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# Aboveground net primary production along a bog-fen-marsh gradient in southern boreal Alberta, Canada[1]

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*Abstract:* Total aboveground plant production in a bog, three rich fens and two marshes were determined via the multiple harvest and cranked wire techniques. These peatlands follow a gradient of increasing pH, water flow, and surface water nutrient concentrations from the bog to the rich fens to the eutrophic marshes. The net primary production (NPP) values were as follows: (*i*) bog, 390 g $m^{-2}$ year$^{-1}$, (*ii*) three rich fens (riverine sedge fen, lacustrine sedge fen, and floating sedge fen), 409 g $m^{-2}$ year$^{-1}$, 277 g $m^{-2}$ year$^{-1}$ and 356 g $m^{-2}$ year$^{-1}$, respectively, and (*iii*) one riverine and one lacustrine marsh, 323 g $m^{-2}$ year$^{-1}$ and 757 g $m^{-2}$ year$^{-1}$, respectively. Overall, the bog and the three fens had a similar NPP but they were significantly less productive than the marshes. Along this bog-fen-marsh gradient, moss and shrub production decreased and herb production increased. Herb and moss production exhibited a greater variation between years than among sites within each year. Shrub production remained similar during both years of this study. A significant tree stratum was only present in the bog. Generally, NPP was greater in 1994 than in 1993. Comparisons with other NPP data from bogs, fens, and marshes throughout North America showed that the results of this study complement a latitudinal gradient of NPP for bogs. The latitudinal gradient for NPP in fens and marshes is less pronounced.

*Keywords:* bog, fen, marsh, boreal, aboveground production, latitudinal gradient.

*Résumé:* La production végétale aérienne totale dans une tourbière ombrotrophe, dans trois tourbières minérotrophes (fen) riches et dans deux marais a été déterminée grâce à de multiples récoltes et par la technique des tiges coudées. Lorsque l'on passe de la tourbière ombrotrophe aux tourbières minérotrophes puis aux marais, on observe un gradient croissant de pH, de circulation d'eau et de concentration en éléments nutritifs dans les eaux de surface. Les valeurs de production primaire nette (PPN) sont les suivantes: (*i*) tourbière ombrotrophe: 390 g par $m^2$ par année, (*ii*) tourbières minérotrophes: 409 (fen de carex riverain), 277 (fen de carex lacustre) et 356 (fen de carex flottant) g par $m^2$ par année, et (*iii*) marais: 323 (marais riverain) et 757 (marais lacustre) g par $m^2$ par année. En général, la tourbière ombrotrophe et les tourbières minérotrophes ont une PPN similaire, mais elles sont significativement moins productives que les marais. Le long de ce gradient (tourbière ombrotrophe-tourbières minérotrophes-marais), la productivité des mousses et des arbustes diminue alors que celle des plantes herbacées augmente. La productivité des plantes herbacées et des mousses est plus variable d'une année à l'autre qu'entre les différents sites à l'étude pour une année donnée. La productivité des arbustes est demeurée similaire au cours des deux années de l'étude. Une strate arborescente significative n'est présente que dans la tourbière ombrotrophe. En général, la PPN était plus grande en 1994 qu'en 1993. La comparaison de ces données avec celles en provenance d'autres tourbières et marais de l'Amérique du Nord montre que les résultats de cette étude complètent le réseau actuel de données sur la PPN des tourbières ombrotrophes et ce, le long d'un gradient latitudinal. Le gradient latitudinal de la PPN des tourbières minérotrophes et des marais est moins prononcé que celui des tourbières ombrotrophes.

*Mots-clés:* tourbière ombrotrophe, tourbière minérotrophe, marais, boréal, production aérienne, gradient latitudinal.

## Introduction

Peatlands cover approximately 14% of Canada's and 21% of Alberta's surface (Natural Wetlands Working Group, 1988). They are defined as waterlogged ecosystems (Gorham, 1991), where plant production exceeds the rate of decomposition (Zoltai, 1988), and the peat thickness is greater than 30-40 cm (Gorham, 1991). Peatlands are among the world's most important ecosystems (Natural Wetlands Working Group, 1988), and just recently have been understood to be sources, sinks, and transformers of a multitude of chemical, biological and genetic materials (Mitsch & Gosselink, 1993). Therefore, peatlands have great economic, recreational, agricultural, water resource, wildlife, and fishing values (Alberta Water Resources Commission, 1993).

Several European and North American studies have examined non-vascular and vascular aboveground net primary production (Neill, 1993; Francez, 1992; Wieder *et al*., 1989; Bartsch & Moore, 1985; Grigal, Buttleman & Kernik, 1985; Vasander, 1982; Mason & Bryant, 1975; Forrest & Smith, 1975; Reader & Stewart, 1972). The majority of these studies were conducted in tundra/subarctic or deciduous forest regions. Despite Alberta's wealth of peatlands, most studies have concentrated on either bryophyte (Vitt, 1990) or sedge (Gorham & Somers, 1973) NPP. Only recently has a study been carried out that examined the total net primary production along a bog to extreme-rich fen gradient in this region (Szumigalski & Bayley, 1996). Values of belowground production are scarce in the literature (Wallén, 1992) due to the difficulty of collecting belowground tissues of plants. It has been estimated that up to 90% of the total biomass of wetland plants is in belowground tissues (Wallén, 1992; Sjörs, 1991), and that the variation in the ratio of belowground to above-

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ground biomass varies considerably even within the same species. Also, Wallén (1992) determined that the proportion of belowground biomass with respect to the total biomass is species specific for wetland plants.

We examined five peatlands in 1993 and 1994, and an additional sixth in 1994 in central Alberta, Canada. They were a bog, three rich fens, and two eutrophic marshes. These peatlands represent a gradient based on the elevation of surface water, inflow of nutrients, nutrient concentrations, pH, (Thormann & Bayley, 1997), vegetation type, and peat accumulation characteristics (Mitsch & Gosselink, 1993). Bogs are ombrotrophic, acidic, *Sphagnum spp*. dominated peatlands that receive nutrients only from precipitation. Fens and marshes are minerotrophic peatlands that receive nutrients from precipitation as well as from surface and groundwater flow. Water level fluctuations throughout the year are greater in marshes than in fens (Vitt *et al*., 1996). The pH in fens and marshes is acidic to neutral to alkaline. Fens are dominated by *Sphagnum spp*. (poor fens), brown mosses (rich and extreme-rich fens), sedges, grasses, and shrubs, and they are mesotrophic with organic soil. Marshes are generally eutrophic peatlands that are dominated by sedges, reeds, and grasses, with shrubs and mosses generally lacking. Sjörs (1952) determined that the pH, relative conductivity, surface water $Ca^{++}$ concentrations, and the number of indicator species increases from bogs to fens. This increasing gradient of surface water chemistry parameters was shown by Vitt & Chee (1990) in poor, moderate-rich, and rich fens in Alberta, but this increase may not apply to nitrogen (N) and phosphorus (P) in the surface water (Vitt & Chee, 1990; Malmer, 1986); however, fens receive more nutrients than bogs due to their greater in- and efflux of water (Sparling, 1966). Marshes are usually eutrophic and have the highest concentrations of N and P compared to fens and bogs (Thormann & Bayley, 1997; Mitsch & Gosselink, 1993), and Sjörs' (1952) increasing gradient of relative conductivity and $Ca^{++}$ can be extended from fens to marshes (Mitsch & Gosselink, 1993). In addition, peat depth is generally greater in bogs than in fens (National Wetlands Working Group, 1988). Marshes are characterized by the presence of a wet mineral soil in many areas but a shallow, well decomposed layer of peat may be present in some areas as well (National Wetlands Working Group, 1988). Both marshes in this study have peat accumulations (Thormann & Bayley, 1997).

The ecological relationships of the NPP of individual vegetation strata (mosses, herbs, shrubs), and total production are discussed in Thormann & Bayley (1997). Also, physical and surface water chemical parameters are presented in that manuscript. Briefly, we found that herb and shrub production correlated positively and negatively with water levels, respectively, and moss production correlated significantly with climatic variables (growing degree days, mean annual growing season temperature, and precipitation) in those sites that had a notable moss stratum (bog, floating sedge fen, and lacustrine sedge fen) (Thormann & Bayley, 1997). Furthermore, total NPP (vascular and non-vascular plants) in these fens correlated significantly with $NO_3^-$ and total phosphorus in 1993 and 1994. Total NPP in the marshes correlated significantly with alkalinity in 1993, and soluble reactive phosphorus in 1994 (Thormann & Bayley, 1997). We refer the reader to Thormann & Bayley (1997) for a detailed treaty on the relationships between NPP and physical, chemical, and climatic parameters within these peatlands.

In this paper, we present the non-vascular (moss), vascular (herbs, shrubs, and trees), and total aboveground net primary plant production values for a bog, three rich fens, and two eutrophic marshes in central Alberta. This is the first study that examines aboveground net primary plant production along a bog-fen-marsh peatland gradient in North America simultaneously. Most production studies concentrate on a particular peatland type (bog, fen, marsh, swamp), and year to year variation of parameters, such as water level fluctuations and surface water nutrient concentrations, presents problems comparing production values obtained from different peatlands in different years. This study represents an extension of the bog to poor fen to rich fen to extreme-rich fen peatland gradient of Szumigalski & Bayley (1996). Also, information on the net primary production in western Canadian peatlands is essential in understanding peat accumulation potentials and rates and responses to global climate changes. We hypothesize that the NPP increases from bogs to fens to marshes in southern boreal Alberta due to the increased nutrient availability towards the eutrophic end of the gradient.

## Study area and site descriptions

The five study sites that were examined in 1993 and 1994 (three fens and two marshes) and an additional sixth in 1994 (the bog) represent the range of peatlands present in the southern boreal region of western Canada. These sites were classified according to hydrologic and surface water chemical characteristics (Thormann & Bayley, 1997). 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), 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).

The climate of the area is characterized by mild summers and cold, snowy winters (Vitt *et al*., 1995). The long term mean annual temperature is 1.7°C (Environment Canada, 1982), and the total mean precipitation is approximately 500 mm for all sites. Vitt *et al*. (1995) give a detailed description of the vegetation and the water chemistry of the bog, the floating sedge fen (their moderate-rich fen), and the lacustrine sedge fen (their extreme-rich fen). All six peatlands lie within the Subhumid Low Boreal ecoclimatic region of Canada (Ecoregions Working Group, 1989). The brown moss and *Sphagnum* nomenclatures follow Anderson, Grum & Buck, (1990) and Anderson (1990), respectively, while that of the vascular plants follows Moss (1983).

### BOG

The bog is a large, raised ombrotrophic island with 5 m (Vitt *et al*., 1995) of peat within a large peatland complex. The peat is arranged in large, dry hummocks which are separated by intermittent wetter hollows. A sparse tree layer of *Picea mariana* (Mill.) B.S.P. covers about 25% of the wooded part of the bog, while *Ledum groenlandicum* Oeder dominates the ericaceous shrub layer (percent cover is approximately 75%). The sparse herb stratum consists primarily of *Smilacina trifolia* (L.) Desf., and *Sphagnum fuscum* (Schimp.) Klinggr. comprises about 90% of the moss layer. Vitt *et al.* (1995) provide a more detailed description of this site.

### LACUSTRINE SEDGE FEN (LSF)

This site is a large expanse of sedge-dominated peatland situated beside a large body of water (approximately 0.8 km$^2$). This fen's topography is mainly flat with the occasional small hummock (about 5% of the peatland surface). In 1993, the water level was below the peat surface but in 1994, this site was flooded, possibly due to beaver dams blocking outflows of drainage channels. The vascular vegetation stratum consists primarily of *Carex lasiocarpa* Ehrh. and *C. diandra* Schrank. 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* (Mitt.) Warnst. and *Calliergon giganteum* (Schimp.) Kindb. in wet pools. A more detailed description of this site is in Vitt *et al.* (1995).

### 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. It receives water from a discrete inflow at the southern end and an outflow at the northern end controls the water table height. The water table was above the peat surface during the 1993 and 1994 growing seasons. The vascular vegetation strata are dominated by *Carex aquatilis* Wahlenb., *C. rostrata* Stokes, and *C. lasiocarpa* which together comprise about 95% of the cover. Mosses are very sparsely distributed, and shrubs are absent.

### FLOATING SEDGE FEN (FSF)

This fen is a floating mat surrounding a small body of water (approximately 0.2 km$^2$). The peat surface is a uniform carpet which fluctuates with the water table of the associated slough. The herb stratum is dominated by *Carex lasiocarpa*, while the shrub layer consists predominantly of *Salix pedicellaris*. The moss stratum is dominated by *Sphagnum warnstorfii* Russ. and *Aulacomnium palustre* (Hedw.) Schwaegr. Vitt *et al.* (1995) provide a more detailed description of this site.

### RIVERINE MARSH (RM)

This site is located on the floodplain of Tawatinaw River. During 1993, this marsh was periodically inundated with water and the water table was consistently above the peat surface. In 1994, a beaver dam just above the study area retained much of the stream flow, and the water table dropped well below the peat surface. The vascular vegetation layer is dominated by *Carex aquatilis* during spring and early summer with *Calamagrostis canadensis* (Michx) Beauv. and *C. inexpansa* A. Gray dominant during late summer and early fall. A number of other herb species are present but only sparsely distributed. There is no moss stratum present.

### LACUSTRINE MARSH (LM)

This marsh is situated on the northwestern shore of Wakomao Lake (approximately 3.6 km$^2$). During 1993, the water table was below the peat surface; however, in 1994, this site was flooded with water possibly due to beaver dams or constructed dams blocking the outflow(s) of the adjacent lake. The lake receives secondarily treated wastewater from Clyde (population < 1000) each spring and additional nutrients from agricultural run-off. No moss or shrub strata exist and the vascular vegetation layer is dominated by *Carex aquatilis, C. rostrata* and *C. atherodes* Spreng. (percent cover is approximately 95%). Also, *Typha latifolia* L. flourishes at the lake shore and *Scirpus microcarpus* Presl., *Galium labradoricum* Wieg. and *Hippuris vulgaris* L. comprise the remaining 5% of cover.

## 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 m × 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, 1996). These plots were randomly established within each site. Five randomly placed transects of 20 wires, placed about 5 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 m × 25 m (125 m$^2$) was established in June 1993. *Sphagnum warnstorfii* and *Aulacomnium palustre* are 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$^{-2}$ year$^{-1}$), the mass per unit length per surface area (g cm$^{-1}$ year$^{-1}$) was required. This was determined by extracting five cores of 85 cm$^2$ surface area (1/118 of 1 m$^2$) 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 4 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, Vitt & Bayley, 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 top one cm of each core was cut off, weighed, and this weight was multiplied by a surface area correction factor (118, see above) to attain a weight per one cm per square meter. The production values were obtained by multiplying these values by the yearly measured length increments from the cranked wires (cm year$^{-1}$).

Since the peat 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 depends directly on the peat surface at each site. To estimate the actual peat 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 peat surface was measured (cm). The coordinates ($x$, $y$) of all grid nodes in association with the depths to the peat 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, 1996), the LSF, and the FSF. The average ratio of actual peat 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 value (g $m^{-2}$ $year^{-1}$) (Table I).

The LSF had very few hummocks, and Clymo's 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 m × 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 (Vitt & Pakarinen, 1977; Vasander, 1982). 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 m × 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 randomly established plots used to measure moss production within the applicable sites. Due to the smaller area available in the FSF, the two plots were 5 m × 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 m × 0.50 m (0.25 $m^2$) randomly placed quadrats (5 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 1993.

All herbaceous plant material was clipped at the ground level during each harvest 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 sp., Betula sp.* and *Ledum sp.* were estimated from Szumigalski & Bayley (1996), 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 analysed for differences in vascular plant production between years, sites, transects within sites, and samples within transects. Belowground production of the vegetation in these sites was not determined as part of this study.

TABLE I. Growth and net primary plant production of moss species in three peatlants in 1993 and 1994. Bulk density is in grams per centimeter per square meter, growth in in centimeters and production is in grams per square meter per period

| Site/species | | | 1993 | | 1994 | |
|---|---|---|---|---|---|---|
| | Bulk density | Surface area correction factor | May-October growth | May-October production | May-October growth | May-October production |
| BOG | 474 | 1.09* | | | | |
| *Sphagnum fuscum* | | | 0.38 | 155.9 | 0.65 | 267.8 |
| FSF | 92 | 1.11 | | | | |
| *Sphagnum warnstorfii* | | | 0.54 | 33.2 | 4.46 | 275.3 |
| *Aulacomnium palustre* | | | 0.72 | 136.2 | 2.15 | 404.7 |
| LSF | 419 | 1.01 | | | | |
| *Drepanocladus aduncus* | | | 0.26 | 26.8 | 1.18 | 120.8 |

*The surface area correction factor was adopted from Szumigalski & Bayley (1996)

### *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 (1996) in our analyses. These values were determined by measuring large (> 1.8 m) and small (< 1.8 m) trees, employing tree height, diameter at breast height (approximately 1.3 m), basal diameter, and leader length measurements.

### STATISTICAL ANALYSES

Randomized nested-block ANOVA designs (samples nested in transects, nested in plots, nested in sites) were used to analyse the vascular (herbs, shrubs, and trees) and the total production (herbs, shrubs, trees, and mosses) separately. After significance was detected in the ANOVA procedures, Tukey significant difference tests were performed. Furthermore, *t*-tests were used to detect significant differences in NPP between years within each site. All statistical analyses were performed on SAS (SAS Institute Inc., 1989).

Since we only examined one bog, the problem of pseudoreplication arises due to the absence of replication within this peatland class. The fens and marshes were grouped into two separate peatland classes for comparisons among all three peatland types (bog, fens, and marshes). Combining the three rich fens and two marshes into two peatland classes was possible because of the homogeneity of variances (Zar, 1984) of the NPP data within the three fens and two marshes.

## Results

### MOSS PRODUCTION

Mosses were present in three of the six sites (bog, FSF, LSF). In these three sites, there were generally more differences in moss production between years than there were among sites. Moss production was significantly ($p < 0.05$) lower in 1993 than in 1994. The LSF had the lowest moss production in 1993 (27 g $m^{-2}$ $year^{-1}$) and 1994 (121 g $m^{-2}$ $year^{-1}$) (Figure 1). The FSF and the bog had values of 52 and 287 g $m^{-2}$ $year^{-1}$ and 156 and 268 g $m^{-2}$ $year^{-1}$ in 1993 and 1994, respectively. Moss production was significantly different ($p < 0.05$) among the sites in 1993. Although there was no significant difference ($p < 0.05$) between the bog and the FSF in 1994, together, they were significantly different from the LSF. Moss NPP decreased along the bog-fen-marsh peatland gradient (Figure 5). There were no significant differences of moss production among transects, and between plots within the bog, FSF, and LSF.

### HERB PRODUCTION

The peak herb standing crops (maximum net aboveground primary productivity) were significantly different ($p < 0.05$) among the sites. The sequence from maximum to minimum mean peak herb production of the sites was as follows: LM > RSF = RM > LSF = FSF > bog (Figure 2). Peak herb production was attained during the month of August in most sites, except for the RM (July), during both growing seasons. The peak herb crop was greater in 1994 than in 1993, except for the RM, where this trend was reversed. The greatest increase (285%) in total herb production was observed in the LSF (from 80 g $m^{-2}$ $year^{-1}$ in 1993 to 300 g $m^{-2}$ $year^{-1}$ in 1994). Conversely, the RM exhibited the greatest decrease (58%) in total herb production (from 349 g $m^{-2}$ $year^{-1}$ in 1993 to 201 g $m^{-2}$ $year^{-1}$ in 1994). The LM (757 g $m^{-2}$ $year^{-1}$) had significantly ($p < 0.05$) higher mean herb production values than the RM (345 g $m^{-2}$ $year^{-1}$) during both years of this study (Figure 2). Herb NPP increased along the bog-fen-marsh peatland gradient (Figure 5). There were no significant differences in total

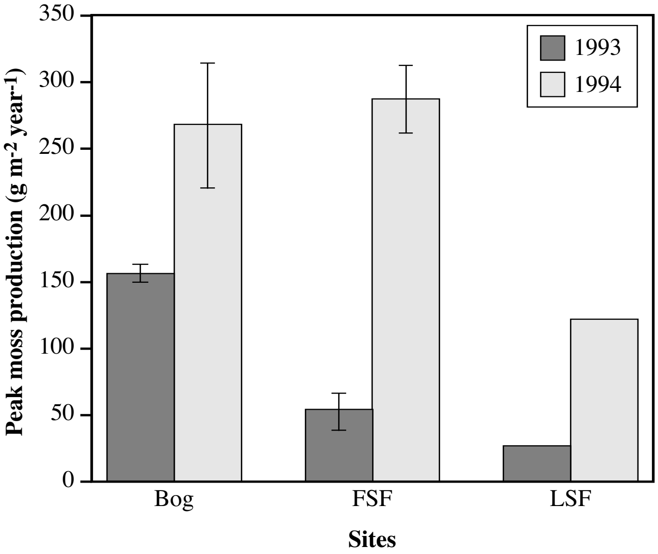

FIGURE 1. Comparison of moss production (mean ± SE) assuming 100% cover of the ground layer by the dominant species in three peatlands (bog, FSF: floating sedge fen, LSF: lacustrine sedge fen). No significant moss stratum was present in the RSF and it was absent in both marshes. SE < 2.5 g $m^{-2}$ $year^{-1}$ at columns without error bars.

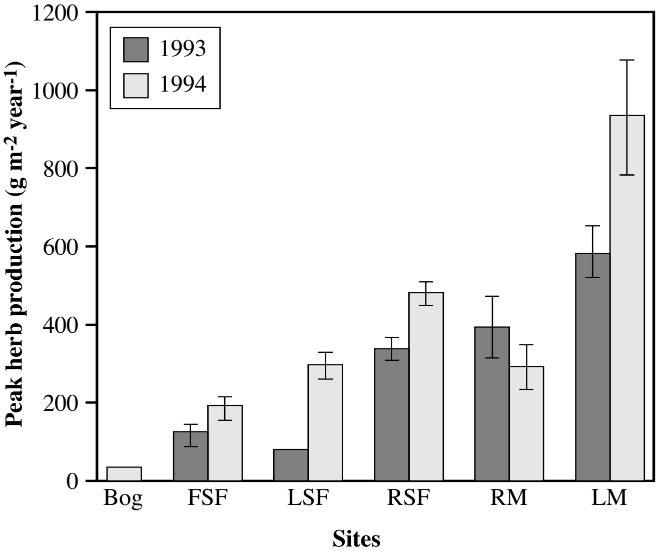

FIGURE 2. Comparison of aboveground peak herb production (mean ± SE) in six peatlands (bog, FSF: floating sedge fen, LSF: lacustrine sedge fen, RSF: riverine sedge fen, RM: riverine marsh, LM: lacustrine marsh). The bog was sampled only in 1994. SE < 10 g $m^{-2}$ $year^{-1}$ at columns without error bars.

herb production among samples within each transect, and between transects within each site.

### SHRUB AND TREE PRODUCTION

Shrub aboveground production decreased along the bog-fen gradient; however, no shrub stratum was present in the RSF, RM, and LM (Figure 3). Total shrub net primary production varied significantly ($p < 0.05$) among those sites that exhibited a shrub stratum (14 to 126 g $m^{-2}$ $year^{-1}$). The minerotrophic sites which exhibited a shrub stratum had a range of mean production values from 14 to 41 g $m^{-2}$ $year^{-1}$ for the FSF and LSF, respectively (Figure 3). The order of these sites from greatest to least shrub production was: bog > FSF > LSF. Shrub production was not significantly different ($p > 0.05$) in any site between 1993 and 1994. Shrub NPP decreased along the bog-fen-marsh peatland gradient (Figure 5). There were no significant differences in total shrub production among samples within each transect, and between transects within each site.

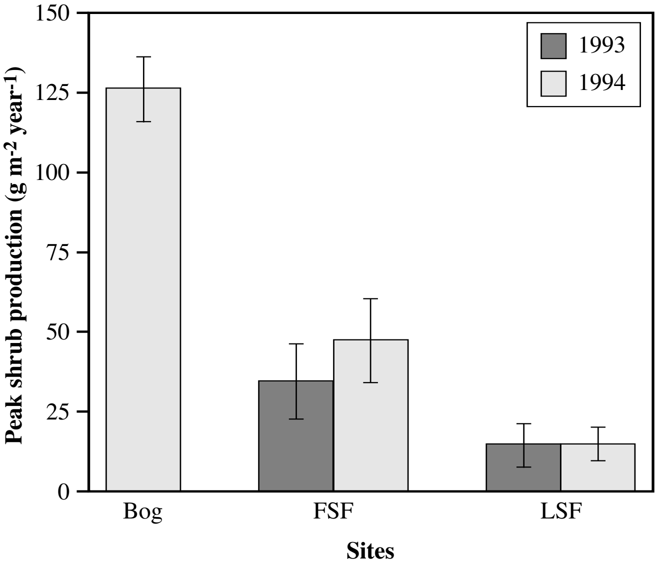

FIGURE 3. Comparison of peak aboveground terminal shrub production (mean ± SE) in three peatlands (bog, FSF: floating sedge fen, LSF: lacustrine sedge fen). The bog was sampled only in 1994 and no shrub stratum was present in the RSF and both marshes.

Only the bog exhibited a tree stratum and NPP values from this layer were adopted from Szumigalski & Bayley (1996) (27 g $m^{-2}$ $year^{-1}$) who studied the same site in 1991 and 1992.

### VASCULAR PLANT PRODUCTION (EXCLUDING TREES)

A significant difference in aboveground vascular plant production (excluding trees) was apparent among sites and between years ($p < 0.05$) (1993 < 1994). Total vascular plant production values ranged from 94 (LSF in 1993) to 933 (LM in 1994) g $m^{-2}$ $year^{-1}$ (Figure 4). The sites ranked as follows (from highest to lowest NPP): LM > RM = RSF > FSF = LSF in 1993, and LM > RSF > LSF > FSF = RM > bog in 1994. The lacustrine fens (FSF and LSF) and the bog had the lowest herb and shrub production combined (1993/1994 mean), whereas the riverine sedge fen (RSF) and both marshes (RM and LM) had the highest. Herb production increased from the bog to the fens to the eutrophic marshes (Figure 2), and shrub production decreased along the same gradient (Figure 3).

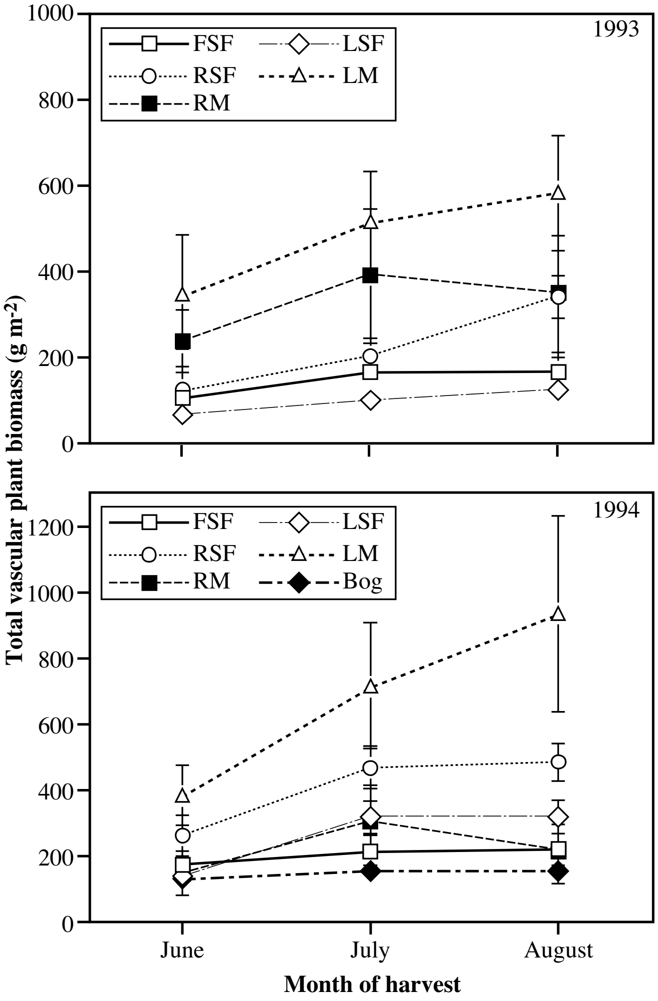

FIGURE 4. Aboveground total vascular plant biomass (mean ± SE) at three monthly harvest periods in six peatlands (bog, FSF: floating sedge fen, LSF: lacustrine sedge fen, RSF: riverine sedge fen, RM: riverine marsh, LM: lacustrine marsh). The bog was sampled only in 1994. SE < 20 g $m^{-2}$ $year^{-1}$ at symbols without error bars.

### TOTAL PLANT PRODUCTION

Total mean aboveground plant production (trees, shrubs, herbs, and mosses) for all sites did not increase along the bog-fen-marsh gradient in central Alberta (Figure 5). From most to least productive sites, the study sites ranked as follows: LM > RSF > Bog = FSF = RM > LSF. The LM had the highest mean aboveground plant production (757 g $m^{-2}$ $year^{-1}$), followed by the RSF (409 g $m^{-2}$ $year^{-1}$), and the LSF had the lowest mean plant production at 277 g $m^{-2}$ $year^{-1}$ in 1993 and 1994.

## Discussion

### MOSS PRODUCTION

Moss NPP varied significantly between years and

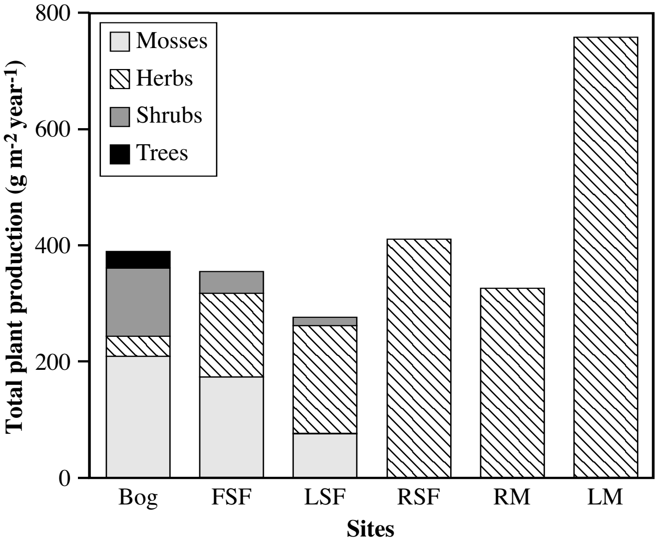

FIGURE 5. Comparison of total aboveground plant production in six peatlands (bog, FSF: floating sedge fen, LSF: lacustrine sedge fen, RSF: riverine sedge fen, RM: riverine marsh, LM: lacustrine marsh). Bars represent the means of 1993 and 1994, except for tree production (where applicable), which is based on Szumigalski & Bayley (1996). The bog was sampled only in 1994.

ranged from 27 g m$^{-2}$ year$^{-1}$ (LSF in 1993) to 287 g m$^{-2}$ year$^{-1}$ (FSF in 1994) (Figure 1). A trend of significantly different moss production between years was previously reported by Wallén, Falkengren-Grerup & Malmer (1988), Moore (1989), Rochefort, Vitt & Bayley (1990), Francez (1992), and Szumigalski & Bayley (1996). Other studies also showed small differences in moss production among a variety of peatlands within the same year (Rochefort, Vitt & Bayley, 1990; Szumigalski & Bayley, 1996). These latter studies were conducted in several minerotrophic and ombrotrophic peatlands in Ontario and along a bog to extreme-rich fen gradient in central Alberta, respectively. Bartsch & Moore (1985) also found similar trends in poor, rich, and transitional fens in Canada's subarctic regions (Table II). Moss production decreased along the bog-fen gradient, and they were altogether absent in the marshes (Figure 1). This decrease or absence of moss growth paralleled water level position with respect to the peat surface and water level fluctuations (Thormann & Bayley, 1997).

Moss production in this bog (212 g m$^{-2}$ year$^{-1}$) is similar to the mean moss production of boreal bogs in North America (190 g m$^{-2}$ year$^{-1}$) (Table II). However, a gradient of increasing moss production with decreasing latitudes exists (Table II) and may be the result of more favourable climatic conditions (higher mean annual temperatures, increased number of growing degree days) which were shown to significantly affect moss growth in Alberta peatlands (Thormann & Bayley, 1997). Moss production in fens is more variable throughout boreal North America (Table II), and no clear trends are detectable. The mean moss production is 81 g m$^{-2}$ year$^{-1}$, and the Alberta fens deviate from this mean substantially (Table II). Thus, site specific characteristics, such as hydrology and surface water nutrient concentrations, may have a more significant effect on moss

TABLE II. Aboveground net primary plant production (g m$^{-2}$ year$^{-1}$) of different strata and totals for North American peatlands in order of decreasing latitude. Columns may not add up to totals due to rounding

| Wetland type | Location and source | Latitude | Moss | Herb | Shrub | Tree | Total |
|---|---|---|---|---|---|---|---|
| BOGS | | | | | | | |
| Bog | Alberta, Szumigalski & Bayley (1996) | 54° 41’ N | 155 | 11 | 87 | 27 | 280 |
| | Alberta, this study | 54° 41’ N | 212 | 34 | 117 | 27[*] | 390 |
| Muskeg | Manitoba, Reader & Stewart (1972) | 49° 53’ N | 17 | 0 | 267 | 58 | 342 |
| Bog | Manitoba, Reader & Stewart (1972) | 49° 53’ N | 55 | 0 | 308 | 8[**] | 371 |
| Raised bog | Minnesota, Grigal, Buttleman & Kernik (1985) | 47°-48° N | 320 | 14 | 200 | 100 | 634 |
| Perched bog | Minnesota, Grigal, Buttleman & Kernik (1985) | 47° 30’ N | 380 | 22 | 43 | 310 | 755 |
| Means | | | 190 | 14 | 120 | 88 | 462 |
| FENS | | | | | | | |
| Poor fen | Québec, Bartsch & Moore (1985) | 54° 43’ N | 38 | 27 | 49 | 0 | 114 |
| Rich fen | Québec, Bartsch & Moore (1985) | 54° 43’ N | 41 | 233 | 61 | 0 | 335 |
| Transitional fen | Québec, Bartsch & Moore (1985) | 54° 43’ N | 39 | 90 | 47 | 0 | 176 |
| Poor fen | Alberta, Szumigalski & Bayley (1996) | 54° 41’ N | 123 | 54 | 134 | 0 | 310 |
| Floating sedge fen | Alberta, this study | 54° 28’ N | 170 | 148 | 38 | 0 | 356 |
| Wooded moderate-rich fen | Alberta, Szumigalski & Bayley (1996) | 54° 28’ N | 142 | 65 | 108 | 44 | 360 |
| Lacustrine sedge fen | Alberta, Szumigalski & Bayley (1996) | 54° 28’ N | 43 | 163 | 8 | 0 | 214 |
| | Alberta, this study | 54° 28’ N | 74 | 190 | 13 | 0 | 277 |
| Riverine sedge fen | Alberta, this study | 54° 28’ N | n.d. | 409 | 0 | 0 | 409 |
| Extreme-rich fen | Alberta, Szumigalski & Bayley (1996) | 53° 42’ N | 149 | 89 | 6 | 0 | 245 |
| Marginal fen | Minnesota, Reiners (1972) | 45° N | 0 | 49 | 6 | 655 | 710 |
| Means | | | 81 | 138 | 43 | 64 | 319 |
| MARSHES | | | | | | | |
| Riverine marsh | Alberta, this study | 54° 28’ N | 0 | 323 | 0 | 0 | 323 |
| Lacustrine marsh | Alberta, this study | 54° 28’ N | 0 | 757 | 0 | 0 | 757 |
| Lacustrine marsh | Manitoba, Neill (1993) | 50° 11’ N | 0 | 955 | 0 | 0 | 955 |
| High fluctuating water table marsh | Minnesota, Bray (1963) | 45° N | 0 | 1360 | 0 | 0 | 1360 |
| Means | | | 0 | 849 | 0 | 0 | 849 |

[*] NPP values estimated from Szumigalski & Bayley (1996).

[**] NPP values estimated from Reader & Stewart (1972).

n.d.: value was not determined.

growth in these minerotrophic peatlands.

Grigal (1985) determined that moss growth in hollows is greater than on hummocks. We assume that moss growth is fairly uniform within the bog and the FSF since both sites consist primarily of hummocks. Therefore, no adjustments were made to account for Grigal's (1985) microtopographical difference in moss growth. Moss production in the LSF was based on a hollow growing species. We assume that our production values are good estimates of total moss production as moss cover was uniform within the sites and those species measured had more than 80% ground cover. However, Grigal (1985) claims that moss production values attained via the cranked wire method may underestimate the actual moss production.

The RM and the LM did not have a moss stratum during the years of this study. No peat cores were collected to ascertain whether mosses grew in this site previously.

### HERB PRODUCTION

The bog had the lowest herb production (35 g m$^{-2}$ year$^{-1}$) of all six sites (Figure 2). This value is higher than Szumigalski & Bayley's (1996) findings, who reported a mean value of 11 g m$^{-2}$ year$^{-1}$ for the same site in 1991 and 1992. The marshes in this study generally exhibited higher peak herb production values (158 to 409 g m$^{-2}$ year$^{-1}$) than the fens (Figure 2). Herb production was substantially higher in the RSF than in the RM in 1994. This is due to the more favourable water regime for herb growth in the fen compared to the marsh (Thormann & Bayley, 1997). Beaver dams blocked the water flow of the associated stream of the RM, and herb production decreased due to low water availability. Conversely, the water level rose in the RSF during the second year of this study (Thormann & Bayley, 1997), resulting in increased herb growth. Szumigalski & Bayley (1996) previously studied the LSF in 1991 and 1992 and reported peak herb production values of 122 and 203 g m$^{-2}$ year$^{-1}$ (mean of 163 g m$^{-2}$ year$^{-1}$). These values are similar to our results of 80 to 300 g m$^{-2}$ year$^{-1}$ in 1993 and 1994 (mean of 190 g m$^{-2}$ year$^{-1}$). Total herb production increased along the bog-fen-marsh peatland gradient (Figure 2). Herb production correlated significantly with water level position relative to the peat surface (Thormann & Bayley, 1997), whereby a higher water table leads to increased herb production in peatlands.

Herb production in North American boreal bogs is similar among sites (Table II). Herb production in fens is similar as well; however, herb production in the RSF is substantially higher than in the remaining boreal fens (Table II). In contrast to the generally similar herb production values of bogs and fens, marsh herb production varies substantially and appears to increase with decreasing latitude (Table II). The hydrologic regimes within North American bogs, fens, and marshes may account for a large proportion of the variation in herb production observed (Table II).

The measurement for aboveground net primary plant production by the multiple harvest method can underestimate herb production due to shoot mortality, different time of peak biomass for different herb species, and herbivory. It can also overestimate herb production due to overwintering of green shoots and translocation from old parts to new ones (Wheeler & Shaw, 1991; Bernard & Gorham, 1978; Reader 1978; Richardson, 1978). Furthermore, up to 90% of the total production of herbs occurs in belowground structures (roots, rhizomes) (Wallén, 1993; Sjörs, 1991), thus, our herb production values may significantly underestimate the actual herb production values within each peatland. However, since belowground tissues of many sedges, such as *Carex rostrata* and *C. aquatilis*, are perennial in nature (Bernard & Gorham, 1978), the majority of plant tissues that lead to peat accumulation in peatlands originates from aboveground tissues that die annually (stems, leaves).

### SHRUB PRODUCTION

Shrub NPP, including radial production, in the bog was 126 g m$^{-2}$ year$^{-1}$ (sampled only in 1994) (Figure 3). This value was higher than Szumigalski & Bayley's (1996) findings of 77 to 97 g m$^{-2}$ year$^{-1}$ in the same bog. Szumigalski & Bayley (1996) reported shrub production values ranging from 6 to 9 g m$^{-2}$ year$^{-1}$ in the LSF in 1991 and 1992. These values are similar to our findings for the two growing seasons following their study.

Shrub production varies substantially in bogs in boreal North America (Table II), and no latitudinal gradient exists. Poor and wooded fens have substantially more shrub production than open, sedge-dominated fens, whereby the latter fens are similar in shrub production in North America (Table II). The decreasing gradient of shrub production paralleled the one observed for moss production in these peatlands (Figure 3). The relative position of the water table with respect to the peat surface affects shrub production in peatlands, whereby a higher water table limits shrub growth (Thormann & Bayley, 1997; Szumigalski & Bayley, 1996).

The RSF, RM, and LM had no shrub stratum, possibly due to high water tables in these sites (Thormann & Bayley, 1997) which may inhibit seed germination of woody plants. The raised water table decreases oxygen transfer to seedlings and roots, resulting in the reduction in vegetative and reproductive growth and often death (Kozlowski, Kramer & Pallardy, 1991).

Our estimates for shrub net primary production may be low because the current year's leaves and stems may continue to grow until October (Backéus, 1985) (our last harvest was conducted in late August). Furthermore, we did not determine radial growth of dwarf shrubs; however, their radial production is believed to be minimal (Vasander, 1982). Furthermore, Szumigalski & Bayley's (1996) estimates of radial production of the major shrub species are low as they did not take into account stem mortality and burial by peat (Forrest & Smith, 1975). Losses due to retranslocation, litter fall, and herbivory may decrease estimates of shrub NPP throughout the growing season as well.

### TOTAL VASCULAR PLANT PRODUCTION

Total vascular NPP varied significantly among sites and between years, ranging from 94 (LSF in 1993) to 933 (LM in 1994) g m$^{-2}$ year$^{-1}$ (Figure 4). During both years of this study, the LM had the highest NPP of all sites. In 1993, total aboveground vascular and total herb NPP exhibited the same trends. The LM and LSF had the highest and lowest total aboveground vascular and herb NPP, respectively, with the remaining sites exhibiting intermediate NPP values (Figures 2 & 4). This trend was most apparent during 1994 as well; however, vascular and herb NPP values decreased significantly in the RM due to lower water levels (beaver dams blocked the stream above the study site) (Thormann & Bayley, 1997), and vascular and herb NPP increased significantly in the LSF and FSF from 1993 to 1994 (Figure 2). These increases in herb NPP were attributed to more favourable water level changes in these two fens as well (Thormann & Bayley, 1997).

Total vascular NPP in the bog was 178 g m$^{-2}$ year$^{-1}$ in 1994 (Table II). This value is similar to the mean total vascular NPP for North American bogs (222 g m$^{-2}$ year$^{-1}$) (Table II). However, an increasing gradient of total vascular NPP with decreasing latitudes does exist for boreal North American bogs (Table II). Such a latitudinal gradient is not apparent in fens. The mean total vascular NPP for the fens of this study (266 g m$^{-2}$ year$^{-1}$) is similar to the North American mean for boreal fens (245 g m$^{-2}$ year$^{-1}$) (Table II). A latitudinal gradient of total vascular NPP in North American boreal marshes is less pronounced than that found in bogs (Table II). Mean vascular NPP for these marshes was 540 g m$^{-2}$ year$^{-1}$ and the North American mean is 849 g m$^{-2}$ year$^{-1}$ (Table II). It appears that the latitudinal gradient of increasing total vascular NPP with decreasing latitudes is pronounced in boreal marshes; however, due to the significantly decreased vascular NPP in the RM in 1994 (Figure 4), our low mean NPP in the marshes of this study may be skewed, magnifying vascular NPP differences among North American boreal marshes. Total vascular NPP increases along the bog-fen-marsh gradient in this study. It appears that the mean vascular NPP is similar in bogs and fens in North America (222 and 245 g m$^{-2}$ year$^{-1}$, respectively); however, their mean vascular NPP is substantially lower than that found in boreal marshes (849 g m$^{-2}$ year$^{-1}$) (Table II). This may be attributed to the dominance of the herb stratum in affecting total plant NPP in North American peatlands and the more favourable water regime for herb growth in marshes than in fens and bogs. The lower contribution of herb NPP to the total vascular NPP in bogs compared to fens is offset by the comparably larger contribution of shrub NPP to the total vascular NPP in the bogs compared to the fens. This results in similar total vascular NPP values for these two peatland types.

### TOTAL PLANT PRODUCTION

Total NPP in the bog was 390 g m$^{-2}$ year$^{-1}$ during the 1994 growing season (Figure 5, Table II). This value is higher than plant production values reported by Szumigalski & Bayley (1996) for the same site during the 1991 and 1992 growing seasons (mean of 273 g m$^{-2}$ year$^{-1}$). A latitudinal gradient of aboveground net primary plant production is present for bogs, with lower NPP at higher latitudes and higher NPP at more southern locations (Table II). The mean total plant production in boreal bogs in North America is 462 g m$^{-2}$ year$^{-1}$ (Table II). European bogs are generally less productive compared to North American ombrotrophic systems as indicated by Vasander (1982). However, Forrest & Smith (1975) reported similar values from British blanket bogs.

The fens ranged from 277 to 409 g m$^{-2}$ year$^{-1}$ in mean total aboveground plant production (Figure 5, Table II). A latitudinal gradient of NPP exists for fens as well. However, this gradient of increasing NPP with decreasing latitudes is not as pronounced as it is with bogs in North America (Table II). Factors other than climate, such as hydrology and vegetation composition, may be influencing NPP in fens.

The RSF was the most productive fen (409 g m$^{-2}$ year$^{-1}$), whereas the LSF was the least productive fen (277 g m$^{-2}$ year$^{-1}$) (Figure 5). Szumigalski & Bayley (1996) examined the same LSF in 1991 and 1992 and measured a mean aboveground NPP of 214 g m$^{-2}$ year$^{-1}$. This is significantly lower than our mean NPP for the two years following their study. This site underwent significant changes to its hydrological regime during the early 1990s, which may explain this difference in NPP (121 and 433 g m$^{-2}$ year$^{-1}$ in 1993 and 1994, respectively). The water table began to drop in 1991 (Szumigalski & Bayley, 1996) and then began to rise again in 1994 (Thormann & Bayley, 1997). This is directly correlated with the changes in NPP observed over this time period in this site. The LSF is dominated by *Carex lasiocarpa, C. diandra* and *C. rostrata*, and Wheeler & Shaw (1991) and Verhoeven *et al.* (1983) reported NPP values of 210 to 250 g m$^{-2}$ year$^{-1}$ in fens with a similar vegetation composition in Europe.

The LM and RM exhibited mean NPP values of 757 and 323 g m$^{-2}$ year$^{-1}$, respectively, during the 1993 and 1994 growing seasons (Figure 5, Table II). These values for southern boreal marshes are low compared to findings by van der Valk & Davis (1978), Anderson (1976), Auclair, Bouchard & Pajaczkowski (1976), Mason & Bryant (1975), Bray (1963), and Bray, Lawrence & Pearson (1959). However, all of these studies were conducted in marshes at lower latitudes, and a gradient of increasing NPP with decreasing latitudes exists for marshes. As with fens, climate is not the only factor influencing NPP in these peatlands, but hydrology, specifically water levels (Mitsch & Gosselink, 1993), and the dominant vegetation (van der Valk & Davis, 1978) influence NPP in marshes as well.

## Conclusion

We have examined five peatlands in 1993 and an additional sixth in 1994 in central Alberta, Canada. They were a bog, a floating sedge fen (FSF), a lacustrine sedge fen (LSF), a riverine sedge fen (RSF), a riverine marsh (RM), and a lacustrine marsh (LM). All three fens are rich fens.

Our hypothesis of increasing aboveground net primary plant production along this bog-fen-marsh gradient was rejected by our results. The total aboveground NPP increased from bogs to marshes; however, the bog did not exhibit a significantly lower NPP than the fens in this study. In fact, the LSF was significantly less productive, on average, than the bog. Since belowground NPP was not determined but may account for up to 90% of the total production of some sedges (Wallén, 1993; Sjörs, 1991), it is possible that total production in these fens and marshes was significantly underestimated; therefore, an increasing gradient of NPP from bogs to fens to marshes may still exist in southern boreal peatlands in Alberta.

The bog exhibited an aboveground NPP of 390 g $m^{-2}$ $year^{-1}$ in 1994 and this value is intermediate for bogs in North America. The fens had NPP values ranging from 277 to 409 g $m^{-2}$ $year^{-1}$, which is also intermediate for North American fens; however, the marshes of this study (323 to 757 g $m^{-2}$ $year^{-1}$) were significantly less productive than other North American marshes. The bog complements a latitudinal gradient of increasing NPP with decreasing latitudes. Fen aboveground NPP is similar in boreal regions of North America, and a latitudinal gradient is less pronounced. Production values of marshes differ considerably, depending on the dominant vegetation of the marsh (van der Valk & Davis, 1978), but a similar, although not as prominent, latitudinal gradient is present as well (Table II). Moss and shrub production decreased along this bog-fen-marsh gradient in central Alberta, whereby herb production increased along the same gradient. Trees were found only in the bog and their NPP was small compared to the production of the other vegetation strata. Shrub and moss strata were absent in both marshes. Moss and herb production was more variable between years than among sites, whereas shrub production remained similar during both years of this study. Generally, all sites had a greater total aboveground NPP in 1994 than in 1993 (except the riverine marsh, whose water was blocked by beaver dams in 1994).

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