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Effects of hydrologic changes on aboveground production and surface water chemistry in two boreal peatlands in Alberta: Implications for global warming

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Abstract

Aboveground net primary production (NPP) and surface water chemistry variables were monitored in a lacustrine sedge fen and a bog for four years. There were no significant differences in precipitation, mean growing season annual temperature, and number of growing degree days from 1991 to 1994. The mean annual water levels in the lacustrine sedge fen differed significantly, whereas they were similar in the bog during these four years. We measured 15 surface water variables in the lacustrine sedge fen and the bog, and found that only two correlated significantly with water level fluctuations. In the lacustrine sedge fen, calcium correlated positively ($r^2 = 0.56$) and nitrate correlated negatively ($r^2 = 0.20$) with water levels. In the bog, potassium correlated positively ($r^2 = 0.88$) and total dissolved phosphorus correlated negatively ($r^2 = 0.62$) with water levels. The remaining chemical variables showed no significant correlations with water level fluctuations.

Net primary production of the different vegetation strata appeared to respond to different environmental variables. In the lacustrine sedge fen, graminoid production was explained to a significant degree by water levels ($r^2 = 0.53$), whereas shrub production was explained to a significant degree by surface water chemistry variables, such as nitrate ($r^2 = 0.74$) and total phosphorus ($r^2 = 0.22$). In the bog, temperature was the only variable that explained moss production to a significant degree ($r^2 = 0.71$), whereas ammonium explained graminoid production ($r^2 = 0.66$) and soluble reactive phosphorus explained shrub production to significant degrees ($r^2 = 0.71$).

There are few direct data on the impact of climatic warming in boreal wetlands, although paleoecological and 2xCO_2 model data have provided some indications of past and possibly future changes in vegetation composition, respectively. Our results suggest that the lacustrine sedge fen may succeed to a bog dominated by *Sphagnum* spp. and *Picea mariana*, whereas the bog may succeed to an upland-type forest ecosystem.

Introduction

The majority of ecosystem models predict grassland and forest ecosystem responses to global climate warming, and only recently have peatlands received any attention. For example, peatland models by Gignac et al. (unpublished), Nicholson et al. (1997), and Gignac & Vitt (1994) predict bryophyte species responses to a $2 \times CO_2$ climate scenario. Other models predict whether peatlands will be sinks or sources of carbon (C) under warmer climatic condition by measuring methane (CH_4) and carbon dioxide (CO_2) fluxes from peatlands (Moore, 1994; Yavitt et al., 1993; Roulet et al., 1993; Armentano & Menges, 1986). Data documenting the responses of vascular plant species in peatlands to climatic warming are scarce. Most studies rely on drainage experiment (Vasander, 1982) and not on naturally occurring annual water level fluctuations.

The hydrology of peatlands is influenced by climate, microtopography, and surficial geology and plays a major role in peatland ecology (Chapin III et al., 1988) and biogeochemistry (Gorham, 1994). The degree of groundwater upwelling (Shedlock et al., 1993; Glaser et al., 1990) is expected to change under global warming (Gorham, 1994; Gorham, 1988). This is predicted to result in alterations of the peatland microclimate, such as surface radiation, peat temperature regime, and evapotranspiration. These microclimatic alterations affect plant growth, nutrient mineralization, and emissions of trace gases, such as CO_2 and CH_4 (Dise et al., 1993).

Our objectives were to monitor seasonal fluctuations of the water table, and to determine the effects of these fluctuations on aboveground plant production and 15 surface water chemistry variables. Inferences regarding the possible effects of global climate warming on aboveground plant production and surface water chemistry in these two peatlands are drawn from our results based on these seasonal fluctuations. Our study differs from those involving the drainage of peatlands (Vasander, 1982) in that it examines naturally occurring fluctuations of the water level in unaltered peatlands. Aboveground plant production, water level fluctuations, and surface water chemistry variables were measured in a lacustrine sedge fen and a bog in southern boreal Alberta from 1991 through 1994. We hypothesize that: (1) production of graminoids and mosses will decrease as the water level drops, because graminoid and moss production correlate positively with water levels (Szumigalski & Bayley, 1997; Thormann & Bayley, 1997b; Zoltai and Vitt, 1990), (2) production of shrubs will increase, because shrub production correlates negatively with water levels (Szumigalski & Bayley, 1997; Thormann & Bayley, 1997b), and (3) surface water nutrient concentrations will decline with a drop in the water level due to decreased water flow rates.

Study area and site descriptions

The bog is located north of Bleak Lake (54° 41′ N and 113° 28′ W) and the lacustrine sedge fen is located east of Perryvale (54° 28′ N, 113° 19′ W) (Figure 1). Vitt et al. (1995) studied this bog and this lacustrine sedge fen (their 'extreme-rich fen') previously. The climate of the area is characterized by mild summers, and cold, snowy winters (Environment Canada, 1982). Table 1 summarizes climatic variables for these two peatlands from the Athabasca 2 weather station (Environment Canada, 1982). Both peatlands lie within the Subhumid Low Boreal ecoclimatic region of Canada (Ecoregions Working Group, 1989). Nomenclature for *Sphagnum* follows Anderson (1990) and for other mosses Anderson et al. (1990), while that of the vascular plants follows Packer (1983). General descriptions of the two sites are as follows:

Bog

The bog is a large, raised ombrotrophic island within a large peatland complex (approximately 260 ha). The peat is 5 m thick and is raised 0.3–0.5 m above an abjacent poor fen water track. A sparse tree layer of *Picea mariana* (Mill.) BSP. covers about 25% of the wooded part of the bog, whereby the remainder of this site is open. In the entire bog, *Ledum groenlandicum* Oeder dominates the ericaceous shrub layer (percent cover is approximately 75%), while the sparse graminoid 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

This site is a large expanse of sedge-dominated peatland (approximately 270 ha) with 2–2.5 m of peat situated beside a large body of water (approximately 62 ha). The vascular vegetation consists primarily of *Carex lasiocarpa* Ehrh. and *C. diandra* Schrank. Shrubs comprise only about 5% of the peatland cover and consist exclusively of *Salix pedicellaris* Pursh and *Betula pumila* L. *var. glandulifera* Regel. The moss stratum is discontinuous and dominated by *Drepanocladus aduncus* (Hedw.) Warnst. There is no tree stratum in this fen.

Methods

Detailed descriptions of the methods employed to measure the aboveground net primary plant production (NPP) of the moss, graminoid, shrub, and tree strata are presented in Thormann & Bayley (1997a). Briefly, Clymo's (1970) cranked wire method was employed to measure moss growth in the bog three times each year. Due to the microtopography of the lacustrine sedge fen, the moss mat was harvested in quadrats three times each year, and growth of the dominant species was determined from innate characteristics (difference in leaf colour between new and previous year's growth) (cf. Vasander, 1982; Vitt & Pakarinen, 1977). Random multiple aboveground harvests along two transects (five quadrats per transect) in both sites were performed in late June, late July, and late August from 1991 to 1994 (vascular NPP was not determined in the

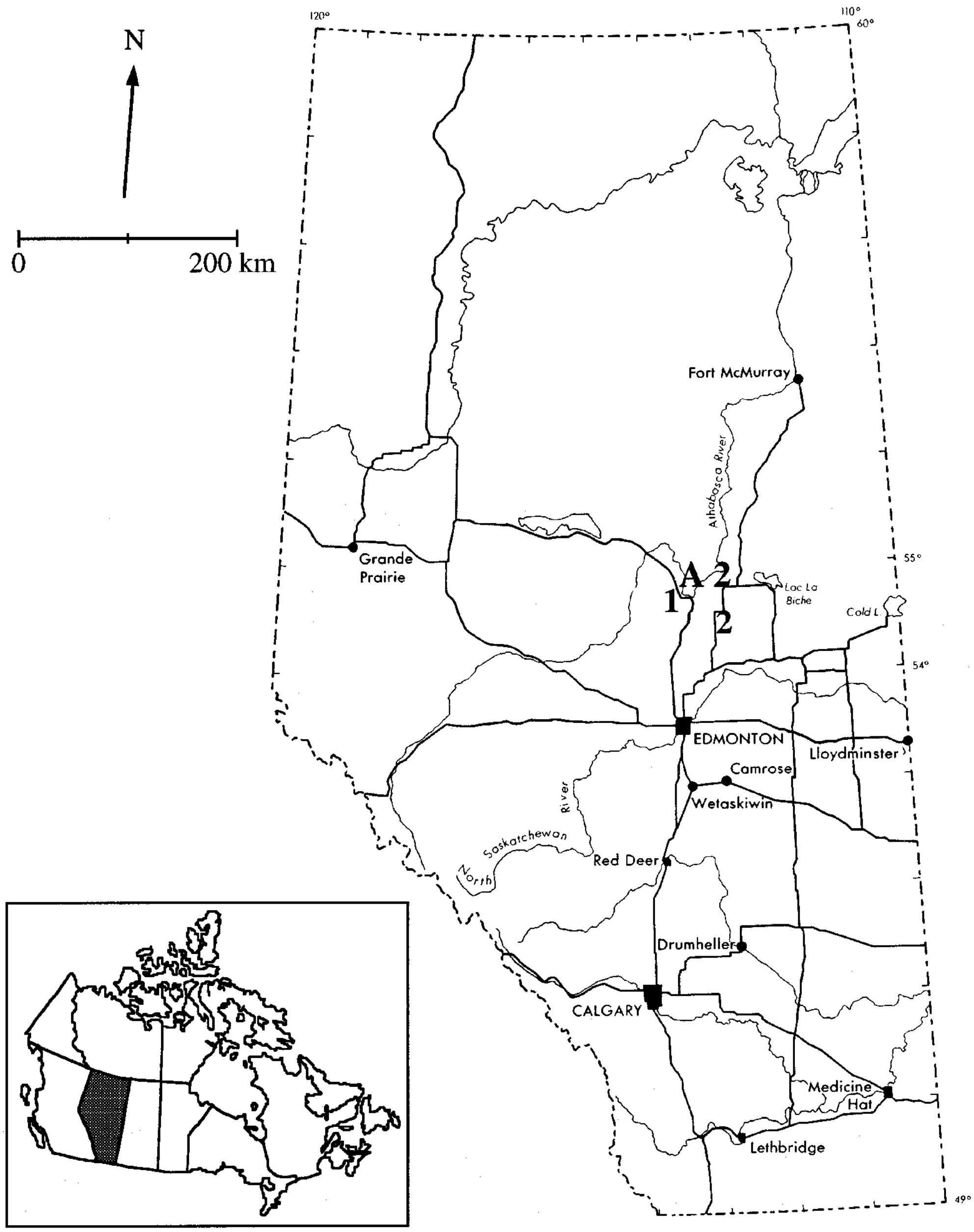

Figure 1. Relative location of the two peatlands (1 = bog, 2 = lacustrine sedge fen) and the Athabasca 2 weather station (A2) in central Alberta, Canada.

bog in 1993) to measure aboveground production of the graminoid and shrub (terminal and radial production) strata, and to determine their peak production annually. Tree production in the bog was estimated from Szumigalski & Bayley (1996). Belowground biomass was not determined as part of this study; however, it may account for up to 90% of the total production of sedges (Wallén, 1993; Sjörs, 1991; Bernard & Gorham, 1978). Therefore, our production values for *Carex* spp. in the lacustrine sedge fen may be substantially underestimated, affecting total graminoid and total plant production values.

The methods employed to collect and analyze water samples follow Vitt et al. (1995). Water samples were

Table 1. Climatic data for May–August 1991 to 1994 and long term (1951–1980) averages from the Athabasca 2 weather station. Growing degree days (GDD) are measured as the sum of daily temperatures above 5 degrees Celcius.

Athabasca 2 weather station	May	June	July	August	May–August Means and Totals
1991					
Mean temp (˚C)	11.5	13.8	16.8	18.3	15.1
GDD	203.3	265.0	366.7	412.6	1247.6
Precip. (mm)	60.4	100.2	54.2	43.4	258.2
Precip. days	11.0	17.0	14.0	9.0	51.0
1992					
Mean temp (˚C)	9.6	15.1	15.1	14.3	13.5
GDD	153.9	302.9	314.0	290.1	1060.9
Precip. (mm)	50.2	55.2	84.0	45.6	235.0
Precip. days	11.0	12.0	16.0	8.0	47.0
1993					
Mean temp (˚C)	11.4	13.4	14.9	14.7	13.6
GDD	198.0	251.9	306.1	300.2	1056.2
Precip. (mm)	39.2	73.4	237.4	83.8	433.8
Precip. days	6.0	12.0	21.0	13.0	52.0
1994					
Mean temp (˚C)	10.9	14.1	16.7	15.7	14.4
GDD	197.0	271.4	361.6	331.1	1161.1
Precip. (mm)	65.4	110.2	116.2	30.6	322.4
Precip. days	11.0	15.0	17.0	6.0	49.0
Long term average					
Mean temp (˚C)	10.1	14.1	16.2	14.8	13.8
Precip. (mm)	44.9	80.1	90.0	68.2	283.2

collected at monthly intervals in 1991 and 1992 (Szumigalski & Bayley, 1997) and at bimonthly intervals in 1993 and 1994 from the same small depressions dug into the peat throughout the ice-free season. Water samples were analyzed for nitrate (NO_3^-), ammonium (NH_4^+), soluble reactive phosphorus (SRP), total dissolved phosphorus (TDP), total phosphorus (TP), potassium (K^+), sodium (Na^+), calcium (Ca^{2+}), magnesium (Mg^{2+}), chloride (Cl^-), sulfate (SO_4^{2-}), pH, alkalinity, bicarbonate (HCO_3^-), and conductivity (adjusted for pH and temperature).

Environment Canada (1982) provided climatic data from the Athabasca 2 weather station (Figure 1), including the quantity and timing of precipitation, number of growing degree days (GDD, the sum of mean daily temperatures above 5 ˚C), and air temperatures (Table 1).

Water level fluctuations were measured with Steven's F water level recorders in the lacustrine sedge fen from 1991 through 1994 (Szumigalski & Bayley, 1997; Thormann & Bayley, 1997b). In the bog, a Steven's F water level recorder was used in 1991 and 1992 (Szumigalski & Bayley, 1997), while a permanently attached meter stick was used to monitor water level fluctuations in 1993 and 1994 (Thormann & Bayley, 1997b). In both sites, the meter stick measurements were related to measurements from a pore water sampler, which was used to determine the relative position of the water table to the moss surface. We did not measure water flow rates in either site.

The depth of oxidation was determined in 1991 and 1992 as outlined by Bridgham et al. (1991) by measuring the depth of rust on steel welding rods inserted into the peat. The rods were retrieved at monthly intervals from May to October, and the distance from the moss surface to the lowest extent of rust on the rods was measured and assumed to be the depth of the acrotelm (oxygenated peat horizon).

Moss, graminoid, and shrub aboveground production, amounts of precipitation, growing degree days, and air temperatures (dependent variables) were analyzed with one-way ANOVAs to determine significant

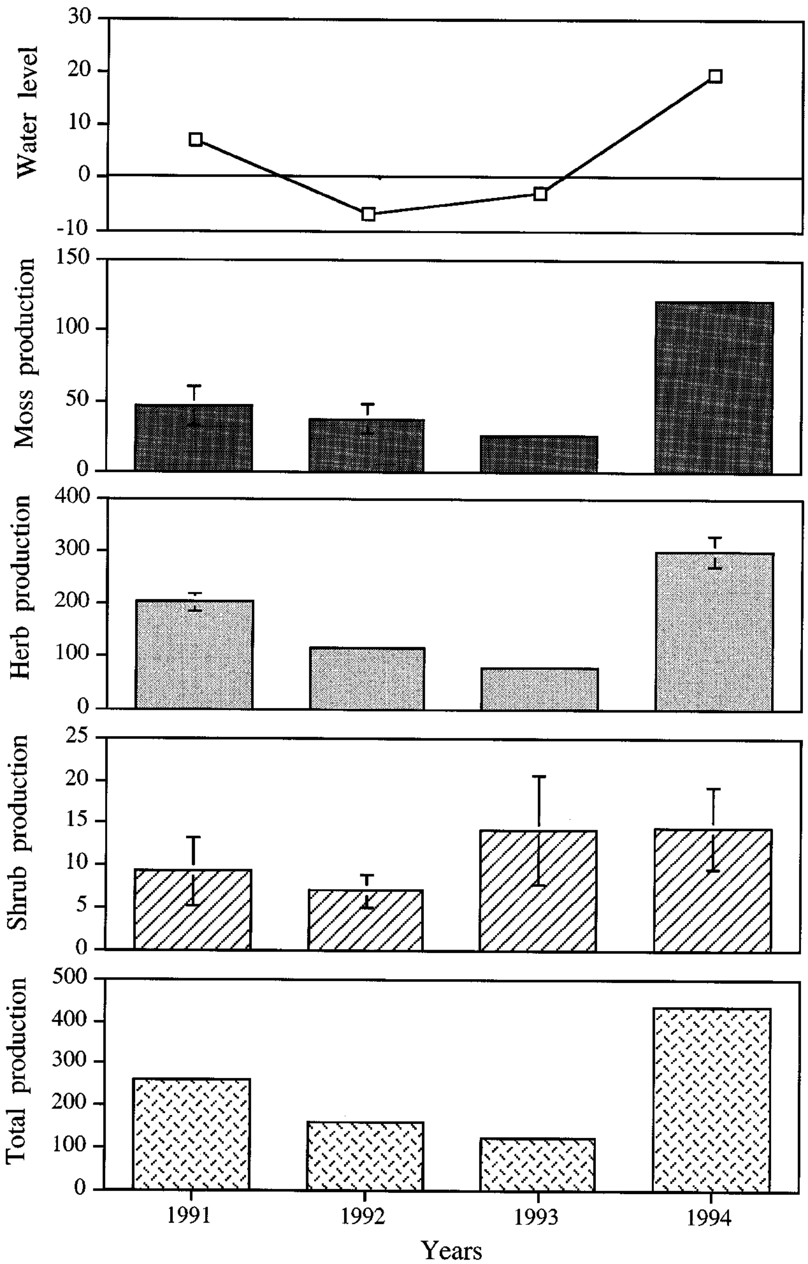

Figure 2. Mean (± SE) peak vascular and non-vascular aboveground plant production and total aboveground plant production (g m^{-2} $year^{-1}$) in the lacustrine sedge fen from 1991 to 1994 in relation to the water level (relative to the moss surface, 0 cm) . Error bars absent where SE $<$ 10 g m^{-2} $year^{-1}$ (columns) and SE $<$ 1.5 cm (symbols) (mean annual water levels). Note the different scales on the y-axes.

variations among and within years (independent variables) from 1991 through 1994 for each site. Tukey tests were used to make pairwise comparisons after the detection of significance from the ANOVAs. Total aboveground plant production could not be analyzed using ANOVAs due to the differential responses of different vegetation strata to the same environmental variable (Szumigalski & Bayley, 1996); however, total annual aboveground NPP values with standard errors are provided in Figures 2 and 3. Multiple stepwise regressions were used to examine the relationships among surface water chemistry and climatic variables

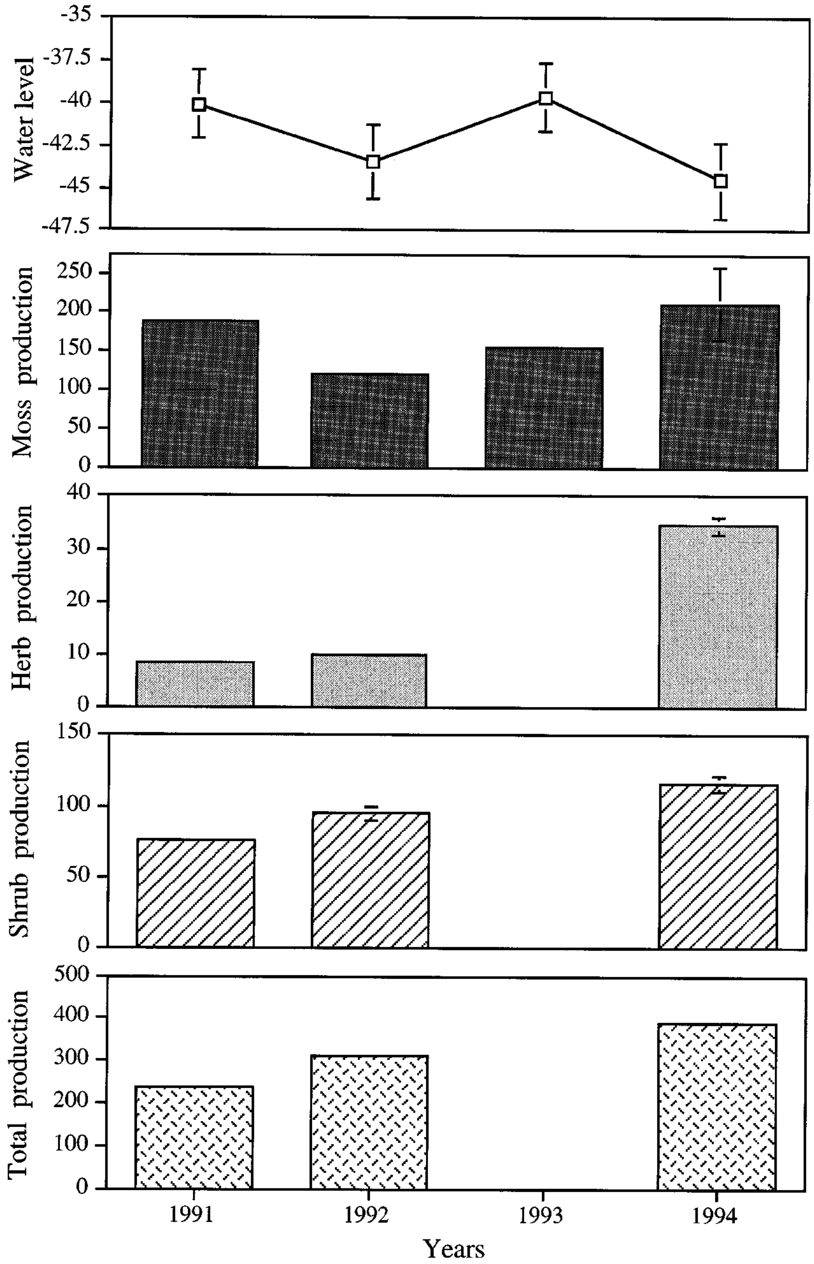

Figure 3. Mean (± SE) peak vascular and non-vascular aboveground plant production and total aboveground plant production (g m^{-2} $year^{-1}$) in the bog from 1991 to 1994 in relation to the water level (relative to the moss surface, 0 cm). Vascular and total aboveground plant production were not measured in 1993. Error bars absent where SE < 8 g m^{-2} $year^{-1}$. Note the different scales on the y-axes.

and moss, graminoid, and shrub aboveground production from 1991 through 1994. Regressions and correlation coefficients were determined between all surface water chemistry variables (some data were transformed) and water levels. Autocorrelation analyses were performed for all surface water nutrient variables to determine any correlation between successive samples within each site, and Pearson correlation coefficients were determined among all surface water chemistry and climatic variables within each site to establish if any of the nutrient or climate variables were correlated with each other. Some data deviated slightly from

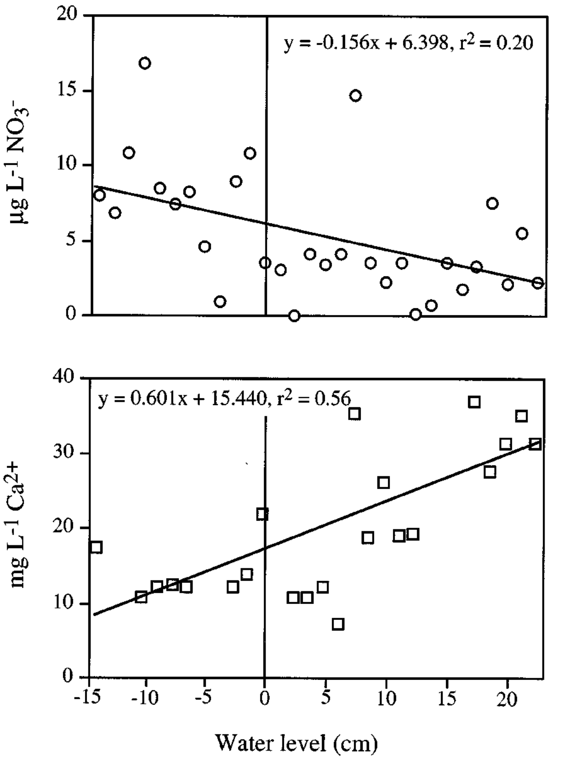

Figure 4. Nitrate (NO_3^-, μg l^{-1}) calcium ion (Ca^{2+}, mg l^{-1}) surface water concentrations in relation to the water level relative to the moss surface (0 cm) in the lacustrine sedge fen from 1991 to 1994.

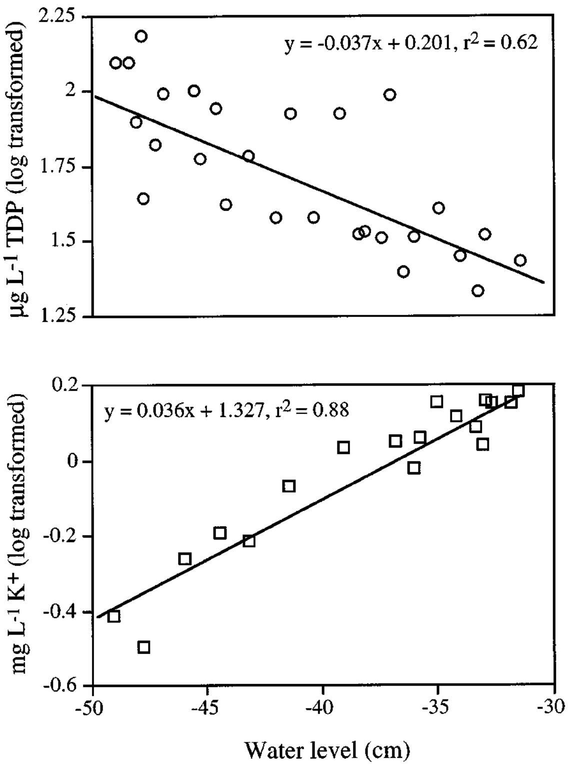

Figure 5. Total dissolved phosphorus (TDP, μg l^{-1}, log transformed) and potassium ion (K^+, mg l^{-1}, log transformed) surface water concentrations in relation to the water level relative to the moss surface (0 cm) in the bog from 1991 to 1994.

normality and homogeneity of variances; however, the statistical tests used are robust to some deviations from these conditions (Zar, 1984). Most statistical analyses were performed on SAS (SAS Institute Inc., 1989), except for the autocorrelation analyses, which were performed on SYSTAT (SYSTAT Inc., 1992).

Results

Detailed aboveground NPP values (mosses, graminoids, shrubs, trees, total vascular, and total plant production), and surface water chemistry variables are in Szumigalski & Bayley (1997), Thormann & Bayley (1997a), Thormann & Bayley (1997b), and Szumigalski & Bayley (1996).

The effects of water level on aboveground plant production

Graminoid and shrub NPP was explained to significant degrees by water level fluctuations in the lacustrine sedge fen (Table 2). Production of graminoids, primarily *Carex lasiocarpa*, ranged from 80 g m^{-2} $year^{-1}$ (1993) to 300 g m^{-2} $year^{-1}$ (1994) with intermediate NPP values in 1991 and 1992, whereas shrub production ranged from 7 g m^{-2} $year^{-1}$ in 1992 to 14 g m^{-2} $year^{-1}$ in 1994 (Figure 2). Production of *Drepanocladus aduncus* (the dominant moss) ranged from 27 g m^{-2} $year^{-1}$ in 1993 to 121 g m^{-2} $year^{-1}$ in 1994 (Figure 2). Total plant production ranged from 121 g m^{-2} $year^{-1}$ in 1993 to 435 g m^{-2} $year^{-1}$ in 1994 (Figure 2).

In the bog, production of *Sphagnum fuscum* (the dominant moss) ranged from 119 g m^{-2} $year^{-1}$ (1992) to 211 g m^{-2} $year^{-1}$ (1994) (Figure 3). Graminoid NPP ranged from 8 g m^{-2} $year^{-1}$ in 1991 to 35 g m^{-2} $year^{-1}$ in 1994, and shrub production ranged from 77 g m^{-2} $year^{-1}$ (1991) to 116 g m^{-2} $year^{-1}$ (1994) (Figure 3). Total plant production increased from 235 g m^{-2} $year^{-1}$ in 1991 to 390 g m^{-2} $year^{-1}$ in 1994 (Figure 3).

Table 2. Correlation coefficients of moss, herb, and shrub production with surface water chemistry and climatic parameters in the bog and the lacustrine sedge fen (LSF) from 1991 through 1994. Abbreviations include: GDD = growing degree days, SRP = soluble reactive phosphorus, TP = total phosphorus, * $0.05 > p > 0.01$, ** $0.01 > p > 0.001$, and *** $0.001 > p > 0.0001$. Sample size (n) corresponds to the number of data points used in the regression analyses for the individual vegetation strata (moss, herb, and shrub strata).

	Bog			LSF		
	n	Parameter	r-square	n	Parameter	r-square
Moss production	11	Temperature	0.71**	3	Not determined due to small sample size ($n = 3$)	
Herb production	8	Ammonium	0.66*	12	Water level	0.53***
					Temperature	0.10*
Shrub production	6	SRP	0.71*	12	Nitrate	0.74*
		GDD	0.27**		TP	0.22*
					Water level	0.05**

The effects of water level on surface water chemistry

In the lacustrine sedge fen, NO_3^- and Ca^{2+} surface water concentrations correlated best with water level fluctuations. As the water level dropped, NO_3^- surface water concentrations increased, and surface water concentrations of Ca^{2+} decreased (Figure 4). The water level ranged from a mean growing season minimum of - 6.8 cm below the moss surface in 1992 to a maximum of 19.6 cm above the moss surface in 1994 (Figure 2). The depth of oxidation was greatest during the driest year and smallest during the wettest year. The pH ranged from annual means of 6.4 to 7.0. Adjusted conductivity was significantly lower in 1991 and 1992 than in 1993 and 1994, and alkalinity and HCO_3^- were both significantly lower in 1992 and 1993 than in 1994 (all $p < 0.05$). All other surface water chemistry parameters were similar from 1991 to 1994 ($p > 0.05$).

In the bog, surface water concentrations of K^+ and TDP correlated positively and negatively with water level fluctuations, respectively (Figure 5). The water level fluctuated a maximum of five cm between years. The lowest mean annual water level was measured in 1994 and the highest in 1993, with intermediate values in 1991 and 1992 (Figure 3). The depth of oxidation paralleled the water level fluctuations, with greater depths of oxidation in years with lower mean annual water levels. The pH ranged from annual means of 3.6 to 4.2, and adjusted conductivity, alkalinity, and HCO_3^- were zero, due to the high acidity of bog waters. Surface water concentrations of K^+ were significantly greater in 1994, the year with the lowest water level, than in any of the preceding three years, whereas Ca^{2+} concentrations were significantly lower in 1994 than in 1991 to 1993 (both $p < 0.05$). The remaining surface water chemistry variables were not significantly different during the four years of this study ($p > 0.05$).

The effects of climate on aboveground plant production

In the lacustrine sedge fen, air temperature was the only climatic variable that explained annual aboveground graminoid production to a significant degree (Table 2). Conversely, shrub and moss aboveground NPP were not explained to a significant degree by any climatic factor in the fen.

In the bog, production of *Sphagnum fuscum* and aboveground shrub NPP were explained to a significant degree by air temperature and GDD, respectively (Table 2). No other climatic variables explained aboveground plant production to a significant degree in the bog.

Discussion

The effects of water levels on aboveground plant production

Lacustrine sedge fen

Water levels explained graminoid aboveground production to a significant degree in this fen (Table 2). A similar relationship between water levels and graminoid production in Alberta peatlands has previously been reported by Szumigalski & Bayley (1997) and Thormann & Bayley (1997b). Also, Laitinen (1990) showed that graminoids, specifically *Carex* spp., are more tolerant of water saturated soils than shrubs. Thormann & Bayley (1997b) showed that the water level rose by 22.4 cm from 1993 to 1994, and graminoid production increased by 376%. Szumigalski & Bayley (1997) reported that a drop of 14 cm in the water level caused the graminoid NPP to decrease by 40% in the same site between 1991 and 1992.

Total aboveground shrub production (terminal and radial NPP) in Alberta peatlands was explained to a significant degree by water levels (Thormann & Bayley, 1997b; Szumigalski & Bayley, 1997). The results of this study seemingly contradict previous findings as the relationship between water level and shrub production was positive between 1991 and 1994 (Table 2); however, this may have been an artifact. Our relationship was weak, possibly because shrubs in this fen almost exclusively inhabited dry hummocks and were rarely found growing in wet hollows. Moore (1989) and Wallén et al. (1988) demonstrated that shrub production is greater on hummocks than in hollows, as waterlogged soils inhibit oxygen absorption by shrub roots (Reader, 1978). The non-significant increase in shrub production observed over the four years of this study can be attributed to the larger size of the plants harvested. Larger individuals will have a greater productivity than smaller ones and a small increase in production from 1991 to 1994 can be expected (the size increases of the sampled shrubs were incidental over the four-year period).

Vance et al. (1995) showed that between 6,000 and 9,000 years ago, the southern boreal forest regions in Alberta experienced summer temperatures between 0.5 and 3.0 ˚C higher than at present. As a result, the water table dropped, which led to a northward migration of grasslands. Pollen diagrams from Lofty Lake (approximately 150 km north east of Edmonton) showed that woody plant species, such as *Salix* spp. and *Populus* spp., and Gramineae (grasses) exhibited a greater abundance during that period than during the cooler and moister period thereafter until the present (Lichti-Federovich, 1970). Furthermore, basal dates from peatlands in western Canada suggest that the water table was also lower in peatlands, which inhibited moss growth in fens (Zoltai & Vitt, 1990).

Bog

Aboveground graminoid and shrub production were explained most significantly by surface water concentrations of NH_4^+ and SRP, respectively (Table 2). Even though the water level did not significantly affect moss, graminoid, and shrub production from 1991 to 1994, the water level relative to the peat surface does influence the solubility of nutrients by affecting the redox potential of the peat. Under anoxic peat conditions, phosphorus solubility is enhanced, whereas nitrification rates are reduced (Bayley et al., 1985). Ullrich et al. (1984) demonstrated that ammonium affected the electrical membrane characteristics in *Lemna gibba* Gl., which resulted in a reduced K^+ uptake rate into the roots of this aquatic herb. In addition, a transient NH_4^+-induced K^+ efflux from roots in sweet potatoes has been reported by Munn & Jackson (1978). We speculate that a similar mechanism affected the graminoid species in the bog and that the effects of this mechanism were compounded by the low concentrations of K^+ in the surface water in those two years. This may have led to a K^+ deficiency and low graminoid production in the bog in 1991 and 1992 (Figure 3). In 1994, NH_4^+ concentrations in the surface water were substantially lower and K^+ concentrations were significantly higher, possibly resulting in a diminished toxicity effect of NH_4^+ on graminoid growth and leading to a significant increase in graminoid production (Figure 3).

Surface water concentrations of SRP exhibited a strong positive relationship with shrub growth (Table 2). SRP concentrations in the surface water did not vary significantly among years; however, they were higher in 1992 and 1994 compared to 1991 (Thormann & Bayley, 1997b; Szumigalski & Bayley, 1997), possibly leading to increased shrub production.

The effects of water levels on surface water chemistry

Lacustrine sedge fen

Nitrate and calcium surface water concentrations correlated negatively and positively with water levels, respectively (Figure 4). We suggest that Ca^{2+} levels decreased due to decreased ground and surface water flow over and through calcium-rich bedrock and mineral soil. Thus, calcium influx into this fen may have been reduced during the years with lower water levels, although we did not measure water flow in either site as part of this study. If the water level and Ca^{2+} concentrations drop and are limiting in this fen, graminoid production may decrease.

Shrub production related best to NO_3^- surface water concentrations (Table 2). A negative correlation between water level and NO_3^- surface water concentrations (Figure 4) indicates that shrub production may increase under better aerated soils and greater availability of nutrients, as such processes as nitrification by soil microbes may be enhanced at lower water levels (Bayley et al., 1985). However, water and other nutrients, especially Ca^{2+}, may eventually limit shrub NPP if the water table drops significantly, and groundwater flow rates are altered as a result of increased atmospheric temperatures.

Bog

Only TDP and K^+ exhibited significant correlations with water levels in the bog (Figure 5). As the water level dropped, TDP surface water concentrations increased and K^+ concentrations decreased. Vitt et al. (1995) hypothesized that this bog may be influenced by regional groundwater flow, thus, if the groundwater level drops, concentrations of highly soluble ions, such as K^+, may decrease in the surface water as well. Also, Pakarinen (1978) determined that soluble ions leach readily from the peatland surface to deeper peat layers in bogs during periods of low water levels. Furthermore, Clymo (1983) and Damman (1978) showed that K^+ concentrations rapidly decrease with increasing peat depths, whereas other ions may be more tightly bound by *Sphagnum* spp. and thus remain largely unaffected by the groundwater. Therefore, a lowered water level may lead to decreased K^+ surface water concentrations in this bog.

Our results contradict those of Bayley et al. (1985) who showed that phosphorus concentrations in the water column increased with higher water levels in a Florida marsh due to the increased solubility of phosphorus under reducing conditions; however, Richardson et al. (1978) and Vitt et al. (1995) reported that TDP concentrations are substantially higher at greater peat depths in peatlands (the latter study was conducted in the same bog). Therefore, we speculate that TDP concentrations increased in the surface water as water levels decreased due to a decreased dilution of TDP in the remaining water.

The effects of climate on plant production

Lacustrine sedge fen

Gorham (1974) previously demonstrated that summer air temperatures explained *Carex* spp. production in eight North American and northern European wetlands between 42° to 68 °N latitude to a significant degree ($r^2 = 0.71$, $p < 0.01$). His relationship was substantially stronger than ours (Table 2), which, we speculate, is the result of the prominent role water level fluctuations played on graminoid production in the lacustrine sedge fen (Table 2). Furthermore, water level fluctuations significantly affected the concentration of some surface water chemistry variables (Figure 4), which could have further diminished the influence of growing season air temperature on graminoid production. The number of growing degree days (Droste, 1984) and latitude (Bernard & Gorham, 1978) have also been found to significantly affect graminoid production in North American wetlands; however, latitude was not a factor in this study and total growing season GDD were not significantly different from 1991 to 1994.

If climatic warming causes a drop in the water level, the results of this study suggest that shrub production will increase and graminoid production will decrease in this fen. Our four-year relationship between water level and shrub production was weak and contradicts previous findings for Alberta peatlands (Thormann & Bayley, 1997b; Szumigalski & Bayley, 1997). Decreased water availability and lower Ca^{2+} concentrations in the surface water may limit graminoid growth. Conversely, shrubs may have greater access to nutrients and water due to their frequent endo- and ectomycorrhizal associations that aid in nutrient uptake, especially phosphorus, and decrease water stress (Dhillion, 1994). Graminoids, especially members of the Cyperaceae, have generally low levels or no endo- and ectomycorrhizal infections of their root systems (Read & Haselwandter, 1981). An extensive examination of the mycorrhizal status of the dominant peatland plants in southern boreal Alberta is currently being conducted (unpubl. data). *Drepanocladus aduncus*, a hollow species, may also be limited by nutrients, water, and increased atmospheric temperatures, and we speculate that production of this drought-intolerant species (Gignac et al., 1991) will decrease as well. Therefore, we suggest that the vegetation composition of this lacustrine sedge fen will change if the water level drops in response to a warmer climate.

Gorham (1990) described the succession from sedge-dominated fens to poor fens to bogs. It is possible that this lacustrine sedge fen may undergo a similar succession under a drier, warmer climate, which would decrease the flow of nutrient-richer water from adjacent uplands into this fen. Shrubs may become the dominant vegetation by replacing graminoids, and *Sphagnum* spp. may replace the presently dominant non-*Sphagnum* moss species. This fen might gradually convert into a poor fen and, if the basin is large and moist enough, ultimately into a bog (Gorham,

1990) dominated by *Picea mariana* and *Sphagnum* spp. (Glaser & Janssens, 1986). However, peat growth is crucial for the formation of a bog from a poor fen, because it will ultimately result in the separation of the plant roots from the mineral ground water.

Bog

A strong correlation between *Sphagnum* spp. production and temperature has previously been reported by Moore (1989) in five poor to moderate-rich fens in Quebec, Canada. His relationship was substantially weaker than ours ($r^2 = 0.30$ versus $r^2 = 0.71$) (Table 2) and may be the result of the variation in the peatlands he examined, whereas ours refers to the same bog over four years. Other studies found significant correlations between moss growth and timing of precipitation (Backéus, 1988) and the position of the water table with respect to the peat surface (Brock & Bregman, 1989). Neither of these two variables were significant in this study as the mean annual water level and timing and total amounts of precipitation did not vary significantly from 1991 to 1994 (Figure 3, Table 1).

Data on the effects of climatic variables on shrub production are scarce, and water level fluctuations (Thormann & Bayley, 1997b; Szumigalski & Bayley, 1997; Gorham, 1991; Hillman et al., 1990; Moore, 1989; Vasander, 1982) and surface water chemistry variables may affect shrub production to a greater extent and possibly mask the effects of climatic variables. The small observed increase in shrub production from 1991 to 1994 may be attributed to (1) the increased concentrations of soluble reactive phosphorus in the surface water, and (2) the age of the plants.

The mean annual water level did not vary significantly among years (Figure 3) and did not affect moss, graminoid, or shrub production directly. The effects of NH_4^+ and low K^+ surface water concentrations on graminoid production and tissue N concentrations were discussed earlier and ammonium toxicity in mosses has also been reported previously (Thormann & Bayley, 1997b; Vasander, 1982). Shrub and moss production were explained to significant degrees by GDD and air temperature, respectively, thus, increased atmospheric temperatures may lead to increased production of these two strata. Furthermore, a lowered water level resulting from warmer air temperatures may also lead to increased production of shrubs and trees. This relationship has been demonstrated in bogs in Finland (Vasander, 1982) and Alberta (Hillman et al., 1990) previously. In addition, Pakarinen (1978) determined that leaching rates of nutrients and minerals, especially K^+, from surface to deeper peat layers are enhanced in bogs with a lowered water table. This may further compound the potential NH_4^+ toxicity on graminoid species and reduce their productivity. Therefore, we speculate that the vegetation composition of this bog may change in response to a warmer and drier climate. Moss and graminoid production may decline and deeper rooted mycorrhizal shrubs and trees may become the dominant vegetation strata by retaining their access to water, nutrients, and minerals. Fires may become more frequent (Flannigan & Van Wagner, 1991) and burn off peat (Gorham, 1994), possibly leading to the disappearance of peat from this site. Even though the peat layer is 5 m thick in this bog, decreases in peat thickness may also result due to increased rates of decomposition caused by increased atmospheric temperatures and lower water levels (Nicholson et al., 1997; Gignac and Vitt, 1994).

Conclusions

The net primary production (NPP) of the moss, graminoid, and shrub strata, surface water chemistry variables, and water level fluctuations were measured in a bog and a lacustrine sedge fen from 1991 through 1994. Based on the data collected by Szumigalski & Bayley (1997) and Thormann & Bayley (1997b), inferences concerning global warming were made regarding these variables in the two peatlands. Although climatic variables explained only moss NPP to a significant degree in the bog, higher atmospheric temperatures may lead to decreased water levels (Shedlock et al., 1993) and affect the peatland microclimate. These changes may affect plant growth and nutrient mineralization (Dise et al., 1993) by affecting the redox potential of the peat. This study shows that even annual fluctuations of the water level significantly affect some surface water chemistry variables and aboveground plant production in this lacustrine sedge fen and bog. Shrub NPP increased and moss and graminoid NPP decreased, supporting hypotheses one and two. Hypothesis three was rejected, as only two surface water chemistry variables showed significant correlations with water levels in either site, thus, not all surface water nutrients may become limiting to plant growth due to decreased water levels in response to increased atmospheric temperatures. Although peatland drainage experiments have shown that the vegetation composition and plant production of the pre- and post-drained peatland differs significantly (Vasander, 1982), such experiments are disruptive to the ecosystem. Our study is not disruptive and still shows that aboveground plant production is significantly affected by water level changes that may ultimately result from higher atmospheric temperatures.

We speculate that a warmer and drier climate may lead to a succession from the lacustrine sedge fen to a poor fen and ultimately to a bog (if peat growth can separate the vegetation strata from the mineral ground water flow). Graminoid and non-*Sphagnum* moss species may be displaced by shrubs and trees or replaced with *Sphagnum* spp., respectively. Peat may disappear due to increased fire occurrences and increased rates of decomposition, whereby the bog may succeed into an 'upland-type' forest ecosystem, where shrubs and trees dominate and mosses contribute less significantly to the total production of the ecosystem. Sedge-dominated fens may experience these changes before shrub- and tree-dominated bogs due to the different environmental requirements of the dominant vegetation strata in these two types of peatlands. This remains speculation though, as our data can not predict future vegetation composition changes; however, Nicholson et al.'s (1997) model predicted similar vegetation responses and a 780 km northward migration of southern boreal peatlands under a $2xCO_2$ scenario in central Alberta. Furthermore, Gignac and Vitt (1994) predicted the disappearance of bryophyte indicator species from bogs and fens in southern boreal peatlands in western Canada as a results of global warming as well.

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References

Anderson, L. E., 1990. A checklist of *Sphagnum* in North America north of Mexico. Bryologist 93: 500–501.

Anderson, L. E., H. A. Crum & W. R. Buck, 1990. List of the mosses of North America north of Mexico. Bryologist 93: 448–499.

Armentano, T. V. & E. S. Menges, 1986. Patterns of change in the carbon balance of organic soil-wetlands of the temperate zone. J. Ecol. 74: 755–774.

Backéus, I., 1990. Production and depth distribution of fine roots in a boreal open bog. Ann. bot. fenn. 27: 261–265.

Backéus, I., 1988. Weather variables as predictors of *Sphagnum* growth in a bog. Holarctic Ecol. 11: 146–150.

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

Bernard, J.M. & E. Gorham, 1978. Life history aspects of primary production in sedge wetlands. In R. E. Good, D. F. Whigham & R. L. Simpson (eds), Freshwater Wetlands: Ecological Processes and Management Potential. Academic Press, New York, NY, USA: 39–53.

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

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

Chapin III, F. S., N. Fetcher, K. Keilland, K. R. Everett & A. E. Linkens, 1988. Productivity and nutrient cycling of Alaskan tundra: Enhancement of flowing soil water. Ecology 69: 693– 702.

Clymo, R. S., 1983. Peat. In A. J. P. Gore (ed.), Mires: Swamp, Bog, Fen and Moor. Vol. A, General Studies. Elsevier Scientific Publishing, Amsterdam, The Netherlands: 159–224.

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

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

Dhillion, S. S., 1994. Ectomycorrhizae, arbuscular mycorrhizae, and *Rhizoctonia* sp. of alpine and boreal *Salix* spp. in Norway. Arc. Alp. Res. 26: 304–307.

Dise, N. B., E. Gorham & E. S. Verry, 1993. Environmental factors controlling methane emissions from peatlands in northern Minnesota. J. Geophys. Res. Atmos. 98: 10583–10594.

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

Ecoregions Working Group, 1989. Ecoclimatic regions of Canada, first approximation. Canada Committee on Ecological Land Classification, Ecological Land Series, No. 23. Sustainable Development Branch, Canadian Wildlife Service, Conservation and Protection, Environment Canada, Ottawa, Ontario, Canada, 118 pp.

Environment Canada, 1982. Canadian Climate Normals, 1951–1980, Temperature and Precipitation, Prairie Provinces. Canadian Climate Program, Ottawa, Ontario, Canada, 429 pp.

Flannigan, M. D. & C. E. Van Wagner, 1991. Climate change and wildfire in Canada. Can. J. For. Res. 21: 66–72.

Gignac, L. D. & D. H. Vitt, 1994. Responses of northern peatlands to climate change: Effects on bryophytes. J. Hattori Bot. Lab. 75: 119–132.

Gignac, L. D., D. H. Vitt, S. C. Zoltai & S. E. Bayley, 1991. Bryophyte response surfaces along climate, chemical, and physi-

cal gradients in peatlands in western Canada. Nova Hedwigia 53: 27–71.
Glaser, P. H. & J. A. Janssens, 1986. Raised bogs in eastern North America: Transitions in landforms and gross stratigraphy. Can. J. Bot. 64: 395–415.
Glaser, P. H. J. A. Janssens & D. I. Siegel, 1990. The response of vegetation to chemical and hydrological gradients in the Lost River Peatland, northern Minnesota. J. Ecol. 78: 1021–1048.
Gorham, E., 1994. The future of research in Canadian peatlands: A brief survey with particular reference to global change. Wetlands 14: 206–215.
Gorham, E., 1991. Northern peatlands: Role in the carbon cycle and probable responses to climate warming. Ecol. Applic. 1: 182–195.
Gorham, E., 1990. Biotic impoverishment in northern peatlands. In G. M. Woodwell (ed.), The Earth in Transition: Patterns and Processes of Biotic Impoverishment. Cambridge University Press, Cambridge, England: 65–98.
Gorham, E., 1988. Canada's peatlands: Their importance for the global carbon cycle and possible effects of 'greenhouse' climatic warming. Transactions of the Royal Society of Canada, Series V, 3: 21–23.
Gorham, E., 1974. The relationship between standing crop in sedge meadows and summer temperature. J. Ecol. 62: 487–491.
Hillman, G. R., J. D. Johnson & S. K. Takyi, 1990. The Canada-Alberta wetlands drainage and improvement for forestry program. qForestry Canada/Alberta Forestry, Lands and Wildlife, Project # 1413-1417-86, 66 pp.
Laitinen, J., 1990. Periodic moisture fluctuations as a factor affecting mire vegetation. Aquilo. Ser. Bot. 28: 45–55.
Lichti-Federovich, S., 1970. The pollen stratigraphy of a dated section of late Pleistocene lake sediment core from central Alberta. Can. J. Earth Sci. 7: 938–945.
Moore, T. R., 1994. Trace gas emissions from Canadian peatlands and the effects of climate change. Wetlands 14: 223–228.
Moore, T. R., 1989. Growth and net production of *Sphagnum* at five fen sites, subarctic eastern Canada. Can. J. Bot. 67: 1203–1207.
Munn, D. A. & W. A. Jackson, 1978. Nitrate and ammonium uptake by rooted cuttings of sweet potato. Agron. J. 70: 312–316.
Nicholson, B. J., L. D. Gignac, S. E. Bayley & D. H. Vitt, 1997. Vegetation responses to global warming: Interactions between boreal forest wetlands and regional hydrology. In S. J. Cohen (ed.), Mackenzie Basin Impact Study (MBIS). Environment Canada, University of British Columbia, Vancouver, B. C., Canada: 125–145.
Packer, J. G., 1983. Flora of Alberta by E. H. Moss, 2nd edn. University of Toronto Press, Toronto, Ontario, Canada, 687 pp.
Pakarinen, P., 1978. Production and nutrient ecology of three *Sphagnum* species in southern Finnish raised bogs. Ann. bot. fenn. 15: 15–26.
Read, D. J. & K. Haselwandter, 1981. Observations of the mycorrhizal status of some alpine plant communities. New Phytol. 88: 341–352.
Reader, R. J., 1978. Primary production in northern bog marshes. In R. E. Good, D. F. Whigham & R. L. Simpson (eds), Freshwater Wetlands: Ecological Processes and Management Potential. Academic Press, New York, NY, USA: 53–63.
Richardson, C. J., D. L. Tilton, K. A. Kadlec, J. P. M. Chamie & W. A. Wentz, 1978. Nutrient dynamics of northern wetland ecosystems. In R. E. Good, D. F. Whigham & R. L. Simpson (eds), Freshwater Wetlands: Ecological Processes and Management Potential. Academic Press, New York, NY, USA: 217–241.
Roulet, N., R. Ash, W. Quinton & R. R. Moore, 1993. Methane flux from drained northern peatlands: Effects of a persistent water table lowering on flux. Global biogeochem. Cycles 7: 749–769.
SAS Institute Inc., 1989. SAS/STAT Release 6.08 Edition. Cary, NC, USA.
Shedlock, R. J., D. A. Wilcox, T. A. Thompson & D. A. Cohen, 1993. Interactions between ground water and wetlands, southern shore of Lake Michigan, USA. J. Hydrol. 141: 127–155.
Sjörs, H., 1991. Phyto- and necromass above and below ground in a fen. Holarctic Ecol. 14: 208–214.
SYSTAT Inc., 1992. SYSTAT Version 5.2 Edition. Evanston, IL, USA.
Szumigalski, A. R. & S. E. Bayley, 1997. Net aboveground primary production in peatlands of central Alberta in relation to water levels and water chemistry. Écoscience 4: 385– 393.
Szumigalski, A. R. & S. E. Bayley, 1996. Net aboveground primary production along a bog-rich fen gradient in central Alberta. Wetlands 16: 467–476.
Thormann, M. N. & S. E. Bayley, 1997a. Aboveground net primary production along a bog – fen – marsh gradient in southern boreal Alberta, Canada. Écoscience 4: 374–384.
Thormann, M. N. & S. E. Bayley, 1997b. Aboveground plant production and nutrient content of the vegetation of six peatlands in Alberta, Canada. Plant Ecology 131: 1–16.
Ullrich, W. R., M. Larsson, C. M. Larsson, S. Lesch & A. Novacky, 1984. Ammonium uptake in *Lemna gibba* Gl. and related membrane potential changes and inhibition of anion uptake. Physiol. Plant. 61: 369–376.
Vance, R. E., A. B. Beaudoin & B. H. Luckman, 1995. The paleological record of 6 ka bp climate in the Canadian prairie provinces. Géographie physique de Quaternaire 49: 81–98.
Vasander, H., 1982. Plant biomass and production in virgin, drained and fertilized sites in a raised bog in southern Finland. Ann. bot. fenn. 19: 103-125.
Vitt, D. H. & P. Pakarinen, 1977. The bryophyte vegetation, production, and organic components of Truelove Lowland. In L. C. Bliss (ed.), Truelove Lowland, Devon Island, Canada: A High Arctic Ecosystem. University of Alberta Press, Edmonton, Alberta, Canada: 225–244.
Vitt, D. H., S. E. Bayley, L. Halsey & T.-L. Jin, 1995. Seasonal variation in water chemistry over a bog-rich fen gradient in continental western Canada. Can. J. Fish. aquat. Sci. 52: 587–606.
Wallén, B., 1993. Methods for studying below-ground production in mire ecosystems. Suo 43: 155–162.
Wallén, B., U. Falkengren-Grerup & N. Malmer, 1988. Biomass, productivity and relative rate of photosynthesis at different water levels on a south Swedish peat bog. Holarctic Ecol. 11: 70–76.
Yavitt, J. B., R. K. Wieder & G. E. Lang, 1993. CO_2 and CH_4 dynamics of a *Sphagnum*-dominated peatland in West Virginia. Global biogeochem. Cycles 7: 269–274.
Zar, H. H., 1984. Biostatistical Analyses, 2nd edn. Prentice Hall, Englewood Cliffs, New Jersey, NJ, USA, 718 pp.
Zoltai, S. C. & D. H. Vitt, 1990. Holocene climate change and the distribution of peatlands in western interior Canada. Quat. Res. 33: 231–240.