

# Contrasting responses of growing season ecosystem CO<sub>2</sub> exchange to variation in temperature and water table depth in two peatlands in northern Alberta, Canada

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[1] The large belowground carbon stocks in northern peatland ecosystems are potentially susceptible to release because of the expected differential responses of photosynthesis and respiration to climate change. This study compared net ecosystem CO<sub>2</sub> exchange (NEE) measured using the eddy covariance technique at two peatland sites in northern Alberta, Canada, over three growing seasons (May–October). We observed distinct differences between the poor fen (*Sphagnum* moss dominated) and extreme-rich fen (*Carex* sedge dominated) sites for their responses of NEE to interannual variation in temperature and water table depth. The rates of growing season cumulative NEE at the poor fen were very similar among the three study years with an average ( $\pm$  standard deviation) of  $-110.1 \pm 0.5$  g C m<sup>-2</sup> period<sup>-1</sup>. By contrast, the growing season cumulative NEE at the extreme-rich fen varied substantially among years ( $-34.5$ ,  $-153.5$ , and  $-41.8$  g C m<sup>-2</sup> period<sup>-1</sup> in 2004, 2005, and 2006, respectively), and net uptake of CO<sub>2</sub> was lower (on average) than at the poor fen. Consistent with the eddy covariance measurements, analysis of <sup>210</sup>Pb-dated peat cores also showed higher recent net rates of carbon accumulation in the poor fen than in the rich fen. Warm spring temperatures and sufficient water availability during the growing season resulted in the highest-magnitude ecosystem photosynthesis and NEE at the extreme-rich fen in 2005. Cool spring temperatures limited photosynthesis at the extreme-rich fen in 2004, while reduced water availability (lower water table) in 2006 constrained photosynthetic capacity relative to 2005, despite the warmer spring and summer temperatures in 2006. The combination of contrasting plant functional types and different peat water table features at our two study sites meant that the poor fen showed a reduced response of ecosystem CO<sub>2</sub> exchange to environmental variation compared to the extreme-rich fen.

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## 1. Introduction

[2] Over the last century, significant air temperature warming has been observed over most of the world's surface, with positive temperature anomalies in the interior of northwestern North America being among the highest recorded [Solomon *et al.*, 2007]. Mean annual precipitation is also projected to rise across North America owing to climate change, but soil moisture may decline because the moderate precipitation increase predicted in the future for middle and high latitudes will be associated with warmer

temperatures and higher evaporation rates [Tarnocai, 2006; Solomon *et al.*, 2007]. In the boreal forest region, which contains 64% of Canadian peatlands [Tarnocai, 2006], enhanced evaporation will likely completely offset increases in precipitation [Hogg and Hurdle, 1995]. Global climate models also suggest a greater frequency of extreme weather events, including longer and more severe summer dry periods [Solomon *et al.*, 2007], likely resulting in more prolonged droughts in Canada's western interior [Lemmen *et al.*, 2008].

[3] Northern peatland ecosystems are generally carbon (C) sinks that have long-term net C uptake rates of 20–30 g C m<sup>-2</sup> yr<sup>-1</sup> [Gorham, 1991; Turunen *et al.*, 2002]. The total C accumulated in peatlands worldwide is approximately 200–450 Pg, an amount that accounts for up to one third of the global soil C pool [Gorham, 1991; Turunen *et al.*, 2002]. This high carbon stock results from low rates of plant production that exceed those of even lower respiration and

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decomposition rates [Gorham, 1991]. Decomposition is suppressed by the cool temperatures and anaerobic conditions that typically occur in Northern peatland ecosystems. Warm and dry conditions can decrease peatland C uptake, sometimes resulting in annual net losses of C [Alm *et al.*, 1999; Roulet *et al.*, 2007]. A shift toward warmer and drier conditions could, therefore, alter the balance between production and decomposition and change the status of peatlands from a net C sink to a net source. The peatland C budget includes both growing season and wintertime CO<sub>2</sub> fluxes, CH<sub>4</sub> fluxes, and DOC losses, all of which may significantly influence the annual net uptake or loss of C from the ecosystem [Moore *et al.*, 1998; Aurela *et al.*, 2002; Christensen *et al.*, 2007; Roulet *et al.*, 2007; Nilsson *et al.*, 2008]. This study focuses on CO<sub>2</sub> fluxes during the growing season.

[4] Net ecosystem CO<sub>2</sub> exchange (NEE) is determined by the difference between gross photosynthesis (GPP) and total ecosystem respiration (TER). Higher temperatures can stimulate photosynthesis in northern ecosystems via several mechanisms [Updegraff *et al.*, 2001; Syed *et al.*, 2006; Cai *et al.*, 2010]. For example, warmer temperatures can lead to earlier leaf development (or later senescence) and a longer growing season, higher leaf area index, and greater biochemical capacity for leaf-level photosynthesis [Moore *et al.*, 1998; Aurela *et al.*, 2004, 2007]. Ecosystem respiration can be simultaneously stimulated by the temperature-induced increase in plant biomass and input of carbohydrate to rhizosphere and heterotrophic microbes from higher ecosystem photosynthesis activity. In addition, even under conditions of constant biomass abundance and substrate availability, respiration increases strongly with temperature [Davidson and Janssens, 2006]. However, the temperature optimum for ecosystem photosynthesis and respiration usually differ so that higher net uptake of carbon is favored at lower temperatures [Larcher, 1980]. In general, photosynthesis and respiration also have bell-shaped, optimum responses to variation in moisture [Davidson and Janssens, 2006]. Lower water tables have been shown to stimulate photosynthesis in some peatlands [Sulman *et al.*, 2010], but if the water table becomes too low, drought will then become limiting [Shurpali *et al.*, 1995; Bubier *et al.*, 2003; Sulman *et al.*, 2010]. Previous studies have observed contrasting responses of respiration to variation in water table depths [Silvola *et al.*, 1996; Updegraff *et al.*, 2001; Lafleur *et al.*, 2005; Aurela *et al.*, 2007; Sulman *et al.*, 2009]. This may be related, in part, to the strong interacting effects between temperature and moisture changes. Parmentier *et al.* [2009] suggested that while variation in respiration may not always be related to changes in water table, respiration does vary with soil moisture, making water table an important control on respiration in peatlands in which soil (peat) moisture is sensitive to water table decline.

[5] The complex interactions that occur among photosynthesis, respiration, temperature and moisture make it very difficult to accurately model and predict the response of different peatland ecosystems to future climate change. Added to this complexity is the wide range of characteristics that differ among peatlands such as plant species composition, peat chemical characteristics, nutrient availability, and hydrology. Currently we have limited understanding of the

potential future responses of diverse peatlands to warmer temperatures and reduced moisture associated with climate change. The large carbon store in peatlands is potentially susceptible to release because of the differential responses of photosynthesis and respiration to climate change. If this occurred, it would provide a positive feedback to increasing atmospheric CO<sub>2</sub> concentration and enhance future climate change [Davidson and Janssens, 2006]. In order to better predict the effects of climate change on peatland C stocks, it is important to understand how different types of peatland ecosystems respond to change in environmental conditions.

[6] The primary goal of this study was to compare the response of CO<sub>2</sub> exchange at two peatland sites in northern Alberta, Canada, to seasonal and interannual variation in temperature and moisture conditions. The sites were located approximately 150 km apart and experienced similar variations in weather among three study years, but differed considerably in plant species composition, nutrient status and water table variation. The first site was a poor fen dominated by *Sphagnum* mosses, while the second was an extreme-rich fen dominated by *Carex* sedges. These sites represented two common types of peatland ecosystems, and the two broad groups into which fens can be classified on the basis of contrasting nutrient levels and dominant vegetation types (i.e., poor fen and rich fen) [Rydin and Jeglum, 2006]. We measured NEE during the growing season in 2004, 2005 and 2006 using the eddy-covariance (EC) technique. This study expands on the work of Glenn *et al.* [2006], who compared CO<sub>2</sub> exchange between these same sites in one growing season during 2004. Glenn *et al.* [2006] found that in 2004 both sites were significant net sinks for CO<sub>2</sub> during the growing season, but that net uptake was three times greater at the poor fen than at the extreme-rich fen, and that this was primarily due to the difference in the dominant plant functional types between the sites. In expanding the comparison to three growing seasons, our major objectives were to determine whether these peatlands remained net sinks for CO<sub>2</sub> in other years with different environmental conditions, and to investigate potential differences between the sites in temperature and moisture controls on NEE. It was hypothesized that warmer temperatures, particularly in spring and fall, would lengthen the period in which plants were photosynthetically active and enhance the total net CO<sub>2</sub> uptake during the growing season. In particular, this was expected at the *Sphagnum*-dominated poor fen, while at the sedge-dominated extreme-rich fen warmer temperatures were expected to lead to earlier leaf emergence and enhanced biomass production, but also to higher respiration and decomposition in the fall, which would limit the potential for net CO<sub>2</sub> uptake. If warmer temperatures were accompanied by drier conditions (i.e., decreased precipitation and lower water tables), it was hypothesized that photosynthesis would be limited at both sites by the decreased water availability, causing net CO<sub>2</sub> uptake over the growing season to be reduced and possibly causing the sites to shift from sinks to sources of CO<sub>2</sub>.

## 2. Materials and Methods

### 2.1. Study Sites

[7] The two study sites were a poor fen (55.53939°N, 112.33528°W; 725 m a.s.l., linear dimensions: 520 m ×

390 m) and an extreme-rich fen (54.47225°N, 113.32593°W; 670 m a.s.l., linear dimensions: 800 m × 200 m) located in north central Alberta, approximately 120 km northeast and 30 km south of Athabasca, AB (54.71930°N, 113.28606°W), respectively. Glenn *et al.* [2006] provided a detailed description of these sites, including aboveground biomass production and plant community characteristics, which is briefly summarized here. These were auxiliary sites to the Western Peatland main flux station, which is part of the Canadian Carbon Program (previously the Fluxnet-Canada Research Network, FCRN) [Syed *et al.*, 2006]. The poor fen was located in the Central Mixedwood Subregion and the extreme-rich fen in the Dry Mixedwood Subregion of the Boreal Forest Natural Region of Alberta [Natural Regions Committee, 2006]. The climate in this region is subhumid continental, and the mean annual and growing season (May–October) temperatures for the area, measured at Athabasca, are 2.1°C and 11.7°C, respectively [Environment Canada, 2010]. Mean annual precipitation at Athabasca is 504 mm, with 382 mm falling as rain.

[8] The poor fen was classified as a “patterned fen” following Vitt *et al.* [1998], with alternating open wet pools and drier elevated areas that were oriented perpendicular to the direction of water flow. There was a distinct microtopography of alternating hummocks and hollows, and the site was dominated by a continuous (100%) ground cover of *Sphagnum* mosses (primarily *S. angustifolium* ([C. Jens. ex Russ.] C. Jens. in Tolf), *S. magellanicum* (Brid.), and *S. fuscum* ([Schimp.] Klinggr.), therefore we assumed that *Sphagnum* effective photosynthetic LAI was 1 m<sup>2</sup> m<sup>-2</sup>. Of the total peak live aboveground biomass (230.9 ± 15.3 g m<sup>-2</sup>, ±SE, n = 6) and peak leaf area index (LAI; 1.52 ± 0.03, ±SE, n = 6) measured at the site in 2004, *Sphagnum* mosses accounted for approximately 68% and 66%, respectively [Glenn *et al.*, 2006]. Other major species present included the dwarf evergreen shrub *Andromeda polifolia* (L.), the sedge *Carex limosa* (L.), the herb *Smilacina trifolia* ([L.] Desf.), and dwarf *Picea mariana* ([Mill.] BSP.) trees, each contributing ≤10% of the live aboveground biomass. The extreme-rich fen was part of a larger wetland complex described by Vitt *et al.* [1995]. The microtopography of the site was mainly flat, with occasional small hummocks. It was a sedge-dominated ecosystem, in which the species *Carex lasiocarpa* (Ehrh.) contributed approximately 47% of the total peak aboveground biomass (157.1 ± 16.6, ±SE, n = 6) and 60% of the total peak LAI (1.09 ± 0.06, ±SE, n = 6) during 2004 [Glenn *et al.*, 2006]. There was also significant cover of brown mosses (*Drepanocladus aduncus* ([Hedw.] Warnst.), *Aulacomnium palustre* ([Hedw.] Schwaegr.) at the site, which were 48% of the live aboveground biomass. Shrubs and herbs were present in low numbers. Corresponding with its classification, the extreme-rich fen had surface water with higher nutrient and base cation concentrations (NH<sub>4</sub><sup>+</sup>, NO<sub>3</sub><sup>-</sup>, total P, K<sup>+</sup>, Ca<sup>2+</sup>, Mg<sup>2+</sup>) than the poor fen. The surface water at the poor fen was more acidic (pH 4.0) than at the extreme-rich fen (pH 6.5).

## 2.2. Peat Core Nutrient Content, Age Measurements, and Rates of Recent Carbon Accumulation

[9] A short peat core (approximately 34 cm depth at the poor fen, and 50 cm depth at the extreme-rich fen) was sampled using a 10.16 cm inside diameter of polyvinyl

chloride (PVC) pipe (with sharpened edge) inserted into the peat. The PVC pipe with peat core inside was placed into a freezer as soon after collection as possible (within one day). After the core was frozen, it was removed from the PVC pipe and cut into approximately 2 cm depth segments before thawing. The thickness and area of each depth segment was measured, the segments were weighed and placed into separate paper bags for drying and subsequent analyses (see below). A deep core was also collected using a Russian peat corer at the rich fen site (the loose peat and unstable surface did not allow the collection of a deep core at the poor fen site). After removal of the first 50 cm from the short core, a Russian peat corer with a 50 cm by 5 cm chamber was used to sequentially extract peat cores until the clay sediment was reached at the base of the peat (approximately 1.9 m depth). The Russian peat core samples were separated into 10 cm increments in the field and stored in bags. Samples from both core types were dried at 60°C, dry weights were determined, and then the samples were ground to a fine powder using a coffee grinder.

[10] The total nitrogen and total carbon contents were analyzed on N<sub>2</sub> and CO<sub>2</sub> gases, respectively, that were generated from combustion/reduction of the dried peat tissue in an elemental analyzer (Carlo Erba NC2500) and quantified using a gas isotope ratio mass spectrometer (Delta Plus, Finnigan Mat, San Jose, CA, USA) at the University of Lethbridge. All 2 cm peat segments from the short cores were analyzed for total carbon and nitrogen contents. Additional macronutrient analysis (total content of: P, K, Mg, Ca, S) was conducted on peat tissue that was dry-ashed and then digested using a dilute HNO<sub>3</sub> and HCl mixture, and then quantified using an Inductively Coupled Plasma (ICP) spectroscopic analysis technique at Norwest Labs, Lethbridge. Only every third peat depth segment (2 cm interval) was analyzed for these additional macronutrients over the top approximately 32 cm depth of the short cores.

[11] Subsamples of the 2 cm depth segments of the peat were dated using the <sup>210</sup>Pb technique based on measurements made at Flett Research Ltd, Winnipeg, Canada. The technique assumes that the <sup>210</sup>Pb concentrations in peat samples decrease exponentially with depth, approaching a value taken to represent the supported <sup>210</sup>Pb activity formed within the soil, in contrast to that deposited from the atmosphere. The <sup>210</sup>Pb activity was estimated by measuring the alpha-emitting <sup>210</sup>Po granddaughter isotope after spiking samples with <sup>209</sup>Po yield tracer. The constant rate of supply (CRS) model of Appleby and Oldfield [1978] was applied to calculate the ages of the peat samples. The <sup>210</sup>Pb technique worked well on the one peat core sample collected at the extreme-rich fen. The first two peat cores from the poor fen had to be excluded because the profile of measured <sup>210</sup>Pb activity was inconsistent and this made it unreliable to construct age chronologies. This may have been related to the relatively low-density (loose) peat and the unstable peat surface at the poor fen. However, a third peat core from the poor fen was reliably dated using the <sup>210</sup>Pb technique.

[12] The cumulative dry mass of peat on an area basis (g m<sup>-2</sup>) was calculated from measurements on the 2–3 cm depth segments in the shallow cores and was converted to carbon accumulation on the basis of the peat carbon content

determined by elemental analysis. We applied the peat growth model of *Clymo* [1984, equation (1)],

$$x = \frac{p}{k} (1 - e^{-kt}), \quad (1)$$

to estimate the rate of carbon addition to the peat acrotelm ( $p$ , g C m<sup>-2</sup> yr<sup>-1</sup>) and the acrotelm peat decay rate coefficient ( $k$ , yr<sup>-1</sup>) from fits of equation (1) to the relationship between measured depth profiles of peat age ( $t$ , years; from <sup>210</sup>Pb dates) and cumulative carbon stock per area ( $x$ , g C m<sup>-2</sup>) on the short peat core from each site. Nonlinear least squares regressions were used to calculate estimates of  $p$  and  $k$  using the Gauss-Newton method in SYSTAT10.

[13] A basal peat sample from the deep core sampled at the rich fen was dated using <sup>14</sup>C at the IsoTrace Radiocarbon Laboratory at the University of Toronto. The <sup>14</sup>C result we present is the average (±SD) of four separate analyses (high precision). The <sup>14</sup>C values were corrected for natural and sputtering isotope fractionation using measured <sup>13</sup>C/<sup>12</sup>C ratios. The peat sample age is quoted as an uncalibrated conventional radiocarbon date in years before present, using the Libby <sup>14</sup>C mean life of 8033 years. We used the second last 10 cm segment from the deep core for the <sup>14</sup>C analysis, as this sample had a carbon content similar to all other peat segments from positions higher in the core, while in the last segment of the peat core the carbon content dropped to approximately 12% upon reaching clay mineral sediment.

### 2.3. Eddy Covariance and Meteorological Measurements

[14] Net ecosystem CO<sub>2</sub> exchange, latent heat flux and sensible heat flux were measured at each study site during the growing season (1 May to 31 October) in 2004, 2005 and 2006 using the eddy covariance (EC) technique [Baldocchi et al., 1988; Moncrieff et al., 1997; Aubinet et al., 1999; Baldocchi, 2003]. At both study sites, two 3 m tall instrumentation towers for mounting EC and meteorological instrumentation were established prior to the 2004 growing season and they remained in place for the duration of the study. In all study years, a mobile EC system was moved alternately between the two study sites, with each measurement campaign at a site lasting between 8 and 19 days. This EC system and data processing were described in detail by Glenn et al. [2006]. Briefly, the EC system consisted of a three-dimensional sonic anemometer-thermometer (SAT; CSAT3, Campbell Scientific, Logan, UT, USA) to measure wind speed and direction and a fast-response open-path infrared gas analyzer (IRGA; LI7500, LI-COR Inc., Lincoln, NE, USA) to measure CO<sub>2</sub> and water vapor concentrations in the air. The SAT and IRGA were mounted on the EC instrumentation tower at a height of 3 m on adjacent horizontal booms oriented west, the prevailing wind direction. Signals from the SAT and IRGA were recorded at a frequency of 10 Hz with a data logger (CR5000, Campbell Scientific) and flash memory storage card.

[15] The performance of the mobile, open-path IRGA EC system described above was compared to a closed-path IRGA EC system at the main site (treed, moderately rich fen) of the Western Peatland flux station during 1–7 September, 2004. The closed-path EC system used at the main site of the Western Peatland has been previously described

[Syed et al., 2006; Cai et al., 2010]. In addition, the main site flux system was evaluated using the FCRN calibration EC system as per protocols developed within the FCRN network. There was excellent agreement between sensible heat flux, latent heat flux and net ecosystem CO<sub>2</sub> exchange measurements when the open-path and closed-path systems were compared side-by-side [Glenn, 2006]. For example, the relationships between measurements of the closed-path ( $x$ ) and open-path ( $y$ ) instruments had the following statistics (±95% confidence interval): sensible heat flux, slope =  $0.95 \pm 0.03$ ,  $y$  intercept =  $-0.17$ ,  $r^2 = 0.95$ ,  $n = 158$ ; latent heat flux, slope =  $1.04 \pm 0.06$ ,  $y$  intercept =  $7.59$ ,  $r^2 = 0.88$ ,  $n = 122$ ; net ecosystem CO<sub>2</sub> exchange, slope =  $0.99 \pm 0.06$ ,  $y$  intercept =  $0.40$ ,  $r^2 = 0.89$ ,  $n = 113$ . Some of the slight difference between the two systems was attributed to the relatively cool temperatures, high relative humidity and occasional precipitation that occurred during the comparison period, and the limitations of the open-path IRGA under such environmental conditions [Glenn, 2006].

[16] A flux-footprint analysis was performed by Glenn et al. [2006] at each study site for 2004, using the simple parameterization of Kljun et al. [2004] (N. Kljun et al., A simple parameterisation for flux footprint predictions, online footprint, available at <http://footprint.kljun.net/>, 2004). Flux-footprint model estimations were produced for a number of scenarios with different model inputs representing different atmospheric conditions. The output from model estimations gave the horizontal distances (m) from the EC tower with the maximum contribution to measured fluxes ( $X_{\max}$ ) and within which 90% of measured fluxes originated ( $X_{90\%}$ ). The values of  $X_{\max}$  and  $X_{90\%}$  that were found varied with atmospheric conditions. At the poor fen,  $X_{\max}$  ranged from 30 to 50 m and  $X_{90\%}$  ranged from 90 to 125 m, while at the extreme-rich fen,  $X_{\max}$  ranged from 35 to 45 m and  $X_{90\%}$  ranged from 110 to 120 m. Fetch distances to the west, north, east and south were 250 m, 100 m, 80 m and 300 m, respectively, at the poor fen, and 120 m, over 600 m, 80 m and 220 m, respectively, at the extreme-rich fen. Therefore,  $X_{\max}$  was less than fetch in all directions at both sites, suggesting that the peak surface contribution to measured fluxes originated from within the peatland at both sites. When comparing  $X_{90\%}$  to fetch from the EC tower, fetch was found to be slightly limited (i.e., fetch <  $X_{90\%}$ ) to the north, northeast and east at the poor fen and to the east at the extreme-rich fen. However, Glenn et al. [2006] concluded that there was adequate fetch at both sites to achieve representative fluxes for the majority of measurements, since the region's predominant winds were from the west and southwest.

[17] Friction velocity ( $u_*$ , m s<sup>-1</sup>) was used to determine when NEE measurements were likely unreliable as a result of calm conditions. Glenn et al. [2006] examined the relationship between NEE and  $u_*$  at both the poor fen and extreme-rich fen, and determined the appropriate  $u_*$  threshold to be  $0.15 \text{ m s}^{-1}$  at both sites. This threshold was used to screen flux measurements prior to conducting further analyses and carbon budget calculations. Unless otherwise stated, the convention that a negative flux indicates uptake by the ecosystem is used in this paper.

[18] Identical meteorological instrumentation was operated continuously for the duration of the study (May 2004 to October 2006) at each site to monitor environmental con-

ditions. On each meteorological instrumentation tower, a net radiometer (NR Lite, Kipp & Zonen, Delft, The Netherlands) and quantum sensor (LI-190SA, LI-COR Inc.) were mounted at a height of 3 m to measure net radiation and incoming photosynthetic photon flux density (PPFD), respectively. An air temperature and humidity probe (HMP45C, Vaisala Inc., Helsinki, Finland) within a vented radiation shield (41002, Gill MultiProbe, R.M. Young Company, Traverse City, MI, USA) was mounted at a height of 2 m. Soil temperature was measured with thermistors (107B Soil Temperature Probe, Campbell Scientific) at 2, 5, 10, 20, 50 and 100 cm depths below the surface. Water table depth was measured in a water well (3 m length of 15 cm diameter plastic pipe installed in the peat) using a float and counterweight system attached to a calibrated potentiometer. The water table depth was measured relative to a fixed point marked on the water well, but it was expressed relative to the average hummock height recorded at the start of the study in 2004 at both sites. We did not make measurements of the peat surface height fluctuations during the study, but it was likely that the peat surface height at the poor fen site varied strongly in association with changes in water level. This is in contrast to the situation at the extreme-rich fen, where it was unlikely that any significant peat surface movement occurred in association with water table changes. Precipitation was measured with a tipping bucket rain gauge (TBRG; CS700, Campbell Scientific). All meteorological signals were scanned at 5 s intervals and recorded as 30 min means on a data logger (CR23X, Campbell Scientific), with the exception of the TBRG, which measured total precipitation at 30 min intervals. Small gaps in temperature and PPFD data ( $\leq 6$  half-hour periods) were filled by linear interpolation, while longer gaps ( $> 6$  half-hour periods) were filled with data determined from the average diurnal trend of the three days previous to and following the gap period. Gaps in water table data were filled only by linear interpolation.

## 2.4. Growing Season Carbon Budget Calculations

[19] During the 2004 growing season, five measurement campaigns were completed at both study sites. There were six campaigns at the poor fen and five at the extreme-rich fen in 2005, seven campaigns at the poor fen and six campaigns at the extreme-rich fen in 2006. For each measurement campaign, mean diurnal patterns of NEE, PPFD and air temperature ( $T$ ) were determined by bin-averaging data over the campaign period by time of day (half hour). The relationship between NEE and PPFD and temperature was described with the following model:

$$NEE = \frac{A_{\max} \alpha \text{PPFD}}{A_{\max} + \alpha \text{PPFD}} + R_{10} Q_{10}^{\left(\frac{T-10}{10}\right)}, \quad (2)$$

in which  $\alpha$  (mol CO<sub>2</sub> mol<sup>-1</sup> photons) is the apparent quantum yield or light-use efficiency,  $A_{\max}$  is maximum GPP ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) at infinite PPFD ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ),  $R_{10}$  is TER ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) at a reference temperature of 10°C, and  $Q_{10}$  is the rate of change in respiration for a 10°C change in temperature. To estimate  $A_{\max}$ ,  $\alpha$ ,  $R_{10}$  and  $Q_{10}$  for each campaign period, equation (2) was fit to the measured NEE data with nonlinear least squares regression and the Gauss-Newton method using MATLAB (The MathWorks, Inc.).

Model parameters were bound by the following ranges at both sites:  $A_{\max}$ , 0.1 to 40.0  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ;  $\alpha$ , 0.001 to 0.08 mol CO<sub>2</sub> mol<sup>-1</sup> photons;  $R_{10}$ , 0.1 to 6.0  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ; and  $Q_{10}$ , 1.8 to 2.2.

[20] Relationships between model parameters ( $A_{\max}$ ,  $\alpha$ ,  $R_{10}$  and  $Q_{10}$ ) and time (day of year at the middle of the corresponding campaign period) were developed for each site in each growing season, in order to calculate integrated monthly and growing season carbon budgets. Third-order polynomial regressions fit to these relationships were used to estimate parameter values for days during the growing season without measured data (e.g., between campaign periods or due to exclusion of measured values because of low turbulence ( $u_*$  screening)). Half-hourly NEE was modeled using equation (2) with these estimated parameters and measurements of air temperature and PPFD. In some cases outside of the measurement period (i.e., before the first day or after the last day of measurement in the growing season) the polynomial regression models did not provide reasonable estimates of the parameter values. For example, the polynomial regression sometimes went below zero or began to increase following a decreasing trend in the latter half of the growing season. This occurred in all years at both sites, for time periods lasting between 3 and 25 days, 3 and 27 days, 0 and 19 days, and 0 and 34 days for  $A_{\max}$ ,  $\alpha$ ,  $R_{10}$ , and  $Q_{10}$ , respectively. In these cases the last estimated parameter value that fell within the boundaries set when fitting equation (2) was extended to the remaining days in the growing season (or was extended from the first value within the boundaries to the beginning of the growing season for cases before the first day of measurement). Half-hourly TER was similarly modeled using

$$TER = R_{10} Q_{10}^{\left(\frac{T-10}{10}\right)}. \quad (3)$$

To determine the reliability of the modeled data, the strength of the linear relationship between half-hourly values of modeled NEE ( $NEE_{\text{mod}}$ ) and measured NEE ( $NEE_{\text{obs}}$ ;  $u_* \geq 0.15$ ) was determined using Model II (geometric mean) linear regression and the modeling efficiency (ME) statistic [*Janssen and Heuberger*, 1995; *Reichstein et al.*, 2002], in which  $\overline{NEE_{\text{obs}}}$  represents the average of measured NEE values:

$$ME = 1 - \frac{\sum_{i=1}^n (NEE_{\text{obs}} - NEE_{\text{mod}})^2}{\sum_{i=1}^n (NEE_{\text{obs}} - \overline{NEE_{\text{obs}}})^2}. \quad (4)$$

A combination of measured and modeled flux data was used in the determination of integrated monthly and growing season carbon budgets. After  $u_*$  threshold screening, measured data were used for half-hour periods in which they were available. Modeled values were substituted when NEE and TER measurements were not available between measurement campaigns or because of gaps caused by  $u_*$  screening, IRGA maintenance and calibration, power outages or bad diagnostics due to interference in the path of the sensor (e.g., fog, dew, rain, or insects). Integrated monthly and growing season carbon budgets for each site in each year were calculated from these data sets of combined measured and modeled data. GPP was calculated as  $GPP = NEE - TER$ . Carbon budgets determined using only modeled fluxes (data not presented) were found to be similar to those determined with both measured and mod-

**Table 1.** Comparison of Average ( $\pm$  Standard Deviation) Macro-nutrient Content and Density of Short Peat Cores Sampled at the Poor Fen and Extreme-Rich Fen<sup>a</sup>

	Poor Fen	Extreme-Rich Fen
N (mg g <sup>-1</sup> )	9.51 $\pm$ 1.81	28.27 $\pm$ 4.91
P (mg g <sup>-1</sup> )	0.43 $\pm$ 0.08	1.30 $\pm$ 0.35
K (mg g <sup>-1</sup> )	0.98 $\pm$ 1.19	0.74 $\pm$ 0.57
Mg (mg g <sup>-1</sup> )	0.50 $\pm$ 0.14	1.82 $\pm$ 0.23
Ca (mg g <sup>-1</sup> )	2.50 $\pm$ 0.33	15.28 $\pm$ 3.87
S (mg g <sup>-1</sup> )	1.02 $\pm$ 0.22	1.90 $\pm$ 0.25
Density (kg m <sup>-3</sup> )	46.5 $\pm$ 7.5	83.1 $\pm$ 18.3

<sup>a</sup>Peat cores were cut into approximately 2 cm depth segments for analyses, and density and N content were analyzed in all segments in the top 32 cm of each core (poor fen:  $n = 16$ ; extreme-rich fen:  $n = 14$ ). Only every third 2 cm depth segment was analyzed for P, K, Mg, Ca, and S (poor fen:  $n = 6$ ; extreme-rich fen:  $n = 5$  in the top 32 cm of each core).

eled fluxes ( $\leq 3.6\%$  and  $\leq 19.5\%$  change in growing season totals at the poor fen and extreme-rich fen, respectively).

[21] The response of gross photosynthesis ( $GEP = -GPP$ ) to daily average acclimation temperature ( $T_{\text{accl}}$ ) was assessed for each site in each growing season.  $T_{\text{accl}}$  accounts for the lagged response of GEP due to the acclimation of vegetation to changes in air temperature [Mäkelä *et al.*, 2004]. Daily  $T_{\text{accl}}$  were calculated starting from 1 March using the change in  $T_{\text{accl}}$  for each day as described by

$$dT_{\text{accl}} = \left( \frac{(T_{\text{avg}} - T_{\text{accl\_in}})}{\tau} \right) dt, \quad (5)$$

where  $T_{\text{avg}}$  is the daily average air temperature,  $t$  is time (24 h time step),  $T_{\text{accl\_in}}$  is  $T_{\text{accl}}$  in the previous time step, and  $\tau$  is the lag period (200 h). Air temperature data measured at the Environment Canada weather station located at Athabasca, AB, were used for days prior to the beginning of the growing season (1 March to 31 April) when data were not measured at the study sites. The relationships between GEP and  $T_{\text{accl}}$  were described by

$$GEP = \frac{a}{1 + e^{-b(T_{\text{accl}} - c)}}. \quad (6)$$

Equation (6) was fitted to the data using nonlinear least squares regression and the Gauss-Newton method in Systat10.2. Here  $a$  is maximum GEP at infinite  $T_{\text{accl}}$ ,  $b$  is the maximum rate of change in GEP, and  $c$  is the temperature at which GEP is 50% of the maximum.

## 2.5. Uncertainty in Carbon Budget Calculations

[22] Potential errors in carbon budget calculations originate from random and systematic errors associated with EC flux measurements [Moncrieff *et al.*, 1996]. Random errors include instrument measurement errors and those associated with varying flux footprint size and surface heterogeneity [Moncrieff *et al.*, 1996; Aurela *et al.*, 2002]. Uncertainty due to random errors ( $E_R$ ) was determined for each site in each growing season from the difference between the measured and modeled half-hourly NEE fluxes, following the method used by Aurela *et al.* [2002]:

$$E_R = \sqrt{\sum_{i=1}^n \frac{(NEE_{\text{obs}} - NEE_{\text{mod}})^2}{(n-1)n}}, \quad (7)$$

in which  $n$  is the number of half-hourly NEE measurements during the corresponding growing season.

[23] The systematic error in carbon budgets particularly results from the choice of the  $u_*$  threshold and resultant data screening for low turbulence [Goulden *et al.*, 1996; Aurela *et al.*, 2002]. The sensitivity of growing season carbon budgets to different  $u_*$  thresholds (0.10 and 0.20 m s<sup>-1</sup>) was assessed to estimate uncertainty in the carbon budgets due to systematic errors ( $E_S$ ).  $E_S$  was estimated as the average difference in integrated growing season NEE calculated with  $u_*$  thresholds of 0.10 and 0.20 m s<sup>-1</sup> relative to that calculated initially ( $u_*$  threshold = 0.15 m s<sup>-1</sup>). Total uncertainty ( $E_T$ ) was calculated using

$$E_T = \sqrt{E_R^2 + E_S^2}. \quad (8)$$

## 3. Results

### 3.1. Peat Core Nutrient Content, Age Measurements, and Rates of Recent Carbon Accumulation

[24] The carbon content of peat did not vary with depth, and the average ( $\pm$ SD) carbon content was equal at the two sites (extreme-rich fen: % C = 47.9  $\pm$  1.4,  $n = 14$ ; poor fen: % C = 46.9  $\pm$  1.3,  $n = 16$ ). The content of other macro-nutrients in the peat core from the extreme-rich fen was higher than that of the poor fen peat core for all nutrients measured except potassium, which was approximately equal at both sites (Table 1). In addition, peat density was almost twice as high at the extreme-rich fen than at the poor fen.

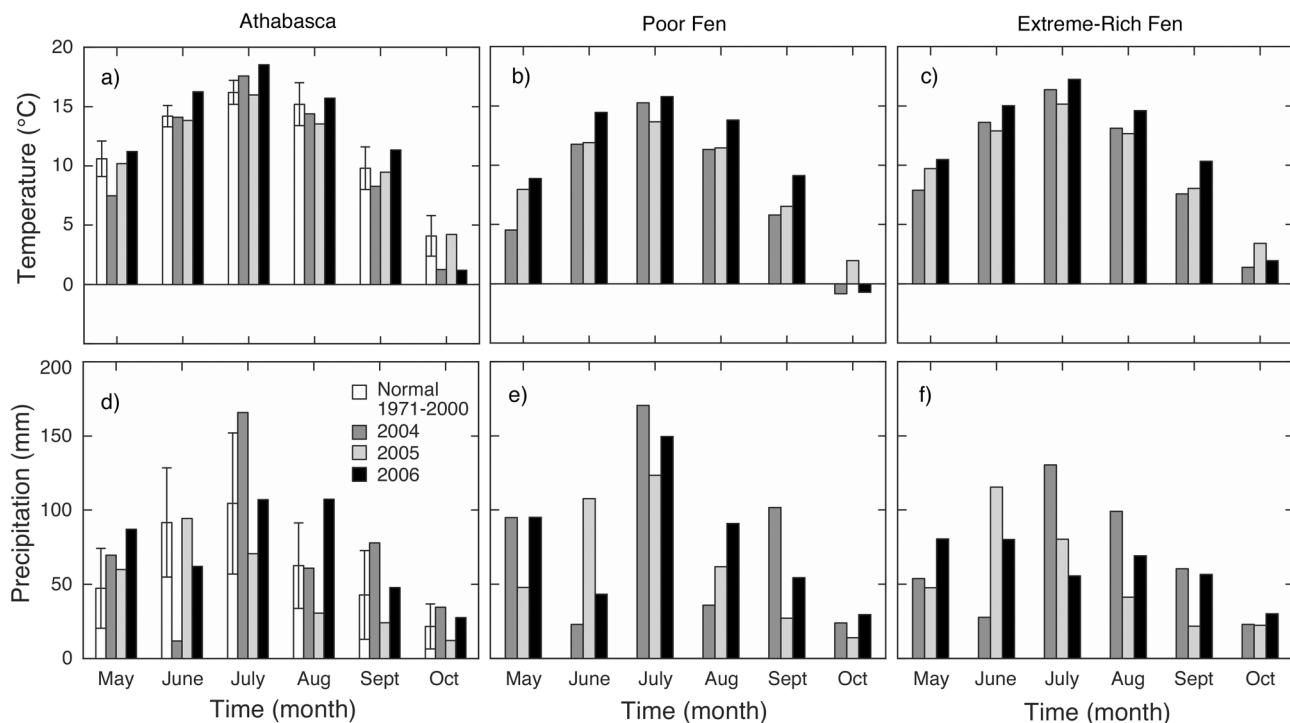
[25] Fits of equation (1) to the relationship between peat age and cumulative carbon stock produced values for (1) the rate of carbon addition to the peat acrotelm ( $p$ ) of 160.2 (poor fen) and 77.8 (rich fen) g C m<sup>-2</sup> yr<sup>-1</sup> and (2) the peat decay rate coefficient ( $k$ ) of 0.024 (poor fen) and 0.015 (rich fen) yr<sup>-1</sup> (Table 2). The balance between carbon addition to ( $p$ ), and total loss of carbon from ( $kx$ ), the top dated portions of the short peat cores was 36.2 (poor fen) and 20.6 (rich fen) g C m<sup>-2</sup> yr<sup>-1</sup> (Table 2). Thus the recent rate of carbon accumulation in the peat cores was higher at the poor fen than at the extreme-rich fen.

[26] The penultimate basal peat sample from the deep core at the rich fen site had an uncalibrated conventional radiocarbon date of 3940  $\pm$  60 years before present. The cumu-

**Table 2.** Age and Depth of the Oldest Dated Segments for Short Peat Cores Based on <sup>210</sup>Pb Dating<sup>a</sup>

Characteristic	Poor Fen	Extreme-Rich Fen
Age of oldest dated segment (years)	62.1	88.5
Depth of oldest dated segment (cm)	29.9	11.4
Productivity, $p$ (g C m <sup>-2</sup> yr <sup>-1</sup> )	160.2	77.8
Decay rate, $k$ (yr <sup>-1</sup> )	0.024	0.015
$n$	7	5
$r^2$	0.99	0.99
Input-output for acrotelm, $p - kx$ (g C m <sup>-2</sup> yr <sup>-1</sup> )	36.2	20.6

<sup>a</sup>Also shown are calculations of terms ( $p$ ,  $k$ ) in the *Clymo* [1984] model of peat growth (equation (1)). The sample size ( $n$ ) refers to the number of different peat segments that were dated and used in the nonlinear regression fit to equation (1). The  $r^2$  value shows the proportion of variation in the data that was explained by the regression.



**Figure 1.** Seasonal variation in (a–c) monthly average temperatures and (d–f) monthly total precipitation, measured at Athabasca, Alberta [Environment Canada, 2010], the poor fen site, and the extreme-rich fen site during the growing season (May–October) in 2004, 2005, and 2006. The 30 year normal (1971–2000) measured at Athabasca, Alberta, is given as the average  $\pm$  standard deviation for each month (Figures 1a and 1d).

lative amount of carbon in the deep peat core at the penultimate basal depth segment (180 cm) was  $92,040 \text{ g C m}^{-2}$ . The apparent long-term average rate of net carbon sequestration in the extreme-rich fen calculated from these measurements was:  $23 \text{ g C m}^{-2} \text{ yr}^{-1}$ .

### 3.2. Comparison of Environmental Conditions

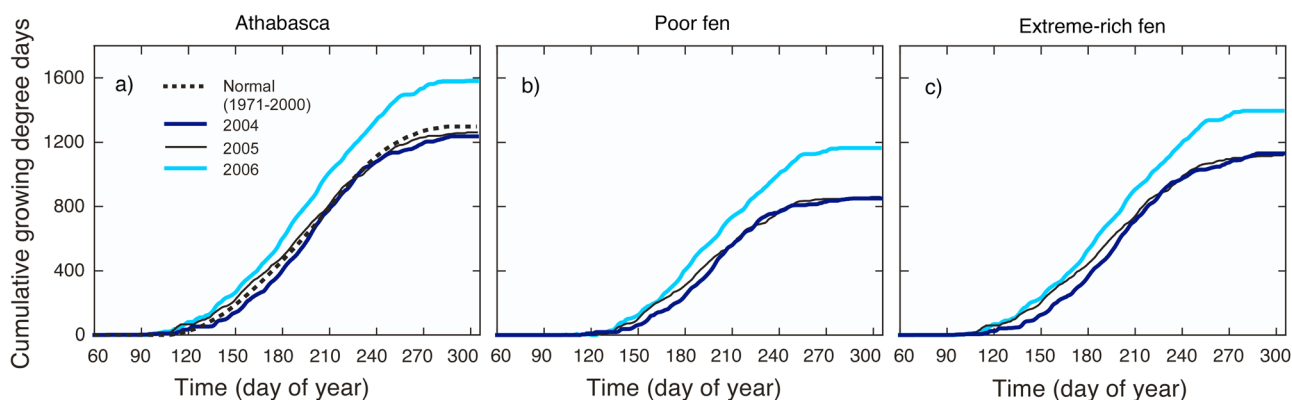
#### 3.2.1. Temperature

[27] Monthly average air temperature variation among years was compared at both study sites and at the Environment Canada climate station in nearby Athabasca, AB, in order to provide perspective on conditions during the study period 2004–2006 relative to the long-term (1971–2000) climate normal for the area. Monthly average temperature in 2005 at Athabasca was within one standard deviation (SD) of the climate normal for all months of the growing season (May–October) (Figure 1a). By contrast, monthly average temperature in 2006 at Athabasca was greater than one SD above the normal for two months (June and July) and was only cooler than normal in October (more than one SD below the long-term average). Temperatures at Athabasca in 2004 were cooler than normal in May and October and only slightly warmer than normal in July (Figure 1a). Averaged over the six growing season months, the temperature in 2005 ( $11.2^\circ\text{C}$ ) was near the 30 year average ( $\pm\text{SD}$ ) ( $11.0 \pm 0.7^\circ\text{C}$ ), 2006 was warmer than normal ( $12.4^\circ\text{C}$ ), and 2004 was cooler than normal ( $10.5^\circ\text{C}$ ). The pattern of change in cumulative growing degree days (above a threshold base of  $5^\circ\text{C}$ ) at Athabasca illustrated that 2004 and 2005 had similar season totals of growing degree days that were slightly

below normal, but that 2005 followed an average or typical pattern of warming in the early growing season, while the cool temperatures in May 2004 delayed accumulation of growing degree days at the start of the 2004 growing season (Figure 2a). The consistently warmer conditions in 2006 resulted in a faster accumulation and a higher season total growing degree days (by approximately 400) compared to 2004 and 2005.

[28] The patterns of variation in temperature among 2004–2006 at Athabasca were consistent with measurements made at the two study sites. At both the poor fen and extreme-rich fen, the early growing season temperature in 2005 and 2006 was higher than in 2004 (Figures 1b and 1c). For example, average air temperatures in May were  $1.8$  to  $4.3^\circ\text{C}$  higher in 2005 and 2006 than in 2004 at both study sites (Figures 1b and 1c). The warmer temperatures in 2006 were sustained throughout the growing season with higher temperatures in 2006 than in other years in all months except October, which was warmest in 2005. Temperatures were low from June to August in 2005 relative to the other two years, particularly at the extreme-rich fen site. Overall, the average growing season temperature at both sites was highest in 2006 ( $10.2^\circ\text{C}$ , poor fen;  $11.6^\circ\text{C}$ , extreme-rich fen), intermediate in 2005 ( $8.9^\circ\text{C}$ , poor fen;  $10.3^\circ\text{C}$ , extreme-rich fen) and coolest in 2004 ( $8.0^\circ\text{C}$ , poor fen;  $10.0^\circ\text{C}$ , extreme-rich fen). The pattern of variation among years in cumulative growing degree days at the two study sites was very similar to that observed in Athabasca (Figure 2). Most notable were the similar seasonal total growing degree days in 2004 and 2005, despite the warmer early season condi-





**Figure 2.** Comparison of cumulative growing degree days (1 March to 31 October) in 2004, 2005, and 2006 at (a) Athabasca, Alberta, (b) the poor fen, and (c) the extreme-rich fen. For Athabasca, cumulative growing degree days for each year and the 30 year normal (1971–2000) were calculated using daily average temperatures measured by *Environment Canada* [2010].

tions in 2005, and the consistently warmer conditions observed throughout the growing season in 2006 (Figure 2). Monthly average temperatures and cumulative growing degree days were lower at the poor fen than at the extreme-rich fen, which was consistent with the more northern location of the poor fen.

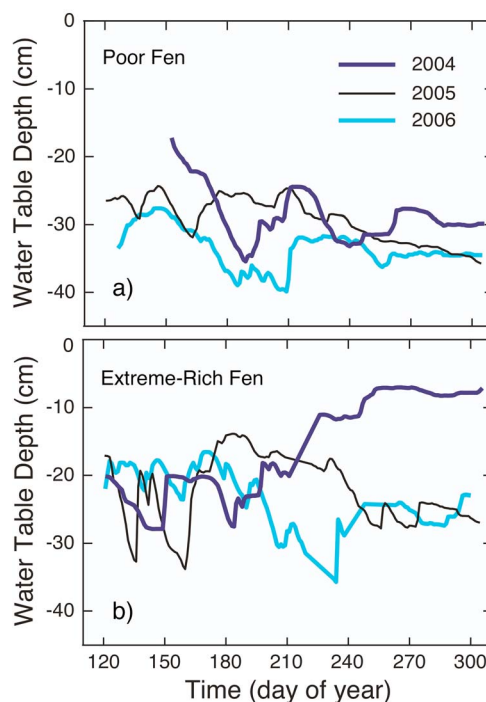
### 3.2.2. Precipitation

[29] The total precipitation received during the growing season months at Athabasca in the study period (421, 292 and 439 mm in 2004, 2005 and 2006, respectively) was within one SD of the 30 year average ( $\pm$ SD) ( $370 \pm 81$  mm). However, there was large variation in the seasonal distribution of the precipitation in the different years. In 2004 precipitation during June at Athabasca was only about 20% of the long-term average, but this was partially compensated for by the 60% above-normal precipitation received in July, while all remaining months in 2004 had average or above average precipitation (Figure 1d). In 2005 precipitation was within one SD of the long-term average in all months except August, when precipitation was only about 50% of normal values. During 2006 the monthly total precipitation at Athabasca was within one SD of the long-term average in all months except May and August, when it was greater than one SD above normal values (Figure 1d). In general, broadly similar patterns of precipitation were recorded at the two study sites as was observed in Athabasca (Figures 1d–1f).

### 3.2.3. Water Table Depth

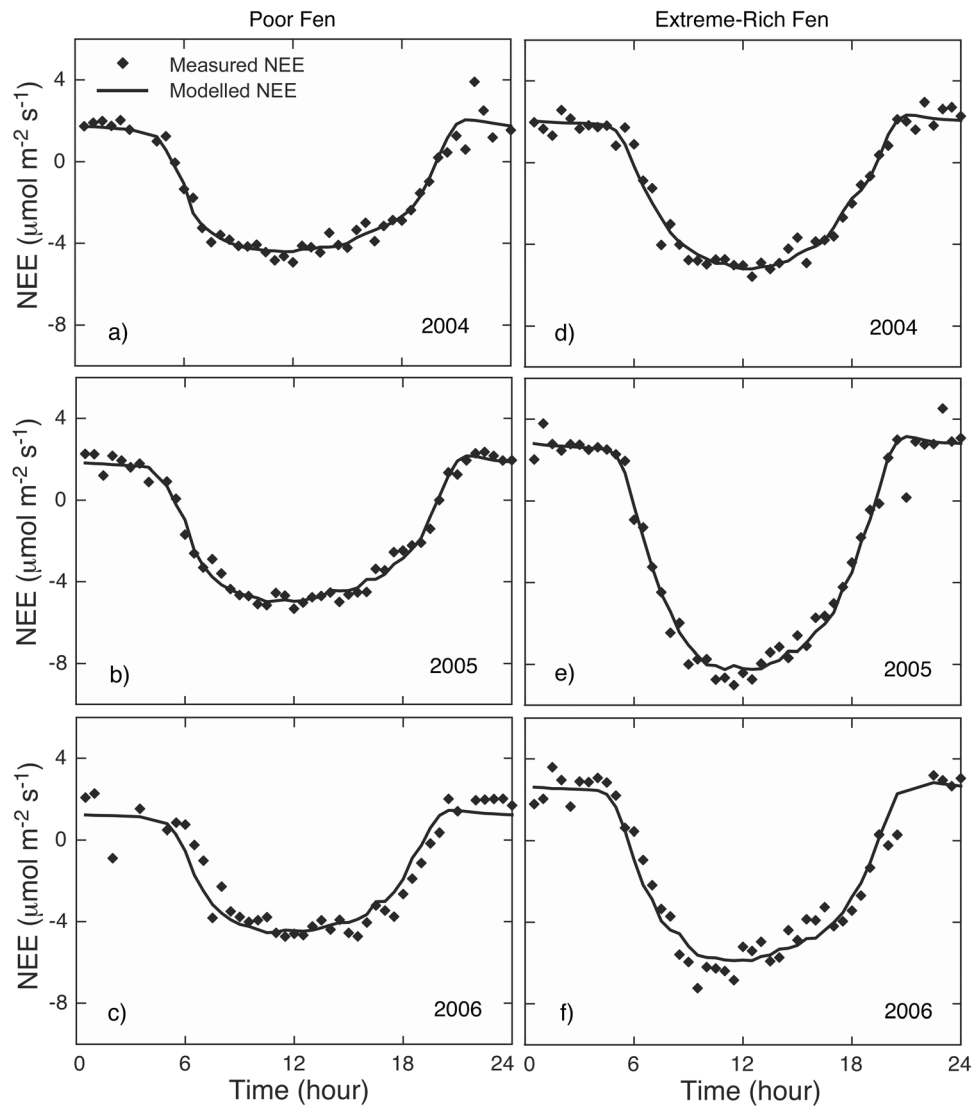
[30] The variation in temperature and precipitation observed among years had important effects on water table depths recorded at the extreme-rich fen (Figure 3b). The close-to-normal temperatures and precipitation recorded during 2005 resulted in relatively minor fluctuations in the water table depth in this year, except for relatively short-term drops recorded in mid-May (near day 135) and early June (near day 160) (Figure 3b). The water table depth in 2004 was quite similar to that recorded in 2005 during the first half of the growing season (until approximately day 210), but higher precipitation in the months of August and September in 2004 compared to 2005 (Figure 1f) resulted in a divergence after day 210 with the water table moving higher in 2004 and lower in 2005 (Figure 3b). A difference of approximately 20 cm was apparent in the water

table depth between 2004 and 2005 during most of September and October (days 244–305). The water table depth in 2006 was similar to, or higher than, that recorded in the other study years through May and June. However, during the important middle of the growing season in July and August of 2006, the water table was at times 10–15 cm below the level recorded in 2005 (Figure 3b). Water table depths returned to very similar levels in September and October of 2005 and 2006. The relatively low water table



**Figure 3.** Comparison of growing season daily average water table depths among study years (2004, 2005, and 2006) at (a) the poor fen site and (b) the extreme-rich fen site. Water table depth was measured relative to a fixed height on the water well and expressed relative to the average hummock height measured in 2004.





**Figure 4.** Mean diurnal trends in measured net ecosystem exchange (NEE;  $u_* \geq 0.15 \text{ m s}^{-1}$ ) at the peak of the growing season in 2004, 2005, and 2006 at (a–c) the poor fen and (d–f) the extreme-rich fen. Points represent measured NEE data that were bin-averaged by time of day. Solid lines represent modeled NEE calculated using equation (2) and the model parameters determined by fitting equation (2) to measured NEE data as described in section 2.4. Peak season periods include days of year 189–207 (Figure 4a), 190–208 (Figure 4b), 207–221 (Figure 4c), 209–226 (Figure 4d), 209–222 (Figure 4e), and 195–206 (Figure 4f).

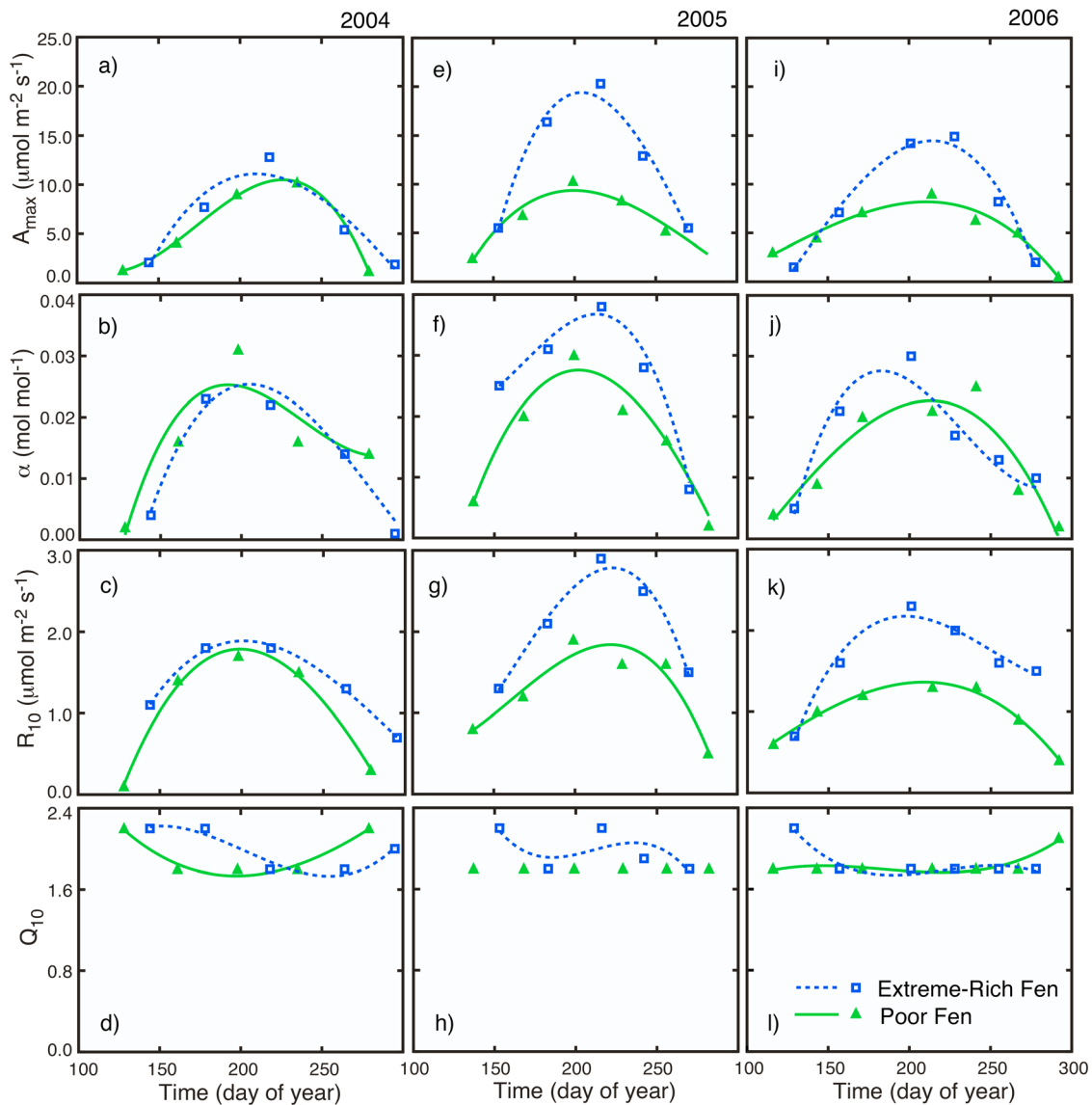
that developed in July and August 2006 was associated with the generally warm temperatures in 2006 and it occurred despite the relatively high precipitation in August 2006 (Figure 1).

[31] Water table depth varied much less at the poor fen than at the extreme-rich fen (Figure 3). In addition, as noted above, we suggest that the peat was floating at the poor fen site, as the surface was very unstable, the peat density was low (Table 1), and it was difficult to extract peat cores from this site because of the loose nature of the peat. Therefore, it is possible that the peat surface height varied in association with changes in water level, so that there was little or no movement of the water table relative to the peat surface at the poor fen site, although this was not confirmed with measurements of peat surface movement. This was in con-

trast to the situation at the extreme-rich fen, where peat density was very high (Table 1) and it was unlikely that there was any significant peat surface movement. As a consequence, the poor fen did not experience any significant dry period, despite relatively large variation in precipitation inputs recorded during the study period (Figure 1e).

### 3.3. Eddy Covariance Measurements and Model Parameters

[32] The mean diurnal pattern of measured NEE at peak season was very similar in all study years at the poor fen site (Figure 4). As a consequence, fitted parameters of equation (2) ( $A_{\max}$ ,  $\alpha$  and  $R_{10}$ ) had similar maximum values and showed very similar temporal variation during the growing season in all study years (Figure 5). By contrast,

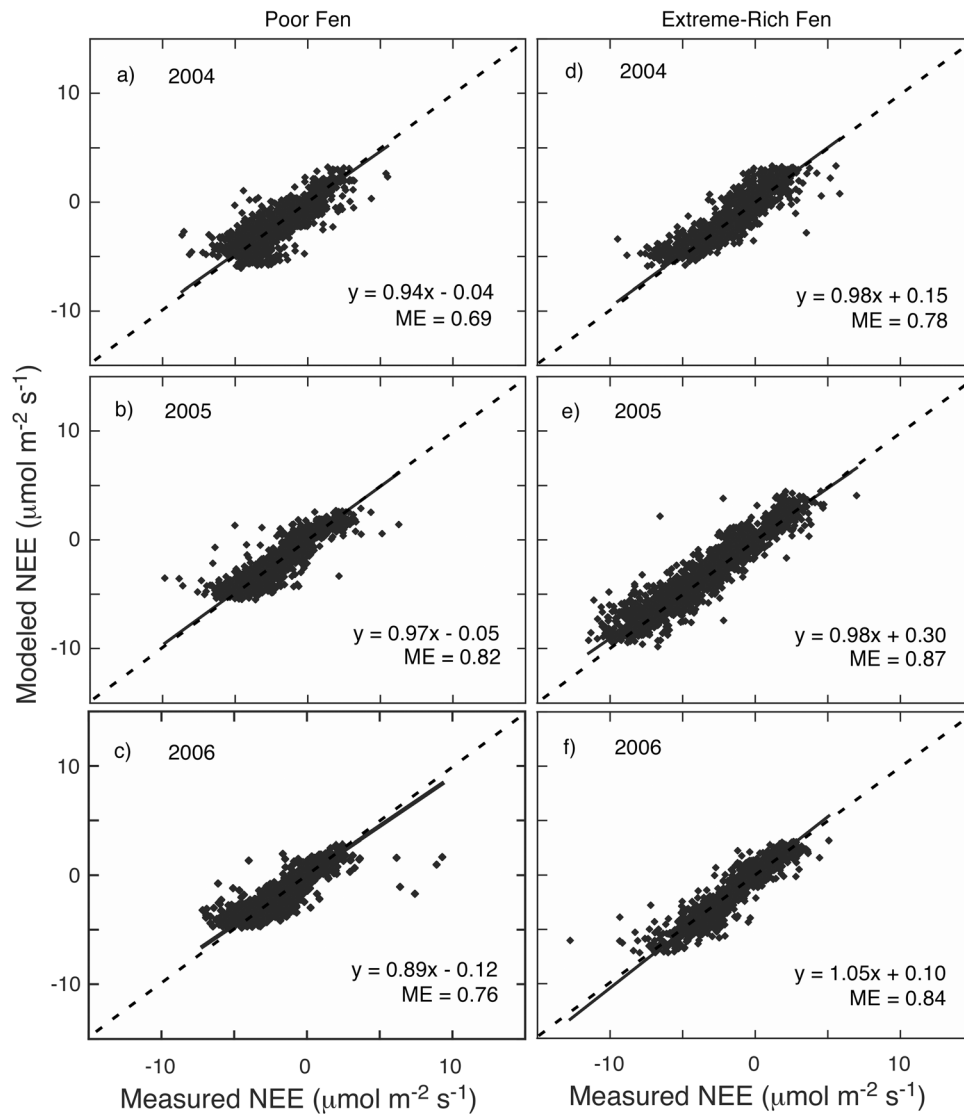


**Figure 5.** Seasonal trends in fitted parameters of equation (2) ( $A_{\max}$ ,  $\alpha$ ,  $R_{10}$ , and  $Q_{10}$ ) for the growing season in (a–d) 2004, (e–h) 2005, and (i–l) 2006 at the poor fen and extreme-rich fen sites. Points represent model parameter estimates for each measurement campaign period, derived by fitting equation (2) to measured NEE data. Lines represent third-order polynomial regressions fitted to the model parameter estimates as a function of time (day of year). There was no regression fit to  $Q_{10}$  values measured at the poor fen in 2005 (Figure 5h), as they did not vary throughout the growing season.

the mean diurnal pattern of measured NEE at peak season varied considerably among study years at the extreme-rich fen site (Figure 4). The greatest maximum NEE at peak season occurred in 2005, when it reached  $-8 \mu\text{mol m}^{-2} \text{s}^{-1}$ , almost twice the maximum observed in 2004 (approximately  $-5 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). Maximum NEE was intermediate in 2006 (near  $-6 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). Peak season NEE was less negative (i.e., lower CO<sub>2</sub> uptake) at the poor fen than at the extreme-rich fen in 2005 and 2006, but was similar between sites in 2004. The maximum values of the  $A_{\max}$ ,  $\alpha$  and  $R_{10}$  were highest at the extreme-rich fen in 2005 and lowest in 2004, with 2006 values being intermediate (Figure 5). There was no obvious pattern of variation in  $Q_{10}$  between the sites or among years. There was a strong linear relationship between  $R_{10}$  and  $A_{\max}$  at both the poor fen ( $R_{10} =$

$0.14A_{\max} + 0.29$ ,  $r^2 = 0.67$ ,  $p < 0.0001$ ) and the extreme-rich fen ( $R_{10} = 0.09A_{\max} + 0.82$ ,  $r^2 = 0.78$ ,  $p < 0.0001$ ). These relationships were not significantly different between the sites (slope comparison:  $|t| = 1.90 < t_{0.05(2),30} = 2.04$ ; intercept comparison:  $|t| = 1.90 < t_{0.05(2),33} = 2.04$ ).

[33] The fit of equation (2) to NEE data was typically strong, with  $r^2 \geq 0.72$  for 85% of the fitted relationships. For the remaining relationships,  $r^2$  was between 0.34 and 0.69. These lower  $r^2$  values occurred early and late in the growing season when there was lower diurnal variation in temperature and PPFD, and in NEE as a result. The polynomial regression relationships between model parameters ( $A_{\max}$ ,  $\alpha$ ,  $R_{10}$  and  $Q_{10}$ ) and time (day of year) were also strong, with  $r^2$  values in the following ranges:  $A_{\max}$ , 0.91 to  $>0.99$ ;  $\alpha$ , 0.83 to 0.98;  $R_{10}$ , 0.92 to  $>0.99$ ;  $Q_{10}$ , 0.54



**Figure 6.** Relationships between modeled NEE and measured NEE in the growing seasons of 2004, 2005, and 2006 at (a–c) the poor fen and (d–f) the extreme-rich fen. Points represent half-hourly values, and solid lines represent model II (geometric mean) linear regression fits. Dashed lines are the 1:1 line. Modeled NEE values were derived using equation (2) with measurements of PPFD and temperature and parameter estimates determined using the polynomial regression relationships presented in Figure 5.

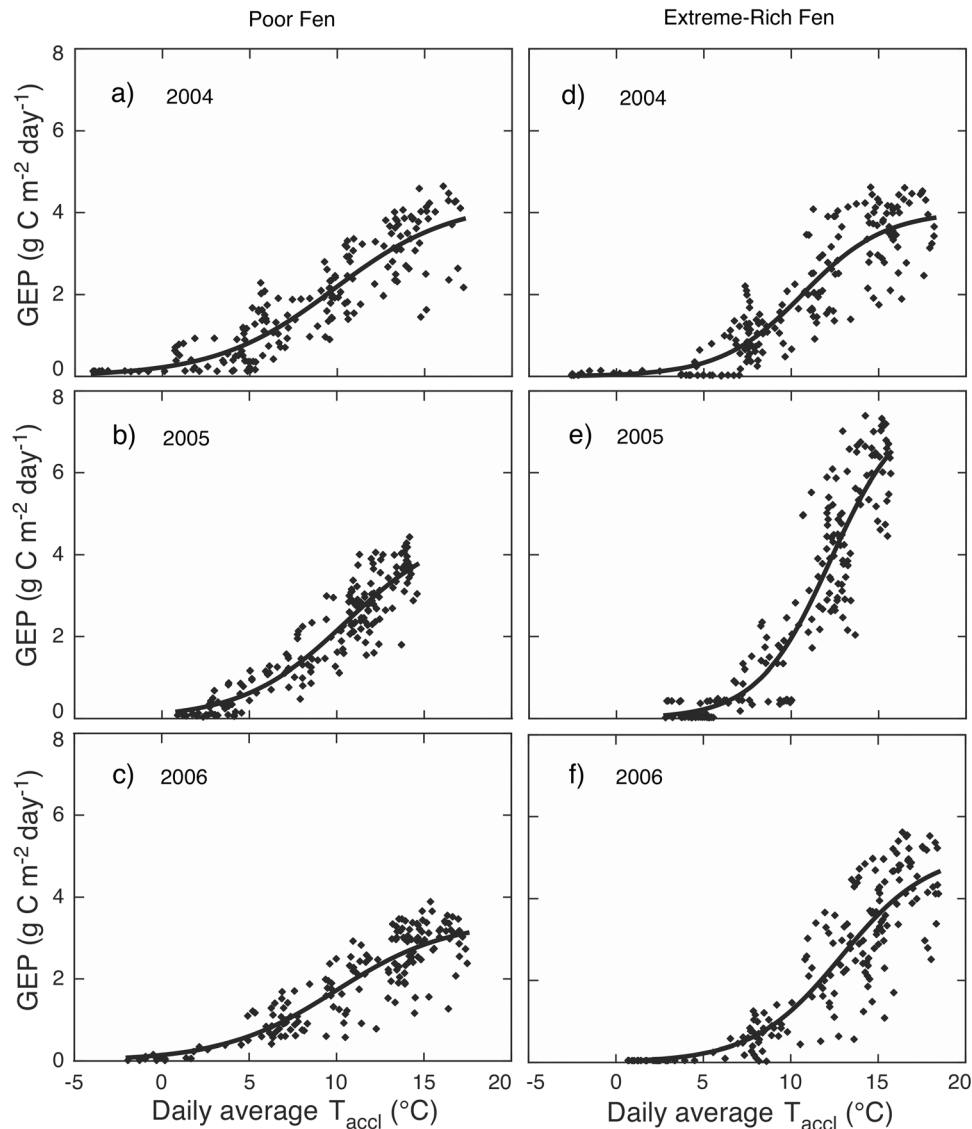
to 0.95 (Figure 5). Modeled NEE, determined using equation (2) with parameters estimated using the polynomial regression relationships (Figure 5) and measurements of temperature and PPFD, agreed well with measured NEE (Figure 6).

[34] The pattern of change in daily integrated GEP with  $T_{\text{accl}}$  at the poor fen was similar among all study years, and there was relatively modest variation in calculated maximum GEP ( $a = 4.3, 4.7$  and  $3.4$  in 2004, 2005 and 2006, respectively) (Figure 7). By contrast, the relationship varied considerably among study years at the extreme-rich fen. In particular, in 2005 GEP increased much more rapidly as temperature warmed, and the calculated maximum GEP was much higher than in the other study years ( $a = 4.03, 7.72$  and  $5.17$  g C m<sup>-2</sup> day<sup>-1</sup> in 2004, 2005 and 2006, respectively). In all study years, GEP initiated at lower temperatures at the poor fen than at the extreme-rich fen,

but responded more slowly to changes in temperature (Figure 7). The rate of change in daily integrated GEP with  $T_{\text{accl}}$  was consistently greater at the extreme-rich fen ( $b = 0.40$  to  $0.48$ ) than at the poor fen ( $b = 0.30$  to  $0.34$ ). The temperature at which GEP was 50% of maximum, was consistently lower for the poor fen ( $c = 9.8$  to  $10.5$ ) than at the extreme-rich fen ( $c = 10.7$  to  $12.0$ ).

### 3.4. Growing Season and Monthly Carbon Budgets

[35] Measured NEE data were used in carbon budget calculations at the poor fen for 19.3%, 22.6% and 18.5% of half-hour periods in 2004, 2005, and 2006, respectively, and modeled NEE data were used for the remaining half-hour periods. At the extreme-rich fen, measured data were used for 19.9%, 17.9% and 16.3% of half-hour periods in 2004, 2005, and 2006, respectively. Uncertainty estimates for integrated growing season NEE were expressed as a percentage relative



**Figure 7.** Response of daily integrated gross photosynthesis ( $\text{GEP} = -\text{GPP}$ ) to changes in daily average acclimation temperature ( $T_{\text{accl}}$ ) during the growing season in 2004, 2005, and 2006 at (a–c) the poor fen site and (d–f) the extreme-rich fen site. Points represent measured values and solid lines represent equation (4), which was fit to the measured data.  $T_{\text{accl}}$  accounts for the lagged response of GEP due to the acclimation of vegetation to changes in air temperature.

to growing season NEE determined using the  $u_*$  threshold of  $0.15 \text{ m s}^{-1}$  (Table 3). Estimates of total uncertainty were used to assign error bars to integrated monthly and growing season NEE, TER and GPP (Figures 8 and 9), in order to assess differences in fluxes between sites and among years.

[36] The integrated growing season (May–October) values for NEE, TER and GPP were very similar among study years at the poor fen site (Figure 8). Temporal variation in the monthly integrated carbon budget values was also quite similar among study years at the poor fen (Figure 9). By contrast, integrated growing season NEE was much more negative (i.e., higher CO<sub>2</sub> uptake) in 2005 at the extreme-rich fen than in 2004 and 2006, while the latter two years had very similar NEE values (Figure 8). This enhanced net C uptake at the extreme-rich fen was primarily a result of higher-magnitude GPP during June to August in 2005 than

during that period in 2004 and 2006, which resulted in higher-magnitude total GPP during the growing season than in the other two years (Figures 8 and 9). Monthly values of TER were similar among study years, so this greater GPP during the summer months resulted in much greater NEE during June–August of 2005 than in 2004 and 2006. In addition, NEE at the extreme-rich fen was approximately zero during May and in September and October of 2005, while a relatively large net loss of C occurred in September and October of 2006. Although growing season GPP was less negative in 2006 than in 2005, growing season TER was similar in the two years, which resulted in less net uptake of CO<sub>2</sub> during the growing season 2006 than in 2005.

[37] Monthly integrated GPP exceeded TER at the poor fen in all months during the growing season in all study

**Table 3.** Total Uncertainty ( $E_T$ ) in Estimates of Integrated Growing Season NEE due to Random Errors ( $E_R$ ) and Systematic Errors ( $E_S$ ) in Eddy Covariance Flux Measurements<sup>a</sup>

Site	Year	May–October NEE (g C m <sup>-2</sup> period <sup>-1</sup> )			Uncertainty (%)		
		$u_* > 0.10$	$u_* > 0.15$	$u_* > 0.20$	$E_S$	$E_R$	$E_T$
Poor fen	2004	-110	-113	-120	±6.0	±1.9	±6.3
	2005	-110	-110	-101	±3.7	±1.4	±4.0
	2006	-111	-101	-113	±3.3	±1.8	±3.7
Extreme-rich fen	2004	-35	-51	-30	±17.3	±3.3	±17.7
	2005	-154	-149	-146	±4.0	±1.2	±4.1
	2006	-42	-33	-37	±16.7	±2.4	±16.9

<sup>a</sup> $E_S$  was estimated as the average difference in integrated growing season NEE determined with  $u_*$  thresholds of 0.10 and 0.20 m s<sup>-1</sup> relative to that determined with a  $u_*$  threshold of 0.15 m s<sup>-1</sup>.  $E_R$  was calculated from the difference between measured and modeled half-hourly NEE using equation (7).  $E_T$  was calculated using equation (8).

years, so that net C uptake occurred in all months at this site (Figure 9). At the extreme-rich fen, GPP was considerably greater than TER only during June–August of all study years, so that the period of net C uptake was much shorter than at the poor fen. At both sites, the integrated growing season GEP exceeded TER in all three years, so that both sites were net C sinks during the growing season (Figure 8).

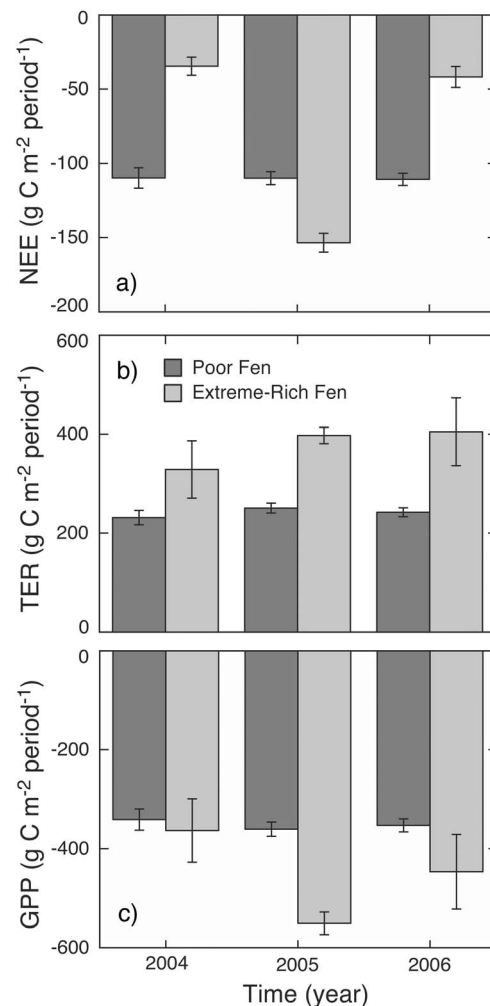
## 4. Discussion

### 4.1. Environmental Responses and Contrasting Plant Functional Types

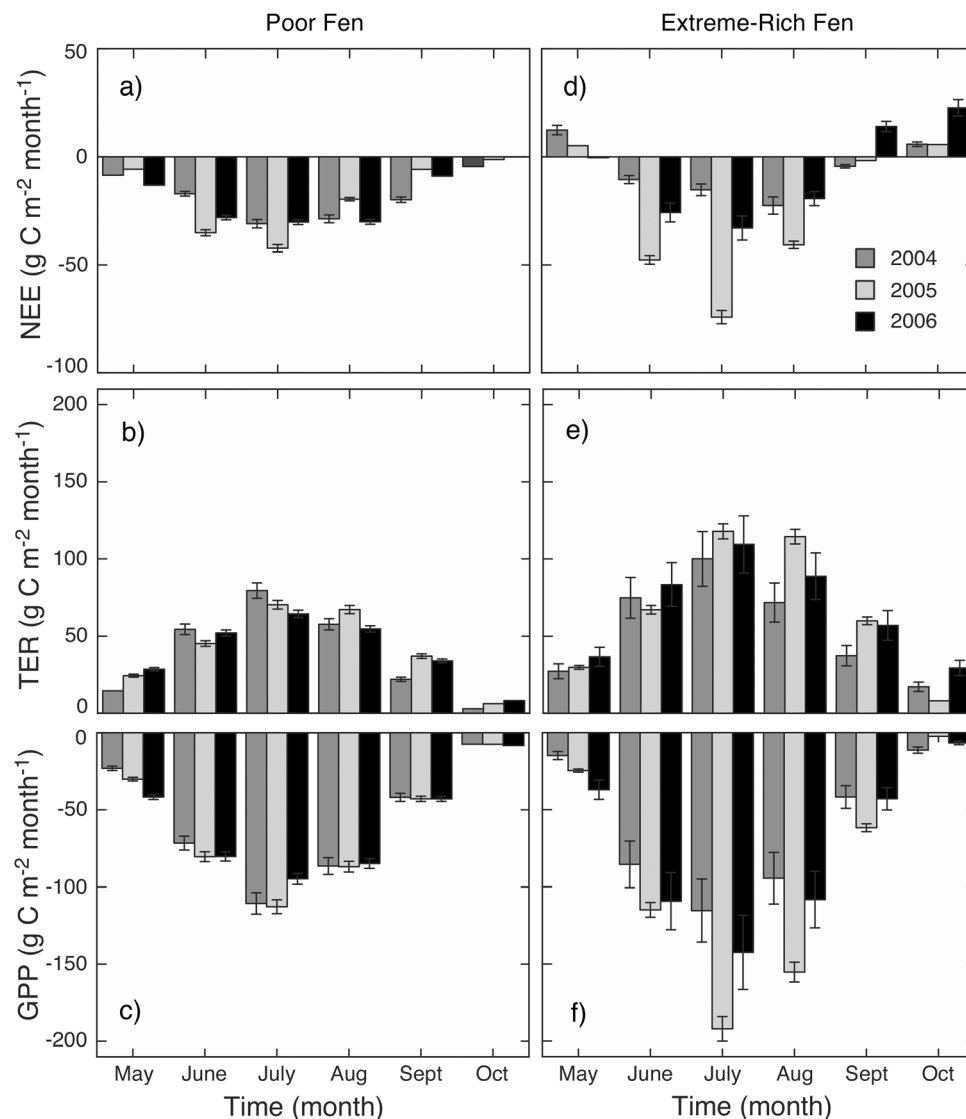
[38] We observed distinct differences between the poor fen and extreme-rich fen sites for their responses of ecosystem carbon dioxide exchange to interannual variation in temperature and water table conditions. The differences between sites resulted from several factors including (1) contrasting plant functional types, (2) environmental differences, particularly the importance of water table fluctuations at the extreme-rich fen, and (3) interactions between temperature and water table depth for effects on ecosystem CO<sub>2</sub> exchange. Each of these three factors will be discussed further in the paragraphs below.

[39] The poor fen was dominated by *Sphagnum* spp., while the extreme-rich fen was dominated by the deciduous perennial sedge *C. lasiocarpa* and brown mosses. The poor fen had a longer period of net CO<sub>2</sub> uptake, with net uptake in at least five months (May through September), while the rich fen was normally only a net sink during three months of the year (June through August). While significant seasonal variation in photosynthetic and respiratory capacity does occur in *Sphagnum* (Figure 5) [Williams and Flanagan, 1998; Zarter et al., 2006], these mosses do not need to build completely new leaf tissue at the start of the growing season and complete senescence of deciduous tissue does not occur at the end of the growing season. Because they lack roots, *Sphagnum* can also begin to photosynthesize almost immediately following snowmelt, when only the surface of the moss has thawed [Bubier et al., 1998; Lafleur et al., 2003; Moore et al., 2006]. Therefore, *Sphagnum* mosses and other evergreen vascular plants at the poor fen can remain photosynthetically active for a longer period of time within the growing season than the deciduous vegetation can at the extreme-rich fen. Also, photosynthetic

and respiratory capacities at the poor fen may vary less among years with different environmental conditions because there is not completely new leaf tissue development at the beginning of each growing season. Whereas, at the extreme-rich fen the growth of new leaf tissue and, therefore, the capacity for photosynthesis and respiration may be influenced more strongly by environmental variation among years. The growth of new leaf tissue, particularly in *Carex lasiocarpa*, at the extreme-rich fen appeared to respond very quickly to variation in spring and early summer temperatures. The differences in dominant plant functional types between the sites, therefore, appeared to control the magnitude of response to environmental change that was possible.



**Figure 8.** Comparisons of the integrated growing season (1 May to 31 October) values of (a) NEE, (b) total ecosystem respiration (TER), and (c) gross photosynthesis (GPP) in 2004, 2005, and 2006 at the poor fen and extreme-rich fen study sites. Cumulative growing season values were determined using a combination of measured and modeled half-hourly flux data. Modeled NEE values were derived using equation (2) with measurements of PPFD and temperature and parameter estimates determined using the polynomial regression relationships presented in Figure 5. Error bars represent total uncertainty estimates for the NEE model.



**Figure 9.** Comparisons of the integrated monthly values of (a, d) NEE, (b, e) TER, and (c, f) GPP for months during the growing season in 2004, 2005 and 2006 at the poor fen and extreme-rich fen study sites. Integrated monthly values were determined using a combination of measured and modeled half-hourly flux data. Modeled NEE values were derived using equation (2) with measurements of PPFD and temperature and parameter estimates determined using the polynomial regression relationships presented in Figure 5. Error bars represent total uncertainty estimates for the NEE model.

[40] The two study sites also differed significantly in peat type and water table fluctuations. The extreme-rich fen had high peat density (Table 1) and relatively large fluctuation in water table depth (Figure 3). The poor fen had low peat density, an unstable surface, and we believe that the peat was likely not anchored to the bottom mineral soil sediments, as it was at the extreme-rich fen. Variation in the water table at the poor fen, therefore, may have been associated with similar changes in peat surface height, so that there was little or no movement of the water table relative to the peat surface. In this case, “soil” moisture availability would not vary significantly at the poor fen. By contrast, change in water table depth likely caused significant changes in “soil” moisture availability at the extreme-rich fen. Previous studies have shown that change in water table depth has little influence on peatland ecosystem CO<sub>2</sub> exchange if the water table variation

is not accompanied by significant change in soil moisture content [Parmentier *et al.*, 2009].

[41] Warmer spring temperatures when accompanied by sufficient water availability throughout the period of leaf growth (as occurred in 2005) resulted in the highest ecosystem photosynthetic capacity ( $A_{\max}$ ) at the extreme-rich fen, likely primarily associated with high leaf area index, but also possibly enhanced photosynthetic rates per unit leaf area. In contrast, the cool spring temperatures in 2004 appeared to inhibit  $A_{\max}$  and leaf area development at the extreme-rich fen. Aurela *et al.* [2004] also found a very strong relationship between warmer spring temperatures and increased annual CO<sub>2</sub> uptake at a subarctic fen in northern Finland. In a Canadian arctic tundra site, Lafleur and Humphreys [2008] observed higher  $A_{\max}$  in spring and mid-summer associated with warmer spring temperatures. How-



ever, reduced water availability (lower water table) from the beginning of July onward in 2006 at the extreme-rich fen constrained development of high ecosystem photosynthetic capacity relative to 2005, despite the warm spring and summer temperatures in 2006. From the start of July until mid-August, photosynthetic capacity continued to increase in 2005, while in 2006 during this period photosynthetic capacity leveled off (Figures 5e and 5i). Prior to the decline in water table, conditions for growth were favorable in 2006, with warmer air and soil temperatures and a higher water table than in 2005, suggesting that reduced water availability was the primary factor contributing to the difference in peak photosynthetic capacity between 2005 and 2006. Warm temperatures in 2006, and the associated increase in evaporative demand, may have exacerbated the effect of declining water table on maximal leaf development in July and August. This demonstrates the important interactions that occur between temperature and water availability in peatland ecosystems [Griffis *et al.*, 2000; Bubier *et al.*, 2003; Aurela *et al.*, 2007]. Previous studies have shown that warm and dry summer conditions can reduce net CO<sub>2</sub> uptake in peatlands by limiting photosynthesis and/or increasing respiration [Alm *et al.*, 1999; Arneth *et al.*, 2002; Bubier *et al.*, 2003; Aurela *et al.*, 2007; Cai *et al.*, 2010], and by promoting earlier leaf senescence in deciduous plants [Bellisario *et al.*, 1998; Bubier *et al.*, 2003]. The effects of moisture stress on photosynthesis and respiration have been observed in both sedge-dominated [Griffis *et al.*, 2000; Aurela *et al.*, 2007; Sonnentag *et al.*, 2010] and *Sphagnum*-dominated peatlands [Shurpali *et al.*, 1995; Silvola *et al.*, 1996; Alm *et al.*, 1999]. The different responses to water table variation at our two study sites was possibly due to a floating peat surface at the poor fen, and so the poor fen may not have been exposed to significant reductions in “soil” moisture as occurred at the extreme-rich fen.

#### 4.2. Net Ecosystem CO<sub>2</sub> Exchange

[42] The rates of growing season cumulative NEE at the poor fen were very similar among the three study years with an average ( $\pm$ SD) of  $-110.1 \pm 0.5$  g C m<sup>-2</sup> period<sup>-1</sup>. By contrast, the growing season cumulative NEE at the extreme-rich fen varied substantially among years ( $-34.5$ ,  $-153.5$ , and  $-41.8$  g C m<sup>-2</sup> period<sup>-1</sup> in 2004, 2005, and 2006, respectively) and the extreme-rich fen was, on average, a lower net sink for CO<sub>2</sub> than the poor fen. Consistent with the eddy covariance measurements, analysis of the <sup>210</sup>Pb-dated peat cores also showed higher recent net rates of carbon accumulation in the poor fen than the extreme-rich fen. For example, calculations using *Clymo*'s [1984] peat growth model (equation (1)) suggested that aboveground net primary productivity (NPP) or carbon input to the acrotelm was twice as high at the poor fen (160 g C m<sup>-2</sup> yr<sup>-1</sup>) than at the extreme-rich fen (78 g C m<sup>-2</sup> yr<sup>-1</sup>) (Table 2). However, estimates of the transfer of carbon to the catotelm below ( $p - kx$ ) was only 36 g C m<sup>-2</sup> yr<sup>-1</sup> at the poor fen and 21 g C m<sup>-2</sup> yr<sup>-1</sup> at the rich fen because of decay occurring in the acrotelm (Table 2). If subsequent decay in the catotelm is very slow, then net carbon sequestration should be similar to the rate of transfer into the catotelm. Consistent with this suggestion, measurements of the cumulative carbon stock near the base of the peat profile at the extreme-rich fen divided by its radiocarbon age provided an estimate of the long-term average carbon accumulation

rate of 23 g C m<sup>-2</sup> yr<sup>-1</sup>. Similar long-term average peat carbon accumulation rates of 14–25 g C m<sup>-2</sup> yr<sup>-1</sup> have been recorded in other peatland studies [Clymo *et al.*, 1998; Vitt *et al.*, 2000; Gorham *et al.*, 2003; Turunen *et al.*, 2004; Roulet *et al.*, 2007].

[43] Ecosystem CO<sub>2</sub> exchange rates measured at both of our study sites were within the range that has been reported for other peatland ecosystems. Daily maximum NEE at peak season at both sites was within the range found by Humphreys *et al.* [2006] for seven Canadian peatlands in a cool and wet summer ( $-4$  to  $-11.5$   $\mu$ mol m<sup>-2</sup> s<sup>-1</sup>). Arneth *et al.* [2002] also found peak NEE within this range at two boreal ombrotrophic bogs in Russia (E. Russia:  $-6$  to  $-7$   $\mu$ mol m<sup>-2</sup> s<sup>-1</sup>; W. Siberia:  $-4$  to  $-5$   $\mu$ mol m<sup>-2</sup> s<sup>-1</sup>), and while peak NEE declined in a particularly warm dry summer that occurred at one of the sites (E. Russia:  $-4$   $\mu$ mol m<sup>-2</sup> s<sup>-1</sup>) it remained within the range observed by Humphreys *et al.* [2006]. It is more difficult to compare cumulative growing season NEE, as growing season length varies among sites and few studies report total NEE for the May–October period. Growing season NEE at the poor fen was much greater in all study years than that found at a *Sphagnum*-dominated open peatland in Minnesota in a cool wet year ( $-32$  g C m<sup>-2</sup> from mid-May to mid-October) [Shurpali *et al.*, 1995]. Interestingly, growing season NEE at the extreme-rich fen in 2004 and 2006 was more similar to that observed at the *Sphagnum*-dominated Minnesota peatland than was NEE at the poor fen, which had more similar vegetation. Growing season NEE at the poor fen in all study years and at the extreme-rich fen in 2005 was more comparable to the values that have been found for nutrient rich, treed peatlands. Suyker *et al.* [1997] found that total NEE from mid-May to early October at a boreal minerotrophic fen in central Saskatchewan was  $-88$  g C m<sup>-2</sup>. The net uptake of CO<sub>2</sub> during May–October 2005 at the extreme-rich fen was high compared to other studies, and NEE approached the  $-176$  g C m<sup>-2</sup> that Syed *et al.* [2006] found at a nearby moderately rich treed fen in northern Alberta. Our results show that comparisons among sites are highly dependent on peatland type and on the temperature and moisture conditions during the growing season, which can vary significantly from year to year.

[44] Our analyses made use of air temperature rather than shallow soil temperature for comparing the response of the two peatlands to interannual variation in conditions. Glenn *et al.* [2006] have previously shown that peat soil temperature increased faster throughout the soil depth profile (2–100 cm) during May–July at the poor fen than at the extreme-rich fen. In addition, the near surface depths (2–10 cm) cooled down faster during August–October at the poor fen compared to the extreme-rich fen. The differences between sites in peat density likely contributed to these patterns of change in soil temperatures. So the poor fen had relatively constant ecosystem CO<sub>2</sub> exchange characteristics in response to interannual variation in air temperature and this may represent a relatively conservative conclusion given that shallow soil temperature can show larger seasonal fluctuations at the poor fen compared to the extreme-rich fen.

#### 5. Conclusions

[45] The combination of contrasting plant functional types and different peat water table features at our two study sites

meant that the poor fen showed reduced response of ecosystem CO<sub>2</sub> exchange to environmental variation compared to the extreme-rich fen. In addition, the absolute magnitude of air temperature differences observed among study years was quite large. For example, there was at least a 2°C difference in monthly average temperature between 2005 and 2006 during June–September at both sites (Figures 1b and 1c). The cumulative value for growing degree days in 2006 was higher by approximately 400 degree days than that observed in 2004 and 2005 at both sites (Figure 2). This degree-day temperature difference is equivalent to a change in elevation of approximately 600 m [Berg *et al.*, 2007]. The study years also included conditions that were cooler than average and warmer than average, based on the 30 year climate normal recorded at nearby Athabasca (Figures 1 and 2). As a consequence, we suggest that our study of ecosystem response to interannual environmental variation has relevance to consideration of the potential responses of these two ecosystems to future climate change. This suggests that the poor fen will probably be quite resilient to anticipated warmer and drier conditions, as long as current hydrological features of the site are not disrupted. By contrast, our data indicate that the extreme-rich fen should be much more susceptible to predicted warmer and drier conditions. The response of the extreme-rich fen to the very warm conditions in 2006 was constrained by reduced moisture availability in mid growing season, and this occurred in a year when the cumulative precipitation during May–October was higher than normal (Athabasca 2006: 439 mm; normal: 381 ± 81 mm). This suggests that in the future, combined warmer- and drier-than-normal conditions could substantially affect ecosystem CO<sub>2</sub> exchange at the extreme-rich fen.

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