

# Modelling the interannual variability of net ecosystem CO<sub>2</sub> exchange at a subarctic sedge fen

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## Abstract

This paper presents an empirical model of net ecosystem CO<sub>2</sub> exchange (NEE) developed for a subarctic fen near Churchill, Manitoba. The model with observed data helps explain the interannual variability in growing season NEE. Five years of tower-flux data are used to test and examine the seasonal behaviour of the model simulations. Processes controlling the observed interannual variability of CO<sub>2</sub> exchange at the fen are examined by exploring the sensitivity of the model to changes in air temperature, precipitation and leaf area index. Results indicate that the sensitivity of NEE to changing environmental controls is complex and varies interannually depending on the initial conditions of the wetland. Changes in air temperature and the timing of precipitation events have a strong influence on NEE, which is largely manifest in gross ecosystem photosynthesis (GEP). Climate change scenarios indicate that warmer air temperatures will increase carbon acquisition during wet years but may act to reduce wetland carbon storage in years that experience a large water deficit early in the growing season. Model simulations for this subarctic sedge fen indicate that carbon acquisition is greatest during wet and warm conditions. This suggests therefore that carbon accumulation was greatest at this subarctic fen during its early developmental stages when hydroclimatic conditions were relatively wet and warm at approximately 2500 years before present.

*Keywords:* climate change, interannual variability, modelling, net ecosystem CO<sub>2</sub> exchange, phenology, sensitivity analysis, subarctic fen

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## Introduction

It is estimated that northern peatlands cover 346 million hectares of the Earth's surface and represent a soil carbon sink of 455 Pg (Gorham 1991). Northern peatland development has reduced atmospheric CO<sub>2</sub> concentrations and provided feedback to the global climate system by reducing the greenhouse effect (Moore *et al.* 1998). Recent evidence, however, suggests that these ecosystems have experienced a reduction in net CO<sub>2</sub> acquisition and in some cases are releasing more CO<sub>2</sub> back to the atmosphere (Vourlitis & Oechel 1997; Schreader *et al.* 1998; Griffis *et al.* 2000a).

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These northern environments are unique because they are typically underlain by permafrost, maintain a water table near the surface, and have a diverse vegetation cover consisting of both vascular and nonvascular plants. Climatic change therefore is anticipated to have pronounced effects on these landscapes (Gorham 1991). Future warming of northern latitudes is expected to lengthen the snow-free period, increase precipitation, enhance evaporation, promote surface drying, increase the length of the growing season, advance active layer deepening, and have a significant impact on photosynthesis, plant respiration and organic decomposition rates (Gorham 1991; Oechel & Billings 1992; Rouse *et al.* 1997). Resulting changes to energy, water and carbon dioxide exchange of northern peatlands will provide significant

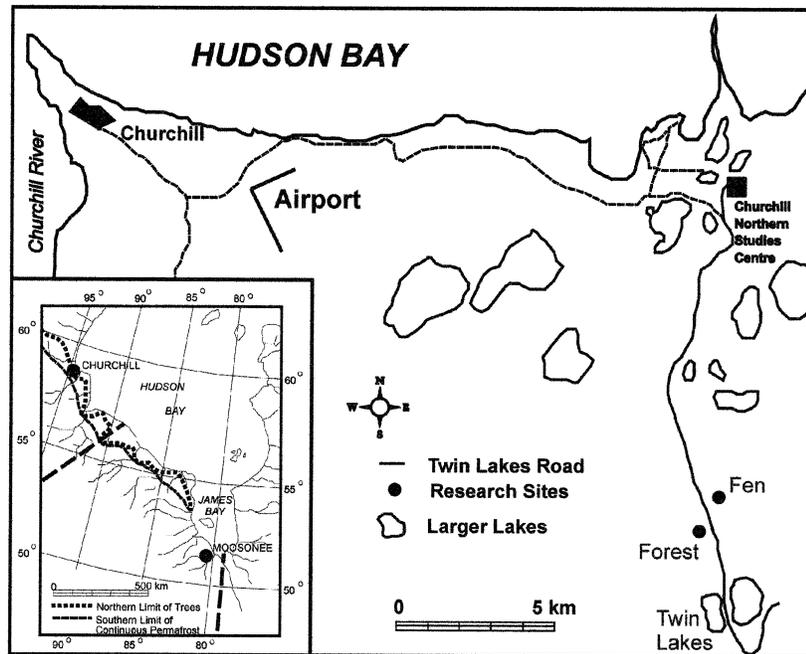


Fig. 1 Location of research area and study site.

feedback to the global climate system given their unique physical and biological properties and vast spatial coverage.

Field studies show that northern peatlands can change from a sink to a source of atmospheric  $\text{CO}_2$  both seasonally and interannually (Shurpali *et al.* 1995; Griffis *et al.* 2000a). This large variability is a consequence of the impact of hydroclimatic conditions on plant growth, photosynthesis, and soil and plant respiration. Few studies (Vourlitis & Oechel 1997; Joiner *et al.* 1999; Griffis *et al.* 2000a) have examined the magnitude and cause of interannual variability in net ecosystem  $\text{CO}_2$  exchange (NEE) in northern peatlands. Recently, Griffis *et al.* (2000a) hypothesized that the interannual variability in NEE is largely manifest in the year-to-year variability in gross ecosystem photosynthesis (GEP), and speculated that the timing of snowmelt and spring hydroclimatic conditions has an important impact on phenology and the biological vigour of the vascular canopy through the entire growing season. Although their study estimated the variability in landscape-scale GEP and ecosystem respiration (ER), their analysis did not explicitly account for the processes and feedbacks affecting photosynthesis, ecosystem respiration, plant growth, and their combined impact on NEE. In an eight-year study involving field manipulations, Johnson *et al.* (2000) demonstrated that plant photosynthesis and plant respiration were more variable than soil respiration and therefore a larger determinant of NEE. These rather surprising results illustrate the need for a better understanding of the feedbacks involving photosynthesis, plant respiration,

soil respiration, NEE, and climatic change in these northern environments.

Modelling of the interannual variability in NEE for these peatlands is needed therefore to increase the understanding of the feedback processes controlling NEE, to provide better temporal and spatial estimates of NEE, and to help understand the impact of climatic change on the local and global carbon cycle. Vourlitis *et al.* (2000) have shown that it is possible to extend simple physiological models of photosynthesis and ecosystem respiration using a 'minimum data' approach to estimate NEE at the landscape scale. Further modelling studies are needed in order to test their reliability at predicting longer-term interannual variation in NEE.

The goal of the present paper is to synthesize a number of studies involving energy balance, plant physiological and gas flux experiments conducted at a subarctic sedge fen near Churchill, Manitoba, from 1976 to present, in order to model the  $\text{CO}_2$  exchange. The model presented here is empirical and comprises a number of algorithms describing the energy, water and  $\text{CO}_2$  exchange of the Churchill fen. The model is developed in an attempt to: (i) help better understand the complex interrelationship between climate and phenology and their influence on NEE; (ii) explore the causes of interannual variability of NEE; (iii) examine how  $\text{CO}_2$  cycling will vary given a changing climate; (iv) identify processes that require better biophysical explanation.

Although there is a need to move toward more physically based models, the approach outlined herein is intended to highlight the processes and feedback

mechanisms necessary to explain the interannual variability in CO<sub>2</sub> exchange.

## Materials and methods

### Research site

The experimental area is located on the southwestern shore of Hudson Bay, within the Hudson Bay Lowland (Fig. 1). The research site is an extensive fen, located 20 km east of the town of Churchill, Manitoba (58°45' N, 94°04' W), and 12.5 km south of the Hudson Bay shoreline. This fen is characterized by nonpatterned, hummock-hollow terrain with hummocks comprising 47%, hollows 48% and large hummocks 5% of the landscape (Griffis *et al.* 2000b). Brown moss (*Scorpidium turgescens*) is the dominant vegetation found in the wet hollows. The moss *Tomenthypnum nitens* and vascular species *Carex aquatilis*, *C. limosa*, *C. saxatilis* and *C. gynocrates* cover the small hummock sites. Larger hummocks support vascular species (*Betula glandulosa*, *Ledum decumbens* *Salix arctophila* or *Carex* spp.) and species of lichen (*Cladina stellaris*, *C. rangiferina*) and moss (*Dicranum undulatum*). The fen has a mean peat depth of 0.25 m and is underlain by glaciomarine till, consisting of fine silts and clays with interspersed layers of carbonate shingles.

### Data collection

Ongoing field experiments at the Churchill fen and other wetlands within the experimental area began in 1976. Summer season energy and water balance measurements have been continuous at the fen since 1987 and landscape-scale CO<sub>2</sub> measurements were initiated in 1991. The Bowen ratio and aerodynamic gradient methods, and robust eddy covariance measurements have been used to estimate the energy balance and carbon dioxide budget of the fen. Nonsteady-state chamber measurements of CO<sub>2</sub> exchange were made frequently during the 1997 growing season and were compared to micrometeorological flux estimates of CO<sub>2</sub> exchange in 1997 (Griffis *et al.* 2000b). Methodological approaches to the energy, water and CO<sub>2</sub> flux measurements and associated sources of error have been described previously in Halliwell & Rouse (1989); Burton *et al.* (1996); Schreuder *et al.* (1998) and Griffis *et al.* (2000a). The daytime average error in the gradient-derived CO<sub>2</sub> flux can approach 30%.

### Power spectral analysis

Power spectral analysis was used to examine the half-hour gradient-derived CO<sub>2</sub> flux from five growing seasons to help identify the underlying processes

influencing the variability in NEE. The technique used is the power spectral density 'psd' function available from The MATLAB Signal Processing Toolbox (MATLAB V5.2, The Math Works, Inc., Natick, MA), which employs Welch's method (Welch 1967) of averaging periodograms. A Fast Fourier Transform (FFT) was performed on 15-d windows in order to compute the mean spectrum of the 375-d signal (18,000 half-hour flux measurements). The 95% confidence intervals were also computed to identify the periods statistically different from random noise.

## Results

### Model development

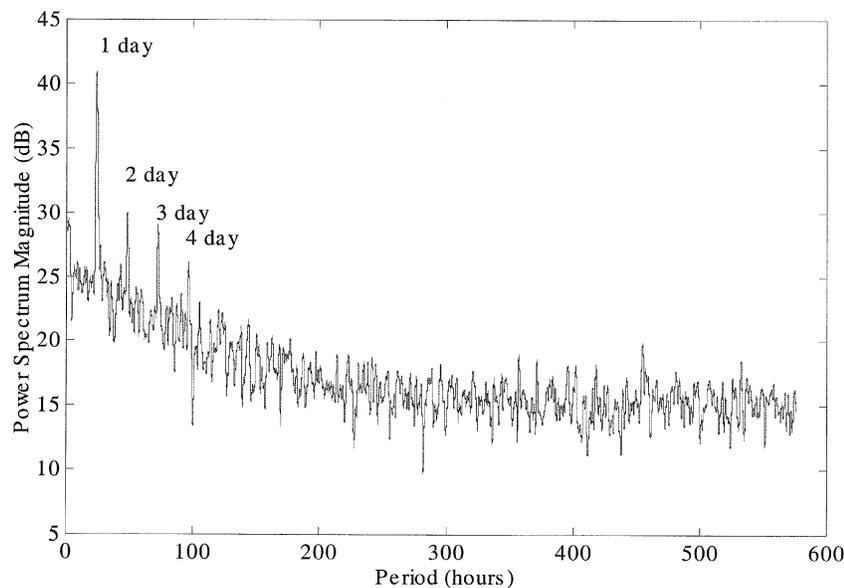
The power spectrum (Fig. 2) of the measured tower-flux data revealed significant power in periods ranging from 1 to 4 days. High power in the 1-d period is related to diurnal changes in photosynthetically active radiation and air temperature, and it is hypothesized that the significant power in lower periods (> 1 d) results from synoptic weather events, fluctuations in water table position, the wetting and drying cycle of mosses, and their combined influence on photosynthesis, respiration and plant growth. The energy of each of the periods was calculated by integrating the power magnitude over the frequency interval. From the 5-y record of NEE it is found that the 1-d period accounts for 12% of the total spectrum energy and that periods ranging up to 3 days account for 98% of the spectrum energy. The broadband behaviour (significant power in a number of periods), combined with the energy level of each period, provide an important set of diagnostics in which to test model dynamics.

The model presented here uses a half-hour time step in order to simulate the observed NEE time series. Model inputs include: net radiation ( $R_n$ ), photosynthetically active radiation ( $Q$ ), air temperature ( $T_a$ ), precipitation ( $P$ ), and vapour pressure deficit ( $vpd$ ). Model variables, parameters, and model coefficients ( $a-v$ ) are listed in Appendix A1.

### Water balance

The water balance functions were developed and tested by Rouse (1998). A brief description is given here along with new developments in its formulation. The model is initialized with a known water table depth ( $WT_1$ ) following snowmelt and begins calculating the potential latent heat flux ( $QeP$ ) as a bilinear function of net radiation and air temperature

$$QeP = a_1 R_n + a_2 T_a \quad (1)$$



**Fig. 2** Power spectrum of five growing seasons (1994, 1996–99) of net ecosystem CO<sub>2</sub> exchange at the Churchill fen. The power spectrum is given as a function of period from time scales of 0.5 to 600 h (25 days). The spectrum was computed from 18000 half-hour periods (375 days) using a 15-d window. Labelled periods are statistically significant at the 95% confidence interval. These data were measured using micrometeorological gradient techniques and are provided by Schreuder *et al.* (1998) and Griffis *et al.* (2000a).

The actual latent heat flux ( $Q_e$ ) is estimated by relating  $Q_eP$  to a surface resistance ( $R_s$ ).  $R_s$  is the ratio of  $Q_e/Q_eP$  as it varies with the change in water table depth ( $WT$ )

$$R_s = b_1 + b_2WT. \quad (2)$$

$R_s$  increases as the water table drops below the surface of the wetland since less surface water is exposed to the atmosphere and the soil water molecules must travel a longer path length before entering the atmosphere. The actual latent heat flux is therefore

$$Q_e = Q_ePf(R_s), \quad (3)$$

with the cumulative half-hour water budget,  $ds$ , calculated as

$$ds = (P - E), \quad (4)$$

where  $P$  is precipitation and  $E$  is the amount of water evaporated (in metres). The water table position is updated according to the half-hour change in  $ds$ . In order to calculate the effect of  $ds$  on  $WT$  position it is necessary to know the percentage area of the wetland that is submerged. A detailed survey of the site was used to estimate the proportion of the wetland residing above and below the relative water table position (Fig. 3) from the following sigmoid relationship

$$w_a = \frac{Wa_{\max}}{c_1 + e^{-\left(\frac{WT - c_2}{\epsilon_3}\right)}} \quad (5)$$

where  $w_a$  represents the fractional area of wetland submerged. Given the initial position of the water table, the relative surface area of water, the change in  $ds$ , and

the specific yield of the soil  $SY$ , the new water table position can be estimated as

$$WT_{t+1} = WT_t + \frac{ds}{SY}(1 - w_a) + ds w_a. \quad (6)$$

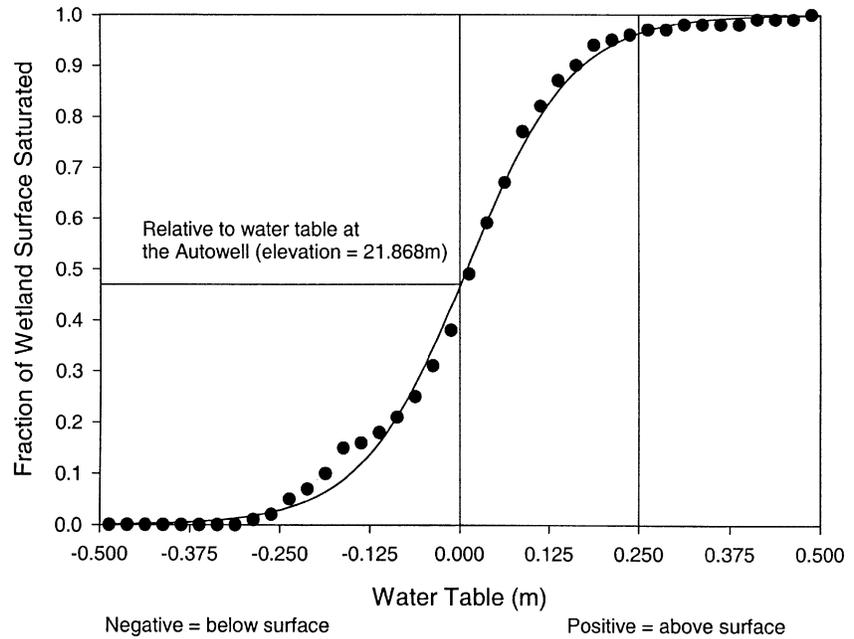
From (6), when the entire wetland is submerged ( $WT > 0.50$  m),  $SY$  equals 1.0.  $SY$  varies from 0.36 at the peat surface and decreases to 0.06 in the deeper marine clay soil layers at a depth below 0.25 m.

Volumetric soil moisture ( $\Theta_s$ ) at the base of the moss layer (0.025 m) at the edge of small hummock sites can be predicted from an exponential relationship with  $WT$  position (Fig. 4). The soil moisture content is predicted as

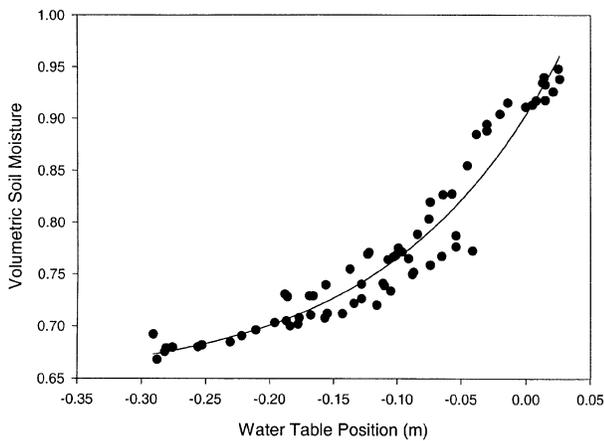
$$\Theta_s = d_1 + d_2 e^{(d_3 WT)} \quad (7)$$

#### Phenology and plant fitness

There is a scarcity of information regarding the phenology and fitness characteristics of *Carex* spp. The timing of events such as germination, breaking of dormancy and flowering has been shown to have important consequences on plant fitness (Kalisz 1986; Purrington & Schmitt 1998). Purrington & Schmitt (1998) have shown that the timing of seedling emergence can affect plant mortality rates and reproductive performance. In the plant *Silene latifolia* early emergence caused high mortality rates through the growing season. Optimum fitness (low mortality rates and high flower production) was



**Fig. 3** Modelled fractional area of wetland surface submerged below the water table level. Data points represent surveyed topography from 4 cardinal directions within a 150-m radius of the main micrometeorological tower site.



**Fig. 4** Relationship between surface volumetric soil moisture and water table position. Soil moisture was measured during the 1997 and 1998 growing season using water content reflectometry (CS615, Campbell Scientific).

attained for seedlings that experienced intermediate emergence times. The sedge species *Eriophorum vaginatum* has been shown to germinate rapidly following snowmelt at surface temperatures between 23 and 27 °C (Gartner *et al.* 1986). In addition, Gerritsen & Greening (1989) have shown that *Carex* spp. have higher germination rates at low water table positions in marsh environments because lower water table permits greater oxygen diffusion to the vicinity of dormant seeds. To our knowledge, information does not exist on the relationship between the timing of *Carex aquatilis* emergence and its impact on fitness or mortality rates.

Estimating leaf area index is difficult because of temporal and spatial variability in aboveground biomass. The number of shoots produced each season depends on a number of factors ranging from predation on seeds and rhizomes (Srivastava & Jefferies 1996; Jano *et al.* 1998), to the failure of seeds and rhizomes to break dormancy given unfavourable spring or winter conditions (Vleeshouwers *et al.* 1995). It is assumed that all shoots emerge at the time that the present model is given the initial LAI.

At the Churchill fen, shoot densities have been shown to vary between 1000 and 1500 shoots m<sup>-2</sup>, reaching maximum density between mid-June and mid-July (Petroni 1996; Schreader *et al.* 1998; Rolph 1999). It is assumed that all seed germination commences after snowmelt once surface temperatures exceed freezing. When dormancy has been broken, the model estimates the initial leaf area index (LAI). The initial LAI and fitness of the vascular canopy is based on the timing of snowmelt and the water table position. Three initial conditions are used to describe the state of the phenology and its fitness consequences to the vascular plants. These estimates are based on personal field observations at the study site and are currently being investigated with on going remote sensing studies (Appendix A2).

*Fitness Condition 1: Normal to late snowmelt.*

Snowmelt commences within  $\pm 1$  week of 1 June. Water table position is above the surface causing low soil oxygen diffusion. As a result, breaking of seed and rhizome dormancy is delayed and shoot emergence is slow. When the water table position recedes and hum-

mock tops become exposed the initial LAI is set to 0.001. The maximum LAI given these initial growing conditions (a descriptor of plant fitness) ranges between 0.47 and 0.60. These values are supported by field observations (Petronne 1996; Rolph 1999; Griffis *et al.* 2000b).

*Fitness Condition 2: early snowmelt and dry spring.*

Snowmelt is completed at least 1 week prior to 27 May, precipitation events are infrequent and the growing season begins with a water deficit (Rouse 1998). Water table position is below  $-0.01$  m. Vascular vegetation does not reach maturity before experiencing considerable drought stress. In this case, the phenology and climatic conditions adversely affect the fitness of the vascular species. The dry conditions experienced during this intense period of plant development cause many of the shoots to have high mortality rates. The initial LAI is 0.001 but a lower maximum LAI of 0.35 is attained (Schreader *et al.* 1998).

*Fitness Condition 3: early snowmelt and no-water deficit.*

Snowmelt commences at least 1 week earlier than 27 May, however, ample precipitation prevents the water table level from dropping to levels that would adversely affect germination and plant growth. The early snowmelt and ideal water table position increase the fitness of the vascular plants. The initial LAI is set to 0.15 (Brown 1999) as a consequence of the longer growing period leading up to the start of model calculations, because data collection commences 13 June (DOY 164). A maximum LAI is set at 0.60. It is hypothesized that the longer growing period allows greater root development and the ability of the vascular canopy to avoid drought stress later in the season.

Although these fitness parameters are at the present time gross assumptions, they do provide a qualitative starting point to the problem of phenology vs. fitness and biological vigour in these ecosystems. Phenology and fitness is also relevant to bryophytes (Johanson *et al.* 1995); however, these characteristics have received relatively little attention in the scientific literature and have not been studied at the Churchill fen. Moreover, the change from net source to net sink at the Churchill fen is correlated with the timing of leaf-out (Schreader *et al.* 1998).

Once LAI and fitness have been described, plant growth is controlled by the rate of photosynthesis, respiration, and carbon allocation parameters. The LAI is updated half-hourly and typically attains a maximum value within 3–4 weeks of emergence. Drought stress and cold temperatures bring about the onset of dormancy and senescence. Sustained levels of highly negative soil moisture potentials ( $< -400$   $\Sigma$ mpa, summed half-hourly) are used to trigger the onset of dormancy based on observations from the 1994 growing season (Schreader *et al.* 1998). Sub-freezing temperatures

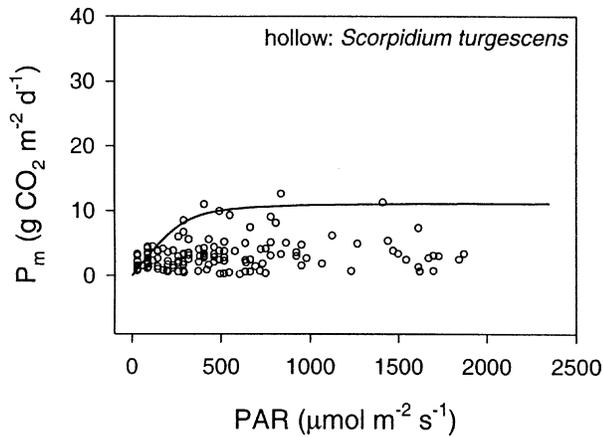
also initiate plant dormancy. Once senescence has been initiated the process is irreversible and the remaining leaf area decays at an assumed rate of 1% per day.

### *Carbon economics and plant growth*

One of the greater challenges in modelling and understanding the carbon budgets of ecosystems is accounting for the transport and allocation of photosynthetic products to the different plant organs and partitioning those products into new growth structures, storage, and the respiration resulting from biosynthesis, maintenance of biomass and the maintenance of ion gradients (Penning de Vries 1975; Heide *et al.* 1985; Van der Werf *et al.* 1988; Poorter *et al.* 1990; Atkin *et al.* 1996).

Carbon economics differ between plants and relatively little information is available for *Carex aquatilis*, and, *Scorpidium turgescens* remains uninvestigated. However, studies have examined some *Carex* spp. (Van der Werf *et al.* 1998) and generalizations can be made between fast- and slow-growing plant species (Poorter *et al.* 1990). Poorter *et al.* (1990) report on the carbon and nitrogen economics of 24 different wild species with respect to relative growth rate (RGR). Slow growing ( $RGR < 110$   $\text{mg g}^{-1} \text{d}^{-1}$ ) species in their study showed approximately 27% of the daily photosynthate products were allocated to new leaf growth, 13% to shoot growth, 18% root growth, 24% above-ground respiration and 19% belowground respiration. Allocation patterns are even more complex in natural settings. Heide *et al.* (1985) has shown that day length can have a significant effect on the allocation to below- and aboveground structures. During long days, a greater portion of carbon is invested in shoot and leaf growth, whereas short days result in greater carbon partitioning into root structures. Larger respiration rates have also been found in slow-growing alpine and lowland *Poa* spp. (Atkin *et al.* 1996). Atkin *et al.*'s study showed that 45–60% of the daily photosynthetic flux is lost to respiration. The greater expense of respiration in slow-growing and arctic species has been hypothesized to be related to a lower efficiency in producing respiratory products, or alternatively, that the respiratory energy efficiency is low. Tenhunen *et al.* (1992) hypothesized a greater need for protein turnover to adapt to the cold conditions.

In the present parameterization, 24% of the photosynthate production is used to form new shoot and leaf growth and 74% is used for root growth. This assumption is based on the above- and belowground biomass findings of Rolph (1999). Two percent of the photosynthetic production is stored as sugars in the plant structures. Leaf and shoot respiration resulting from maintenance and growth processes (autotrophic



**Fig. 5** Boundary curve describing moss community photosynthesis as a function of photosynthetically active radiation. These data ( $n = 128$ ) were acquired from nonsteady-state chamber measurements made at the Churchill fen during the 1997 growing season (Griffis *et al.* 2000b).

respiration,  $R_a$ ) account for 30% of the photosynthetic production. The effect of environmental conditions (day length effects and nutrient conditions) on transport and distribution of photosynthate carbon to above- and belowground structures is currently ignored. However, the amount of  $R_a$  from the plant is increased by 1% for every 1° increase above the optimum temperature of 15 °C. This parameter value is assigned arbitrarily but is justified by the fact that warmer temperatures increase protein turnover in plants and the amount of energy production used in respiration.

From the carbon budget of the plant, the growth of the vascular leaf area is estimated as

$$LAI_{t+1} = LAI_t G_l \quad (8)$$

where  $G_l$  is a growth parameter describing the conversion of leaf photosynthate into leaf biomass.

### Gross photosynthesis

Photosynthetic activity of the moss community can occur when the air temperature exceeds freezing. Based on chamber measurements from the 1997 growing season, a boundary analysis approach was used and the maximum observed chamber flux ( $P_{mmax}$ ) scaled according to PAR (Fig. 5) and volumetric water content. The moss contribution to gross ecosystem photosynthesis can be described as

$$P_m = P_{mmax} f(A_{mQ}) f(A_{m\theta}), \quad (9)$$

where

$$f(A_{mQ}) = \left( \frac{\phi_m Q + P_{mmax} - \sqrt{(\phi_m Q + P_{mmax})^2 - 4\phi_m Q k P_{mmax}}}{2k P_{mmax}} \right) \quad (10)$$

and

$$f(A_{m\theta}) = \frac{(h_1 + h_2 e^{h_3 \theta_m})}{P_{mmax}} \quad (11)$$

$A_{mQ}$  describes the response of moss net photosynthesis to variations in  $Q$ . Equation 10 was proposed by Prioul & Chartier (1977). The parameter  $\phi_m$  is the apparent quantum efficiency for moss ( $\phi_v$  for vascular plants) describing the conversion of light to photochemical products and  $k$  is the scaling parameter defining the change in slope between the light-limited and light-saturated region of the curve.

Equation 11 describes the limitation of decreased volumetric moisture on moss gross photosynthesis. This relationship is idealized and not supported by empirical data at present from the Churchill fen. However, previous research supports the contention that water content of bryophytes plays an important role in their photosynthetic capacity (Tenhunen *et al.* 1992; Green & Lange 1994). Moss moisture content,  $\theta_m$ , is estimated from the water table soil moisture curve (eqn 7).

Vascular photosynthesis is based on chamber measurements made during the 1997 growing season (Griffis *et al.* 2000b) combined with a stomatal conductance model developed for *Carex aquatilis* by Blanken & Rouse (1995). Gross photosynthesis is described as

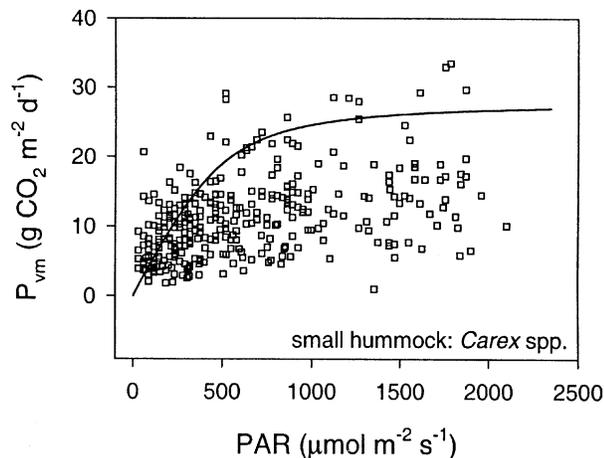
$$P_v = (P_{vmax} - P_m) f(A_{vQ}) f(g_s) \quad (12)$$

$$f(A_{vQ}) = \left( \frac{\phi_v Q + P_{vmax} - \sqrt{(\phi_v Q + P_{vmax})^2 - 4\phi_v Q k P_{vmax}}}{2k(P_{vmax} - P_m)} \right) \quad (13)$$

$$f(g_s) = \frac{LAI}{LAI_{max}} f(T_s) f(VPD) f(\psi_s), \quad (14)$$

$$f(T_s) = \frac{m_1 + m_2 T_s + m_3 T_s^2}{g_{smax}} \quad (15)$$

$$f(vpd) = \frac{n_1 + n_2 VPD}{g_{smax}}, \quad (16)$$



**Fig. 6** Boundary curve describing vascular community photosynthesis as a function of photosynthetically active radiation. These data ( $n = 332$ ) were acquired from nonsteady-state chamber measurements made at the Churchill fen during the 1997 growing season (Griffis *et al.* 2000b).

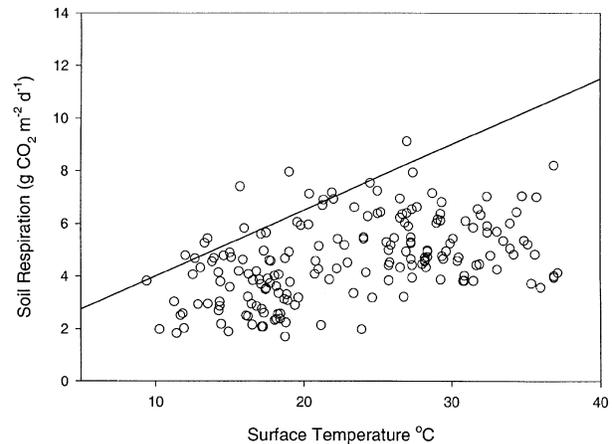
$$f(\psi_s) = \frac{p_1 + p_2\psi_s}{g_{smax}} \quad (17)$$

Because bryophytes carpet the entire fen landscape, (13) separates the modelled moss net photosynthesis from the vascular community. Vascular photosynthesis,  $P_v$ , is described as a function of  $Q$  following Prioul & Chartier (1977) (Fig. 6).

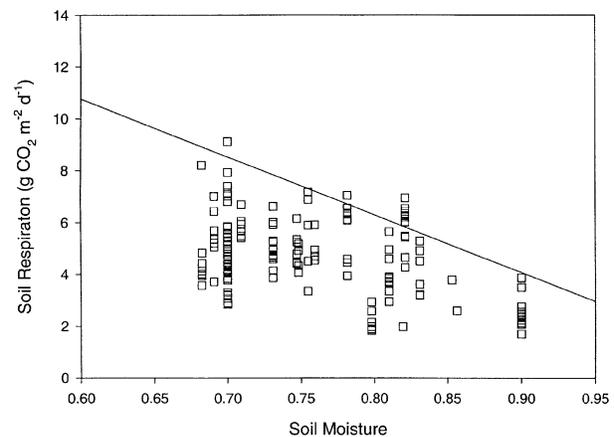
The conductance model ( $g_s$ ) is described in detail by Blanken & Rouse (1995). The model has been adapted so that it is used to scale the photosynthetic flux and not as an absolute conductance value. The conductance model was also developed from a boundary analysis approach and is a function of surface temperature ( $T_s$ ), vapour pressure deficit, soil water potential ( $\theta_s$ ) and the ratio of the observed leaf area ( $LAI$ ) to the maximum potential leaf area ( $LAI_{max}$ ). The maximum observed conductance value ( $g_{smax}$ ) is used to scale each of the stomatal conductance functions to a fraction of 1.0.

### Soil respiration

Soil respiration (heterotrophic respiration,  $R_h$ ) is separated from plant respiration despite the complexities in the relationship between them and, additionally, the difficulties of measuring these fluxes in the field. Based on chamber measurements where the vegetation was removed at the beginning of the growing season, a soil respiration relationship was developed based on temperature (Fig. 7) and soil moisture (Fig. 8).



**Fig. 7** Boundary curve describing soil respiration as a function of surface temperature. These data ( $n = 190$ ) were acquired from nonsteady-state chamber measurements made at the Churchill fen during the 1997 growing season. Soil respiration was estimated by removing the surface vegetation prior to sampling.



**Fig. 8** Boundary curve describing soil respiration as a function of surface moisture. These data ( $n = 190$ ) were acquired from non steady-state chamber measurements made at the Churchill fen during the 1997 growing season. Soil respiration was estimated by removing the surface vegetation prior to sampling.

$$R_h = R_{hmax}f(T_s)f(\theta_s), \quad (18)$$

$$f(T_s) = \frac{q_1 + q_2T_s}{R_{hmax}} \quad (19)$$

$$f(\theta_s) = \frac{v_1 + v_2\theta_s}{R_{hmax}} \quad (20)$$

$R_{hmax}$  is the maximum observed soil respiration flux from chamber measurements.

**Table 1** General climatic and net ecosystem CO<sub>2</sub> exchange characteristics during the five growing seasons at the Churchill fen. Growing periods include Pre-green (DOY 164–172), Green (DOY 173–219), and Post-green (DOY 220–238)

(a) Mean daily air temperature by growing period and season (°C)

Year	Pre-green	Green	Post-green	Season
1994	12.5 (+5.7)	12.3 (+1.0)	11.1 (–0.4)	12.0 (+1.2)
1996	7.0 (+0.2)	13.0 (+1.7)	11.5 (0.0)	11.9 (+1.1)
1997	6.1 (–0.7)	13.8 (+2.5)	13.0 (+1.5)	12.7 (+1.9)
1998	5.5 (–1.3)	14.1 (+2.8)	12.9 (+1.4)	12.8 (+2.0)
1999	13.0 (+6.2)	12.6 (+1.3)	12.1 (+0.6)	12.5 (+1.7)
Normal	6.8	11.3	11.5	10.8

\*bracket indicates departure from normal

(b) Total precipitation by growing period and season (mm).

Year	Pre-green	Green	Post-green	Season
1994	4 (–9)	32 (–47)	37 (0)	73 (–56)
1996	35 (+22)	70 (–9)	41 (+4)	145 (+16)
1997	8 (–5)	109 (+30)	7 (–30)	125 (–4)
1998	23 (+10)	58 (–21)	35 (–2)	118 (–11)
1999	0 (–13)	72 (–7)	45 (+8)	118 (–11)
Normal	13	79	37	129

\*bracket indicates departure from normal

(c) Cumulative net ecosystem CO<sub>2</sub> exchange and estimate of maximum probable error (g CO<sub>2</sub> m<sup>–2</sup>)

Year	Pre-green	Green	Post-green	Season
1994	+55 (± 17)	–12 (± 4)	+33 (± 10)	+76 (± 23)
1996	–20 (± 6)	–135 (± 41)	–80 (± 24)	–235 (± 71)
1997	+12 (± 4)	–61 (± 18)	0 (± 0)	–49 (± 15)
1998	–22 (± 7)	–189 (± 57)	–17 (± 5)	–228 (± 68)
1999	–0.6 (± 0.2)	–41 (± 12)	+8 (± 2)	–34 (± 10)
Days	9	48	18	75

\*bracket indicates maximum probable error. Adapted from Griffis *et al.* (2000a)

### Net ecosystem exchange

The net ecosystem exchange of carbon dioxide at the fen is the net balance between production and decomposition processes. Gross ecosystem photosynthesis (GEP) includes production from the mosses ( $P_m$ ) and vascular plants ( $P_v$ ). Ecosystem respiration (ER) comprises the dark respiration from the mosses ( $R_m$ ) and vascular plants ( $R_v$ ) and also the respiration from soil microbial decomposition ( $R_h$ ).

$$\text{GEP} = P_m + P_v, \quad (21)$$

$$\text{ER} = R_m + R_v + R_h, \quad (22)$$

$$\text{NEE} = \text{GEP} - \text{ER}. \quad (23)$$

### Model testing

#### Climatic conditions and net ecosystem CO<sub>2</sub> flux data

Table 1 summarizes the general climatic conditions and NEE data for the five growing seasons examined in this study (Griffis *et al.* 2000a). The 1994 season was uncharacteristically dry and experienced a net loss of +76 g CO<sub>2</sub> m<sup>–2</sup> to the atmosphere over the measurement period (13 June to 28 August, DOY 164–238). In 1996, climatic conditions were wetter than normal and NEE showed a net gain of –235 g CO<sub>2</sub> m<sup>–2</sup>. The 1997 and 1998 seasons were climatically similar throughout the measurement period. Both seasons were warmer than the 30-y Churchill normal with near-normal precipitation. Each season was a sink of CO<sub>2</sub>. In (1999) growing season precipitation was near normal with a pronounced dry spring period. The fen was a weak net sink of –34 g CO<sub>2</sub> m<sup>–2</sup>.

#### Sensitivity analysis of model parameters

A sensitivity analysis of the model parameters listed in Appendix A1 was performed to help identify potential causes of model bias. Sensitivity was examined by varying each of the parameters by ±5% and assessing their effect on the model simulations for the 1996 season. The sensitivity of NEE to the estimate of  $\theta_m$  caused a 20% change in the modelled seasonal cumulative CO<sub>2</sub> exchange. Simultaneous increases in LAI<sub>max</sub> and  $G_1$  caused a 13% change in seasonal NEE. Varying  $P_{vmax}$  showed an 8% difference in the seasonal NEE. Testing of all other parameters resulted in changes of less than 5% for the simulated seasonal NEE. The sensitivity analysis indicates that the assumptions surrounding estimates of moss moisture content and vascular plant growth have the strongest influence on the modelled seasonal NEE.

#### Seasonal NEE

The behaviour of the model is tested against five years of growing season NEE data. These data have been described previously in Griffis *et al.* (2000a). The five-year series of NEE, cumulative seasonal NEE, diurnal NEE, and the time series of half-hour fluxes for 1996 and 1997 are examined in order to evaluate model performance.

The power spectrum for the continuous series of the five modelled data years is presented in Fig. 9. Periods with high relative power are similar to those shown in Fig. 2 for the observed data series. However, the model exhibits significantly higher power in additional low periods of up to 8 days. It is encouraging that the model captures the broadband behaviour at periods less than 3 days. The energy of the model spectra, however, is

concentrated (> 90%) in the 1-d period. Greater attention is needed therefore in improving the model dynamics beyond the 1-d period. This may require better simulation of the wetting and drying cycle of mosses and phenology of both vascular and moss species.

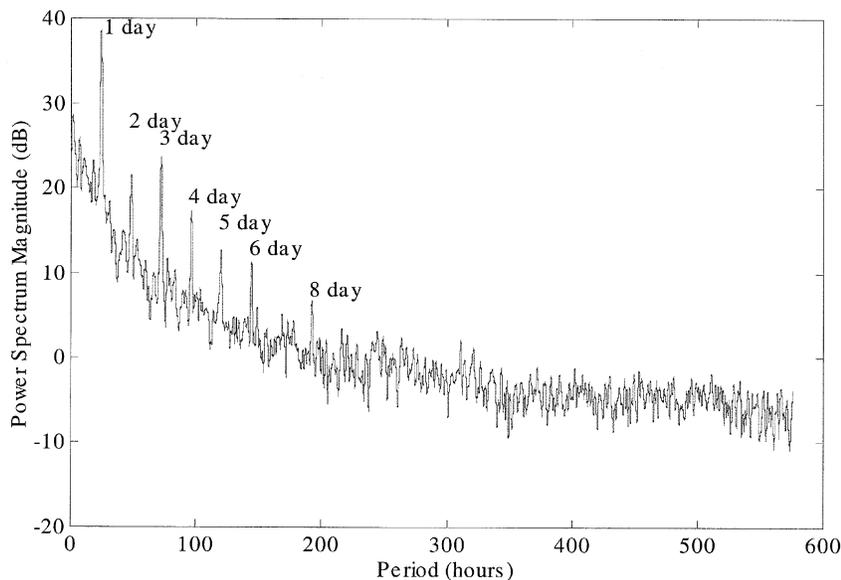
#### *Seasonal net ecosystem exchange*

The model accurately predicts those years that experienced a net gain and a net loss of CO<sub>2</sub>. Figure 10 displays the actual and modelled cumulative NEE for the five test years. On a seasonal basis the model performs reasonably well in four of the five years. In 1994, the model underestimates the net loss of CO<sub>2</sub> during the early portion of the growing season (Fig. 10a). Although the magnitude of the modelled flux disagrees with the measured data, the behaviour of the model shows strong similarities to the observed trend. During the mid-growing season, the observed and modelled net loss of CO<sub>2</sub> from the wetland reach a near equilibrium because of the emergence of the vascular species. Following an early vascular senescence, initiated in mid-July, both signals experience an increase in the loss of CO<sub>2</sub> from the wetland. The model overestimated the net loss by 10 g CO<sub>2</sub> m<sup>-2</sup>; however, this is within the maximum margin of error in the flux measurements. Figure 11(a) indicates that the net loss of CO<sub>2</sub> during the 1994 growing season was the result of low photosynthetic rates from both the moss and vascular species relative to ecosystem respiration.

In 1996, the model accurately estimates a strong sink year (Fig. 10b). Acquisition of CO<sub>2</sub> is rapid

during the early part of the growing season and is attributed to the wet spring conditions that promoted a large photosynthetic flux from the mosses (Fig. 11b). However, the model does not maintain the rate of CO<sub>2</sub> acquisition and begins to underestimate the cumulative gain in early July (DOY 180 and DOY 200). The underestimate is likely caused by the large reduction in moss net photosynthesis as a consequence of the drier surface conditions and, additionally, a low vascular net photosynthetic flux. Model behaviour improves once the vascular leaf area has reached its maximum of 0.6 at mid-season. By the end of the growing season, the modelled cumulative CO<sub>2</sub> exchange underestimated the actual result by 37 g CO<sub>2</sub> m<sup>-2</sup>. Although this is a significant underestimate it is within the error of the flux measurements.

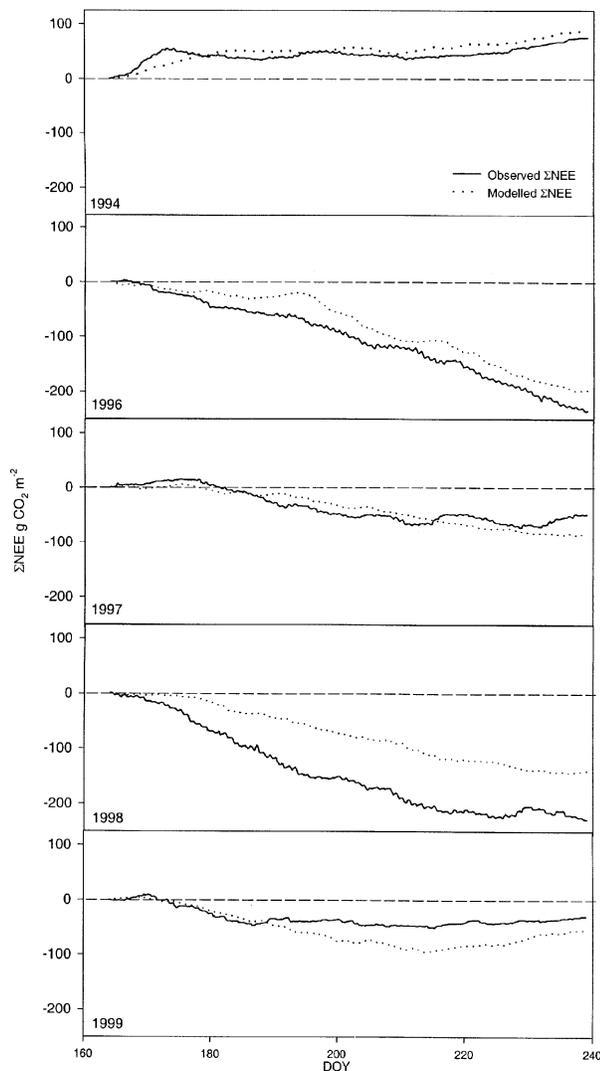
There is good agreement between the modelled and observed cumulative CO<sub>2</sub> flux in 1997 (Fig. 10c). During the early growing season the model underpredicts the loss of CO<sub>2</sub> to the atmosphere and switches from a net source to a net sink earlier in the season. Model behaviour is similar to the observed data during the mid-growing period; however, there is some discrepancy between the simulated and observed data near the end of the growing season. That the divergence is the result of strong vascular photosynthetic activity late in the growing season, is supported by Figure 11(c). Modelling the shoulder season components appears to be problematic because of the current description of phenology. The simulation overestimated the net gain by 37 g CO<sub>2</sub> m<sup>-2</sup>, which is within the maximum probable error of the measured cumulative flux.



**Fig. 9** Power spectrum of five growing seasons (1994, 1996–99) of modelled net ecosystem CO<sub>2</sub> exchange at the Churchill fen. The power spectrum is given as a function of period from time scales of 0.5 to 600 h (25 days). The spectrum was computed from 18000 half-hour periods (375 days) using a 15-d window. Labeled periods are statistically significant at the 95% confidence interval.

The model simulation for the 1998 growing season performed poorly during the early growth period, which led to a gross underestimate of the observed cumulative NEE (Fig. 10d). It is possible that the vascular photosynthetic contribution is underestimated in the model (Fig. 11d). During independent tests, model performance improved when a larger initial vascular leaf area was prescribed. However, at the present time this large LAI value cannot be justified, as early growing season leaf area data are not available. The model underestimated the observed cumulative NEE flux by 88 g CO<sub>2</sub> m<sup>-2</sup> and exceeded the error in the measurements.

The simulated cumulative NEE for (1999) shows realistic behaviour during the early growing season but



**Fig. 10** Comparison of modelled and observed cumulative net ecosystem CO<sub>2</sub> exchange for five growing seasons at the Churchill fen. Observed data are tower-flux measurements provided by Schreuder *et al.* 1998 and Griffis *et al.* 2000a.

diverges later in the season (Fig. 10e). This suggests that the fitness parameter describing the maximum LAI is incorrect or that senescence was initiated earlier because of the dry surface conditions (Fig. 11e). The model overestimated the net acquisition by 23 g CO<sub>2</sub> m<sup>-2</sup> and was within the error of measurement.

#### Diurnal patterns of CO<sub>2</sub> exchange

On a half-hour time-step the model failed to reproduce the mean diurnal pattern of net ecosystem CO<sub>2</sub> exchange for each of the seasons (Fig. 12). The best comparison is observed for the 1997 season (Fig. 12c). The half-hour variability in NEE is generally noisy in the measured signal and the model fails to reproduce this variability. Large bias is apparent for the night-time respiration and for the early morning maximum peak in net CO<sub>2</sub> acquisition.

The diurnal variation in moss moisture content may be causing some of the bias in NEE. The GEP values do not decrease as expected through the mid-day period. Because mosses are prone to surface drying, a significant reduction in GEP would be expected through the day. Furthermore, Blanken & Rouse (1995) and Schreuder *et al.* (1998) have shown that *Carex aquatilis* exhibits evidence of water conservation. Modelled diurnal patterns of stomatal conductance do not show similar patterns to the observed NEE. It is possible, therefore, that the mid-day reduction in carbon acquisition is a result of photoinhibition of both the moss and vascular species. Murray *et al.* (1993) have shown that *Sphagnum* moss production decreases at high PAR levels (> 800 μmol m<sup>-2</sup> s<sup>-1</sup>), which may be related to low tissue nitrogen.

#### Time series of half-hour fluxes

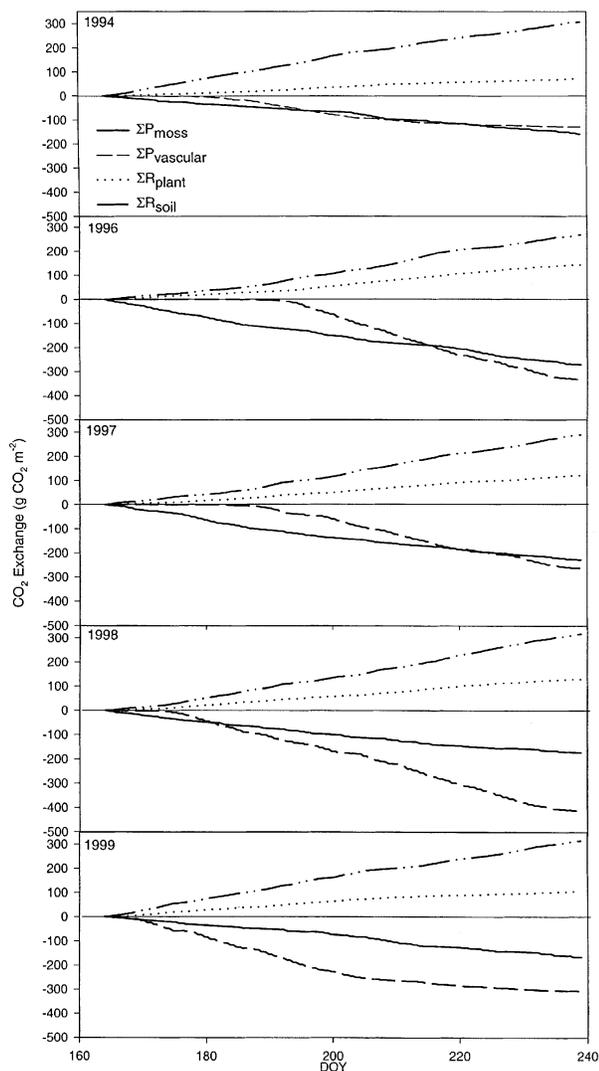
Observed and simulated half-hour fluxes of NEE for 21 days (DOY 170 to DOY 190) from the 1996 and 1997 seasons are presented in Fig. 13. The time period includes the beginning of leaf emergence to approximately full canopy at the fen. In 1996, the model simulation between DOY 177 and 179 is particularly problematic. This period coincides with warm and sunny conditions, which ended an 8-d period of relatively cold and wet conditions in Churchill. Because this period occurs early in the growing season, the inability of the model to capture the abrupt change in NEE may be attributed to underestimation of moss GEP under these potentially optimal conditions. In 1997, the model simulation is especially poor between DOY 187 and 189. This period was characterized by relatively warm daytime temperatures (>25°C), with a single precipitation event seven days previously. The simulation indicates an

overestimate of night-time ecosystem respiration and underestimate of daytime NEE in response to drying surface conditions. Although tower flux measurements are prone to errors at night (Schreuder *et al.* 1998), the disparity between daytime fluxes illustrates the strong sensitivity of the model to surface moisture conditions.

### Sensitivity to climate variability

In this section the sensitivity of NEE to changes in air temperature, precipitation, and leaf area index is examined, and the potential response of the Churchill fen to transient and equilibrium changes in climate explored.

*Air temperature.* Many of the algorithms used in this model are temperature dependent. It is expected,



**Fig. 11** Simulated cumulative CO<sub>2</sub> fluxes of moss and vascular photosynthesis, plant respiration, and soil respiration.

therefore, that modelled GEP, ER and NEE will show high sensitivity to temperature change in the system. In the present analysis, the observed temperature was varied in each year by  $\pm 4^\circ\text{C}$  in order to assess the sensitivity of NEE, GEP and ER to temperature change (Table 2).

In general, net photosynthesis was enhanced between 15 and 20% for warmer air temperatures and decreased between 24 and 26% for cooler air temperatures. The response is attributed largely to the higher conductance values under warmer temperatures. It has been argued that arctic plants photosynthesize below their optimum temperature over the majority of the growing season (Tieszen 1973; Semikhatova *et al.* 1992). The largest increase in net photosynthesis was observed in 1996, which was the coldest season. Increased temperature generally results in higher stomatal conductance and larger photosynthetic rates. The smallest increase in net photosynthesis was observed in 1997, which experienced the highest daytime temperatures. The decrease in net photosynthesis resulting from colder air temperatures showed strong similarity between all seasons.

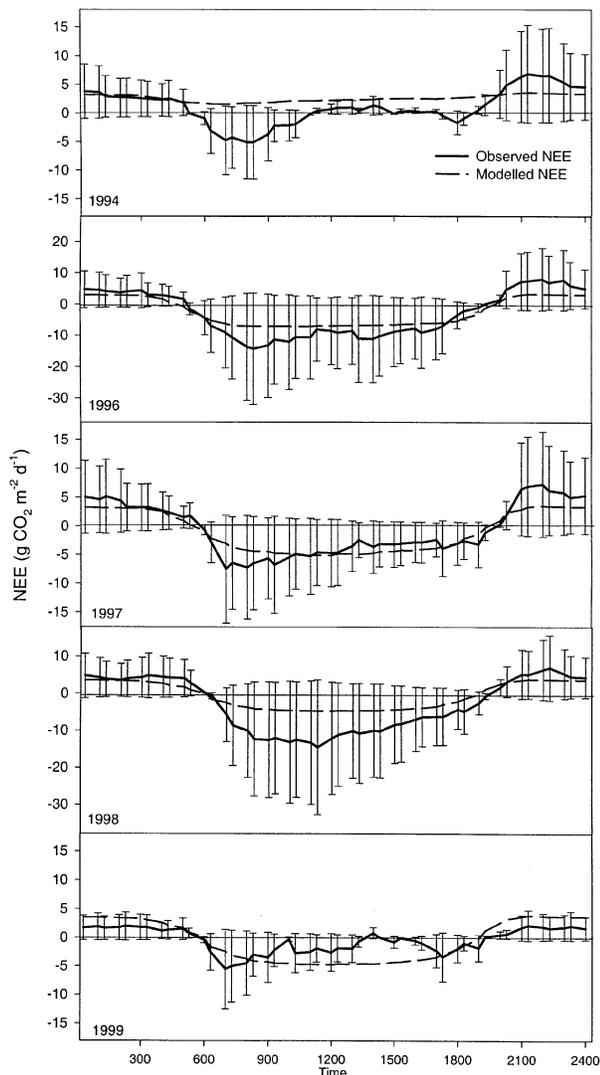
Ecosystem respiration showed a similar response to the  $\pm 4^\circ\text{C}$  temperature change in all years. Efflux of CO<sub>2</sub> under the warmer scenario increased by about 20% and decreased by a similar amount for the colder scenario in each year.

The effect of temperature change on NEE is a consequence of the differences caused in GEP and ER. Increasing temperature caused NEE to vary between 3 and 25%. In 1994, the loss of CO<sub>2</sub> from the wetland was increased by 25%. Although GEP was enhanced by 17%, the increase in ER resulted in an increased net loss of carbon from the wetland. Lower temperatures caused NEE to change between 1 and 61%. Lower temperatures caused substantial reductions in net photosynthesis. This was a result of a higher frequency of air temperatures below the temperature optimum of photosynthesis. Photosynthesis decreased more than the ecosystem respiration in all seasons, causing an increase in the observed carbon loss in 1994 and reducing the carbon acquisition in the other years.

*Precipitation.* The sensitivity of CO<sub>2</sub> exchange to changes in precipitation was explored by varying the magnitude of the observed precipitation events in each year by  $\pm 30\%$ . Climate simulations from GCMs indicate a 20% increase in precipitation for  $2 \times \text{CO}_2$  scenarios in the central arctic (Maxwell 1992). The larger value of 30% is used herein to accentuate the NEE response in the model simulations. The effects of precipitation distribution and frequency of rain events on CO<sub>2</sub> exchange were also examined. In order to accomplish this the total observed seasonal precipita-

tion in each year was distributed either to the early summer season (ES: DOY 164 to DOY 201) or to the late summer season (LS: DOY 202 to DOY 238) while employing an artificial 2-d rainfall frequency to examine the impact of a wet spring/dry summer vs. a dry spring/wet summer on NEE.

*Precipitation magnitude.* Increasing the magnitude of precipitation events enhanced GEP in all years between 1 and 4% (Table 3). ER decreased between 0 and 2% despite the greater productivity of the plants. This



**Fig. 12** Comparison of modelled and observed mean diurnal patterns of net ecosystem CO<sub>2</sub> exchange. Observed data are tower-flux measurements provided by Schreuder *et al.* 1998 and Griffis *et al.* 2000a. Error bars represent the maximum probable error in the measured data.

indicates that soil respiration was reduced relative to plant respiration. Changes in NEE varied between 6 and 24% for all years.

Reducing the magnitude of precipitation events by 30% caused GEP to decrease between 2 and 20%. The largest change occurred in 1998 as the result of the onset of an early senescence. The smallest change was observed for 1996, and attributed to the wet surface conditions that persisted through that season. ER increased between 0.3 and 4%. Changes in NEE were large and ranged from 10% in 1996 to 71% in 1998.

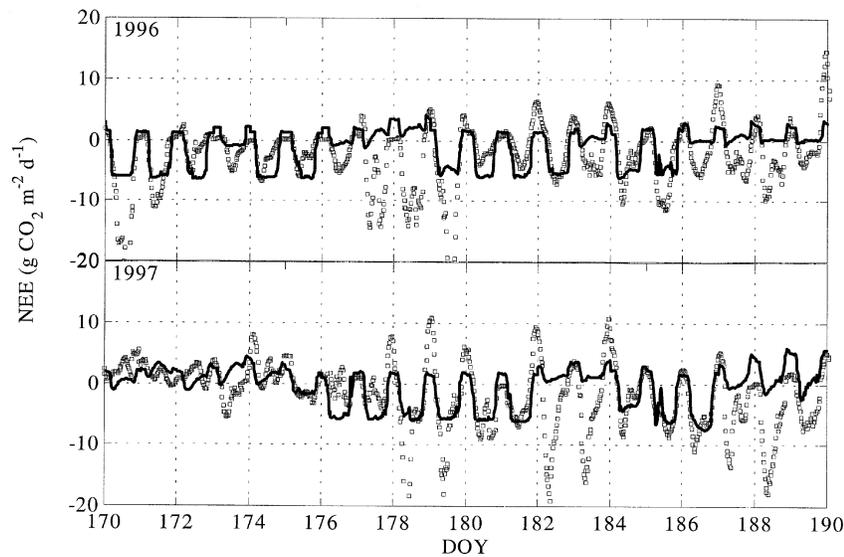
*Precipitation distribution and frequency.* Changing the distribution and frequency of the observed rainfall in each year caused substantial differences in GEP and NEE. The model is highly sensitive to the timing of rainfall events. Given frequent early summer precipitation events (wet spring/dry late summer), GEP increased by 32% in 1994 and decreased by 4% in 1996 (Table 4). ER increased in all years excluding 1998.

The wet late summer scenario caused a reduction in GEP for all years ranging between 4 and 30%. The largest decrease was observed in 1998 resulting from the onset of a premature senescence. The changes in ER are complex. In some cases, ER increases as a result of greater plant respiration while in other cases ER decreases because of higher soil water contents.

The influence of precipitation distribution and frequency on NEE is pronounced and depends on the initial conditions of the wetland. In 1994, the frequent early season rainfall delayed the senescence of the vascular canopy and caused the net loss of CO<sub>2</sub> from the system to be reduced by 85%. In 1996, the simulated wet spring reduced the net gain of carbon by 17%, which resulted from desiccation of the moss canopy occurring later in the season. In 1999, there was a 70% increase in net carbon acquisition following more frequent wetting of the moss surface and, additionally, the delayed senescence of the vascular canopy. This analysis indicates the high level of complexity in NEE and shows that it can largely manifest itself in GEP.

#### Leaf Area Index

The sensitivity of NEE to a  $\pm 10\%$  change in LAI was high in all cases, varying from 11% in 1994 to 45% in 1999 (Table 5). This demonstrates the need for better estimates of LAI. GEP increased from 4% in 1994 to 6% in 1998 and 1999. ER increased 0.5–2% because of greater plant production. Reducing LAI caused similar changes in the opposite direction for all years.



**Fig. 13** Comparison of half-hour modelled and measured net ecosystem  $\text{CO}_2$  exchange for a 21-d period during the 1996 and 1997 growing seasons. Boxes represent half-hour tower-flux measurements (Griffis *et al.* 2000a).

**Table 2** Sensitivity of GEP, ER, and NEE to a  $\pm 4^\circ\text{C}$  change in air temperature

Year	GEP			ER			NEE		
	+4°C	P	-4°C	+4°C	P	-4°C	+4°C	P	-4°C
<b>1994</b>									
$\Sigma$	341	291	218	448	377	306	↑108	↑86	↑87
$\Delta$	+17%		-25%	+19%		-19%	+25%		+1%
<b>1996</b>									
$\Sigma$	729	607	450	496	410	326	↓234	↓198	↓124
$\Delta$	+20%		-26%	+21%		-21%	+18%		-37%
<b>1997</b>									
$\Sigma$	570	494	371	486	408	328	↓84	↓86	↓44
$\Delta$	+15%		-25%	+19%		-20%	-3%		-49%
<b>1998</b>									
$\Sigma$	687	587	443	531	446	359	↓156	↓141	↓84
$\Delta$	+17%		-25%	+19%		-20%	+11%		-40%
<b>1999</b>									
$\Sigma$	551	474	362	501	420	341	↓51	↓53	↓21
$\Delta$	+16%		-24%	+19%		-19%	-5%		-61%

P, Present Condition; GEP, gross ecosystem production; ER, ecosystem respiration; NEE, net ecosystem exchange;  $\Sigma$ , cumulative seasonal flux ( $\text{g CO}_2 \text{ m}^{-2}$ );  $\Delta$ , percentage change in flux;  $\uparrow$ , net exchange of  $\text{CO}_2$  to the atmosphere;  $\downarrow$ , net exchange of  $\text{CO}_2$  to the wetland

### Climate change scenario

Climate models forecast warming at high latitudes given a  $2 \times \text{CO}_2$  scenario. There is great uncertainty surrounding the expected changes in precipitation both in magnitude and frequency. In these scenarios a  $4^\circ\text{C}$  warming is assumed with a  $\pm 30\%$  increase in precipitation of the

observed rainfall from each season. The transient response considers conditions where no change in aboveground biomass occurs. The equilibrium response case assumes that the vascular canopy has adjusted to a lower water table position, longer growing season, and increased nutrient turnover. Although the present model does not account for nutrient changes explicitly, it is assumed that LAI is enhanced under a  $2 \times \text{CO}_2$  scenario

**Table 3** Sensitivity of GEP, ER, and NEE to a  $\pm 30\%$  change in precipitation magnitude

Year	GEP		ER		NEE				
	+30%; P	-30%	+30%	P	-30%	+30%	P	-30%	
<b>1994</b>									
$\Sigma$	303	291	278	375	377	378	↑72	↑86	↑100
$\Delta$	+4%		-5%	-0.5%		+0.3%	-12%		+16%
<b>1996</b>									
$\Sigma$	615	607	594	404	410	415	↓211	↓198	↓179
$\Delta$	+1%		-2%	-2%		+1%	+6%		-10%
<b>1997</b>									
$\Sigma$	505	494	480	400	408	415	↓107	↓86	↓65
$\Delta$	+2%		-3%	-2%		+2%	+24%		-24%
<b>1998</b>									
$\Sigma$	598	587	470	441	446	430	↓157	↓141	↓41
$\Delta$	+2%		-20%	-1%		-4%	+11%		-71%
<b>1999</b>									
$\Sigma$	482	474	462	420	420	422	↓62	↓53	↓41
$\Delta$	+2%		-3%	0		+0.5%	+15%		-23%

P, Present Condition; GEP, gross ecosystem production; ER, ecosystem respiration; NEE, net ecosystem exchange;  $\Sigma$ , cumulative seasonal flux (g CO<sub>2</sub> m<sup>-2</sup>);  $\Delta$ , percentage change in flux; ↓, net exchange of CO<sub>2</sub> to the atmosphere; ↑, net exchange of CO<sub>2</sub> to the wetland

as a result of greater nutrient availability (Griffis *et al.* 2000b). The Equilibrium change assumes a 50% increase in LAI.

#### Transient 2 × CO<sub>2</sub> response

The warm and wet scenario (WW) produced greater carbon sequestration in all years excluding the 1994 season. Increases ranged from 10% in 1999 to 25% in 1996 (Table 6). The large increase in 1996 is attributed to the increase in air temperature resulting in more frequent optimum conditions for photosynthesis. GEP increased by 21% and ER increased by 19%. Increases in GEP were larger than ER in all years excluding the 1999 season.

The warming and drying scenario (WD) accelerated the net loss of carbon at the fen in 1994. Increased ER exceeded the gains in GEP. During 1996, the fen gained carbon despite the drier conditions. This substantiates the proposition that cold temperatures limited GEP. However, 1997, 1998 and 1999 all experienced large reductions in net carbon acquisition, as a consequence of large increases in ER relative to GEP. In 1998, the decreased moisture and higher temperatures caused an earlier senescence of the vascular canopy resulting in a 4% GEP decrease.

#### Equilibrium 2 × CO<sub>2</sub> response

In all cases the equilibrium response (EQ) showed substantial increases in carbon acquisition. In each of the sink years carbon acquisition increased between 43 and 240% (Table 6). GEP increased between 28 and 54%. Again, the largest increase in GEP was observed in the 1996 season owing to the warmer temperatures and more frequent optimum photosynthetic temperature. Increases in ER were substantial and ranged from 23 to 33%. The 1994 season remained a net source of CO<sub>2</sub> to the atmosphere. Despite having greater leaf area, the dry surface conditions caused ER to exceed GEP. This suggests that increased above-ground biomass in response to drier conditions may not be sufficient to change these ecosystems from sources to sinks of atmospheric carbon under extremely dry conditions.

## Discussion

### Model performance

The NEE model presented here can predict, on a seasonal basis, the strong sink and source years and therefore can be used as a tool to help explain observations and hypotheses surrounding the interannual variability of CO<sub>2</sub> exchange. The model performance is highly sensitive to assumptions made herein about moss moisture content and its impact on photosynthesis, and descriptions of phenology, fitness and plant growth. These factors will require further field study in order to improve these model algorithms.

### Interannual variability

The interannual variability in NEE at the Churchill fen results from phenological and hydroclimatic variations. In an environment with a relatively short growing season, the impact of daily weather and climate on phenology is pronounced. During 1993, autumn and winter precipitation at Churchill failed to restore the summer water deficit (Rouse 1998; Schreuder *et al.* 1998). Early snowmelt, coupled with high evaporation rates in the spring of 1994 reduced the photosynthetic capacity of the wetland, and the vascular species experienced premature dormancy (Fig. 11a). Cumulative GEP from the moss and vascular plants was approximately 130 and 110 g CO<sub>2</sub> m<sup>-2</sup>, respectively. While cumulative soil and plant respiration was 300 and 40 g CO<sub>2</sub> m<sup>-2</sup>, respectively.

The 1998 growing season provides a marked contrast to the 1994 season. Heavy rains during the 1997 autumn season recharged the soil moisture reservoir prior to freeze back. Relatively warm winter and spring tem-

**Table 4** Sensitivity of GEP, ER, and NEE to a change in precipitation distribution and frequency

Year	GEP			ER			NEE		
	ES	P	LS	ES	P	LS	ES	P	LS
<b>1994</b>									
$\Sigma$	384	291	275	397	377	377	↑13	↑86	↑101
$\Delta$	+32%		-6%	+5%		0%	-85%		+17%
<b>1996</b>									
$\Sigma$	582	607	556	418	410	422	↓165	↓198	↓135
$\Delta$	-4%		-8%	+2%		+3%	-17%		-32%
<b>1997</b>									
$\Sigma$	494	494	466	413	408	418	↓80	↓86	↓49
$\Delta$	0%		-7%	+1%		+3%	-7%		-43%
<b>1998</b>									
$\Sigma$	610	587	414	442	446	410	↓167	↓141	↓4
$\Delta$	+4%		-30%	-1%		-8%	+18%		-97%
<b>1999</b>									
$\Sigma$	623	474	454	444	420	419	↓179	↓53	↓35
$\Delta$	+31%		-4%	+5%		-0.2%	+70%		-34%

P, Present Condition; ES, wet early summer and dry late summer; LS, wet late summer and dry spring; GEP, gross ecosystem production; ER, ecosystem respiration; NEE, net ecosystem exchange;  $\Sigma$ , cumulative seasonal flux ( $\text{g CO}_2 \text{ m}^{-2}$ );  $\Delta$ , percentage change in flux;  $\uparrow$ , net exchange of  $\text{CO}_2$  to the atmosphere;  $\downarrow$ , net exchange of  $\text{CO}_2$  to the wetland

peratures following the 1997/1998 El Niño phenomenon (Griffis *et al.* 2000a) caused an early snowmelt and greater than normal spring precipitation. The wet and warm surface conditions during the pregreen and early green period caused large photosynthetic fluxes from the moss-covered surfaces and also allowed early leaf development in the vascular plants (Fig. 11d). Cumulative GEP from the moss and vascular plants was 190 and 400  $\text{g CO}_2 \text{ m}^{-2}$ , respectively. Soil and plant respiration accounted for about 300 and 100  $\text{g CO}_2 \text{ m}^{-2}$ , respectively. The early breaking of dormancy during favourable growing conditions appears to have helped the vascular canopy withstand the drier summer conditions experienced later in the growing season (Griffis *et al.* 2000a). Scott *et al.* (1997) have also suggested that early spring hydroclimatic conditions are critical to the growth of trees at treeline in the vicinity of Churchill.

Sink years, however, are not always associated with early leaf development. In 1996, late snowmelt and cool spring conditions prevented early leaf development. Carbon acquisition in this particular year was large as a result of high productivity of the mosses early in the season and from the vascular plants later in the season (Fig. 11b). Moss and vascular GEP was 300 and 340  $\text{g CO}_2 \text{ m}^{-2}$ , respectively.

**Table 5** Sensitivity of GEP, ER, and NEE to change a  $\pm 10\%$  in leaf area index

Year	GEP		ER		NEE		
	+10%	P	-10%	+10%	P	-10%	+10%
<b>1994</b>							
$\Sigma$	302	291	279	379	377	374	↑77
$\Delta$	+4%		-4%	+0.5%		-0.8%	-11%
<b>1996</b>							
$\Sigma$	638	607	576	415	410	403	↓223
$\Delta$	+5%		-5%	+1%		-1%	+13%
<b>1997</b>							
$\Sigma$	518	494	469	413	408	403	↓105
$\Delta$	+5%		-5%	+1%		-1%	+22%
<b>1998</b>							
$\Sigma$	626	587	548	453	446	438	↓173
$\Delta$	+6%		-7%	+2%		-2%	+23%
<b>1999</b>							
$\Sigma$	502	474	445	425	420	415	↓77
$\Delta$	+6%		-6%	+1%		-1%	+45%

P, Present Condition; GEP, gross ecosystem production; ER, ecosystem respiration; NEE, net ecosystem exchange;  $\Sigma$ , cumulative seasonal flux ( $\text{g CO}_2 \text{ m}^{-2}$ );  $\Delta$ , percentage change in flux;  $\uparrow$ , net exchange of  $\text{CO}_2$  to the atmosphere;  $\downarrow$ , net exchange of  $\text{CO}_2$  to the wetland

Water table position and soil moisture content play a key role in controlling the dormancy and phenology of the fen vegetation. Dry surface conditions can cause mosses to lie dormant until rewetting, and low soil moisture content can trigger the dormancy of vascular plants as in 1994 and 1999. The idea of plant fitness or biological vigour (the relationship between phenology and hydroclimatic conditions) is a qualitative parameter used in the present model to help explain the complex interaction between plant growth and mortality rates as determined by early season hydroclimatic conditions during the time that dormancy is broken. There is currently a lack of understanding of these fitness relationships.

#### Sensitivity of NEE to climate

Model sensitivity analysis illustrates that the response of NEE to changes in the environmental variables is dependent on the initial conditions of the wetland. The strength of the NEE response to individual variables varies considerably between the years. In general, warmer temperatures act to increase GEP more than ER. This evidence supports the hypothesis of Griffis *et al.* (2000a) and the explanation that the interannual variability in NEE is largely manifest in GEP. The effect of increased temperature on GEP is more pronounced in cooler and wetter years such as the 1996 season. These

**Table 6** Transient and equilibrium response of GEP, ER, and NEE to climate change scenarios

Year	GEP				ER				NEE			
	WW	P	WD	EQ	WW	P	WD	EQ	WW	P	WD	EQ
<b>1994</b>												
$\Sigma$	351	291	328	410	446	377	450	466	↑95	↑86	↑122	↑57
$\Delta$	+21%		+13%	+41%	+18%		+19%	+24%	+11%		+42%	-34%
<b>1996</b>												
$\Sigma$	736	607	716	932	489	410	502	547	↓247	↓198	↓215	↓386
$\Delta$	+21%		+18%	+54%	+19%		+22%	+33%	+25%		+9%	+95%
<b>1997</b>												
$\Sigma$	581	494	556	715	477	408	494	527	↓104	↓86	↓162	↓188
$\Delta$	+18%		+13%	+45%	+17%		+21%	+29%	+17%		-28%	+119%
<b>1998</b>												
$\Sigma$	701	587	561	753	527	446	512	550	↓175	↓141	↓49	↓202
$\Delta$	+16%		-4%	+28%	+18%		+15%	+23%	+19%		-65%	+43%
<b>1999</b>												
$\Sigma$	559	474	540	720	500	420	503	539	↓59	↓53	↓38	↓181
$\Delta$	+15%		+14%	+52%	+19%		+20%	+28%	+10%		-28%	+240%

P, Present Condition; GEP, gross ecosystem production; ER, ecosystem respiration; NEE, net ecosystem exchange;  $\Sigma$ , cumulative seasonal flux (g CO<sub>2</sub> m<sup>-2</sup>);  $\Delta$ , percentage change in flux; WW, warm and wet scenario (+4 °C and +30% P); WD, warm and dry scenario (+4 °C and -30% P); EQ, equilibrium climate change (+4 °C and -30% P and +50% LAI); ↑, net exchange of CO<sub>2</sub> to the atmosphere; ↓, net exchange of CO<sub>2</sub> to the wetland

results support the idea that arctic ecosystems photosynthesize below their temperature optimum over the majority of the growing season.

Precipitation distribution and frequency of precipitation events are important factors controlling the inter-annual variability in NEE. In seasons such as 1994, 1997 and 1999, mid- to late-season precipitation events failed to increase the CO<sub>2</sub> acquisition of the fen. However, 1998 illustrates how wet spring conditions can lead to greater CO<sub>2</sub> acquisition through much of the growing period even when drier conditions persist. The sensitivity of the modelled NEE agrees with these field observations. In all simulations, excluding the 1996 season, increased frequency of precipitation events early in the growing season lead to greater carbon acquisition over the course of the growing season.

#### *Climatic change and net ecosystem CO<sub>2</sub> exchange*

The historical rate of carbon acquisition by northern peatlands has been estimated at about -29 g C m<sup>-2</sup> y<sup>-1</sup> (Gorham 1991). At the Churchill fen, carbon gain has been approximately -7 g C m<sup>-2</sup> y<sup>-1</sup> over its 2200-year history. However, the contemporary annual CO<sub>2</sub> balance of the Churchill fen is potentially a net loss based on the five growing seasons of data and the estimated non-growing season respiration losses reported in Griffis *et al.* (2000a). The recent trend suggests that carbon loss is

proceeding at a rate of nearly three times the historical gain. It would appear, therefore, that hydroclimatic conditions have changed resulting in reduced carbon acquisition and frequent net loss at the fen. This hypothesis assumes that vegetation has not changed significantly and that interannual differences in phenology and plant fitness balance over longer time scales. Preliminary macrofossil analyses (Cristine 1998) confirm that the fen has been composed of mosses and sedges throughout its history. This suggests that hydroclimatic conditions may be the causal mechanism of the contemporary change from net sink to net source.

Modelled net ecosystem CO<sub>2</sub> exchange response to climatic change scenarios indicate that warmer and wetter conditions would promote greater carbon acquisition at this fen site. Given that the local area is rising following isostatic rebound (currently 0.01 m y<sup>-1</sup>), improved drainage could be impacting the surface water budget, thereby influencing the long-term CO<sub>2</sub> balance. The contemporary trend of reduced carbon gain and perhaps switch to carbon loss suggests a progression toward drier conditions than in the past. Reduction in both summer and winter precipitation may be important for the recent trend in CO<sub>2</sub> exchange. Payette & Morneau (1993) and Gajewski *et al.* (1993), using palaeoclimate reconstructions from the Eastern Arctic, argue that climate in the region was warmer and more humid during the late Holocene with cooling and increased occurrence of fire during the last

millennium. It may be that the Hudson Bay Lowland peat complex stored the majority of its carbon during its early developmental phases.

## Conclusions

Model simulations and landscape-scale measurements of NEE substantiate the importance of spring hydroclimatic conditions on growing season Net Ecosystem CO<sub>2</sub> Exchange. Warm surface temperatures combined with wet soil conditions in the early growing season increase above ground biomass and carbon acquisition throughout the summer season. Sensitivity analysis supports the contention that warmer and wetter conditions are optimal for carbon acquisition at this northern wetland. If climatic warming is characterized by greater winter and summer precipitation, northern wetlands should therefore become larger sinks for atmospheric CO<sub>2</sub>.

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## Appendix A

Table A1. Model variables and parameters

Variable	Parameter	Value	Units
QeP	a <sub>1</sub>	0.59	-
	a <sub>2</sub>	1.08	-
Rs	b <sub>1</sub>	0.80	-
	b <sub>2</sub>	0.50	-
Wa	wa <sub>max</sub>	1.0	-
	c <sub>1</sub>	1.0	-
	c <sub>2</sub>	0.01	-
	c <sub>3</sub>	0.07	-
ds		0.36 to 0.06	m
SY			m
WT			m <sup>3</sup> m <sup>-3</sup>
Θs	d <sub>1</sub>	0.60	-
	d <sub>2</sub>	0.28	-
	d <sub>3</sub>	4.4	-
LAI	G <sub>1</sub>	0.02	m <sup>2</sup> m <sup>-2</sup>
	LAI <sub>max</sub>	0.60	m <sup>2</sup> g <sup>-1</sup> C
AmQ			m <sup>2</sup> m <sup>-2</sup>
Pm	Pm <sub>max</sub>	13.0	g CO <sub>2</sub> m <sup>-2</sup> d <sup>-1</sup>
	φ <sub>m</sub>	0.044	g CO <sub>2</sub> m <sup>-2</sup> d <sup>-1</sup>
QmΘ	k <sub>m</sub>	0.9	g CO <sub>2</sub> m <sup>-2</sup> d <sup>-2</sup>
	h <sub>1</sub>	0.003	umol <sup>-1</sup> PAR
	h <sub>2</sub>	0.025	-
AvQ		6.9	-
	Pv <sub>max</sub>	39.0	g CO <sub>2</sub> m <sup>-2</sup> d <sup>-1</sup>
	0 <sub>v</sub>	0.069	g CO <sub>2</sub> m <sup>-2</sup> d <sup>-1</sup>
gs	k <sub>v</sub>	0.85	g CO <sub>2</sub> m <sup>-2</sup> d <sup>-2</sup>
	gs <sub>max</sub>	1312.4	umol <sup>-1</sup> PAR
gs(Ts)	m <sub>1</sub>	-2399.2	mmol s <sup>-1</sup> m <sup>-2</sup>
	m <sub>2</sub>	335.2	-
	m <sub>3</sub>	-8.1	-
gs(vpd)	n <sub>1</sub>	1312.4	-
	n <sub>2</sub>	-237.6	-
gs(φs)	p <sub>1</sub>	1285.2	-
	p <sub>2</sub>	265.7	-
R <sub>h</sub>	R <sub>hmax</sub>	9.1	g CO <sub>2</sub> m <sup>-2</sup> d <sup>-1</sup>
R <sub>h</sub> (Ts)	q <sub>1</sub>	1.5	g CO <sub>2</sub> m <sup>-2</sup> d <sup>-1</sup>
	q <sub>2</sub>	0.25	-

R <sub>h</sub> (Θs)			-
	v <sub>1</sub>	26.5	-
	v <sub>2</sub>	-25.0	-
GEP			g CO <sub>2</sub> m <sup>-2</sup> d <sup>-1</sup>
ER			g CO <sub>2</sub> m <sup>-2</sup> d <sup>-1</sup>
NEE			g CO <sub>2</sub> m <sup>-2</sup> d <sup>-1</sup>

All coefficients (excluding G1 and LAI<sub>max</sub> were estimated using linear or non-linear least squares regression.

Table A2. Initial conditions for each model simulation

Year	Date of snowmelt	Initial water table height	Fitness condition
1994	10 May	- 0.01 m	2
1996	1 June	0.058 m	1
1997	5 June	0.079 m	1
1998	12 May	0.002 m	3
1999	22 April	- 0.005 m	3