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# Aboveground plant production and nutrient content of the vegetation in six peatlands in Alberta, Canada

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## Abstract

We examined the effects of water level, surface water chemistry, and climatic parameters on aboveground primary plant production, and the tissue nutrient concentrations in the dominant herb species in a bog, three fens, and two marshes. In the fens, total NPP correlated best with $NO_3^-$ and total phosphorus surface water concentrations in 1993 and 1994. Total NPP in the marshes correlated best with alkalinity in 1993, and with soluble reactive phosphorus in 1994. Climatic parameters, such as mean annual growing season temperature, growing degree days, and precipitation, had the most notable effect on moss growth, whereas shrub and herb production correlated significantly with the water level relative to the moss surface. Herb production correlated positively and shrub production correlated negatively with the water level relative to the moss surface. Tissue nutrient concentrations of carbon (C), nitrogen (N), and total phosphorus (TP), and the C:N quotient in *Carex lasiocarpa* exhibited similar trends in the fens and the marshes. Carbon tissue concentrations in *C. lasiocarpa* remained unchanged, whereas N and TP tissue levels decreased throughout the growing season. In the site with the highest NPP and presumably the highest stand density, *C. lasiocarpa* exhibited the highest tissue N and TP levels. Furthermore, TP tissue concentrations in *C. lasiocarpa* were substantially higher in the marshes than in the fens. Tissue nutrient concentrations in *Eriophorum vaginatum* in the bog showed variable response patterns. N tissue levels increased, whereas tissue TP concentrations decreased from late June to late August. In the bog, *E. vaginatum* exhibited similar tissue TP levels to *C. lasiocarpa* in the fens; however, they were both substantially lower than those found in *C. lasiocarpa* from the marshes.

## Introduction

Boreal peatlands sequester large amounts of carbon from the atmosphere via photosynthesis and release only small quantities via decomposition thereafter (Gorham 1991; Gorham 1988). Rates of carbon accumulation are estimated at 0.096 Pg $y^{-1}$ (1 Pg = $10^{15}$ g) during the postglacial period (Gorham 1991), and Riley (1987) and Riley & Michaud (1987) estimated that approximately 51.7% of Canada's carbon is stored in wetlands. The accumulation of carbon in wetlands is believed to be the result of slow rates of decomposition of plant matter rather than large rates of net primary production (Vitt 1990; Farrish & Grigal 1988; Clymo 1965).

The effects of environmental parameters, such as water level, water chemistry, and climate, on net primary production (NPP) are not clearly understood (Gorham 1982; Reader 1978; Richardson 1978) and only a few studies exist, which relate these parameters to NPP. Moore (1989) and Forrest & Smith (1975) examined the relationship of water levels to NPP in peatlands and Backéus (1990), Bartsch & Moore (1985), and Szumigalski & Bayley (unpublished) related water levels, surface water chemistry, and some climatic parameters to NPP in peatlands. The effect of temperature on peatland NPP was previously investigated by Droste (1984), Damman (1979), and Gorham (1974). The majority of these studies concentrated on bogs and fens, whereby marshes have received less attention, especially at more northerly latitudes. The paucity of data regarding the effects of environmental parameters on marsh plant production in boreal regions necessitated further investigation, especially in fens and marshes during the same period.

*Eriophorum vaginatum* and *Carex lasiocarpa* are two common plant species in boreal North American peatlands. They are both perennial sedges which grow from belowground rhizomes each year and may produce shoots even when covered by snow and ice during the winter months (Bernard & Gorham 1978). These 'winter shoots' give them a competitive advantage over other species within the same ecosystem. Decreases in tissue nutrient levels occur each fall due to leaching and translocation of nutrients from above- to belowground tissues (Kistritz et al. 1983). Their life histories have been extensively studied (Bernard & Gorham 1978; Auclair 1977; Wein 1973), and their tissue nutrient concentrations have been monitored throughout the growing season (Chapin III et al. 1988; Kistritz et al. 1983). Tissue nutrient concentrations of *C. lasiocarpa* have not been quantified simultaneously in fens and marshes in western boreal Canada previously. The data that are available are usually restricted to either fens or marshes or to non-boreal sites (Good et al. 1978).

The objectives of this paper were to (a) discuss the surface water chemistry of these six peatlands, (b) examine the effects of water levels, surface water nutrients, and selected climatic parameters on aboveground NPP, and (c) report on the %C, %N, and TP tissue concentrations of *Carex lasiocarpa* in these three fens and two marshes, and *Eriophorum vaginatum* in the bog in central Alberta.

## Study area and site descriptions

The five study sites which were examined in 1993 and 1994 and an additional sixth in 1994 represent the range of peatlands present in Alberta, Canada. They are not contiguous. These included a bog, a floating sedge fen (FSF), a riverine sedge fen (RSF), a lacustrine sedge fen (LSF), a riverine marsh (RM), and a lacustrine marsh (LM). The bog is located north of Bleak Lake at 54°41′ N and 113°28′ W, while the FSF (54°28′ N, 113°17′ W), the LSF (54°28′ N, 113°19′ W), and the RSF (54°28′ N, 113°18′ W) are located east of Perryvale. The RM is located northwest of Perryvale at 54°28′N and 113°23′ W, and the LM is located northeast of Clyde (54°10′ N, 113°34′ W) (Figure 1).

Mild summers and cold, snowy winters characterize the climate of central Alberta, whereby the long term mean annual temperature is 1.7 °C, and the total mean precipitation is approximately 500 mm for all sites (Environment Canada 1982). All six peatlands lie within the Subhumid Low Boreal ecoclimatic region of Canada (Ecoregions Working Group 1989). Vascular plant nomenclature follows Packer (1983), whereas 'brown' moss nomenclature follows Anderson et al. (1990), and *Sphagnum* nomenclature is in accordance with Anderson (1990). Only the dominant vegetation taxa are listed in these site descriptions. A detailed description of these peatlands is in Thormann (1995).

### *Bog*

The bog is a large, raised ombrotrophic island within a large peatland complex. The peat is 5 m thick and is arranged in large, dry hummocks, which are separated by intermittent wetter hollows. A sparse tree layer of *Picea mariana* (Mill.) BSP. covers about 25% of the wooded part of this bog. *Ledum groenlandicum* Oeder dominates the ericaceous shrub layer (covers about 75%), while the sparse herb stratum consists primarily of *Smilacina trifolia* (L.) Desf. and *Eriophorum vaginatum* L. *Sphagnum fuscum* (Schimp.) Klinggr. comprises about 90% of the moss layer.

### *Lacustrine Sedge Fen (LSF)*

This site is a large expanse of sedge dominated peatland situated aside a large body of water (approximately 62 ha) in a former north-south drainage channel (Vitt et al. 1995) with 2–2.5 m of peat. The vascular vegetation consists primarily of *Carex lasiocarpa* Ehrh. Shrubs comprise only about 5% of the peatland cover and consist of *Salix pedicellaris* Pursh and *Betula pumila* L. *var. glandulifera* Regel exclusively. The moss stratum is discontinuous and dominated by *Drepanocladus aduncus* (Hedw.) Warnst. in wet pools, and by *Aulacomnium palustre* (Hedw.) Schwaegr. on top of dry hummocks. Szumigalski & Bayley (1996b), who studied this site in 1991 and 1992, referred to this fen as 'lacustrine sedge fen' (SF).

### *Riverine Sedge Fen (RSF)*

This peatland is part of an extensive wetland complex adjacent to the aforementioned lacustrine sedge fen and has an approximate peat depth of 1 m. The vascular vegetation stratum is dominated by *Carex aquatilis* Wahlenb. and *Carex lasiocarpa*, mosses are very sparsely distributed, and shrubs are absent.

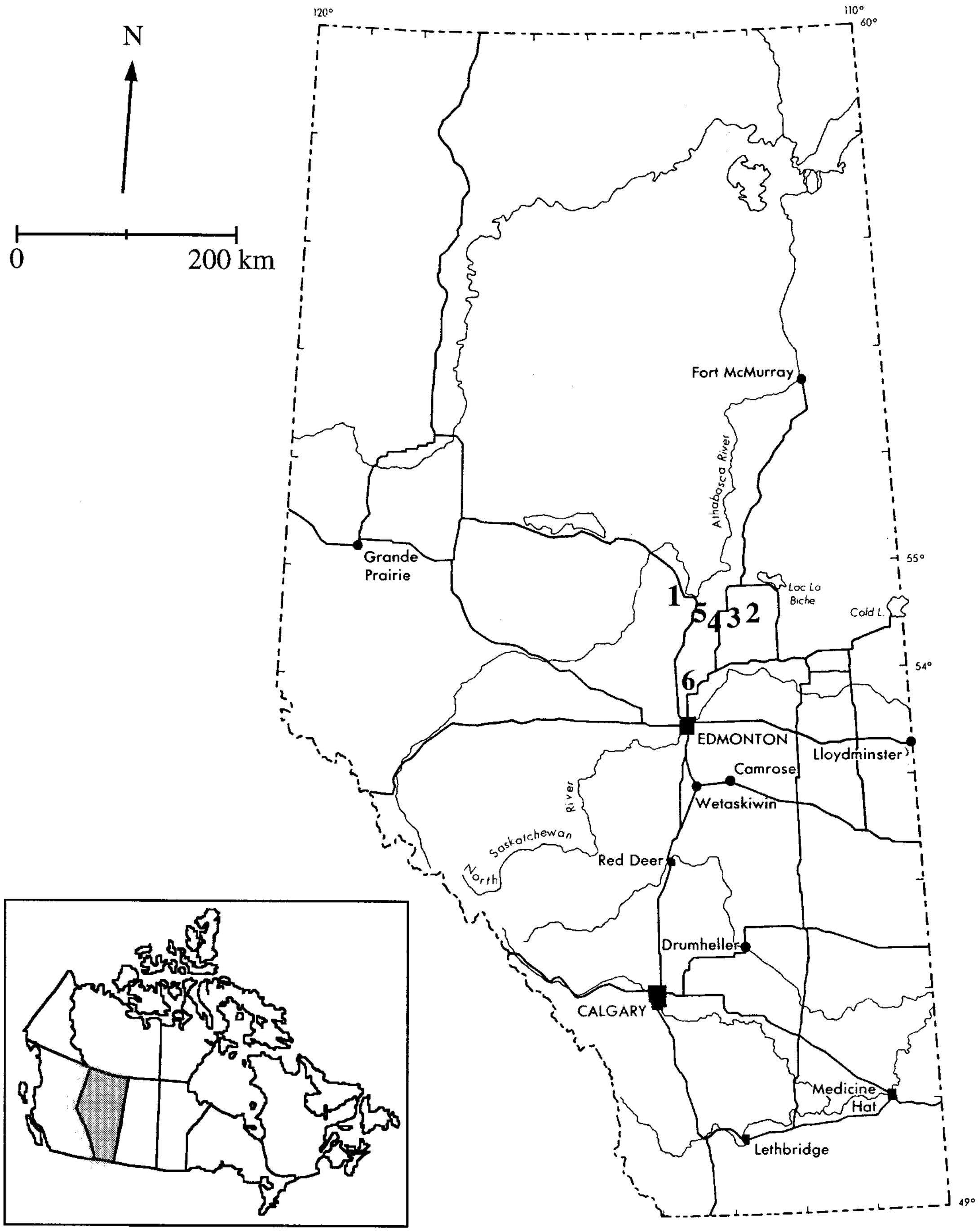


*Figure 1.* Relative locations of the six peatlands in central Alberta, Canada (1 = bog, 2 = floating sedge fen, 3 = riverine sedge fen, 4 = lacustrine sedge fen, 5 = riverine marsh, 6 = lacustrine marsh).

*Floating Sedge Fen (FSF)*

This fen is a floating mat surrounding a small body of water (approximately 0.5 ha). The peat is approximately 1 m thick and floats over 1–1.5 m of water, below which an additional 1–1.5 m of peat are located. The vascular plant stratum is dominated by

*Carex lasiocarpa* and in addition to four other species of *Carex* cover about 90% of the surface. Other herbs present are *Triglochin maritima* L., *Potentilla palustris* (L.) Scop. and the insectivorous, perennial herb *Drosera rotundifolia* L. The shrub layer consists predominantly of *Salix pedicellaris* and *Andromeda polifolia* L., whereas the moss stratum is dominated by *Sphagnum warnstorfii* Russ. and *Aulacomnium palustre* (Hedw.) Schwaegr. The latter two species comprise about 80% of the moss cover in this fen.

*Riverine Marsh (RM)*

This site is located on the floodplain of Tawatinaw River and has less than 1 m of peat. The vascular vegetation layer is dominated by *Carex aquatilis* and *C. lasiocarpa* during spring and early summer, but *Calamagrostis canadensis* (Michx.) Beauv. and *C. inexpansa* A. Gray were dominant during late summer and early fall. During their period of vegetation domination, these species cover about 95% of the surface. A number of other herb species are sparsely distributed. There are no moss and shrub strata present.

*Lacustrine Marsh (LM)*

This marsh is situated on the northwestern shore of Wakomao Lake (approximately 360 ha) with a peat depth of approximately 1.5–1.75 m. The lake receives secondarily treated wastewater from Clyde (population $< 1000$) each spring and additional nutrients from agricultural run-off. No moss stratum exists, and the vascular vegetation layer is dominated by *Carex aquatilis*, *C. lasiocarpa*, and *Typha latifolia* L. Together, these three species cover approximately 90% of the surface.

## Methods

*Production measurements*

*Mosses*

Clymo's (1970) cranked wire method was employed to measure the moss growth in the bog and the FSF. Two 5 by 50 m (250 m$^2$) plots were established in the bog in early June 1991 to determine the growth and production of the dominant moss species, *Sphagnum fuscum* (Szumigalski & Bayley 1996b). Five randomly placed transects of 20 wires, placed about five cm apart, were established in each plot (a total of 200 wires). Due to the smaller dimensions of the FSF, only one plot of 5 by 25 m (125 m$^2$) was established in June 1993. *Sphagnum warnstorfii* and *Aulacomnium palustre* were the two dominant species in this site. Three circular transects of 20 wires were set up for each moss species (60 wires per species). Growth in length was measured four times during each growing season, which was estimated to begin in early May and end in mid-October each year, in both sites. To convert the linear growth increments (cm year$^{-1}$) to production values (g m$^{-2}$ y$^{-1}$), the mass per unit length per surface area (g cm$^{-2}$ y$^{-1}$) was required. This was determined by extracting five cores of 85 cm$^2$ surface area in early October of 1993 and 1994 for each of the species measured for growth and production. The number of individual stems in each core was counted, and the top four cm of each plant was cut off from the remainder of the plant, dried at 60 °C, and weighed to the nearest 0.01 g. The capitulum of *Sphagnum* spp. was removed before drying and weighing under the assumption that it does not grow significantly during the growing season (Rochefort et al. 1990). The dry weight of each core was then converted to an average weight per one cm per square meter (g cm$^{-1}$ m$^{-2}$) for each moss species. The production values were obtained by multiplying these values by the yearly measured length increments from the cranked wires (cm y$^{-1}$).

Since the moss surface within the FSF and the bog are not perfectly flat, the calculated production values were corrected for hummock elevations by multiplying the production values by a correction factor that depended directly on the moss surface at each site. To estimate the actual moss surface area per vertically projected area, a 2500 cm$^2$ quadrat was set up into a grid of 25 equal 100 cm$^2$ squares. This was accomplished by stringing wires across the quadrat, resulting in 36 evenly spaced grid nodes on the quadrat surface. At each circular sample transect, this quadrat was leveled, and the distance from each grid node to the moss surface was measured (cm). The coordinates $(x, y)$ of all grid nodes in association with the depths to the moss surface $(z)$ could then be used by the computer program MacGridzo to calculate the surface area within each quadrat. This procedure was carried out in the bog (Szumigalski & Bayley 1996b), the LSF, and the FSF. The average ratio of actual moss surface area to vertical projected area was determined for the LSF and the FSF, and the calculated moss production values were multiplied by the corresponding site correction factor to arrive at the actual moss production figure (g m$^{-2}$ y$^{-1}$). These were 1.09 (Szumigalski & Bayley 1996b) for *Sphagnum fuscum* in the bog, 1.11 for *S. warnstorfii* and *Aulacomnium palustre* in the FSF, and 1.01 for *Drepanocladus aduncus* in the LSF.

The LSF had very few hummocks, and Clymo's (1970) cranked wire method for determining moss production could not be applied here. Instead, moss production was determined by multiple harvests of the moss mat. A 0.25 by 0.25 m (0.0625 $m^2$) quadrat was employed to extract five samples of the dominant moss species, *Drepanocladus aduncus*, three times during both growing seasons. From each harvested quadrat, a sub-sample of 25 moss plants was taken, and the ratio of the mass of new growth, as estimated from pigmentation change, to the total biomass of the sample was determined (cf. Vasander 1982; Vitt & Pakarinen 1977). To estimate the total moss production per harvested quadrat, the ratio of the weight of the new growth to total weight was multiplied by the total harvested moss mass per quadrat. All samples were dried at 60 °C before weighing. The sample period with the peak biomass was used as an estimate of the total NPP.

*Herbs and shrubs*

These two vegetation layers were measured in two 5 by 50 m (250 $m^2$) plots. These were established in early May (bog, FSF, LSF, RM, and LM) or early June (RSF) in 1993, and ran parallel to the plots used to measure moss production within the applicable sites. Due to the smaller area available in the FSF, the two plots were 5 by 25 m (125 $m^2$) each. The aboveground vascular vegetation was harvested three times during each growing season, in late June, late July, and late August. Ten 0.50 by 0.50 m (0.25 $m^2$) randomly placed quadrats (five per plot) were clipped during each harvest period. These quadrats were never the same throughout either growing season. The bog was added as a sixth study site in 1994; therefore, no vascular plant production values are available for the 1993 growing season.

All herbaceous plant material was clipped at the ground level during each sample period, dried at 48 °C, and sorted into live and dead plant matter. The dead plant matter from (the) previous year(s) was discarded, and the live plant material was further separated into individual taxa and then weighed. The maximum aboveground herb production for each site was estimated by using the month (June, July, or August) with the peak live standing crop.

Shrub NPP was determined similarly to herb production with the exception that shrubs are evergreens or deciduous with secondary growth (radial growth). The radial growth plus the new terminal growth (leaves, flowers, new twigs) is an approximate estimate of the aboveground annual NPP. Radial production for *Salix pedicellaris*, *Betula pumila var. glandulifera* and *Ledum groenlandicum* were estimated from Szumigalski & Bayley (1996b) who modified techniques previously used by Reader & Stewart (1972). First, leaves were removed and the total stem biomass was determined for the major species within each quadrat. Then, the total terminal stem production was weighed. Lastly, the total shrub stem weight was divided by the average quadrat age (as determined by the number of bud scale scars of the major shrub species) to obtain a mean stem production per annum. The total radial production is the difference between the terminal shrub production and the total shrub stem weight. Consequently, total shrub production is the sum of the total terminal and total radial productions within each quadrat. These values were incorporated into the total NPP for the bog, LSF, and FSF before statistical analyses were carried out. The radial production of dwarf shrubs is believed to be minimal (Vasander 1982) and was not determined. To estimate total herbaceous and shrubby vascular plant aboveground NPP, the August herb and shrub total biomass from each quadrat was combined and then statistically analyzed for differences in vascular plant production between years, sites, and transects within sites.

*Trees*

The only site with a significantly developed tree canopy was the bog (*Picea mariana*). Since the climatic data between 1991 and 1994 were similar in average temperature, total precipitation, and growing degree days on a per annum basis, we adopted the tree NPP values determined by Szumigalski & Bayley (1996b) in our analyses. These values were determined by measuring large ($>$ 1.75 m) and small ($<$ 1.75 m) trees, employing tree height, diameter at breast height (approximately 1.30 m), basal diameter, and leader length measurements.

*Water chemistry*

Water samples were collected bimonthly from May until the end of October each year. These samples were taken from the same location within each site, a depression dug into the peat surface. The conductivity of each sample was measured in the lab within 24 h of collection, and later corrected for pH and temperature (Sjörs 1950).

All water samples were filtered initially with GFC filters. Base cations ($Na^+$, $Ca^{2+}$, $Mg^{2+}$, $K^+$) were fixed with 0.5 mL concentrated $HNO_3$ and then analyzed with a Perkin-Elmer Atomic Absorption Spectrometer. Nitrate ($NO_3^-$), soluble reactive phosphorus (SRP), and total dissolved phosphorus (TDP) samples were re-filtered with a 0.45 $\mu$m millipore filter. Nitrate and ammonium ($NH_4^+$) samples were analyzed on a Technicon Auto Analyser II within 24 h of collection. Total phosphorus (TP), SRP, and TDP analyses followed Bierhuizen & Prepas (1985). Alkalinity was determined via the electrometric titration technique employing the phenolphthalein technique developed by Environment Canada (1979).

*Water levels*

Steven's F water level recorders were used to monitor the water table fluctuations within each site during most of the ice-free season in 1993 and 1994 (early May to late October). Additionally, manual measurements were taken from meter sticks attached to permanent wooden stakes driven into the mineral substrate. These measurements follow those outlined in Szumigalski & Bayley (1996a). Measurements from a pore water sampler were used to determine the annual average water level relative to the moss surface within each site. These measurements were then compared to the current reading on the water level recorders and the meter stick.

*Depth of oxidation*

A total of 15 steel welding rods (1.0 m long) were placed in each site in early May, 1994. These were inserted to a depth of 0.8 m into the peat, and three replicates were removed at monthly intervals until October. The distance from the moss surface to the lowest extent of rust on each rod was measured and assumed to be the depth of the acrotelm. The mean of all measurements from June until October inclusively determined the depth of the acrotelm within each site. The methods for this technique follow those outlined by Bridgham et al. (1991).

*%C, %N, and TP analyses*

Carbon (C) and nitrogen (N) were analyzed as described by Szumigalski & Bayley (unpublished). Total phosphorus (TP) was analyzed with the molybdophosphovanadate method with an Auto Analyzer as outlined by Prepas & Rigler (1982) and Parkinson & Allen (1975). Plant samples were collected from quadrats clipped as part of the production study in late June, late July, and late August within each site.

*Eriophorum vaginatum* from the bog and *Carex lasiocarpa* from the remaining three fens and two marshes were selected for analyses of C, N, and TP tissue concentrations. Four randomly selected samples from each site from late June, late July, and late August in 1993 and 1994 were ground and analyzed for C and N content in a Model 440 Elementary Analyzer (Control Equipment Corp.). The nutrients were expressed as %C and %N of total dry weight and the C:N quotient was determined by dividing %C by %N for each sample. TP was expressed as $\mu$g $g^{-1}$ of dry weight, or as %TP.

*Statistical analyses*

Linear simple regressions between the water level relative to the moss surface and peak herb (maximum net primary production) and terminal shrub production (leaves, flowers, new twigs) values were performed for 1993 ($n = 4$ sites, $n = 10$ samples site$^{-1}$) and 1994 ($n = 5$ sites, $n = 10$ samples site$^{-1}$). Peak herb and terminal shrub production values were square-root and natural-logarithm transformed, respectively, to normalize the data before statistical analyses. Pearson correlation coefficients were determined to indicate the relationship between these two parameters.

ANOVAs were employed to examine changes of the C:N quotient and total phosphorus (TP) tissue concentrations of the dominant vegetation (*Eriophorum vaginatum* in the bog, *Carex lasiocarpa* in the fens and marshes) from late June to late August within and among sites ($n = 6$ sites, $n = 4$ samples site$^{-1}$ sampling period$^{-1}$ year$^{-1}$). Tukey tests were performed to make pairwise comparisons between %C, %N, C:N, and TP within and among sites over this period. Multiple stepwise regressions (forward) were used to examine the relationship among surface water nutrients ($n = 13$ samples nutrient$^{-1}$ year$^{-1}$) and vascular and total plant net primary production in fens ($n = 3$) and marshes ($n = 2$) individually and combined ($n = 5$). The bog was not included in these analyses because it was sampled only in 1994 and did not have sufficient data points for a regression.

Autocorrelation analyses were performed for each surface water nutrient within each site in order to establish any correlation between successive samples. Pearson correlation coefficients were determined between all surface water nutrients within each site to establish if any of these nutrients were correlated with each other. Most statistical analyses were performed on SAS (SAS Institute Inc. 1989) except for the simple linear regressions, which were performed on Quattro Pro (Borland International Inc. 1992), and the autocorrelation analyses, which were done in SYSTAT (SYSTAT Inc. 1992).

## Results

*Surface water chemistry and water level characteristics of the six peatlands*

The LSF had the lowest surface water concentrations of nitrate ($NO_3^-$), total dissolved nitrogen (TDN), soluble reactive phosphorus (SRP), total dissolved phosphorus (TDP), and total phosphorus (TP) (Table 1). The LM exhibited the highest nutrient concentrations of $NO_3^-$, ammonium ($NH_4^+$), TDN, SRP, TDP, TP, sodium ($Na^+$), and calcium ($Ca^{2+}$). The remaining peatlands exhibited surface water nutrient levels intermediate to those found in the LSF and LM. $NO_3^-$ did not vary significantly ($p > 0.05$) among the sites, except for the LM, where surface water concentrations were significantly higher ($p < 0.05$) (Table 1). $NH_4^+$ was similar in the bog and the three fens but it was significantly higher in the marshes. Surface water concentrations ranged from means of 29 $\mu$g L$^{-1}$ to 366 $\mu$g L$^{-1}$ in the fens and marshes, respectively. TDN exhibited trends similar to $NH_4^+$. Significantly lower ($p < 0.05$) surface water concentrations of TDN prevailed in the bog and the three fens (mean of 1,117 $\mu$g L$^{-1}$) compared to the marshes (mean of 2,135 $\mu$g L$^{-1}$). SRP concentrations were similar in most sites (mean of 18 $\mu$g L$^{-1}$), except for the LM, which exhibited a mean concentration of 161 $\mu$g L$^{-1}$ (significant at $p < 0.05$) during both growing seasons (Table 1), possibly due to additions of wastewater to the lake from the nearby community. The LSF had the lowest concentrations of SRP (mean of 4 $\mu$g L$^{-1}$) (Table 1). TDP exhibited trends similar to SRP (Table 1). The bog and the fens had similar surface water concentrations of TP but they were significantly lower than those found in the marshes. Mean values ranged from 103 $\mu$g L$^{-1}$, in the bog and the three fens, to 373 $\mu$g L$^{-1}$, in both marshes, a 3.5-fold increase (Table 1).

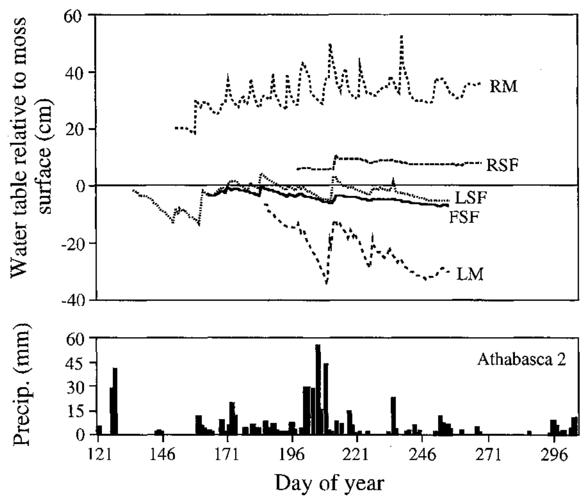


*Figure 2.* Water level fluctuations relative to the moss surface (0 cm) in five peatlands (FSF = floating sedge fen, LSF = lacustrine sedge fen, RSF = riverine sedge fen, RM = riverine marsh, LM = lacustrine marsh) during the 1993 growing season compared to daily precipitation at the nearby weather station (Athabasca 2).

The pH ranged from 3.9 (bog) to means of 6.8 for the fens and 7.4 for the marshes, and adjusted conductivity, alkalinity, and $HCO_3^-$ surface water concentrations increased along the bog - fen - marsh gradient in 1993 and 1994 (Table 1). Concentrations of base cations increased along the peatland gradient. $Na^+$ and $Ca^{2+}$ surface water concentrations were significantly higher in the marshes than in the fens and the bog ($p < 0.05$), whereas $Mg^{2+}$ concentrations were similar in all sites ($p > 0.05$) (Table 1).

Significant water level differences between 1993 and 1994 were detected in the LSF, the RM, and the LM ($p < 0.01$) (Table 1, Figures 2 and 3). In the LSF and the LM, the water levels were below the moss surface in 1993 but above the moss surface in 1994 (Figures 2 and 3). The RM exhibited a converse trend. No significant water level differences between years were observed in the FSF and the RSF ($p > 0.05$). A lower water level was correlated with the depth of the acrotelm (measured as depth of oxidation in 1994). The bog had the lowest water level relative to the moss surface during the 1993 and 1994 growing seasons (mean of -42 cm), and the depth of oxidation was greatest in this site (28 cm) (Table 1). The LM had a mean water level above the peat surface (23 cm in 1994), and the peat was completely anoxic (as determined by the rust- free steel rod below the peat surface) (Table 1).

*Table 1.* Means (ranges) af surface water parameters in six peatlands (bog, FSF = floating sedge fen, RSF = riverine sedge fen, LSF = lacustrine sedge fen, RM = riverine marsh, LM = lacustrine marsh) in 1993 and 1994.

| Characteristic | Bog | FSF | RSF | LSF | RM | LM |
|---|---|---|---|---|---|---|
| pH | 3.9 | 6.2 | 7.1 | 7.0 | 7.4 | 7.4 |
| | (3.4 – 4.1) | (5.5 – 7.4) | (6.3 – 8.1) | (6.2 – 7.8) | (6.7 – 8.4) | (6.6 – 8.1) |
| * Adjusted conductivity ($\mu$S) | 8 | 75 | 231 | 197 | 433 | 780 |
| | (0 – 44) | (51 – 86) | (128 – 342) | (57 – 286) | (293 – 717) | (651 – 1186) |
| Alkalinity (mg/L $CaCO_3$) | 0 | 27 | 99 | 75 | 201 | 242 |
| | – | (13 – 40) | (56 – 168) | (20 – 136) | (75 – 299) | (78 – 380) |
| $HCO_3^-$ (mg/L) | 0 | 33 | 121 | 92 | 244 | 295 |
| | – | (15 – 48) | (68 – 204) | (24 – 166) | (91 – 365) | (95 – 463) |
| $N0_3^-$ ($\mu$g/L) | 7 | 7 | 7 | 6 | 8 | 24 |
| | (2 – 17) | (1 – 36) | (2 – 44) | (1 – 21) | (2 – 20) | (3 – 233) |
| $NH_4^+$ ($\mu$g/L) | 29 | 36 | 17 | 32 | 299 | 432 |
| | (1 – 202) | (2 – 145) | (2 – 110) | (0 – 470) | (2 – 2275) | (4 – 3516) |
| TDN ($\mu$g/L) | 1185 | 1185 | 1072 | 1027 | 1620 | 2649 |
| | (629 – 2304) | (936 – 1781) | (665 – 1837) | (613 – 1594) | (405 – 6251) | (1537 – 5633) |
| SRP ($\mu$g/L) | 20 | 9 | 21 | 4 | 36 | 161 |
| | (3 – 75) | (3 – 21) | (3 – 93) | (0 – 14) | (2 – 114) | (9 – 867) |
| TDP ($\mu$g/L) | 59 | 29 | 39 | 19 | 59 | 207 |
| | (23 – 132) | (13 – 42) | (13 – 100) | (9 – 46) | (3 – 117) | (23 – 1146) |
| TP ($\mu$g/L) | 110 | 99 | 143 | 57 | 313 | 433 |
| | (37 – 297) | (34 – 529) | (18 – 461) | (13 – 197) | (97 – 1014) | (79 – 1864) |
| $Na^+$ (mg/L) | 1 | 2 | 3 | 5 | 8 | 34 |
| | (1 – 2) | (2 – 3) | (3 – 4) | (2 – 7) | (3 – 13) | (3 – 64) |
| $Ca^{2+}$ (mg/L) | 3 | 9 | 18 | 21 | 47 | 55 |
| | (0 – 20) | (8 – 14) | (15 – 21) | (7 – 51) | (30 – 64) | (43 – 66) |
| $Mg^{2+}$ (mg/L) | 1 | 6 | 8 | 8 | 14 | 11 |
| | (0 – 8) | (4 – 9) | (7 – 9) | (3 – 26) | (11 – 18) | (0 – 22) |
| 1993 Water table depth (cm) | -39.6 | -4.2 | 7.9 | -2.8 | 32.4 | -22.0 |
| | (-28.1 – -49.8) | (-7.1 – -1.3) | (5.7–11) | (-12.7 – +4.7) | (18.9–50.2) | (-33.0 – -6.4) |
| 1994 Water table depth (cm) | -44.5 | -3.2 | 7.6 | 19.6 | -11.2 | 22.8 |
| | (-32.9 – -51.2) | (-10.1 – +4.5) | (-8.1 – +26.9) | (6.4–27.5) | (-14.7 – +17.3) | (13.6 – 40.1) |
| Depth af oxidation (cm) | 27.5 | 9.8 | 5.4 | 3.9 | 13.5 | ** |
| | (22.3 – 30.36) | (7.4 – 13.05) | (2.5 – 7.4) | (2.43 – 5.73) | (9.76 – 15.96) | ** |

Note: TDN = total dissolved nitrogen, SRP = soluble reactive phosphorus, TDP = total dissolved phosphorus, TP = total phosphorus, * measured only in 1994, and ** peat was completely anoxic.

*Net aboveground primary production in six peatlands*

Aboveground production of individual strata, total vascular, and total plant production are provided elsewhere (Thormann 1995; Thormann & Bayley in press). Briefly, the mean moss production in the bog (212 g $m^{-2}$ $y^{-1}$) was greater than in the fens (122 g $m^{-2}$ $y^{-1}$) during both years of this study. In FSF, moss NPP averaged 170 g $m^{-2}$ $y^{-1}$. NPP averaged 74 g $m^{-2}$ $y^{-1}$ in the LSF in 1993 and 1994. Mosses were very sparsely distributed in the RSF and their NPP was not determined. There was no moss stratum in either marsh.

Herb production increased significantly along the bog - fen - marsh peatland gradient ($p < 0.01$). The bog exhibited the lowest herb NPP of all the sites (35 g $m^{-2}$ $y^{-1}$, or 9% of its total NPP). The fens and marshes averaged an herb NPP of 249 g $m^{-2}$ $y^{-1}$ (72% of the total NPP) and 540 g $m^{-2}$ $y^{-1}$ (100% of the total NPP) during 1993 and 1994, respectively. Shrub production decreased significantly along the bog - fen - marsh gradient ($p < 0.05$). Neither marsh had a shrub stratum. A significant tree cover was present only in the bog and it contributed 7% to the total production within this site (approximately 27 g $m^{-2}$ $y^{-1}$).

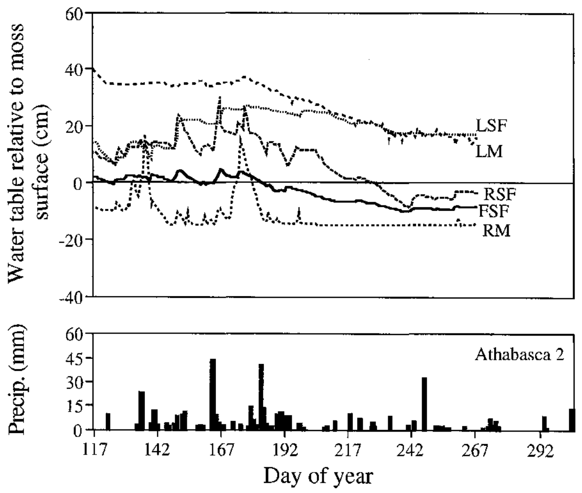


*Figure 3.* Water level fluctuations relative to the moss surface (0 cm) in five peatlands (FSF = floating sedge fen, LSF = lacustrine sedge fen, RSF = riverine sedge fen, RM = riverine marsh, LM = lacustrine marsh) during the 1994 growing season compared to daily precipitation at the nearby weather station (Athabasca 2).

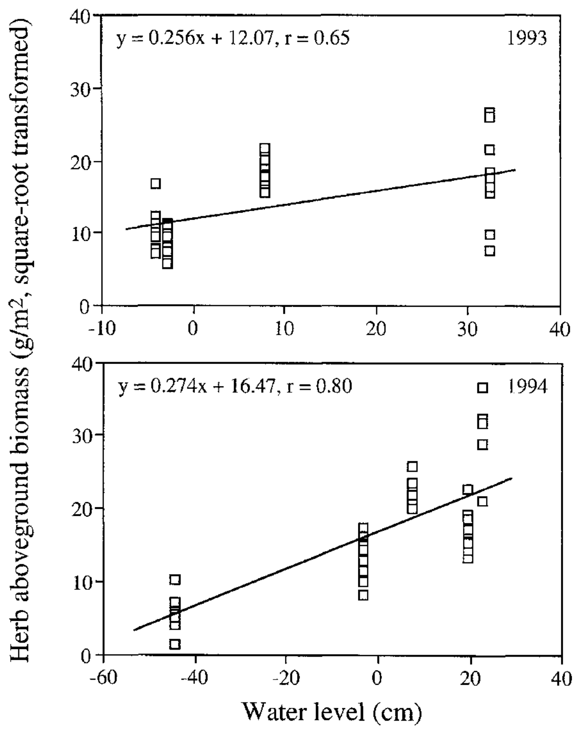


*Figure 4.* Peak herb aboveground biomass (square-root transformed) in relation to the mean site water level relative to the moss surface (0 cm). Symbols represent harvested quadrats from four (floating sedge fen, lacustrine sedge fen, riverine sedge fen, riverine marsh) and five (bog, floating sedge fen, riverine sedge fen, lacustrine sedge fen, lacustrine marsh) peatlands in 1993 and 1994, respectively.

Aboveground vascular plant production ranged from 178 g $m^{-2}$ $y^{-1}$ in the bog to means of 266 g $m^{-2}$ $y^{-1}$ in the three fens and 540 g $m^{-2}$ $y^{-1}$ in the two marshes during 1993 and 1994. Total aboveground plant production ranged from 390 g $m^{-2}$ $y^{-1}$ in the bog to means of 347 g $m^{-2}$ $y^{-1}$ in the three fens and 540 g $m^{-2}$ $y^{-1}$ in the two marshes during both years of this study. Our marshes were significantly more productive than these fens and the bog ($p < 0.05$). However, total aboveground NPP was similar in the bog and the fens ($p > 0.05$).

*Effects of water level, surface water nutrients, and climatic variables on aboveground plant production*

Herb aboveground NPP was positively correlated with water levels ($r = 0.65$ in 1993, $r = 0.80$ in 1994) (Figure 4), whereas terminal shrub NPP correlated negatively with this parameter ($r = -0.76$ in 1993, $r = -0.72$ in 1994) (Figure 5) during both years of this study.

Surface water concentrations of $NO_3^-$ ($r = 0.85$, 1993) and TP ($r = 0.74$, 1994) correlated best with the total plant NPP within the three fens (Table 2). Marsh vascular and total plant NPP correlated best with alkalinity ($r = 0.87$, 1993) and SRP ($r = 0.92$, 1994) (Table 2). Both vascular and total production in all six peatlands correlated best with adjusted conductivity ($r = 0.80$, $r = 0.78$) and SRP ($r = 0.76$, $r = 0.69$) during 1993 and 1994 (Table 3). $NO_3^-$ was also correlated significantly with vascular and total plant NPP in 1993 ($r = 0.53$, $r = 0.48$, respectively).

None of the climatic variables (temperature, growing degree days, precipitation) correlated significantly with aboveground plant production in these six peatlands.

*Carbon, nitrogen, and total phosphorus content of tissues from the dominant plant species*

The carbon content of *Carex lasiocarpa* and *Eriophorum vaginatum* in June ranged from 43.5% to 44.9% in 1993, and from 43.9% to 45.3% in 1994. There were no significant differences in the carbon content of the plant tissues among sites, years or species, nor within sites throughout either growing season ($p > 0.05$).

The nitrogen content in tissues of *Carex lasiocarpa* ranged from 1.6% to 2.8% in June 1993, and from 1.9% to 2.5% in June 1994 (Table 4). *Eriophorum vaginatum* tissues contained 1.8% N in June of 1994

*Table 2.* Correlation coefficients of vascular and total plant productivity (vasc. and tot. prod.) with various surface water chemistry parameters in five peatlands (fens: floating sedge fen, lacustrine sedge fen, riverine sedge fen; marshes: riverine marsh, lacustrine marsh) in 1993 and 1994. SRP = soluble reactive phosphorus, TP = total phosphorus, TDP = total dissolved phosphorus and TDN = total dissolved nitrogen, * = 0.05 > $p$ > 0.01, ** 0.01 > $p$ > 0.001.

| Type | 1993 | | | 1994 | | |
|---|---|---|---|---|---|---|
| | Parameter | r | p | Parameter | r | p |
| Fens | | | | | | |
| Vasc. prod. | SRP | 0.80 | ** | TP | 0.67 | * |
| | $NO_3^-$ | 0.53 | ** | $NO_3^-$ | 0.65 | ** |
| | TDN | 0.24 | * | | | |
| | TDP | 0.13 | ** | | | |
| Tot. prod. | $NO_3^-$ | 0.85 | ** | TP | 0.75 | * |
| | SRP | 0.40 | * | TDP | 0.43 | * |
| | pH | 0.30 | * | | | |
| Marshes | | | | | | |
| Vasc. and Tot. prod. | Alkalinity | 0.87 | * | SRP | 0.92* | |

*Table 3.* Correlation coefficients of vascular and total plant productivity with various surface water chemistry parameters in five peatlands (floating sedge fen, lacustrine sedge fen, riverine sedge fen, riverine marsh, lacustrine marsh) in 1993 and 1994. SRP = soluble reactive phosphorus, TDN = total dissolved nitrogen, adj. cond. = adjusted conductivity, NPP = net primary production, * = 0.05 > $p$ > 0.01, ** 0.01 > $p$ > 0.001, *** 0.001 > $p$ > 0.0001.

| | 1993 | | | 1994 | | |
|---|---|---|---|---|---|---|
| NPP | Parameter | r | p | Parameter | r | p |
| Vascular | Adj. Cond. | 0.80 | *** | SRP | 0.76 | ** |
| | $NO_3^-$ | 0.53 | ** | TDN | 0.39 | * |
| | $NH_4^+$ | 0.24 | * | | | |
| | pH | 0.20 | * | | | |
| Total | Adj. Cond. | 0.78 | *** | SRP | 0.69 | ** |
| | $NO_3^-$ | 0.48 | ** | TDN | 0.46 | * |
| | $NH_4^+$ | 0.30 | ** | | | |

(tissue nutrient levels were not determined for this herb in 1993). *Carex lasiocarpa* tissue nitrogen concentrations decreased in all minerotrophic sites; however, *E. vaginatum* tissue nitrogen levels increased in the bog from late June to late August. The only significant change in tissue nitrogen levels occurred in the RM in 1993 ($p < 0.05$).

June C:N quotients of *Carex lasiocarpa* ranged from 16 to 27 in 1993, and from 19 to 24 in 1994. The C:N quotient of *Eriophorum vaginatum* in June was 25 (only determined in 1994) and did not change significantly ($p > 0.05$) (Table 4). The C:N quotient increased in all minerotrophic sites but decreased in the bog in 1993 and 1994 due to the changes in N tissue content. C:N quotients changed significantly in the LM, RM, FSF, and RSF in 1993 and 1994, and in the LSF only in 1994 (all $p < 0.05$).

Total phosphorus concentrations of *Carex lasiocarpa*-ranged from 1,410 (0.14%) to 2,620 $\mu g\ g^{-1}$ dry weight (0.26%) in June 1993 and from 1,628 (0.16%) to 2,626 $\mu g\ g^{-1}$ dry weight in June 1994 (0.26%) (Table 5). TP concentrations of *Eriophorum vaginatum* were 1,538 $\mu g\ g^{-1}$ dry weight (0.15%) in June 1994 (not determined in 1993). Significant decreases in TP tissue levels occurred only in the RSF in 1993 and 1994, and in the LM in 1994 (all $p < 0.05$) (Table 5).

## Discussion

### *Aboveground plant production in relation to environmental variables*

#### *Mosses*

Mean *Sphagnum fuscum* NPP in the bog was greater than the mean NPP of the fen moss species (*Aulacomnium palustre* and *Sphagnum warnstorfii* in the FSF, and *Drepanocladus aduncus* in the LSF) (Thormann 1995; Thormann & Bayley in press). In those sites where moss production was determined, the NPP increased substantially from 1993 to 1994. Moss NPP exhibited greater variation among sites than between years, indicating the importance of climatic parameters for this stratum. Mosses were very sparsely distributed in the RSF and their NPP was not determined. A moss stratum was absent in both marshes in 1993 and 1994.

Backéus (1988) reported a correlation between the timing and quantity of precipitation and *Sphagnum* spp. growth during the month of June. Our results support his findings. Although there were more days with precipitation in June 1993 than in June 1994 (12 days versus 9 days in 1994, respectively), the total precipitation was greater in June 1994 (90.2 mm versus 73.4 mm in 1993). Also, Brock & Bregman (1989) and Moore (1989) found a positive correlation between air temperature and *Sphagnum* spp. growth. The mean temperature from May to October was 1 °C higher

*Table 4.* Mean percent nitrogen and C:N quotients of the dominant plant species (bog = *Eriophorum vaginatum*, all other sites = *Carex lasiocarpa*) in six peatlands (bog, FSF = floating sedge fen, RSF = riverine sedge fen, LSF = lacustrine sedge fen, RM = riverine marsh, LM = lacustrine marsh) in 1993 and 1994. The bog was sampled only in 1994.

| Site | 1993 | | | | | | 1994 | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | June 26 % N | July 26 % N | Aug. 26 % N | June 26 C:N | July 26 C:N | Aug. 26 C:N | June 26 % N | July 26 % N | Aug. 26 % N | June 26 C:N | July 26 C:N | Aug. 26 C:N |
| Bog | – | – | – | – | – | – | 1.8 | 1.9 | 2.1 | 25 | 24 | 22 |
| | – | – | – | – | – | – | (0.06) | (0.05) | (0.14) | (0.63) | (0.60) | (1.60) |
| FSF | 1.9 | 1.9 | 1.6 | 23 | 24 | 28 | 1.9 | 1.5 | 1.3 | 24 | 30 | 36 |
| | (0.08) | (0.08) | (0.06) | (0.90) | (0.95) | (1.14) | (0.10) | (0.08) | (0.07) | (1.25) | (1.56) | (2.07) |
| RSF | 2.2 | 1.7 | 1.5 | 21 | 27 | 31 | 2.0 | 1.3 | 1.3 | 24 | 36 | 35 |
| | (0.15) | (0.08) | (0.03) | (1.62) | (1.20) | (0.65) | (0.15) | (0.07) | (0.07) | (1.99) | (2.24) | (1.97) |
| LSF | 1.8 | 1.6 | 1.5 | 26 | 28 | 29 | 1.9 | 1.5 | 1.3 | 24 | 31 | 35 |
| | (0.07) | (0.08) | (0.04) | (1.07) | (1.33) | (0.80) | (0.08) | (0.08) | (0.06) | (1.32) | (1.60) | (1.68) |
| RM | 2.8 | 2.2 | 1.7 | 16 | 21 | 26 | 2.5 | 2.3 | 2.1 | 19 | 19 | 21 |
| | (0.20) | (0.15) | (0.15) | (1.23) | (1.65) | (2.36) | (0.36) | (0.14) | (0.19) | (3.02) | (1.25) | (1.94) |
| LM | 1.6 | 1.7 | 1.2 | 27 | 27 | 37 | 2.0 | 1.8 | 1.2 | 22 | 25 | 36 |
| | (0.12) | 0.19) | (0.12) | (2.11) | (3.09) | (3.10) | (0.19) | (0.16) | (0.10) | (2.11) | (2.72) | (3.18) |

*Table 5.* Comparison of TP (total phosphorus, $\mu g\ g^{-1}$) content of two plant species in six peatlands (bog, FSF = floating sedge fen, RSF = riverine sedge fen, LSF = lacustrine sedge fen, RM = riverine marsh, LM = lacustrine marsh) in 1993 and 1994. The bog was sampled only in 1994.

| Site | Species | 1993 | | | 1994 | | |
|---|---|---|---|---|---|---|---|
| | | June | July | August | June | July | August |
| Bog | *Eriophorum vaginatum* | – | – | – | 1,538 | 1,698 | 1,179 |
| FSF | *Carex lasiocarpa* | 1,411 | 1,417 | 1,221 | 1,628 | 1,521 | 1,164 |
| RSF | *Carex lasiocarpa* | 1,930 | 1,829 | 1,418 | 2,034 | 1,557 | 1,369 |
| LSF | *Carex lasiocarpa* | 1,567 | 1,364 | 1,349 | 1,903 | 1,425 | 1,324 |
| RM | *Carex lasiocarpa* | 2,620 | 2,177 | 1,488 | 2,393 | 2,196 | 1,807 |
| LM | *Carex lasiocarpa* | 1,690 | 1,673 | 1,560 | 2,626 | 2,135 | 1,298 |

in 1994 (12.4 °C) and the number of growing degree days (GDD) was greater in 1994 (1,416 versus 1,350 in 1993). Therefore, temperatures may have been more favorable for the growth of *S. fuscum* in the second year of this study.

Several studies have shown that moss growth may be limited by nutrients, particularly nitrogen and phosphorus (Aerts et al. 1992; Malmer 1990; Vitt 1990; Brock & Bregman 1989). Higher concentrations of $NH_4^+$, SRP, TDP, and TP were detected in the surface water in the bog in 1994, possibly resulting in the large increase in moss NPP in this site ($p < 0.05$). All other surface water nutrient concentrations were similar in 1993 and 1994. It is unclear whether the lowered water level or the higher nutrient concentrations contributed to the increase in moss growth.

We speculate that moss growth in the FSF and LSF was also positively influenced by these more favourable climatic variables during the second year of this study in addition to the effects of surface water nutrient concentrations.

*Herbs*

Herb production increased along the bog - fen - marsh peatland gradient (Thormann 1995; Thormann & Bayley in press), and varied significantly among sites. Herb NPP was positively correlated with water levels ($r = 0.65$ in 1993, $r = 0.80$ in 1994) (Figure 4); however, our correlations were weaker than those of Szumigalski & Bayley (unpublished).

Laitinen (1990) showed that herbs, specifically *Carex* spp., are more tolerant of water saturated soils than shrubs. The mean growing season water level dropped by 43.6 cm from the first to the second year in the RM (Table 1), and peak herb production decreased by 25%. Conversely, in the LM, the mean growing season water level rose by 44.8 cm from 1993 to 1994 (Table 1), and herb production increased by 60%. However, the most prominent herb production increase occurred in the LSF. The mean growing season water level rose by 22.4 cm from 1993 to 1994 (Table 1), and herb production increased by 376%. Szumigalski & Bayley (unpublished) reported that a drop of 14 cm in the water level caused the herb NPP to decrease by 40% in the same site between 1991 and 1992. It appears that the nutrients associated with the water column played a more prominent role affecting herb NPP in the nutrient-poorer LSF than they did in the nutrient-richer LM. This is evident from the comparably 'small' mean water level change in the LSF between 1993 and 1994, which resulted in the most significant increase in herb NPP. Similar positive correlations between herb production and water levels were previously reported by Hillman et al. (1990), Bayley et al. (1985), Lieffers & Shay (1982), and Richardson (1978) in other North American wetlands. Climatic variables, such as growing degree days, mean annual temperature and precipitation, and surface water nutrient concentrations did not correlate significantly with herb production in these sites.

*Shrubs*

Shrub production decreased significantly along the bog - fen - marsh peatland gradient (Thormann 1995; Thormann & Bayley in press), and showed a significant negative correlation to the water level ($r = -0.76$ in 1993 and $r = -0.72$ in 1994) (Figure 5). Hillman et al. (1990) showed that deciduous shrubs had an increase in production, and that ericaceous shrubs had either less growth and vigor or no change in production at lower water levels. The bog had the lowest water level (Table 1) and the greatest deciduous shrub production (36 g $m^{-2}$ $y^{-1}$ in 1994). The FSF and LSF averaged 14 g $m^{-2}$ $y^{-1}$ in 1993 and 1994 of deciduous shrub production. Even though these mean NPP values are not different in the latter two sites, deciduous shrub production tended to decrease with higher water levels. Shrubs grew almost exclusively on dry hummocks rather than in wet hollows in the LSF. Our results are supported by those of Szumigalski & Bayley (unpublished), Backéus (1990), Hillman et al. (1990), Moore (1989), and Wallén et al. (1988), as waterlogged soils inhibit oxygen absorption by shrub roots (Reader 1978).

Shrub strata were absent in the RSF and both marshes, possibly a result of the consistently high water level, which may inhibit seed germination. Kozlowski et al. (1991) showed that a raised water level decreases oxygen transfer to seedlings and roots of woody plants. This may reduce vegetative and reproductive growth and may lead to death.

Few studies relate shrub production to surface water nutrients, and their results differ substantially (Szumigalski & Bayley unpublished; Reader 1982). Climatic variables, such as growing degree days, temperature, and precipitation did not correlate significantly with shrub production in this study.

*Trees*

The bog exhibited the only significant tree cover of all sites, but this stratum did not provide a notable contribution towards total NPP (Thormann 1995; Thormann & Bayley in press). Hillman et al. (1990) showed that tree growth is enhanced in aerated and dry peatland soils in northern Alberta. Supportingly, Jeglum (1974) demonstrated that tree growth is inhibited in wet, waterlogged soils in northern Ontario. Our results support both of these studies, as the bog had the lowest water level relative to the moss surface (mean of -42 cm) and the greatest depth of oxidation (27.5 cm in 1994) (Table 1). All other sites had higher water levels relative to the peat surface, and shallower depths of oxidation (Table 1).

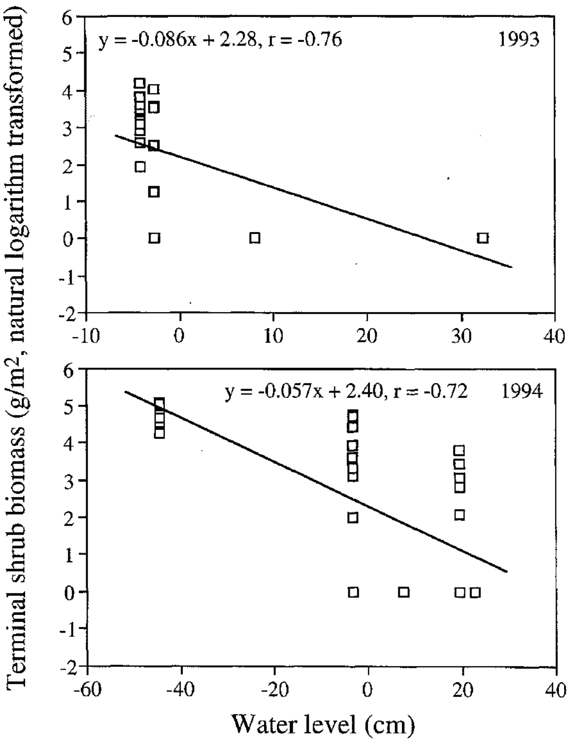


*Figure 5.* Peak shrub terminal aboveground biomass (new leaves and stems) (natural-log transformed) in relation to the mean site water level relative to the moss surface (0 cm). Symbols represent harvested quadrats from four (floating sedge fen, lacustrine sedge fen, riverine marsh, lacustrine marsh) and five (bog, floating sedge fen, lacustrine sedge fen, riverine marsh, lacustrine marsh) peatlands in 1993 and 1994, respectively.

*Vascular and total plant production*

Vascular plant NPP in fens related best to surface water concentrations of SRP ($r = 0.80$) and TP ($r = 0.67$) in 1993 and 1994, respectively (Table 2), whereas total plant NPP in these fens related best to $NO_3^-$ ($r = 0.85$) and TP ($r = 0.75$) in 1993 and 1994, respectively. Marsh vascular and total plant NPP related best to alkalinity ($r = 0.87$) in 1993 and to SRP ($r = 0.92$) in 1994 (Table 2). The variation in both vascular and total plant production in all six peatlands correlated best with adjusted conductivity ($r = 0.80$, $r = 0.78$) and SRP ($r = 0.76$, $r = 0.69$) surface water concentrations in 1993 and 1994 (Table 3).

It is generally believed that either nitrogen (N), phosphorus (P), or potassium (K) limits plant production in peatlands (Mitsch & Gosselink 1993; Reader 1978). Updegraff et al. (1995) determined that the temperature, soil type, and aeration of the organic soil significantly affect nutrient mineralization rates in wetlands (specifically those of C and N). These factors primarily affect the small labile bioavailable fraction of nutrients within the wetland, rather than the larger biounavailable nutrient pool. Thus, organic soils may have large quantities of N or P tied up in organic forms; however, these nutrients may be unavailable to plants, and, thus, limiting to plant growth (Updegraff et al. 1995; Mitsch & Gosselink 1993). Furthermore, rates of water flow, water level fluctuations, rates of nutrient mineralization, and succession within each site may all influence vegetation production and mask the effects of chemical factors. Gorham (1950) determined that competition between vegetation strata also decreases the effects of surface water nutrients on plant growth in peatlands. Therefore, results from similar studies will vary, and no generalizations regarding the effects of surface water nutrients on vascular and total plant productions can be made.

*Carbon, nitrogen, and total phosphorus content of tissues from the dominant indigenous vegetation*

*Carex lasiocarpa in three fens and two marshes*

Tissue nitrogen concentrations were variable in these fens and marshes, ranging from 1.6 to 2.8% in late June (Table 4). *Carex lasiocarpa* from the RM had the highest nitrogen tissue concentrations in 1993 and 1994, whereby the remaining fens and marsh had tissue nitrogen levels up to 1.2% lower (Table 4). In all cases, these levels decreased from late June to late August (Table 4). Generally, tissue nutrient concentrations of N and TP in *C. lasiocarpa* were similar among the fens and marshes in late June and late August, and they followed a similar decreasing trend during the 1993 and 1994 growing seasons (Tables 4 and 5).

Auclair (1977) determined that *Carex* spp. N and P tissue concentrations are positively correlated to the stem density of the stand. He suggested that with a high stem density each plant would have relatively higher tissue nutrient concentrations. Plants growing in a high stem density environment require smaller quantities of carbon-rich tissues for structural support; however, plants growing in a low stem density environment require larger quantities of carbon-rich tissues, since they do not have the structural support from neighboring plants. Auclair's (1977) results are supported by this study. Even though stand densities were not determined in this study, we assume that they correlate positively with NPP. TP and N tissue concentrations in June increased as production increased within the LM and the LSF from 1993 to 1994. In the RM, the total NPP decreased from the first to the second year, as did the tissue nutrient concentrations. However, not all of these changes were significant from 1993 to 1994. Total aboveground NPP was similar in the RSF in 1993 and 1994 (Thormann 1995; Thormann & Bayley in press), thus, tissue N and TP concentrations were also similar during both years of this study (Tables 4 and 5).

Simultaneous carbon, nitrogen, and phosphorus tissue concentrations (N, TP) from *Carex* spp. in boreal wetlands are rare in the literature. Most studies examine these variables in either bogs, fens, or marshes (Chapin III et al. 1988; Kistritz et al. 1983; Richardson et al. 1978; Klopatek 1978; Auclair 1977; Small 1971). From these and our study, no clear trends in tissue nutrient concentrations of N and TP in *Carex* spp. are detectable among North American wetlands.

Differences in TP and N tissue concentrations can in part be explained by the different ecosystems in which the herb grew (tussock tundra versus bogs), different surface water concentrations of nutrients, and the different *Carex* spp. examined. Rates of decomposition and nutrient mineralization differ among ecosystems, nutrient requirements vary among different *Carex* spp., and nutrients leach at varying rates from different plants, possibly even from plants of the same genus and/or species. It is difficult to compare our tissue nutrient levels to those of other studies without knowing standing crops of vegetation biomass, site species composition, surface water nutrients, collection dates of the analyzed plant material, or the location of the collected plant material within a site (margin versus centre of site) (Richardson et al. 1978). Thus, direct comparisons of our data to those of other studies require caution.

*Eriophorum vaginatum in the bog*

Tissue nutrient concentrations of *Eriophorum vaginatum* showed a variable response pattern. The nitrogen tissue concentrations increased from late June to late August by 22% (the C:N quotient decreased) (Table 4), whereas TP tissue levels decreased by 23% over the same period (Table 5).

Similar tissue nutrient concentration analyses in *E. vaginatum* were done by Chapin III et al. (1988), Lechowicz & Shaver (1982), and Small (1971). As with tissue nutrient concentrations of N and TP of *Carex lasiocarpa*, no clear trends are detectable in these data. When comparing the results of these previous studies to ours, it appears that N tissue concentrations in this species are independent of latitude. Our results are comparable to both Chapin III et al.'s (1988) and Small's (1971). However, in all previous studies, the N tissue concentrations decreased towards the end of the growing season, whereas they increased from late June to late August in this bog (Table 4). This is possibly due to higher surface water nitrogen concentrations in this site compared to those of the other studies. The increase in tissue N concentrations caused a decrease in the C:N quotient from late June to late August (Table 4). Fertilization experiments showed that P caused the greatest increase in NPP, indicating that P, rather than N, is limiting growth of *E. vaginatum* in this site (Thormann 1995; Thormann & Bayley in press). Therefore, tissue phosphorus concentrations will decrease before tissue nitrogen concentrations. It may also explain the lower TP levels in this species in the bog compared to those found in the same species in other bogs and the Alaska tussock tundra.

Even though the TP content in *Eriophorum vaginatum* may vary in magnitude among studies, these differences can partially be explained by different surface water nutrient concentrations of the different sites, and the differing ecosystems (bogs versus tussock tundra). In all cases, the TP content in *E. vaginatum* tissues decreases towards the end of the growing season due to leaching and translocation of phosphorus from aboveground to belowground tissues. Direct comparisons with other studies require caution due to the aforementioned reasons.

## Conclusions

Moss NPP was primarily affected by climatic parameters, whereas herb and shrub production correlated significantly with water levels. In these fens, vascular and total plant production generally correlated with phosphorus related parameters (SRP and TP), indicating that phosphorus may be the most limiting surface water nutrient in central Alberta fens. In the marshes, alkalinity and SRP correlated most significantly with vascular and total plant production.

Tissue nutrient concentrations of N and TP of *Carex lasiocarpa* in the nutrient richer fens and marshes and *Eriophorum vaginatum* in the nutrient poorer bog seemed to be affected by stand densities and the nutrient status of the peatland, respectively.

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