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Interannual Variability in Net Ecosystem CO₂ Exchange at the Arctic Treeline

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Abstract

Net ecosystem exchange (NEE) of carbon dioxide was measured at treeline forest and fen tundra sites near Churchill, Canada during three consecutive growing seasons (1997–1999). Although both sites demonstrated a net uptake of CO₂ in each of the years, there was considerable variation in the flux between sites and between years. Mean daily NEE at the forest varied from -1.5 (±0.25 SD) g $CO_2 \text{ m}^{-2} \text{ d}^{-1}$ in 1997 to $-7.3 \ (\pm 0.39) \text{ g } CO_2 \text{ m}^{-2} \text{ d}^{-1}$ in 1999. The fen mean daily NEE varied from $-1.1 (\pm 0.36)$ g CO₂ m⁻² d⁻¹ in 1997 to $-3.1 (\pm 0.50)$ g CO₂ m⁻² d⁻¹ in 1998. Integrated over the 65-d measurement period the forest was a net sink of -100, -313, and -478 g CO_2 m⁻² in 1997, 1998, and 1999, respectively, and the fen net sink was -73, -202, and -38 g CO₂ m⁻², respectively. Interannual variations in the fen NEE were closely related to water table drawdown (soil wetness), the forest NEE was unaffected by water table change. The forest seasonally cumulative NEE was closely associated with timing of snowmelt and accumulated heat content prior to leaf-out. Earlier snowmelt and greater heat accumulation produced a larger growing season sink. It is likely these events also influenced the fen NEE, but the relationship is complicated by water table effects. These results suggest that carbon dioxide exchange varies considerably across the northern treeline, and that there may be an important biospheric feedback between climate warming, treeline advance, and carbon cycling.

Introduction

In recent years there has been considerable interest in carbon exchange of northern ecosystems, particularly northern peatlands because of their large carbon stock (Gorham, 1991) and sensitivity to climate change (Oechel and Billings, 1992; Oechel et al., 1993; Oechel and Vourlitis, 1994). Although limited in number, previous studies of CO₂ exchange of arctic and subarctic ecosystems have focused on tundra terrain. These studies indicate considerable variation between sites. Some have shown a net loss of CO₂ during the growing season (Fan et al., 1992; Oechel et al. 1993; Oechel et al. 1995; Schreader et al., 1998), while others have found a net CO₂ gain (Coyne and Kelly, 1975; Vourlitis and Oechel, 1997). Studies which have investigated interannual variations in CO2 exchange at a given site have found that the same peatland ecosystem can act as either a net source or sink for CO₂ (Oechel et al., 1993; Shurpali et al., 1995; Joiner et al., 1999; Griffis et al., 2000a). In most cases it is changes in water table (soil moisture) indirectly driven by climate variability which have the greatest impact on the sourcesink strength of the peatland.

To the best of our knowledge there have been only two studies of subarctic forest carbon exchange: Fan et al. (1995) and Lafleur (1999). Although conducted in geographically distinct regions and in different years, both of these studies found that the open forest was a net sink for $\rm CO_2$ during a single growing season. We are not aware at this time of any previous direct comparisons of carbon exchange for adjacent tundra and treeline forest sites.

In the present study we examine net ecosystem CO_2 exchange (NEE) at two treeline sites near Churchill, Manitoba, Canada: open conifer forest and sedge fen tundra. The measurements extend over three growing seasons (1997–1999). Thus,

we are able to investigate differences in NEE between the two sites and between seasons. Such a comparison is important for several reasons. These two ecosystems constitute a major component of the low arctic landscape (Billings, 1987; Gilmanov and Oechel, 1995) and as such play an important role in the arctic carbon budget. Records of treeline advance and retreat in recent historical times are well established (Ritchie, 1984, 1987). Several studies have investigated the biophysical impacts of treeline movement on climate (Harvey, 1988; Bonan et al., 1992, 1995; Thomas and Rowntree, 1992). Most have concluded that there is a large positive feedback between climate and treeline movement, initiated by the changes in albedo and roughness where forest replaces tundra (or vice versa). Although the importance of the biogeochemical impact of arctic land cover change is still largely speculative, it is suggested that changes in carbon storage are likely as forest replaces tundra (Prentice and Fung, 1990; Smith et al., 1992). However, there is little direct field data available with which to assess the potential importance of this significant, but as yet poorly understood, biospheric feedback between global climate change and the arctic ecosystem. We hope the present study fulfills part of this knowledge gap.

Sites

The sites are located about 20 km east of Churchill, Canada (58°45′N, 94°04′W), and 11 to 14 km south of the Hudson Bay coast. The local treeline runs east-west and is located 12.5 km from the Bay, with an extensive sedge fen tundra to the north and open conifer forest extending south. The fen instrument site was located 1.2 km north of the treeline and the forest tower was 1.1 km south of the forest edge.

Climate in the Churchill region is classified as arctic continental. The mean annual temperature is -7.5° C, with January

being the coldest month (-26.9°C) and July the warmest (11.8°C) . Mean annual precipitation is 412 mm, 57% of which falls as rain during May to October. The growing season typically extends from June to August, and has an average temperature of 9.7°C and total precipitation of 151.4 mm.

The forest is composed of 52% spruce (Picea mariana and P. glauca) and 48% tamarack (Larix laricina). Mean height of the trees is 5.4 m but the tallest trees reach 10-12 m. The best estimate of maximum tree leaf area index (LAI) is 1.5. The trees are widely spaced apart, growing as individuals or in small clumps. The understory is a sparse shrub layer of willow (Salix spp.), birch (Betula glandulosa), and Labrador tea (Ledum groenlandicum). Leaf area index of the understory is between 0.5 and 0.7. The forest floor has a hummock/hollow microtopography with nonvascular ground cover throughout. Mosses (Sphagnum spp.) grow in the moist interhummock regions and, where there is standing water, in the deepest hollows a brown moss (Scorpidium spp.) is dominant with some sedges (Carex spp.). The hummock tops are generally dry and support a cover of lichens (Cladina stellaris, C. rangiferina). In areas where tree density is low, the lichen mat is quite thick (10 to 15 cm). Soils at the site are moist consisting of 30 cm of peat, underlain by glaciomarine sediments of silt/clay. The site slopes gently upward to the south, and therefore receives lateral runoff from up slope. Permafrost is sporadic throughout the forest, and is usually found only in the larger peat hummocks.

The sedge fen is a flat, nonpatterned hummock-hollow terrain, with maximum relief between hummocks and hollows of 0.75 m. Vegetation in the hollows is dominantly brown moss (Scorpidium turgescens), with a sparse overstory of sedges (Carex aquatilis, C. limosa, C. saxatilis) in the shallowest hollows and on small hummocks. The larger hummocks support stunted shrubs (Betula glandulosa, Ledum decumbens, Salix actifolia) and a ground cover of lichen (C. stellaris, C. raniferina) and moss (Dicranum sp.). Leaf area index of the vascular canopy ranges between 0.35 and 0.5. The peat topsoil at the site averages 25 cm in depth, with clay/silt sediment interspersed with layers of carbonate shingles below. Permafrost is continuous in the fen; maximum depth of the active layer in summer is typically between 1 and 1.2 m.

Methodology

Instrument towers have been established in accessible areas at both sites. Minimum fetch for the fen tower was 1200 m to the south of the treeline. Fetch around the forest tower varied from 1000 m to the northeast, to 500 m in the southwest where there was a small lake, to >1500 m in all other directions. Extensive descriptions of the instruments and methods for the sites have been reported elsewhere (see Lafleur [1999] for the forest; Schreader et al. [1998] and Griffis et al. [2000a] for the fen). Here we present a summary of this information.

Fluxes of heat, water vapor, and CO₂ at the forest site were measured via the eddy covariance technique. Sensible heat was measured with a single axis sonic anemometer and fine wire thermocouple (model CA27, Campbell Scientific, Logan, Utah). Vapor density fluctuations were measured with a krypton hygrometer (model KH20, Campbell Scientific, Logan, Utah, U.S.A.). CO₂ concentration was measured with a fast response infrared gas analyzer, IRGA (model LI6252, LI-COR, Lincoln, Nebraska, U.S.A.). The sonic anemometer, krypton hygrometer and intake for the CO₂ sampling were located at the top of the tower at 18 m from the ground surface. Air was drawn down the sampling tube (6.35-mm i.d. Bev-a-line IV tubing) at 4.5

SLM through a particle filter (model Gelman, 1-mm pore size, LI-COR, Lincoln, Nebraska), to the IRGA, and then through a mass flow sensor (model 5860E, Rosemount Instruments, Calgary, Alberta, Canada). Temperature of the air leaving the sample cell in the IRGA was measured with a thermocouple and pressure inside the IRGA sample cell was measured with a gauge pressure sensor (model PX163–005BD, Omega Eng. inc., Stamford, Connecticut, U.S.A.). The absolute CO₂ concentration was measured via the IRGA's DAC channel. The IRGA was calibrated manually each week using a range of span gases (320 ppmv and 390 ppmv) and CO₂-free nitrogen for the zero.

Signals from the sonic and propeller anemometers, fine wire thermocouple, hygrometer, and the fast response channel of the IRGA were monitored on a data logger (21X, Campbell Scientific, Logan, Utah) every 0.1 s and the logger covariance software was used to compute 30-min averages and covariances. Data were later corrected for fluctuations in temperature and water vapor density (Webb et al., 1980; Leuning and Moncrieff, 1990) and oxygen absorption by the krypton hygrometer (Tanner et al., 1993).

Since the Campbell sonic anemometer is sensitive to rain and adverse weather, a single axis propeller anemometer was used as a backup signal for vertical wind fluctuations. Blanford and Gay (1992) have discussed the utility of this system for sensible heat measurements. Lafleur (1999) later demonstrated it could be used for CO₂ measurements at the Churchill site. A response correction for the propeller was computed by comparing standard deviations of the vertical wind speed measured by the sonic anemometer to the propellers using the 1997 data. A similar exercise was performed in this study on the 1998 and 1999 data and an identical correction factor was found. Therefore, fluxes were calculated using the sonic anemometer when it was available and then from the propeller system when the sonic system was inoperable. The amount of data measured with the sonic anemometer varied from a maximum of 56% in 1997 to a minimum of 40% in 1999.

The supporting meteorological measurements included air temperature and relative humidity with shielded probes (model HMP35 CF, Campbell Scientific, Logan, Utah) and wind speed with cup anemometers (model 12102, R.M. Young, Traverse City, Michigan, U.S.A.), at heights of 16.0 and 2.5 m. Wind direction was measured with a vane mounted at the top of the tower. Net radiation was measured with a net radiometer (model Q*6, REBS, Seattle, Washington, U.S.A.) and incoming photosynthetically active radiation with a quantum sensor (model LI190 SZ, LI-COR, Lincoln, Nebraska). Soil heat flux was measured with four heat flux transducers (model CN-3, Middleton Inc., Melbourne, Australia) wired in parallel. Soil temperatures at depths of 5, 10, 40, and 80 cm and tree bole temperatures were measured with copper-constantan thermocouples. Precipitation was measured with a tipping-bucket rain gauge located in a small clearing in the forest.

The IRGA, mass flow sensor, gauge pressure sensor, and suction pump were powered from a small gas generator. The generator was located 50 m to the southwest of the tower. This arrangement caused loss of data in two ways. First, at times throughout the study the generator failed causing a loss of data. Second, to ensure that the generator exhaust had no effect on the measurements, data were eliminated from the data set when winds were from a 30° arc centered on the direction of the generator.

Energy fluxes at the fen were measured via the Bowen ratio-energy balance technique. Wet- and dry-bulb temperatures were measured at six levels (0.35, 0.70, 1.10, 1.60, 2.30, and

3.20 m). The Bowen ratio, β (i.e., the ratio of sensible to latent heat), was computed from the slope of vapor pressure plotted against temperature. Net radiation, Q^* , was measured with a net radiometer (model Q*6, REBS, Seattle, Washington), and soil heat flux, Q_G , was measured with four sets of heat flux transducers and companion arrays of thermocouples placed in representative terrain. The heat flux transducer readings were then corrected via calorimetric computations using the soil temperature profile data. Turbulent fluxes of sensible, Q_H , and latent, Q_E , were then calculated as from β and available energy (i.e., Q^* - Q_G).

Wind speed was measured with a profile of cup anemometers (model 12102, R.M. Young Co., Travis City, Michigan) set at the same levels as the psychrometers and direction was measured with a vane at the top (3.5 m) of the mast. Precipitation was measured with a tipping-bucket rain gauge and water-table depth measured automatically with a home-made float-potentiometer system. All of these signals were recorded on a data logger (CR7, Campbell Scientific, Logan, Utah), where signals were sampled every 1 s, and 30-min averages were computed.

The flux of CO_2 , F_c , at the fen was measured via a gradient technique, where

$$F_c = -K_c \cdot \partial \rho_c / \partial z \tag{1}$$

and K_c is the turbulent transfer coefficient for CO_2 , and $\partial \rho_c/\partial z$ is the time averaged vertical gradient of CO_2 concentration. K_c was derived from the sensible heat flux and air temperature profile measurements as

$$K_c = K_H = -Q_H/(\partial T/\partial z) \cdot c_p \cdot \rho_a \tag{2}$$

in which K_H is the turbulent transfer coefficient for heat, $\partial T/\partial z$ is the time averaged vertical gradient of temperature, c_p is specific heat of air, and ρ_c is density of air. The assumption of similarity between turbulent transfer coefficients for heat and CO₂ follows Oke (1987) and Verma (1990).

CO₂ concentrations were measured at the same height intervals as temperature and wind speed by drawing air from an intake in the psychrometer housings through sampling lines to the IRGA (model 6252, LICOR, Lincoln, Nebraska). All sample tubes were of equal length (6.5 m) 0.54-mm i.d. Bev-a-line. Air was drawn down the sample tubes by two 12 V pumps to individual 1 l buffer volumes and then to the IRGA via a switching system. One pump drew air continuously through all lines and the other drew air from individual lines to the IRGA. The switching system consisted of a manifold and six 12 V solenoid-actuated valves so that air from each line could be sampled sequentially. Flow was maintained between 1.8 and 2.0 L min⁻¹ and monitored with a flow meter. As it took air approximately 7 s to travel from the intake to the IRGA, each line was sample every 10 s. The IRGA was encased in a polystyrene foam insulated cabinet and samples were drawn through a copper tube situated on the top of the analyzer hosing in an effort to use the heat of the IRGA to keep the sample temperatures near the optical bench temperature of 37°C. Temperature of the sample gas entering the IRGA was measured with a fine wire thermocouple inserted into the sample line immediately upstream of the IRGA intake.

A data logger (21X, Campbell Scientific, Logan, Utah) controlled the sampling sequence and duration. The same logger also monitored the output from the IRGA and the temperature of the sample. The IRGA was run in absolute mode and calibrated on an every-other-day basis. Ultrahigh purity nitrogen gas was used to zero the IRGA and a span gas (334 ppmv) was used to calibrate CO₂ concentration. The IRGA, data logger, sample

TABLE 1

Monthly mean temperature and precipitation during the snowfree period in 1997 and 1998 and long-term normals. All data are from the Environment Canada meteorological station at Churchill airport.

	May	June	July	August	Season
		Air	Temperature	e (°C)	
1997	-3.5	7.4	14.7	13.2	8.0
1998	1.4	8.8	12.7	15.1	9.5
1999	3.3	10.9	13.3	12.0	9.9
Normal	-1.1	6.1	11.8	11.3	7.0
		Pre	cipitation (r	nm)	
1997	7.3	29.7	64.0	82.5	183.5
1998	50.3	29.0	46.2	51.5	177.0
1999	36.7	44.8	57.7	50.0	189.2
Normal	30.5	44.5	50.7	60.5	185.2

buffers, and switching manifold were placed in an insulated car top carrier for weather proofing. CO_2 fluxes were calculated in a specially designed computer program during data postprocessing. F_c was calculated from the 0.5-h time averaged concentrations, and the flux corrected for density variations relating to the latent heat flux (Webb et al.,1980).

Data Handling

Measurement of the CO₂ fluxes is fraught with considerable difficulty. Power failures, adverse weather conditions, low wind speeds, and instrument malfunctions all caused data losses. These problems were most frequent at the forest site, partly due to the nature of the equipment employed. As a result 43% of the forest data record was missing in 1997, 18% in 1998, and 49% in 1999. It is necessary to fill in the missing data in order to compute a net CO₂ budget for the growing season. Various methods of filling missing data were investigated by Lafleur (1999). In this study separate empirical models were used to fill in missing nighttime and daytime periods. The nighttime data were estimated with a relationship between air temperature and NEE and daytime data were filled with a rectangular hyperbola model of NEE on photosynthetically active radiation (PAR). For both night and day periods, separate models were developed for each growing season.

Missing data constituted a much smaller proportion of the record at the fen, about 5% in each of the years. The missing data were filled by inserting the appropriate half hours from ensemble diurnal average curves constructed for each of three phenological periods, pregreen, green, and postgreen periods (Griffis et al., 2000a).

The data records vary in length and period for each year. Since the main purpose of this study was to compare between sites we selected a 65-d period (DOY 167–231) when flux measurements were available in all years at both sites for the following analyses. This period roughly corresponds to the typical growing season in the Churchill region.

Results

SEASONAL CLIMATIC CONDITIONS

Monthly meteorology for the three growing seasons is compared to long-term normals in Table 1. In general, the three study years were warmer than normal and precipitation was near the long-term normal. The most noticeable difference between the

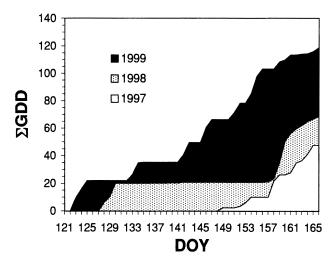


FIGURE 1. Summed growing degree-days (Σ GDD) from DOY 121 (1 May) to the start of the measurement period DOY 167 (16 June).

study years was in spring (May) temperatures, which were below normal in 1997, 2.5°C above normal in 1998 (an El Niño year), and more than 4°C above normal in 1999. Final snowmelt in each season was recorded from a time series of daily albedo (i.e., the ratio of incoming to reflected global solar radiation) at the forest site. Final melt in 1997 occurred on DOY 150 (31 May), and about 3 wk earlier in 1998 (DOY 129; 8 May). However, in 1999 final melt occurred on DOY 114 (24 April). The net effect of the spring meteorology is summarized in Figure 1, where we have plotted the summed growing degree-days from DOY 121 (1 May) until the start of the measurement period (DOY 167). The large warming in May 1999 resulted in about 2.5 times more growing degree-days than in 1997 and almost two times more than in 1998.

Precipitation totals for the three seasons were within $\pm 7\%$ of normal. However, the soil water balance during the study period showed considerable variation because of differences in timing of snowmelt and frequency of rain events (Fig. 2). Water table is generally high at the start of the growing season with short-term flooding occurring at the fen site immediately after snowmelt, as seen in 1997. The effect is not present in 1998 and 1999 because of the earlier snowmelt. Water tables at both sites decline throughout summer. Maximum draw-down varied between years, occurring about DOY 217–219 in 1998, at the end of the study (DOY 231) in 1998, and earliest in 1999 near DOY 201. The greatest observed water table depth at both sites was reached in 1999.

SEASONAL ENERGY EXCHANGE

Daily average energy balance for both sites is given in Table 2. These findings can be summarized as follows. Net radiation was smallest in 1998 and largest in 1999, with slightly larger fluxes at the forest except in 1999. Soil heat flux and latent heat flux were larger at the fen than forest, and sensible heat flux was larger at the forest site. The net result is that Bowen ratios at the forest are two to three times larger than at the fen.

DAILY NEE

Time series of daily NEE for the two sites showed distinct differences both between sites and between years (Fig. 3). The sign convention used throughout this paper is to plot CO₂ uptake

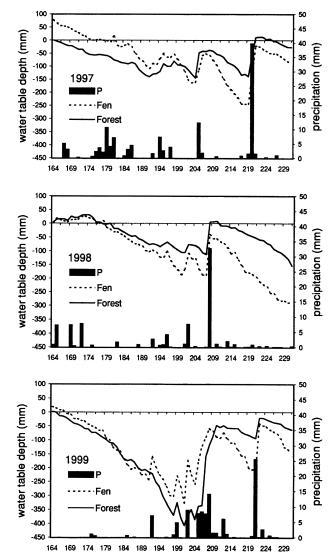


FIGURE 2. Daily water table depth for the fen and forest sites and precipitation (forest site) during the study periods.

DOY

by the ecosystem (a loss from the atmosphere) as negative and ecosystem losses (gains to the atmosphere) as positive. Although there was considerable daily variation at both sites, the fen showed generally smaller daily NEE uptake and a greater number of daily losses than the forest in all years. For the 3 yr, mean daily NEE ranged from -1.5 to -7.3 g CO₂ m⁻² d⁻¹ at the forest and from -0.6 to -3.1 g CO₂ m⁻² d⁻¹ at the fen (Table 3). The ratio of NEE_{forest}/NEE_{fen} varied from 1.4 in 1997 to 12.4 in 1999.

TABLE 2

Mean daily energy balance for growing season (DOY 167–231) for 1997, 1998 and 1999. Fluxes in W m^{-2} . β is Bowen ratio (Q_H/Q_E) .

	Year	Q*	Q_G	Qн	Q_E	β
Fen	1997	129	18	36	74	0.49
	1998	126	15	40	72	0.56
	1999	157	15	48	94	0.51
Forest	1997	145	8	70	57	1.22
	1998	133	9	63	54	1.17
	1999	151	9	73	51	1.43

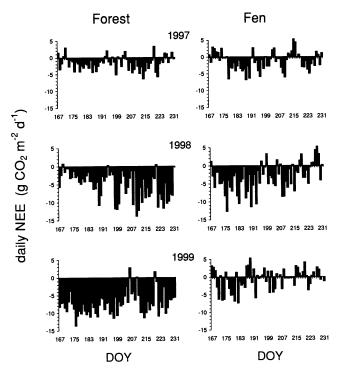


FIGURE 3. Daily net ecosystem exchange of CO_2 (NEE) for fen and forest during 1997, 1998, and 1999.

Maximum daily NEE at the forest was smallest in 1997 (≈ -6 g CO2 m⁻² d⁻¹) and similar in magnitude in 1998 and 1999 (≈ -12 to -14 g CO_2 m⁻² d⁻¹). The fen experienced similar maximum daily NEE in 1997 and 1999 (≈ -6 to -7 g CO₂ m⁻² d^{-1}), with the largest daily uptakes in 1998 (≈ -10 to -12 g CO₂ m⁻² d⁻¹). The pattern of daily NEE varied considerably between these years. During 1997, fen and forest displayed similar trends in daily NEE, except for a marked period of daily losses at the fen between DOY 213-220. In 1998, the fen showed strong daily uptake during the early part of the growing period and declining thereafter, with daily losses dominating at the end of the study. In contrast NEE at the forest increased rapidly during the first 20 d of 1998 and remained strong throughout the growing season. In 1999 the forest experienced strong daily uptake of CO₂ throughout the study, while the fen showed strong uptake only at the start of the study period (until about DOY 185) and thereafter was dominated by daily CO₂ losses with occasional weak daily uptake.

Ensemble-average diurnal patterns of NEE were constructed for each site (Fig. 4). These patterns reflect the differences noted above. NEE at the forest followed a typical concave pattern in all years, with maximum daily uptake occurring near noon. There were distinct differences in maximum daytime uptake, which was smallest in 1997, intermediate in 1998 and largest in 1999. Nighttime NEE at the forest varied little between years. On the other hand, the fen exhibited considerable variation in the diurnal pattern of NEE. In 1998, fen NEE demonstrated a concave pattern symmetrical about noon similar to the forest. However, in 1997 and 1999 peak uptake was achieved during the morning and NEE decreased (i.e., became less negative) throughout the day. Daytime NEE was most reduced in 1999, with daytime losses occurring near mid-day. Fen nighttime fluxes were similar in magnitude in 1997 and 1998, but were considerably smaller in 1999. This difference did not appear to be related to soil temperatures, as mean nighttime soil temperatures were smallest in 1997, intermediate in 1999 and largest in 1998. Instead, we hypothesize this effect was due to the extreme drying

TABLE 3

Subarctic forest and fen mean daily net ecosystem exchange (NEE) for a 65-d growing season, day of year 167–231.

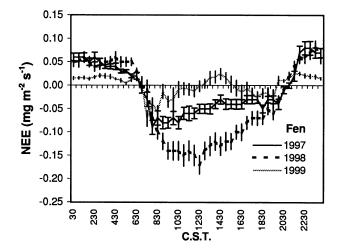
Standard error in parentheses.

	Year	NEE (g CO ₂ m ⁻² d ⁻¹)
Fen	1997	-1.12 (0.36)
	1998	-3.11 (0.50)
	1999	-0.59 (0.37)
Forest	1997	-1.54 (0.25)
	1998	-5.09 (0.46)
	1999	-7.35 (0.39)

which took place in 1999 (Fig. 2), which could have resulted in lower photosynthetic and plant respiration rates, and a reduction in soil respiration as suggested in Silvola et al. (1996).

SEASONAL NEE

The difference in CO_2 fluxes between the two study years is clearly illustrated in plots of seasonal cumulative NEE (Σ NEE) (Fig. 5). Both sites were weak seasonal CO_2 sinks during 1997, -73 and -100 g m $^{-2}$ for fen and forest, respectively. In 1998 Σ NEE for the fen was a net uptake of -202 g m $^{-2}$ and



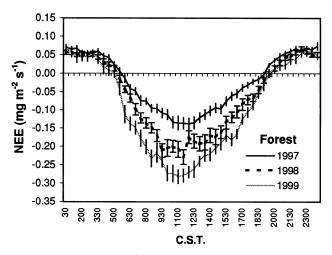


FIGURE 4. Fen and forest ensemble-average diurnal trends of net ecosystem exchange of CO₂ (NEE) for 1997, 1998, and 1999. Each point is the average from all available measured data for that half-hour, vertical bars are standard errors.

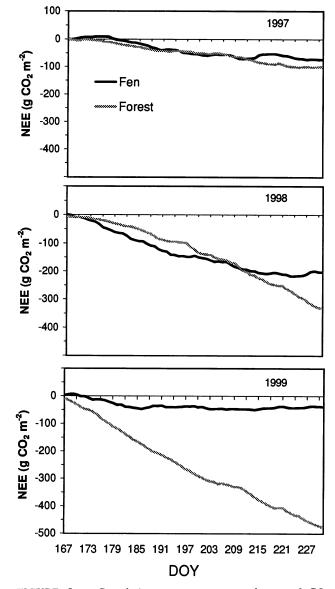


FIGURE 5. Cumulative net ecosystem exchange of CO_2 (ΣNEE) for forest (gray lines) and fen (black) for the study periods. Includes both measured and modeled data.

for the forest the accumulated uptake was $-331~g~m^{-2}$ at the forest. The difference in ΣNEE between sites for 1998 was largely realized in the final 20 d of the study, when the rate of CO_2 accumulation at the fen declined to near zero, but was unchanged at the forest. The largest difference in ΣNEE between sites occurred in 1999, when the forest showed a steady rate of CO_2 accumulation throughout the study period and the fen experienced an accumulation of CO_2 for the first 20 d only and no increase thereafter. The result was an net uptake of only $-38~g~m^{-2}$ for the fen, whereas the forest accumulated some 12.5 times more CO_2 ($-478~g~m^{-2}$).

Discussion

The results presented here show that there are large differences in growing season NEE between these treeline forest and fen tundra sites. Seasonal CO₂ uptake was always greater at the forest site even though instantaneous and daily CO₂ fluxes at the fen can be as large as those at the forest. The larger NEE at the forest might be expected simply on the basis of the difference in biomass between these sites. Total leaf area at the forest (trees

and shrubs) is two to three times larger than at the fen and the moss and lichen ground cover is considerably thicker and more widespread at the forest. The fact that seasonal NEE at the forest varied from 1.4 to 12.5 times larger than at the fen suggests that there are important interannual variations in the factors controlling carbon exchange at these sites. Since these sites are close together (<1.5 km) they experience the same overhead meteorological conditions, making it unlikely that differences in temperature, radiation, humidity, or precipitation were important in producing such variability between sites. Instead, we hypothesize that these differences can be explained in terms of two factors: local soil moisture controls on NEE and spring climate effects on phenology.

In each year of the study water table deficits developed at these sites (Fig. 2). The largest occurred in 1999 when field notes indicated a dramatic desiccation of the brown mosses at the fen. Griffis et al. (2000b) suggest that at the fen the critical water table limit at which daily photosynthesis appears to be severely reduced is -250 mm, which corresponds to the peat/mineral substrate interface. When the water table drops below this point, continuity between the peat soil matrix and the water supply (i.e., the water table) is broken. As a result the moisture to the shallow root zone of the vascular plants and to the brown mosses in the interhummock pools is severely restricted. The timing of this event was DOY 217, DOY 225, and DOY 191 in 1997, 1998, and 1999, respectively. Each of these events corresponds closely to the point on the SNEE curve where the rate of accumulation of CO₂ at the fen is reduced to zero. Indeed, in a longer study Griffis et al. (2000a) indicate that growing season NEE at the fen has varied considerably during the period 1994 to 1999, ranging from a net sink of -235 g CO₂ m⁻² in a warm, wet year, 1996, to a net loss of 76 g CO₂ m⁻² in 1994, the warmest and driest year of their study.

Although water table deficits also developed at the forest in each year, Σ NEE showed no response to this deficit. We believe that this lack of response to water table change arises because the peat/mineral soil boundary is deeper at this site (\approx -375 mm). Water table draw down did not reached this boundary in 1997 or 1998, and did so only for a brief period in 1999. Therefore, water supply to the forest rooting zone (50–200 mm) was unrestricted for most for the study.

Magnitude and behavior of the CO₂ fluxes at the fen are consistent with past studies concerning interannual variability of carbon dioxide exchange in northern and arctic peatlands. Several authors have suggested that variation in growing season NEE was most strongly controlled by temperature and soil water status during the growing season (Oechel et al., 1993; Oechel et al., 1995; Shurpali et al., 1995; Griffis et al., 2000a). Elsewhere, Joiner et al. (1999) measured growing season CO₂ exchange at a high boreal fen for two summers and found similar mid-summer NEE but large differences in post-snowmelt and senescence period CO₂ respiration losses. They computed an integrated NEE over a 124-d period from spring to late summer as a net loss in one year and a net uptake in another.

There was a 4.7 fold increase in forest Σ NEE between the year with the smallest uptake (1997) and the greatest uptake (1999). Since the year with the greatest water table draw-down (1999) was also the year of greatest NEE uptake, it is likely that water table variations did not affect seasonal NEE at the forest. Given similar meteorological conditions during the three growing seasons, an explanation for the large seasonal variation in Σ NEE is needed. We hypothesize that the forest Σ NEE was most likely influenced by phenology and spring climate. No quantitative assessments of phenology were made, however, field notes

indicated the timing of leaf-out in each year. In 1997 melting of the winter snowpack was complete on 1 June (DOY 152) and leaf-out commenced about the same time as the beginning of the field experiments, 16 June (DOY 167). This is typical of the timing of leaf-out in the Churchill area (Scott et al., 1987). Although snowmelt occurred 3 wk earlier in 1998, it was followed by generally cool and overcast weather that delayed leaf-out to the extent that it occurred only a few days earlier than the 1997 date. In 1999 however, snowmelt occurred at the end of April and warm conditions through May initiated leaf-out 3 to 4 wk earlier than in 1998. Thus in 1999 phenology was well advanced by the time the field measurements began. As a result of these variation in spring conditions, there was a close correspondence between the summed growing degree-days in spring (Fig. 1) and forest Σ NEE for the measurement period (Fig. 5). These findings are in agreement with work by Myneni et al. (1997), who suggested that earlier initiation of snowmelt and lengthening of the growing season in northern regions from 1981 to 1991 were concordant with an increase in the amplitude of the seasonal cycle of atmospheric carbon dioxide. We believe that spring conditions would also have influenced NEE at the fen in a manner similar to the forest, as indicated by the strong uptake at the start of the 1998 and 1999 periods. However, the effects of water table draw-down discussed above obscure the seasonal relationship.

What is not understood as yet is the true nature of the biophysiological linkages between timing of snowmelt, leaf-out, and growing season Σ NEE. Undoubtedly, this is a complex relationship and involves the link between carbon and nutrient budgets, which are closely coupled in arctic ecosystems (Shaver et al., 1992; Johnson et al., 2000). In most arctic ecosystems soil turnover rates are slow and nutrients are strongly limited. As a result plant biomass and carbon acquisition are sensitive to even small additions of nutrients (Shaver et al., 1992; Shaver et al., 1998). Researchers have shown that net nitrogen mineralization immediately following snowmelt is critical for growing season productivity in some arctic systems (Giblin et al., 1991; Nadelhoffer et al., 1997). If this is true for the Churchill ecosystems, in a "normal" year, where leaf-out takes place within 1 to 2 wk of snowmelt, the postmelt N pool may be small and productivity is largely dependent upon nitrogen mineralization taking place during the growing season. However, in exceptional years, such as 1999 when snowmelt was very early, an extended period of nitrogen release prior to leaf-out may have enhanced carbon uptake during the growing season. An observable effect of the enhanced productivity would be greater above-ground biomass. Although we have little field data to confirm this, it may be possible to investigate the phenomenon using remote sensing. Such studies are ongoing.

One element that we feel is poorly represented in this discussion is the importance of the moss and lichen ground cover to the carbon balance of these ecosystems. Phenology of the moss and lichen is a very subtle process and their contribution to carbon sequestration is difficult to assess with micrometeorological techniques. Other studies have shown that mosses begin photosynthesizing immediately after snowmelt (Bubier et al., 1998). Thus, it is likely that these plants were significant contributors to the strong uptake recorded in our study at the beginning of the 1998 and 1999 measurement periods.

Finally, it is important to recognize that the growing season measurements described here do not necessarily reflect the annual carbon balance at these sites. Several studies have shown that carbon exchange in the nongrowing period, which amounts to some nine months at Churchill, has a significant impact on the annual carbon budget (Goulden et al., 1998; Oechel et al., 2000; Lafleur et al., 2001). In arctic and subarctic regions $\rm CO_2$ losses during the long winter season can affect the annual budget to the point that some ecosystems change from net sinks during growing seasons to annual net sources (Fahnestock et al., 1999; Oechel et al., 2000). Although the implications of these results for the present study are not entirely clear, there is no doubt that winter losses at these sites would reduce the seasonal sinks found in this study. Based on winter values from these previous studies, we believe that, on an annual basis, the fen is probably a $\rm CO_2$ source in most years. On the other hand, the forest would likely remain a sink in most years.

Conclusions

We have shown that there are significant differences in growing season NEE between treeline forest and sedge tundra sites and that controls on the seasonal carbon exchange vary between fen and forest. The open forest appears to be a larger and more conservative sink for CO₂ than the sedge fen tundra. The tundra CO₂ exchange is highly sensitive to moisture deficits during the growing season. Carbon exchange at both sites appears to be strongly linked to spring climate conditions and date of leaf-out. These results have important implication in terms of the biospheric feedback between treeline and climate. The movement of treeline in response to climate change may play an important role in the global CO2 cycle. The effects of such a feedback would, of course, only be felt over long time scales and more research on modeling this feedback is needed. As well, the biophysical components of global climate models need to capture both growing season and the non-growing season biological processes. Thus, the linkages between the climate, snow cover and biophysical processes need further investigation.

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