laricina	small	Biomass	10.744	24.200	(Diam. sq.) ht.	6	0.998	This study
P. mariana	large	Log Biomass	2.185	2.248	Log dbh			Grigal et al. (1984)
L. laricina	large	Biomass	584.910	32.612	(dbh) ht.	243	0.972	Lavigne (1982)
P. mariana	all	Log Production	-1.303	1.055	Log Biomass	19	0.954	This study
L. laricina	all	Log Production	-0.922	0.885	Log Biomass	20	0.915	This study

NOTE: Diam. sq. = basal diameter squared (cm-squared), ht. = height (m), dbh = diameter at breast height (cm), biomass and production (g).

Table 2.2: Average (+/- SE) bulk density, surface area correction factor, growth and net primary production of moss species in four peatlands during 1991 and 1992. Annual growth and production represent May to October growth period. The June-October period was used in the analysis (paired t-test) to compare production between years. See methods for further explanations. Bulk density is in grams per centimeter per square meter, growth is in centimeters and production is in grams per sqaure meter per period.

Site/Species	Bulk density	Surface area correction factor	1991 June-Oct. growth	1991 June-Oct. prod.	1991 Annual growth*	1991 Annual prod.*	1992 June-Oct. growth	1992 June-Oct. prod.	1992 Annual growth	1992 Annual prod.
BOG										
Sphagnum fuscum	267 (35) n = 5	1.09 (0.02) n = 10	0.45 (0.03) n = 180	131 (8) n = 180	0.65	189	0.22 (0.02) n = 175	64 (6) n = 175	0.41 (0.02) n = 175	119 (7) n = 175
POOR FEN										
S. teres	45 (5) n = 5	1.20 (0.05) n = 10	1.91 (0.11) n = 129	103 (6) n = 129	2.64	143	1.38 (0.08) n = 122	75 (4) n = 122	1.87 (0.12) n = 105	101 (6) n = 105
S. angustifolium	43 (3) n = 5	1.20 (0.05) n = 10	1.89 (0.17) n = 48	98 (9) n = 48	3.21	166	0.99 (0.13) n = 46	51 (7) n = 46	1.85 (0.24) n = 30	95 (12) n = 30
WOODED-RICH FEN										
Tomenthypnum nitens	91 (14) n = 5	1.13 (0.02) n = 10	1.08 (0.04) n = 164	111 (4) n = 164	1.65	170	0.61 (0.05) n = 141	63 (5) n = 141	1.12 (0.06) n = 141	115 (6) n = 141
EXTREME-RICH FEN										
T. nitens	167 (21) n = 5	1.12 (0.02) n = 3	0.73 (0.05) n = 140	137 (10) n = 140	1.09	204	0.22 (0.02) n = 137	41 (5) n = 137	0.51 (0.04) n = 132	95 (7) n = 132
S. warnstorfii	n.d.	n.d.	1.44 (0.14) n = 35	n.d.	1.96	n.d.	0.60 (0.10) n = 38	n.d.	1.12 (0.15) n = 38	n.d.

* 1991 annual growth and production were estimated (see methods), n.d. = not determined, n = sample size

Table 2.3: Comparison of above ground tree biomass, production and litter fall between the wooded bog and wooded-rich fen. Total tree net primary production was estimated by combining biomass production and litter fall. Biomass is in grams per square meter while production and litter fall are in grams per square meter per year.

Component	Wooded bog	Wooded-rich fen
Above ground biomass		
Picea mariana	592	39
Larix laricina	0	312
Total tree	592	351
Biomass production		
P. mariana	46	3
L. laricina	0	16
Total tree	46	19
Litter fall		
P. mariana	8	2
L. laricina	0	23
Total tree	8	25
Total tree production	54	44

Table 2.4: Above ground net primary production (grams per square meter per year) of different strata and totals for North American peatlands in order of decreasing latitude. Columns may not add up to totals due to rounding.

Peatland type	Location and Source	Latitude	Moss	Herb	Shrub	Tree	Total
BOGS							
Open bog	Alberta This study	54° 41' N	167	11	86	-	264
Wooded bog	Alberta This study	54° 41' N	143	12	88	54	297
Muskeg	Manitoba Reader and Stewart (1972)	49° 53' N	17	-	267	58	342
Bog	Manitoba Reader and Stewart (1972)	49° 53' N	55	-	308	*8	371
Raised bogs	Minnesota Grigal et. al. (1985)	47 - 48° N	320	14	200	100	634
Perched bogs	Minnesota Grigal et. al. (1985)	47° 30' N	380	22	43	310	755
Bog	West Virginia Wieder et. al. (1989)	39° 07' N	449	209	387	-	1045
FENS							
Poor fen	Quebec Bartsch and Moore (1985)	54° 43' N	38	27	49	-	114
Rich fen	Quebec Bartsch and Moore (1985)	54° 43' N	41	233	61	-	335
Transitional fen	Quebec Bartsch and Moore (1985)	54° 43	39	90	47	-	176
Poor fen	Alberta This study	54° 41' N	123	54	134	-	310
Wooded moderate-rich fen	Alberta This study	54° 28' N	142	65	108	44	360
Sedge fen	Alberta This study	54° 28' N	43	163	8	-	214
Extreme-rich fen	Alberta This study	53° 42' N	149	89	6	-	245
Lagg	Manitoba Reader and Stewart (1972)	49° 53' N	76	*300	*650	-	1026
Marginal fen	Minnesota Reiners (1972)	45° N	-	49	6	655	710
Leather leaf-bog birch fen	Michigan Richardson et. al. (1976)	44° N	-	3	338	-	341

* production of stratum estimated from data

3. DECOMPOSITION ALONG A BOG-RICH FEN GRADIENT IN CENTRAL ALBERTA, CANADA

Introduction

Peatlands are an important component in the global carbon cycle because they store large amounts of organic carbon and comprise a significant area of the boreal and sub-arctic regions in the northern hemisphere (Gorham, 1991). Several authors have suggested that peat accumulation is controlled by slow decomposition rates rather than rapid net primary production rates (Clymo, 1965; Malmer, 1986; Farrish and Grigal, 1988; Vitt, 1990). Decomposition rates are reduced in peatlands because of unfavourable (anoxic, cold, acidic or nutrient poor) environmental conditions (Bartsch and Moore, 1985; Farrish and Grigal, 1988; Gorham, 1991) and/or poor substrate quality (Brinson *et al.*, 1981; Bridgham and Richardson, 1992).

Decomposition (or decay) are general terms that encompass a number of processes. These include: organic matter losses by leaching, micro-organism attack or removal by animals; loss of physical structure and changes in the chemical constituents (Clymo, 1983). Methods which have been employed to quantify decomposition in peatlands include measuring soil respiration (Bridgham and Richardson, 1992), changes in peat macrostructure (Johnson *et al.*, 1990), the degree of humification (Aaby and Tauber, 1974; Malmer, 1986) and the C:N ratio of the peat (Malmer and Holm, 1984).

Perhaps the most common method of determining rates of decomposition in peatlands has been to measure the weight loss of a substrate (natural or artificial) placed in the peat over a period of time. Numerous authors have investigated the decay of plant material found on the site with most moss decomposition studies focusing on *Sphagnum* (Clymo, 1965; Bartsch and Moore, 1985; Brock and Bregman, 1989; Johnson *et al.*, 1990; Rochefort *et al.*, 1990; Johnson and Damman, 1991). Less research has been done on "brown moss" decay (Reader and Stewart, 1972; Vitt, 1990). Several vascular plant decomposition studies have been carried out on minerotrophic peatlands emphasizing above ground tissues of sedges or shrubs (Chamie and Richardson, 1978; Bartsch and Moore, 1985; Ohlson, 1987; Moore, 1989; Verhoeven and Arts, 1992), while very few have investigated vascular plant decomposition in bogs (Reader and

Stewart, 1972). Research on decomposition rates of boreal mires in Western Canada has been scarce (Vitt, 1990).

To compare decomposition rates in a variety of wetland types many researchers have used cellulose as a standard substrate (Bartsch and Moore, 1985; Farrish and Grigal, 1985; Farrish and Grigal, 1988; Lieffers, 1988; Verhoeven *et al.*, 1990; Santelmann, 1992; Verhoeven and Arts, 1992). Utilization of natural plant material for this purpose has been rare (Ohlson, 1987; Lieffers, 1988; Johnson and Damman, 1991). Natural material (e.g. *Carex*) provides a source of nutrients (e.g. N, P and K) for the decomposers in addition to carbon while the cellulose method provides only carbon.

This paper is part of a long term project investigating decomposition in five different peatlands (bog, poor fen, open-rich fen, wooded-rich fen and rich sedge fen) in central Alberta, Canada. These peatlands represent the poor-rich vegetation gradient (*sensu* Du Rietz, 1949) where numbers of indicator species, pH, base cations, reduced conductivity and water flow all increase along the gradient (Sjörs, 1950; Malmer, 1986). The objectives of this study were to: 1) measure the decomposition rates of dominant species in each site; 2) relate differences in weight loss of litter types to substrate quality (i.e. C:N ratios and percent N); 3) compare the rates of decomposition in the sites as measured by weight loss of a common substrate type; and 4) relate these differences to site environmental parameters.

Two major hypotheses were tested in this study with the first related to substrate or tissue type. I hypothesize that the tissue types with lower C:N ratios and greater percent N should decompose faster in all sites because of greater N availability for decomposers. The second hypothesis is related to environmental parameters. Rates of decomposition as measured by a common substrate should increase among the sites along the bog-rich fen gradient due to higher pH which may favour decomposer activities.

Study area and site descriptions

The sites sampled include a bog, poor fen (PF), open moderate-rich fen (ORF), wooded moderate-rich fen (WRF), and sedge fen (SF). The bog and poor fen are located north of Bleak Lake, Alberta at 54° 41' N and 113° 28' W, while the wooded- and open-rich fens (54° 28' N, 113° 17' W) and sedge fen (54° 28' N, 113° 20' W) are east of Perryvale (Fig 3.1). All study sites are located within the Boreal Forest Region of Canada (Rowe, 1972).

The climate of the area is characterized by mild summers and cold, snowy winters (Vitt *et al.*, in press). The long-term mean annual temperature (Environment Canada, 1982) is 1.7 °C for the area (average of two weather stations: Meanook and Athabasca 2). The total mean annual precipitation is about 500 mm. Climate data for the growing seasons of 1991 and 1992 compared to the long-term average are summarized in Appendix 1. Table 3.1 lists means and ranges of surface water parameters at the sites, while Figs. 4.2 and 4.3 (in Chapter Four) show water level fluctuations at the sites (excluding ORF) during the 1991 and 1992 growing seasons. Details of the vegetation and water chemistry are also described in Vitt *et al.* (in press). Authority names follow Ireland *et al.* (1987) for bryophytes and Moss and Packer (1983) for vascular plants. Cover values of the dominant species were estimated in 10 by 10 m plots.

General descriptions of the sites are as follows:

Bog

This site is a large, raised ombrotrophic island within a peatland complex bordered by a poor fen water track. The peat surface is raised about 0.3-0.5 m above the associated water track and is composed of large, dry hummocks separated by a few wetter hollows. This peatland has a sparse tree layer of small *Picea mariana* (Mill.) BSP. covering about 25% of the area with an ericaceous shrub stratum dominated by *Ledum groenlandicum* Oeder with a cover value of about 75%. The moss layer is dominated by *Sphagnum fuscum* (Schimp.) Klinggr. with a cover of about 90%.

Poor Fen

This fen is the water track adjacent to the bog island. The poor fen has a hummocky microtopography, but is wetter than the bog, with open water usually present in some areas during the ice-free season. This site has a well-developed shrub layer of *Betula pumila* L. var. *glandulifera* Regel. (40% cover) and *Salix pedicellaris* Pursh (20%). The herb layer is dominated by *Smilacina trifolia* (L.) Desf., *Menyanthes trifoliata* L. and *Carex* species. The ground layer has a *Sphagnum* cover of about 90% with *S. teres* (Schimp.) Aongstr. ex C. Hartm. and *S. angustifolium* (C. Jens. ex Russ.) C. Jens. in Tolf, the most common species.

Open-Rich Fen

This moderate-rich fen is located on a floating mat surrounding a small lake. The peat surface is a uniform carpet, about one meter thick, that fluctuates with the water level of the associated pond.

This site is largely sedge-dominated with *Carex lasiocarpa* Ehrh., *C. diandra* Schrank and *C. chordorrhiza* L.f. the most common species. The dominant mosses are *Drepanocladus vernicosus* (Mitt.) Warnst., *Calliergonella cuspidata* (Hedw.) Loeske and *Calliergon giganteum* (Schimp.) Kindb.

Wooded-Rich Fen

This site forms a grounded, forested fen adjacent to the open-rich fen. The peat surface consists of large hummocks and wet lawns, with pools of water present during much of the season. This moderate-rich fen has an open tree canopy dominated by *Larix laricina* (Du Roi) K. Koch (25% cover), while *Betula pumila var. glandulifera* is the dominant shrub with a cover of 30%. The dwarf shrub layer is also well-developed (25%) with *Oxycoccus microcarpus* Turcz. and *Andromeda polifolia* L. the most important species. The herb layer has a cover of about 20% and includes mostly *Carex* species and *Menyanthes trifoliata*, while the ground layer is brown moss-dominated with *Tomenthypnum nitens* (Hedw.) Loeske covering about 75% of the study area.

Sedge Fen

This peatland is situated in a former north-south drainage channel that presently contains several large bodies of open water, separated by large expanses of sedge-dominated wetlands. The microtopography is mainly flat with a few isolated, small hummocks constituting less than 5% of the surface. The site was inundated with water for most of 1991, and therefore has characteristics of a marsh, but began to dry out during the 1992 season. Vitt *et al.* (in press) designated this site as an extreme-rich fen and that it is probably transitional between a moderate- and extreme-rich fen. The vascular plant vegetation is almost completely sedge-dominated with *Carex lasiocarpa* and *C. diandra* the two most important species. The moss layer is discontinuous covering only about 75% of the surface. *Drepanocladus aduncus* (Hedw.) Warnst. (65%) is the dominant species, forming mats at the bases of sedge plants.

Methods

Decomposition measurements

Aerial portions of the dominant moss species from each site (except the sedge fen) and *Carex* species (local *Carex*) from the fens were collected on September 16, 1990. Leaves and young branches (upper 15 cm) of the dominant shrub (*Betula pumila* var. *glandulifera*) were also collected in the poor fen and wooded-rich fen. All vascular plant samples appeared to be senescent at the time of collection. After oven-drying at 60 °C for 24 hours, 0.3-2.7 g samples of dried moss or *Carex* were placed in weighed nylon mesh bags (approximately 2.5 x 2.5 cm, 1 mm mesh). *Betula* samples contained 0.55 g of leaves and 0.45 g of stems for a total of 1.0 g per bag. The decomposition bags were placed horizontally in the peat, at their respective collection sites, so that the upper surface of each was at ground level. During October 1991 and 1992 at least five replicates of each litter type were removed from each site, except the local *Carex* at the PF was not removed in 1992. Roots and debris present in the bags were carefully removed with forceps. The bags were then dried at 60 °C for 24 hours and weighed to the nearest 0.001 g.

To compare decomposition between all the sites one standard species, *Carex lasiocarpa* (collected from the sedge fen), was used. This *C. lasiocarpa* litter was placed into all the sites following the same procedures as above.

The percent weight loss (k') over a period of one or two years was expressed using the following equation (*cf.* Reader and Stewart, 1972; Bartsch and Moore, 1985):

$$k' = \frac{Xo - X}{Xo}(100)$$

where Xo represents the initial dry litter mass before decomposition and X the final dry litter mass after removal from the field.

C/N analyses

Methods used to analyze tissue samples for carbon and nitrogen follow those in Bayley and Szumigalski (under review). Plant samples were ground and analyzed for total C and total N using a Model 440 Elemental Analyzer (Control Equipment Corp.). Amounts were expressed as %N (percent N) and %C (percent C) of total dry weight and C:N ratios were determined by dividing %C by %N for each sample. Initial %C, %N and C:N values were derived from averages of three samples of each litter type collected, while final values of these parameters were determined from the incubated samples removed after either one or two years of decomposition.

Water levels

Water level fluctuations were monitored at each site (except ORF) with Steven's F water level recorders and manually with permanently attached meter sticks during most of the ice-free season. The average water level relative to the moss surface at each site was determined by calculating the mean of the daily water table depths for each year. The daily water table depth was defined as the relative position of the water table at approximately noon each day.

Water chemistry

Measurements of surface water pH and temperature were done in the field monthly using a Beckman pH meter and thermometer. The open-rich fen was only sampled in 1991 and not 1992. Water samples for laboratory analysis were collected concurrently. As much as possible, the readings and samples were collected from the same locations (holes dug in the peat) within each site. Conductivities were measured in the lab within 24 hours of collection and corrected for pH and standardized to 20 °C (Sjörs, 1950).

Chemical analyses of water samples follow the methods of Vitt et al. (in press). All samples were filtered initially with glass fibre (GFC) filters. Base cations (Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}) were fixed with 0.5 ml of concentrated HNO_3 and analyzed with a Perkin-Elmer Atomic Absorption Spectrometer. Nitrate, soluble reactive phosphorus (SRP) and total dissolved phosphorus (TDP) samples were refiltered with a 0.45 µm millipore (HAWP) filter. Water samples for NO_3^- and NH_4^+ were analyzed on a Technicon Auto Analyser II within 24 hours of collection. Total phosphorus (TP), SRP and TDP were measured by the methods of Bierhuizen and Prepas (1985). Dissolved organic carbon (DOC) was measured with a Model 1505 Programmable Carbon Analyser.

Depth of oxidation

Measurements of oxidation depth followed the methods of Bridgham *et al.* (1991). Steel welding rods of one m length were placed in the sites (except ORF) in June 1992. A total of 8 rods (4 in hummocks and 4 in hollows) were inserted into the peat at each site exposing only the top 20 cm of the rod. One rod per microhabitat per site was removed at monthly intervals and the depth of solid rust relative to the peat surface was measured. Depth of oxidation was determined by averaging site microhabitats and all 4 measurements from July to October.

Statistical analyses

Analysis of covariance (ANOCOVA) was used to test for significant differences in weight loss between the litter types (including the *Carex lasiocarpa* standard) incubated in the bog, poor fen, open-rich fen and wooded-rich fen. Separate ANOCOVA tests were performed on each of these four sites with the initial weight of the litter in each bag as the covariate and the the final weight of the litter after incubation as the dependent variable. Both of these were log-transformed before the analyses. Mean comparisons of the final weights of the various litter types within sites were made using Tukey tests (Zar, 1984). A similar ANOCOVA was also done to test for significant differences in the *C. lasiocarpa* standard litter weight loss between all five sites.

Correlation analyses were performed between the *C. lasiocarpa* standard percent weight loss (k') after one year (all sites) and various mean site parameters. Nitrate (NO_3^-), NH_4^+ and TP were excluded from these analyses because there were no significant differences (ANOVA) in surface water concentrations of any of these parameters between sites in 1991. Correlations were also done between k' after one and two years with the initial and final C:N ratios and %N of the dominant litter types within the five sites.

All analyses were performed on Systat version 5.2.1.

Results and discussion

Decomposition of dominant species at each site

There was a significant difference ($p < 0.001$) in weight loss between the litter types in the bog, poor fen, open-rich fen and wooded-rich fen. The dominant moss species consistently had the lowest rate of loss ($p < 0.001$) compared to vascular plant litter, while the local *Carex* litter always decomposed faster than ***Betula*** leaves and stems (Fig. 3.2).

Other researchers have also reported differences in the rate of decay between vegetation types. Reader and Stewart (1972) and Bartsch and Moore (1985) found mosses to be more resistant to decomposition than vascular plants in peatlands, while Heal and

French (1974) and Taylor *et al.* (1991) found similar results in tundra and coniferous forest ecosystems respectively. Graminoid and shrub leaves appear to decompose at similar rates (Reader and Stewart, 1972; Chamie and Richardson, 1978; Bartsch and Moore, 1985). The slower rates of decay for *Betula* than *Carex* in this study may be due to the presence of stems in the samples of the former. Chamie and Richardson (1978) found *B. pumila* leaves to decompose more rapidly than stems and attributed this to the greater content of cellulose, hemicellulose and lignin in woody stems. Of all materials, forbs seem to decompose the fastest (Moore, 1989; Slapokas and Granhall, 1991; Taylor *et al.*, 1991).

Moss litter weight losses ranged from 10% (*Drepanocladus vernicosus* in the ORF) to 22% (*Tomenthypnum nitens* in WRF) in the first year and from 16% (*Sphagnum teres* in the PF) to 32% (*T. nitens* in the WRF) after two years. The two species of *Sphagnum* (*S. teres* in the PF and *S. fuscum* in the bog) showed similar trends losing very little additional mass after the first year (Fig. 3.2). This contrasts with *D. vernicosus* which had a constant rate of loss over the two years. The *T. nitens* litter decay rate was generally constant with only a slight decrease the second year.

The average first year decomposition loss (k') for *Sphagnum fuscum* (14%) is high compared to other values reported in the literature for this species. For example, Reader and Stewart (1972) recorded values of only 0.1 and 1.7% for this peat moss in two Manitoba peatlands. Rochefort *et al.* (1990) found *S. fuscum* lost 12% after 14 months in north-west Ontario while Johnson and Damman (1991) reported losses of 10.8-11.7% after 10 months in a Swedish raised bog. Hummock sphagna such as *S. fuscum* are known to be more resistant to decay than sphagna from hollows (Clymo, 1965; Rochefort *et al.*, 1990; Johnson and Damman, 1991; Johnson *et al.*, 1992). In my study, *S. teres* (a hollow species from the poor fen) did not decompose significantly faster than the *S. fuscum* on hummocks in the adjacent bog. Bartsch and Moore (1985) also found no difference between hummock and hollow sphagna in several subarctic fens. In both of these cases it is impossible to separate site differences from species differences.

The brown moss species in this study also decayed at slow rates, although they had greater weight losses after two years than the sphagna (Fig. 3.2). Decomposition of brown mosses has not been studied as widely as *Sphagnum*. The moss species *Hypnum pratense* W. Koch ex Spruce, in a lagg from south-east Manitoba, lost 23% in one year (Reader and Stewart, 1972). Vitt (1990) reported decomposition rates for some extreme-rich fen species in Alberta which are comparable to results from the wooded and open-rich fens. For example, *Tomenthypnum nitens* lost 32% after two years in the WRF and averaged 33% after 30 months in the extreme-rich fens of Vitt (1990). Similarly, *Drepanocladus vernicosus* lost 20% after two years in the ORF while *D. revolvens* (Sw.) Warnst. lost 32% after 2.5 years in Vitt's extreme-rich fens. The *D. vernicosus* in my study was one of the only species to show a constant weight loss over two years. All the extreme-rich fen brown moss species recorded by Vitt (1990) showed rates that increased over time. These trends contrast with the decay rates of *Sphagnum* (this study and Rochefort *et al.*, 1990) which lost very little additional weight after the first year.

The *Carex* litter had the fastest rate of decay in all sites, with the local *Carex* losing weight more rapidly than the standard *C. lasiocarpa* litter in the PF, ORF and WRF. The local *Carex* at the WRF had the greatest overall k' values losing 58% during first year and 74% after 2 years of decomposition (Fig. 3.2). During the same period the ORF local *Carex* also had high losses of 50 and 65%, while the poor fen local *Carex* samples lost 50% in the first year as well. The sedge fen local *Carex* (*C. lasiocarpa*) had the slowest rate of decay losing only 31% in the first year and 41% after two years.

The results of *Carex* weight loss after one year (31-58%) are within the range of literature values reported for this genus in peatlands. Bartsch and Moore (1985) cited a low value of 13.4% for *C. rostrata* Stokes in a subarctic rich fen, while Ohlson (1987) reported an 81% weight loss after one year for the same species in a spring area (rich fen).

Betula pumila leaves and stems in the PF and WRF had rates of weight loss that were intermediate to those of the moss and *Carex* litters. At these sites weight losses of the shrub samples were significantly lower than those of local *Carex* ($p < 0.001$), and although lower, were not significantly different from those of the standard *C. lasiocarpa* litter ($p > 0.05$). Values of k' for *Betula* samples were similar in the poor fen (36% after one year, 49% after two years) and wooded-rich fen (37% after one year, 43% after two years).

The *Betula* k' values after one year in the poor and wooded-rich fens (36-37%) are higher than those listed in other studies. For instance, *B. glandulosa* Michx. leaves in subarctic fens lost only 16.6-21.6% after one year (Bartsch and Moore, 1985). *B. pumila* leaves in a Michigan fen also lost 37% (Chamie and Richardson, 1978); however, this value is reduced to 27% when corrected for the proportion of stem material (45%) used in this Alberta study (see methods).

The comparisons with other studies are complicated by several factors: the degree of senescence and prior leaching (Ohlson, 1987);

the drying temperature used (Clymo, 1965); the depth of placement (Farrish and Grigal, 1988; Santelmann, 1992); the length of the growing season and for mosses (Clymo, 1965), the part of the plant included (e.g. capitulum vs. stem). Differences in mesh size will also affect the rate, with larger mesh sizes resulting in greater weight losses (Brinson *et al.*, 1981).

Substrate quality (%C, %N and C:N) of litter types

The initial carbon content (%C) in the litter from the decomposition bags (Table 3.2) ranged from 28% (*D. vernicosus* in ORF) to 41% (*Betula* in PF and WRF). The %C remained fairly constant during the two years of incubation with values of most litter types slightly greater after one year than either the initial values or those after two years. The mosses tended to have lower %C than vascular plant tissues at all stages of decomposition.

The nitrogen content (%N) showed greater change over time than the %C (Table 3.2). Most vascular plant litter had increases in %N over time while moss litter was more variable. *S. fuscum* and *T. nitens* tissues showed few changes in %N while *S. teres* showed decreases and *D. vernicosus* showed increases in %N during the two years. The vascular plant samples had higher %N than mosses with initial values ranging from 0.76 to 1.13 for vascular species and from 0.65 to 0.78 for mosses. Bartsch and Moore (1985) also found that vascular tissues had higher %N than *Sphagnum* tissues in sub-arctic fens.

The trends in the C:N ratios of the various tissue types over the two years were generally the inverse to those of the nitrogen content (Table 3.2). Malmer and Holm (1984) also found that the variation in the C:N ratio within a bog peat profile was opposite to and reflected the variation in N content.

Initial C:N ratios (Table 3.2) also varied according to litter type. Moss and *Betula* samples tended to have higher initial ratios than the *Carex* litter. The initial C:N ratios of the mosses ranged from 44.0 (*D. vernicosus*) to 52.0 (*S. fuscum*). *Betula pumila* leaves and stems in the PF and WRF had similar initial C:N ratios of 44.8 and 43.9 respectively. The initial ratios of *Carex* litter were relatively low (32.7-34.4) in all sites except the *C. lasiocarpa* from the sedge fen which had a surprisingly high value of 48.6.

In most cases the C:N ratio of vascular tissues decreased gradually during the two years of decomposition. Verhoeven and Arts (1992) also found the C:N ratio to decrease during decomposition of *Carex* in Dutch fens. Reductions in the C:N ratio and increases in the N concentration of peat is a result of decay processes (Malmer and Holm, 1984).

The C:N ratios of the moss species (excluding *D. vernicosus* in the ORF) generally did not show this decreasing trend over time and either remained fairly constant (*S. fuscum* and *T. nitens*) or increased gradually (*S. teres*). Similarly, Brock and Bregman (1989) found that the N content in decomposing *S. fallax* (Klinggr.) Klinggr. (= *S. recurvum*) decreased in relation to the organic matter content over a period of one year in the Netherlands. These results contradict those of Bartsch and Moore (1985) who reported increases in the N content of sphagna after one year of decomposition in subarctic fens.

After two years of decay, the local *Carex* litters tended to still have the lowest C:N values (around 28). The *Betula* samples also had relatively low ratios (28.3 in PF, 37.6 in WRF), while the moss tissues had higher C:N ratios than the vascular tissues within their respective sites. *D. vernicosus* had the lowest ratio (33.5) of the mosses while the two species of *Sphagnum* had much higher ratios (52.6 and 54.2) after two years.

Relationship of decomposition to substrate quality

Significant ($p < 0.001$) correlations were found between k' and the C:N ratios and between k' and the N content of the dominant litter types at the sites (Table 3.3). Percent weight loss after one and two years was positively correlated with initial and final percent N and negatively correlated with initial and final C:N ratios.

The negative correlations between weight loss and C:N ratios and positive correlations between weight loss and %N are consistent with other studies. Taylor *et al.* (1991) and Verhoeven and Arts (1992) also found that litter with high initial C:N ratios (or low %N) decomposed slowly. Other authors have also correlated weight loss with initial P or K concentrations as well as N (Coulson and Butterfield, 1978; Bartsch and Moore, 1985; Ohlson, 1987; Slapokas and Granhall, 1991). The initial C:N or C:P ratio is important because many litter types accumulate these nutrients (microbial immobilization) during early decay (Verhoeven *et al.*, 1990; Taylor *et al.* 1991). At high C:N quotients (>20) net immobilization should occur while at lower ratios net mineralization should prevail (Prentki *et al.*, 1978; Verhoeven *et al.* 1990). All of the litter types in my study showed increases in %N in the initial stages of decomposition with the exception of the mosses *Tomenthypnum nitens*, *Sphagnum fuscum* and *S. teres*. The N content of *S. fuscum* and *T. nitens* remained relatively constant over two years while that of *S. teres* gradually decreased from 0.78 to 0.66%. This suggests that some N mineralization may have taken place in these litter types even though they had high initial C:N values (44-52). Net mineralization of N has also been reported in *Sphagnum* peat with high C:N ratios (Bayley and Szumigalski, under review; Malmer and Holm, 1984; Verhoeven *et al.*, 1990). Sikora and Keeney (1983) reported that *Sphagnum* materials readily yield ammonium N even when poorly decomposed. This might help to explain the relatively high concentrations of NH_4^+ in the bog surface water (Table 3.1), as this peatland is the most *Sphagnum*-dominated of all the sites.

Decomposition of standard litter type (*Carex lasiocarpa*)

There were significant differences in weight loss of the standard *C. lasiocarpa* litter between sites ($p < 0.001$). After one year, the standard litter samples lost more weight in the bog (45%), poor fen (45%) and wooded-rich fen (42%) than the samples in the open-rich fen (33%) and sedge fen (31%) decomposition bags (Fig. 3.3).

After two years, the bog litter lost 46% of its original weight which represents additional losses of only 1% during the second year. These results contrast with those of the nearby poor fen which lost another 17% in the second year for a two year total of 62%, the highest of all the sites. Total percent weight losses after two years in the rest of the sites were similar ranging from 41 to 50%. The sites ranked: poor fen > wooded-rich fen > bog > open-rich fen > sedge fen, in order of largest to smallest percent weight loss of the *C. lasiocarpa* standard litter after two years of decay.

Farrish and Grigal (1988) and Verhoeven *et al.* (1990) both found cellulose decomposition to be greater in fens than bogs. In contrast, the bog standard litter in this study lost more weight than the open-rich fen and sedge fen and the same amount as the poor fen and wooded-rich fen after the first year (Fig. 3.3). However, the fens lost much more additional weight than the bog during the second year. Substantial amounts of the first year losses from the *C. lasiocarpa* litter may have been due to the leaching of soluble organic materials, as this is known to be a rapid process (Brinson *et al.*, 1981; Verhoeven and Arts, 1992). Ohlson (1987) found initial leaching accounted for a 14% weight loss in *Carex rostrata* after one week under laboratory conditions. The cellulose used in the above studies (Farrish and Grigal, 1988; Verhoeven *et al.*, 1990) probably did not undergo as much initial leaching as the natural plant material (which contains nutrients) in my study, which may partially explain the different results.

Other researchers have also made comparisons of decay rates between poor and rich fens using the common substrate method. Verhoeven and Arts (1992) found cellulose decomposition to be greater in a rich fen than a poor fen, while Ohlson (1987) reported greater *Carex* weight loss in a spring-fed rich fen than in a *Sphagnum*-dominated intermediate fen. However, Bartsch and Moore (1985) found no difference between sub-arctic poor and rich fens. My results contradict most of these findings as the poor fen *C. lasiocarpa* litter had greater weight losses than the litter in most of the rich fens (Fig. 3.3). These contrasting results may again be due to different standard substrates (cellulose vs. *Carex*) used as well as other differences in methods, such as depth of placement and pre-incubation treatment. These comparisons may also be obscured by differences in climatic factors between study areas.

The changes in %C, %N and C:N of the *C. lasiocarpa* litter in the sites (Table 3.4) were not related to differences in the decomposition rates between sites (Fig. 3.3). The %C of the standard litter was similar in all the sites after one year (38.5-42.0%) and after two years (36.6-44.4%).

The %N showed much greater change over time, increasing in all sites after one year and in most after two years. The sedge fen, which had one of the slowest rates of weight loss, showed the greatest increase in %N after two years, doubling from 0.76% to 1.53%. Conversely, the poor fen, which had one of the fastest rates of weight loss after two years, had one of the lowest values of %N (1.24) for the *C. lasiocarpa* litter after that period. These trends contrast those for the dominant litter types (Table 3.2), where the most decomposed material had greater %N values than the least decomposed material.

In all cases the C:N ratio of the standard litter type decreased gradually over the two year period. C:N ratios were similar in the sites ranging from 31.5 to 38.2 after the first and from 28.4 to 33.5 after the second year.

Relation of decomposition to environmental factors

Of all the environmental characteristics measured at the sites, water level had the best relationship with *C. lasiocarpa* weight loss (Table 3.5). A significant negative correlation ($r = -0.60$, $p < 0.001$) was found between the weight loss (k') of *C. lasiocarpa* after one year and the average position of the water table relative to the moss surface during the growing season (Fig. 3.4).

Of the sites, the sedge fen had the lowest weight loss (31%) during the first year. The surface of this site was also inundated for most of the growing season in 1991, which probably caused anoxic conditions to prevail. Anaerobic environments such as these are known to be unfavourable for decomposition (Brinson *et al.*, 1981; Bridgham and Richardson; 1992). Studies of cellulose loss in bogs have also shown decomposition to be slower under reducing conditions and faster in hummocks than hollows (Farrish and Grigal, 1985; Santelmann, 1992).

Anoxic conditions, as indicated by the average depth of iron oxidation at each site (see methods), also support the water level data (Table 3.1). The depth of rust was greatest in the site with the lowest water levels (bog) and least in the wettest site (SF). The poor fen had a similar depth of rust as the bog even though the latter was much drier than the former. This may be due to greater water movement in the poor fen, since it is a water track, which may result in more oxygenated surface water (Malmer, 1986). This potentially enhanced aeration might also partially explain the rapid weight loss of the standard litter in this fen after two years.

In sites other than the sedge fen the water table was usually well below the surface so that the decomposition bags should have been above the highly reducing conditions for most of the time. However, Farrish and Grigal (1985) suggested that even at incubation levels above the water table, capillary action may fill micropores near the surface, thus reducing aeration and microbial respiration.

Farrish and Grigal (1985) also found lower spring and summer soil temperatures in hollows compared to hummocks, which may also explain their slower rates of decomposition for the hollows. Several others (Clymo, 1965; Brinson *et al.*, 1981; Lieffers, 1988; Bridgham and Richardson, 1992; Hogg *et al.*, 1992; Santelmann, 1992) have also discussed the inhibitory effects of low temperatures on decomposition. Although not measured in this experiment, soil temperature may have accounted for some of the variation in the decomposition data.

Significant inverse relationships (Table 3.5) were also found between the decomposition of the standard litter and characteristics related to the acidity-alkalinity gradient (pH, reduced conductivity, Ca^{2+}, Mg^{2+} and Na^{+}). Dissolved organic carbon (which decreases with site pH) had a significant positive correlation with the decay rate. These results contrast others who have suggested that environments of low pH are unfavourable to decomposition (Farrish and Grigal, 1988; Tóth and Zlinszky, 1989; Verhoeven *et al.*, 1990). However, Farrish and Grigal (1988) and Bridgham and Richardson (1992) found only anaerobic decay to be inhibited by low pH while aerobic decomposition was either unaffected or slightly enhanced by increased acidity. Except for the sedge fen in 1991, anoxic conditions were not evident at the site surfaces where the decomposition bags were placed. Decay of the *C. lasiocarpa* standard litter may not have been inhibited in the sites with low pH (bog, PF) because these sites were well-aerated. In this study, it is difficult to separate the influence of water levels and the pH-related characteristics because they are correlated.

Correlations of standard litter (*C. lasiocarpa*) percent weight loss with major nutrient concentrations in the surface water were not as strong as the relationships with water level and pH-related parameters (Table 3.5). A positive correlation was found between TDP ($r = 0.42$, $p < 0.01$) and the percent weight loss of *C. lasiocarpa* after one year. There were no significant relationships between weight loss and K^+ or SRP. Nitrate, NH_4^+ and TP were excluded from the analyses because their concentrations did not differ significantly between sites (see methods).

The positive correlation between TDP in the surface water and first year *C. lasiocarpa* k' suggests that decomposition may be enhanced by nutrient-rich conditions. However, these results should be interpreted with caution since the correlation with TDP was a weak one. Nevertheless, elements dissolved in surface waters should supplement the nutrient demands of decomposers (Brinson *et al.*, 1981) and therefore nutrient-rich environments should favour decomposition (Clymo, 1983).

Slapokas and Granhall (1991) found that alder leaves in heavily fertilized plots on a low-humified peat bog in Sweden decomposed more rapidly than in poorly fertilized plots and Coulson and Butterfield (1978) demonstrated that nitrogen additions increased the decay rate of *Sphagnum recurvum*. However, Verhoeven and Arts (1992) reported lower cellulose decomposition in a fen that had higher levels of phosphates and greater rates of phosphorus and nitrogen mineralization than in one that had lower rates. Other enrichment experiments done on wetlands also appear to contradict the hypothesis that nutrient-rich wetlands have higher decomposition rates. The "fertilizing" effect of artificial acidification (NO_3^- and SO_4^{2-}) had no apparent effect on the decomposition rates of *Sphagnum* in northeastern Ontario (Rochefort *et al.*, 1990) and N and P enrichments did not increase respiration in soil from southern peatlands (Bridgham and Richardson, 1992). As well, in a Florida marsh, Bayley *et al.* (1985) found that nutrient loading had no effect on decomposition.

Conclusions

In this study, differences in the decomposition rate were observed between tissue types and sites. These differences can be partially explained by variation in the chemical composition of the litter types within sites and by the environmental factors between sites.

The hypothesis of increased decomposition in the native litter with higher N and lower C:N ratios was supported by the results. Weight losses after both one and two years were negatively correlated with initial and final C:N ratios and positively correlated with initial and final %N. Rates of decay within sites differed according to litter types with *Carex* > *Betula* > mosses.

The hypothesis of increasing decomposition from bog to rich fens was not supported by the decay results of the standard litter. After one year, weight losses of *C. lasiocarpa* were negatively correlated with water levels and pH-related parameters and positively correlated with surface water concentrations of TDP. Although the bog and poor fen lost the most weight after one year (45%), the former had negligible losses during the second year while the latter continued to lose weight rapidly. After two years, the sites ranked poor fen > wooded-rich fen > bog > open-rich fen > sedge fen in order of fastest to slowest rate of weight loss of the standard litter type.

All these results suggest that substrate quality may be more important than environmental variables in controlling decomposition in continental, boreal bogs and fens, as the degree of decomposition in fen peat is much greater than that of bog peat (Malmer, 1986). Bartsch and Moore (1985) found similar results in sub-arctic peatlands.

If peat accumulation is controlled more by decomposition than production, then it is expected that *Sphagnum* moss-dominated systems such as the bog will accumulate peat faster than systems with greater herbaceous growth (rich fens).

Literature cited

Aaby, B. and H. Tauber. 1974. Rates of peat formation in relation to degree of humification and local environment, as shown by studies of a raised bog in Denmark. Boreas. 4:1-17.

Bartsch, I. and T. R. Moore. 1985. A preliminary investigation of primary production and decomposition in four peatlands near Schefferville, Quebéc. Can. J. Bot. 63:1241-1248.

Bayley, S. E. and A. Szumigalski. under review. Nitrogen mineralization and decomposition in bogs and fens in Western Canada. Biogeochem.

Bayley, S. E., J. Zoltek, A. J. Hermann, T. J. Dolan and L. Tortora. 1985. Experimental manipulation of nutrients and water in a freshwater marsh: effects on biomass, decomposition, and nutrient accumulation. Limnol. Oceanogr. 30:500-512.

Bierhuizen, J. F. H. and E. E. Prepas. 1985. Relationship between nutrients, dominant ions, and phytoplankton standing crop in prairie saline lakes. Can. J. Fish. Aquat. Sci. 42:1588-1594.

Bridgham, S. D. and C. J. Richardson. 1992. Mechanisms controlling soil respiration (CO_2 and CH_4) in southern peatlands. Soil Biochem. 24:1089-1099.

Bridgham, S. D., S. P. Faulkner and C. J. Richardson. 1991. Steel rod oxidation as a hydrologic indicator in wetland soils. Soil Sci. Soc. Am. J. 55:856-862.

Brinson, M. M., A. E. Lugo and S. Brown. 1981. Primary productivity, decomposition and consumer activity in freshwater wetlands. Ann. Rev. Ecol. Syst. 12:123-161.

Brock, C. M. and R. Bregman. 1989. Periodicity in growth, productivity, nutrient content and decomposition of *Sphagnum recurvum* var. *mucronatum* in a fen woodland. Oecologia 80:44-52.

Chamie, J. P. M. and C. J. Richardson. 1978. Decomposition in northern wetlands, pp. 115-130.*In*: R. E. Good, D. F. Whigham and R. L. Simpson (eds.). Freshwater wetlands: ecological processes and management potential. Academic Press, New York.

Clymo, R. S. 1965. Experiments on breakdown of *Sphagnum* in two bogs. J. Ecol. 53:747-757.

Clymo, R. S. 1983. Peat, pp. 159-224. *In:* A. J. P. Gore (ed.). Ecosystems of the world 4A, mires: swamp, bog, fen and moor. Elsevier Scientific Publishing Company, New York.

Coulson, J. C. and J. Butterfield. 1978. An investigation of the biotic factors determining the rates of plant decomposition on blanket bog. J. Ecol. 66:631-650.

Du Rietz, G. E. 1949. Huvudenheiter och huvugranser i svensk myrvegetation. Svenska botaniska Tidskrift 43:274-309.

Environment Canada. 1979. Analytical methods manual. Inland Water Directorate, Water Quality Branch, Ottawa, Ont.

Environment Canada. 1982. Canadian climate normals, 1951-1980, temperature and precipitation, prairie provinces. Canadian Climate Program. 429 pp.

Farrish, K. W. and D. F. Grigal. 1985. Mass loss in a forested bog: relation to hummock and hollow microrelief. Can. J. Soil Sci. 65:375-378.

Farrish, K. W. and D. F. Grigal. 1988. Decomposition in an ombrotrophic bog and a minerotrophic fen in Minnesota. Soil Sci. 145:353-358.

Gorham, E. 1991. Northern peatlands: Role in the carbon cycle and probable responses to climatic warming. Ecol. Applic. 1:182-195.

Heal, O. W. and D. D. French. 1974. Decomposition of organic matter in tundra, pp. 279-309. *In*: A. J. Holding, O. W. Heal, S. F. Maclean and P. W. Flanagan (eds.). Soil organisms and decomposition in tundra. Tundra Biome Steering Committee, Stockholm.

Hogg, E. H., V. J. Lieffers and R. W. Wein. 1992. Potential carbon losses from peat profiles: effects of temperature, drought cycles and fire. Ecol. Applic. 2:298-306.

Ireland, R. R., G. R. Brassard, W. B. Schofield and D. H. Vitt. 1987. Checklist of the mosses of Canada II. Lindbergia 13:1-62.

Johnson, L. C. and A. W. H. Damman. 1991. Species controlled *Sphagnum* decay on a south Swedish raised bog. Oikos 61:234-242.

Johnson, L. C., A. W. H. Damman and N. Malmer. 1990. *Sphagnum* macrostructure as an indicator of decay and compaction in peat cores from an ombrotrophic south Swedish peat-bog. J. Ecol. 78:633-647.

Lieffers, V. J. 1988. *Sphagnum* and cellulose decomposition in drained and natural areas of an Alberta peatland. Can. J. Soil Sci. 68:755-761.

Malmer, N. 1986. Vegetational gradients in relation to environmental conditions in northwestern European mires. Can. J. Bot. 64:375-383.

Malmer, N. and E. Holm. 1984. Variation in the C/N quotient of peat in relation to decomposition rate and age determination with ^{210}Pb. Oikos 43:171-182.

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

Moss, E. H. and J. G. Packer. 1983. Flora of Alberta. University of Toronto Press, Toronto. 687 pp.

Ohlson, M. 1987. Spatial variation in decomposition rate of *Carex rostrata* leaves on a Swedish mire. J. Ecol. 75:1191-1197.

Prentki, R. T., T. D. Gustafson and M. S. Adams. 1978. Nutrient movements in lakeshore marshes, pp. 169-194. *In*: R. E. Good. D. F. Whigham, and R. L. Simpson (eds.). Freshwater wetlands: ecological processes and management potential. Academic Press, New York.

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

Rochefort, L., D. H. Vitt and S. E. Bayley. 1990. Growth, production and decomposition dynamics of *Sphagnum* under natural and experimentally acidified conditions. Ecology 71:1986-2000.

Rowe, J. S. 1972. Forest regions of Canada. Dept. of Environment, Canadian Forestry Services Publication 1300, Ottawa, Ontario.

Santelmann, M. V. 1992. Cellulose mass loss in ombrotrophic bogs of Northeastern North America. Can. J. Bot. 70:2378-2383.

Sikora, L. J. and D. R. Keeney. 1983. Further aspects of soil chemistry under anaerobic conditions, pp. 247-256. *In:* A. J. P. Gore (ed.). Ecosystems of the world 4A, mires: swamp, bog, fen and moor. Elsevier Scientific Publishing Company, New York.

Sjörs, H. 1950. On the relation between vegetation and electrolytes in north Swedish mire waters. Oikos 2:241-258.

Slapokas, T. and U. Granhall. 1991. Decomposition of litter in fertilized short-rotation forests on a low-humified peat bog. For. Ecol. Manag. 41:143-165.

Taylor, B. R., C. E. Prescott, W. F. J. Parsons and D. Parkinson. 1991. Substrate control of litter decomposition in four Rocky Mountain coniferous forests. Can. J. Bot. 69:2242-2250.

Tóth, L. G. and J. Zlinszky. 1989. The importance of self-oxidation in decomposition and its dependence on the pH of the environment. Water, Air, Soil Poll. 46:213-219.

Verhoeven, J. T. A, E. Maltby and M. B. Schmitz. 1990. Nitrogen and phosphorus mineralization in fens and bogs. J. Ecol. 78:713-726.

Verhoeven, J. T. A. and H. H. M. Arts. 1992. *Carex* litter decomposition and nutrient release in mires with different water chemistry. Aquat. Bot. 43:365-377.

Vitt, D. H. 1990. Growth and production dynamics of boreal mosses over climatic, chemical and topographical gradients. Bot. J. Linn. Soc. 104:35-59.

Vitt, D. H., S. E. Bayley, L. Halsey and T. L. Jin. in press. Seasonal variation in water chemistry over a bog-rich fen gradient in continental western Canada. Can. J. Fish. Aquat. Sci.

Zar, J. 1984. Biostatistical analysis. Prentice-Hall, Toronto. 718 pp.

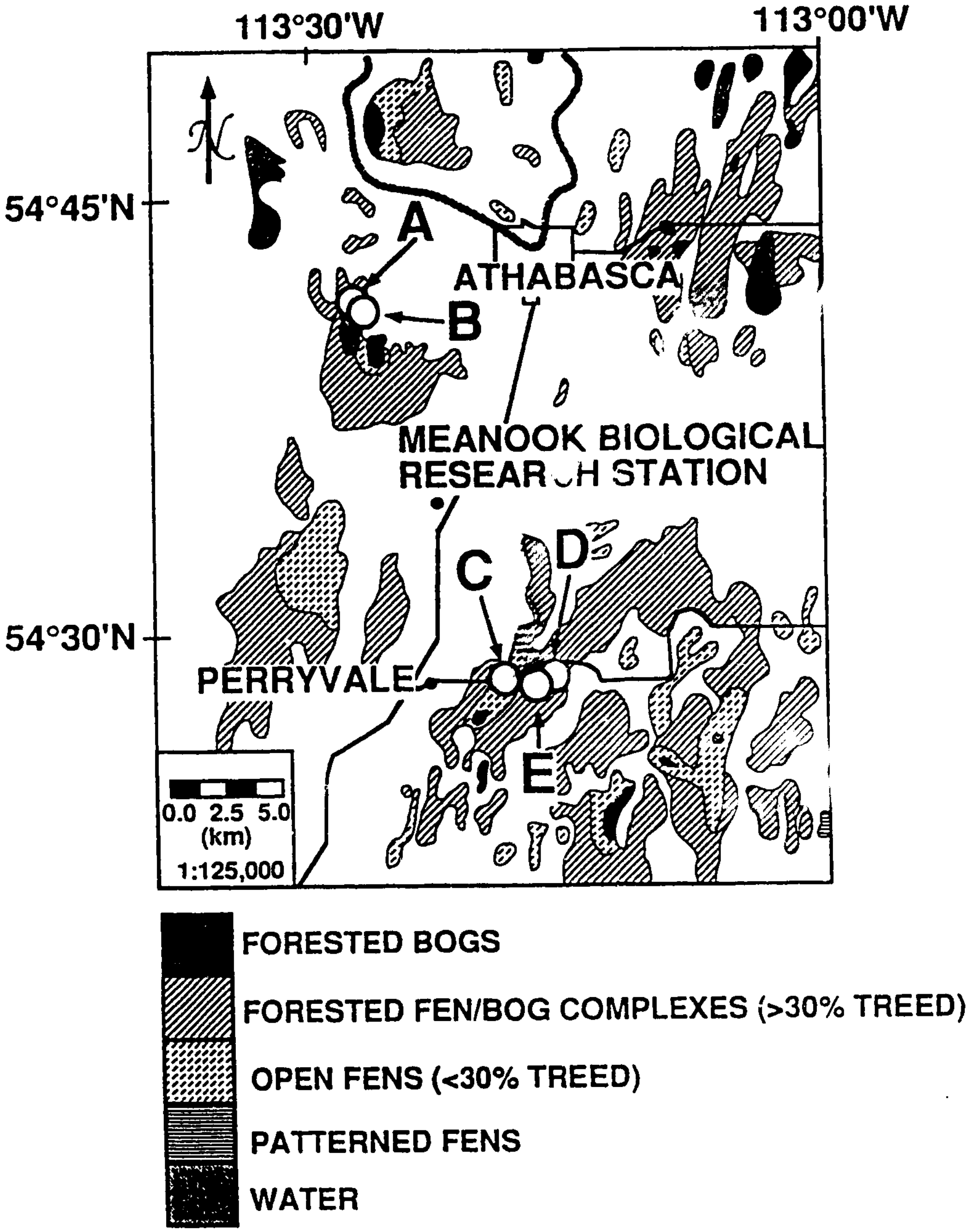


Fig. 3.1. Map of study sites (from Vitt *et al.*, in press). A = bog, B = poor fen, C = sedge fen, D = wooded-rich fen and E = open-rich fen.

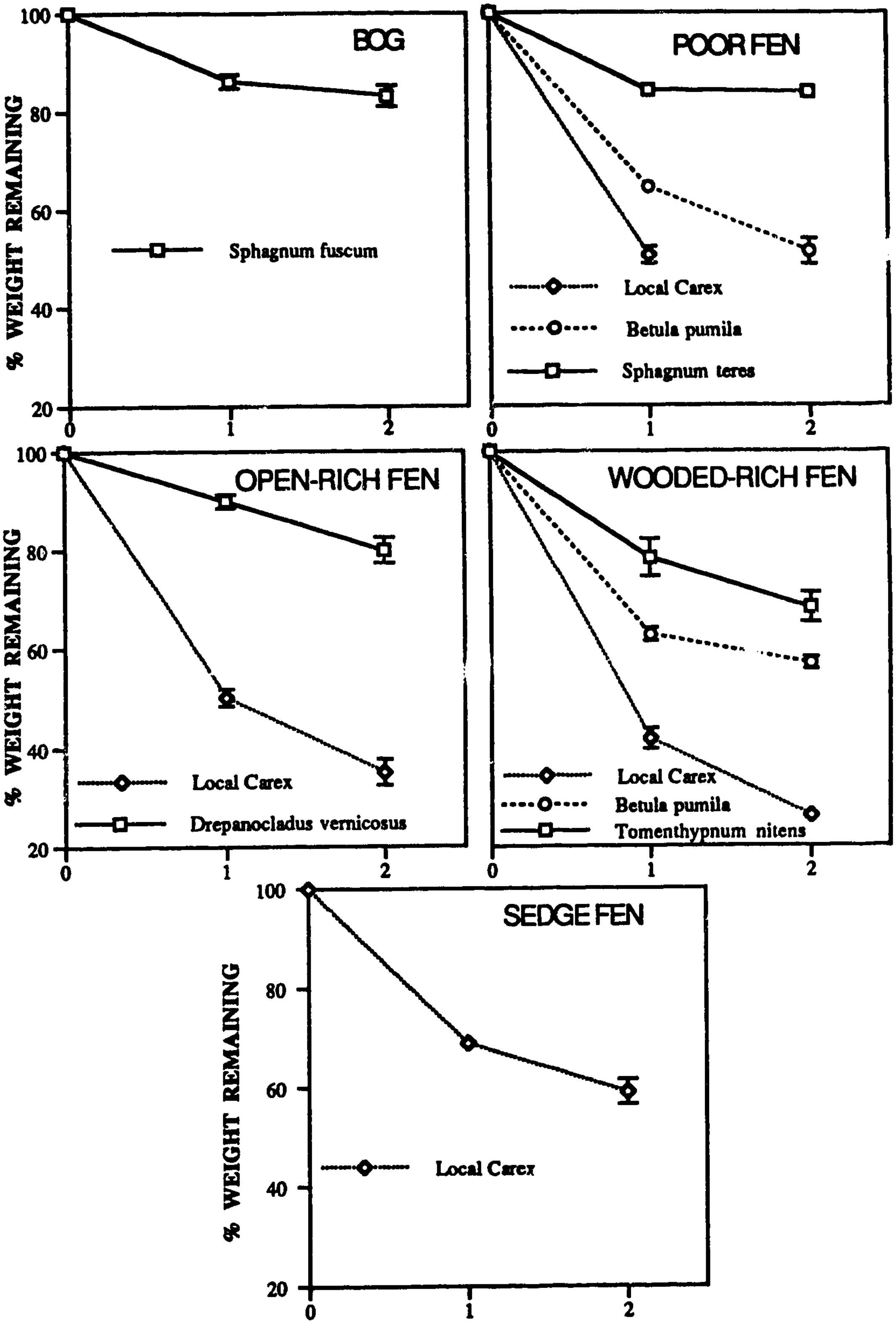


Fig. 3.2: Percent weight loss (mean +/- SE) of the dominant species in five sites over two years. Local *Carex* refers to *Carex* sp. collected on site.

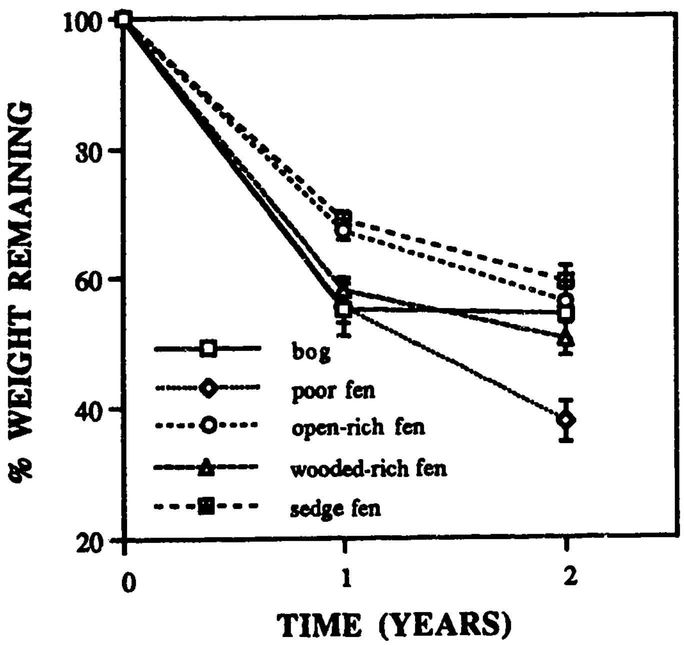


Fig. 3.3: Percent weight loss (mean +/- SE) of *Carex lasiocarpa* litter (used as a standard for cross site comparisons) in five sites over two years.

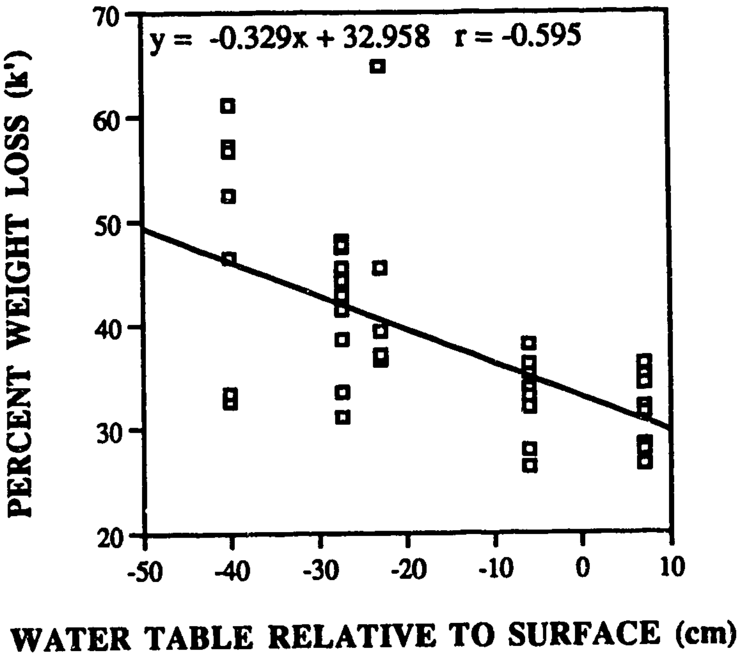


Fig. 3.4: Percent weight loss (k') of *Carex lasiocarpa* litter after one year of incubation in relation to average site water table position relative to moss surface (0 cm) in five peatlands. The sites are bog, wooded-rich fen, poor fen, open-rich fen and sedge fen from left to right.

Table 3.1: Means (ranges) of surface water characteristics at five sites. Chemical parameters were measured monthly during the 1991 (n = 5) and 1992 (n = 6) ice-free seasons. *Open-Rich Fen measured in 1991 only, **depth of oxidation determined at sites in 1992 only, + = water table was above surface. (SRP = soluble reactive phosphorus, TDP = total dissolved P, TP = total P, DOC = dissolved organic carbon)

parameter	Bog	Poor Fen	*Open-Rich Fen	Wooded-Rich Fen	Sedge Fen
field pH	3.86 (3.39 - 4.22)	4.98 (4.28 - 5.22)	5.82 (5.53 - 6.45)	6.06 (5.68 - 6.57)	6.53 (6.12 - 6.85)
reduced conductivity (us)	-17.9 (-32.8 - 3.8)	18.5 (15.2 -26.5)	22.9 (20.6 - 24.7)	26.3 (17.6 - 40.7)	56.2 (38.0 - 79.2)
Ca2+ (mg/l)	3.97 (2.3 - 5.5)	8.08 (5.2 - 11.7)	10.06 (7.7 - 11.9)	11.62 (8.0 - 22.5)	18.35 (7.2 - 35.8)
Mg2+ (mg/l)	1.36 (0.8 - 2.4)	5.12 (3.4 - 7.9)	4.91 (4.4 - 5.2)	5.13 (3.6 - 6.6)	6.63 (2.3 - 12.2)
Na+ (mg/l)	1.78 (1.3 - 2.3)	2.34 (1.9 - 3.1)	2.24 (1.8 - 3.0)	2.16 (1.8 - 2.5)	4.59 (2.8 - 7.4)
K+ (mg/l)	0.91 (0.3 - 1.4)	1.57 (0.1 - 3.1)	0.47 (0.3 - 0.8)	0.35 (0.1 - 0.7)	1.13 (0.3 - 2.3)
NO3- (ug/l)	8.9 (3.4 - 24.4)	10.6 (2.0 - 30.2)	13.5 (4.1 - 33.3)	8.7 (2.0 - 24.5)	7.1 (3.1 - 14.7)
NH4+ (ug/l)	41.8 (12.2 - 107.5)	20.5 (2.9 - 57.9)	26.0 (0 - 62.8)	19.1 (2.1 - 34.4)	20.7 (1.9 - 67.5)
SRP (ug/l)	16.0 (1.4 - 63.3)	71.7 (1.8 - 166.0)	9.9 (5.0 - 15.4)	24.4 (3.2 - 147.4)	5.55 (0.0 - 16.5)
TDP (ug/l)	56.4 (21.4 - 152.9)	115.9 (33.6 - 193.6)	29.9 (24.7 - 37.5)	49.3 (15.3 - 208.0)	23.2 (10.0 - 36.6)
TP (ug/l)	153.2 (34.3 - 386.8)	191.7 (44.1 - 392.3)	146.4 (37.3 - 466.5)	152.6 (27.5 - 357.2)	120.4 (15.1 - 266.9)
DOC (mg/l)	74.2 (67 - 94)	72.4 (56 - 94)	42.0 (39 - 45)	40.1 (22 - 56)	26.3 (15 - 34)
Water table depth (cm)	42 (33 - 52)	24 (12 - 34)	6 -	29 (13 - 39)	0 (+20 - 16)
**1992 depth of oxidation (cm)	30.5 (19.2 - 43.3)	27.0 (12.7 - 41.0)	- -	23.8 (13.7 - 34.5)	16.4 (0.5 - 31.0)

Table 3.2: Mean (+/- SE) percent carbon and nitrogen and C:N ratios of dominant species from decomposition bags in five peatlands (PF = poor fen, ORF = open-rich fen, WRF = wooded-rich fen and SF = sedge fen) over a period of two years Sample size (n) was three for intial samples and 5-10 for samples removed after one and two years.

		%C	%C	%C	%N	%N	%N	C:N	C:N	C:N
SITE	SPECIES	INITIAL	1 YEAR	2 YEARS	INITIAL	1 YEAR	2 YEARS	INITIAL	1 YEAR	2 YEARS
Bog	*S. fuscum*	34.3 (0.5)	36.7 (0.7)	34.9 (0.4)	0.66 (0.04)	0.66 (0.02)	0.65 (0.02)	52.0 (2.7)	56.3 (2.1)	54.2 (1.6)
PF	*S. teres*	34.7 (0.3)	35.3 (1.1)	34.5 (0.3)	0.78 (0.01)	0.75 (0.03)	0.66 (0.03)	44.3 (0.8)	47.3 (1.8)	52.6 (2.1)
	Carex	35.7 (0.6)	35.9 (0.7)		1.08 (0.02)	1.43 (0.05)		33.0 (1.3)	25.3 (0.6)	
	Betula pumila	41.1	44.1 (2.3)	37.8 (1.6)	0.94	1.28 (0.12)	1.36 (0.09)	44.8	36.6 (3.0)	28.3 (1.2)
ORF	*D. vernicosus*	28.2 (2.2)	34.5 (0.4)	36.1 (1.6)	0.65 (0.08)	0.95 (0.04)	1.09 (0.06)	44.0 (3.0)	37.1 (1.7)	33.5 (1.3)
	Carex	37.8 (0.1)	40.6 (0.8)	39.9 (0.7)	1.10 (0.03)	1.28 (0.06)	1.43 (0.03)	34.4 (1.1)	32.3 (1.4)	28.0 (0.8)
WRF	*T. nitens*	32.4 (1.0)	35.3 (1.2)	31.6 (1.5)	0.67 (0.01)	0.72 (0.04)	0.67 (0.06)	48.4 (1.7)	50.5 (3.1)	48.7 (2.9)
	Carex	36.8 (1.6)	37.6 (0.3)	37.3 (1.4)	1.13 (0.08)	1.34 (0.11)	1.39 (0.13)	32.7 (1.3)	29.9 (2.5)	28.1 (3.2)
	B. pumila	41.2	38.3 (1.0)	41.8 (2.5)	0.94	1.15 (0.05)	1.12 (0.04)	43.9	33.8 (1.3)	37.6 (2.4)
SF	*Carex*	36.8 (5.0)	42.0 (1.4)	41.9 (0.4)	0.76 (0.12)	1.14 (0.08)	1.53 (0.12)	48.6 (2.3)	37.8 (1.5)	28.4 (2.2)

Key to moss genera:
S. = *Sphagnum*
D. = *Drepanocladus*
T. = *Tomenthypnum*

Table 3.3: Coefficients (r) for the correlations of percent weight loss (k') with tissue properties (final and initial %N and C:N) for the dominant litter types in five peatlands (bog, poor fen, open-rich fen, wooded-rich fen, sedge fen). The correlations were performed separately after one and two years of decomposition.

Properties	k' (after one year) r	k' (after two years) r
Initial %N	0.908 ***	0.868 ***
Final %N	0.711 ***	0.710 ***
Initial C:N	-0.786 ***	-0.743 ***
Final C:N	-0.673 ***	-0.704 ***

*** $p < 0.001$

Table 3.4: Mean (+/- SE) percent carbon and nitrogen and C:N ratios of *standard litter from decomposition bags in five peatlands (PF = poor fen, ORF = open-rich fen, WRF = wooded-rich fen, SF = sedge fen) over a period of two years. Sample size (n) was three for initial samples and 5-10 for samples removed after one and two years.

	% C	% C	% C	% N	% N	% N	C:N	C:N	C:N
SITE	INITIAL	1 YEAR	2 YEARS	INITIAL	1 YEAR	2 YEARS	INITIAL	1 YEAR	2 YEARS
Bog	36.8 (5.0)	38.5 (1.6)	37.4 (0.8)	0.76 (0.12)	1.16 (0.06)	1.14 (0.05)	48.6 (2.3)	33.5 (1.8)	33.1 (2.0)
PF	36.8 (5.0)	39.0 (0.8)	36.6 (0.8)	0.76 (0.12)	1.29 (0.12)	1.24 (0.03)	48.6 (2.3)	31.5 (3.2)	29.8 (0.8)
ORF	36.8 (5.0)	39.7 (1.3)	44.4 (1.9)	0.76 (0.12)	1.10 (0.05)	1.33 (0.06)	48.6 (2.3)	36.4 (1.5)	33.5 (1.0)
WRF	36.8 (5.0)	38.5 (0.4)	38.3 (1.8)	0.76 (0.12)	1.03 (0.05)	1.27 (0.08)	48.6 (2.3)	38.2 (1.8)	30.6 (1.0)
SF	36.8 (5.0)	42.0 (1.4)	41.9 (0.4)	0.76 (0.12)	1.14 (0.08)	1.53 (0.12)	48.6 (2.3)	37.8 (1.5)	28.4 (2.2)

**Carex lasiocarpa*

Table 3.5: Coefficients (r) for the correlations of first year percent weight loss (k') of standard litter type(1) with mean site water level relative to surface and various surface water parameters for 1991 in five peatlands (bog, poor fen, open-rich fen, wooded-rich fen and sedge fen).

Parameter	r	p
Water level	-0.60	***
pH	-0.48	**
Reduced conductivity	-0.50	***
Ca^{2+}	-0.47	**
Mg^{2+}	-0.47	**
Na^+	-0.48	**
DOC	0.51	***
K^+	0.04	n.s.
SRP	0.29	n.s.
TDP	0.42	**

DOC = dissolved organic carbon
SRP = soluble reactive phosphorus
TDP = total dissolved phosphorus
(1) = Carex lasiocarpa

n.s. $p > 0.05$
** $0.01 > p > 0.001$
*** $p < 0.001$

4. NET ABOVE GROUND PRIMARY PRODUCTION IN PEATLANDS OF CENTRAL ALBERTA IN RELATION TO WATER LEVEL, SURFACE WATER CHEMISTRY AND PEAT ACCUMULATION POTENTIAL

Introduction

Peatland systems are important to the global carbon cycle because they sequester large amounts of carbon (Gorham, 1991). Forestry Canada (1992) estimates that peatlands account for 60% of all organic carbon stored in Canada. The accumulation of organic carbon in these systems is the result of an imbalance between two processes: net primary production (NPP) and decomposition. It is generally believed that a reduced rate of decomposition, rather than an accelerated rate of production, is responsible for the peat accumulation in these wetlands (Clymo, 1965; Malmer, 1986; Farrish and Grigal, 1988; Vitt, 1990). However, few studies have examined the relative rates of total organic matter production and decomposition simultaneously (Reader and Stewart, 1972; Bartsch and Moore, 1985; Moore, 1989b).

The environmental controls (climate, hydrology, nutrient inputs, etc.) of plant growth and decay (see Chapter 3) are poorly understood (Gorham, 1982). Reader (1978) and Richardson (1978) also emphasized the scarcity of research relating total production to environmental parameters such as hydrology, soil and water chemistry and climate. Forrest and Smith (1975) and Moore (1989b) related NPP of mires to water levels, while other authors have stressed the relationship between nutrient availability and production in peatlands (Reader, 1978; Brinson *et al.*, 1981; Bartsch and Moore, 1985; Grigal *et al.*, 1985; Backéus, 1990). The three most important elements that have been found to limit plant growth in peatlands are N, P and K (Reader, 1978). Climate has also been shown to have an important influence on production in wetlands (Gorham, 1974; Damman, 1979; Droste, 1984).

Most peat accumulation studies have focused on bogs (e.g. Aaby and Tauber, 1974; Clymo, 1978), which are ombrotrophic systems that receive nutrient inputs from precipitation only. Research comparing the relative peat accumulation rates between bogs and fens (minerotrophic systems "fed" by ground water as well as precipitation) is scarce (Walker, 1970). Minerotrophic mires can be further divided into poor (*Sphagnum* moss-dominated) and rich (brown moss-dominated) fens. Bogs are reported to generally have greater peat accumulation rates than fens (Malmer, 1986; National Wetlands Working Group, 1988), however, Reader and Stewart (1972) found that a minerotrophic peatland (lagg) had a greater peat accumulation rate than an ombrotrophic site (muskeg) in Manitoba. These results (52 vs. 27 $g/m^2/yr$) were based on long term average rates and not direct measurements of production/decomposition. A shorter term investigation based on amount of original litter remaining after one year of decomposition suggested that their bog site had a greater peat accumulation potential than the lagg.

One objective of this paper is to relate the above ground production of the various strata in five peatlands, representing the bog-rich fen gradient (see Chapter 2; Vitt *et al.*, in press), to environmental parameters such as water level, water chemistry and climate. The hypothesis is that the sites with the highest water levels will be more productive due to greater water and nutrient availability. A second objective is to estimate relative amounts of above ground peat accumulation along this gradient. My hypothesis is that the above ground peat accumulation potential will decrease along the bog-rich fen gradient because decomposition rates will increase relative to production rates.

Study area and site descriptions

Five sites were chosen to represent the bog-rich fen gradient of peatlands present in the central Alberta area. The sites sampled include a bog, poor fen (PF), wooded moderate-rich fen (WRF), open-rich sedge fen (SF) and an extreme-rich fen (ERF). The bog and poor fen are located north of Bleak Lake, Alberta at 54° 41' N and 113° 28' W, while the wooded-rich fen (54° 28' N, 113° 17' W) and sedge fen (54° 28' N, 113° 20' W) are located east of Perryvale (Fig 4.1). The extreme-rich fen is located south of Calahoo at 53° 42' N and 113° 57' W.

The climate of the area is characterized by mild summers and cold, snowy winters (Vitt *et al.*, in press). The long-term mean annual temperature (Environment Canada, 1982) is 1.7 °C for the first four sites (average of two weather stations: Meanook and Athabasca 2) and 2.2 °C for the extreme-rich fen (average of four surrounding weather stations). The total mean annual precipitation is about 500 mm for all sites. Climate data for the growing seasons of 1991 and 1992 compared to the long-term average are summarized in Appendix 1. All study sites are located within the Boreal Forest Region of Canada (Rowe, 1972). Descriptions of the vegetation and water chemistry are also in Vitt *et al.* (in press) for the first four sites and in Rochefort (1987) for the extreme-rich fen. A more complete listing of the composition of the herb and shrub taxa at each site can be found in Appendices 2 and 3. Moss nomenclature follows Ireland *et al.* (1987) while that of vascular plants follows Moss and Packer (1983). Cover values of the dominant species at each site were estimated in 10 by 10 m plots.

General descriptions of the sites are as follows:

Bog

This site is a large, raised ombrotrophic island within a peatland complex bordered by a poor fen water track. The peat surface is raised about 0.3-0.5 m above the associated water track, and is composed of large, dry hummocks separated by a few wetter hollows. This site was further divided into an open bog (OB) and wooded bog (WB). The only difference between these sites is that there is a sparse tree layer of small *Picea mariana* (Mill.) BSP. covering about 25% of the wooded bog. The moss layer is dominated by *Sphagnum fuscum* (Schimp.) Klinggr. with a cover of about 90%. The bog had the lowest surface water pH (see methods) of all the sites (3.4-4.2) and an average peat depth of 5 m (determined by steel rod).

Poor Fen

This fen is a water track adjacent to the bog island. The poor fen has a hummocky microtopography and is wetter than the bog, with open water usually present in some areas during the ice-free season. This site has a well developed shrub layer of *Betula pumila* L. var. *glandulifera* Regel. (40% cover) and *Salix pedicellaris* Pursh (20%). The ground layer has a *Sphagnum* cover of about 90% with *S. teres* (Schimp.) Aongstr. ex C. Hartm. and *S. angustifolium* (C. Jens. ex Russ.) C. Jens in Tolf, the most common species. The surface water pH varied between 4.3 and 5.2 during the study period, while the peat layer was about 4 m thick.

Wooded-Rich Fen

This site forms the grounded, forested fen adjacent to a floating mat fen which surrounds a small open pond. The peat surface consists of large hummocks and wet lawns, with pools of water present during much of the season. This moderate-rich fen has an open tree canopy dominated by *Larix laricina* (Du Roi) K. Koch (25% cover). The ground layer is brown moss-dominated with *Tomenthypnum nitens* (Hedw.) Loeske covering about 75% of the study area. Surface water pH ranged between 5.7 and 6.6 and the peat averaged 4.5 m in depth.

Sedge Fen

This site is situated in a former north-south drainage channel that presently contains several large bodies of open water, separated by large expanses of sedge-dominated wetlands. The microtopography is mainly flat with a few isolated, small hummocks constituting less than 5% of the surface. The site was inundated with water for most of 1991, and therefore has characteristics of a marsh, but began to dry out during the 1992 season. Vitt *et al.* (in press) designated this site as an extreme-rich fen and it is probably transitional between a moderate- and extreme-rich fen. The vascular plant vegetation is almost completely sedge-dominated with *Carex lasiocarpa* Ehrh. and *C. diandra* Schrank the two most important species. The moss layer is discontinuous covering only about 75% of the surface. *Drepanocladus aduncus* (Hedw.) Warnst. (65%) is the dominant moss species, forming mats at the bases of sedge plants. The pH of the water ranged between 6.1 and 6.9, while the peat layer was 2-2.5 m thick.

Extreme-Rich Fen

This small, open, spring-fed fen consists of strings alternating with flarks. Open marl ($CaCO_3$) ponds cover about one third of the site and were not included in the study. The dominant species, the sedge *Scirpus cespitosus* L., covers about 50% of the study area. The insectivorous *Drosera rotundifolia* L. and *D. anglica* Huds. are also important components. The moss layer follows the typical sequence for extreme-rich fens in Western Canada (Vitt 1990). From pools to dry hummock this sequence is: *Scorpidium scorpioides* (Hedw.) Limpr. - *Drepanocladus revolvens* (Sw.) Warnst. - *Campylium stellatum* (Hedw.) C. Jens. - *Tomenthypnum nitens*. Together these species make up 95% of the ground layer with *C. stellatum* (55%) the most important. Surface water pH was high (7.8-8.4) and the average peat depth was 2.5 m.

Methods

Water chemistry

Measurements of surface water pH and temperature were done in the field monthly using a Beckman pH meter and thermometer.

Water samples for laboratory analysis were collected concurrently. As much as possible, the readings and samples were collected from the same locations (holes dug in the peat) within each site. Conductivities were measured in the lab within 24 hours of collection and corrected for pH and standardized to 20 °C (Sjörs, 1950).

Chemical analyses of water samples follow the methods of Vitt *et al.* (in press). All samples were filtered initially with glass fibre (GFC) filters. Base cations (Ca^{2+}, Mg^{2+}, Na^+, K^+) were fixed with 0.5 ml of concentrated HNO_3 and analyzed with a Perkin-Elmer Atomic Absorption Spectrometer. Sulfate (SO_4^{2-}) and Cl^- were analyzed with a Dionex Ion Chromatograph. Nitrate (NO_3^-), soluble reactive phosphorus (SRP) and total dissolved phosphorus (TDP) samples were refiltered with a 0.45 µm millipore (HAWP) filter. Water samples for NO_3^- and NH_4^+ were analyzed on a Technicon Auto Analyser II within 24 hours of collection. Total phosphorus (TP), SRP and TDP were measured by the methods of Bierhuizen and Prepas (1985). The ratios of inorganic N to inorganic P (N:P) were calculated by dividing the sum of NO_3^- and NH_4^+ by SRP for each sample. The N and P values were first converted from µg/l to µeq/l following the methods of Hem (1970). Alkalinity was analyzed by an electrometric titration technique using the phenolphthalein technique (Environment Canada, 1979). Dissolved organic carbon (DOC) was measured with a Model 1505 Programmable Carbon Analyser.

Water levels

Water level fluctuations were monitored at each site with Steven's F water level recorders and manually with permanently attached meter sticks during most of the ice-free season. Water level measurements in the extreme-rich fen site were only taken in 1992, not in 1991. The average water level relative to the moss surface at each site was determined by calculating the mean of the daily water table depths for each growing season. The daily water table depth was defined as the relative position of the water table at approximately noon each day.

Depth of oxidation

Measurements of oxidation depth followed the methods of Bridgham *et al.* (1991). Steel welding rods (one meter in length) were placed in the sites in June 1992. A total of 8 rods (4 in hummocks and 4 in hollows) were inserted into the peat of each site exposing only the top 20 cm of the rod. Due to the diversity of microtopography at the ERF, 12 rods were placed into the peat (4 in strings, 4 in lawns and 4 in carpets). One rod per microhabitat per site was removed at monthly intervals and the depth of solid rust relative to the peat surface was measured. Depth of oxidation was determined by averaging site microhabitats and all 4 measurements from July to October.

Production measurements

Detailed explanations of the methods used in the production measurements for the moss, herb, shrub and tree strata and litter are in Chapter 2.

Moss growth and production were measured in 1991 and 1992 by the cranked wire method of Clymo (1970) in all sites except the sedge fen. Moss production was determined in the sedge fen by harvesting the live moss mat in quadrats and then estimating the new growth by innate markers.

Herb and shrub production were measured by the clipped quadrat method in the same randomly placed 50 cm by 50 cm (0.25 m^2) quadrats in 250 m^2 plots adjacent to those used to measure moss production. Harvest periods were in late June, late July and late August in 1991 and 1992.

Tree biomass and production (biomass increment) were estimated in the wooded bog and wooded-rich fen using the regression equations in Table 2.3 (Chapter 2). Tree radial growth was measured with a Digimic machine. Amounts of annual tree litter fall were added to biomass increments to arrive at total above ground tree production figures.

Shrub and tree litter fall were measured in circular litter traps placed randomly in plots adjacent to the vascular plant plots. Litter production was measured over a one year period from May 1992 to May 1993.

Statistical analyses

Major nutrient (N, P and K) ion concentrations in the surface water were tested with a randomized-block ANOVA (site and year as factors). Paired t-tests were used to test for differences in water levels at sites and radial increment in trees between 1991 and 1992.

Simple correlations were done between August herb and terminal shrub biomass (both square root-transformed) and between each of these strata and mean site water level and chemical parameters. These correlations were performed separately for 1991 and 1992 data.

Statistical analyses were performed with SYSTAT version 5.2.1.

Decomposition measurements

Methods for determining decomposition rates are described in detail in Chapter 3. Percent of original weight lost (k') of the dominant species was measured using 2.5 x 2.5 cm, nylon, 1 mm mesh bags placed just below the surface at the sites in October 1990 and retrieved one or two years later.

The total site decay rates (percent weight loss) of above ground litter were estimated in the bog, poor fen, wooded-rich fen and sedge fen by combining the production and decomposition data. Total moss production values from each site were used to estimate moss litter, while *Carex* litter was estimated from minimal seasonal production (see Chapter 2). Minimum seasonal production was used because it was believed to be a better estimate of the *Carex* litter present at the end of the growing season than peak standing crop, which would tend to over-estimate the litter. *Betula* litter production in the poor and wooded-rich fens was estimated from the annual amount measured in the litter traps. The moss, *Carex* and *Betula* accounted for 73-84% of the total annual above ground litter produced in the sites and were designated as the "measured litter types" because their decomposition rates were calculated (see Chapter 3 for more details). The total site decay rate was determined by dividing the sum of the absolute amount of weight lost (g/m^2) from the measured litter types (after one or two years of decay) by the sum of the litter production (g/m^2/yr) of the measured litter types. This figure was then multiplied by 100 to arrive at percent weight loss. The weight loss of the remaining 16-27% unmeasured litter at each site was estimated using the total site decay rate based on the measured species (*cf.* Reader and Stewart, 1972).

Since the poor fen local *Carex* was not removed in 1992 the *C. lasiocarpa* standard k' (see Chapter 3) was used instead to estimate local *Carex* decomposition after two years, as the two litter types had similar k' values after one year in this site.

Peat accumulation potential measurements

Production/decomposition ratios were determined by dividing average total site above ground NPP ($g/m^2/yr$) by the absolute amount of weight lost ($g/m^2/yr$) from the original tissues after one year of decomposition, as estimated from the total site decay rate.

The weights (g/m^2) of original litter remaining after one and two years of decomposition were also determined from the site decay rates. The absolute amount of litter decomposed (g/m^2) was subtracted from the original weight of litter produced to arrive at the absolute amount of above ground litter remaining (g/m^2) after both one and two years of decay.

Results and discussion

Environmental characteristics of the sites

The pH, reduced conductivity, alkalinity, Ca, Mg and Na of the surface water all increased along the bog-rich fen gradient (Table 4.1). The major nutrient ions (N, P and K) did not show the same trend. Potassium concentrations were significantly different between sites and highest in the ERF and lowest in the WRF. Although the bog appeared to have a higher mean NH_4^+ concentration than the rest of the sites, surface water concentrations of both NO_3^- and NH_4^+ did not differ significantly between sites ($p > 0.05$). Nitrate was the only major nutrient ion to show a significant difference in concentration between years ($p < 0.01$) and was greater in 1991 than 1992. All determinations of P differed significantly between sites ($p \leq 0.05$), with the poor fen having the highest concentrations of SRP, TDP and TP. The sedge fen had the lowest SRP and the extreme-rich fen had the lowest TDP and TP. The poor fen and the wooded-rich fen had the lowest N:P ratios, while the sedge fen and the bog had the highest. The extreme-rich fen and bog were the only sites to have any measurable quantities of SO_4^{2-}, with the ERF having much greater concentrations. Chloride ion (Cl^-) concentrations also showed no distinct trend along the gradient and were greatest in the WRF and lowest in the bog. Dissolved organic carbon (DOC) decreased along the bog-rich fen gradient. Surface water temperature increased along the gradient.

A more detailed study of annual and seasonal fluctuations in the water chemistry of these sites is found in Vitt *et al.* (in press).

Water table height (Figs. 4.2 and 4.3) was lowest in the bog and highest in the sedge fen and sites tended to become wetter along the bog-rich fen gradient. All sites were significantly wetter during the growing season of 1991 than 1992. Depth of oxidation followed the same basic trend as water levels with the drier sites generally having a deeper mean depth of rust (Table 4.1).

Moss production in relation to environmental factors

All sites (excluding the sedge fen) had similar moss production averages, ranging from 123 to 167 g/m^2/yr (Fig. 4.4). The sedge fen had the lowest moss NPP (43 g/m^2/yr). This site was the wettest of all the peatlands and was inundated for most of the first year and part of the second (Figs. 4.2 and 4.3). Water levels rose rapidly in the spring of 1991 and peaked at 20 cm above the surface on July 1st and then declined steadily over the rest of the season and the next year to a minimum of 16 cm below the surface at the end of October 1992. Laitinen (1990) suggested that flooding coupled with a drop in water level and desiccation results in poor moss cover and low bryophyte production.

Moss production in all sites was greater in 1991 than 1992 (Fig. 2.2 in Chapter 2). Water levels in all sites were also significantly higher in 1991, averaging 2-3 cm more in the first year in most peatlands. The SF was an average of 14 cm higher during the first year. Brock and Bregman (1989) also found a correlation between a high water table and *Sphagnum* growth and production, while Wieder and Lang (1983) and Backéus (1988) discussed the desiccation of *Sphagnum* associated with low water levels. Forestry experiments in which peatlands were drained have also resulted in reduced vigour and production of both sphagna and brown mosses (Vasander, 1982; Hillman *et al.*, 1990).

Even though moss production was greater in the sites during the wetter year (1991) compared to the relatively dry year (1992), there was no evidence of increased production in the sites with higher water levels compared to drier sites. Several authors have found greater moss production in wet sites or microhabitats such as lawns and pools as opposed to dry hummocks (Forrest and Smith, 1975; Vitt and Pakarinen, 1977; Hulme and Blyth, 1982; Wallén *et al.*, 1988; Moore, 1989a). However, Bartsch and Moore (1985) and Vitt (1990) reported that moss NPP on hummocks was greater than or equal to that of hollows in poor and rich fens.

Correlations have also been made between moss production and precipitation (Backéus, 1988; Moore, 1989a; Vitt, 1990).

Although water levels were higher at the bog, PF, WRF and SF in 1991, this trend was not reflected in the precipitation records from the nearby Athabasca weather station (Appendix 1). Total precipitation at Athabasca was very similar during the May-October period in 1991 (313 mm) and 1992 (317 mm) but was much greater at the ERF in 1991 (372 mm) versus 1992 (220 mm). Backéus (1988) states that the timing of precipitation may be more important than the total amount of precipitation. He found correlations between *Sphagnum* growth and total June precipitation and number of days in June with precipitation. The Alberta data also appear to support this relationship between moss growth and June precipitation. Rainfall in June (Appendix 1) was much higher in 1991 (100 mm at Athabasca; 98 mm at the extreme-rich fen) than in [illegible] (55 mm at Athabasca; 21 mm at the ERF). There were also mo[illegible] in June with precipitation at Athabasca and the ERF i[illegible]91 than in 1992.

Moss production has also been correlated with air temperature in peatlands (Brock and Bregman, 1989; Moore, 1989a). Wieder and Lang (1983) found that *Sphagnum* production generally increases with decreasing latitude while Moore (1989a) correlated *Sphagnum* production with mean annual temperature. Higher mean temperatures (11.9 °C) from May to October and more growing degree days (1467) were observed in 1991 than the same period in 1992 (10.8 and 1208 respectively). Therefore, temperatures were probably more favourable for moss growth during the first year.

Several studies have also shown that moss growth in peatlands may be N- or P-limited (Brock and Bregman, 1989; Malmer, 1990; Rochefort *et al.* 1990; Vitt, 1990; Aerts *et al.* 1992). Although the effects of nutrients on moss growth were not directly tested in this study, surface waters were regularly monitored for N and P (Table 4.1). There was no significant difference in levels of either NO_3^- or NH_4^+ between sites but there was significantly ($p < 0.01$) more NO_3^- present in the surface waters in 1991 than in 1992. This difference in NO_3^- was two-fold and corresponded with the greater moss production at all sites in the first year.

Herb production in relation to environmental factors

There was much greater variation in herb than moss production between sites. Average above ground herb production ranged from 11-12 $g/m^2/yr$ in the bog to 163 $g/m^2/yr$ in the sedge fen (Fig. 4.4).

Maximum biomass of herbs correlated positively with water level, pH, reduced conductivity, Ca, Mg and Na and negatively with

DOC (Table 4.2). Herb production was not correlated with K or P except in 1992 when there was a weak negative correlation with surface water levels of TDP. Most of these parameters are strongly correlated with each other. For instance, most base cations and conductivity are related to the pH gradient (Malmer, 1986; Vitt *et al.*, in press), while DOC is negatively correlated with this gradient.

Water level is the most consistent parameter that correlates with herb production (Fig. 4.5). One explanation of this relationship between herb growth and site wetness is that herbs (especially sedges such as *Carex lasiocarpa*) appear to be more tolerant of flooding and desiccation than species of shrubs (Laitinen, 1990). These conditions were most prevalent at the SF and ERF, the sites with greatest herb production. Further evidence of the importance of water level is apparent in the annual comparisons of herb NPP at the sedge fen (Fig. 2.3). A drop of 14 cm in mean water level from 1991 to 1992 at the SF corresponded with a 40% reduction in peak herb standing crop from 203 to 122 g/m.

Drainage experiments on peatlands have also resulted in reduced cover and production of sedges and other herbs (Vasander, 1982; Hillman *et al.*, 1990). Similar relationships between water level and herbaceous growth have been demonstrated in other wetland types. For example, Lieffers and Shay (1982) related the standing crop of the sedge *Scirpus paludosus* A. Nels. to mean water depth in prairie saline marshes and Richardson (1978) reported that the extremely productive northern *Typha* and *Scirpus* marshes were generally present in areas of deeper standing water than the less productive *Carex* marshes.

There were no relationships between nutrient concentrations in the surface water and herb peak standing crop (Table 4.2), except for one very weak negative correlation (TDP in 1992). Similarly, Vermeer and Verhoeven (1987) found no correlations between biomass and N, P or K in the soil of herb-dominated mesotrophic fens in the Netherlands. However, they and Verhoeven *et al.* (1983) did find a positive correlation between shoot biomass and the amounts of N, P and K within the vegetation. These two studies also demonstrated that N and to a lesser extent P were limiting to herb production in Dutch mesotrophic fens. Wheeler and Shaw (1991) have also suggested that herbaceous growth in rich fens may be limited by P, while Vasander (1982) reported that fertilization with N, P and K increased the production of the sedge *Eriophorum vaginatum* L. in hollows in a Finnish bog.

Substantial relationships between surface water nutrient concentrations and herb biomass may not have been found because differences in production may be related more to rates of N and P mineralization than amounts of nutrients measured in the water (Verhoeven *et al.*, 1983; Koerselman *et al.*, 1990). Rate of nutrients supplied per unit time by flowing water may be more important than the concentration and competition may also obscure the effects of purely chemical factors (Gorham, 1950).

Temperature is also an important factor influencing herbaceous production. For instance, Gorham (1974) related *Carex* production to summer temperature while Droste (1984) correlated *Carex gracilis* CURT. standing crop with growing degree days. Bernard and Gorham (1978) also found that the above ground NPP of sedge wetlands in North America declines with increasing latitude. In all the sites, except the bog, peak herb standing crop was greater in the warmer year (1991). This year also had higher water levels than 1992, therefore, it is difficult to draw conclusions about the influence of temperature on herb growth in this study.

Shrub production in relation to environmental factors

Shrub production also varied greatly between sites ranging from 6 $g/m^2/yr$ in the extreme-rich fen to 134 $g/m^2/yr$ in the poor fen (Fig. 4.4).

In contrast to herb production, shrub terminal production was negatively correlated with water level, pH, conductivity, Ca, Mg and Na and positively correlated with DOC for both years (Table 4.2). Shrub production was also positively correlated with concentrations of P (SRP, TDP and TP) in the surface waters. The only parameter to show a different relationship in both years was K which had no relationship in 1991 but a significant negative correlation in 1992.

As further evidence of the contrasting responses of herbs and shrubs, correlations were also performed between the August herb biomass and shrub terminal biomass (leaves and current year's stem growth) present in the clipped quadrats (Fig. 4.6). There was a significant negative correlation between the two strata in both 1991 ($r = -0.70$, $p < 0.001$) and 1992 ($r = -0.72$, $p < 0.001$).

Water level appeared to be the most consistent parameter measured that correlated (negatively) with shrub production over the two years (Fig. 4.7). The two wettest sites (SF and ERF) had minimal shrub cover and therefore low shrub biomass and production. In the three sites with substantial shrub cover (bog, PF and WRF) shrub production was also higher in the year with lower water levels (1992), however, these differences were not significant.

In a subarctic fen, Moore (1989b) also measured very low shrub production and biomass in pools and flarks as opposed to strings which had much greater shrub cover than the former habitats. Vasander (1982) and Hillman *et al.* (1990) both found increased shrub growth in peatlands after drainage. Vasander (1982) found draining increased the dwarf shrub layer but had no significant affect on the tall shrub/small tree layer. Hillman *et al.* (1990) reported diminished cover and vigour or no change for ericaceous shrubs but an increase in growth for deciduous shrubs. Some dwarf shrubs such as *Andromeda polifolia* L. are reported to be as productive in hollows as on hummocks while others such as *Vaccinium* spp. generally grow better on hummocks (Backéus, 1985).

There are very few studies relating shrub production to mineral or nutrient levels. The negative correlation of shrub growth in the peatlands with the pH-related characteristics appears to contradict the findings of Reader (1982), who found an increase in ericaceous shrub production in sites with greater conductivities. These contrasting results may be due to the different methods of measurement used in each study. Reader (1982) measured production as mg/shoot while this study used g/m^2. In both studies, water level and pH characteristics are correlated so that interpretations separating these parameters are difficult to make.

The positive relationship between shrub production and concentration of P in the surface water suggests that nutrients levels may play an important role in shrub growth. These results are supported by Vasander (1982), who found that the biomass of both dwarf and tall shrubs increased with N, P and K fertilization in a Finnish bog. Correlations of shrub growth with N were not performed in the Alberta study because there were no significant differences in surface water concentrations of NO_3^- or NH_4^+ between sites.

The interpretation of these shrub production correlations are also further complicated by different rates of water flow and mineralization at the sites and by competition of shrubs with other strata. The successional status of a site may also be an important factor influencing shrub biomass and NPP.

Tree production in relation to environmental factors

Well-developed tree layers were only present on the wooded bog and wooded moderate-rich fen and only made a minor contribution to the total production of each (Fig. 4.4). Total above ground estimated tree production was similar in the wooded bog (54 g/m^2/yr) and wooded-rich fen (44 g/m^2/yr) despite the difference in dominant tree species. These two forested peatlands had the lowest water tables (Figs. 4.2 and 4.3) and also had relatively deep oxidation depths (Table 4.1) compared to the other sites. At both sites radial increments were greater in the dry year (1992) than the wet year (1991). These differences were only significant for the *L. laricina* ($p < 0.001$) sampled in the wooded-rich fen and not for the *P. mariana* from the bog ($p > 0.05$).

These results suggest that site dryness and aeration are important factors determining tree growth on peatlands. Tilton (1978) reported that *L. laricina* generally grew better in peatlands that were drier in Minnesota and suggested that this may be due to better aeration and nutrient cycling. Hillman *et al.* (1990) also demonstrated significant increases in *P. mariana* growth with drainage in a Northern Alberta wetland, while Jeglum (1974) found decreased growth in this species in wetter and poorly aerated wetlands in Northern Ontario.

Nutrient availability is also important for tree growth in peatlands. Tilton (1978) found *L. laricina* to be more productive in "nutrient-rich" fens than "nutrient-poor" bogs and correlated growth with foliar concentrations of N and P. Vasander (1982) reported large increases in biomass and production of *Pinus sylvestris* L. with application of N, P and K on a Finnish raised bog.

Succession and competition may also be important factors influencing tree growth and production on peatlands. The scarcity of trees on the open bog compared to the wooded bog could not be explained by differences in water levels or understory growth as these were similar in the two sites. The most plausible explanation is that *P. mariana* had not yet become established at the open site, but may in the future, as some small seedlings were observed in this area. The relative lack of *P. mariana* trees on the driest hummocks in the poor fen may be due to competition from *Betula* and *Salix* that dominate the thick shrub layer there.

Total production in relation to environmental factors

Total average above ground NPP ranged between 214 and 360 $g/m^2/yr$ for the peatlands (Fig. 4.4), with the highest production in the wooded-rich fen and the lowest production in the sedge fen. The poor fen had the second highest average NPP (310 $g/m^2/yr$) followed by the wooded bog (295 $g/m^2/yr$), open bog (265) and extreme-rich fen (245).

The total NPP of the sites could not be correlated with any single environmental factor. While this could be due to the variety of methods used for the estimation of production, it is more reasonably accounted for by differential responses of strata to the same environmental factor. Herbs and shrubs, for example, responded oppositely to water level, obscuring the correlation for total vascular plants with this environmental factor.

The WRF had intermediate levels of almost all characteristics measured (e.g. pH, nutrients, oxidation depth), however, it had the highest estimated above ground production of all sites. The WRF's total production was shared among four well-developed strata (see Fig. 4.4). The peatlands with relatively extreme environments (e.g. the open bog or sedge fen) possessed only one or two well-developed strata. The presence of many productive strata may be an efficient means of exploiting resources for ecosystem NPP.

Other studies support the higher total production at the WRF. Lucas and Davis (1961) found that the optimal pH for nutrient availability in organic soils was 5.5 to 5.8 which is probably similar to the soil pH of the wooded-rich fen. Vitt (1990) reported that moderate-rich fens have greater amounts of organic N in the surface water than do other peatlands in Alberta. Vitt *et al.* (in press) also found greater concentrations of P in the surface water and deeper water (1.0-1.5 m) and NH_4^+ in the deeper water at the WRF compared to the bog, poor fen or sedge fen. However, my data showed surface water concentrations of P to be the highest in the poor fen which was the second most productive site. Concentrations of nutrients measured in the water may be less important than rates of supply through water movement and mineralization.

Even though ombrotrophic systems are known to be nutrient deficient and unproductive (Vasander 1982; Backéus, 1990), my results suggest that bogs can be just as or more productive than some fens. Similarly, Francez (1992) found no significant difference in NPP between a bog and fen and attributed this to efficient recycling of N from the biomass in the bog. My bog sites actually had greater average NPP than the sedge fen and the ERF. Other authors (Malmer, 1986; Boyer and Wheeler, 1989; Wassen *et al.*, 1990; Wheeler and Shaw, 1991) have suggested that some extreme-rich fens may be limited by P. The ERF, which had relatively low production, also had low levels of TDP and TP accompanied by an abundant cover of insectivorous plants (*Drosera rotundifolia, D. anglica, Utricularia intermedia* Hayne). These plants generally indicate low nutrient availability (Dickinson, 1983). The sedge fen, which was the least productive of all sites, also had low concentrations of surface water P (especially SRP). Wassen and

Barendregt (1992) found similar *Carex lasiocarpa* and *C. diandra* fens to be poor in all major nutrients.

Water level is also an important factor influencing rates of production. The low two year average NPP of the sedge fen was partly due to a very reduced rate of *Carex* production in 1992, which correlated [illegible] sharp drop in water levels. This significant change in local [illegible] was probably caused by the dam-building activities of beavers (*Castor canadensis*).

Although increases in herb NPP have been correlated with high water tables in this study, the wettest site (SF) also had the lowest overall production. Increases in total NPP have been associated with periodic flooding, however, wet, stagnant conditions can result in reduced production (Richardson, 1978; Brinson *et al.*, 1981). *Carex lasiocarpa*, the dominant plant species at the sedge fen is believed to be a major indicator of flooded peatlands (Laitinen, 1990). Laitinen (1990) suggested that flooding and stagnation create oligotrophic conditions, while Reader (1978) discussed the negative impacts of waterlogging on the ability of roots to absorb nutrients and grow. Other studies have shown that vascular plant biomass and production are greater on hummocks than hollows (Backéus, 1985; Wallén *et al.*, 1988; Moore, 1989b). Forrest and Smith (1975) also found a negative correlation between site wetness and total production for five different blanket bogs in the U.K..

Climate variables may also explain some of the variation in the data. Total NPP of wetlands has been documented to generally increase with higher mean temperature and a longer growing season (Reader, 1978; Brinson *et al.*, 1981; Wieder *et al.*, 1989). All of the Alberta sites had greater total NPP in 1991 compared to 1992, which may be related to higher mean growing season temperatures and more growing degree days in 1991 (Appendix 1). Most of this variation in total production is due to moss growth, which of all the strata showed the greatest change between the two years.

Peat accumulation potential in bogs and fens

Peat accumulation results when the rate of production exceeds the rate of decomposition. The loss of weight (decomposition), on a total site basis, appears to increase along the bog-rich fen gradient (Table 4.3). After one year the bog had the lowest value (14%) while the fens had much higher losses (25-31%). The pattern is similar after two years of decomposition with total weight losses increasing from 17 to 41% along the gradient.

One way to assess the potential accumulation of peat is to divide the annual production of organic matter [illegible] the amount lost annually to decay (production/decomposition [illegible]). The peat accumulation rate should be greater in sites where this ratio is relatively high than where it is low. The ratio of production to decomposition decreased along the gradient from the bog to sedge fen (Fig. 4.8). The bog had a much higher ratio [illegible]) than the other sites, while the poor fen and wooded-rich fen had similar ratios of 5.3 and 4.9 respectively. The sedge fen had the lowest rate of production relative to decomposition with a ratio of 3.1.

These results suggest that the peat accumulation rate should decrease along the bog-rich fen gradient as the decomposition rate increases relative to the rate of production. To further investigate this trend, the aerial input of litter compared to losses from decomposition was examined.

The total weight of original aerial litter remaining after one year of decomposition was very similar in the four sites, with the wooded-rich fen (192 g/m^2) having the most material remaining and the sedge fen (150) the least (Fig. 4.9). Reader and Stewart (1972) reported greater amounts of above ground litter remaining after one year in Manitoba peatlands (184-465 g/m^2) than this study. Their lagg also had much higher aerial litter accumulation than their ombrotrophic sites, while the ombrotrophic sites generally had greater subsurface litter accumulation.

After two years of decomposition the bog, poor fen and wooded-rich fen had almost identical (160-164 g/m^2) amounts of the original litter remaining, while the sedge fen had the least (129). These results correspond to the peat thicknesses of the sites which are similar in the bog (5 m), PF (4 m) and WRF (4.5), but lower in the sedge fen (2-2.5 m). The bog and wooded moderate-rich fen had similar amounts of material remaining after two years despite differences in the rates of production and decomposition between them. The high peat accumulation rates in the bog appear to be maintained by low decomposition while similar peat accumulation may occur in the wooded-rich fen because of greater production. The poor fen appears to have a similar rate of peat accumulation as the bog and WRF due to rates of production and decomposition that are both intermediate to those of these two sites. Vitt (1990) also suggested that hummocks in bogs are maintained by low decay rates while those of rich fens are maintained by higher rates of production and predicted that moderate-rich fens should have greater peat accumulation rates than extreme-rich fens because of higher production in the former. Since moderate-rich fens are probably the most common type of peatland in [illegible] peat accumulation in these fens may play a dominant role in carbon storage for this region.

With a hypothetical warming of the boreal climate, both the production and decomposition rates should increase in these peatlands. However, rates of peat accumulation would probably decrease because the ratio of production to decomposition would be lower as is the case in more southerly wetlands.

Conclusions

The NPP of the moss, herb, shrub and tree layers appeared to respond differently to environmental parameters. Moss production generally showed greater variation between years than between sites suggesting the importance of climatic factors. Moss growth was greater in the year (1991) with higher water levels, more NO_3^- in the surface water and higher air temperatures Vascular plant production showed greater variation between sites than years. Herb production correlated with water level and pH-related parameters, while shrub production was negatively correlated with these parameters. Tree contribution to total production was minimal and appeared to be related to site dryness (in the bog and WRF). The hypothesis of increased total NPP with higher water levels was not supported by the results. Total above ground production could not be correlated to any of the parameters that were measured and was greatest in sites with the most diverse plant community stratification (WRF, PF).

The hypothesis related to peat accumulation along the gradient was supported by the results. The peat accumulation potential appeared to decrease along the bog-rich fen gradient. In the bog, peat accumulation may be related to a lower rate of decomposition. In the fens, peat accumulation is apparently maintained by higher rates of production rather than lower decomposition rates.

Literature cited

Aaby, B. and H. Tauber. 1974. Rates of peat formation in relation to degree of humification and local environment, as shown by studies of a raised bog in Denmark. Boreas. 4:1-17.

Aerts, R., B. Wallén and N. Malmer. 1992. Growth-limiting nutrients in *Sphagnum*-dominated bogs subject to low and high atmospheric nitrogen supply. J. Ecol. 80:131-140.

Backéus, I. 1985. Aboveground production and growth dynamics of vascular bog plants in Central Sweden. Acta. Phytogeogr. Suec. 74. 98 pp.

Backéus, I. 1988. Weather variables as predictors of *Sphagnum* growth on a bog. Holarc. Ecol. 11:146-150.

Backéus, I. 1990. Production and depth distribution of fine roots in a boreal open bog. Ann. Bot. Fennici 27:261-265.

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

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

Bierhuizen, J. F. H. and E. E. Prepas. 1985. Relationship between nutrients, dominant ions, and phytoplankton standing crop in prairie saline lakes. Can. J. Fish. Aquat Sci. 42:1588-1594.

Boyer, M. L. H. and B. D. Wheeler. 1989. Vegetation patterns in spring-fed calcareous fens: calcite precipitation and constraints on fertility. J. Ecol. 77:597-609.

Bridgham, S. D., S. P. Faulkner and C. J. Richardson. 1991. Steel rod oxidation as a hydrologic indicator in wetland soils. Soil Sci. Soc. Am. J. 55:856-862.

Brinson, M. M., A. E. Lugo and S. Brown. 1981. Primary productivity, decomposition and consumer activity in freshwater wetlands. Ann. Rev. Ecol. Syst. 12:123-161.

Brock, C. M. and R. Bregman. 1989. Periodicity in growth, productivity, nutrient content and decomposition of *Sphagnum recurvum* var. *mucronatum* in a fen woodland. Oecologia 80:44-52.

Clymo, R. S. 1965. Experiments on breakdown of *Sphagnum* in two bogs. J. Ecol. 53:747-757.

Clymo, R. S. 1970. The growth of *Sphagnum*: methods of measurement. J. Ecol. 58:13-49.

Clymo, R. S. 1978. A model of peat bog growth, pp. 187-223. *In*: O. W. Heal and D. F. Perkins (eds.). Production ecology of British moors and montane grasslands. Springer Verlag, New York.

Damman, A. W. H. 1979. Geographic patterns in peatland development in eastern North America, pp. 42-53. *In*: Proceedings of the International Symposium on Classification of Peat and Peatlands, Hyytiälä, Finland, Sept. 17-21, 1979. International Peat Society.

Dickinson, C. H. 1983. Micro-organisms in peatlands, pp. 225-256. *In*: A. J. P. Gore (ed.). Ecosystems of the world 4A, mires: swamp, bog, fen and moor. Elsevier Scientific Publishing Co., New York.

Droste, M. 1984. Above ground standing crop and production of *Carex gracilis* CURT. in a fen. Arch. Hydrobiol. 100:533-538.

Environment Canada. 1979. Analytical methods manual. Inland Water Directorate, Water Quality Branch, Ottawa, Ont.

Environment Canada. 1982. Canadian climate normals, 1951-1980, temperature and precipitation, prairie provinces. Canadian Climate Program. 429 pp.

Farrish, K. W. and D. F. Grigal. 1988. Decomposition in an ombrotrophic bog and a minerotrophic fen in Minnesota. Soil Sci. 145:353-358.

Forrest, G. I. and R. A. H. Smith. 1975. The productivity of a range of blanket bog vegetation types in the Northern Pennines. J. Ecol. 63:173-202.

Francez, A. J. 1992. Structure, function and evolution of the ecosystem of a peat bog: Primary production and nitrogen flow in a peat bog in central France. Ann. Bot. Fennici. 29:197-211.

Gorham, E. 1950. Variation in some chemical conditions along the borders of a *Carex lasiocarpa* fen community. Oikos 2:217-240.

Gorham, E. 1974. The relationship between standing crop in sedge meadows and summer temperature. J. Ecol. 62:487-491.

Gorham, E. 1982. Some unsolved problems in peatland ecology. Naturaliste Can. 109:533-541.

Gorham, E. 1991. Northern peatlands: role in the carbon cycle and probable responses to climatic warming. Ecol. Applic. 1:182-195.

Grigal, D. F., C. G. Buttleman and L. K. Kernik. 1985. Biomass and productivity of the woody strata of forested bogs in northern Minnesota. Can. J. Bot. 63:2416-2424.

Hem, J. D. 1970. Study and interpretation of the chemical characteristics of natural water. Geological survey water-supply paper 1473. United States Government Printing Office, Washington.

Hillman, G. R., J. D. Johnson and S. K. Takyi. 1990. The Canada-Alberta wetlands drainage and improvement for forestry program. Forestry Canada/Alberta Forestry, Lands and Wildlife, Project #1413-1417-86. 66 pp.

Hulme, P. D. and A. W. Blyth. 1982. The annual growth period of some *Sphagnum* species on the Silver Flowe National Nature Reserve, south-west Scotland. J. Bryol. 12:287-291.

Ireland, R. R., G. R. Brassard, W. B. Schofield and D. H. Vitt. 1987. Checklist of the mosses of Canada II. Lindbergia 13:1-62.

Jeglum, J. K. 1974. Relative influence of moisture-aeration and nutrients on vegetation and black spruce growth in Northern Ontario. Can. J. For. Res. 4:114-126.

Koerselman, W., S. A. Bakker and M. Blom. 1990. Nitrogen, phosphorus and potassium budgets for two small fens surrounded by heavily fertilized pastures. J. of Ecol. 78:428-442.

Laitinen, J. 1990. Periodic moisture fluctuation as a factor affecting mire vegetation. Aquilo. Ser. Bot. 28:45-55.

Lieffers, V. J. and J. M. Shay. 1982. Seasonal growth and standing crop of *Scirpus maritimus* var. *paludosus* in Saskatchewan. Can. J. Bot. 60:117-125.

Lucas, R. E. and J. F. Davis. 1961. Relationships between pH values of organic soils and availabilities of 12 plant nutrients. Soil Sci. 92:177-182.

Malmer, N. 1986. Vegetational gradients in relation to environmental conditions in northwestern European mires. Can. J. Bot. 64:375-383.

Malmer, N. 1990. Constant or increasing nitrogen concentrations in *Sphagnum* mosses on mires in Southern Sweden during the last few decades. Aquilo. Ser. Bot. 28:57-65.

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

Moore, T. R. 1989b. Plant production, decomposition, and carbon efflux in a subarctic patterned fen. Arc. Alp. Res. 21:156-162.

Moss, E. H. and J. G. Packer. 1983. Flora of Alberta. 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 Poly Science Publications, Inc., Montreal, Québec. 452 pp.

Reader, R. J. 1978. Primary production in northern bog marshes, pp. 53-62. *In*: R. E. Good, D. F. Whigham and R. L. Simpson (eds.). Freshwater wetlands: ecological processes and management potential. Academic Press, New York.

Reader, R. J. 1982. Geographic variation in shoot productivity of bog shrubs and some environmental correlates. Can. J. Bot. 60:340-348.

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

Richardson, C. J. 1978. Primary productivity values in freshwater wetlands, pp. 131-145. *In*: Wetland functions and values: the state of our understanding. Proceedings of the National Symposium on Wetlands, Lake Beuna Vista, Florida, Nov. 7-10, 1978.

Rochefort, L. 1987. Biological effects of wet acid deposition on peatland bryophytes. Unpublished M. Sc. thesis, University of Alberta, Edmonton. 171 pp.

Rochefort, L., D. H. Vitt and S. E. Bayley. 1990. Growth, production and decomposition dynamics of *Sphagnum* under natural and experimentally acidified conditions. Ecology 71:1986-2000.

Rowe, J. S. 1972. Forest regions of Canada. Dept. of Environment, Canadian Forestry Services Publication 1300, Ottawa, Ontario.

Sjörs, H. 1950. On the relation between vegetation and electrolytes in north Swedish mire waters. Oikos 2:241-258.

Tilton, D. L. 1978. Comparative growth and foliar element concentrations of *Larix laricina* over a range of wetland types in Minnesota. J. Ecol. 66:499-512.

Vasander, H. 1982. Plant biomass and production in virgin, drained and fertilized sites in a raised bog in southern Finland. Ann. Bot. Fennici. 19:103-125.

Verhoeven, J. T. A., S. Van Beek, M. Dekker and W. Storm. 1983. Nutrient dynamics in small mesotrophic fens surrounded by cultivated land: I. Productivity and nutrient uptake by the vegetation in relation to the flow of eutrophicated ground water. Oecologia 60:25-33.

Vermeer, J. G. and J. T. A. Verhoeven. 1987. Species composition and biomass production of mesotrophic fens in relation to the nutrient status of the organic soil. Acta Œcologica Œcol. Plant. 8:321-330.

Vitt, D. H. 1990. Growth an production dynamics of boreal mosses over climatic, chemical and topographical gradients. Bot. J. Linn. Soc. 104:35-59.

Vitt, D. H., S. E. Bayley, L. Halsey and T. L. Jin. in press. Seasonal variation in water chemistry over a bog-rich fen gradient in continental western Canada. Can. J. Fish. Aquat. Sci.

Vitt, D. H. and P. Pakarinen. 1977. The bryophyte vegetation, production, and organic components of Truelove Lowland, pp. 225-244. *In*: L. C. Bliss (ed.). Truelove Lowland, Devon Island, Canada: a high arctic ecosystem. Univ. of Alberta Press, Edmonton.

Walker, D. 1970. Direction and rate in some British post-glacial hydroseres, pp. 117-139. *In*: D. Walker and R. G. West (eds.). Studies in the vegetation history of the British Isles. Cambridge Univ. Press, London.

Wallén, B., U. Falkengren-Grerup and N. Malmer. 1988. Biomass, productivity and relative rate of photosynthesis at different water levels on a South Swedish peat bog. Holarc. Ecol. 11:70-76.

Wassen, M. J. and A. Barendregt. 1992. Topographic position and water chemistry of fens in a Dutch river plain. J. Veg. Sci. 3:447-456.

Wassen, M. J., A. Barendregt, A. Palczynski, J. T. De Smidt and H. De Mars. 1990. The relationship between fen vegetation gradients, ground water flow and flooding in an undrained valley mire at Biebrza, Poland. J. Ecol. 78:1106-1122.

Wheeler, B. D. and S. C. Shaw. 1991. Above-ground crop mass and species richness of the principal types of herbaceous rich-fen vegetation of lowland England and Wales. J. Ecol. 79:285-301.

Wieder, R. K. and G. E. Lang. 1983. Net primary production of the dominant bryophytes in a *Sphagnum*-dominated wetland in West Virginia. Bryologist 86:280-286.

Wieder, R. K., J. R. Yavitt, G. E. Lang and C. A. Bennett. 1989. Above-ground net primary production at Big Run Bog, West Virginia. Castanea 54:209-216.

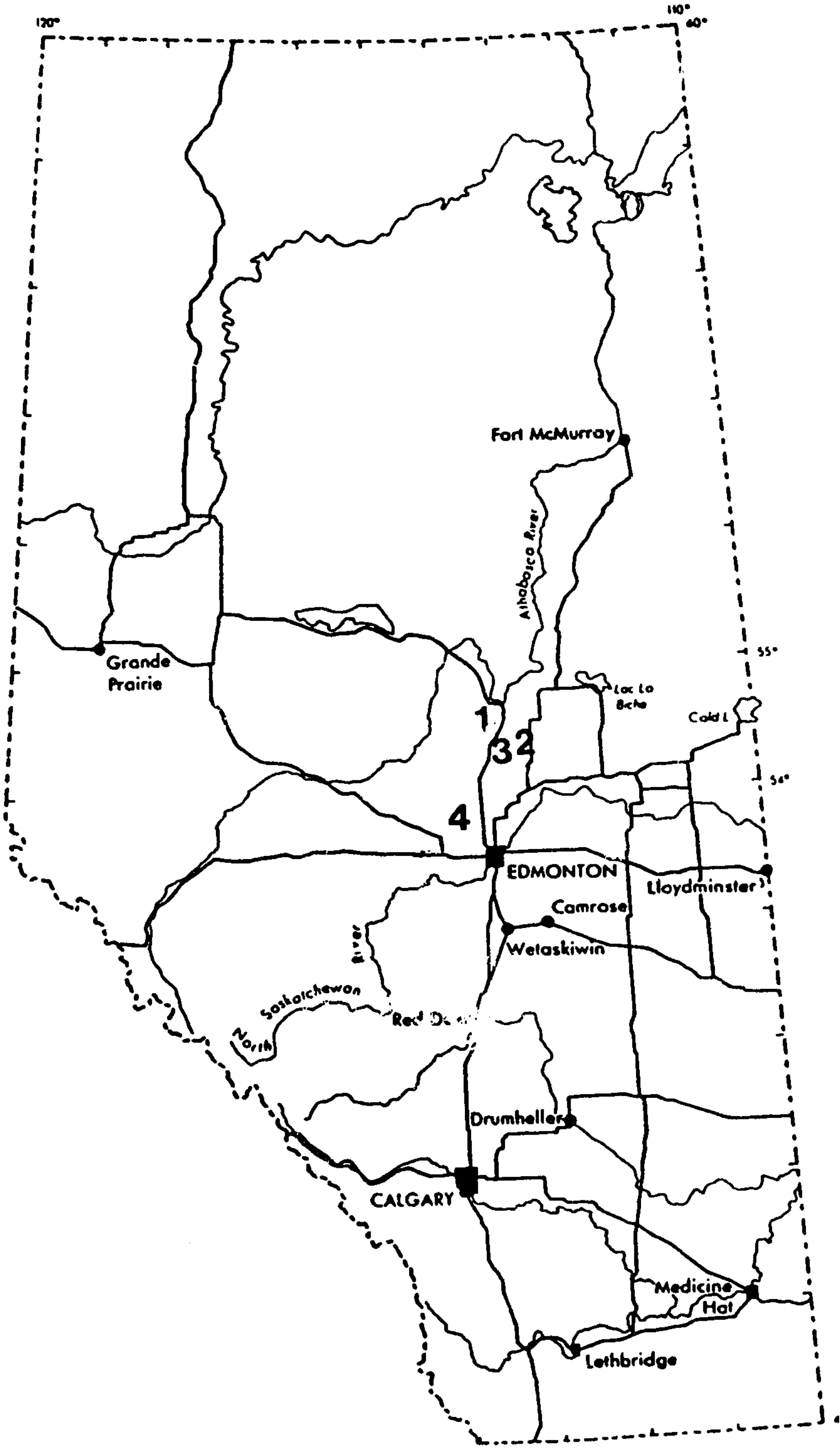


Fig. 4.1. Relative location of the sites in central Alberta (**1** = bog and poor fen, **2** = wooded rich fen, **3** = sedge fen and **4** = extreme-rich fen).

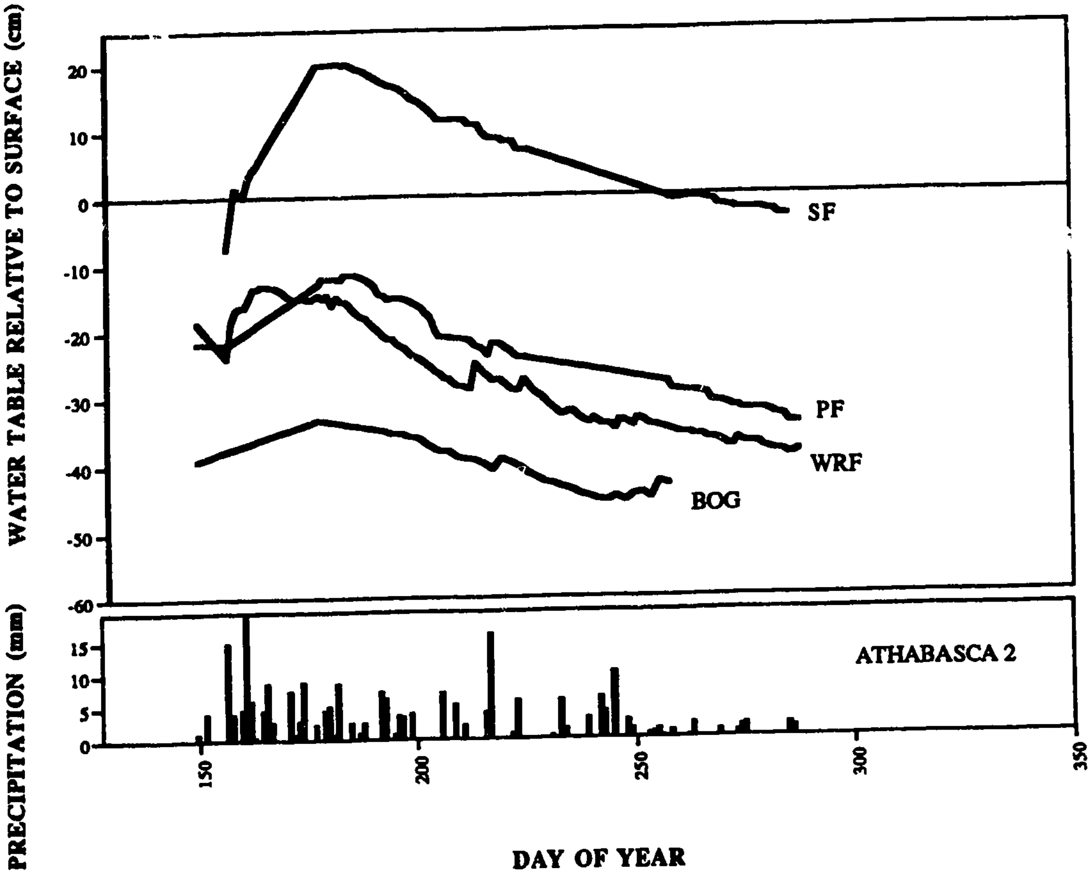


Fig. 4.2: Water level fluctuations relative to the moss surface (0 cm) at four sites (PF = poor fen, WRF = wooded-rich fen, SF = sedge fen) during the growing season in 1991 compared to daily precipitation at a nearby weather station (Athabasca 2).

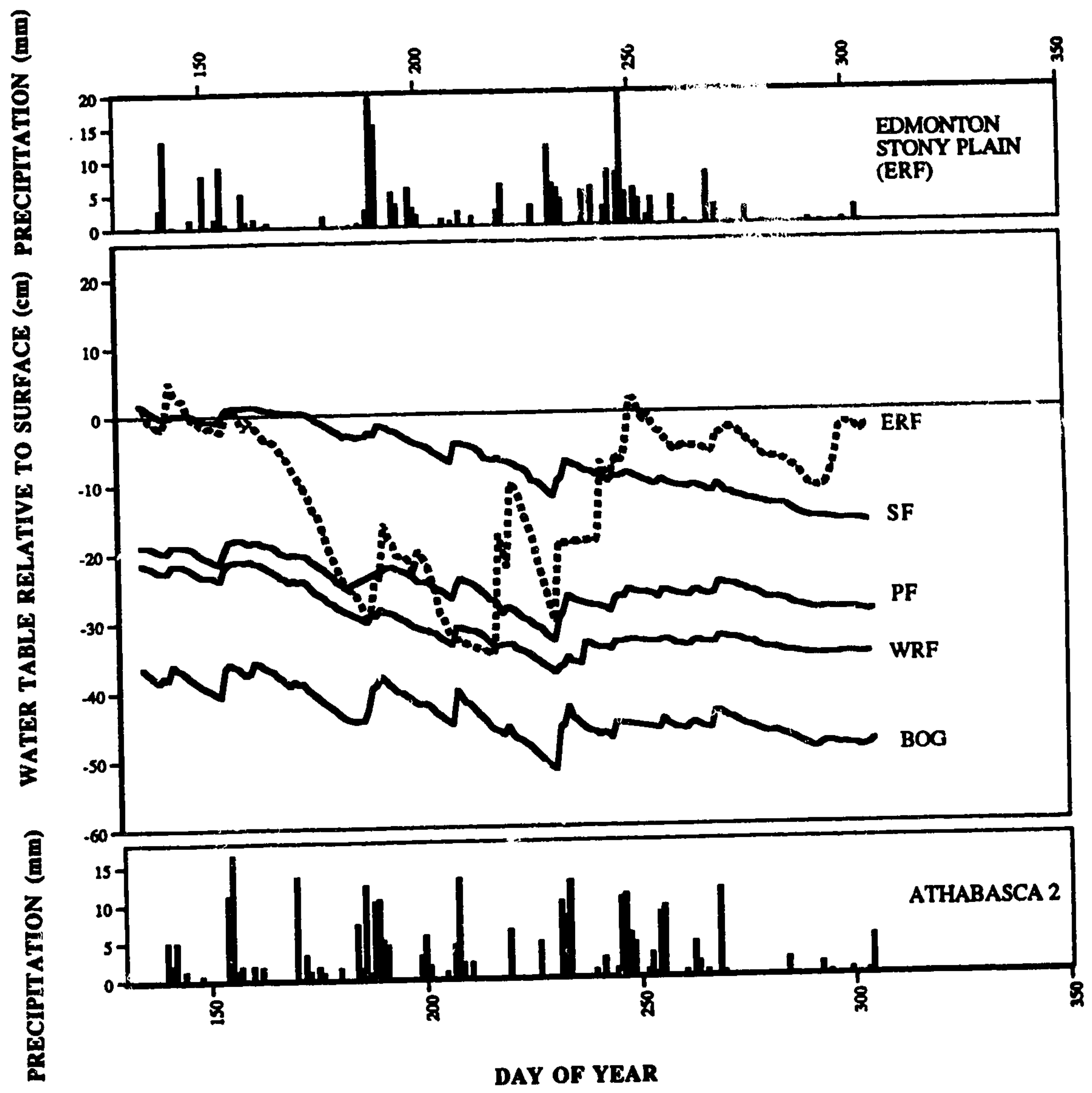


Fig. 4.3: Water level fluctuations relative to the moss surface (0 cm) at five sites (PF = poor fen, WRF = wooded-rich fen, SF = sedge fen, ERF = extreme-rich fen) during the growing season in 1992 compared to daily precipitation from two weather stations (Edmonton Stony Plain is near ERF, Athabasca 2 is near the other sites).

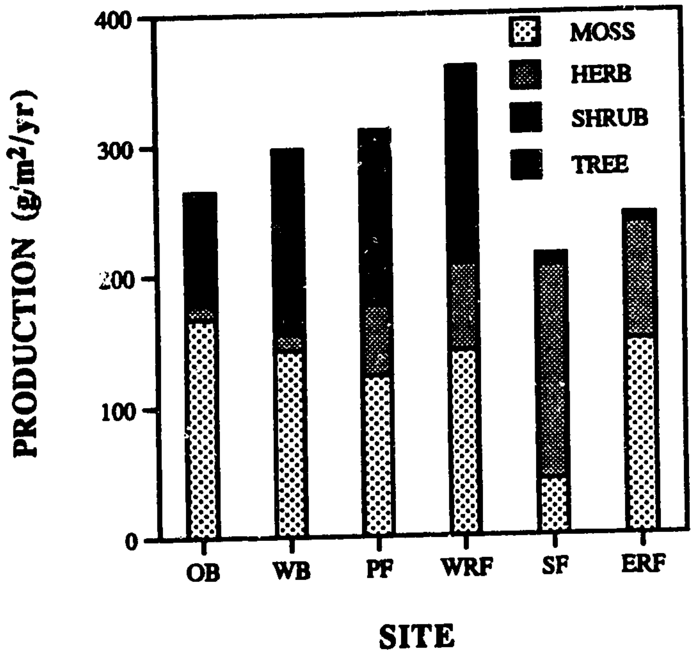
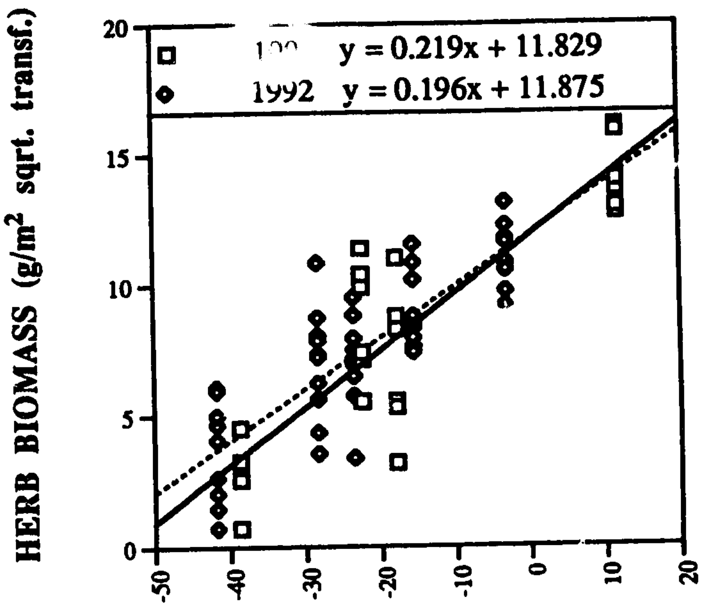


Fig. 4.4: Comparison of total above ground plant production (moss, herb, shrub and tree layers) in six sites (OB = open bog, WB = wooded bog, PF = poor fen, WRF = wooded-rich fen, SF = sedge fen and ERF = extreme-rich fen). Bars represent averages of 1991 and 1992, except sites with trees, where tree production is based on an average of five year growth increments.



WATER TABLE RELATIVE TO SURFACE (cm)

Fig. 4.5: Peak herb above ground biomass (square root-transformed) in relation to mean site water level relative to the moss surface (0 cm) during the 1991 (solid line) and 1992 (dashed line) growing seasons. Symbols represent clipped quadrats from five peatlands (bog, wooded-rich fen, poor fen, extreme-rich fen and sedge fen from left to right). 1991 does not include extreme-rich fen.

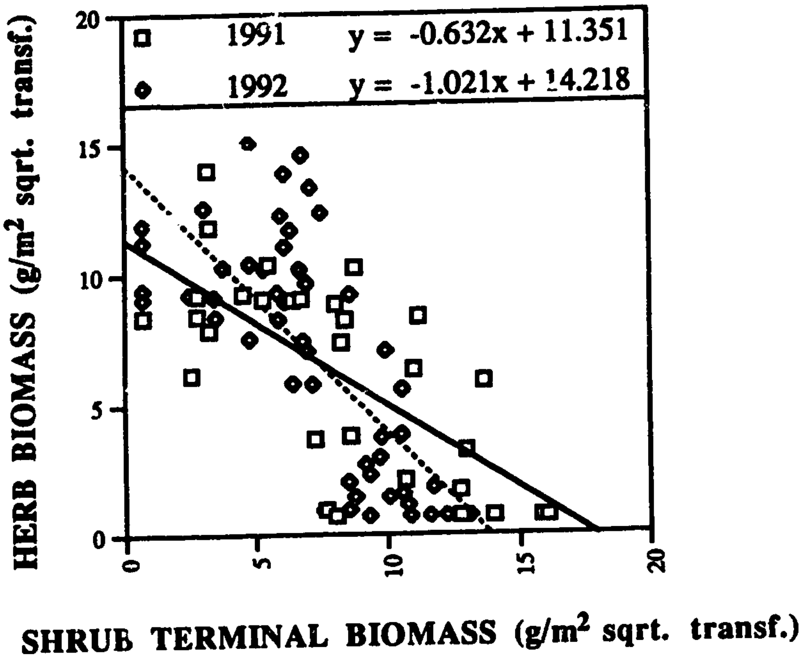


Fig. 4.6: Correlation between August above ground herb biomass and shrub terminal (new leaves and stems) biomass from clipped quadrats in the five peatlands (bog, poor fen, wooded-rich fen, sedge fen and extreme-rich fen) in 1991 and 1992. Solid line represents 1991 while dashed line represents 1992. All biomass values are square root-transformed.

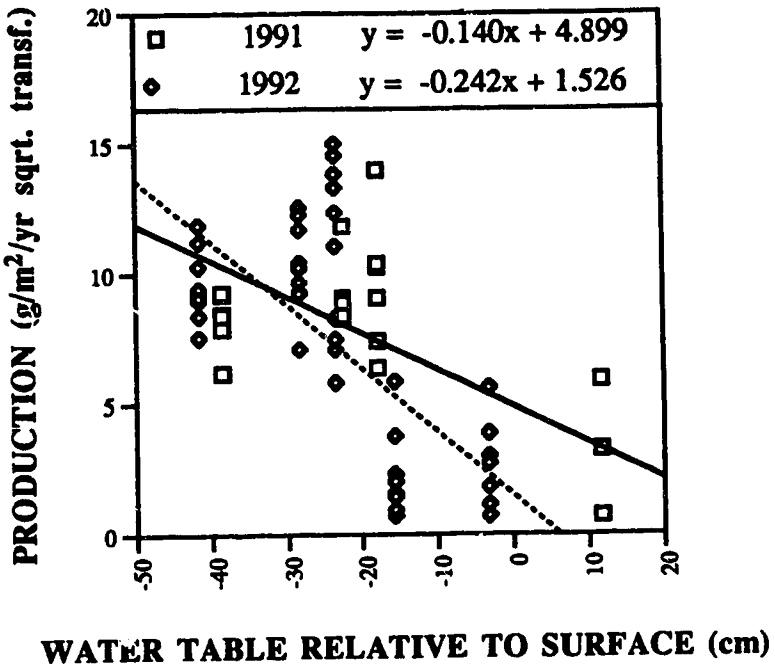


Fig. 4.7: Shrub terminal (new leaves and stems) production (square root-transformed) in relation to mean site water level relative to the moss surface (0 cm) during 1991 (solid line) and 1992 (dashed line) growing seasons. Symbols represent clipped quadrats from five peatlands (bog, wooded-rich fen, poor fen, extreme-rich fen and sedge fen from left to right). 1991 does not include extreme-rich fen.

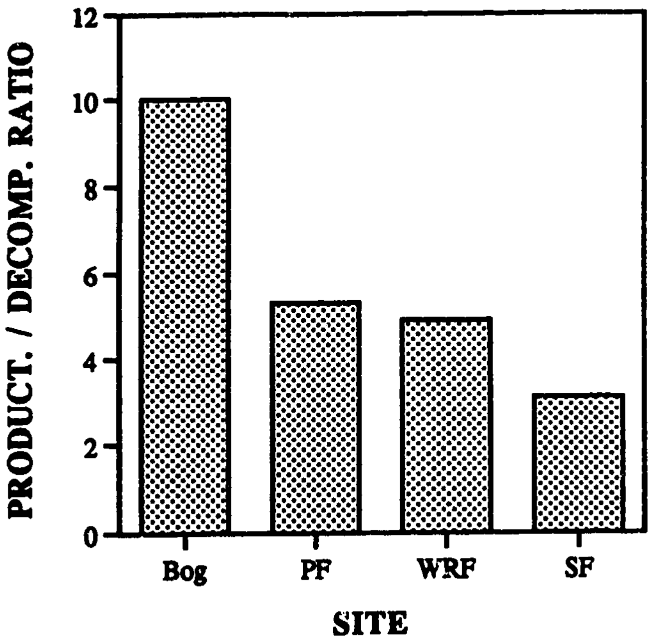


Fig. 4.8: Ratio of above ground production ($g/m^2/yr$) to estimated weight loss ($g/m^2/yr$) of original tissues after one year of decomposition in four peatlands (PF = poor fen, WRF = wooded-rich fen, SF = sedge fen).

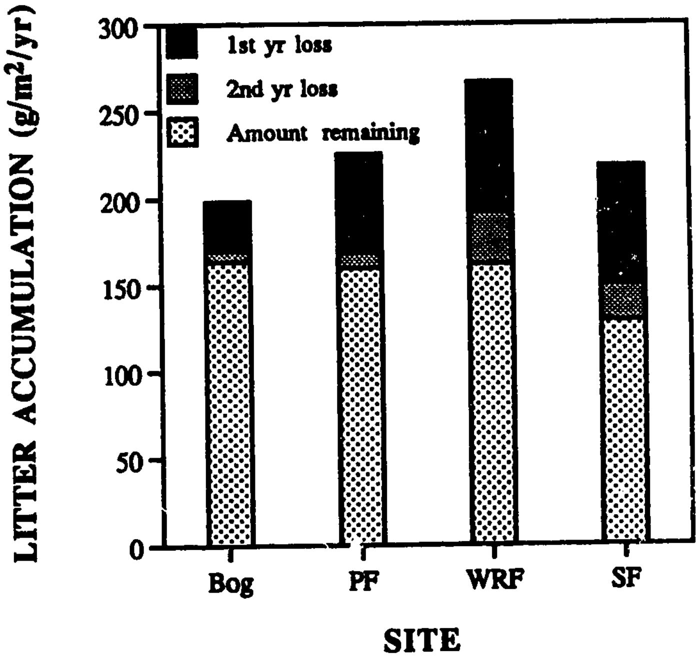


Fig. 4.9: Annual above ground litter accumulation (moss and herb production combined with tree and shrub litter fall) with amounts lost after after 1 and 2 years of decomposition in four peatlands (PF = poor fen, WRF = wooded-rich fen, SF = sedge fen).

Table 4.1: Means (ranges) of surface water characteristics at five sites in 1991 (n = 5) and 1992 (n = 6). *Measured in 1992 only. +Water level was above surface. (SRP = soluble reactive phosphorus, TDP = total dissolved P, TP = total P, DOC = dissolved organic carbon, N:P ratio = NO3- + NH4+ / SRP)

Characteristic	Bog	Poor Fen	Wooded-Rich Fen	Sedge Fen	*Extreme-Rich Fen
field pH	3.86 (3.39 - 4.22)	4.98 (4.28 - 5.22)	6.06 (5.68 - 6.57)	6.53 (6.12 - 6.85)	8.17 (7.83 - 8.35)
reduced conductivity (uS)	-17.9 (-32.8 - 3.8)	18.5 (15.2 - 26.5)	26.3 (17.6 - 40.7)	56.2 (38.0 - 79.2)	232.2 (194.7 - 259.1)
*alkalinity (mg/l CaCO3)	- -	21.5 (8.3 - 58.4)	36.8 (26.1 - 50.0)	61.0 (52.7 - 74.1)	244.1 (205.0 - 269.5)
*HCO3- (mg/l)	- -	26.3 (10.1 - 71.2)	44.9 (31.8 - 61.0)	74.4 (64.3 - 90.3)	290.6 (249.9 - 328.6)
Ca2+ (mg/l)	3.97 (2.3 - 5.5)	8.08 (5.2 - 11.7)	11.62 (8.0 - 22.5)	18.35 (7.2 - 35.8)	87.17 (57.5 - 114.5)
Mg2+ (mg/l)	1.36 (0.8 - 2.4)	5.12 (3.4 - 7.9)	5.13 (3.6 - 6.6)	6.63 (2.3 - 12.2)	27.8 (21.4 - 39.9)
Na+ (mg/l)	1.78 (1.3 - 2.3)	2.34 (1.9 - 3.1)	2.16 (1.8 - 2.5)	4.59 (2.8 - 7.4)	20.35 (16.3 - 24.4)
K+ (mg/l)	0.91 (0.3 - 1.4)	1.57 (0.1 - 3.1)	0.35 (0.1 - 0.7)	1.13 (0.3 - 2.3)	3.47 (2.1 - 4.5)
NO3- (ug/l)	8.9 (3.4 - 24.4)	10.6 (2.0 - 30.2)	8.7 (2.0 - 24.5)	7.1 (3.1 - 14.7)	5.8 (3.4 - 10.1)
NH4+ (ug/l)	41.8 (12.2 - 107.5)	20.5 (2.9 - 57.9)	19.1 (2.1 - 34.4)	20.7 (1.9 - 67.5)	24.0 (1.3 - 79.4)
SRP (ug/l)	16.0 (1.4 - 63.3)	71.7 (1.8 - 166.0)	24.4 (3.2 - 147.4)	5.55 (0 - 16.5)	24.6 (1.5 - 111.8)
TDP (ug/l)	56.4 (21.4 - 152.9)	115.9 (33.6 - 193.6)	49.3 (15.3 - 208.0)	23.2 (10.0 - 36.6)	21.3 (2.3 - 93.4)
TP (ug/l)	153.2 (34.3 - 386.8)	191.7 (44.1 - 392.3)	152.6 (27.5 - 357.2)	120.4 (15.1 - 266.9)	35.0 (8.1 - 111.6)
N:P ratio	18.8 (1.2 - 50.3)	4.0 (0.1 - 23.7)	7.4 (0.1 - 18.4)	29.3 (1.7 - 167.0)	8.1 (1.4 - 21.4)
Sulfate (mg/l)	1.04 (0.59 - 1.48)	below detect. -	below detect. -	below detect. -	57.95 (41.60 - 68.15)
Cl- (mg/l)	0.59 (0.21 - 1.08)	0.94 (0.35 - 1.80)	1.06 (0.53 - 2.47)	0.78 (0.16 - 1.44)	0.99 (0.37 - 2.71)
DOC (mg/l)	74.2 (67 - 94)	72.4 (56 - 94)	40.1 (22 - 56)	26.3 (15 - 34)	17.2 (14 - 20)
water temp. in field (°C)	10.0 (2.0 - 17.0)	13.1 (1.0 - 22.0)	14.4 (6.0 - 19.0)	15.2 (2.0 - 20.0)	19.8 (4.5 - 28.0)
water table depth (cm)	42 (33 - 52)	24 (12 - 34)	29 (13 - 39)	0 (20+ - 16)	12 (5+ - 35)
*depth of oxidation (cm)	30.5 (19.2 - 43.3)	27.0 (12.7 - 41.0)	23.8 (13.7 - 34.5)	16.4 (0.5 - 31.0)	19.4 (9.5 - 36.5)

Table 4.2: Correlation coefficients (r) of peak herb live standing crop and shrub terminal production (both square root-transformed) with mean site water level relative to surface and various surface water parameters for 1991 and 1992. Both years include bog, poor fen, wooded-rich fen and sedge fen, while the extreme-rich fen was added in 1992.

Parameter	Peak herb standing crop (square root-transf.)				Shrub terminal production (square root-transf.)			
	1991		1992		1991		1992	
	r	p	r	p	r	p	r	p
Water level	0.88	***	0.83	***	-0.72	***	-0.70	***
pH	0.85	***	0.65	***	-0.50	*	-0.67	***
Reduced conduct.	0.91	***	0.39	**	-0.68	***	-0.61	***
Ca2+	0.89	***	0.28	*	-0.69	***	-0.57	***
Mg2+	0.90	***	0.28	*	-0.58	**	-0.51	***
Na+	0.86	***	0.29	*	-0.80	***	-0.59	***
K+	0.10	n.s.	0.26	n.s.	-0.16	n.s.	-0.40	**
DOC	-0.74	***	-0.73	***	0.59	**	0.69	***
SRP	-0.19	n.s.	-0.16	n.s.	0.49	*	0.34	*
TDP	-0.36	n.s.	-0.32	*	0.57	**	0.58	***
TP	-0.37	n.s	-0.07	n.s.	0.78	***	0.33	*

DOC = dissolved organic carbon
SRP = soluble reactive phosphorus
TDP = total dissolved phosphorus
TP = total phosphorus

n.s. $p > 0.05$
* $0.05 > p > 0.01$
** $0.01 > p > 0.001$
*** $p < 0.001$

Table 4.3: Average annual litter production, percent weight loss and amount of original litter remaining after one and two years of decomposition in four peatlands. Unmeasured litter represents minor species whose decomposition rate was not determined in the field, but estimated using total site decay rate.

Site	Litter type	Above ground litter production (g/m^2/yr)	% weight loss with one year of decomposition	Amount remaining after one year of decomp. (g/m^2)	% weight loss with two years of decomposition	Amount remaining after two years of decomp. (g/m^2)
Bog						
	Sphagnum fuscum	154	14	132	17	128
	Unmeasured liitter	44	14	38	17	37
	Total	198	14	170	17	164
Poor fen						
	S. teres/S. angustifolium	123	16	103	16	103
	Carex	25	50	13	62	10
	Betula pumila	40	36	26	49	20
	Unmeasured liitter	37	25	28	29	26
	Total	225	25	169	29	160
Wooded-rich fen						
	Tomenthypnum nitens	142	22	111	32	97
	Carex	26	58	11	74	7
	Betula pumila	25	37	16	43	14
	Unmeasured liitter	73	28	53	39	45
	Total	266	28	192	39	162
Sedge fen						
	Carex	159	31	110	41	94
	Unmeasured liitter	59	31	41	41	35
	Total	218	31	150	41	129

5. CONCLUSIONS

These studies demonstrate that there were differences in above ground production, decomposition and peat accumulation between the peatlands and that these differences could be related to changes in environmental characteristics and vegetation along the bog-rich fen gradient. Water level appeared to have the strongest influence on these processes, however, water chemistry and climatic factors were also important.

Moss production was lowest in the sedge fen but was not significantly different between the bog, poor fen, wooded-rich fen or extreme-rich fen. There was greater variation between the two years than there was between these four sites, suggesting that climatic factors have an influence on moss production at these sites. Moss production was greater in all sites during the year (1991) of higher water levels, greater June precipitation, higher mean growing season temperature, more growing degree days and greater NO_3^- concentrations in the surface water.

There was greater variation in vascular production between sites than between years. The sites in the middle of the gradient (poor fen, wooded-rich fen and sedge fen) had greater above ground vascular production than the sites on the ends (bog and extreme-rich fen). There was also greater between site variation in the production of the individual strata (herb, shrub and tree) than the total vascular plant NPP.

Herbaceous production increased along the bog-rich fen gradient while shrub production tended to decrease along this gradient. Herb production increased with site wetness and the pH-related characteristics while shrub production decreased with site wetness and higher pH. These two strata were also negatively correlated with each other. Tree contribution to total production was minimal and also appeared to be related to water levels as canopies were only present in the two driest sites (bog and wooded-rich fen).

The hypothesis of increasing production along the bog-rich fen gradient (Chapter two) was only partially supported by the results. Total above ground NPP was highest in the middle of the gradient and increased from the bog to wooded moderate-rich fen and then abruptly decreased at the sedge and extreme-rich fens. The wooded-rich fen had the highest total above ground production (331-388 $g/m^2/yr$), followed by the poor fen (303-318 $g/m^2/yr$). The open (238-292) and wooded bog (279-311) sites were only slightly lower than the poor fen. The sedge fen (167-260 $g/m^2/yr$) and extreme-rich fen (183-306 $g/m^2/yr$) had low total NPP values and also showed the greatest variation between years. The hypothesis of increased NPP with higher water levels (Chapter four) was only supported by the results for herb production (and to some extent mosses) and not for woody growth (shrubs and trees) or total NPP.

There were significant differences in decay rates between the litter types (moss, local *Carex*, *Betula* and standard *C. lasiocarpa*) incubated in each of the sites. Decomposition, as measured by percent weight loss (k') of the standard substrate (*C. lasiocarpa*), also differed between sites.

Variation in weight loss appeared to be greater between litter types than between sites. Rates of decay were consistently faster in vascular plant tissues than moss tissues, regardless of site, while *Carex* litter decomposed more rapidly than the *Betula* samples. The slower weight loss of the shrub may be due to the presence of twigs in the samples. Local *Carex* samples also lost weight faster than the *C. lasiocarpa* standard.

The hypothesis of rapid decay in litter of good quality (high %N and low C:N) was strongly supported by the differences in k' between the litter types. Substrates of poor quality (low %N and high C:N), such as mosses, decomposed slowly while those of high %N and low C:N (e.g. *Carex*) decomposed rapidly. The *C. lasiocarpa* litter probably decomposed slower than the local *Carex* samples because it had much higher initial C:N ratios than the latter.

First year weight loss of the standard litter decreased along the bog-rich fen gradient with the bog, poor fen and wooded-rich fen samples losing more weight than those of the open-rich and sedge fens. This was contrary to the hypothesis of an increasing decay rate along the gradient (Chapter three). *C. lasiocarpa* weight loss was negatively correlated with water levels and pH-related parameters and positively correlated with surface water concentrations of TDP. Decay rates were lowest in the wettest sites because anaerobic conditions associated with high water tables may have inhibited microbial respiration at the wetter sites. After two years the sites ranked poor fen > wooded-rich fen > bog > open-rich fen > sedge fen in order of fastest to slowest *C. lasiocarpa* decay rate.

The total site percent weight loss (Chapter four) increased along the bog-rich fen gradient (Table 4.3). After both one and two years the bog had the lowest decay rate while the fens had much higher losses. These results support the hypothesis of increasing decomposition along the gradient. The total ecosystem decay rates increased along this gradient mainly because of the changes in vegetation at the sites. For example, site decay rates were slower in the *Sphagnum*-dominated systems (bog, PF) than the sedge-dominated system (SF).

The hypothesis of decreasing peat accumulation (Chapter four) along the bog-rich fen gradient appears to be supported by the ratio of production to decomposition at the sites. The bog had a much higher ratio than the fens, suggesting that peat is accumulating more rapidly at this site. However, the amount of original aerial litter remaining after one and two years of decomposition was similar in the bog, poor fen and wooded-rich, but lower in the sedge fen. The bog and wooded moderate-rich fen had similar amounts of material remaining after two years despite the much higher annual litter production in the latter site. This supports the theory that decomposition determines peat accumulation rates more than production (Malmer, 1986) in the bog, however, the relatively high peat accumulation in the wooded-rich fen appears to be maintained by increased production rather than decreased decomposition as suggested by Vitt (1990).

Literature cited

Malmer, N. 1986. Vegetational gradients in relation to environmental conditions in northwestern European mires. Can. J. Bot. 64:375-383.

Vitt, D. H. 1990. Growth an production dynamics of boreal mosses over climatic, chemical and topographical gradients. Bot. J. Linn. Soc. 104:35-59.

Appendix 1: Climatic data for May-October 1991 and 1992 and long term (1951-1980) averages from weather stations near study sites. Athabasca 2 is the closest station to bog, poor fen, wooded-rich fen and sedge fen, while the extreme-rich fen data is an average of two stations: Edmonton Stony Plain and Edmonton Namao A. GDD is growing degree days measured as the sum of daily mean temp. > 5.0 °C.

	May	June	July	August	September	October	May-October Mean/Total
Athabasca 2							
1991							
Mean temp. (°C)	11.5	13.8	16.8	18.3	10.0	0.7	11.9
GDD	203.3	265.0	366.7	412.6	154.5	64.9	1467.0
Precip. (mm)	60.4	100.2	54.2	43.4	25.0	29.6	312.8
1992							
Mean temp. (°C)	9.6	15.1	15.1	14.3	7.5	3.2	10.8
GDD	153.9	302.9	314.0	290.1	96.9	49.7	1207.5
Precip. (mm)	50.2	55.2	84.0	45.6	72.2	9.7	316.9
LONG TERM AVE.							
Mean temp. (°C)	10.1	14.1	16.2	14.8	9.5	4.6	11.6
Precip. (mm)	44.9	80.1	90.0	68.2	45.2	21.5	349.9
Extreme-rich fen							
1991							
Mean temp. (°C)	10.9	13.9	17.1	18.6	11.5	1.2	12.2
GDD	186.6	265.8	381.3	420.6	195.4	79.2	1528.9
Precip. (mm)	98.9	97.8	23.6	71.8	17.4	62.6	372.1
1992							
Mean temp. (°C)	9.9	16.0	15.9	15.2	8.7	4.8	11.8
GDD	164.8	328.6	337.4	317.4	126.7	72.2	1347.1
Precip. (mm)	27.3	21.2	61.3	47.0	56.5	6.5	219.8
LONG TERM AVE.							
Mean temp. (°C)	10.6	14.4	16.6	15.4	10.3	5.2	12.1
Precip. (mm)	43.1	88.5	86.2	73.5	43.5	19.1	353.[illegible]

Appendix 2: Above ground (g/m^2) production, biomass and necromass of herbs and shrubs from five peatlands in 1991. Herb values are from the period of peak herb standing crop while shrub values are from August harvest period.

Plant type	Bog	Poor fen	Wooded-rich fen	Sedge fen	Extreme-rich fen
Smilacina trifolia					
live	4.3	2.0	7.9		
dead	0.5	1.5	0.3		
Eriophorum vaginatum					
live	2.5				
dead	22.9				
Rubus Chamaemorus					
live	1.7				
dead	8.1				
Menyanthes trifoliata					
live		6.5	41.7		
dead		0.0	7.5		
Sedges (Carex, Scirpus)					
live		44.4	26.7	201.8	54.4
dead		29.6	22.9	371.5	76.5
Muhlenbergia glomerata					
live					15.5
dead					3.9
Triglochin spp.					
live					19.8
dead					3.7
Juncus spp.					
live					1.9
dead					0.7
Minor spp.					
live		2.4	1.8	1.5	5.3
dead		0.0	0.8	2.1	0.2
Ledum groenlandicum					
terminal production	40.2				
radial production	8.6				
biomass	150.3				
Andromeda polifolia					
terminal production	10.0	22.2	32.9		
biomass	28.9	51.3	69.1		
Chamaedaphne calyculata					
terminal production	4.7				
biomass	14.0				
Vaccinium vitis-idaea					
terminal production	10.4				
biomass	23.2				
Oxycoccus spp.					
terminal production	2.7	3.1	8.6		2.3
biomass	6.3	5.9	17.4		3.5
Dead standing ericaceous	33.2	1.3	2.1		0.0
Betula pumila					
terminal production		46.1	21.7	4.5	0.7
radial production		15.3	6.1	1.2	0.1
biomass		190.5	73.4	13.2	1.1
dead		16.2	57.9	1.3	0.0
Salix spp.					
terminal production		25.5	22.8	2.9	2.7
radial production		2.8	4.1	0.7	0.0
biomass		61.1	72.6	8.1	3.5
dead		36.5	26.7	2.3	0.0
Total production	85.1	170.3	174.3	212.6	102.7
Total biomass	231.2	364.1	295.3	224.6	105.0
Total standing dead	64.7	85.1	118.2	377.2	85.0

Appendix 3: Above ground (g/m^2) production, biomass and necromass of herbs and shrubs from five peatlands in 1992. Herb values are from the period of peak herb standing crop while shrub values are from August harvest period.

Plant type	Bog	Poor fen	Wooded-rich fen	Sedge fen	Extreme-rich fen
Smilacina trifolia					
live	9.4	17.3	7.1		
dead	0.1	0.0	0.0		
Eriophorum vaginatum					
live	3.7				
dead	21.9				
Rubus Chamaemorus					
live	1.4				
dead	1.0				
Menyanthes trifoliata					
live		4.4	16.8		
dead		0.0	0.0		
Sedges (Carex, Scirpus)					
live		28.8	26.0	121.4	51.2
dead		6.9	11.2	271.2	41.3
Muhlenbergia glomerata					
live					1.9
dead					1.4
Triglochin spp.					
live					24.0
dead					3.9
Juncus spp.					
live					1.8
dead					0.9
Minor spp.					
live		1.1	2.4	0.9	2.5
dead		0.0	0.0	0.2	0.3
Ledum groenlandicum					
terminal production	66.1	0.7			0.0
radial production	5.6	0.0			0.0
biomass	187.8	2.0			0.1
Andromeda polifolia					
terminal production	8.4	14.6	45.0		
biomass	21.5	34.0	103.0		
Chamaedaphne calyculata					
terminal production	4.1				
biomass	13.3				
Vaccinium vitis-idaea					
terminal production	10.7				0.1
biomass	22.4				0.2
Oxycoccus spp.					
terminal production	2.1	5.8	15.6		1.2
biomass	3.3	10.0	25.6		2.4
Dead standing ericaceous	21.2	2.0	3.8		0.0
Betula pumila					
terminal production		76.5	28.0	0.0	0.6
radial production		28.0	11.0	0.0	0.2
biomass		268.7	102.0	0.0	2.6
dead		20.3	22.3	2.4	0.0
Salix spp.					
terminal production		30.8	18.4	6.4	4.2
radial production		1.0	1.9	0.6	0.0
biomass		58.5	40.2	17.5	6.2
dead		13.0	4.2	0.7	0.3
Total production	111.5	209.0	172.2	129.3	87.7
Total biomass	262.8	424.8	301.3	139.8	92.7
Total standing dead	44.2	42.2	41.5	274.5	48.1

Appendix 4: Litter fall (g/m^2) of shrubs and trees in five peatlands from May 1992 to May 1993 (PF = poor fen, WRF = wooded-rich fen, SF = sedge fen, ERF = extreme-rich fen). Period 1 is from early May to late Aug. 1992, period 2 from Aug. to late Oct. 1992 and period 3 from Oct. to early May 1993. Totals may differ from those in Fig. 2.8 where data was deleted for any lost or damaged traps.

Litter type	Period	Bog	PF	WRF	SF	ERF
Picea mariana	1	2.86	0.12	0.47	0.00	0.09
	2	4.27	0.29	0.76	0.00	0.09
	3	0.57	0.01	0.13	0.00	0.10
	Total	7.70	0.42	1.36	0.00	0.28
Larix laricina	1	0.00	0.00	1.50	0.00	0.01
	2	0.00	0.00	20.98	0.01	0.84
	3	0.00	0.00	0.99	0.00	0.37
	Total	0.00	0.00	23.47	0.01	1.22
Ericaceous	1	5.08	0.75	1.99	0.00	0.00
	2	10.21	1.22	1.06	0.00	0.00
	3	3.84	0.66	0.72	0.00	0.30
	Total	19.13	2.63	3.77	0.00	0.30
Betula pumila	1	0.00	11.11	3.15	0.50	0.14
	2	0.00	23.82	20.00	5.85	2.13
	3	0.00	5.06	1.60	0.57	0.[illegible]
	Total	0.00	39.99	24.75	6.92	2.[illegible]
Salix	1	0.00	2.96	2.85	0.78	0.32
	2	0.00	10.62	7.35	7.12	1.89
	3	0.00	2.19	1.05	0.44	0.16
	Total	0.00	15.77	11.25	8.34	2.37
Total		26.83	58.81	64.60	15.27	6.85