

Interannual variability of net ecosystem CO₂ exchange at a subarctic fen

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Abstract. Landscape-scale net ecosystem CO₂ exchange (NEE) and the energy balance of a subarctic fen were studied during five growing seasons near Churchill, Manitoba. Interannual variability in NEE was large and ranged from a net sink of -235 g CO₂ m⁻² in 1996 to a net source of +76 g CO₂ m⁻² in 1994. Annual estimates of CO₂ exchange indicate that during the present period the fen is losing carbon nearly 3 times faster than its long-term historical gain of about -11 g CO₂ m⁻² yr⁻¹. Our estimates suggest that gross ecosystem photosynthesis may be more variable than ecosystem respiration on diurnal, seasonal, and interannual timescales. Our data strongly indicate that an early snowmelt combined with wet and warm conditions during the spring period lead to large carbon acquisition even when drier conditions were experienced over the majority of the growing season. The phenological stage of the vegetation relative to the climatic conditions experienced is an important cause of the interannual variability in NEE. An accurate representation of phenology in climate models is, therefore, critical to the success of forecasting the carbon budgets of northern wetlands.

1. Introduction

Northern wetlands are an important sink of atmospheric CO₂. They contain approximately one third of the total global soil carbon pool [Gorham, 1991] and represent 60% of the carbon currently stored in the atmosphere [Sundquist, 1993]. Stored carbon in northern wetlands is vulnerable to climatic change [Oechel *et al.*, 1993]. General circulation models (GCMs) forecast warming and decreased soil moisture at higher latitudes [Kattenberg *et al.*, 1996], which will accelerate the decomposition of organic material and the efflux of CO₂ to the atmosphere [Billings *et al.*, 1987a; Moore *et al.*, 1998]. However, increased carbon acquisition resulting from a longer growing season, warmer air temperatures, and increased nutrient turnover could offset this initial increase in decomposition [Oechel and Billings, 1992]. Northern wetlands therefore represent an important biosphere feedback to global climate through the CO₂ - greenhouse effect.

The Hudson Bay Lowland is the second largest contiguous wetland in the world, yet few studies [Neumann *et al.*, 1994; Burton *et al.*, 1996; Schreader *et al.*, 1998; Lafleur, 1999] have examined the CO₂ sink/source magnitudes in this environment. A limited number of studies [Coyne and Kelley, 1975; Fan *et al.*, 1992; Vourlitis and Oechel, 1997; McFadden *et al.*, 1998] have investigated landscape-scale net ecosystem CO₂ exchange (NEE) at other high latitude wetlands. Coyne and Kelley [1975], Fan *et al.* [1992], and Vourlitis and Oechel [1997] working in Alaskan arctic tundra observed a small net acquisition of CO₂ over the growing season, while Burton *et al.* [1996] and Schreader *et al.* [1998] reported significant growing-season losses of CO₂ from a fen site located within the Hudson Bay Lowland (Table 1).

The biophysical processes regulating CO₂ exchange in these ecosystems are complex, and identifying the causal mechanism(s) of interannual variability in CO₂ flux is difficult to assess. NEE is the difference between the efflux of CO₂ resulting from ecosystem respiration (ER) and carbon acquisition through gross ecosystem photosynthesis (GEP). ER is comprised of both heterotrophic soil respiration and autotrophic dark respiration resulting from plant growth and tissue maintenance [Oechel and Billings, 1992; Oberbauer *et al.*, 1992; Moore *et al.*, 1998]. Experimental evidence and field observations indicate that lower water table position and drier soil conditions enhance organic decomposition and increase the rate of ER to the atmosphere [Billings *et al.*, 1983; Peterson *et al.*, 1984; Oechel *et al.*, 1993, 1995]. Plant and root respiration, which may account for 30 to 70% of ER in arctic ecosystems [Semikhatova *et al.*, 1992; Silvola *et al.*, 1996; Bhardwaj, 1997] is affected by environmental factors such as temperature but is more strongly related to the growth stage of the plant [Semikhatova *et al.*, 1992]. Bubier *et al.* [1998] have shown that ER accounts for 33% of GEP under high light conditions and that this relationship varies seasonally as soil moisture, surface temperature, and plant phenology change. Furthermore, ER is affected by the nutrient status of the substrate. Organic material with higher nutrient levels are decomposed and consumed more rapidly than substrates of poor nutrient quality [Moore *et al.*, 1998].

Photosynthesis in arctic plants has been found to range between 10 and 20 g CO₂ m⁻² d⁻¹ [Semikhatova *et al.*, 1992]. The spatial and temporal variability observed in GEP is attributed to plant type, growth stage, nutrient conditions, and variations in soil moisture, photosynthetically active radiation (PAR), and temperature [Green and Lange, 1994; Bubier *et al.*, 1998; Waddington *et al.*, 1998; Griffis *et al.*, 2000]. Vourlitis and Oechel [1997] have shown that the dependence of GEP and NEE on PAR and temperature is strongly correlated to the seasonal development of these ecosystems. The timing of leafout is a major event in the CO₂ balance and is often correlated with a

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Table 1. Landscape-Scale Estimates of Σ NEE and Daily NEE for Northern, Subarctic and Arctic Wetlands

Site	Duration	Σ NEE	Daily	Study
Churchill Manitoba. Fen (58°N, 94°W)	July to Aug. 1993 (27 days)	+30	+1.1	<i>Burton et al.</i> , [1996]
Churchill Manitoba. Fen (58°N, 94°W)	June to Aug. 1994 (75 days)	+76	+1.0	<i>Schreader et al.</i> , [1998]
Churchill Manitoba. Fen (58°N, 94°W)	June to Aug. 1996 (75 days)	-235	-3.1	This study
Churchill Manitoba. Fen (58°N, 94°W)	June to Aug. 1997 (75 days)	-49	-0.7	
Churchill Manitoba. Fen (58°N, 94°W)	June to Aug. 1998 (75 days)	-229	-3.1	
Churchill Manitoba. Fen (58°N, 94°W)	June to Aug. 1999 (72 days)	-34	-0.5	
Thompson Manitoba. Fen (56°N, 98°W)	May to Sept. 1996 (124)	-120	-1.0	<i>Joiner et al.</i> , [1999]
Thompson Manitoba. Fen (56°N, 98°W)	May to Sept. 1994 (124 days)	+40	+0.3	<i>Lafleur et al.</i> , [1997]
Prince Albert Saskatchewan. Fen (53°N, 105°W)	May to Oct. 1994 (136 days)	-366	-2.7	<i>Suyker et al.</i> , [1997]
Alaska U-Pad. Sedge Tundra (70°N, 148°W)	June to Aug. 1994 (90 days)	-66	-0.7	<i>Vourlitis and Oechel</i> [1997]
Alaska U-Pad. Sedge Tundra (70°N, 148°W)	May to Sept. 1995 (90 days)	-48	-0.5	
Alaska 24-Mile. Sedge Tundra (70°N, 148°W)	June to Aug. 1995 (77 days)	-101	-1.3	
Barrow Alaska Wet Tundra (71°N 160°W)	June to July. 1971 (20 days)	-69	-3.5	<i>Coyne and Kelley</i> [1975]
Lake Kinosheo, Ontario Bog (51°N, 81°W)	June to July. 1990 (33 days)	-56	-1.7	<i>Neumann et al.</i> , [1994]
Northern Minnesota. Bog (47°N 93°W)	May to Oct. 1991 (145 days)	+123	+0.9	<i>Shurpali et al.</i> , [1995]
Northern Minnesota. Bog (47°N 93°W)	May to Oct. 1992 (145 days)	-55	-0.4	
Bethel Alaska Mixed Tundra (61°N, 162°W)	July to Aug. 1988 (30 days)	+9	+0.3	<i>Fan et al.</i> , [1992]

Σ NEE is g CO₂ m⁻²; Daily NEE is given in g CO₂ m⁻² d⁻¹.

change from a net loss to a net gain of CO₂ in fens [*Schreader et al.*, 1998]. This is especially important in arctic ecosystems where the growing season is typically less than four months in duration [*Burton et al.*, 1996; *Lafleur et al.*, 1997; *Schreader et al.*, 1998]. Growing season GEP may also be limited by a large soil moisture deficit [*Green and Lange*, 1994] and low air temperatures [*Semikhatova et al.*, 1992].

Daily variability in the overlying meteorological conditions can also have a strong influence on GEP. Synoptic analysis of surface pressure coupled with field measurements of CO₂ exchange have shown that GEP at a subarctic fen near Churchill Manitoba is most efficient when anticyclones are positioned to the east of the study site. These synoptic conditions are associated with clear skies and the advection of warm southerly air into the region providing near optimal temperatures for photosynthesis [T. J. Griffis, R. Petrone, and W. R. Rouse, A synoptic climatological analysis of net ecosystem CO₂ exchange at a subarctic fen, submitted to *Arctic, Ant. Alpine Res.*, 2000]. Furthermore, *Frolking* [1997], using a boreal forest model, showed that NEE is strongly sensitive to the pattern and timing of weather events. The link between climate and the biophysical processes operating in these ecosystems indicate that climatic variability should be the key factor in determining the CO₂ sink and source strength of these ecosystems.

At present, the amount of interannual variability in growing season NEE and its cause is speculative for these ecosystems [*Vourlitis and Oechel*, 1997] due to a scarcity in landscape-scale observations. As a result, our understanding of the sensitivity of CO₂ exchange to climatic variability for these landscapes is limited. There are two main problems that arise from this limitation. First, estimates of CO₂ exchange between northern wetlands and the atmosphere under future climate change scenarios are difficult to quantify, and second the development and validation of carbon exchange models for these environments is lacking.

This paper examines the sensitivity of landscape-scale NEE at a subarctic fen to climatic variability during five growing seasons. The variability in NEE is investigated by quantifying the

changes in GEP and ER through each of the five seasons and by qualitatively relating these changes to key environmental factors of temperature, precipitation, radiation, water deficit, and soil moisture content.

2. Site and Methods

2.1. Research Site

The experimental area is located on the southwestern shore of Hudson Bay, within the Hudson Bay Lowland (Figure 1). Patches of open woodland near the experimental area mark the edge of the northern boreal tree line and the transition to large expanses of open tundra. The region is underlain by continuous permafrost. Hudson Bay has a strong influence on the regional climate and energy balance during the growing season through the advection of cold moist air [*Rouse*, 1991].

The research site is an extensive fen and is 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. Detailed surveying within a 150 m radius of the main micrometeorological measurement tower indicates that small hummocks comprise 47%, hollows comprise 48%, and large hummocks comprise 5% of the landscape with respect to the water table position. The maximum difference in vertical height between large hummocks and hollows is ~ 0.75 m. The configuration and height of the hummocks and hollows determines the depression storage of surface water. A maximum amount of water storage occurs at a mean height of 0.08 m above the base of the hollows (depression storage surface) [*Rouse*, 1998]. As the water table rises above this equilibrium level, lateral drainage of water begins. The water table disappears below the hollow surfaces at a height of -0.08 m relative to the equilibrium storage level.

Average water table height relative to the hummocks and hollows has an important influence on the distribution of vegetation [*Billings*, 1987b; *Bubier et al.*, 1995]. At this fen, brown moss (*Scorpidium turgescens*) is the dominant vegetation found in the wet hollows. Small hummocks exhibit a limited

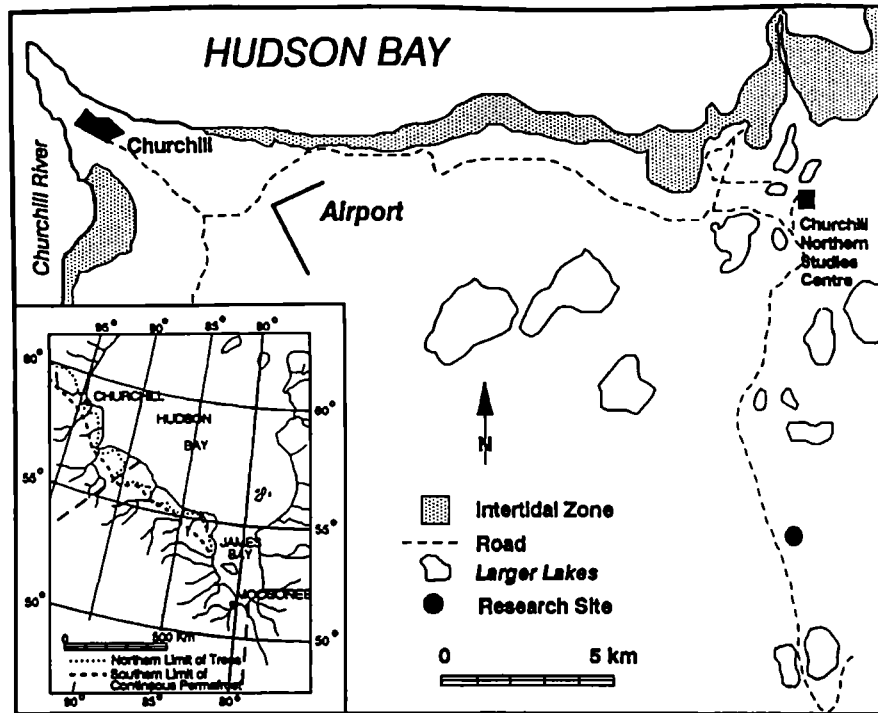


Figure 1. Location of research area and site.

moss cover (*Tomenthypnum nitens*) but are dominated by the vascular species *Carex aquatilis*, *C. limosa*, *C. saxatilis*, and *C. gynocrates*. Larger hummocks support vascular species (*Betula glandulosa*, *Ledum decumbens*, *Salix arctophila* or *Carex* spp.) and nonvascular species of lichen (*Cladina stellaris* and *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. The regional landscape continues to respond to isostatic rebound following the last glaciation. Elevation increase at the research site is ~ 0.01 m yr^{-1} . At present, the fen is ~ 22 m above sea level, and therefore it is estimated that vegetation and peat development was initiated ~ 2200 years ago. The historical rate of carbon accumulation for the fen is estimated at $11 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$.

2.2. Measurement

Measurements in all seasons are similar to those described by Schreader *et al.* [1998]. The Bowen ratio energy balance approach (BREB) was used to calculate the energy balance over the fen. Temperature and vapor pressure profiles were measured with wet-and dry-bulb psychrometers. The sensors were mounted at heights of 0.35, 0.70, 1.10, 1.60, 2.30, and 3.20 m. A wind speed profile was measured using cup anemometers mounted at the same heights. Wind direction was measured at a height of 3.5 m. Data logger sampling was every 2 s, and the averaging period was 0.5 hour. Precipitation was recorded daily using a standard rain gauge and half-hourly with a tipping bucket rain gauge. Water table position was measured relative to the equilibrium water storage level at a manual well and recorded continuously with a float-potentiometer system. Volumetric soil moisture was measured using a water content reflectrometer (CS615, Campbell

Scientific) during 1997, 1998, and 1999. Volumetric soil moisture was measured gravimetrically in 1994 and 1996 and also modeled as an exponential function of water table position ($R^2 = 0.88$)

$$\theta_v = 0.60 + 0.28e^{4.4WT}, \quad (1)$$

where θ_v is the volumetric soil moisture content and WT is the water table position in meters. Net radiation Q^* was measured at a height of 3 m above ground using a Middleton net pyrradiometer. Ground heat flux was measured with four Middleton heat flux plates, which were arranged to give a spatially representative flux. The calorimetric ground heat flux calculation was used to correct the heat flux plate measurements following Halliwell and Rouse [1987] to correct for inconsistencies in thermal conductivity and poor thermal contact between the heat flux plates and the organic soil.

2.3. Net CO₂ Flux Calculation

The theory and methodology for calculating the net CO₂ flux F_c using gradient techniques has been described previously by Burton *et al.* [1996] and Schreader *et al.* [1998]. F_c is derived from the following expression:

$$F_c = -K_c \frac{\partial \rho_c}{\partial z}, \quad (2)$$

where K_c is the turbulent transfer coefficient for CO₂ and $\partial \rho_c / \partial z$ is the time-averaged vertical gradient of CO₂ concentration. K_c is assumed identical to the turbulent transfer coefficient K_h and is derived from the basic energy balance equations,

$$K_c = K_h = \frac{-Q_h}{\left(\frac{\partial T}{\partial z}\right) C_p \rho_a}, \quad (3)$$

where Q_h is the sensible heat flux, $\partial T/\partial z$ is the vertical temperature gradient, C_p is the atmospheric heat capacity, and ρ_a is the air density. Q_h is calculated from the Bowen ratio energy balance expression

$$Q_e = \frac{Q^* - Q_g}{1 + \beta}, \quad (4)$$

where Q_e is the latent heat flux, and $\beta = Q_h/Q_e = \gamma \Delta T/\Delta e$ is the Bowen ratio, γ is the psychrometric constant, and ΔT and Δe are obtained from finite differences in air temperature and vapor pressure measured at their respective levels. Q_h can be calculated as a residual of the energy balance equation

$$Q_h = Q^* - Q_e - Q_g. \quad (5)$$

CO₂ concentrations were measured at the same height intervals as for temperature, vapor pressure, and wind speed. Air from the six levels was drawn through equal length tubing into 1L buffer sample volumes. Buffer volume air was continuously replenished by the pumping system. Sequential sampling from the six buffer volumes was controlled with a solenoid-actuated valve manifold system. Samples were analyzed on an infrared gas analyzer (LI-COR 6262). A time interval of 1 min was used to determine the CO₂ concentration from the six buffer volumes. The net CO₂ flux was calculated from 0.5 hour time averaging and corrected for density variations resulting from the latent heat flux [Webb *et al.*, 1980]. A correction for sensible heat flux was omitted since the samples from each level were analyzed at the same constant temperature [Burton *et al.*, 1996]. Owing to the remote location of the research site, all instrumentation was powered by 12 V storage batteries and charged with a wind generator and solar panels.

2.4. Measurement Accuracy

CO₂ flux measurements derived from the gradient approach are prone to substantial errors resulting from fetch limitations, determination of the turbulent transfer coefficient K_c , and systematic bias in one or more of the measuring sensors. Schreader *et al.*, [1998] give a detailed discussion of these errors, which is summarized as follows.

The measurements were made over a large homogeneous fen with a minimum fetch of 2500 m in the southerly direction. Analysis indicates that 80% of the flux footprint lies within 238 m of the tower and that the most sensitive distance is at 26.5 m from the tower [Schreader *et al.*, 1998]. Calculating the turbulent transfer coefficients K_h and K_c from BREB- Q_h can be problematic when Q^* is small such as at night or during sunrise or sunset. At these times, temperature and humidity gradients tend to be small, and β is often unreliable. Under these conditions K_h has been derived from either the aerodynamic or eddy covariance calculation of Q_h . These data have been provided from micrometeorological stations located at the same site. This approach has been successful due to the relatively vigorous nocturnal wind speeds typically experienced at Churchill. Systematic bias in the sensors has been remedied by using a multiple level flux calculation scheme and software package originally described by Halliwell and Rouse [1989] to test for measurement error and boundary layer problems. However, under calm conditions, K_h is unreliable and the fluxes must be interpolated. Data interpolation used in this study were based on half-hour ensemble averages computed from measured data during the early, middle, and late growing season periods.

The magnitude of the error in F_c resulting from the propagation of errors in the calculation of the energy balance and turbulent transfer coefficient K_h can be estimated using the root mean squared error method (RMSE) outlined by Bevington [1969]. This approach estimates the error in F_c by examining the partial derivatives of F_c (proportionality constants) with respect to each of its dependent variables

$$\Delta F_c = \Delta \left(\frac{d\rho_c}{dz} \right) \frac{\partial F_c}{\partial \left(\frac{d\rho_c}{dz} \right)} + \Delta K_h \left(\frac{\partial F_c}{\partial K_h} \right) \frac{d\rho_c}{dz}. \quad (6)$$

The error propagating through the calculation of F_c can therefore be estimated as

$$\delta F_c = \sqrt{\left[\left(\frac{d\rho_c}{dz} \delta K_h \right)^2 + \left(K_h \frac{d\rho_c}{dz} \frac{\partial G}{\partial C} \right)^2 \right]} \quad (7)$$

where δK_h is the 19% error calculated for K_h and $\partial G/\partial C$ is the 0.3% error in measuring the CO₂ concentration gradient at 350 $\mu\text{mol/mol}$. The second term in equation 7 can be neglected since the random error in measuring CO₂ cancels with time and the systematic bias between levels is offsetting when calculating the finite difference in CO₂ concentration. We estimate a relative maximum probable error of 24% for the measurement of F_c . Further confidence in the quality of CO₂ flux measurements at this site is provided by good agreement between chamber fluxes of net ecosystem CO₂ exchange with the landscape scale micrometeorological measurements [Griffis *et al.*, 2000].

2.5. Estimating Ecosystem Respiration and Gross Ecosystem Photosynthesis

Soil and plant root respiration has been shown to correlate with near-surface temperature [Waddington *et al.*, 1998]. As well, ER increases linearly with lower water table position, which has a direct effect on Redox potential [Moore *et al.*, 1998]. The amount of plant respiration is proportional to the amount of biomass present and also varies with maturity and growth stage [Semikhatova *et al.*, 1992]. Despite these complexities, some success has been achieved in estimating total respiration fluxes from tower and chamber data as functions of temperature and or water table position [Oberbauer *et al.*, 1991; Kim and Verma 1992; Shurpali *et al.*, 1995; Waddington *et al.*, 1998]. We used nighttime (solar radiation = 0 W m⁻²) NEE tower data from four growing seasons to estimate ER as a linear function of surface temperature

$$ER = \alpha T_s + R_{\max} + R_p, \quad (8)$$

where α (0.15 g CO₂ m⁻² d⁻¹ °C⁻¹) is the slope of the ER versus surface temperature relationship describing microbial and plant response to surface temperature change, R_{\max} is the maximum ER rate (4.9 g CO₂ m⁻² d⁻¹) at a surface temperature of 0°C. R_{\max} can be viewed as a relative measure of microbial activity and is also dependent on plant biomass and growth stage. R_p is a correction factor used to adjust the ER estimate to match the observed mean nighttime measured NEE during each growing period of each year. The adjustment was used to account for changes in ER caused by variation in water table, amount of biomass, and phenology within and between the growing seasons. Since these

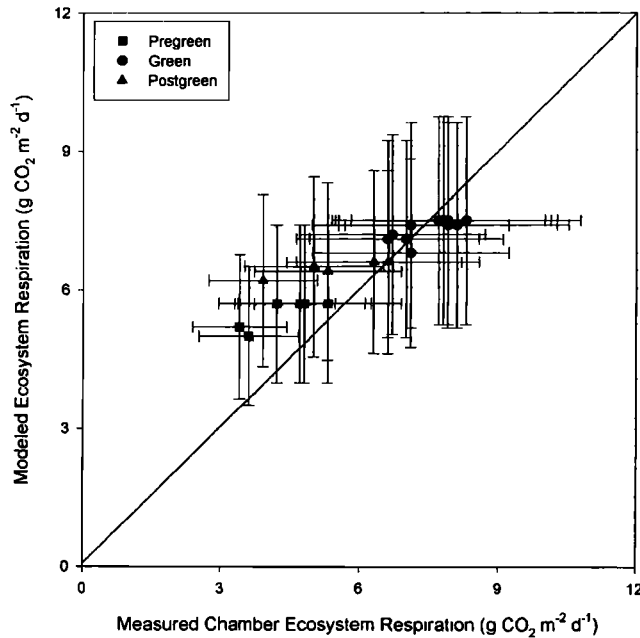


Figure 2. Comparison of modeled ecosystem respiration versus daytime measured chamber ecosystem respiration. Results are averaged for individual half-hour periods during the pregreen, green, and postgreen periods of the 1997 growing season. Error bars represent the maximum probable error.

factors cannot be modeled adequately at the present time, the use of R_p in 8 introduces less bias to the daytime ER estimate. Four years of data were used to construct the model in order to reduce the bias resulting from a relatively small data set, and as well, to facilitate a direct comparison of the daytime ecosystem respiration estimate with chamber measurements made during the 1997 growing season. Figure 2 shows the relationship between

the estimated ER and the measured chamber ER for the 1997 growing season. Further details regarding the chamber measurements and the comparison of community-scaled chamber fluxes of ER and GEP are discussed by *Griffis et al.* [2000]. Although our estimates of GEP and ER do not always give a balance to the observed NEE, our approach permits us to gain some insight into the variability of NEE by studying the climatic effects on GEP and ER.

2.6. Study Years and Growth Periods

The study years include 1994, 1996, 1997, 1998, and 1999. CO₂ fluxes and energy balance data are compared over the measurement period day of year (DOY) 164 (June 13) to DOY 238 (August 26). Owing to equipment failure, the 1999 measurement period ends on DOY 235 (August 23). The measurement period includes the majority of the growing season at this tundra location. For comparative purposes, each growing season has been divided into three periods following *Schreder et al.* [1998]. Period one (normal pregreen) extends from DOY 164 to DOY 172 (June 21). At this time the vascular species emerge but are immature. Period two (normal green) includes DOY 173 to DOY 220 (August 8). In this period, vascular species reach maturity and leaf area index (LAI) reaches a maximum. Period three (normal postgreen) extends from DOY 221 to DOY 238. The normal postgreen period generally coincides with the onset of dormancy.

3. Results

3.1. General Climatic Conditions

Growing season climatic differences between each of the years were relatively small in terms of air temperature and precipitation. However, stronger differences were evident for the pregreen, green, and postgreen periods. Each season was warmer than the Churchill 30 year (1965-1994) normal (Table 2). During

Table 2. Growing Season Climatological Characteristics

Year	Pregreen	Green	Postgreen	Season
<i>Mean Daily Air Temperature by Growing Period and Season.</i>				
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
<i>Total Precipitation by Growing Period and Season (mm)</i>				
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

Normal air temperature and precipitation is based on the Churchill airport record (1965-1994) [Atmospheric Environment Service, 1994] for the Pregreen period (DOY 164 to 172), Green period (DOY 173 to 219) and Postgreen period (DOY 220-238).

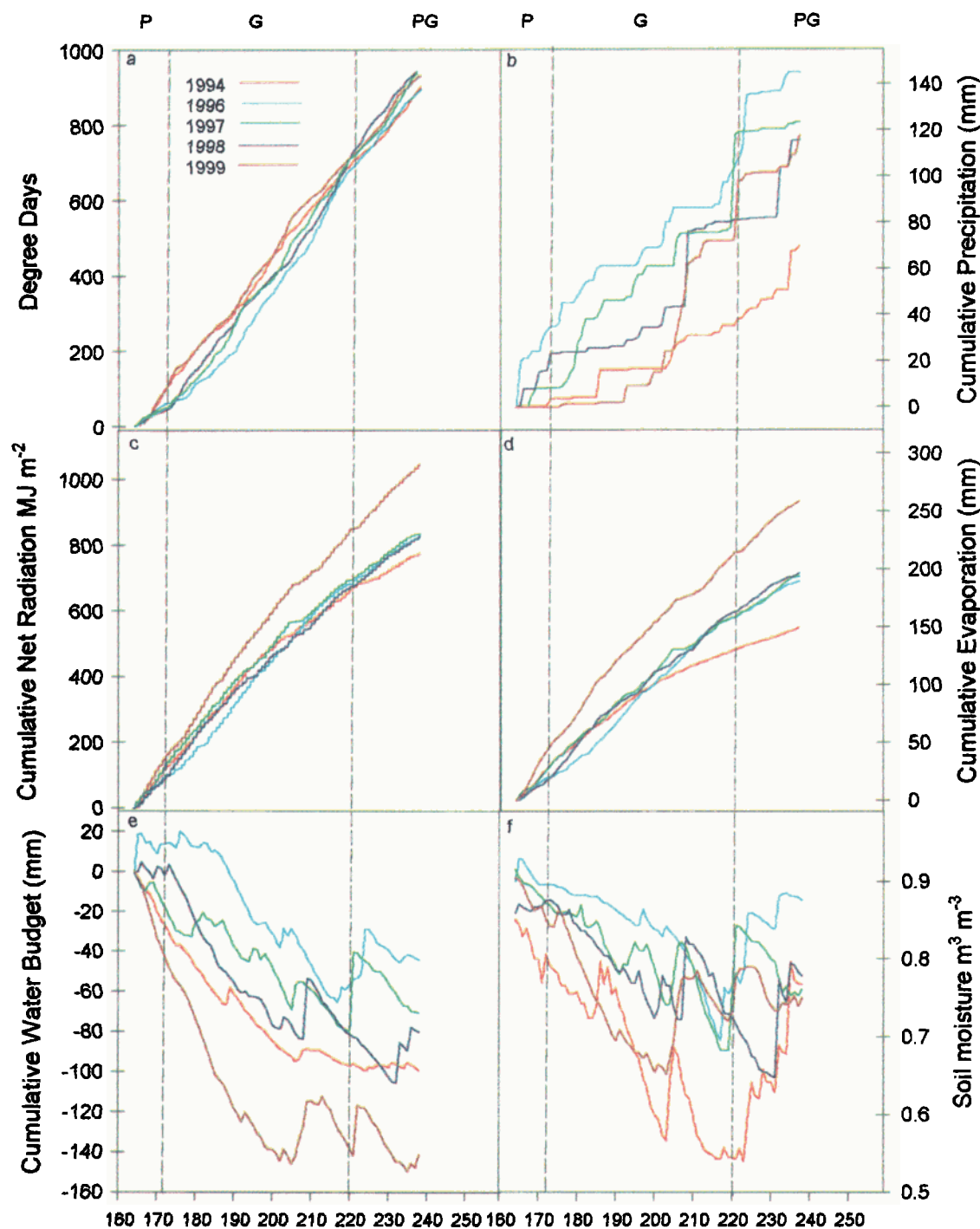


Plate 1. Comparison of hydroclimatological conditions during five seasons of NEE measurements at the Churchill fen. (a) Number of degree days, (b) cumulative precipitation, (c) cumulative net radiation, (d) cumulative evaporation, (e) cumulative water budget $\Sigma(P-E)$, (f) volumetric soil moisture. Years include 1994 (light red), 1996 (cyan), 1997 (green), 1998 (dark blue) and 1999 (dark red). Periods include pregreen (P), green (G), and postgreen (PG).

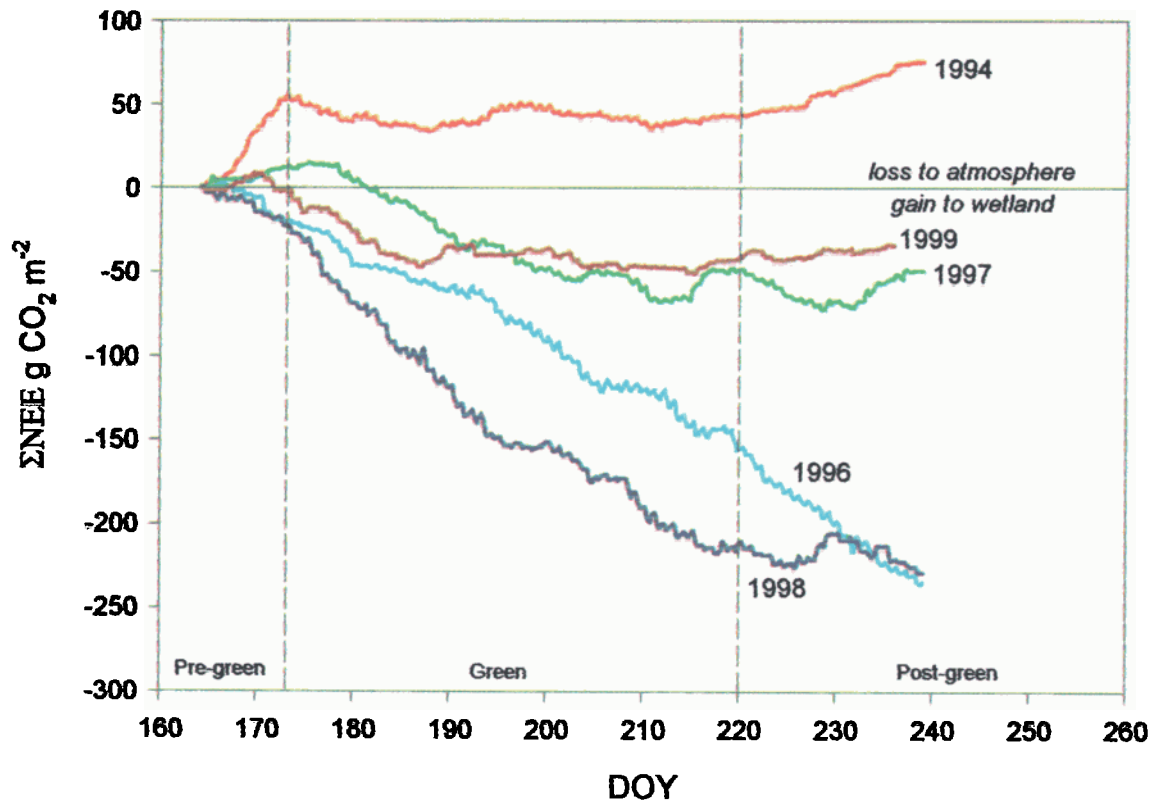


Plate 2. Growing season cumulative net ecosystem CO₂ exchange during five seasons of measurement at a subarctic sedge fen near Churchill, Manitoba. Years include 1994 (light red), 1996 (cyan), 1997 (green), 1998 (dark blue), and 1999 (dark red).

the 1994 pregreen period, air temperature was nearly 6°C above normal. Precipitation in 1994 was also below normal, providing a strong contrast to the other years (Table 2). The 1996 season had above normal precipitation with an especially wet pregreen period. Air temperature and precipitation differences between 1997 and 1998 were small over the entire measurement period (Plate 1a). Each season was ~ 2°C warmer than normal with slightly below normal precipitation. The 1998 season, however, received above normal precipitation during the pregreen period while 1997 had above normal precipitation during the green period (Plate 1b). In 1999, net radiation and evaporation were 20% greater than the other seasons (Plates 1c and 1d). Air temperature was 1.7°C warmer than normal. Precipitation was slightly below normal for the growing season but especially dry during the pregreen and early green period. The approximate timing of snowmelt, based on personal observations and albedo measurements for the 1994, 1996, 1997, 1998, and 1999 seasons, was May 10, May 30, May 31, May 9, and April 22, respectively.

3.2. Cumulative Net Ecosystem CO₂ Exchange

During the 1994 season, cumulative NEE (Plate 2) showed a net loss of +76 g CO₂ m⁻² [Schreader *et al.*, 1998]. Losses increased rapidly to +55 g CO₂ m⁻² in the pregreen period where ~ 63% of the CO₂ loss occurred within this 9-day period (Table 3). GEP balanced ER through the green period. ER exceeded GEP in the postgreen period and accounted for 37% of the total seasonal CO₂ loss.

In 1996 the wetland gained -235 g CO₂ m⁻². GEP exceeded ER losses by day four of the pregreen period (Plate 2). The rate of change in cumulative NEE was relatively constant through the green period, and GEP remained larger than ER through to the end of the measurement period (August 26). The percentage of total cumulative acquisition during the pregreen, green, and postgreen periods was 8, 59, and 32%, respectively.

The wetland gained -49 g CO₂ m⁻² over the 1997 growing season. During the pregreen period, cumulative NEE was positive and did not switch to a net gain until DOY 181 (June 30). NEE oscillated through the green and postgreen period but remained a net CO₂ sink (Plate 2). Postgreen period ER was larger than GEP. Nearly 85% of the net CO₂ loss occurred during the pregreen period, and 15% occurred in the postgreen period.

Cumulative net exchange of CO₂ during 1998 showed strong similarity to the 1996 season (Plate 2). The wetland gained -230 g CO₂ m⁻². GEP was larger than ER at the beginning of the measurement period. The rate of cumulative gain was faster through the pregreen and early green period compared to 1996 but attained a similar rate midway through the season. A sharp reduction in cumulative NEE in the postgreen period correlated with the maximum draw down of the water table that followed the very dry green period. The percentage of total cumulative NEE for the pregreen, green, and postgreen period was 10, 84, and 6%, respectively.

The 1999 season shows some similarity to 1997 (Plate 2), gaining approximately -34 g CO₂ m⁻² by the end of the

Table 3. Cumulative Net Ecosystem CO₂ Exchange and Estimate of Maximum Probable Error

Year	Pregreen	Green	Postgreen	Season
1994	+55 (± 14)	-12 (± 3)	+33 (± 8)	+76 (± 19)
1996	-20 (± 5)	-135 (± 34)	-80 (± 20)	-235 (± 59)
1997	+12 (± 3)	-61 (± 15)	0 (± 0)	-49 (± 12)
1998	-22 (± 6)	-189 (± 47)	-17 (± 4)	-228 (± 57)
1999	-0.6 (± 0.2)	-41 (± 10)	+8 (± 2)	-34 (± 9)
Days	9	48	18	75

Error is given in g CO₂ m⁻².

measurement period. Cumulative NEE was near zero at the end of the pregreen period. The gain of CO₂ during the early green period progressed at a rate near the 1996, 1997, and 1998, seasons. However, on DOY 188 (July 7), the net gain of CO₂ diminished considerably, and GEP and ER were approximately balanced. During the post-green period, ER was larger than GEP causing a net loss of CO₂ to the atmosphere. Approximately 99% of the net CO₂ gain occurred during the green period, while all of the net loss of CO₂ occurred during the postgreen period.

3.3. Seasonal CO₂ Exchange Patterns and Environmental Characteristics

3.3.1. Pregreen period. Strong differences in diurnal NEE, GEP, and ER are observed between each of the years during the pregreen period (Figure 3). In 1994, NEE was positive to the atmosphere for each half-hour period, averaging a net loss of +6.1 g CO₂ m⁻² d⁻¹ (Figure 3a). Pregreen GEP is dominated by bryophytes (*Scorpidium turgescens* and *Tomenthypnum nitens*) prior to vascular leaf emergence. In 1994, GEP averaged -2.6 g CO₂ m⁻² d⁻¹, while ER averaged +8.5 g CO₂ m⁻² d⁻¹. The large net loss of CO₂ from the wetland is attributed to the hot and dry surface conditions. Air temperature was 6°C above normal, and cumulative precipitation was less than 5 mm (Plate 1b). The cumulative water budget, $\Sigma(P-E)$, was negative (Plate 1c) as a result of little precipitation and strong surface evaporation (Plate 1d), and there was a small reduction of soil moisture by the end of the pregreen period (Plate 1f).

During 1996, NEE averaged -2.2 g CO₂ m⁻² d⁻¹ and exhibited a strong diurnal fluctuation (Figure 3b). Estimates of GEP and ER averaged -4.4 and +2.5 g CO₂ m⁻² d⁻¹, respectively. The surface conditions during this period were considerably cooler and wetter than the 1994 year. Cumulative water budget showed a net gain through the pre-green period and maintained soil moisture values near their maximum water holding capacity (Plate 1f).

The 1997 patterns of CO₂ exchange were similar to 1994 (Figure 3c). However, ER was ~ 45% smaller, and two brief episodes of net CO₂ acquisition were observed in the early morning and late afternoon. NEE decreased substantially through the late morning hours and became positive by solar noon, averaging a loss of +1.1 g CO₂ m⁻² d⁻¹. GEP and ER averaged -3.3 and +4.7 g CO₂ m⁻² d⁻¹, respectively. Temperatures were relatively cool compared to 1994 and 1996. The cumulative water budget was negative during the pregreen period due to low rainfall and large evaporation. However, volumetric soil moisture was near saturation at the end of the period due to a relatively late snowmelt and high initial water table position.

NEE during the 1998 pregreen period was similar to 1996, averaging -2.5 g CO₂ m⁻² d⁻¹ (Figure 3d). GEP averaged -7.1 g CO₂ m⁻² d⁻¹, which was significantly larger than any other pregreen period in this study. However, ER was also relatively large and averaged +5.2 g CO₂ m⁻² d⁻¹. Air temperature in 1998

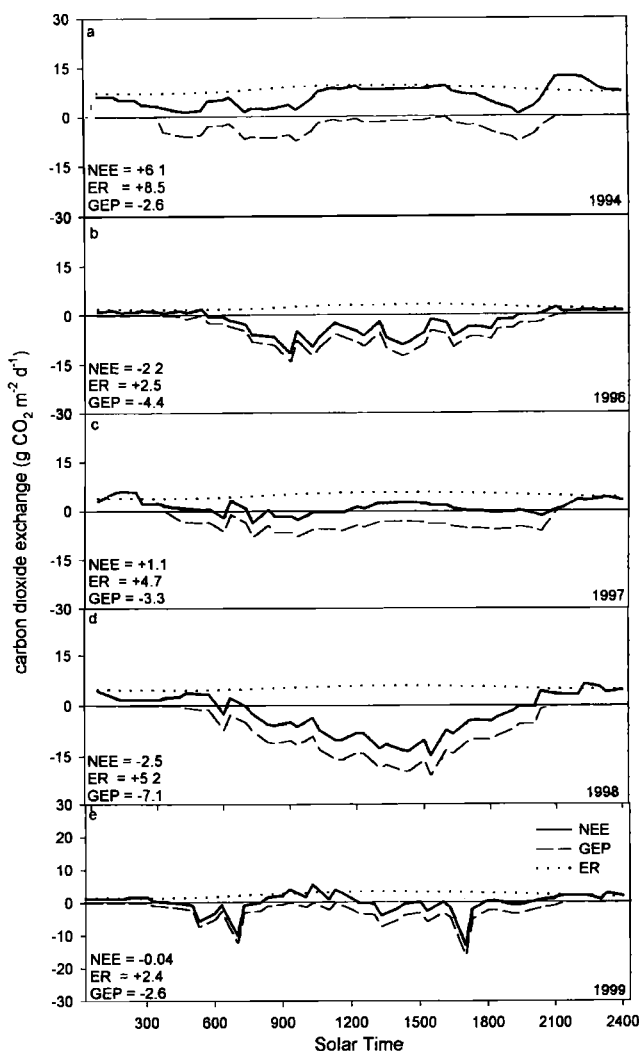


Figure 3. Diurnal patterns of measured NEE (solid line), estimated NEP (dashed line), and estimated ER (dotted line) during the pregreen period (DOY 164-172).

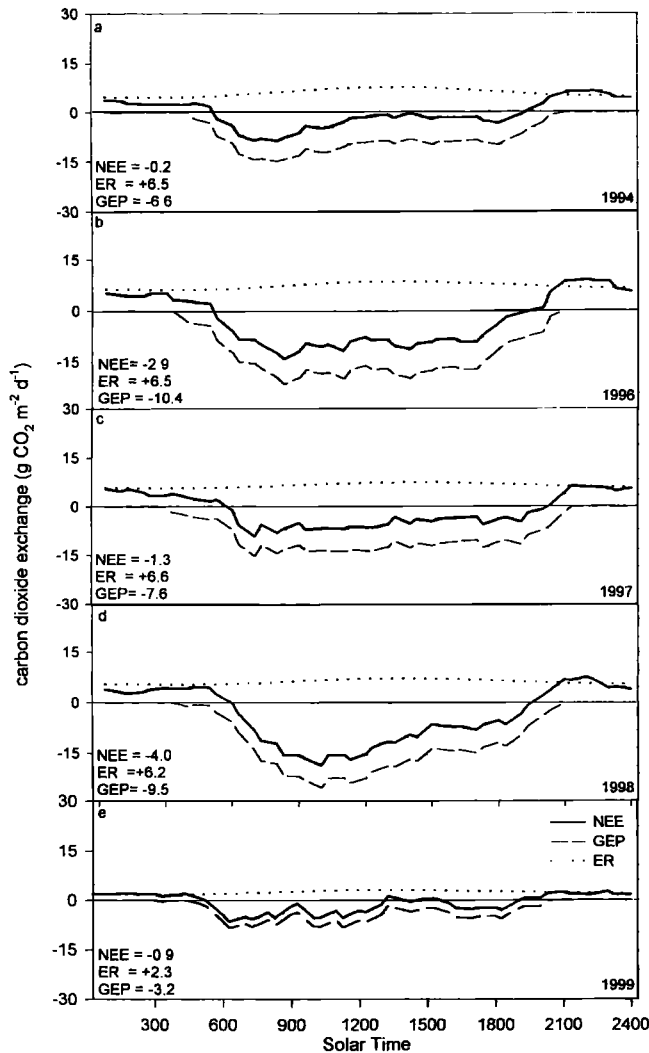


Figure 4. Diurnal patterns of measured NEE (solid line), estimated NEP (dashed line), and estimated ER (dotted line), during the green period (DOY 173-219).

was $\sim 1^{\circ}\text{C}$ below normal. As in 1996, the cumulative water budget was positive through the pregreen period due to above normal precipitation. Consequently, soil moisture content was maintained near its maximum capacity (Plate 1f).

The 1999 patterns of pregreen CO₂ exchange (Figure 3e) are comparable to 1994 and 1997. Only brief periods of net CO₂ gain are observed during the early morning and late afternoon hours, and substantial losses of CO₂ occurred prior to solar noon. Measured NEE showed a net balance. Estimates of ER and GEP averaged $+2.4$ and -2.6 g CO₂ m⁻² d⁻¹. The 1999 pregreen period was $\sim 6^{\circ}\text{C}$ warmer than normal and did not record a single precipitation event. The cumulative water budget was -43 mm, exceeding all other years in this study. However, the volumetric soil moisture remained relatively large at 0.85 due to the initial high water table position. Personal field observations showed that the bryophytes on the larger hummocks were desiccated.

3.3.2. Green period. The diurnal patterns of CO₂ exchange during the green period (Figure 4) differ substantially from

pregreen exchange. In general, the shapes of the curves show stronger similarity between the years, which can be attributed to the emergence and maturing of the vascular species.

In 1994, NEE was negative during most of the daytime period (Figure 4a) and averaged -0.2 g CO₂ m⁻² d⁻¹. GEP averaged -6.6 g CO₂ m⁻² d⁻¹ and showed a strong decline through midday. The mean daily estimate of ER was $+6.5$ g CO₂ m⁻² d⁻¹. Cumulative water budget reached -97 mm, reducing the soil water content to below 0.55. Blanken and Rouse [1996] and Schreader *et al.*, [1998] demonstrated evidence of water conservation via a decrease in stomatal conductance for *Carex* spp. at this site and other wetlands near Churchill. We hypothesize that plant moisture stress was the cause of the observed midday reduction in GEP and NEE. Given the drier and warmer temperature conditions and the increase in biomass, it is surprising that ER decreased from the pregreen period. However, Lafleur *et al.* [1997] reported similar findings for a northern boreal fen in the same year. The reduction may be related to rapid consumption of fresh litter at the surface in the pregreen period [Schreader *et al.*, 1998] and also a depletion of CO₂ supplied from the melting of ice in peat soils of the active layer. Furthermore, it may reflect changes in plant growth or a relaxation in energy supply for tissue maintenance.

Mean NEE was -2.9 g CO₂ m⁻² d⁻¹ in 1996 (Figure 4b). GEP and ER averaged -10.4 and $+6.5$ g CO₂ m⁻² d⁻¹, respectively. A reduction in NEE and GEP during midday is apparent but less pronounced than in the 1994 season. Air temperature was above normal during this period, and the cumulative evaporative flux exceeded precipitation. Soil moisture decreased through the green period (Plate 1f) and reached a season minimum of 0.64 on DOY 218 (August 6).

Patterns of CO₂ exchange in 1997 are similar to 1994 (Figure 4c). NEE averaged -1.3 g CO₂ m⁻² d⁻¹, and estimates of GEP and ER averaged -7.6 and $+6.6$ g CO₂ m⁻² d⁻¹. The diurnal pattern of NEE and GEP exhibit a steady reduction through the late morning and afternoon hours. Air temperature was above normal during this period. Despite the large increase in precipitation, large evaporative fluxes caused the cumulative water budget to become more negative. As a result, the volumetric soil moisture decreased (Plate 1f) and reached a season minimum on DOY 219 (August 7). We hypothesize that the observed increase in ER from the pregreen period is due to the warmer temperatures, lower soil moisture content, and increased plant biomass.

The 1998 green period (Figure 4d) was similar to the 1996 period. NEE, GEP, and ER averaged -4.0 , -9.5 , and $+6.2$ g CO₂ m⁻² d⁻¹, respectively. The main distinction between the 2 years is greater net CO₂ gain during the early morning and stronger midday reduction in GEP during 1998. Air temperature was $\sim 3^{\circ}\text{C}$ warmer than normal and precipitation was near normal for the period. The cumulative water budget decreased substantially during the 1998 period causing a soil moisture deficit, which was, on average, larger than the 1997 period (Plate 1f). Despite the warm temperatures and reduction in soil moisture, the net acquisition of CO₂ remained relatively large compared to 1997 and 1996.

During the 1999 green period, NEE averaged -0.9 g CO₂ m⁻² d⁻¹. The pattern is similar to the 1994 season, exhibiting a strong reduction in net CO₂ gain through the midday period. Both GEP and ER are small compared to the other seasons (-3.2 and $+2.3$ g CO₂ m⁻² d⁻¹) and suggest that the canopy

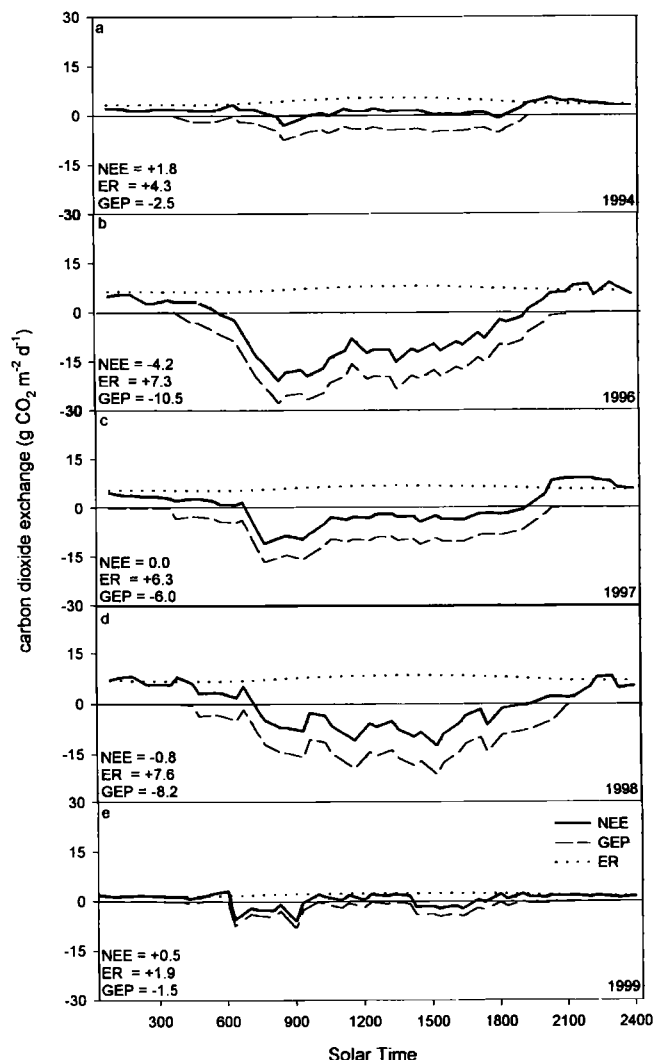


Figure 5. Diurnal patterns of measured NEE (solid line), estimated NEP (dashed line), and estimated ER (dotted line), during the postgreen period (DOY 220-238).

did not develop to its normal potential or that it experienced high mortality rates due to the drier conditions. Precipitation during this period was slightly below normal. Evaporation exceeded precipitation resulting in a large negative cumulative water budget of -134 mm. Volumetric soil moisture was reduced to a minimum of 0.72 (Plate 1f).

3.3.3. Postgreen period. In general, the post-green patterns of CO₂ exchange (Figure 5) indicate a reduction in GEP and the relatively quick transition to dormancy which is most pronounced in the years that experienced dry pregreen conditions. In 1994, the wetland showed a net gain of CO₂ for two short intervals during the early morning and late afternoon (Figure 5a). NEE averaged +1.8 g CO₂ m⁻² d⁻¹. GEP and ER decreased substantially from the green period rates to -2.5 and +4.3 g CO₂ m⁻² d⁻¹. The postgreen period was cooler than normal but had near normal rainfall. The cumulative water budget was positive and raised the volumetric soil water content to 0.80 by the end of the period (Plate 1f). The estimated reduction in GEP indicates that the

vascular vegetation was beginning to senesce. LAI and shoot density of *Carex* spp. had started to decrease by DOY 201 (July 20) [Schreader *et al.*, 1998]. The transition to dormancy of the vascular species appears to have been initiated relatively early due to the persistent drought conditions. Figure 6a illustrates the effects of the dry summer on the vegetation. The mosses in the hollows and sedges on the small hummocks were desiccated. As a result they appear white in Figure 6a. We hypothesize that the reduction in ER from the green period is related to the wetter soil conditions, cooler temperatures, and reduction in living plant tissue.

The 1996 postgreen period gained CO₂ at a faster rate than the green period (Figure 5b). NEE, GEP, and ER averaged -4.2, -10.5, and +7.3 g CO₂ m⁻² d⁻¹, respectively. The increased acquisition of CO₂ resulted from a reduction in ER. The postgreen period was both warmer and wetter than normal. The delayed senescence of the fen vegetation due to the wet seasonal conditions may explain the sustained rate of GEP. Figure 6b illustrates the fen vegetation under wetter conditions and provides a strong contrast to the 1994 season. The hollows appear darker due to the saturated moss cover, and there is generally a healthier appearance to the sedges.

The 1997 postgreen period yielded a net efflux of +0.1 g CO₂ m⁻² d⁻¹ (Figure 5c). The net loss of CO₂ can be attributed to a reduction in GEP relative to ER. The fluxes were -6.0 and +6.3 g CO₂ m⁻² d⁻¹, respectively. Temperature was above normal, and precipitation was below normal. Soil moisture decreased rapidly over the final 15 days of the measurement period.

Patterns of CO₂ exchange in 1998 showed strong diurnal variability (Figure 5d). GEP decreased to -8.2 g CO₂ m⁻² d⁻¹, while ER increased to +7.6 g CO₂ m⁻² d⁻¹. NEE averaged -0.8 g CO₂ m⁻² d⁻¹. The net gain of CO₂ decreased substantially in 1998 due to a near equal increase in ER and reduction in GEP. This reduction in net CO₂ acquisition on the seasonal cumulative exchange is apparent in Plate 2. Air temperature was warmer than normal, and precipitation was near normal during this period. However, soil moisture content reached a minimum on DOY 231 (August 19). This minimum occurred about 12 days later than the other experimental years.

There is strong similarity between 1999 (Figure 5e) and the 1994 postgreen period. We hypothesize that this similarity stems from advanced dormancy caused by drought conditions experienced through the majority of each growing season. NEE averaged a net loss of +0.5 g CO₂ m⁻² d⁻¹. GEP and ER decreased on average to -1.5 and +1.9 g CO₂ m⁻² d⁻¹, respectively. Even though the postgreen period received more precipitation than normal, this failed to rejuvenate the GEP of the canopy.

4. Discussion and Conclusions

4.1. Interannual Variability in NEE

The 5 year experiment captured a wide range of climatic conditions and included the strong El Niño phenomenon of spring 1998. Large interannual variability is observed in the net ecosystem CO₂ exchange ranging from a net source to a net sink over the 5 year study. The cause of interannual variability in NEE is complex, driven by change in the net photosynthetic rate of moss and sedges and, as well, variation in heterotrophic and autotrophic respiration. GEP rates were generally more variable than measured nighttime and estimated daytime ER rates on a diurnal and seasonal basis. Soil moisture, air temperature, and



Figure 6. A visual comparison of the Churchill fen in the postgreen period during (a) the 1994 dry year and (b) the 1996 wet year.

stomatal conductance are important variables in causing the observed diurnal patterns of NEE. The growth stage and phenology of the wetland vegetation are especially important during the pregreen and postgreen periods. Interannual variability in NEE is most pronounced during these shoulder periods. Consequently, it is necessary for climate models to describe phenology and growth cycles properly. Phenology has also been identified as a key variable driving the interannual variability in the global carbon budget. *Kindermann et al.* [1996] using the Frankfurt Biosphere Model to reconstruct annual changes in atmospheric CO₂ concentrations suggest that anomalous sink years might result from early leafing. Furthermore, modeling efforts by *Frolking* [1997] found that the timing of weather patterning had a strong influence on CO₂ exchange for a boreal forest. The link between climate and phenology is emerging as a key determinant in the observed variability in global atmospheric CO₂ concentrations.

Large losses of CO₂ experienced during 1994 are related to the dry and hot surface characteristics of the fen. The climatic conditions during the early spring and pregreen period (when the wetland vegetation is developing) appear from this evidence to have a profound impact on NEE. This impact persists through the remainder of the season. Dry conditions at the beginning of 1997 and 1999 cause a similar diurnal pattern in NEE during the pregreen period as in 1994. Both 1997 and 1994 experienced large losses of CO₂ during this period. Increased precipitation during the green period of 1997 and 1999 and the postgreen period of 1994 did not cause a substantial increase in GEP. In contrast, above normal precipitation during the pregreen period of 1996 and 1998 resulted in a net gain of CO₂. The gain in 1996

was largely due to the high soil moisture content and associated low ER, whereas the gain in 1998 was caused by a large increase in GEP. In 1998, early snowmelt and above normal precipitation and temperature [*T. J. Griffis et al.*, submitted manuscript; 2000] caused an earlier greening of the fen. Wet and warm conditions sustained through the 1996 growing season resulted in a large GEP rate during the green and postgreen periods. There was no sign of the onset of dormancy at the end of the measurement period. The green and postgreen periods in 1998 were drier than the 1996 and 1997 periods. However, GEP remained large, and cumulative NEE was comparable to 1996. Climatic differences between 1998 and 1997 are small over the entire measurement season. The disparity in cumulative NEE between the 2 years is therefore somewhat surprising. However, *P. M. Lafleur et al.* [manuscript in preparation; 2000] have found similar observations for an open subarctic forest site located adjacent to the Churchill fen. This evidence further supports the hypothesis that NEE is strongly influenced by the early spring climatic conditions. Wet and warm conditions during the early growing period increase the photosynthetic capacity, and fitness of the vegetation and largely determine the CO₂ sink/source magnitude of this wetland environment.

4.2. Comparison With Other Landscape-Scale Studies

Table 1 provides a summary of the major studies examining landscape-scale NEE measurements over northern wetlands using eddy covariance or gradient micrometeorological techniques. Twelve of the seventeen field studies show ecosystems that were net sinks of CO₂ over the growing season, however, the majority

of these indicated only weak net sinks of less than $-2.0 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$. Given the errors involved in measurement and the lack of complete CO₂ flux information for the nongrowing season [Zimov *et al.*, 1993; Fahnestock *et al.*, 1999], it is reasonable to conclude that most of these landscapes, on an annual basis, experienced a net loss of CO₂ to the atmosphere. Only three of the studies suggest a net annual CO₂ sink including Suyker *et al.* [1997] and the 1996 and 1998 seasons in Churchill. The CO₂ sink strength for Churchill is speculative given the lack of spring, fall, and wintertime NEE measurements. The three net sink studies indicate that northern wetlands have the potential to sequester significant amounts of CO₂ when climatic conditions are favorable. These favorable conditions for CO₂ sequestration include frequent rain events combined with high water table position and warm temperatures at least during the beginning of the growing-season.

Shurpali *et al.* [1995], Vourlitis and Oechel [1997], Schreader *et al.* [1998], and our results confirm that water balance (soil moisture) is critical to the sink/source strength of these wetlands. The limited number of studies conducted over the past three decades suggest that northern wetlands have experienced a reduction in their average sink strength of approximately $-40 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$ [Gorham, 1991] and in most cases have switched to a net source of atmospheric CO₂. Zimov *et al.* [1993], Vourlitis and Oechel [1997], Oechel *et al.* [1997], and Fahnestock *et al.* [1999] support that wintertime respiration rates have the potential of offsetting summertime CO₂ gains despite the cold conditions in these arctic environments. If we take the average CO₂ exchange for the Churchill fen over the five growing seasons and assume a nongrowing season of 240 days with a soil respiration rate of $+0.5 \text{ g CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ [Zimov *et al.*, 1993], we find that the fen is losing approximately $+30 \text{ g CO}_2 \text{ m}^{-2} \text{ yr}^{-1}$. The 5 year NEE budget of the Churchill fen suggests a contemporary loss of CO₂ that is proceeding at about 3 times the rate of its long-term historical gain.

4.3. Implications for Climate Change

Atmospheric general circulation models predict warmer temperatures and increased precipitation over subarctic and arctic regions given a doubling of atmospheric CO₂ [Kattenberg *et al.*, 1996]. Projected temperatures for the summer range from 1° to 4°C , while winter temperatures are predicted to increase 2° to 5°C . Coupled GCMs forecast an increase in precipitation. Simulations from a number of models predict an increase of $0\text{--}2 \text{ mm d}^{-1}$ during the summer months and $0\text{--}0.5 \text{ mm d}^{-1}$ during the winter months. At the present time it is difficult to conclude with confidence how these climatic changes will immediately affect the net ecosystem exchange of CO₂ at high latitudes. This is due to uncertainty surrounding the changes in (1) evaporation rates, (2) active layer deepening, (3) water balance and water table position, and (4) soil moisture content.

Rouse [1998] developed a model to explore the potential impact of a $2\times\text{CO}_2$ warming on the water balance of the Churchill fen. The model was run with changes in air temperature and precipitation forecast for the Churchill region by a number of GCMs. The scenario employed was an increase in the annual air temperature by 4°C [Mitchell, 1990] and an increase in precipitation of 20% [Maxwell, 1992]. The water balance calculations show that evaporation increases would exceed precipitation increases and cause water deficits to be greater than the recent 30 year normal. The Churchill fen would experience a

lower water table position and decreased soil moisture. These results, coupled to our present study, indicate that ER will increase relative to GEP. Reductions in CO₂ acquisition will be most severe if future spring conditions become drier than present. The transient response of carbon storage at the Churchill fen therefore is likely to be a greater net loss under a $2\times\text{CO}_2$ climate change scenario. However, over longer timescales the wetland may experience greater CO₂ sequestration due to changes in nutrient cycling and plant response [Waddington *et al.*, 1998; Griffiths *et al.*, 2000].

4.4. Conclusions

Growing season net ecosystem CO₂ exchange shows large interannual variability, ranging from a net source to a net sink over the 5 years of measurement. Variability results from daily and seasonal changes in the GEP of the mosses and sedges and from changes in soil and plant respiration rates. We hypothesize that GEP is more variable than ER on a daily and seasonal basis. Our evidence suggests that climatic conditions during the pregrowth and pregreen period are critical to the sink/source strength of the wetland over the growing season. The linkage between phenological stage and climatic conditions is important in determining the CO₂ sink/source strength, especially during the shoulder seasons. It is therefore imperative that climate models describe phenological stage accurately for this type of landscape. Years that experience a drier than normal spring experience either a loss or near balance exchange of CO₂ between the wetland and atmosphere. A comparison of landscape-scale NEE studies from northern latitudes over the last three decades suggests that most wetlands are sequestering considerably less CO₂ from the atmosphere when compared to their historical rates and appear to be net sources of CO₂ to the atmosphere rather than sinks. Future research efforts need to combine process based chamber studies with landscape scale measurements in order to determine and model the contributions of GEP and ER at the community level. The measurement and modeling of nongrowing season respiration is needed in order to improve our understanding of the annual CO₂ budget of northern wetlands.

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