

University of New Hampshire
University of New Hampshire Scholars' Repository

Earth Sciences Scholarship

Earth Sciences

11-27-1999

Net ecosystem productivity and its uncertainty in a diverse boreal peatland

Jill L. Bubier
Mount Holyoke College

Steve Frolking
University of New Hampshire - Main Campus, steve.frolking@unh.edu

P Crill
Stockholm University

Ernst Linder
University of New Hampshire, ernst.linder@unh.edu

Follow this and additional works at: https://scholars.unh.edu/earthsci_facpub

Recommended Citation

Bubier, J. L., S. Frolking, P. M. Crill, and E. Linder (1999), Net ecosystem productivity and its uncertainty in a diverse boreal peatland, *J. Geophys. Res.*, 104(D22), 27683–27692, doi:10.1029/1999JD900219.

This Article is brought to you for free and open access by the Earth Sciences at University of New Hampshire Scholars' Repository. It has been accepted for inclusion in Earth Sciences Scholarship by an authorized administrator of University of New Hampshire Scholars' Repository. For more information, please contact nicole.hentz@unh.edu.

Net ecosystem productivity and its uncertainty in a diverse boreal peatland

J.L. Bubier,^{1,2} S. Frolking,¹ P.M. Crill,¹ and E. Linder³

Abstract. Net ecosystem exchange (NEE) of CO₂ was measured in four peatlands along plant community, hydrologic, and water chemistry gradients from bog to rich fen in a diverse peatland complex near Thompson, Manitoba, as part of the Boreal Ecosystem-Atmosphere Study (BOREAS). A simple model for estimating growing season net ecosystem productivity (NEP) using continuous measurements of photosynthetically active radiation (PAR), and peat temperature was constructed with weekly chamber measurements of NEE from May to October 1996. The model explained 79–83% of the variation in NEE across the four sites. Model estimation and parameter uncertainty calculations were performed using nonlinear regression analyses with a maximum likelihood objective function. The model underestimated maximum NEE and respiration during the midseason when the standard errors for each parameter were greatest. On a daily basis, uncertainty in the midday NEE simulation was higher than at night. Although the magnitude of both photosynthesis and respiration rates followed the trophic gradient bog less than poor fen less than intermediate fen less than rich fen, NEP did not follow the same pattern. NEP in the bog and rich fen was close to zero, while the poor and intermediate fens had higher NEP due to a greater imbalance between uptake and release of CO₂. Although all sites had a positive growing season NEP, upper and lower 95% confidence limits showed that the bog and rich fen were either a source or sink of CO₂ to the atmosphere, while the sedge-dominated poor and intermediate fens were accumulating approximately 20–100 g CO₂ C m⁻² over the 5 month period in 1996. Peatland ecosystems may switch from a net sink to a source of carbon on short timescales with small changes in soil temperature or water table position. Since the difference between production and decomposition is small, it is important to understand and quantify the magnitude of uncertainty in these measurements in order to predict the effect of climatic change on peatland carbon exchange.

1. Introduction

Peatlands are important ecosystems in the global carbon cycle because they store approximately one third (455 Pg (=10¹⁵g)) of the total terrestrial pool of soil carbon. Although they have been accumulating 20–40 g C m⁻² annually over the last 5000–10,000 years since deglaciation [Gorham, 1991; Tolonen and Turunen, 1996; Harden *et al.*, 1992], they have the potential to become net sources of C to the atmosphere under a warmer and drier climate. Other studies have shown that northern ecosystems can switch from a net sink to a source of CO₂ on short timescales (months to years) with small changes in either soil temperature or water table position [Oechel *et al.*, 1995; Shurpali *et al.*, 1995; Waddington and Roulet, 1996; Johnson *et al.*, 1996; Goulden *et al.*, 1998]. Several studies have measured net CO₂ exchange in northern peatlands using chambers and micrometeorological techniques [Whiting *et al.*, 1992; Whiting, 1994; Shurpali *et al.*, 1995; Waddington and Roulet, 1996; Ball, 1996; Bhardwaj, 1997; Alm *et al.*, 1997; Lafleur *et al.*, 1997; Suyker *et al.*, 1997; Carroll and Crill, 1997; Bellisario *et al.*, 1998; Joiner *et al.*, this issue]; but few have quantified the

uncertainty surrounding the seasonal to annual carbon balance. Since the difference between production and decomposition is small, it is important to understand and quantify the magnitude of uncertainty in these measurements.

As part of the Boreal Ecosystem-Atmosphere Study (BOREAS), Bubier *et al.* [1998] measured seasonal patterns and controls on net ecosystem exchange (NEE) in a diverse peatland complex near Thompson, Manitoba. To further our understanding of CO₂ exchange in peatland environments, the purposes of this study were (1) to develop a simple statistical model for determining net ecosystem productivity (NEP) using a few parameters that have a physiological basis and can be measured continuously, such as temperature, water table position, and photosynthetically active radiation (PAR); (2) determine the uncertainty in the NEE and NEP estimates in order to assess the confidence limits of the sink/source CO₂ estimates in peatlands; and (3) compare ecological differences in NEP along a bog-rich fen gradient.

2. Study Site

The peatland complex in this study was chosen for its diverse representation of plant communities, thermal and hydrochemical gradients, and the presence of peat plateaus, palsas, and collapse scars. The field experiment was located in the northern study area of BOREAS [Sellers *et al.*, 1995, 1997], near Thompson, Manitoba (55.91° N., 98.42° W). The average annual temperature and precipitation for the region are -3.9°C and 542 mm (40% as snow, 60% as rain). The sampling year 1996 was normal, within 1 standard deviation of 30 year precipitation and temperature means.

¹Complex Systems Research Center, University of New Hampshire, Durham.

²Now at Environmental Studies Program, Mount Holyoke College, South Hadley, Massachusetts.

³Department of Mathematics, University of New Hampshire, Durham.

Copyright 1999 by the American Geophysical Union.

Paper number 1999JD900219.
0148-0227/99/1999JD900219\$09.00

The underlying substrates supporting the wetlands are Glacial Lake Agassiz sediments overlying the regional bedrock of Canadian Shield Precambrian gneissic granite. Soils are derived predominantly from Glacial Lake Agassiz sediments and consist mostly of clays and organics. Wetlands are common in the region because of poor drainage across the flat terrain. The wetlands include a wide range of types found in northern peatlands from rich fen to bog [Zoltai, 1988]. Plant associations in rich fens are diverse, dominated by brown mosses (e.g., *Drepanocladus* spp., *Scorpidium* spp.) and deciduous shrubs (e.g., *Salix* spp., *Betula* spp.) Sedges (particularly *Carex* spp.) are common in poor and intermediate fens with water tables close to the surface. Permafrost underlies many of the peatlands; frozen palsas and peat plateaus are dry and wooded with upland plant communities such as black spruce (*Picea mariana*), feathermosses (e.g., *Pleurozium schreberi*), and ericaceous shrubs (e.g., *Ledum groenlandicum*). Areas of permafrost degradation are found interspersed in the frozen features. These collapse scars can become bogs (species-poor, *Sphagnum*-dominated communities) if they collapse completely internal to a peat plateau and remain isolated from groundwater. Collapse scars may develop into fens if they occur on the edge of peat plateau, which allows groundwater to intrude [Vitt et al., 1994; Zoltai, 1993].

Four sites were chosen within the larger peatland complex: rich fen, intermediate fen, poor fen, and bog. Within each site, six collars were placed along moisture, thermal, plant community and chemical gradients to capture the full range of environmental conditions. The rich fen (pH 6.7-7.2) had the largest range of plant communities from the drier shrub-dominated *Larix laricina* and *Salix pedicellaris* communities underlain by *Sphagnum warnstorffii* to the wetter sites dominated by *Betula pumila*, *Menyanthes trifoliata*, and brown mosses (e.g., *Scorpidium scorpioides* and *Limprichtia revolvens*). The poor fen (pH 4.3-4.7), a collapse scar adjacent to a peat plateau, was dominated by the sedges *Carex aquatilis* and *C. limosa*, while *Sphagnum riparium* comprised the moss layer. The intermediate fen (pH 5.8-6.2) was a sedge-rich (*Carex rostrata*) community, with *Sphagnum riparium* and *Warnstorffia exannulata* in the moss layer. Finally, the bog site (pH 3.9-4.2), a collapse scar completely enclosed by frozen peat plateau, had the lowest species diversity (14 species compared with 57 in the rich fen). This site was dominated by ericaceous shrubs (*Chamaedaphne calyculata*, *Vaccinium oxycoccus*) and *Sphagnum* mosses (e.g., *Sphagnum fuscum* and *S. angustifolium*) See Bubier et al. [1995, appendix, 1998] for more detailed study site descriptions and plant species lists, Glaser et al. [1990] for general relationships between plant communities and hydrochemical gradients in peatlands, and Halsey et al. [1997] for distribution of peatland types in Manitoba.

3. Materials and Methods

3.1. CO₂ Measurements

Net ecosystem CO₂ exchange (NEE), photosynthetically active radiation (PAR), relative humidity (RH), and chamber temperature were measured with a LI-COR 6200 portable photosynthesis system, which includes a LI-6250 infrared gas analyzer, thermistor, hygrometer, quantum sensor, and data logger. Whole ecosystem measurements of NEE were made with clear, climate-controlled chambers modeled after a chamber described by Whiting [1991] and Carroll and Crill [1997], designed and constructed at the University of New Hampshire. All plants, including shrubs, were enclosed by the chambers. The chamber walls were constructed of clear Lexan and Teflon film with a removable top to allow equili-

bration of plant communities to ambient conditions between sampling runs. The climate-control system consisted of a heat exchanger (Dodge Motors transmission cooler) and a cooler to store cold water that was pumped through the heat exchanger. Fans mounted on the inside of the chamber circulated air across the heat exchanger, maintaining the enclosed air within 1°C of outside air temperature. The area of the base of the chambers was 3660 cm² (60 x 60 cm) to fit a collar with the same area. Chamber heights were either 45 cm or 90 cm to accommodate the varying heights of the vegetation at the different sites. Aluminum collars with a groove for chamber placement were inserted into the peat in the fall of 1995 so that measurements could begin during the thaw period of 1996 with minimal peat disturbance. The groove was filled with water before each sampling run to ensure an airtight seal. In order to establish relationships between NEE and PAR on each sampling day, shrouds with different mesh sizes were used to reduce the light entering the chamber to one-half and one-fourth full light. An opaque shroud was placed over the chamber to eliminate all light for measuring ecosystem respiration (autotrophic and heterotrophic). Four 2.5 min sampling runs at different light levels were conducted at each collar location on a weekly basis from April 15 to October 23, 1996. See Bubier et al. [1998] for more details on NEE methods.

3.2. Environmental Variables

Water table position relative to the peat surface and peat temperature at 5, 10, 20, and 50 cm depth were recorded continuously at each collar location with CR10 and CR7 data loggers (Campbell Scientific, Inc.). Water table measurements were made with a float and counter weight attached to a wheel and potentiometer [Roulet et al., 1991] mounted on a platform that was anchored to a wooden post driven into the clay below the peat (peat thickness varied from 2 to 5 m). Wells were constructed of PVC tubing, and the height of the peat surface in each collar was measured with a tube level referenced to the nearest well. Peat temperatures were measured with thermocouples attached at four depths to wooden stakes and inserted into the peat in October 1995. The pH of surface water was measured at monthly intervals from May to October 1996 at each site with a portable pH meter. Calcium, magnesium, and specific conductance were measured at each site in 1994 and are reported by Bubier et al. [1995].

3.3. Vegetation Sampling

Plant species composition was recorded in each collar by percent cover of vascular plant and bryophyte species [Daubenmire, 1968]. Nomenclature follows Anderson et al. [1990] for true mosses, Anderson [1990] for *Sphagnum* moss species, Stotler and Crandell-Stotler [1977] for liverworts, and Fernald [1950] for vascular plant species. Sites were classified after a modification of the Canadian peatland classification system [Zoltai, 1988; Riley, 1987], which uses vegetation physiognomy (tree, shrub, graminoid) and water chemistry (pH, calcium, magnesium) [Chee and Vitt, 1989] as the primary variables: for example, open sites had < 10% tree cover; treed sites had 10-30% tree cover; the pH of bogs was 3.8-4.7; poor fens, 4.5-5.1; intermediate fens, 5.1-6.2; rich fens, 6.2-7.2.

3.4. Data Analyses

A simple model, using hourly rates of photosynthetically active radiation (PAR) and temperature at 5 cm peat depth, was developed to calculate hourly rates of photosynthesis and respiration and to

interpolate between the weekly measurements of CO₂ exchange throughout the entire growing season. We chose a simple model with a minimum number of parameters but one with a physiological basis. Net ecosystem exchange (NEE) of CO₂ is the instantaneous difference between gross photosynthesis (PSN) and respiration (RSP):

$$NEE = \frac{mT_{5cm}}{mT_{season}} \frac{\alpha \cdot PAR \cdot GP_{max}}{\alpha \cdot PAR + GP_{max}} - 10^{(9T_{5cm} - 0.1)} \quad (1)$$

The first term imposes a seasonality on the calculated PSN using a 7 day running average of the peat temperature at 5 cm (mT_{5cm}) (see Figure 2b for seasonal pattern of soil temperature) divided by the mean seasonal temperature at 5 cm (mT_{season} , e.g., 12) to derive a factor from 0 to 1. For our period of measurements the running mean was always greater than zero. The second term is a rectangular hyperbolic curve fit [Thornley and Johnson, 1990] of PSN ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) to PAR ($\mu\text{mol photon m}^{-2} \text{ s}^{-1}$). PAR data were recorded every 5 s and averaged every 30 min [Joiner et al., this issue]. The asymptote GP_{max} of the curve fit is the maximum rate of carbon fixation at infinite PAR ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), and α ($\mu\text{mol CO}_2 / \mu\text{mol photon}$) is the initial slope of the curve (the apparent quantum yield). The entire data set was used to determine GP_{max} and α parameter estimates (Table 1). However, by imposing a simple seasonal phenology with peat temperature, the α and GP_{max} functions of the hyperbolic curve fit also change as the season progresses. The final term is the RSP response curve determined by the fit (slope (s) and intercept (0.1)) of the instantaneous peat temperature at 5 cm (T_{5cm}) to the logarithm of the carbon exchange measured at PAR = 0. Water table position was strongly correlated with peat temperature and did not add a significant independent parameter to the model. All the data were fit to one equation, instead of separating the data into PSN and RSP, in order to estimate uncertainty in the estimated NEE values. However, we have reported separate fits of respiration to temperature and water table elsewhere [Bubier et al., 1998].

We adopted the sign convention of CO₂ uptake by the ecosystem as positive and CO₂ emission from respiration as negative. The dark chambers measured ecosystem respiration (total efflux of CO₂ due to the combined metabolic activities of enclosed plants, roots, and soil microbes). Since light and dark measurements were made within a few minutes of each other, the difference between NEE at full or fractional light and NEE with a dark chamber (respiration) was considered to represent the gross photosynthesis at that light level for the vegetation within the chamber.

Model estimation and parameter uncertainty calculations were performed using nonlinear regression analyses [Bates and Watts, 1988] with a maximum likelihood objective function. Uncertainty in the modeled hourly NEE was determined using the Delta method [Arnold, 1990], which is based on a first-order Taylor series approximation of the response function $NEE = h(GP_{max}, \alpha, s)$. For

three parameters GP_{max} , α , and s in equation (1), the approximate variance (var) in NEE is

$$\begin{aligned} \text{var}(NEE) = & \text{var}(h(GP_{max}, \alpha, s)) = ((\partial h/\partial GP_{max})^2 \text{var}(GP_{max}) \\ & + (\partial h/\partial \alpha)^2 \text{var}(\alpha) + (\partial h/\partial s)^2 \text{var}(s)) \\ & + (2(\partial h/\partial GP_{max})(\partial h/\partial \alpha) \text{cov}(GP_{max}, \alpha)) \quad (2) \\ & + (2(\partial h/\partial GP_{max})(\partial h/\partial s) \text{cov}(GP_{max}, s)) \\ & + (2(\partial h/\partial \alpha)(\partial h/\partial s) \text{cov}(\alpha, s)) \end{aligned}$$

where $\text{cov}(GP_{max}, \alpha)$ is the usual covariance, which is calculated as (correlation of GP_{max} and α)(SE GP_{max})(SE α).

See Table 1 for correlation and standard error (SE) estimates for each parameter. Upper and lower confidence limits were calculated as $NEP \pm (1.96 \text{ SE}(NEE))$, where $\text{SE}(NEE) = (\text{var}(NEE))^{1/2}$.

Net ecosystem production (NEP) was defined as the sum of the hourly NEE values for the entire growing season (mid-May through mid-October). Winter CO₂ fluxes and losses of C from CH₄, DOC, or leaching were not included in the calculation. Taylor series approximations were applied to the variance of the sum of the accumulated hourly variances to estimate variance for NEP:

$$\begin{aligned} \text{var}(NEP) = & ((\sum \partial h/\partial GP_{max})^2 \text{var}(GP_{max}) + (\sum \partial h/\partial \alpha)^2 \text{var}(\alpha) \\ & + (\sum \partial h/\partial s)^2 \text{var}(s) + (2(\sum \partial h/\partial GP_{max})(\sum \partial h/\partial \alpha) \\ & \cdot \text{cov}(GP_{max}, \alpha)) + (2(\sum \partial h/\partial GP_{max})(\sum \partial h/\partial s) \\ & \cdot \text{cov}(GP_{max}, s)) + (2(\sum \partial h/\partial \alpha)(\sum \partial h/\partial s) \text{cov}(\alpha, s)) \quad (3) \end{aligned}$$

To assess the effect of temporal and spatial autocorrelation on model uncertainty, we tested for autocorrelation in the model residuals. Data analyses were performed with the statistical software JMP-IN [SAS Institute, Inc., 1996].

4. Results

4.1. Parameter Estimates

The relationship between NEE and PAR varied among the four sites with maximum photosynthetic capacity following the ecological gradient of bog to rich fen. Parameter estimates for GP_{max} in Table 1 indicate that the bog had the lowest maximum carbon uptake ($5.12 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), the rich fen had the greatest ($12.01 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), with values at the poor and intermediate fens of 7.52 and $8.15 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively. The difference among sites was the greatest during the height of the growing season from mid-June to mid-July (Figure 1)(see Bubier et al. [1998] for early and late season parameter estimates). Standard error for GP_{max} is greatest for the rich fen (1.02) reflecting the greater spatial variability in vegetation types than the bog, which had the lowest standard error for GP_{max} (0.28).

Table 1. Parameter Estimates, Standard Errors (SE), and Correlation Coefficients for GP_{max} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), α ($\mu\text{mol CO}_2/\mu\text{mol Photon}$), and Slope (s) of the Respiration-Temperature Relationship

Site	GP_{max}	SE_ GP_{max}	α	SE_ α	s	SE_ s	corr_ GP_{max}/α	corr_ GP_{max}/s	corr_ α/s
CB	5.1242	0.2848	0.0092	0.0009	0.0331	0.0011	-0.7034	0.1357	0.4341
PF	7.5228	0.5617	0.0173	0.0027	0.0345	0.0429	-0.6315	0.1318	0.2949
IF	8.1511	0.4524	0.0165	0.0017	0.0326	0.0009	-0.7241	0.0951	0.4558
RF	12.0098	1.0206	0.0142	0.0018	0.0355	0.0047	-0.7363	0.0678	0.0429

See equations (1) and (2) in text. Sites are collapse bog (CB), poor fen (PF), intermediate fen (IF), and rich fen (RF)

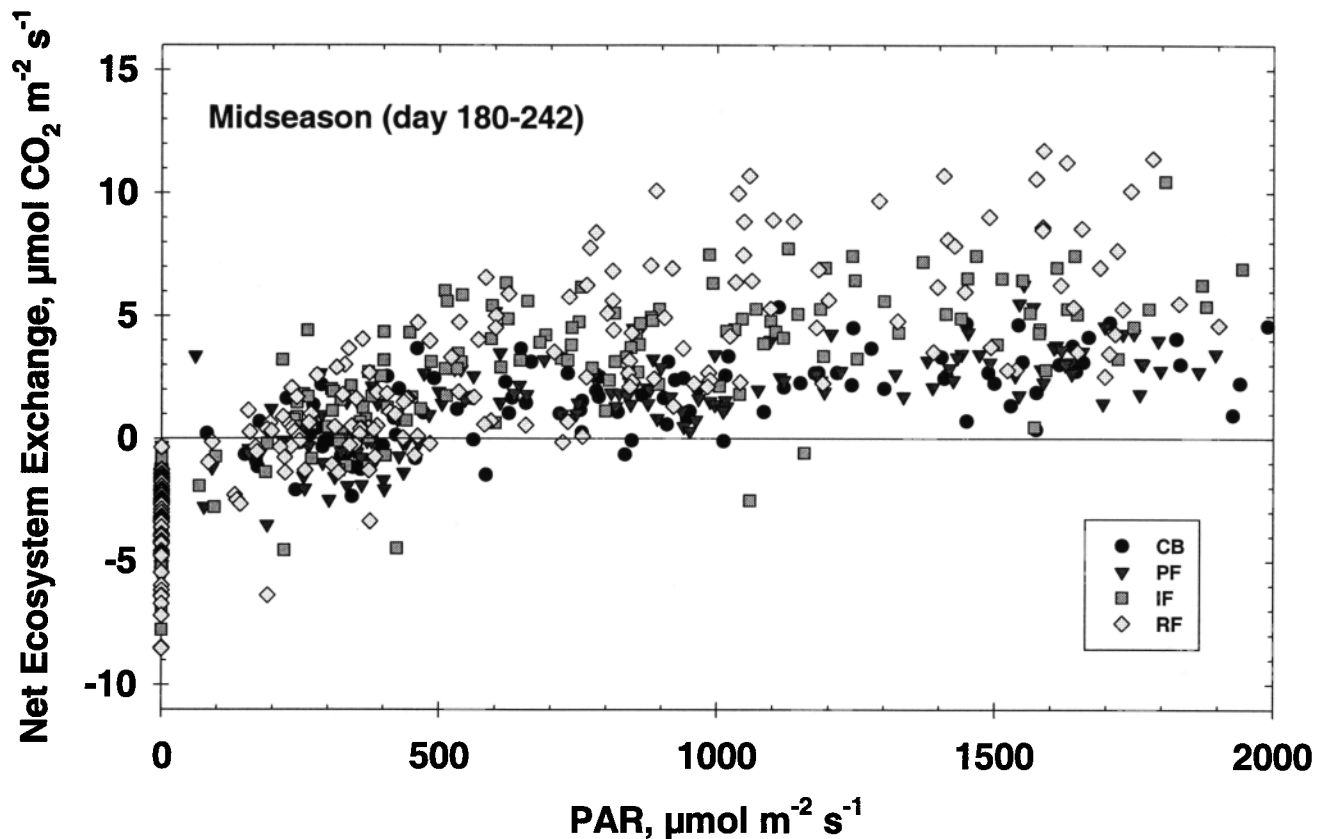


Figure 1. Relationship between net ecosystem exchange (NEE) of CO_2 and photosynthetically active radiation (PAR) ($\mu\text{mol photon m}^{-2} \text{s}^{-1}$) for collapse bog (CB), poor fen (PF), intermediate fen (IF), and rich fen (RF) for the period June 28 to August 29, 1996. Midseason parameter estimates (standard error) for GP_{max} , α , and R (y intercept) for CB, PF, IF, and RF in order are (1) GP_{max} : 6.29 (0.56), 8.44 (0.56), 11.52 (0.83), 17.33 (1.78); (2) α : 0.011 (0.002), 0.017 (0.002), 0.022 (0.003), 0.017 (0.002); and (3) R: -2.44 (0.16), -3.20 (0.17), -3.16 (0.25), -3.45 (0.29). See Table 1 for parameter estimates for whole season for each site. See Bubier *et al.* [1998] for early and late season parameter estimates.

The values for α do not follow the same sequence. The initial slope of the rectangular hyperbola is greatest for the poor (0.0173) and intermediate fens (0.0165), with the rich fen slightly lower (0.0142), and the bog lowest (0.0092). This suggests that the poor and intermediate fens respond more rapidly at low light levels than either the bog or the rich fen. The standard error for α is highest for the poor fen and lowest for the bog. GP_{max} and α are negatively correlated at all four sites, indicating that α is lowest when GP_{max} is highest. This relationship is consistent with enzyme activities reported in other ecosystems [e.g., Schlesinger, 1997].

Respiration was correlated more significantly with temperature at 5 cm depth than with temperatures at deeper portions of the profile (Figure 2a). Spring thawing of the peat at 50 cm depth lagged surface temperatures by as much as 2-3 weeks (Figure 2b). The onset of carbon uptake in the spring correlated with the rise of 5 cm temperature above 0°C [see Bubier *et al.*, 1998]. The slope of the respiration-temperature relationship (s in Table 1) was higher at the poor and rich fens (0.0345 and 0.0355, respectively) and lower at the bog (0.0331) and intermediate fen (0.0326). The standard error for s was greatest at the poor fen (0.0429) and lowest for the intermediate fen (0.0009). Correlations between GP_{max} and s were low at all sites, while correlations between α and s were slightly higher, particularly at the bog (0.43) and intermediate fen (0.46).

4.2. Model Results

Interpolation results show that the model using hourly values of PAR and peat temperature to predict NEE explained between 79% and 83% of the variation in NEE (Table 2). The predicted versus observed data (Figure 3) are close to the 1:1 line (slope of the model versus data regressions varies from 0.99 to 1.01 in Table 2). The data are divided into early, middle, and late season to show the fit of the model at different times of year. Modeled versus measured NEE values for the bog and intermediate fen are shown in Figure 4. Measured data vary during each day with different levels of PAR, which explains the range in NEE values on a given day. The model follows the seasonal pattern of carbon uptake and release reasonably well but tends to underestimate maximum NEE and respiration midseason as well as overestimate NEE in the early season. At the bog (Figure 4a) the spring period of measured carbon uptake matches the model simulation more closely than at the intermediate fen (Figures 3b and 4b), but the midsummer simulation underestimates both maximum photosynthesis and respiration. The observed decline in CO_2 uptake and release in the fall matches the simulated CO_2 exchange very well at both the bog and the intermediate fen.

Daily integrated NEE values at the intermediate fen (Figure 5a) are negative until day 152 when photosynthesis is greater than

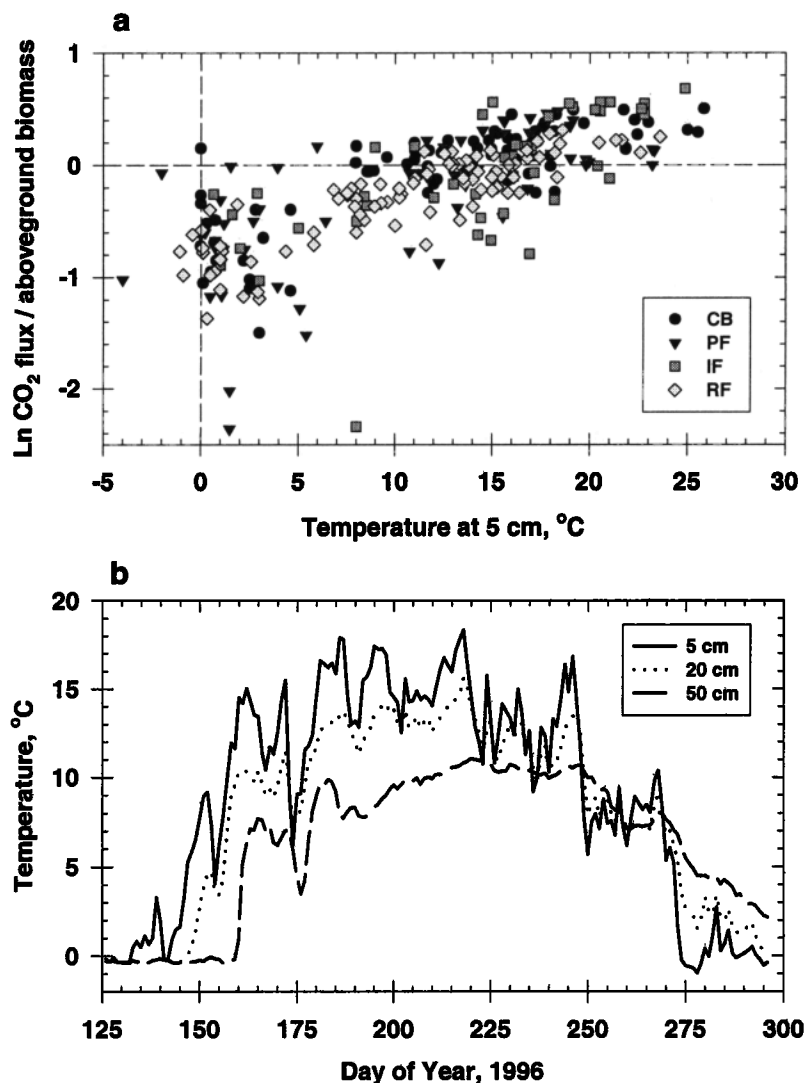


Figure 2. (a) Relationship between respiration and temperature at 5 cm peat depth, normalized for aboveground vascular plant biomass, which is strongly correlated with aboveground net primary productivity (ANPP) (see Bubier *et al.* [1998] for ANPP values for each site). $\text{Log CO}_2 \text{ flux/aboveground biomass} = 0.052 T_{5\text{cm}} - 0.784$ ($r^2 = 0.57$; $p < 0.01$; $n = 566$); (b) seasonal pattern of daily average peat temperature at 5, 20, and 50 cm below the peat surface from May to October 1996 at a rich fen hummock.

respiration on average. This is the point when the 5 cm peat temperature rises above freezing. However, the ecosystem vascillates between positive and negative values until day 165 when the largest increase in NEE occurs. The intermediate fen is a net sink of carbon on balance from day 160 to day 260 but occasionally loses CO₂ to the atmosphere over a 24 hour period. Around day 265, photosynthesis drops off sharply, resulting in a net loss of CO₂

of approximately $-1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. The decline in CO₂ uptake matches the drop in the 5 cm peat temperature at the end of the season (Figure 2). Peat temperatures are warm enough, however, to sustain a small degree of respiration. A closer examination of a midsummer period that includes days of both net CO₂ gain and release (Figure 5b) shows that respiration stays fairly constant throughout the period, but photosynthesis varies considerably depending on the PAR levels.

Table 2. Observed Versus Predicted NEE ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) Relationships for NEP Model

Site	Observed NEE	Standard Error	r^2	n
CB	0.99 predicted NEE +0.02	0.027	0.82	232
PF	1.00 predicted NEE -0.01	0.042	0.83	217
IF	0.99 predicted NEE +0.04	0.028	0.79	312
RF	1.01 predicted NEE -0.12	0.043	0.80	240

Standard error (SE) for predicted NEE and correlation coefficients (r^2) reported ($p < 0.0001$)

4.3. Model Uncertainty

Upper and lower confidence limits for daily and hourly NEE are shown in Figures 5a and 5b. The components of the uncertainty in NEE, which include the standard errors for the model parameters (GP_{max} , α , s) and the correlations between the pairs of parameters (equation (2)), are shown in Table 1. The hourly estimates of uncertainty (Figure 5b) show that the uncertainty is greatest during midday, the time when both PAR and temperature are at their daily maximum. The NEE-PAR relationship has its greatest uncertainty

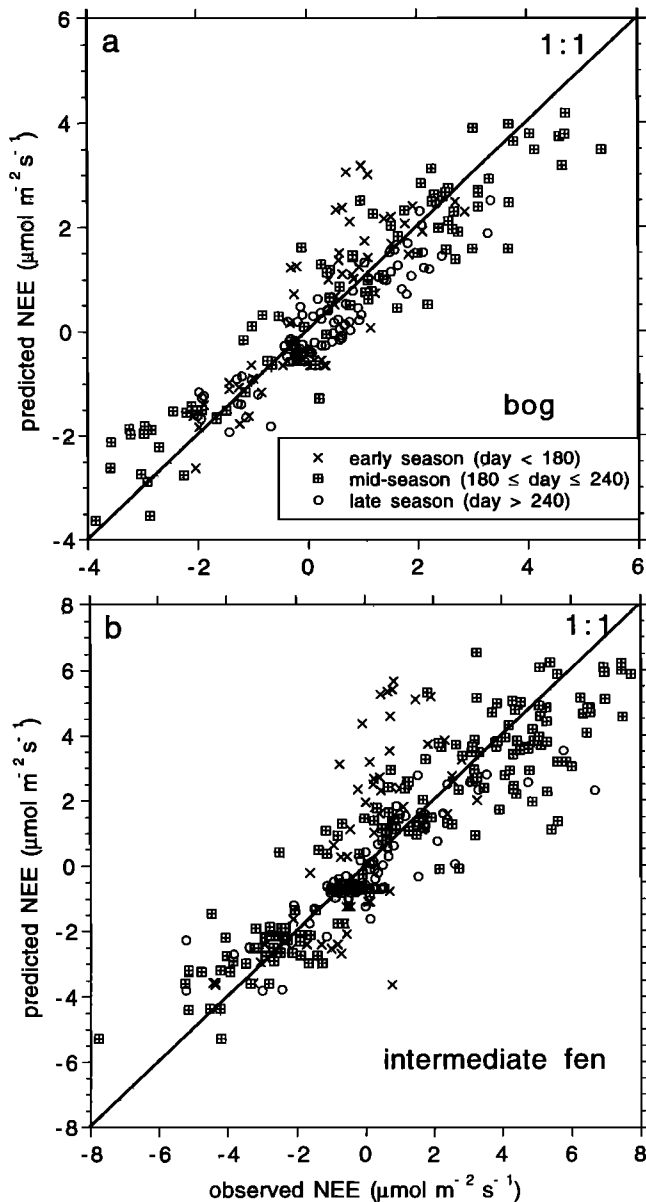


Figure 3. Predicted versus measured values of NEE for (a) collapse bog, and (b) intermediate fen from May to October 1996. The 1:1 line is shown. Separate symbols for early, middle and late season are shown (these time periods correspond to the seasonal components reported by Bubier *et al.* [1998]). See Table 2 for predicted versus observed equations and correlation coefficients for each site. The model explains 79–83% of the variation in NEE.

at maximum values of PAR, and the log-linear respiration-temperature relationship also has the greatest variation at maximum temperatures (Figure 2a).

The daily standard errors (Figure 5a) are calculated from the variances of the sum of the hourly variances, which are all positive. However, since the daily NEE values are the sum of both positive and negative hourly NEE values over a 24 hour period, the daily SE becomes larger relative to daily NEE. The accumulated uncertainty for the growing season (see equation (3) in methods) is shown in Figure 6. Upper and lower confidence limits for net ecosystem productivity (NEP) are greatest for the poor fen and lowest for the bog. This reflects the variation in standard error for the three parameters.

Analyses of model residuals showed that temporal and spatial autocorrelation did not affect uncertainty estimates significantly. Temporal autocorrelation at the daily scale tends to be present due primarily to imperfect model fits and not because of any particular temporal autocorrelation structure. Since the sampling intervals were irregular, we could not incorporate temporal autocorrelation or other processes impacting NEE at the daily scale in the model. However, uncertainties in the annual NEP would have been reduced further if we were able to include this source of variation in the model. Analyses of spatial autocorrelation showed that there is a slight effect of individual chambers on site variability. However, these effects account for less than 5% of the residual variation.

4.4. Net Ecosystem Productivity

The sum of the hourly NEE values from May to October is the net ecosystem productivity for the growing season (Figure 6). Uncertainty in NEP is calculated from equation (3). Unlike the sequence bog less than poor fen less than intermediate fen less than rich fen for GP_{max} in the NEE-PAR relationship (Figure 1), NEP does not follow the same trend. The poor and intermediate fens have greater $\text{CO}_2\text{-C}$ accumulation over the season than either the bog or rich fen. NEP for the bog ($3 \pm 9 \text{ g CO}_2\text{-C m}^{-2}$) and rich fen ($13 \pm 24 \text{ g CO}_2\text{-C m}^{-2}$) are near zero, with lower confidence limits below zero, suggesting that both of these ecosystems could be losing carbon on an annual basis. The poor fen ($65 \pm 47 \text{ g CO}_2\text{-C m}^{-2}$) and intermediate fen ($31 \pm 14 \text{ g CO}_2\text{-C m}^{-2}$) have higher NEP, with lower confidence limits above zero.

5. Discussion

5.1. Model Results and Uncertainty

The simple model using PAR and peat temperature explains 79–83% of the variance in NEE over the growing season for a wide ecological range of peatlands. This provides a useful tool for predicting changes in peatland NEP with a few easily measurable environmental variables. The uncertainty estimates are extremely important because they will contribute to more reliable predictions of the present and future carbon balances in peatlands.

The greatest discrepancy between the measured chamber NEE data and the simulated NEE interpolation occurs in the midseason. The model underestimates maximum photosynthesis at full light and maximum respiration (Figure 4). Because we are fitting to all the data simultaneously instead of breaking the data into PSN and RSP components, the curves will necessarily pass through the middle of the points and will underestimate the highest and lowest values. The largest uncertainty (standard errors) in the model also occur at high levels of PAR and maximum temperatures (Figure 5b). Because the temperature - respiration relationship is a log-linear one, the greatest variation occurs at high temperatures during the day. At night, when PAR = 0, temperature is the only contributing variable, which reduces total uncertainty. Also, the standard errors in GP_{max} midseason may be due to the variation in photosynthetic capacity of different plant species within each site. This is especially true of the rich fen, which has the greatest diversity of plant communities.

The model also overestimates NEE in the spring at the intermediate fen (Figure 4b) but less so at the bog. One explanation may be that the ericaceous shrubs and mosses at the bog have evergreen leaves and are capable of fixing carbon as soon as the surface peat thaws and there is sufficient light. Therefore the seasonal pattern of soil temperature correlates well with plant phenology. The poor and

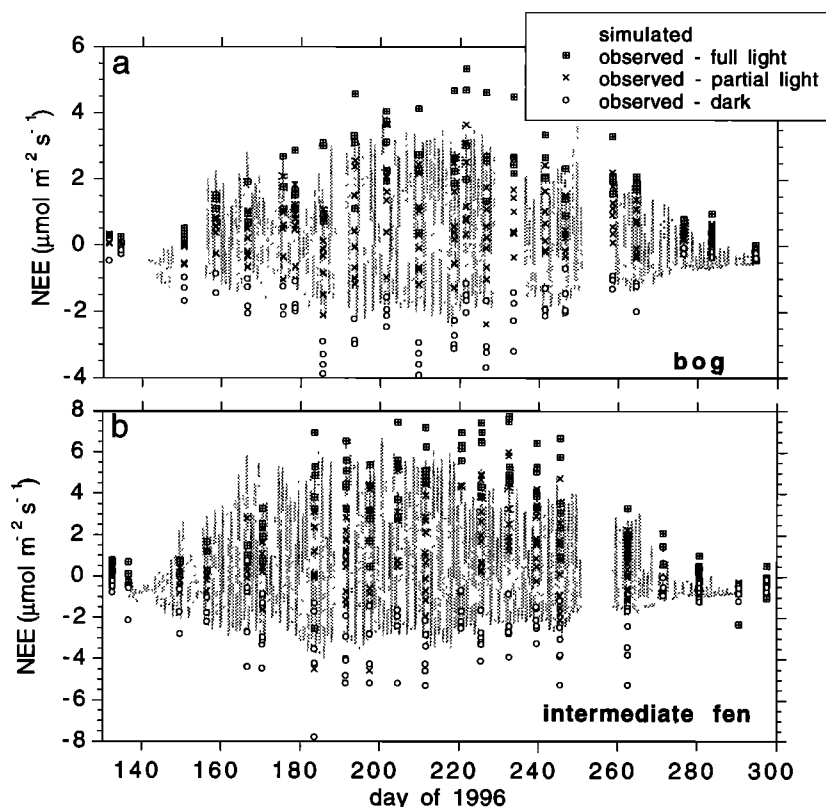


Figure 4. Simulated hourly values versus weekly measured chamber values of NEE for (a) collapse bog and (b) intermediate fen from May to October 1996. Positive values indicate net CO₂ uptake by the ecosystem, and negative indicates loss of CO₂ to the atmosphere. The variation in measured data on a given day is due to different levels of PAR entering the chamber. Light levels varied either naturally or with shrouds placed over the chamber. Full light indicates that no shrouds were used (PAR ranged from 257 to 1980 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ in the bog and from 145 to 1944 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ in the fen). Partial light indicates that shrouds with different mesh sizes were used permitting one quarter to one half of the available light to enter the chamber (partial light ranged from 82 to 1175 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ in the bog and from 68 to 1163 $\mu\text{mol photon m}^{-2} \text{s}^{-1}$ in the fen). Dark values indicate that opaque shrouds were used to completely eliminate light from the chamber.

intermediate fens, however, are dominated by herbaceous vascular plants, particularly sedges, which must develop new leaves each year. There is a greater lag time between the warming of surface peats and the onset of carbon uptake in these ecosystems because of this difference in the development of photosynthetic plant tissue. Although the bog plant communities have lower photosynthetic capacity than the fens (see GP_{max} in Table 1 and Figure 1), they begin to fix carbon earlier in the spring. However, the higher α values at the poor and intermediate fens, relative to the bog and rich fen (Table 1), suggest that the sedge-dominated ecosystems are capable of fixing more carbon at low light once the plants have developed. Since the model is constructed only with PAR and peat temperature using the seasonal soil temperature trend to simulate plant phenology, it does not take into account the differences in plant physiology and development of biomass between bogs and fens. Both types of ecosystems seem to respond similarly to the decline in PAR and surface temperatures in the fall (Figure 4).

Other sources of variation, such as temporal and spatial autocorrelation, were not included in the model because of the sampling design and simplicity of the model. Analyses of the model residuals show, however, that although these sources of variation were not significant, incorporating them into the model could have reduced the uncertainty estimates even further.

5.2. Net Ecosystem Productivity

The net accumulation of CO₂ for each of the four ecosystems varied from near 0 to 65 g CO₂-C m⁻² over the period mid-May to mid-October 1996 (Figure 6). Although GP_{max} in the rich fen was over twice that of the bog, NEP was only slightly higher. Both respiration and photosynthesis were higher in the rich fen than at the bog [Bubier *et al.*, 1998]; but both processes were nearly in balance resulting in a NEP of near zero for both ecosystems. In contrast, NEP in the poor and intermediate fens was much higher, and the lower confidence limits were above zero because of a greater imbalance between photosynthesis and respiration.

One of the most important findings of this study is that NEP does not follow the trophic gradient even though photosynthetic capacity and respiration follow the sequence bog less than poor fen less than intermediate fen less than rich fen [Bubier *et al.*, 1998]. The relative difference between photosynthesis and respiration determines NEP, not the absolute rates of uptake or release of CO₂. This has several important implications. First, one cannot determine NEP only by photosynthetic capacity or richness gradients. Frohking *et al.* [1998] showed that peatlands have significantly lower photosynthetic capacity than upland ecosystems, yet they store significantly more carbon. Second, certain plant communities

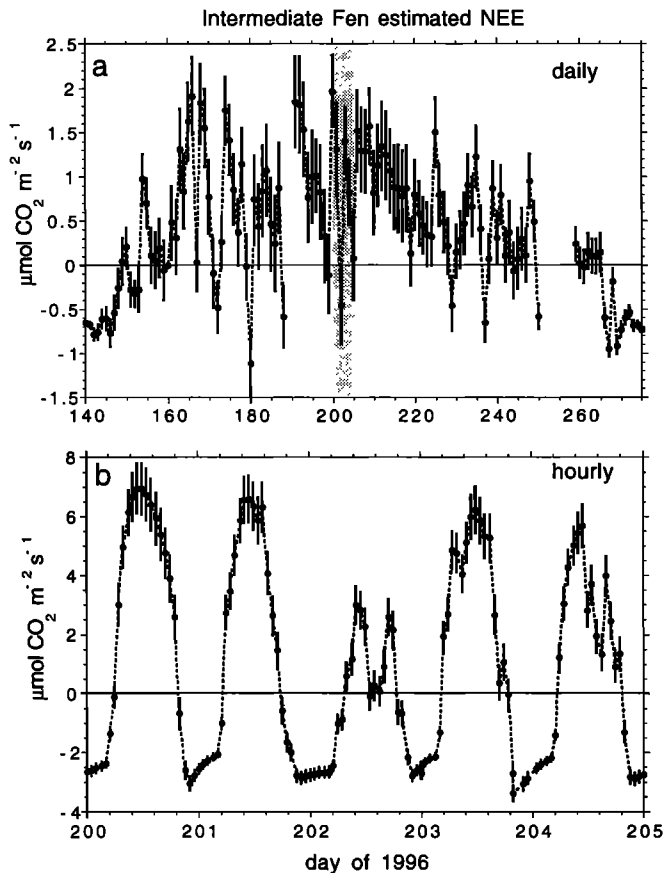


Figure 5. (a) Daily integrated values of NEE with upper and lower confidence limits ($NEE \pm 1.96$ standard error (NEE)) for intermediate fen site from May to October 1996. See equations (1) and (2) in text for calculations of NEE and standard error. Positive indicates net CO_2 uptake by the ecosystem; negative indicates loss of CO_2 to the atmosphere; (b) hourly estimated values of NEE with standard errors are shown for five days in mid-season highlighted by the shaded area in Figure 5a).

(such as sedge-dominated peatlands) may have unique characteristics, such as greater below/aboveground plant production ratios, which may be more important for determining NEP than maximum rates of ecosystem production.

Measurements of NEE in 1994 at the same ecosystems showed the same pattern as the 1996 results, with the bog and rich fen having the lowest NEP rates, compared with the poor and intermediate fens [Bellisario *et al.*, 1998]. In that study, aboveground sedge biomass was correlated with NEP, suggesting that *Carex* species are highly productive vascular plants [e.g., Thormann and Bayley, 1997]. Within pin fen microsites, Alm *et al.* [1997] also found that *Carex* sites had the highest growing season NEP compared with hummocks, saturated flarks, and *Eriophorum* lawns. Long-term carbon accumulation rates in these same ecosystems [Trumbore *et al.*, this issue] show the same pattern as the growing season NEP measurements with poor and intermediate fens having the highest C accumulation rates over the last 30-100 years.

Growing season NEP is not the same as annual C accumulation. This study did not include losses of C from dissolved organic carbon (DOC) leaching, winter CO_2 flux, or CH_4 flux. However, we can estimate the range of these additional losses to compare the ranges of C accumulation or loss in each of these four ecosystems. DOC and leaching losses are in the range of 4-6 $g\ m^{-2}\ C\ yr^{-1}$ (T.

Moore, personal communication, 1997). CH_4 emissions from the same measurement period in 1996 show that these peatlands lost from 1 to 5 $g\ CH_4-C\ m^{-2}$ (J. Bubier, unpublished data, 1996), and nongrowing season CO_2 losses based on measurements made in late winter and fall are probably in the range of 5-20 $g\ CO_2-C\ m^{-2}$ (J. Bubier, unpublished data, 1996). For the two sites with the highest NEP, poor and intermediate fen, the additional C losses could change the lower confidence limits to 3-10 $g\ C\ m^{-2}$. For the rich fen and bog, two sites that are not clearly sinks or sources of C for the 1996 growing season, upper confidence limits would be close to zero. This suggests that the poor and intermediate fens are still net carbon sinks even with the error bars, but the bog and rich fen are less likely to be net sinks for the 1996 annual period.

Since peatland soils are usually saturated, lowering of the water level can result in net ecosystem losses of carbon by increasing aerobic respiration rates [e.g., Silvola *et al.*, 1996; Carroll and Crill, 1997]. Shurpali *et al.* [1995] reported a net gain of 32 $g\ CO_2-C\ m^{-2}$ in a wet summer and net loss of 71 $g\ CO_2-C\ m^{-2}$ in a drier than average year in a Minnesota peatland. Waddington and Roulet [1996] also found substantial interannual variation in NEP as a result of differences in mean water table position in a Swedish bog. At the rich fen site in this study, Joiner *et al.* [this issue] and Lafleur *et al.* [1997] reported a net loss of 30.8 $g\ C\ m^{-2}$ to the atmosphere in 1994 and a net ecosystem gain of 91.6 $g\ C\ m^{-2}$ for 124 days in 1996 from micrometeorological CO_2 exchange measurements. Chamber measurements of NEE in 1994 showed that the bog and rich fen lost carbon during the latter half of the growing season in response to the third driest season in the last 30 years [Bellisario *et al.*, 1998]. Rates of respiration were greater than photosynthesis resulting in a net loss of CO_2 to the atmosphere. In this study based on 150 days in 1996, the lower confidence limits of the bog and rich fen were below zero, showing the sensitivity to these ecosystems on either end of the ecological gradient to slight imbalances in photosynthesis and respiration. The water table did not contribute additional predictive ability because it was strongly

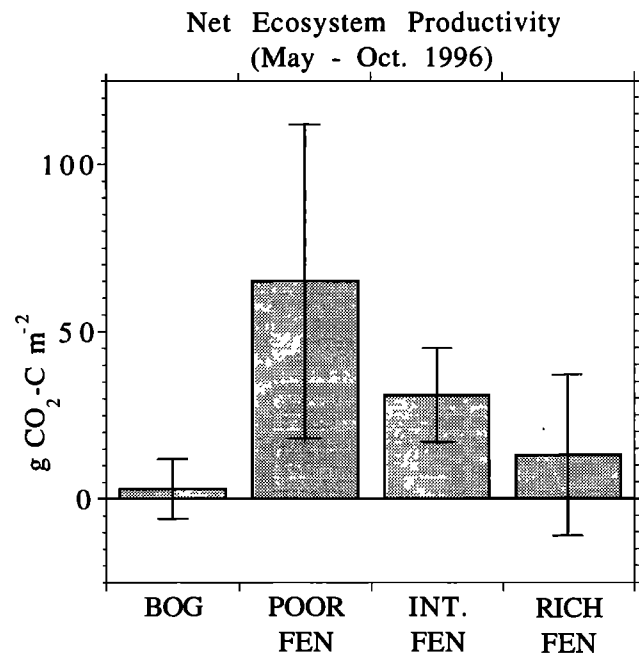


Figure 6. Net ecosystem productivity (NEP) for the four peatland sites based on the integration of simulated hourly NEE values from May to October 1996. Upper and lower 95% confidence limits are $NEP \pm (1.96$ standard error).

correlated with peat temperature. However, in a drier year, the large variation in water table position over the season did contribute to the NEP model [Bellisario *et al.*, 1998].

Spatial variation in water table position within a peatland can be as significant as interannual differences in affecting C accumulation rates. Drier hummocks generally accumulate more C than wetter hollows [Waddington and Roulet, 1996]. Microtopographic features also respond differently to changes in temperature and water table. Alm *et al.* [1997] found that water table position was important as an additional parameter only when significant microtopographic variation occurred within a site.

The standard errors in NEP, reported in this study, illustrate the importance of understanding not only the average C loss or accumulation but also the uncertainty around the annual figure. Although all four sites showed a net gain of CO₂-C during the 1996 growing season, the error bars for the bog and rich fen indicate that the possibility of net loss is within 95% confidence limits. Since the difference between photosynthesis and respiration is usually very small for these northern ecosystems, reporting the uncertainty becomes important.

These differences in NEP among the peatland ecosystems have implications for climate change because the *Carex*-dominated poor and intermediate fens are associated with the collapse of frozen peat plateaus in the zone of discontinuous permafrost [Zoltai *et al.*, 1993]. Camill and Clark [1997] reported that *Carex*-dominated scars are younger and more unstable than *Sphagnum fuscum* bog collapse scars that are completely enclosed by permafrost. A warmer climate could result in the collapse of permafrost; but the younger collapse scars may be sequestering more CO₂ than other peatlands, which is a negative feedback on climate warming. However, *Carex*-dominated collapse scars are also large sources of atmospheric methane [Bubier *et al.*, 1995], which is a positive feedback. On shorter timescales the sensitivity of unfrozen rich fen ecosystems to lower water levels and warmer peat temperatures may lead to an increase in net CO₂ emission.

Acknowledgments. We thank Andy and Cindy Mosedale, Ruth Varner, and Kathleen Savage for their enthusiastic assistance in the field and laboratory; Peter Lafleur and Harry McCaughey for access to tower facilities; Scott Mifflin and the NASA BOREAS team for logistical support; NASA grants to P.M. Crill and S. Frolking and NSERC grants to T.R. Moore for the BOREAS experiment; and a DOE Distinguished Global Change Postdoctoral Fellowship to J.L. Bubier.

References

- Alm, J., A. Talanov, S. Saarnio, J. Silvola, E. Ikkonen, H. Aaltonen, H. Nykanen, and P. J. Martikainen, Reconstruction of the carbon balance for microsites in a boreal oligotrophic pine fen, Finland, *Oecologia*, **110**, 423-431, 1997.
- Anderson, L. E., A checklist of *Sphagnum* in North America north of Mexico, *Bryologist*, **93**, 500-501, 1990.
- Anderson, L. E., H. A. Crum, and W. R. Buck, List of the mosses of North America north of Mexico, *Bryologist*, **93**, 448-499, 1990.
- Arnold, S.F., *Mathematical Statistics*, Prentice Hall, Englewood Cliffs, N.J., 1990.
- Ball, T., Seasonal transitions in fluxes of carbon dioxide and methane from an ombrotrophic peatland, Frontenac Bog, southern Quebec, M.Sc. thesis, Geogr. Dep., McGill Univ., Montreal, 1996.
- Bates, D.M., and D.G. Watts, *Nonlinear Regression Analysis and Its Applications*, John Wiley, New York, 1988.
- Bellisario, L., T. R. Moore, and J. L. Bubier, Net ecosystem CO₂ exchange in a boreal peatland, northern Manitoba, *Ecoscience*, **5**, 534-541, 1998.
- Bhardwaj, A., Seasonal variability of net carbon dioxide exchange in a headwater bog, Kenora, Ontario, M.Sc. thesis, Geogr. Dep., McGill Univ., Montreal, 1997.
- Bubier, J. L., T. R. Moore, L. Bellisario, N. T. Comer, and P. M. Crill, Ecological controls on methane emissions from a northern peatland complex in the zone of discontinuous permafrost, Manitoba, Canada, *Global Biogeochem. Cycles*, **9**, 455-470, 1995.
- Bubier, J.L., P.M. Crill, T.R. Moore, K. Savage, and R.K. Varner, Seasonal patterns and controls on net ecosystem CO₂ exchange in a boreal peatland complex, *Global Biogeochem. Cycles*, **12**, 703-714, 1998.
- Camill, P., and J.S. Clark, Climate change disequilibrium of boreal permafrost peatlands caused by local processes, *Am. Nat.*, **151**, 207-222, 1997.
- Carroll, P., and P. M. Crill, Carbon balance of a temperate poor fen, *Global Biogeochem. Cycles*, **11**, 349-356, 1997.
- Chee, W.-L., and D. H. Vitt, Vegetation, surface water chemistry and peat chemistry of moderate-rich fens in central Alberta, Canada, *Wetlands*, **9**, 227-261, 1989.
- Daubenmire, R. F., *Plant Communities: A Textbook of Plant Synecology*, Harper and Row, New York, 1968.
- Fernald, M. L., *Gray's Manual of Botany*, Van Nostrand, New York, 1950.
- Frolking, S., et al., The relationship between photosynthetically active radiation and ecosystem productivity for northern peatlands, *Global Biogeochem. Cycles*, **12**, 115-126, 1998.
- Glaser, P. H., J. A. Janssens, and D. I. Siegel, The response of vegetation to chemical and hydrological gradients in the Lost River Peatland, northern Minnesota, *J. Ecol.*, **78**, 1021-1048, 1990.
- Gorham, E., Northern peatlands: Role in the carbon cycle and probable responses to climatic warming, *Ecol. Appl.*, **1**, 182-195, 1991.
- Goulden, M. L., et al., Sensitivity of boreal forest carbon balance to soil thaw, *Science*, **279**, 214-217, 1998.
- Halsey, L., D. Vitt, and S. Zoltai, Climatic and physiographic controls on wetland type and distribution in Manitoba, Canada, *Wetlands*, **17**, 243-262, 1997.
- Harden, J. W., E. T. Sundquist, R. F. Stallard, and R. K. Mark, Dynamics of soil carbon during deglaciation of the Laurentide Ice Sheet, *Science*, **258**, 1921-1924, 1992.
- Johnson, L.C., G.R. Shaver, A.E. Giblin, K.J. Nadelhoffer, E.R. Rastetter, J.A. Laundre, and G.L. Murray, Effects of drainage and temperature on carbon balance of tussock tundra microcosms, *Oecologia*, **108**, 737-748, 1996.
- Joiner, D.W., P.M. Lafleur, J.H. McCaughey, and P.B. Bartlett, Interannual variability in carbon dioxide exchanges at a boreal wetland in the BOREAS northern study area, *J. of Geophys. Res.*, this issue.
- Lafleur, P. M., J. H. McCaughey, D. W. Joiner, P. A. Bartlett, and D. E. Jelinski, Seasonal trends in energy, water, and carbon dioxide fluxes at a northern boreal wetland, *J. Geophys. Res.*, **102**, 29,009-29,020, 1997.
- Oechel, W. C., G. L. Vourlitis, S. J. Hastings, and S. A. Bochkarev, Change in arctic CO₂ flux over two decades: Effects of climate change at Barrow, Alaska, *Ecol. Appl.*, **5**, 846-855, 1995.
- Riley, J. L., *Peat and Peatland Resources of Northeastern Ontario*, Ont. Geol. Surv., Minist. of Northern Mines and Dev., 1987.
- Roulet, N., S. Hardill, and N. Comer, Continuous measurement of the depth of water table (inundation) in wetlands with fluctuating surfaces, *Hydrol. Process.*, **5**, 399-403, 1991.
- SAS Institute, Inc. JMP-IN Statistics, version 3.2.1, 1996.
- Schlesinger, *Biogeochemistry: An Analysis of Global Change*, 2nd ed., Academic, San Diego, Calif., 1997.
- Sellers, P. J., et al., Boreal-Ecosystem Atmosphere Study (BOREAS): An overview and early results from the 1994 field year, *Bull. Am. Meteorol. Soc.*, **76**, 1549-1577, 1995.
- Sellers, P. J., et al., BOREAS in 1997: Experiment overview, scientific results, and future directions, *J. Geophys. Res.*, **102**, 28,731-28,769, 1997.
- Shurpali, N. J., S. B. Verma, and J. Kim, Carbon dioxide exchange in a peatland ecosystem, *J. Geophys. Res.*, **100**, 14,319-14,326, 1995.
- Silvola, J., J. Alm, U. Ahlholm, H. Nykanen, and P. J. Martikainen, CO₂ fluxes from peat in boreal mires under varying temperature and moisture conditions, *J. Ecol.*, **84**, 219-228, 1996.
- Stotler, R., and B. Crandell-Stotler, Checklist of liverworts and hornworts of North America, *Bryologist*, **80**, 405-428, 1977.
- Suyker, A. E., S. B. Verma, and T. J. Arkebauer, Season-long measurement of carbon dioxide exchange in a boreal fen, *J. Geophys. Res.*, **102**, 29,021-29,028, 1997.
- Thormann, M. N., and S. E. Bayley, Aboveground net primary production along a bog-fen-marsh gradient in southern boreal Alberta, Canada, *Ecoscience*, **4**, 374-384, 1997.
- Thornley, J. H. M., and I. R. Johnson, *Plant and Crop Modeling: A Mathematical Approach to Plant and Crop Physiology*, Clarendon, Oxford, England, 1990.
- Tolonen, K., and J. Turunen, Accumulation rates of carbon in mires in

- Finland and implications for climate change, *Holocene*, 6, 171-178, 1996.
- Trumbore, S.E., J.L. Bubier, J.W. Harden, and P.M. Crill, Carbon cycling in boreal wetlands: A comparison of three approaches, *J. Geophys. Res.*, this issue.
- Vitt, D. H., L. A. Halsey, and S. C. Zoltai, The bog landforms of continental western Canada in relation to climate and permafrost patterns, *Arct. Alp. Res.*, 26, 1-13, 1994.
- Waddington, J. M., and N. T. Roulet, Atmosphere-wetland carbon exchanges: Scale dependency of CO₂ and CH₄ exchange on the developmental topography of a peatland, *Global Biogeochem. Cycles*, 10, 233-245, 1996.
- Whiting, G. J., CO₂ exchange in the Hudson Bay lowlands: Community characteristics and multispectral reflectance properties, *J. Geophys. Res.*, 99, 1519-1528, 1994.
- Whiting, G. J., J. P. Chanton, D. Bartlett, and J. Happell, Relationships between CH₄ emission, biomass, and CO₂ exchange in a subtropical grassland, *J. Geophys. Res.*, 96, 13,067-13,071, 1991.
- Whiting, G. J., D. S. Bartlett, S. Fan, P. S. Bakwin, and S. C. Wofsy, Biosphere/atmosphere CO₂ exchange in tundra ecosystems: Community characteristics and relationships with multispectral surface reflectance, *J. Geophys. Res.*, 97, 16,671-16,680, 1992.
- Zoltai, S. C., Wetland environments and classification, in *Wetlands of Canada*, pp. 3-26, Polysci. Publ., Inc., Montreal, 1988.
- Zoltai, S. C., Cyclic development of permafrost in the peatlands of northwestern Alberta, Canada, *Arct. and Alp. Res.*, 25, 240-246, 1993.

J. L. Bubier, Environmental Studies Program, Mount Holyoke College, S. Hadley, MA 01075. (jbubier@mtholyoke.edu)

P. M. Crill and S. Frolking, Complex Systems Research Center, University of New Hampshire, Durham, NH 03824-3525. (patrick.crill@unh.edu; steve.frolking@unh.edu)

E. Linder, Department of Mathematics, University of New Hampshire, Durham, NH 03824. (elinder@hopper.unh.edu)

(Received July 30, 1998; revised February 11, 1999; accepted March 22, 1999.)