

# Scaling net ecosystem CO<sub>2</sub> exchange from the community to landscape-level at a subarctic fen

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## Abstract

Landscape- and community-level CO<sub>2</sub> measurements were made at a subarctic sedge fen near Churchill Manitoba during the 1997 growing season. Climatic conditions were warmer and drier than the 30-y normal. Landscape-scale micrometeorological measurements indicated that the wetland gained 49 g CO<sub>2</sub> m<sup>-2</sup> during the growing season. Chamber-scale measurements from the main vegetation community types showed that small hummocks (*Carex* spp. sites) dominated the CO<sub>2</sub> exchange, yielding an effective scaling factor of 70%. Scaled parameters of two algorithms describing photosynthesis and respiration for each community type show strong similarity to those derived at the landscape level. Scaling photosynthesis, respiration, and net ecosystem CO<sub>2</sub> exchange from the community to landscape-level over the season is within the maximum probable error of each methodological approach and helps substantiate the 1997 CO<sub>2</sub> budget. We explore the equilibrium response of net ecosystem CO<sub>2</sub> exchange of this fen to climatic change by examining the feedback of water table position on vegetation distribution and nitrogen availability. Based on the effective scaling factors computed for each community type, we hypothesize that a small decrease in mean water table position could nearly triple the net uptake of CO<sub>2</sub> at this wetland.

*Keywords:* climatic change, net ecosystem CO<sub>2</sub> exchange, scaling, subarctic fen

*Received 8 April 1999; revised version received 18 August and accepted 9 November 1999*

## Introduction

Northern wetlands cover approximately 346 million ha of the earth's surface and play an important role in the global carbon cycle (Gorham 1991). The majority of these wetlands is located in high latitudes and coincides with the boreal zone. There is concern that these ecosystems will experience a net loss of stored carbon to the atmosphere in response to high latitude warming (Billings *et al.* 1982; Billings 1987a; Oechel *et al.* 1993). This biological feedback process may further amplify the greenhouse effect by releasing stored CO<sub>2</sub> to the atmosphere.

Many landscape-level CO<sub>2</sub> exchange studies (Griffis *et al.* in press; Burton *et al.* 1996; Lafleur *et al.* 1997; Vourlitis & Oechel 1997; Schreuder *et al.* 1998) indicate that northern wetlands experience a significant reduction in net CO<sub>2</sub> uptake and can become a source on an annual basis when spring and summer conditions are hot and

dry. Field data for a subarctic sedge fen near Churchill Manitoba, Canada, indicate that the net loss of CO<sub>2</sub> is caused by a strong reduction in photosynthetic activity and a small increase in ecosystem respiration (Griffis *et al.* submitted).

Over longer timescales (tens to hundreds of years), however, wetlands may display homeostatic behaviour through a number of internal feedback processes. Increased microbial activity due to warmer and drier soils may release stored organic nitrogen, thereby enhancing the productivity of wetland systems (Shaver *et al.* 1986; Shaver *et al.* 1998), and vegetation succession, induced by climatic change, may lead to increased productivity (Waddington *et al.* 1998). To date, field evidence of homeostatic adjustment under natural conditions remains speculative (Vourlitis & Oechel 1997). Long-term monitoring at the appropriate scale is needed to establish baseline measurements for evaluating such system adjustment. The characteristic heterogeneity in wetness and vegetation type observed in northern

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wetlands suggests that carbon exchange processes vary strongly across time and space. Future changes in the energy and water balance due to climatic forcing will impact the carbon exchange processes due to changes in wetness, nutrient cycling, and vegetation succession. Thus, understanding how the ecosystem will change will require observations at the landscape, community and plant level.

Studying the balance and potential response of net ecosystem CO<sub>2</sub> exchange (NEE) to changing environmental conditions has most commonly been approached by using either landscape-level micrometeorological techniques (gradient and eddy covariance measurements) or community-level chamber methods (static and dynamic chambers). Landscape-level monitoring does not provide mechanistic information about the components of NEE at the community-scale since micrometeorological methods cannot differentiate between photosynthetic and respiration responses of different vegetation communities to varying light, temperature, humidity, moisture, and nutrient conditions. This lack of resolution is important because individual vegetation communities respond differently to changing environmental conditions (Bubier *et al.* 1998). Consequently, the ability to predict changes in NEE to climatic change could be biased. For example, communities characterized by mosses may experience a large reduction in photosynthesis under dry surface conditions, while vascular species-dominated communities continue to photosynthesize near their potential because of roots in the deeper saturated zone. More importantly, changes in community composition and distribution

within a wetland could result in poor estimates of NEE if model parameters do not account for plant or community scale processes.

Measurements at the community-/chamber-level have their own limitations as they can influence the plant and soil environment directly (Matthias *et al.* 1978; Moore & Roulet 1991; Knapp & Yavitt 1992; Dugas 1993; Norman *et al.* 1997). Moreover, calculating landscape-scale budgets from chamber data can be problematic due to the uncertainty associated with lower temporal and spatial sampling (Waddington & Roulet 1999; Moore *et al.* 1998). Gaining a better understanding of the response of northern wetland carbon cycling to climatic change therefore requires study of these systems at a variety of spatial scales. However, to our knowledge, scaling CO<sub>2</sub> fluxes from the community- to the landscape-level has never been attempted for this environment. The objective of this study, therefore, is to combine both landscape- and community-scale approaches simultaneously in order to: (i) understand the scale complexity of net ecosystem CO<sub>2</sub> exchange at a subarctic fen in Churchill Manitoba; and (ii) help substantiate the growing season CO<sub>2</sub> budget.

## Materials and methods

### Research site

The experimental area is located on the south-western shore of Hudson Bay, within the Hudson Bay Lowland (Fig. 1). Patches of open woodland near the experimental area mark the edge of the northern boreal tree line and the transition to open tundra. Continuous permafrost

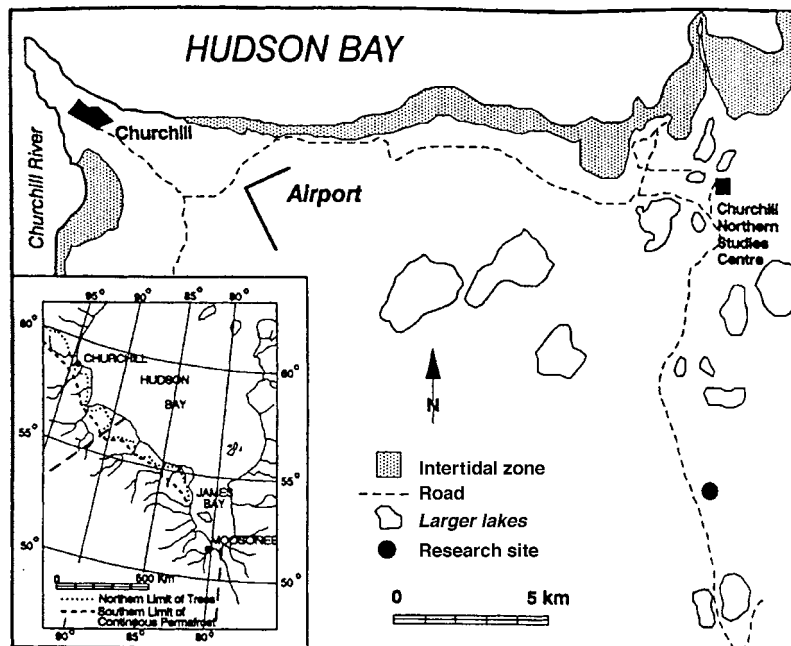


Fig. 1 Local study area and research site

begins to the south of the region. The 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 48% and large hummocks 5% of the landscape with respect to the water table position. The maximum difference in vertical height between large hummocks and hollows is approximately 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 falls 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 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*, *C. rangiferina*) and moss (*Dicranum undulatum*).

The fen has a mean peat depth of 0.25 m and is underlain by glaciomarine till, comprising fine silts and clays interspersed with layers of carbonate shingles. The regional landscape continues to respond to isostatic rebound following the last glaciation. Elevation increase at the research site is about 0.01 m y<sup>-1</sup>. At present, the fen is approximately 22 m a.s.l., and, therefore, it is estimated that vegetation and peat development was initiated about 2200 years ago. Combining this with peat depth, bulk density, and carbon content, we estimate the long-term rate of carbon accumulation for this fen at 11 g CO<sub>2</sub> m<sup>-2</sup> y<sup>-1</sup>.

### Study periods

CO<sub>2</sub> fluxes are examined over the measurement period DOY 164 (13 June) to DOY 238 (26 August). This includes the majority of the growing season at this tundra location. Each growing season has been divided into

three periods following Griffis *et al.* (in press). Period one (pregreen) extends from DOY 164 to DOY 172 (21 June). At this time the vascular species emerge but are immature. Period two (green) includes DOY 173 to DOY 220 (8 August). In this period vascular species reach full maturity and leaf area index (LAI) reaches a maximum. Period three (postgreen) extends from DOY 221 to DOY 238. The postgreen period generally coincides with the onset of senescence but this varies substantially from year to year.

### Landscape-level instrumentation and measurements

Measurements during the 1997 growing season are similar to those described in Griffis *et al.* (in press). The Bowen ratio energy balance approach (BREB) was used to calculate the energy balance over the fen. Temperature and vapour 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. Data logger sampling was performed every 2 s, and the averaging period was 0.5 h. 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. Net radiation  $Q^*$  was measured at a height of 3 m above ground using a Middleton net pyrradiometer. Incoming  $K\downarrow$  and reflected  $K\uparrow$  solar radiation were measured with Eppley pyranometers. Photosynthetic active radiation PAR was measured with a Licor Quantum sensor. Surface temperature was monitored using a series of thermocouple arrays. Ground heat flux was measured with 4 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 & Rouse (1987) to correct for inconsistencies in thermal conductivity and poor thermal contact between the heat flux plates and the organic soil.

### Landscape-level net CO<sub>2</sub> flux measurements

The theory and methodology for calculating the net CO<sub>2</sub> flux  $F_c$  using gradient techniques has been described previously in Burton *et al.* (1996), Schreder *et al.* (1998) and Griffis *et al.* (submitted).  $F_c$  is derived from the following expression

$$F_c = -K_c \left( \frac{\partial \rho_c}{\partial z} \right), \quad (1)$$

where  $K_c$  is the turbulent transfer coefficient for CO<sub>2</sub> and  $\partial \rho_c / \partial z$  is the time-averaged vertical gradient of CO<sub>2</sub>

concentration.  $K_c$  is assumed identical to the turbulent transfer coefficient for sensible heat  $K_h$  and is derived from the BREB approach.

Atmospheric gradients of  $\text{CO}_2$  concentration were measured from the same height intervals as for temperature, vapour pressure and wind speed. Due to the remote location of the research site, all instrumentation was powered by 12-V storage batteries and charged using a wind generator and solar panels. Air from the six levels was drawn through equal length tubing into 1-L 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 analysed on an infrared gas analyser (LI-COR 6262). A time interval of 1 minute was used to determine the  $\text{CO}_2$  concentration from the six buffer volumes. The net  $\text{CO}_2$  flux was calculated from 0.5 h time averaging and corrected for density variations resulting from the latent heat flux (Webb *et al.* 1980).

#### *Estimating landscape-level ecosystem respiration and photosynthesis*

Ecosystem respiration (ER) consists of heterotrophic soil respiration and autotrophic plant respiration. Both soil and plant respiration have been shown to vary strongly with soil and plant temperatures, respectively. In addition, soil respiration is a function of water table position, which has a direct affect on Redox potential and therefore microbial activity. Plant respiration is proportional to the amount of biomass present and also varies with phenological stage. 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 (Kim & Verma 1992; Oberbauer *et al.* 1992; Shurpali *et al.* 1995; Waddington *et al.* 1998). We used night-time ( $K \downarrow = 0$ ) net  $\text{CO}_2$  tower data from four different growing seasons to estimate respiration as a linear function of surface temperature. From this bulk relationship, we adjusted the  $y$ -intercept of the function until it matched the measured half-hourly night-time respiration recorded at the tower for each period during the 1997 season. Adjusting the linear fit as the season progressed was necessary since ER varied with changes in water table, amount of biomass, and phenology. The goal was not to model respiration explicitly, but to separate respiration from NEE in order to provide a best estimate of the photosynthetic flux.

#### *Community-level instrumentation and measurements*

A semidynamic chamber system (surface area  $0.05 \text{ m}^2$ , volume 20 L) was constructed from clear Plexiglas. The

chamber was outfitted with circulation fans and a water-bath-cooling unit to help maintain ambient conditions. On average, chamber temperatures were maintained to within  $\pm 0.3^\circ\text{C}$ . However, in a few instances chamber temperatures differed from ambient by  $5^\circ\text{C}$ . PAR extinction resulting from the Plexiglas material was approximately 13%. PVC collars were inserted into the peat to maintain a seal between the ground surface and chamber, and as well, to reduce the chance of episodic  $\text{CO}_2$  release during measurement. Boardwalks were placed near each of the collars to help reduce site disturbance. During  $\text{CO}_2$  sampling the chamber was placed on a collar for a 5-minute interval. The relatively short interval was chosen to reduce the effect of the chamber on the plant and soil environment.  $\text{CO}_2$  concentrations were measured every minute on a PP-systems portable EGM-1 infrared gas analyser (PP Systems, UK). The chamber  $\text{CO}_2$  flux was calculated as

$$F_c = \frac{\Delta\text{CO}_2}{\Delta t}, \quad (2)$$

where  $\Delta\text{CO}_2$  is the change in  $\text{CO}_2$  concentration over the  $\Delta t$ , 5 minute interval. Fluxes were corrected for volume changes resulting from temperature variations within the chamber. NEE was measured using a clear semidynamic chamber while ecosystem respiration was measured using a dark version of the semidynamic chamber. Photosynthesis was then estimated by subtracting ecosystem respiration from NEE. Site selection included 3 hollows (H), 6 small hummocks (SH) and 3 large hummocks (LH). The total number of chamber observations for ER and photosynthesis during the pregreen, green and senescence period was 155, 475 and 361, respectively. Chamber measurements were taken between 08.00 and 16.30 hours solar time. The sign convention for community and landscape-level  $\text{CO}_2$  fluxes is (+) respiration; (-) photosynthesis; (+) net loss of  $\text{CO}_2$  from the wetland to the atmosphere and (-) net gain of  $\text{CO}_2$  to the wetland from the atmosphere.

#### *Measurement accuracy of $\text{CO}_2$ flux calculations*

$\text{CO}_2$  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. Schreuder *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. Calculating the

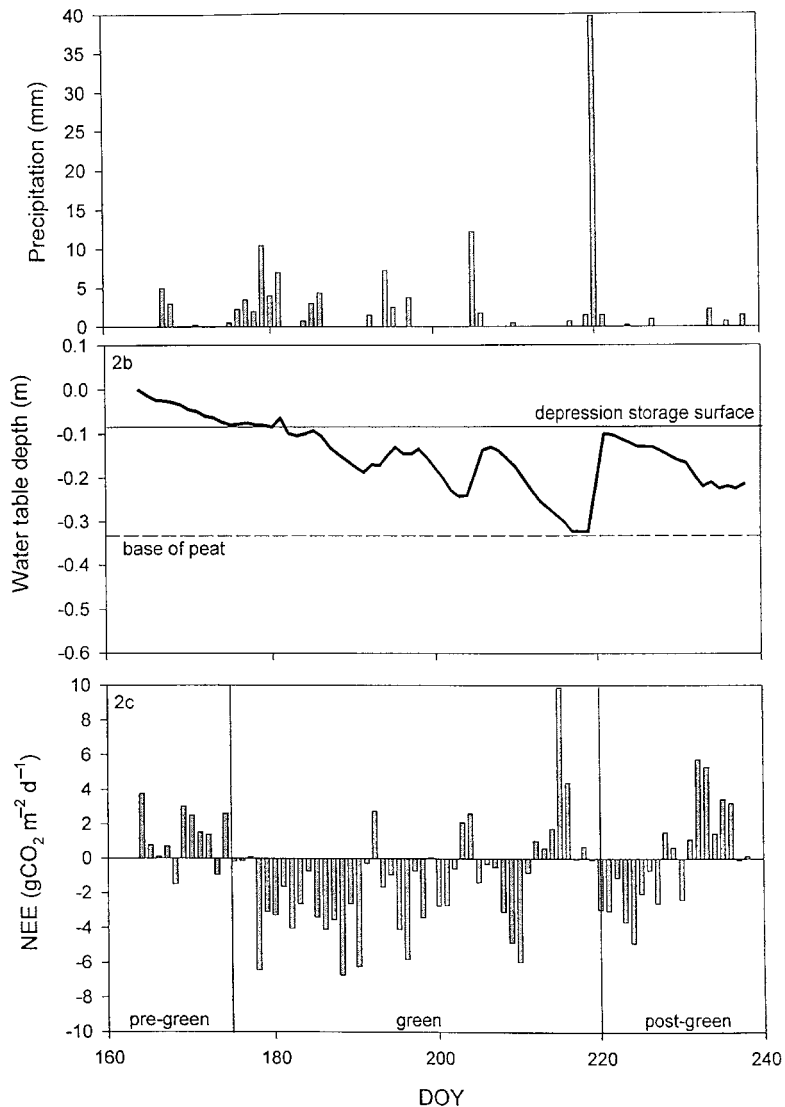
turbulent transfer coefficients  $K_h$  and  $K_c$  from BREB- $Q_h$  can be problematic when  $Q^*$  is small such as at night or during sunrise or sunset. At these times, temperature and humidity gradients tend to be small and  $\beta$  may become unreliable. Under these conditions  $K_h$  has been derived from either the aerodynamic or eddy covariance calculation of  $Q_h$ . 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 & Rouse (1989) to test for measurement error and boundary layer problems. Maximum error in daytime  $F_c$  can approach 30%. Errors associated with chamber measurements are difficult to quantify due to the uncertainty of their effect on the soil and plant environment. For consistency we

have estimated that the error is similar to the tower measurements.

## Results

### *Environmental conditions*

The 1997 growing season was drier and warmer than the Churchill 30-y normal (Griffis *et al.* in press). Total precipitation during the growing season was 125 mm (4 mm below average) and mean air temperature was 12.7°C (1.9°C above average). Precipitation events occurred on average every 3 days and were generally more frequent at the beginning of the season (Fig. 2a). Water table depth remained above the depression storage surface until DOY 180 (29 June) and reached a maximum depth of -0.32 m on DOY 217 (5 August)



**Fig. 2** (a) Seasonal precipitation; (b) Seasonal water table position; (c) Daily landscape-level net ecosystem CO<sub>2</sub> exchange

(Fig. 2b). Leaf area index (LAI) was 0.47 by DOY 192 and decreased to 0.28 10 days following the start of the postgreen period. Photosynthetically active radiation and net radiation was typical for the season. Evaporation was the dominant eERgy sink, consuming 57% of the net radiation. The Bowen ratio averaged 0.49 over the growing season (Griffis *et al.* submitted).

#### Landscape-level CO<sub>2</sub> exchange

The fen represented a net sink of  $-0.7 \text{ gCO}_2 \text{ m}^{-2} \text{ d}^{-1}$ , accumulating a total of  $-49 \text{ gCO}_2 \text{ m}^{-2}$  over the measurement period. Daily losses of CO<sub>2</sub> were experienced through the pregreen period (Fig. 2c). Peak uptake occurred early in the green period. Day-to-day variability in NEE increased during the mid-green period and large losses of CO<sub>2</sub> occurred near the end of the green period. The early postgreen period experienced a net gain of CO<sub>2</sub> while late postgreen CO<sub>2</sub> exchange showed frequent losses. The seasonal diurnal curve of NEE (Fig. 3) indicates maximum CO<sub>2</sub> uptake in the morning (07.00 hours) and a strong reduction through the afternoon hours. Losses of CO<sub>2</sub> were observed from early evening (19.00 hours) to early morning (05.30 hours).

Ecosystem respiration and photosynthesis were both relatively small during the pregreen period. Respiration averaged  $+4.7 \text{ gCO}_2 \text{ m}^{-2} \text{ d}^{-1}$  and photosynthesis averaged  $-3.3 \text{ gCO}_2 \text{ m}^{-2} \text{ d}^{-1}$  (Fig. 4). Green period respiration and photosynthesis increased to  $+6.6 \text{ gCO}_2 \text{ m}^{-2} \text{ d}^{-1}$  and  $-7.6 \text{ gCO}_2 \text{ m}^{-2} \text{ d}^{-1}$ , respectively. Post-green respiration decreased to  $+6.3 \text{ gCO}_2 \text{ m}^{-2} \text{ d}^{-1}$  while photosynthesis decreased to  $-6.0 \text{ gCO}_2 \text{ m}^{-2} \text{ d}^{-1}$ .

#### Community-level CO<sub>2</sub> exchange

The majority of the chamber measurements from this study was taken between 10.30 and 15.30 hours and therefore lower photosynthetic and higher respiration rates are exhibited than would be expected if integrated over the entire daytime period. However, it is the relative difference in CO<sub>2</sub> exchange between the community types that is of primary interest. At the hollow sites respiration averaged  $+3.4 \text{ gCO}_2 \text{ m}^{-2} \text{ d}^{-1}$  with a coefficient of variation (*r*) 51%. Pre-green, green and postgreen respiration averaged  $+0.9$ ,  $+3.8$ , and  $+3.3 \text{ gCO}_2 \text{ m}^{-2} \text{ d}^{-1}$  (Fig. 5a). Seasonal photosynthesis averaged  $-2.1 \text{ gCO}_2 \text{ m}^{-2} \text{ d}^{-1}$  and showed a large amount of spatial and temporal variability (*r* = 83%). Pre-green, green and postgreen photosynthesis averaged  $-0.9$ ,  $-2.5$ , and  $-2.1 \text{ gCO}_2 \text{ m}^{-2} \text{ d}^{-1}$ , respectively (Fig. 5b). Small hummock respiration averaged  $+9.9 \text{ gCO}_2 \text{ m}^{-2} \text{ d}^{-1}$ . Pre-green, green, and postgreen respiration averaged  $+8.1$ ,  $+10.6$ , and  $+9.5 \text{ gCO}_2 \text{ m}^{-2} \text{ d}^{-1}$  (Fig. 5a). The *r* for small hummock respiration at 32% was smaller than for the hollows.

Seasonal photosynthesis averaged  $-8.8 \text{ gCO}_2 \text{ m}^{-2} \text{ d}^{-1}$ . The variability in photosynthesis was also lower (*r* = 52%) than for the hollows. Pre-green, green, and postgreen photosynthesis averaged  $-5.0$ ,  $-9.7$  and  $-9.7 \text{ gCO}_2 \text{ m}^{-2} \text{ d}^{-1}$ , respectively (Fig. 5b). Pre-green photosynthetic rates were relatively large due to the wet mosses and as well the contribution from the emerging vascular species. Photosynthesis remained large during the early postgreen period as senescence had just been initiated. As well, complete senescence had not occurred when the 1997 field study ended on DOY 238. Large hummock respiration rates averaged  $+5.5 \text{ gCO}_2 \text{ m}^{-2} \text{ d}^{-1}$ . Pre-green, green, and postgreen respiration averaged  $+3.9$ ,  $+5.6$ , and  $+4.0 \text{ gCO}_2 \text{ m}^{-2} \text{ d}^{-1}$  (Fig. 5a). Seasonal photosynthesis averaged  $-5.1 \text{ gCO}_2 \text{ m}^{-2} \text{ d}^{-1}$ . Pre-green, green, and postgreen photosynthesis averaged  $-4.2$ ,  $-4.7$  and  $-6.4 \text{ gCO}_2 \text{ m}^{-2} \text{ d}^{-1}$ , respectively (Fig. 5b). The coefficient of variation for large hummock respiration and photosynthesis was 70% and 66%, respectively.

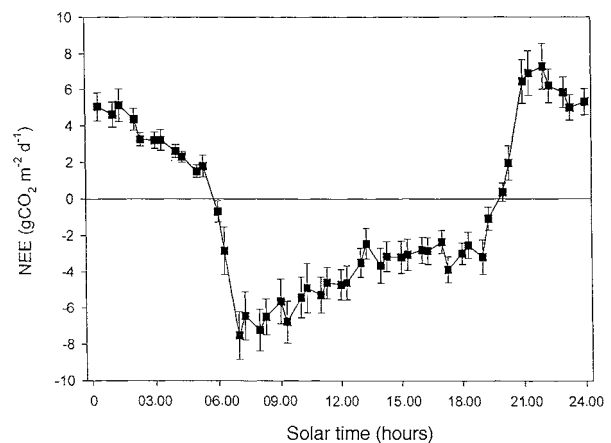


Fig. 3 Diurnal landscape-level net ecosystem CO<sub>2</sub> exchange

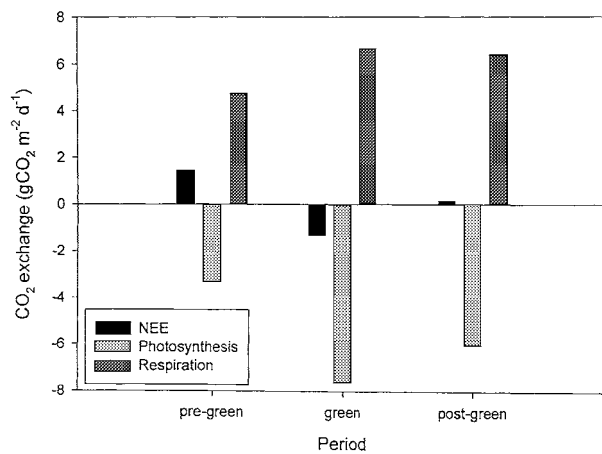


Fig. 4 Mean landscape-level respiration, photosynthesis, and NEE by phenological study period

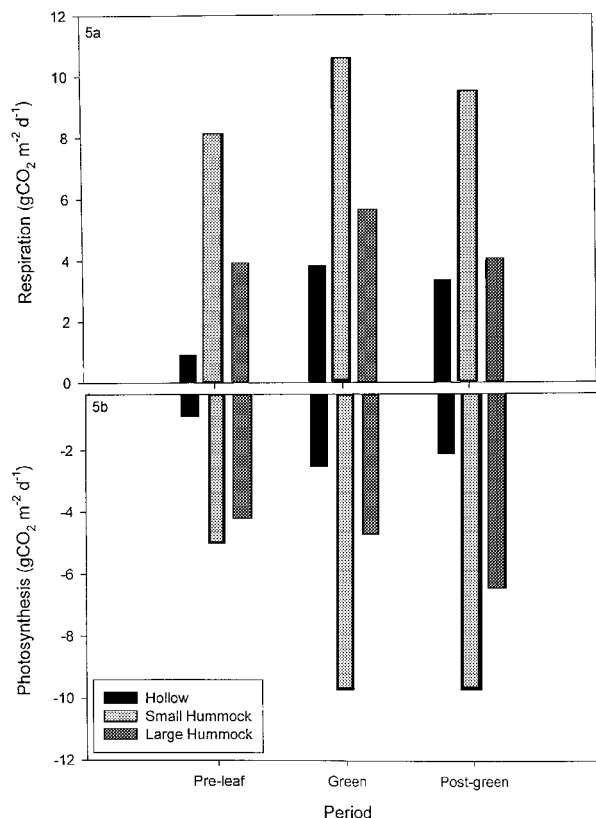
### Scaling from the community to landscape-level

*A priori* selection of the community scale was based on the strong patterning of vegetation type with respect to microtopography. Community- and landscape-scale CO<sub>2</sub> fluxes were analysed to: (i) compare the differences between chamber and tower measurements; (ii) examine the CO<sub>2</sub> exchange differences between community types; and (iii) assess how the process of net photosynthesis and ecosystem respiration differs between the community and landscape level.

*Comparison of chamber and tower data* Simultaneous chamber measurements of photosynthesis, respiration, and NEE over each terrain type were not possible. Therefore, in order to scale from the community to landscape level, it was necessary to integrate all chamber measurements within each of the three phenological study periods. Pre-green, green, and postgreen chamber fluxes were scaled as follows:

$$F_{c_{total}} = 0.48(F_{c_{HW}}) + 0.47(F_{c_{SH}}) + 0.05(F_{c_{LH}}), \quad (3)$$

where  $F_{c_{total}}$  is the scaled-sum of chamber photosynthesis, respiration or NEE resulting from the individual terrain units. The scaling factor is the percentage areal



**Fig. 5** Mean community-level respiration and photosynthesis by phenological study period

coverage of each terrain unit type determined from the detailed survey. Figure 6 shows comparisons between scaled chamber fluxes with tower measurements for common half-hour time intervals during each of the phenological periods. Figure 6(a) indicates good agreement between chamber and tower photosynthesis and respiration in the pregreen period. The scaled chamber method produced lower photosynthetic rates by 4% and respiration by 28%. Figure 6(b) displays the half-hour comparisons for the green period. Scaled chamber photosynthesis was lower than tower photosynthesis by 32% and chamber respiration was greater than the tower respiration by 3%. Photosynthesis estimates between 12.30 and 13.30 hours however, showed only a 3% difference. Consequently, there was a substantial difference in NEE during the morning and afternoon hours. Post-green comparisons of photosynthesis, respiration and NEE show good agreement and are within the maximum expected error (Fig. 6c). Chamber measurements were lower than tower photosynthesis, respiration and NEE by 28%, 17%, and 37%, respectively, during this period. It appears that the best agreement between scaled chamber and tower measurements is during midday for all periods.

*Estimating the community contribution to landscape-level CO<sub>2</sub> exchange* Expected changes in mean water table position resulting from global warming are likely to shift the distribution of plant types within this fen. It is essential, therefore, to understand how each community type within the larger landscape influences CO<sub>2</sub> exchange. The contribution of each community to landscape-scale NEE was estimated by computing an effective scaling factor (ESF) for each terrain unit. In doing so, we identify the communities that have the largest control on CO<sub>2</sub> exchange within the fen. This scaling method is especially useful when the physical processes operating in a system are not understood completely. One caveat to this approach, however, is the assumption that the relative difference between photosynthesis and ecosystem respiration between each community type is conserved diurnally. This potential error has been reduced by using a large number of chamber observations and by developing the effective scaling factor for different phenological periods.

The ESF was calculated by multiplying the terrain unit-scaling factor by the relative difference in respiration and photosynthesis observed for each community (hollow, small hummock, large hummock) (Table 1).

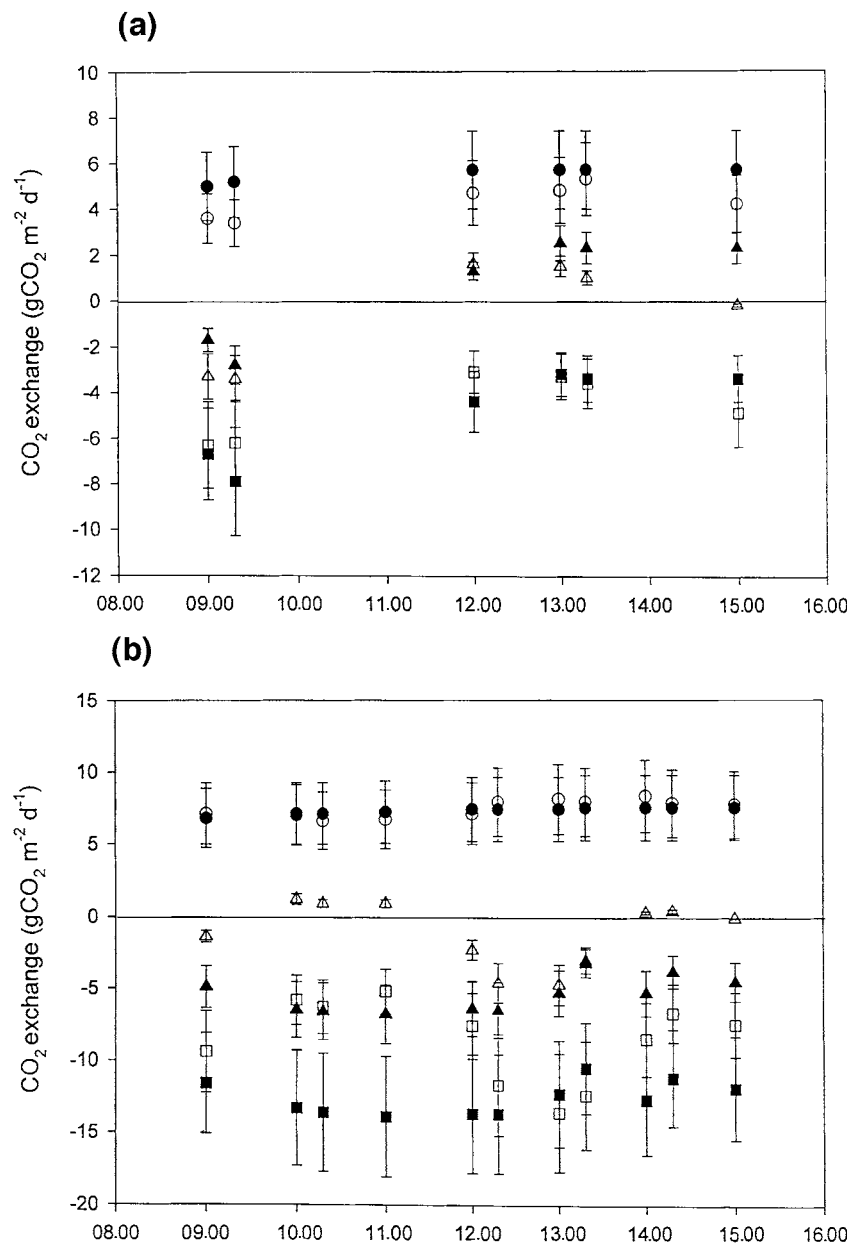
$$ESF = ASF \left( \frac{F_{c_{total}}}{F_{c_{CT}}} \right), \quad (4)$$

where ESF is the effective scaling factor, ASF is the areal scaling factor for each terrain unit or community type,

$F_{CT}$  is the mean  $CO_2$  flux observed from a community type. The ESF was then applied to the landscape-scale NEE measurements to obtain the relative contribution from each community. Figure 7(a) shows the contribution of each terrain unit type to respiration. Over the growing season, small hummocks accounted for  $+4.4 gCO_2 m^{-2} d^{-1}$ . Hollows and large hummocks contributed  $+1.5$  and  $+0.3 gCO_2 m^{-2} d^{-1}$ . Figure 7(b) displays the contribution of individual terrain units to photosynthesis. Small hummocks dominated the overall production of the fen and averaged  $-5.3 gCO_2 m^{-2} d^{-1}$ . Hollows and large hummocks contributed significantly less to the overall production of the fen. Their average estimated produc-

tion was  $-1.3$  and  $-0.3 gCO_2 m^{-2} d^{-1}$ , respectively. Therefore, it appears from this analysis that the *Carex* spp. portion of the landscape represents the major sink of  $CO_2$  to the fen. Small hummock terrain units gave a net balance of  $-0.9 gCO_2 m^{-2} d^{-1}$  while hollows experienced a net loss of  $+0.2 gCO_2 m^{-2} d^{-1}$ . Large hummock photosynthesis and respiration balanced over the season. Summation of all the contributing fluxes results in a net balance of  $-0.7 gCO_2 m^{-2} d^{-1}$ .

*Landscape and community-scale processes: net photosynthesis* NEE and net photosynthesis is commonly described as a function of photosynthetically active radiation (Prioul &



Chartier 1977; Whiting 1994; Frohling *et al.* 1997; Waddington *et al.* 1998). However, the process is complicated by a number of other environmental factors including leaf temperature, soil and leaf water potential, atmospheric moisture deficit, internal and ambient CO<sub>2</sub> concentrations, and nutrient status (Lambers *et al.* 1998). Here, we examine the relationship between net photosynthesis and light using the basic model proposed by Prioul & Chartier (1977):

$$A = \frac{\phi Q + A_{\max} - \sqrt{(\phi Q + A_{\max})^2 - 4\phi Q k A_{\max}}}{2k} - R_{\text{day}} \quad (5)$$

where *A* is the net photosynthetic flux,  $\phi$  is the apparent quantum efficiency (AQE) describing the conversion of light to photochemical products. *Q*, is the photosynthetically active radiation, *A*<sub>max</sub>, the maximum light saturated net photosynthetic rate, *R*<sub>day</sub>, the daylight respiration rate resulting from nonphotorespiration processes and *k*, is a scaling parameter describing the

change of slope between the light-limited and light-saturated region of the curve.

Growing season net photosynthesis at the landscape-level and for each community type shows unique relationships with respect to light levels (Fig. 8). The parameters for each curve-fit and the net photosynthetic flux value (*A*) for *Q* = 1000 μmol m<sup>-2</sup> s<sup>-1</sup> are listed in Table 2.

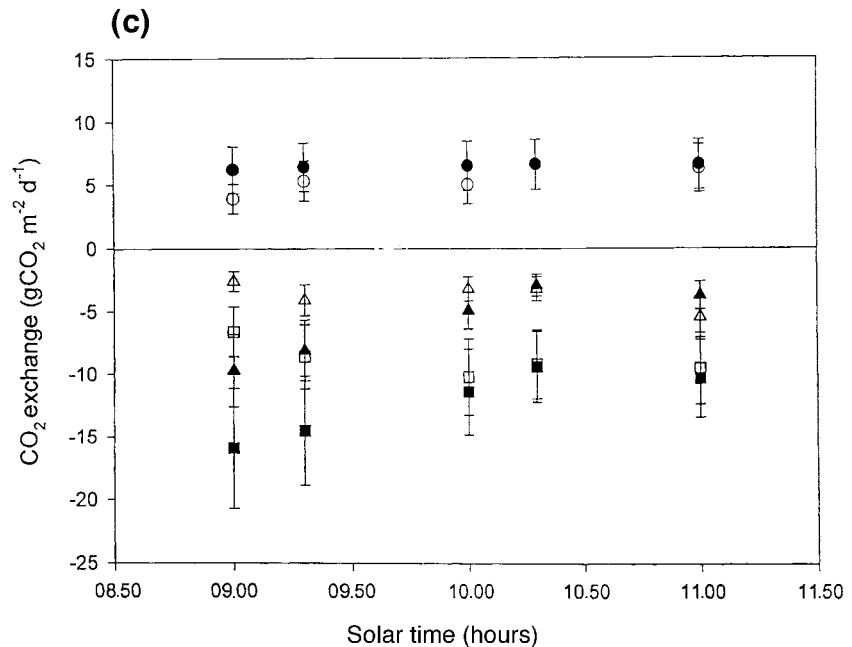
In geERal, each curve-fit exhibits a low correlation coefficient and only the small hummock and landscape-level parameters are statistically significant at the 95% confidence interval. This can be attributed to the fact that a large number of the controlling environmental factors are not included in the above algorithm. Furthermore, we expect a large amount of scatter in the net photosynthetic data due to spatial (biomass) and temporal (phenological stage) heterogeneity within the fen. At the landscape scale, small hummock, hollow and large hummock communities correlation coefficients were 0.40, 0.50, 0.25, and 0.32, respectively. The curve-fits show higher

**Table 1** Effective scaling factors of community contribution to landscape-level CO<sub>2</sub> exchange

Terrain Unit	Pre-green <i>R</i>	Pre-green <i>P</i>	Green <i>R</i>	Green <i>P</i>	Post-green <i>R</i>	Post-green <i>P</i>
Small hummock	0.75	0.79	0.70	0.76	0.71	0.77
Hollow	0.18	0.14	0.26	0.20	0.25	0.17
Large hummock	0.07	0.07	0.04	0.04	0.03	0.05

\**R*, Respiration; *P*, Photosynthesis

**Fig. 6** (a) Pre-green period comparison of scaled chamber and landscape-level CO<sub>2</sub> fluxes (square indicates photosynthesis, circle indicates respiration, triangle indicates NEE, dark symbols indicate landscape-level measurements, open symbols indicate community-scale measurements). (b) Green period comparison of scaled chamber and landscape-level CO<sub>2</sub>. (c) Post-green period comparison of scaled chamber and landscape-level CO<sub>2</sub> fluxes



correlation at the landscape level and small hummock community compared to the hollow and large hummock community. This may be due to the small flux values at the hollow and large hummock sites relative to the errors involved in the measuring process. In addition, since the hollow and large hummock communities are dominated by bryophytes, variations in plant water potential and atmospheric moisture content may lead to large variability in net photosynthesis over a wide range of PAR levels.

At the community scale, small hummock net photosynthesis yielded the smallest AQE and the largest  $A_{\max}$  rate. Hollows and large hummock communities experienced higher AQEs and lower  $A_{\max}$  rates compared to the small hummocks. Landscape-level net photosynthesis exhibited an AQE and  $A_{\max}$  value that was within the range of the community values. Each of the community parameters was scaled according to the areal coverage of the community type:

$$P_{P_{\text{total}}} = 0.48(P_{P_{\text{HW}}}) + 0.47(P_{P_{\text{SH}}}) + 0.05(P_{P_{\text{LH}}}), \quad (6)$$

where  $P_p$  is the areal weighted sum of the net photosynthesis community parameters  $\phi$ ,  $A_{\max}$ ,  $R_{\text{day}}$  and  $k$ . The scaled community relationship yields para-

meters that are close to those found at the landscape level. For comparative purposes we determined the net photosynthetic rate for the landscape level, individual community types, and the scaled community parameters for  $Q = 1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ . The observed difference in net photosynthesis between the landscape-level and scaled community composite is about 21%.

*Landscape and community-scale processes: Ecosystem Respiration* Empirical approaches to estimating ER fluxes from functions of soil temperature and or water table position have been adopted by numerous authors (Oberbauer *et al.* 1991; Kim & Verma 1992; Shurpali *et al.* 1995; Waddington *et al.* 1998). In general, these relationships have performed poorly due to the large amount of spatial and temporal variability observed in the fluxes. ER plotted as a function of surface temperature for the landscape-scale and each community type is shown in Fig. 9. The landscape-scale ER fluxes have been grouped into small temperature intervals and averaged. This classification was necessary in order to smooth the large number of data points and better depict the relationship with surface temperature. A similar approach was employed by Waddington *et al.* (1998) for ER at the community scale. Also note that the night-time

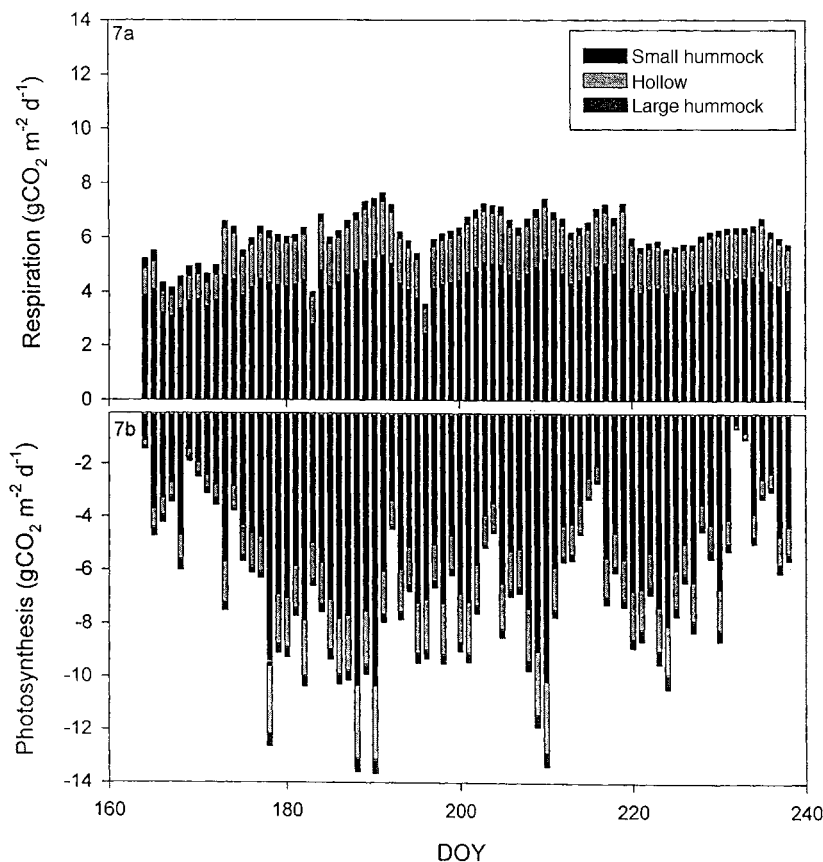


Fig. 7 (a) Community-level contribution to landscape-scale respiration. (b) Community-level contribution to landscape-scale photosynthesis

temperature range is small (−1.4–15.5°C) relative to each of the community types where measurements were made during the daytime. A linear equation was fit to each of the datasets to estimate ER as a function of surface temperature

$$ER = \alpha \cdot T_s + R_{\max} \quad (7)$$

where  $\alpha$  is the slope of the ER vs. surface temperature ( $T_s$ ) relationship describing microbial and plant response to surface temperature change and  $R_{\max}$  is the maximum ER rate 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 phenological stage. Each of the parameters along with  $Q_{10}$  factors are listed in Table 3.

The correlation coefficient for the landscape, small hummock, hollow and large hummock communities was 0.83, 0.46, 0.58 and 0.29, respectively. ER at the small hummock community yields the largest respiration rate at the freezing temperature. Hollows experience small

respiration rates under cold conditions. The large hummock communities experienced slightly higher respiration rates than hollows at freezing. The  $Q_{10}$  sensitivity factor indicates that the hollow communities respond the most rapidly to surface-temperature change. This is likely autocorrelated with lower water table position given higher surface temperature; however, no significant relationship was found between ER and water table position or soil moisture content. The landscape- and community-scale parameters were within the same order of magnitude.

Each of the community parameters was scaled according to the areal coverage of the community type:

$$P_{R_{\text{total}}} = 0.48(P_{R_{\text{HW}}}) + 0.47(P_{R_{\text{SH}}}) + 0.05(P_{R_{\text{LH}}}), \quad (8)$$

where  $P_R$  is the areal weighted total of the ER community parameters  $\alpha$ , and  $R_{\max}$ . The scaled community composite resulted in similar parameters, however, overestimated  $\alpha$  and underestimated  $R_{\max}$ . For a surface temperature of 25°C the community composite relation-

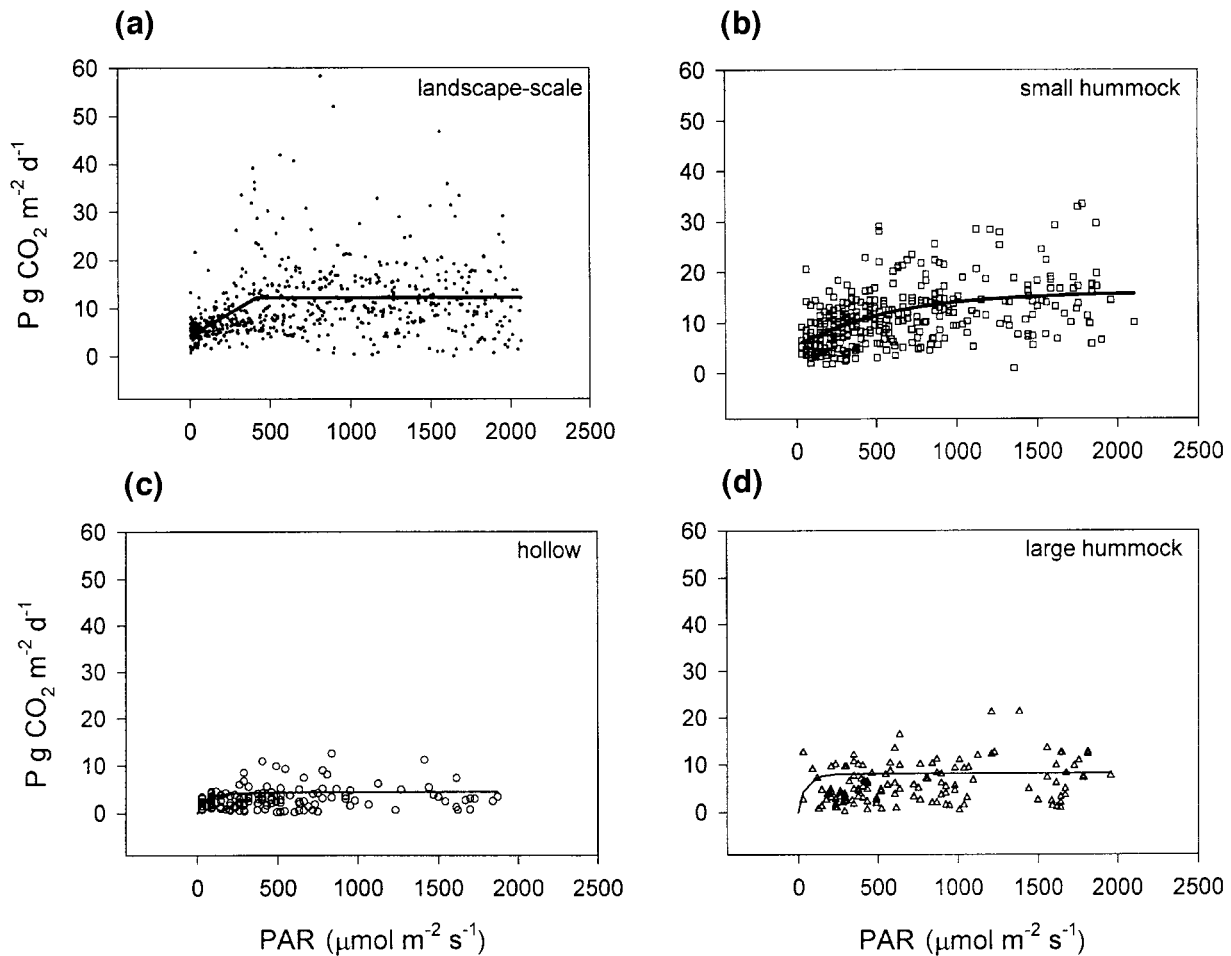


Fig. 8 Landscape and community-scale net photosynthesis as a function of photosynthetically active radiation

ship underestimated landscape-level respiration by about 26%. The landscape-level and the community-scaled composite revealed a similar  $Q_{10}$  response.

## Discussion

### Landscape-level NEE

During the relatively dry and warm growing season the Churchill fen experienced a small net gain of  $\text{CO}_2$ . The daily photosynthetic flux did not exceed ecosystem respiration until about DOY 178 when leafing had commenced. Maximum uptake of  $\text{CO}_2$  occurred early during the green period when LAI reached near maximum and coincided with relatively wet surface-conditions. As the season progressed the water table position dropped and NEE became more variable. Maximum draw down in the water table near the end of the green period coincided with five days of large  $\text{CO}_2$

losses from the wetland. However,  $\text{CO}_2$  uptake increased following a large rain event that occurred at the end of the green period. The data suggest that NEE may become more sensitive to precipitation events as the water table is lowered. Consequently, synoptic conditions exert an important control on the  $\text{CO}_2$  exchange at the fen.

### Scaling

At the community scale, all fluxes showed a large amount of spatial and temporal variability as indicated by the large coefficients of variation. However, respiration rates were less variable than photosynthesis. This observation supports the findings of Griffis *et al.* (in press) where the interannual variability in landscape-scale NEE at a subarctic fen was attributed to large seasonal and daily differences in photosynthesis. Furthermore, Kindermann *et al.* (1996), using the Frankfurt Biosphere Model, attributed global-scale inter-

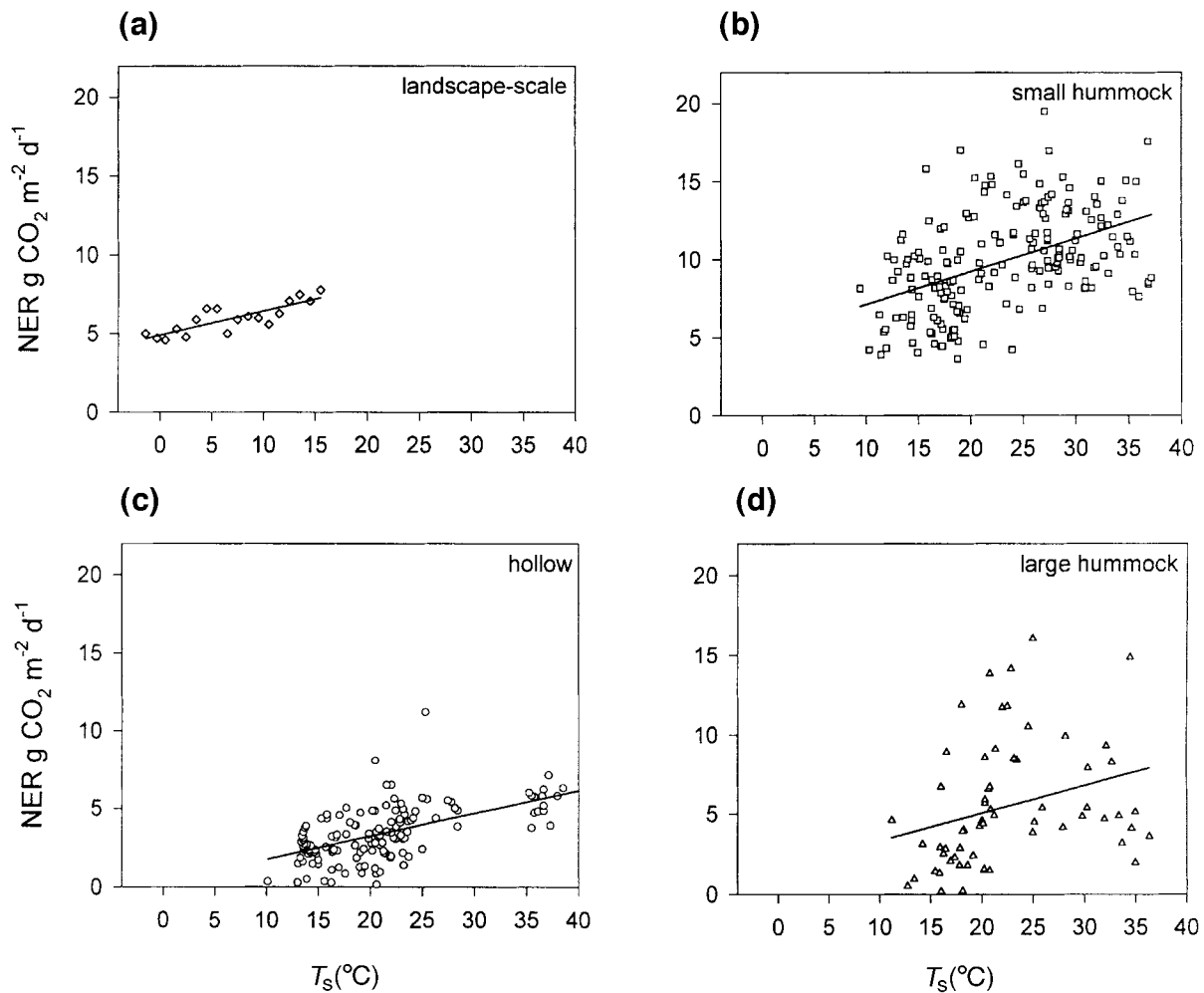


Fig. 9 Landscape and community-scale ecosystem respiration as a function of surface temperature.

**Table 2** Curve-fit parameters for landscape and community-scale net photosynthesis described as a function of photosynthetically active radiation

Terrain type	$\phi$	$A_{\max}$	$R_{\text{day}}$	$k$	$A_{(Q=1000)}$
Small hummock	0.014	11.3	5.8	0.76	14.2
Hollow	0.026	3.0	1.5	0.84	4.4
Large hummock	0.040	5.0	3.1	0.96	8.1
Landscape	0.019	7.9	4.3	1.0	12.2
Scaled community	0.021	7.0	3.6	0.81	10.1

$\phi$ , gCO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup> μmol<sup>-1</sup> PAR

$A_{\max}$ , gCO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>

$R_{\text{day}}$ , gCO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>

$k$ , dimensionless

All curve-fit parameters are statistically different at the 95% confidence interval.

**Table 3** Parameters for landscape- and community-scale net ecosystem respiration described as a function of surface temperature

Terrain type	$\alpha$	$R_{\max}$	$Q_{10}$
Small hummock	0.21	5.1	1.3
Hollow	0.14	0.32	1.6
Large hummock	0.17	1.6	1.4
Landscape	0.15	4.9	1.2
Scaled community	0.17	2.6	1.3

$\alpha$ , gCO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup> °C<sup>-1</sup>

$R_{\max}$ , gCO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>

All curve-fit parameters are statistically different at the 95% confidence interval.

annual variability in atmospheric CO<sub>2</sub> concentrations to differences in photosynthesis.

The small hummock community (*Carex* spp.) exerted the strongest control on landscape-scale NEE. This is due to their relatively large surface coverage, but also, more importantly, the large flux value observed for both photosynthesis and respiration. Small hummocks exhibited the largest effective scaling factor during all periods of study. Therefore, the observed diurnal pattern in landscape-scale NEE is driven largely by CO<sub>2</sub> exchange at the small hummock sites. Strong reduction in CO<sub>2</sub> uptake through the late morning and afternoon hours is likely due to a reduction in stomatal conductance at the small hummock sites. Blanken & Rouse (1996) and Schreuder *et al.* (1998) provide evidence of water conservation in *Carex* species. Furthermore, estimates of landscape-scale photosynthesis (Griffis *et al.* in press) show a strong reduction through the late morning and afternoon hours especially during warm and dry years. Positive NEE (losses of CO<sub>2</sub>) from the wetland following the

maximum draw-down in the water table is likely due to a large reduction in photosynthesis and a small increase in ecosystem respiration.

Scaling the chamber measurements to the landscape level over the season indicates that estimates of tower photosynthesis and respiration, as well as measured NEE, is within the maximum margin of error of both methods. This helps substantiate that the fen was a net sink of -49 gCO<sub>2</sub> m<sup>-2</sup> over the measurement season. There is a need for detailed analysis of the error associated with chamber measurements. It is apparent that chambers tend to underestimate the fluxes. This may be due to: (i) lack of spatial representation — a limited number of sampling points was available for the early morning and late afternoon hours; (ii) gradient problems — build-up of CO<sub>2</sub> in the chamber could have suppressed the respiration flux while depletion of CO<sub>2</sub> might have reduced the photosynthetic flux. Re-examination of the photosynthesis CO<sub>2</sub> gradients from our data suggests that the 5-minute sampling interval is too long for some sites; and (iii) chamber heating which may have enhanced photorespiration rates. Better results might have been achieved with a more sophisticated dynamic chamber.

#### Ecological implications

Previous studies of landscape-scale NEE (Lafleur *et al.* 1997; Griffis *et al.* in press) indicate that the transient response of northern wetlands to hot and dry spring–summer conditions is a net loss of CO<sub>2</sub> while warm and wet summers enhance CO<sub>2</sub> uptake. Based on the results of the community- and landscape-scale analysis it is possible to hypothesize about the equilibrium response of this fen to climatic warming.

A water-balance model developed by Rouse (1998) for the Churchill fen suggests that soil moisture will decrease during the main growing season given a future two-fold CO<sub>2</sub> warming of 4 °C and a substantial 20% increase in precipitation. In time, this small reduction in water table position at the fen could enhance its productivity by (i) changing the vegetation distribution within the fen, and (ii) increasing the mineralization of organic nitrogen. The strong patterning of vegetation in relation to microtopography and mean water table position suggests that a long-term reduction in the water table position at the fen would allow for the invasion of vascular species into the drier hollows. For example, a similar distribution of *Carex* spp. at the hollow and small hummock sites would have changed the 1997 NEE dramatically (Table 4). In effect, this vegetation feedback would approximately double the LAI of the fen from 0.47 to 0.94. Moreover, this analysis may also serve as a simple analogue for increased productivity resulting

**Table 4** Potential change in landscape-scale NEE resulting from vegetation feedback

Distribution	Small hummocks	Hollows	Large hummocks
<b>Current</b>			
Cumulative <i>P</i>	-394	-98	-23
Cumulative <i>R</i>	+328	+115	+19
<i>P</i> - <i>R</i>	-66	+17	-4
Seasonal NEE	-53 gCO <sub>2</sub> m <sup>-2</sup>		
Daily NEE	-0.7 gCO <sub>2</sub> m <sup>-2</sup> d <sup>-1</sup>		
<b>Scenario 1</b>			
Cumulative <i>P</i>	-788		-23
Cumulative <i>R</i>	+656		+19
<i>P</i> - <i>R</i>	-132		-4
Seasonal NEE	-136 gCO <sub>2</sub> m <sup>-2</sup>		
Daily NEE	-1.8 gCO <sub>2</sub> m <sup>-2</sup> d <sup>-1</sup>		

*P*, Photosynthesis gCO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>

*R*, Ecosystem Respiration gCO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>

Results based on 1997 Environmental Characteristics

from greater nitrogen availability due to drier soil conditions. It is well known that the productivity of arctic ecosystems is limited strongly by either nitrogen and/or phosphorous (Shaver & Chapin 1991; Shaver & Chapin 1995; Shaver *et al.* 1998). In this scenario, *Carex* spp. would not necessarily change their distribution but would increase their leaf blade dimensions. Experiments by Shaver *et al.* (1998) demonstrated that increased nitrogen and or phosphorous supply to wet sedge tundra in northern Alaska caused significant increases in above- and below-ground biomass; changed species composition and increased both ecosystem production and respiration on an areal basis. Leaf area increased 4–6 times in nitrogen plus phosphorous addition experiments. Communities dominated by sedges showed significant increases in the abundance of *Carex corrdor-rhiza*, a species that yielded the highest nutrient concentrations in control treatments. Ecosystem photosynthesis and respiration fluxes increased mainly due to changes in biomass. Recent work by Rolph (1999) has shown similar findings for the Churchill fen. In this 4-y nitrogen addition experiment (FERTEX), significant changes were found in both species composition and above-ground biomass. Higher abundance of *Carex aquatilis* and *Carex limosa* was found for fertilized plots in both hollow and small hummock environments. LAI reached 1.5 at the peak of the growing season, which was approximately three times larger than at the control site. The effects of community composition and biomass changes on chamber-level CO<sub>2</sub> exchange are currently under investigation at the FERTEX study site.

It is possible that one or both of the above feedbacks could occur. Based on the 1997 climatic conditions, a doubling of LAI would have amplified net CO<sub>2</sub> uptake by about 2.6 times, resulting in a net sink of -136 gCO<sub>2</sub> m<sup>-2</sup>. However, our analysis assumes that soil respiration and stomatal conductance would respond conservatively to the changing water table position. Current modelling efforts (Griffis & Rouse submitted) are examining the sensitivity of these potential feedbacks.

### Modelling implications

A combination of community- and landscape-level observations reveals the complex nature of CO<sub>2</sub> cycling at the Churchill fen. While predicting the future response of NEE will require detailed physical representation of the exchange processes at the appropriate scales, this paper has shown that landscape-level monitoring is critical in verifying that all the important community-level processes have been identified and described accurately. While it was not the goal of this paper to describe in detail the physical processes regulating CO<sub>2</sub> exchange at the community and landscape levels, we provide two simple examples that demonstrate how photosynthesis and ER behave differently at each scale and between community types. Community-scale analysis indicates that stomatal control on photosynthesis is a key variable influencing CO<sub>2</sub> exchange at the Churchill fen. Mechanistic models of NEE should therefore be developed from lower-order processes (plant level) and scaled to the landscape level using community information. This would provide an opportunity to use satellite data to monitor community distribution changes and allow for the adjustment of model scaling parameters.

### Acknowledgements

The National Science and Engineering Research Council of Canada and the Department of Indian and Northern Affairs have supported this work through research grants and scholarships. The Churchill Northern Studies Centre has provided the logistical support for this research endeavour. We would like to thank Rich Petrone and Sandra Rolph for their expertise in the field. Finally, we would like to thank the GCB subject editor and the anonymous reviewers of this paper for their helpful criticisms and suggestions.

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