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NET ABOVE-GROUND PRIMARY PRODUCTION ALONG A BOG-RICH FEN GRADIENT IN CENTRAL ALBERTA, CANADA

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Abstract: The above-ground net primary production (NPP) and litter fall of five peatlands (bog, poor fen, wooded moderate-rich fen, lacustrine sedge fen, and extreme-rich fen) representing the bog-rich fen gradient in central Alberta, Canada were measured during two growing seasons. Total above-ground NPP increased along the gradient from the bog to moderate-rich fen and then decreased in the sedge and extreme-rich fens. Above-ground NPP in the bog (264–297 $g \cdot m^{-2} \cdot yr^{-1}$) was low compared to other North American bogs, while the Alberta fens had intermediate values of NPP (214–360 $g \cdot m^{-2} \cdot yr^{-1}$) compared to other North American fens. Moss NPP was lowest in the sedge fen but did not differ significantly between the other peatlands. Vascular plant NPP was highest in the poor fen, moderate-rich fen, and sedge fen and lowest in the bog and extreme-rich fen. Herb NPP tended to increase along the bog-rich fen gradient, while shrub NPP tended to decrease along the gradient. Litter fall was greatest in the poor and moderate-rich fens and lowest in the sedge and extreme-rich fens.

Key Words: net primary production, litter fall, bogs, fens, boreal peatlands, Alberta, Canada

INTRODUCTION

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

There have been a number of studies quantifying above-ground peatland NPP in North America (Reader and Stewart 1972, Wein and Bliss 1974, Bartsch and Moore 1985, Grigal et al. 1985, Wieder et al. 1989) and Europe (Forrest 1971, Doyle 1973, Forrest and Smith 1975, Wielgolaski 1975, Vasander 1982, Francez 1992a), while there have been fewer investigations into below-ground NPP (e.g., Reader and Stewart 1972, Vasander 1982, Backéus 1990, Sjörs 1991). Most NPP research has focused on either ombrotrophic or tundra/sub-arctic ecosystems, while few studies of total NPP have incorporated southern-boreal minerotrophic systems (Reader and Stewart 1972, Richardson et al. 1976). Despite the abundance of peatlands in Alberta, NPP studies of these systems have been scarce and limited to either bryophytes (Busby et al. 1978, Vitt 1990) or sedges (Gorham and Somers 1973). Information on the NPP of peatlands in Western Canada is essential to the understanding and prediction of peat accumulation rates and responses to global climate change.

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

(1971) generally correlated trophic status with pH in peatlands.

The objective of this paper is to document the above-ground NPP of the different strata (moss, herb, shrub, and tree) to arrive at an estimate of total above-ground NPP for each of the sites. We hypothesized that total NPP will increase along the bog-rich fen gradient, due to enhanced nutrient availability toward its rich end.

STUDY AREA AND SITE DESCRIPTIONS

The five sites (all within 150 km of Edmonton) generally represent the range of peatland types in the central Alberta area. The bog and poor fen were located north of Bleak Lake at 54°41′N and 113°28′W, while the moderate-rich fen (54°28′N, 113°17′W) and sedge fen (54°28′N, 113°20′W) were east of Perryvale. The extreme-rich fen was south of Calahoo at 53°42′N and 113°57′W.

The climate of the area is characterized by mild summers and cold, snowy winters, with a long-term mean annual temperature of 1.7 °C for the first four sites and 2.2 °C for the extreme-rich fen (Environment Canada 1982). The mean annual precipitation is about 500 mm for all sites. These peatlands were located within the Boreal Forest Region of Canada (Rowe 1972). Detailed descriptions of the vegetation and water chemistry are also in Vitt et al. (1995) for the first four sites and in Rochefort (1987) for the extreme-rich fen. General descriptions of the sites are as follows:

Bog

This site, a raised ombrotrophic island within a peatland complex, was bordered by the poor fen water track. The peat surface of the bog was composed mainly of large, dry hummocks with a few hollows. The peat depth was about 5 m, while the surface water pH ranged from 3.4 to 4.2 during the study period. This site consisted of an open bog (OB), and a sparsely wooded bog (WB) dominated by *Picea mariana* (Mill.) BSP [vascular plant nomenclature follows Moss (1983)]. The shrub stratum of the bog was dominated by *Ledum groenlandicum* Oeder, while the moss layer consisted almost entirely of *Sphagnum fuscum* (Schimp.) Klinggr. [bryophyte nomenclature follows Ireland et al. (1987)].

Poor Fen (PF)

The PF had a hummocky microtopography and was wetter than the bog. The surface water pH varied between 4.3 and 5.2, and peat thickness was about 4 m. This site had a well developed shrub layer of *Betula pumila* L. var. *glandulifera* Regel. and *Salix pedicellaris* Pursh. The herb stratum consisted mainly of *Smilacina trifolia* (L.) Desf., *Menyanthes trifoliata* L., and *Carex* spp. (*C. brunescens* (Pers.) Poir., *C. aquatilis* Wahlenb., and *C. chordorrhiza* L.f.). The ground layer was *Sphagnum*-dominated; *S. teres* (Schimp.) Aongstr. ex C. Hartm., and *S. angustifolium* (C. Jens. ex Russ.) C. Jens in Tolf, were the most common species.

Wooded Moderate-Rich Fen (WRF)

This site, a forested fen with large hummocks and wet lawns, was adjacent to a floating mat fen surrounding a pond. Peat depth at the WRF was about 4.5 m, while surface water pH ranged between 5.7 and 6.6. The fairly sparse tree canopy was dominated by *Larix laricina* (Du Roi) K. Koch, while the most prominent shrubs were *B. pumila* var. *glandulifera*, *S. pedicellaris*, and *Andromeda polifolia* L. The most abundant herbs were *M. trifoliata*, *S. trifolia*, and *Carex* spp. (*C. lasiocarpa* Ehrh., *C. diandra* Schrank, and *C. chordorrhiza*). The moss layer consisted mainly of *Tomenthypnum nitens* (Hedw.) Loeske.

Lacustrine Sedge Fen (SF)

This rich fen was situated within a large expanse of sedge-dominated wetlands with several bodies of open water nearby (Vitt et al. 1995). The peat surface was level, except for a few isolated hummocks. During 1991, the SF was inundated with water; however, it began to dry out in 1992. The water pH ranged between 6.1 and 6.9, while peat thickness was from 2 to 2.5 m. *C. lasiocarpa* and *C. diandra* dominated the vascular plant strata, while the sparse moss layer consisted mostly *Drepanocladus aduncus* (Hedw.) Warnst.

Extreme-Rich Fen (ERF)

This spring-fed fen consisted of strings and flarks with marl ($CaCO_3$) mud bottoms. These marl ponds were not included in the study. Peat depth was about 2.5 m, and surface water pH ranged from 7.8 to 8.4. *Scirpus cespitosus* L. was the dominant herb, while *Drosera rotundifolia* L. was also common. The woody strata were very sparse at the ERF. The moss layer followed the typical sequence, from pool to dry hummock, for extreme-rich fens in western Canada (Vitt 1990): *Scorpidium scorpioides* (Hedw.) Limpr.–*Drepanocladus revolvens* (Sw.) Warnst.–*Campylium stellatum* (Hedw.) C. Jens.–*T. nitens*.

METHODS

Production Measurements

All biomass, production, and litter samples were oven-dried at 60 °C before weighing. The different strata were measured using the following methods.

Mosses. Growth and NPP of dominant moss species were measured by the cranked wire method of Clymo (1970) in all sites except the SF. In June 1991, 200 cranked wires were established at each of these sites. Growth was measured during the growing season (defined as early May to mid-October). Since the wires were set up in June, part of the growing season (May 1 to June 10) was missed in 1991. Moss growth during approximately the same period in 1992 was used to estimate the amount missed in 1991.

The NPP of the dominant moss species (*S. fuscum* in the bog; *S. teres* and *S. angustifolium* in the PF; *T. nitens* in the WRF and ERF) was used to estimate total moss NPP, since the dominant species generally had a cover of 75% or more and total moss cover approached 100%. *T. nitens* NPP was used as an approximation of total moss production in the ERF, since Vitt (1990) showed *T. nitens* and total moss NPP to be very similar over three years in two different extreme-rich fens in Alberta.

Moss production in the SF was estimated using innate markers (cf. Vitt and Pakarinen 1977, Vasander 1982).

Herbs and Shrubs. Production of these strata was estimated from randomly placed 0.25 m^2 quadrats. In 1991, six quadrats were sampled per site per harvest period (late June, late July, and late August), while in 1992, the sample size was increased to 10.

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

At the final (August) harvest period, all shrub material was clipped at ground level, and terminal production (current year's leaf and stem growth) was collected for all species. Radial production was estimated for the larger shrubs (*Betula, Salix,* and *Ledum*) by a modification of the methods of Reader and Stewart (1972). The radial production of smaller dwarf shrub species is believed to be insignificant (Vasander 1982) and, therefore, was not measured. Total shrub NPP was determined by summing terminal and radial production in each quadrat.

To estimate total vascular plant above-ground NPP (excluding trees and shrub radial production), the August herb biomass and shrub terminal production from the quadrats were combined.

Trees. At the end of October 1992, two linear plots of 2 m by 50 m (100 m^2) were established in both the WB and WRF to estimate tree biomass and production. Within the plots, each tree was classified as large ($\geq$1.90 m) or small ($<$1.90 m). The dbh (diameter at 1.3 m) and height of each large tree were measured, while the small trees were measured for basal diameter, height, and leader length. Cross-sectional disks were removed at the dbh level from large trees (9 *P. mariana* in the bog; 14 *L. laricina* in the WRF) in each site, representing the range of sizes. Ten small *P. mariana* from the bog and 6 small *L. laricina* from the WRF were harvested and had basal disks removed for measurement. These trees were then separated into various components (trunk, live branches, dead branches, etc.).

The biomass increment (ΔB) of the trees was predicted with the equation

$$\Delta B = B_2 - B_1;$$

where B_2 is the biomass at the end of the growing season and B_1 is the biomass at the beginning of the growing season. B_2 and B_1 were estimated using the regression equations in Table 1. The diameter (basal or dbh) and height (small trees only) used to estimate B_1 were determined by

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

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

Regression equations to estimate annual above-ground biomass change using current biomass as the independent variable were then developed for each species combining both large and small trees (Table 1). Final tree NPP values were derived by combining annual biomass increment with annual tree litter fall (Grigal et al. 1985).

Litter Traps. Litter traps were randomly placed on the peat surface at the beginning of the growing season (early May) in 1992 and left out for a period of about one year. The traps were constructed of circular em-

Table 1. Regression equations used to estimate above-ground tree biomass and biomass increment. Equations follow the general format: $y = a + bx$, where y is the dependent variable, x is the independent variable, and a and b are the y-intercept and slope, respectively.

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

diam. sq. = basal diameter squared (cm^2); ht. = height (m); dbh = diameter at breast height (cm); biomass and biomass increment (g); n = tree sample size; and r-square = coefficient of determination. * Small trees < 1.90 m and large trees ≥ 1.90 m.

broidery hoops with a diameter of 14.5 cm and 1-mm-mesh nylon screen on the bottom. Fifty traps were placed in each of the bog, PF, and WRF, while 25 each were placed in the SF and ERF. The contents were collected three times: late August/early September 1992, mid-October 1992, and early May 1993.

Statistical Analyses

Moss NPP was tested using a nested ANOVA design (Zar 1984). Since the SF was sampled differently, it was excluded from this analysis. Differences in moss NPP between sites were tested separately for 1991 and 1992. To test for differences between years, a paired *t*-test was performed using only the growth period from June to October. In the PF, there was no significant difference in NPP between *S. teres* and *S. angustifolium* (*t*-test, $p > 0.05$) both years. These two species, therefore, were treated as the same population and their data pooled for the statistical analyses.

Randomized block-nested ANOVA designs were used to test minimum seasonal herb, maximum herb, terminal shrub, and vascular plant production. Litter fall was tested between sites using a one-way ANOVA. Since only the WB site had a tree layer within the bog, the WB and OB were presented separately when comparing total production and litter fall between peatlands. The data from the WB and OB were combined for all other analyses because there were no significant differences (*t*-tests, $p > 0.05$) in moss, herb, shrub, and vascular plant (excluding trees) production between the two bog sites.

To maintain homogeneity of variances and normality, most of the data were either square root- or log-transformed before the analyses (Zar 1984). All analyses were performed on SYSTAT (SYSTAT Inc. 1992).

RESULTS AND DISCUSSION

Moss Production

The SF had the lowest moss production (47 $g \cdot m^{-2} \cdot yr^{-1}$ in 1991 and 38 $g \cdot m^{-2} \cdot yr^{-1}$ in 1992) of all the sites (Figure 1). The low moss cover and NPP at this site may have been a function of large water-level fluctuations and flooding, which can be detrimental to moss survival and growth (Laitinen 1990).

The bog, PF, WRF, and ERF had values between 146 and 203 $g \cdot m^{-2} \cdot yr^{-1}$ in 1991 and from 95 to 120 $g \cdot m^{-2} \cdot yr^{-1}$ in 1992. There were no significant differences between these four sites; however, there was a significant difference between years ($p < 0.001$). In every site, moss NPP was lower in 1992, ranging from 50% to 80% of the 1991 rates. This difference may be due to much lower water levels in all sites during 1992. Large variations in moss NPP between years have also been reported in other studies (Wallén et al. 1988, Moore 1989, Rochefort et al. 1990, Francez 1992b). Others have also shown that moss NPP may differ minimally between peatland types (Bartsch and Moore 1985, Rochefort et al. 1990, Vitt 1990). However, Reader and Stewart (1972) found moss NPP to differ widely between peatland types in Manitoba, and Moore (1989) recorded greater moss NPP in a sub-arctic extreme-rich fen than other nearby fens.

The moss production averages of the bog (120–189 $g \cdot m^{-2} \cdot yr^{-1}$) and PF (98–146 $g \cdot m^{-2} \cdot yr^{-1}$) are within the range of values from the oligotrophic (74–206 $g \cdot m^{-2} \cdot yr^{-1}$) and minerotrophic (75–223 $g \cdot m^{-2} \cdot yr^{-1}$) sites of Rochefort et al. (1990). Reader and Stewart (1972), and Moore (1989) recorded lower values in a Manitoba bog (55 $g \cdot m^{-2} \cdot yr^{-1}$) and in sub-arctic poor fens (70–84 $g \cdot m^{-2} \cdot yr^{-1}$), respectively. The moss NPP of our two *Sphagnum*-dominated sites was much lower than values (320–380 $g \cdot m^{-2} \cdot yr^{-1}$) cited for Minnesota bogs (Grigal 1985); probably reflecting the more southerly location (i.e., higher temperature and precipitation) of the latter sites.

Total moss NPP of the brown moss-dominated WRF (115–170 $g \cdot m^{-2} \cdot yr^{-1}$) and ERF (95–203 $g \cdot m^{-2} \cdot yr^{-1}$) showed more variation between years than the two boreal extreme-rich fens of Vitt (1990), which remained fairly constant over three years (125–131 $g \cdot m^{-2} \cdot yr^{-1}$).

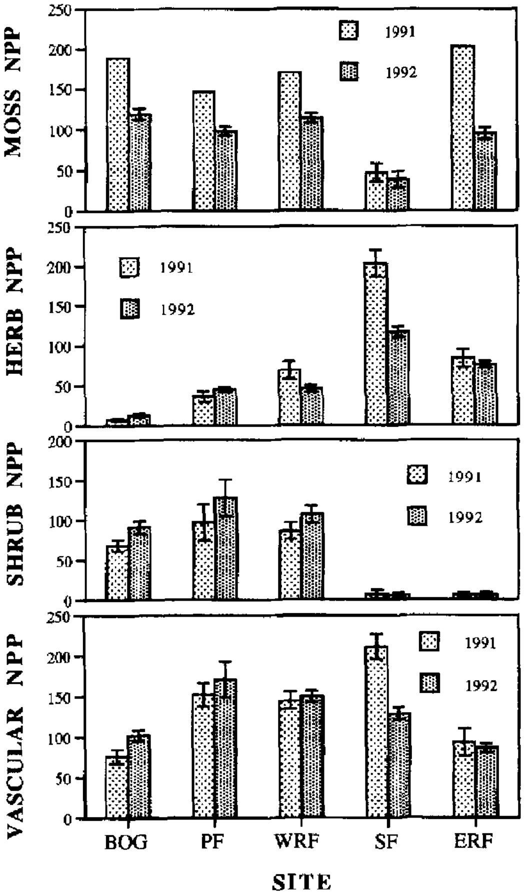

Figure 1. Moss, herb, shrub, and vascular plant above-ground production (mean ± SE) along the bog to extreme-rich fen gradient (PF = poor fen, WRF = moderate-rich fen, SF = sedge fen, and ERF = extreme-rich fen) in 1991 and 1992. All values are in g·m^{-2}·yr^{-1}. Moss NPP was derived assuming 100% cover of ground layer by dominant species. Note that there are no error bars on the 1991 moss NPP values partially estimated from 1992 growth. Herb NPP is from minimum seasonal production. Shrub NPP consists of terminal production only. Vascular plant NPP does not include shrub radial and tree production.

Our sites may have been subjected to a greater yearly variation in water levels and climate than those of the latter study.

Our NPP values may be low because the cranked wire method has been shown to under-estimate moss NPP (Grigal 1985, Wallén et al. 1988). There may also have been errors in the estimation of moss production in the SF due to difficulties in determining growth by innate characteristics.

Herb Production

Minimum seasonal herb production and peak herb standing crop (maximum production) were both significantly different ($p < 0.01$) between sites (Figures 1 and 2). Herb NPP increased along the bog-rich fen gradient, possibly due to increasing water levels across the gradient. Minimum seasonal production ranged from 7 to 203 g·m^{-2}·yr^{-1} in the order: SF > ERF > WRF > PF > bog. With the exception of the bog in 1992, peak standing crops were attained in either July or August both years (Figure 2). Peak standing crops were greater in 1991 in all sites except the bog. The SF showed the greatest yearly change in maximum production, dropping from 203 g·m^{-2}·yr^{-1} in 1991 to 122 g·m^{-2}·yr^{-1} in 1992—probably a result of much lower water levels during the second year.

The low values of peak herb standing crop in the bog (8 and 14 g·m^{-2}) are consistent with the results of other studies done on ombrotrophic systems (Paavilainen 1980, Vasander 1982, Grigal et al. 1985, Malmer 1986).

The maximum herb NPP of our minerotrophic sites is also similar to other fens studied. Bartsch and Moore (1985) recorded 27 g·m^{-2}·yr^{-1} in a sub-arctic poor fen, which is somewhat lower than the PF (52–55 g·m^{-2}·yr^{-1}). Total herb NPP in their rich fens (90–233 g·m^{-2}·yr^{-1}) seems to be slightly higher than the WRF (52–78 g·m^{-2}·yr^{-1}) and ERF (81–97 g·m^{-2}·yr^{-1}) but similar to the SF (122–203 g·m^{-2}·yr^{-1}). Reader and Stewart (1972) also found similar herb NPP (164 g·m^{-2}·yr^{-1}) in a Manitoba lagg.

The SF had much lower herb production than other North American sedge wetlands reported by Bernard and Gorham (1978). Above-ground NPP of the latter ranged from 340 to 1500 g·m^{-2}·yr^{-1}; however, several of these wetlands were located at much lower latitudes.

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

Shrub Production

Above-ground shrub NPP seems to decrease along the bog-rich fen gradient (Figure 1), which may be a function of increasing wetness along the gradient. Total terminal shrub production was highly significant ($p < 0.001$) between sites, ranging from 6 to 128 g·m^{-2}·yr^{-1}. The bog, PF, and WRF had much greater shrub production than the SF and ERF. Shrub terminal production was generally higher in 1992; however, this difference was not significant ($p > 0.05$). The estimated radial production of the major shrub species was low compared to the terminal production. This secondary wood growth only accounted for an additional 2–26% (mean of 12%) of the terminal production.

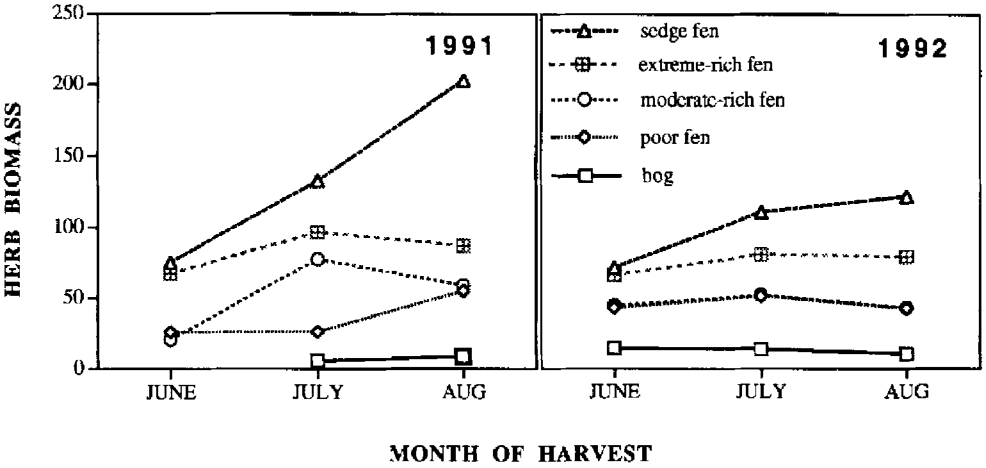

Figure 2. Above-ground herb biomass ($g \cdot m^{-2}$) at three monthly harvest periods in five peatlands during the summers of 1991 and 1992.

Total (terminal and radial) shrub NPP in the bog (77–97 $g \cdot m^{-2} \cdot yr^{-1}$) was slightly higher than that recorded by Reader and Stewart (1972) in a Manitoba bog forest (53 $g \cdot m^{-2} \cdot yr^{-1}$) but lower than their sparsely-treed muskeg (241 $g \cdot m^{-2} \cdot yr^{-1}$) and tree-less bog (308 $g \cdot m^{-2} \cdot yr^{-1}$). Grigal et al. (1985) also reported higher mean shrub NPP (200 $g \cdot m^{-2} \cdot yr^{-1}$) in Minnesota raised bogs but lower values in perched bogs (40 $g \cdot m^{-2} \cdot yr^{-1}$).

The PF (115–152 $g \cdot m^{-2} \cdot yr^{-1}$) and WRF (96–120 $g \cdot m^{-2} \cdot yr^{-1}$) had high total shrub production compared to similar fens in sub-arctic Québec (Bartsch and Moore 1985), where values ranged from 43 to 71 $g \cdot m^{-2} \cdot yr^{-1}$. Reader and Stewart (1972) in Manitoba, and Richardson et al. (1976) in Michigan, reported much higher shrub NPP (458 and 338 $g \cdot m^{-2} \cdot yr^{-1}$, respectively) in fens.

The SF (7–9 $g \cdot m^{-2} \cdot yr^{-1}$) and ERF (6 $g \cdot m^{-2} \cdot yr^{-1}$, both years) had the lowest total shrub production, probably because of their high water levels compared to the other sites. These shrub NPP values are similar to that of a Minnesota marginal fen (7 $g \cdot m^{-2} \cdot yr^{-1}$) studied by Reiners (1972).

The estimates of above-ground shrub NPP may be low because of losses due to retranslocation, litter fall, and herbivory. Ericaceous terminal NPP also could have been under-estimated because current leaves and stems may continue to increase in weight until October (Backéus 1985), while our harvests were performed in late August.

Vascular Plant Production

There was a significant difference ($p < 0.05$) in above-ground vascular plant (excluding trees and radial production of shrubs) NPP between sites, but there was no significant difference between the two years ($p > 0.05$). The two sites at the ends of the gradient (bog and ERF) had the lowest vascular plant NPP (Figure 1), while the rest of the sites had values that were similar. Mean vascular NPP ranged from 76 to 211 $g \cdot m^{-2} \cdot yr^{-1}$ but was less variable than between site comparisons of either herb or shrub NPP.

Tree Production

Total above-ground estimated tree production was similar in the WB and WRF despite different dominant tree species (Table 2). The bog had slightly greater

Table 2. Comparison of above-ground tree biomass, biomass increment, litter fall, and production between the wooded bog and moderate-rich fen. Total tree net primary production was estimated by combining biomass increment and litter fall.

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

* Biomass is in $g \cdot m^{-2}$; biomass increment, litter fall, and production are in $g \cdot m^{-2} \cdot yr^{-1}$.

NPP (54 g·m^{-2}·yr^{-1}), mainly due to the larger biomass estimates and growth increments of *P. mariana*, while about half of the estimated WRF tree production (44 g·m^{-2}·yr^{-1}) was measured as *L. laricina* leaf litter.

P. mariana biomass (592 g·m^{-2}) and NPP (54 g·m^{-2}·yr^{-1}) in the WB were similar to biomass (368 g·m^{-2}) and NPP (58 g·m^{-2}·yr^{-1}) measured by Reader and Stewart (1972) for the same species in a Manitoba muskeg. Their bog forest; however, had much greater tree biomass (4186 g·m^{-2}) and NPP (303 g·m^{-2}·yr^{-1}). Minnesota bogs (Grigal et al. 1985) also had much greater *P. mariana* biomass (3,100–10,000 g·m^{-2}) and NPP (100–310 g·m^{-2}·yr^{-1}).

In Minnesota, tree biomass and NPP in a *Fraxinus nigra* Marsh. and *Thuja occidentalis* L.—dominated fen were 9800 g·m^{-2} and 650 g·m^{-2}·yr^{-1}, respectively (Reiners 1972). These were much higher than the *L. laricina*-dominated WRF, where a biomass of 351 g·m^{-2} and a NPP of 44 g·m^{-2}·yr^{-1} were estimated.

The regression equations used to predict the biomass of large trees were developed outside of Alberta and, therefore, may not provide accurate estimations for the sites. Also, the biomass and NPP were probably under-estimated from the log-log equations (Table 1) when antilog-transformed (Baskerville 1972, Beauchamp and Olson 1973, Crow and Laidly 1980).

Total Production

Total above-ground NPP, when averaged for the two years (Figure 3), seems to increase along the gradient from bog to PF to WRF, but then it abruptly decreases towards the rich end of the gradient. The WRF had the greatest average production (360 g·m^{-2}·yr^{-1}), followed by the PF (310 g·m^{-2}·yr^{-1}). This supports Vitt (1990), who suggested that moderate-rich fens have higher nutrient levels than the other mire types and, therefore, should be more productive. The SF (214 g·m^{-2}·yr^{-1}) and ERF (245 g·m^{-2}·yr^{-1}) had the lowest values. The average NPP of the bog sites was intermediate; the WB (297 g·m^{-2}·yr^{-1}) was slightly higher than the OB (264 g·m^{-2}·yr^{-1}).

Total NPP in the bog was among the lowest reported for North American bogs, which range from 342 to 1045 g·m^{-2}·yr^{-1} (Table 3). Above-ground NPP in the Alberta fens (214–360 g·m^{-2}·yr^{-1}) was intermediate compared to other North American fens (114–1026 g·m^{-2}·yr^{-1}). There seems to be a strong trend of increasing NPP with decreasing latitude in North American bogs (Table 3). This trend is not as pronounced in fens, suggesting the importance of local hydrology on the NPP of minerotrophic systems.

Our least productive fens were the SF and ERF. In Europe, *C. lasiocarpa/C.diandra* wetlands similar to the SF have lower standing crops than other nearby fens (Verhoeven *et al.* 1983, Wheeler and Shaw 1991). Extreme-rich fens have also been demonstrated to have low NPP (Boyer and Wheeler 1989, Wassen et al. 1990, Wheeler and Shaw 1991). Wheeler and Shaw (1991) attribute this to low phosphorus availability.

Below-ground NPP was not measured in this study; however, it may have accounted for a large proportion of total NPP and biomass at the sites, especially in the SF. Sjörs (1991) found that below-ground biomass in a sedge fen was extremely large, representing 93% of total biomass. Reader and Stewart (1972) estimated that below-ground NPP accounted for 25 to 75% of the total NPP in peatlands of southeastern Manitoba, while Backéus (1990) found that fine roots may represent 38 to 59% of the total vascular plant NPP in a Swedish open bog.

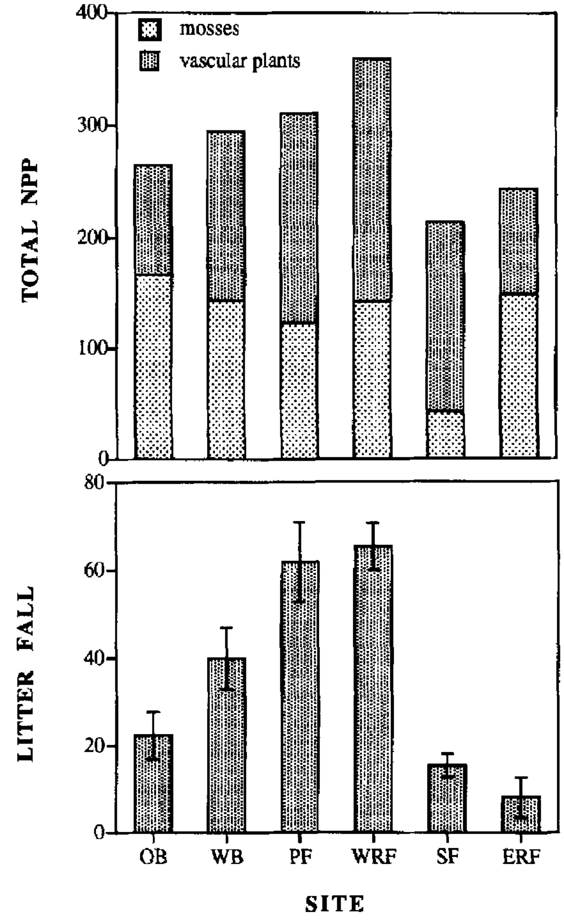

Figure 3. Comparison of mean total above-ground plant production and litter fall (g·m^{-2}·yr^{-1}) between six peatlands (OB = open bog, WB = wooded bog, PF = poor fen, WRF = moderate-rich fen, SF = sedge fen, and ERF = extreme-rich fen). Total NPP values represent averages of 1991 and 1992 for all strata, except tree production (where applicable), which is based on an average of five year growth increments. The error bars on the litter fall graph refer to ± SE. Note the different scales on the y-axes.

Table 3. Above-ground net primary production ($g \cdot m^{-2} \cdot yr^{-1}$) of different strata and totals for North American peatlands in order of decreasing latitude. Strata may not add up to totals due to rounding.

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

Estimates of sites from this study represent two-year averages (except trees). * Production of stratum estimated from data.

Litter Fall

There were significant differences in total litter (Figure 3), shrub litter, and tree litter fall between the sites ($p < 0.001$). The WRF (65.3 $g \cdot m^{-2} \cdot yr^{-1}$) and PF (61.8 $g \cdot m^{-2} \cdot yr^{-1}$) had the greatest total litter production, indicating the importance of litter fall in peat accumulation at these sites. The ERF and SF had the lowest litter fall (8.1 and 15.3 $g \cdot m^{-2} \cdot yr^{-1}$, respectively), while the OB (22.3 $g \cdot m^{-2} \cdot yr^{-1}$) and WB (39.9 $g \cdot m^{-2} \cdot yr^{-1}$) were intermediate. The WRF also had the highest tree litter fall (24.7 $g \cdot m^{-2} \cdot yr^{-1}$), while the PF had the greatest shrub litter fall (61.7 $g \cdot m^{-2} \cdot yr^{-1}$).

Total litter fall (Figure 3) was greatest in the PF and WRF, due to their high cover of deciduous woody species. The bog had relatively low litter production because it was dominated by evergreen species, while the very low litter fall in the ERF and SF was a result of their reduced tree and shrub cover.

Few studies have directly measured litter fall in peatlands. Grigal et al. (1985) reported values of 130 $g \cdot m^{-2} \cdot yr^{-1}$ for raised and 250 $g \cdot m^{-2} \cdot yr^{-1}$ for perched bogs in Minnesota. These results are 3 to 6 times greater than the total litter fall measured in the WB (40 $g \cdot m^{-2} \cdot yr^{-1}$); however, tree and shrub biomass were also much larger in the Minnesota sites. Reiners (1972) recorded a much higher value (412 $g \cdot m^{-2} \cdot yr^{-1}$) in a Minnesota fen dominated by deciduous trees.

Litter production may have been under-estimated in our traps because of leaching, decomposition, materials being blown out by wind, animal removal, and failure of the traps to catch litter from dwarf and prostrate shrubs.

CONCLUSIONS

The hypothesis of increasing NPP along the bog-rich fen gradient was only partially supported by the data. Total above-ground NPP increased from the bog to WRF and then abruptly decreased in the SF and ERF. Our hypothesis may have been more strongly supported if below-ground NPP was included, since a very large proportion (>90%) of biomass in sedge fens may be subterranean (Sjörs 1991).

Moss NPP generally showed greater variation between years than sites, with all sites having similar moss production, except for the SF, which had much lower values. Herb NPP increased along the bog-rich fen gradient, while shrub NPP tended to decrease along the gradient. Tree NPP contributed minimally to the total production of the bog and WRF. Total tree and shrub litter fall followed a trend similar to total NPP; that is, greatest in the middle of the gradient in the PF and WRF and lowest at the rich end of the gradient in the SF and ERF.

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