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Interannual Variability in Carbon Dioxide Exchange from a High Arctic Fen Estimated by Measurements and Modeling

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Abstract

The response of high arctic ecosystems' carbon dioxide exchange to changing climate is uncertain and may be important from a climate-change perspective. In this study, the net ecosystem carbon dioxide exchange during four growing seasons is examined by combining measurements and modeling from a high arctic fen in northeastern Greenland. The summer-season net ecosystem exchange shows large interannual variations, fluctuating from an uptake of -50 g C m^{-2} to -123 g C m^{-2}. Through ecosystem modeling, we can observe that leaf area index development and the maximum Rubisco capacity are more important controls on the interannual variability of net ecosystem carbon dioxide exchange than meteorological conditions. Furthermore, we present a hypothesis linking the interannual variability in maximum Rubisco capacity with leaf nitrogen content and leaf area index development. This hypothesis may provide a method to model seasonal net ecosystem carbon dioxide exchange in detail without having to resort to elaborate fitting procedures using measured carbon dioxide flux data.

Introduction

Approximately 30% of global terrestrial soil organic carbon is stored in boreal and arctic peatland soils (Gorham, 1991). The waterlogged characteristics of fens and bogs, as well as their slow decomposition rates, have resulted in a buildup of the organic carbon store. Future climate warming may affect both the uptake and release of organic carbon from these soils. Centuries of carbon accumulation may be reversed by a net carbon release in greenhouse gases, such as carbon dioxide and methane. Indications of this reversal have already been observed in Alaska (Oechel et al., 1993).

The response of arctic and boreal ecosystems to climate change is still uncertain. Generally, the ecosystems in the northern hemisphere seem to have increased their vegetation mass during the previous decades (Myneni et al., 1997; Tucker et al., 2001). The same period also shows positive temperature trends over a large part of the northern hemisphere (Serreze et al., 2000). Some of these changes may be a result of the polar amplification of global warming taking place in the Arctic (Holland and Bitz, 2003), but they may also be a result of decadal fluctuations in climate due to the Arctic Oscillation/North Atlantic Oscillation (Moritz et al., 2002). A long-term experimental study by Mack et al. (2004) suggests that the nutrient release associated with higher temperatures leads to an increase in the aboveground carbon storage in plants; however, the decrease in soil carbon storage caused by increased decomposition outweighs this effect, resulting in a positive feedback effect to the atmosphere.

Detailed studies of carbon dioxide flux from arctic and boreal ecosystems occurred sporadically in the 1970s (e.g., Coyne and Kelley, 1975) and 1980s, and such studies have become more frequent since the 1990s. The relatively short study period makes it difficult to observe long-term changes, and the studies that have been done present a diverse picture of carbon dioxide flux in these regions. Oechel et al. (2000) showed that an Alaskan tussock tundra shifted from losses of carbon dioxide of ~450 g C m^{-2} to an uptake of ~100 g C m^{-2} over a period of 15 yr. At a high arctic, polar, semidesert site, the ecosystem shifted from being a net summer sink of carbon dioxide to a source from one summer to another, but did so with much less variability than the Alaskan site (±5 g C m^{-2}) (Lloyd, 2001b). At another high arctic site, the ecosystem's growing-season carbon dioxide uptake was 96 g C m^{-2}, and a modeling study suggested that this ecosystem was far from being a source of carbon dioxide (Soegaard and Nordstroem, 1999).

Most of the detailed carbon dioxide flux studies have been carried out in the boreal and the lower arctic regions (e.g., Oechel et al., 1993, 2000; Aurela et al., 1998; Shurpauli et al., 1995; Joiner et al., 1999; Arneth et al., 2002). This paper focuses on the high arctic where only a few studies have been made, for example, in Greenland (e.g., Nordstroem, 1999; Nordstroem et al., 2001; Soegaard and Nordstroem, 1999; Soegaard et al., 2000) and in Svalbard (Lloyd, 2001a, 2001b).

The objective of this study is to quantify the interannual variability of the growing season's net ecosystem carbon dioxide exchange and to investigate the factors responsible for the variability. The net ecosystem carbon dioxide exchange (NEE) is the sum of net primary production (net photosynthetic assimilation of carbon dioxide) and soil-respiration losses of carbon dioxide. Arctic ecosystems only act as sinks for carbon dioxide during the growing season when photosynthesis occurs. Soil respiration may take place over the entire year (Zimov et al., 1993) and can be substantial. Wintertime respiration may range between 17 and 81% of the annual net ecosystem carbon dioxide exchange (Hobbie et al., 2000). Because of the remoteness of the Arctic and sensor limitations, wintertime carbon dioxide fluxes are hard to quantify, whereas summertime measurements are more feasible. Because of seasonal measurement limitations, this study will focus only on the summer season; however, we recognize that understanding and quantifying wintertime respiration is an important aspect in the overall evaluation the annual NEE for arctic ecosystems.

Studies of carbon dioxide flux of a high-arctic wetland were initiated in 1996 at the Zackenberg research station in northeastern Greenland and continued each summer until 1999. The measured fluxes from 1996 (Soegaard and Nordstroem, 1999) and 1997 (Soegaard et al., 2000) were compared against photosynthesis and soil respiration simulated with a model. Rather than using the model by Soegaard and Nordstroem (1999) for studying the data covering the

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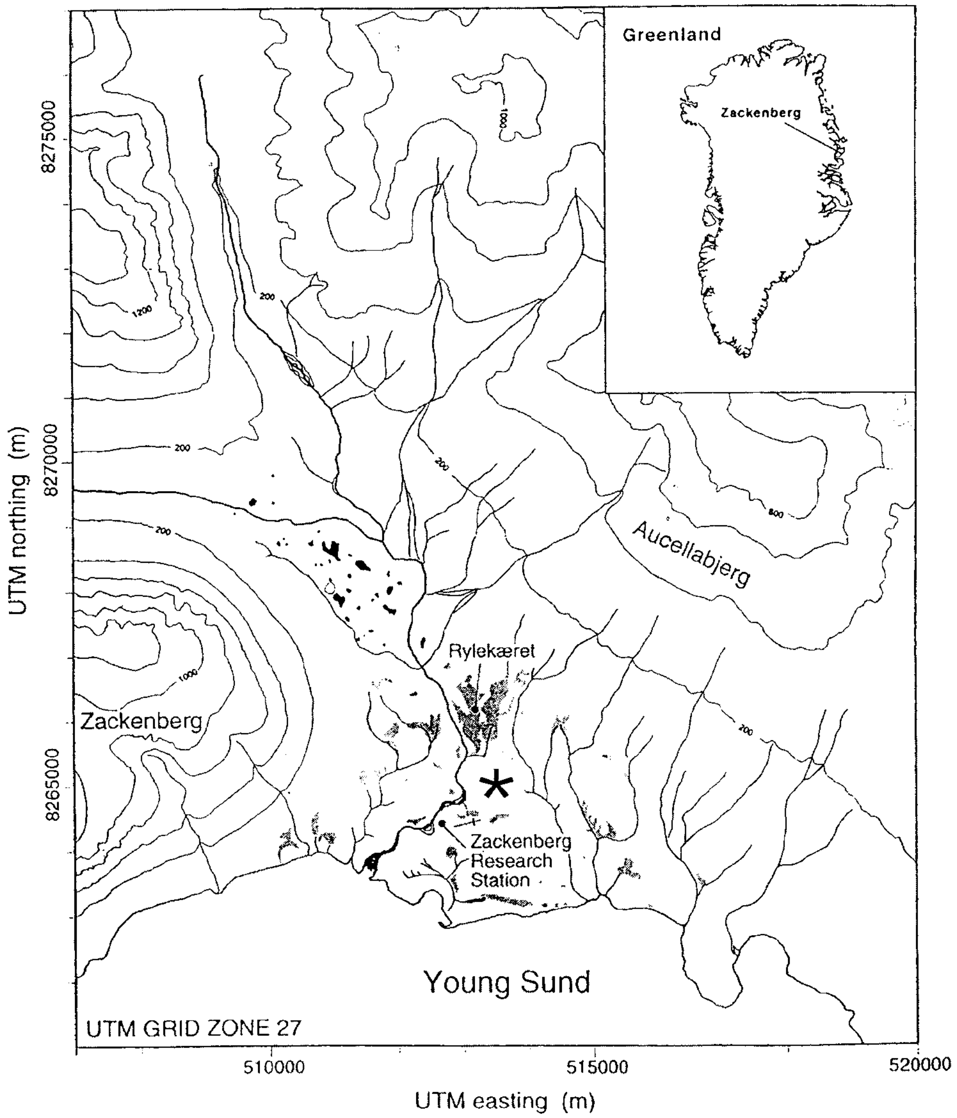

FIGURE 1. Zackenberg Valley, showing the fen Rylekæret (shaded; the study site). The star denotes the location of the supplementary meteorological masts operated by Zackenberg Ecological Research Operation (ZERO).

4 yr of interannual variation, we decided to apply a more generally established model based on the U.K.'s Meteorological Office Surface Exchange Scheme (MOSES, Cox et al., 1999). Besides relying less on sophisticated parameters such a leaf surface temperature, MOSES also makes better use of standard meteorological parameters. To optimize the validity of the findings, it was furthermore decided to utilize both already published data (1996 and 1997) and unpublished data (1998 and 1999) in the analysis.

Methods

SITE DESCRIPTION

The study site is the Rylekæret fen in the Zackenberg Valley located in the National Park of North and East Greenland at 71.28°N and 20.34°W (Fig. 1). Zackenberg Valley is located between the Greenland Ice Cap and the Greenland east coast. Mountains surround the valley on three sides. A fjord (Young's Sund) forms the southern boundary of the valley.

The fen covers ~600 m by 1200 m of the valley floor and is situated ~3 km north of the Zackenberg Research Station. The dominant plants in the fen are vascular plants, such as sedges and grasses, but mosses and lichens are also present. The most common species are arctic cotton grass (*Eriphorum scheuchzeri*), arctic red grasses (*Arctagrostis latifolia*) and *Eriphorum triste*, *Dupontia psilosantha*, and *Carex Saxatilis* (Nordstroem et al., 2001; Soegaard et al., 2000). The mineral soil in Rylekæret is covered by a peat layer of ~0.2–0.5-m thickness.

Zackenberg is a high arctic environment (Maxwell, 1992) with continuous permafrost. In the summer, the surface of the permafrost thaws and forms an active layer to a depth of ~0.2 to 0.8 m (Meltofte and Thing, 1997). The mean temperature is ~4°C in the warmest month (July) and –18°C in the coldest month (February). The annual precipitation is ~200 mm, 87% of which falls as snow.

MICROMETEOROLOGICAL AND NET ECOSYSTEM CARBON DIOXIDE EXCHANGE (NEE) MEASUREMENTS

The main instruments for measuring fluxes and climatic parameters were mounted in the center of the Rylekæret fen. A source-area analysis showed that the instrument fetch area was composed of ~73% continuous and hummocky fen and 16% grassland; the remainder was heath and willow snowbed (Soegaard et al., 2000). At the Rylekæret site, fluxes and climatic measurements were made during the period 1996–1999. The data from 1996 and 1997 have been used in previous publications (Soegaard and Nordstroem, 1999; Soegaard et al., 2000, 2001; Nordstroem, 1999; Nordstroem et al., 2001), and the data collection is described in detail in Nordstroem (1999). Here the data collection is reviewed briefly for completeness.

An eddy covariance system was used to measure half-hourly fluxes of carbon dioxide, water vapor, and sensible heat. The carbon dioxide flux measured above the ecosystem with the eddy covariance system includes fluxes from both vegetation and soil, and thus the flux is a measure of the net ecosystem carbon dioxide exchange (NEE). The system consisted of a sonic anemometer (Gill Instruments Ltd., U.K.) to measure wind speed and a LI-COR 6262 IRGA (Infra Red Gas Analyzer LI-COR Inc., U.S.A.) to measure carbon dioxide and water vapor concentrations. The sonic anemometer and the tube inlet to the IRGA were mounted on a tower, 3 m above the ground surface. Data were sampled at 21 Hz by using the EdiSol software package (Moncrieff et al., 1997). In calculating the fluxes from the raw data, the time lag between vertical wind speed and carbon dioxide and water vapor measurements was determined and corrected by maximizing the covariance between these variables. Data detrending, axis-coordinate rotation, air-density fluctuation corrections, sensor separation, and corrections for the fluctuations in the sampling tube were made according to Moncrieff et al. (1997).

Half-hourly measurements of meteorological parameters consisted of net radiation, incoming solar radiation, photosynthetic photon flux density, near-infrared radiation, air temperature, relative humidity, wind speed, wind direction, surface temperature, soil moisture, soil temperature, and soil heat flux. Supplemental hourly meteorological data were provided by ASIAQ (ASIAQ is Greenland Survey under the Greenland Home Rule), which manages the two meteorological towers in the Zackenberg Valley as a part of the Zackenberg Ecological Research Operations (ZERO) program. The towers are situated ~3 km south of the main instrument site in Rylekæret (Fig. 1). Data from the nearby weather station Daneborg (~30 km east of Zackenberg) were provided by the Danish Meteorological Institute (DMI, 2000).

MODELING

Model Description

MOSES was used to model growing-season fluxes of carbon dioxide, energy, and water in a single grid cell assumed to be representative of the fen ecosystem (see Cox et al. [1999] for a detailed model description). The meteorological forcing inputs consist of air temperature, air humidity, wind speed, net radiation, and incoming solar radiation. The soil is divided into four layers; the top two layers and the bottom two layers are parameterized as peat soil and as mineral soil, respectively. The fen is described by a set of model parameters that include the initial conditions and characteristics of the vegetation and soil. MOSES was modified to include seasonally varying leaf area index (LAI) and maximum Rubisco capacity, a heat-advection term, and a soil-respiration model (Fig. 2). The modifications are described later.

Precipitation input drives the water balance, which consists of plant interception, throughfall, infiltration, gravitational drainage, evapotranspiration, and surface and subsurface runoff. Surface runoff is either saturation excess or infiltration excess runoff. The energy balance is driven by net radiation, which is given as a meteorological forcing and consists of the sensible heat flux, latent heat flux, snowmelt heat flux, and groundwater heat flux. The latent heat flux is described with a Penman-Monteith function, extended to account for heat transfer through the soil. The sensible heat flux and the soil heat flux are both described with gradient-resistance functions. Soil and surface temperatures are diagnostic variables in the energy balance. Energy- and water-balance equations are solved separately for the grid-cell fractions of bare soil, vegetation, and snow.

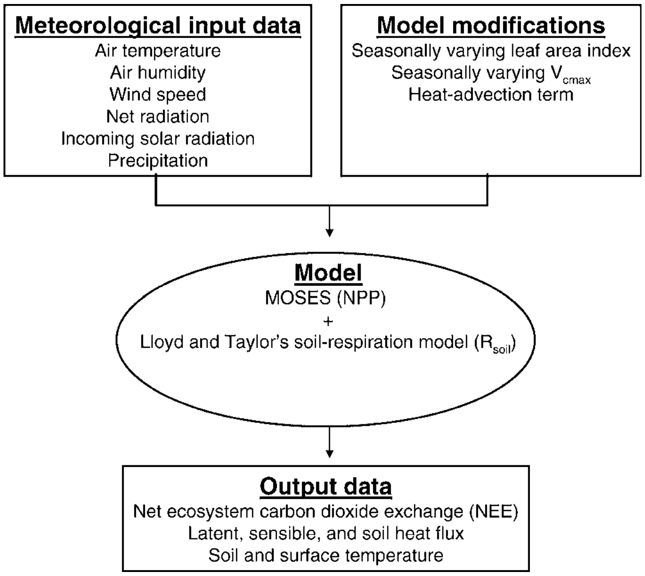

FIGURE 2. Schematic figure of the model. Meteorological input data and input of seasonally varying leaf area index drives MOSES and the soil-respiration model to produce output variables describing the net ecosystem carbon dioxide exchange and surface energy and water balance.

The carbon dioxide model produced by MOSES simulates the canopy net primary production (NPP) by subtracting the gross primary production (GPP) from the plant respiration (R_p). Plant respiration consists of both maintenance and growth respiration. It takes place in leaves, stems, and roots and is a function of canopy gross primary production, canopy dark respiration, and plant nitrogen content. Gross primary production is the product of the upscaled leaf net primary production and the leaf dark respiration. The upscaling of fluxes from the leaf to canopy level is dependent on the LAI (equation 1). In our simulations, the upscaling was independent of the vegetation fraction of the grid cell, as we chose to scale the fluxes to one for the whole grid cell.

$$\prod = \frac{1 - \exp^{-kL}}{k}, \qquad (1)$$

where $\prod$ is the sunlit area of the vegetation, which is used for upscaling, L is leaf area index, and k is the extinction coefficient. The extinction coefficient is calculated as the cosine of the mean leaf to sun angle divided by the cosine of the zenith angle (Norman, 1993). Cox et al. (1999) used an extinction coefficient of 0.5. Owing to low sun angles in the Arctic, Soegaard and Nordstroem (1999) found an extinction coefficient of 0.9 to be more appropriate, and we used this value in our simulations.

The leaf-level photosynthetic model is based on Collatz et al.'s (1991) biogeochemical model. The modeled leaf net primary production is determined as the minimum of three potential photosynthetic rates: the rate controlled by the Rubisco capacity, the rate controlled by the absorbed photosynthetic photon flux density, and the rate controlled by the removal of assimilates. For C_3 plants, both the photosynthetic rate controlled by the Rubisco capacity and the rates controlled by light are linear functions of the Rubisco capacity (V_m). The Rubisco capacity describes the activity of the CO_2-fixing enzyme Rubisco. In the model, the activity is doubled for every 10°C and scaled by the maximum Rubisco capacity (V_{cmax}). The leaf dark respiration, which is also modeled according to Collatz et al. (1991), is also a function of the maximum Rubisco capacity.

Modifications to MOSES

In a study of a mixed temperate deciduous forest, Wilson et al. (2001) showed that temporal trends in photosynthetic capacity can be

TABLE 1

Climate and vegetation characteristics.

	1996	1997	1998	1999
Snow depth on June 1st (Hinkler et al., 2003)	40 cm	80 cm	80 cm	110 cm
Snow-cover end date	170	172	178	181
Growing-season start (defined as start of LAI development)	178	184	184	195
Growing-season end (defined as end of positive LAI)	245	245	245	242
Growing-season length (number of days with nonzero LAI)	67	59	61	47
Measured sink-season start (defined as first day with nonzero daily NEE)	184	198		203
Measured sink-season end (defined as last day with nonzero daily NEE)		238	240	243
First frost night	228	223	232	225
Max LAI	1.21	1.1	1.0	0.53
Precipitation (June–August)	11 mm	45 mm	112 mm	35 mm
Sink-season NEE (sink season is defined as the period with negative daily CO_2 fluxes)	-123 g C m^{-2}	-84 g C m^{-2}	-88 g C m^{-2}	-53 g C m^{-2}
Measured sink-season NEE		-63 g C m^{-2}		-50 g C m^{-2}

very important in determining the seasonal variation and magnitude of carbon dioxide fluxes. They showed that neglecting these trends can result in serious overestimation of the annual carbon uptake. Wang et al. (2003) came to similar conclusions when they studied forests in climates ranging from boreal to mediterranean. We modified MOSES to account for seasonal variation in photosynthetic capacity by replacing the mean values of leaf area index (LAI) and maximum Rubisco capacity (V_{cmax}) with seasonally varying values. Both variables are important for estimating canopy carbon dioxide flux: the LAI for upscaling fluxes from leaf to canopy level and V_{cmax} for determining the photosynthetic rate controlled by the Rubisco capacity. In addition to model runs with seasonally and interannually varying LAI and V_{cmax}, model runs were made with constant V_{cmax} and LAI (LAI and V_{cmax} determined as the 4-yr means over the period June–August) to investigate the effect of using generalized LAI and V_{cmax} data.

Seasonally varying LAI was derived from spectral measurements of near-infrared and photosynthetic active radiation. The LAI data for 1996 and 1997 were taken from Soegaard and Nordstroem (1999) and Soegaard et al. (2000), respectively. LAI for 1998 and 1999 was determined by following the method of Soegaard and Nordstroem (1999). They determined LAI by using a linear relationship between LAI and the ratio of the reflectances of near-infrared (R_{NIR}) and photosynthetic photon flux density (R_{PAR}) (equation 2) as proposed by Hinzman et al. (1986):

$$L = c\left(\frac{R_{\mathrm{NIR}}}{R_{\mathrm{PAR}}} - r_0\right), \qquad (2)$$

where L is leaf area index, c is an empirical constant, and r_0 is the reference reflectance ratio of R_{NIR} and R_{PAR} when the LAI is zero. Soegaard and Nordstroem (1999) calibrated the c constant to 0.24, and this value was used for LAI determination for all the years studied. The reflectance ratio ($R_{\mathrm{NIR}}/R_{\mathrm{PAR}}$) was calculated from diurnal sums of near-infrared radiation and photosynthetic photon flux density. The reference reflectance ratio (r_0) was determined with the reflectance from pre-growing-season data and was found to be 2.8 in 1996 and 1997, 2.0 in 1998, and 3.0 in 1999.

At the end of the growing season, the reflectance ratio was higher than in the beginning, which caused the LAI to be unrealistically high. This result could be an indication of changing magnitudes of soil and vegetation spectral characteristics over the season. To remove this effect, the linear LAI function (equation 2) was replaced by a piecewise linear function following the result of equation 2 until senescence, when the function was forced to decline to zero at day 245 in 1998 and 1999.

The V_{cmax} was initially kept at a fixed value that was found previously through calibration (Soegaard and Nordstroem, 1999). We denote the initial fixed V_{cmax} value for peak maximum Rubisco capacity. After the first frost, the maximum Rubisco capacity was forced to decline by 5% per day until the end of the growing season. We choose the first frost day to represent the changing climate conditions that characterize the senescent period. The first frost night varied by as many as 9 d over the 4-yr period (Table 1), and the 5% decline was arbitrarily chosen.

Eddy covariance measurements of energy fluxes typically leave a residual of between 10 and 20% when sensible, latent, and ground heat fluxes are subtracted from net radiation measurements (Massman and Lee, 2002). In fen ecosystems, lateral surface and subsurface runoff can play a significant role in the water balance (Rouse, 1998), and heat drainage associated with this lateral runoff may partly explain the energy-balance residual (Soegaard et al., 2001). Because MOSES closes the energy balance, overestimation of energy-balance components (sensible, latent, and ground heat flux) is a likely outcome. To counteract this overestimation, a heat-advection term (Q_{A}) was added to the MOSES energy-balance equation:

$$Q_{\mathrm{N}} = Q_{\mathrm{H}} + Q_{\mathrm{E}} + Q_{\mathrm{S}} + Q_{\mathrm{SNOW}} + Q_{\mathrm{A}}, \qquad (3)$$

where Q_{N} is the net radiation, Q_{H} is the sensible heat flux, Q_{E} is the latent heat flux, Q_{S} is the soil heat flux, Q_{SNOW} is the snow heat flux, and Q_{A} is the introduced heat-advection term (all in units of W m^{-2}). Because the modeling is made after snowmelt, Q_{SNOW} was zero in the simulations.

Soil-Respiration Modeling and Modeling of NEE

To model the summertime net ecosystem carbon dioxide exchange (NEE), MOSES was used in combination with Lloyd and Taylor's (1994) model for soil respiration R_{soil}. NEE is the sum of net primary production and soil respiration:

$$\mathrm{NEE} = \mathrm{NPP} + R_{\mathrm{soil}}, \qquad (4)$$

where NEE is net ecosystem carbon dioxide exchange, NPP is the net primary production, and R_{soil} is the soil respiration (equation 5). With regard to the sign convention, the NPP value is negative, resulting in

TABLE 2

Model parameters describing the soil. The peat soil values are the median values found for fibric (little decomposed) and sapric (highly decomposed) peat found by Letts et al. (2000) in their literature review of parameter values, except heat capacity and heat conductivity that were calculated according to Williams and Smith (1989) and Campbell and Norman (1998). The values for the third and fourth soil layers represent coarse mineral soil texture and are taken from Table 2 in Cox et al. (1999).

Parameter	Upper soil layer (peat)	Second soil layer (peat)	3rd and 4th soil layer (mineral soil)
Layer thickness	0.1 m	0.25 m	0.55 and 2 m, respectively
Saturated hydraulic conductivity	2.8×10^{-4} m s^{-1}	1.0×10^{-7} m s^{-1}	7.57×10^{-6} m s^{-1}
Saturated hydraulic suction	1.03×10^{-2} m	1.01×10^{-2} m	3.29×10^{-2} m
Clapp-Hornberger's B constant	2.7	12	4.5
Soil-moisture content at wilting point	0.04 m^3 m^{-3}	0.15 m^3 m^{-3}	0.06 m^3 m^{-3}
Soil-moisture content at critical point (field capacity)	0.24 m^3 m^{-3}	0.70 m^3 m^{-3}	0.15 m^3 m^{-3}
Soil-moisture content at saturation	0.90 m^3 m^{-3}	0.80 m^3 m^{-3}	0.40 m^3 m^{-3}
Dry-soil heat capacity	0.25×10^6 J m^{-3} K^{-1}	0.60×10^6 J m^{-3} K^{-1}	1.25×10^6 J m^{-3} K^{-1}
Dry-soil heat conductivity	0.03 W m^{-1} K^{-1}	0.04 W m^{-1} K^{-1}	0.272 W m^{-1} K^{-1}

TABLE 3

Site-specific parameters. All values are taken from Soegaard and Nordstroem (1999) except the constant heat drain Q_A, which is introduced and determined in this study.

Parameter	Value
Maximum rubisco capacity (V_{cmax})	50 μmol CO$_2$ m^{-2} s^{-1}
Quantum efficiency (α)	0.04
Constant in photosynthetic rate controlling assimilate removal (C_j)	1.0
Coupling factor β_1	0.95
Coupling factor β_2	0.98
Light extinction factor (k)	0.90
Constant heat drain (Q_A)	10 W m^{-2}

a negative NEE, when photosynthetic assimilation (CO$_2$ uptake) is larger than the respiration losses of carbon dioxide.

Lloyd and Taylor's model for soil respiration is written as

$$R_{soil} = R_{10} \exp\left[308.56\left(\frac{1}{56.02} - \frac{1}{T_{soil} - 227.15}\right)\right], \qquad (5)$$

where R_{10} is the reference soil respiration at 10°C and T_{soil} is the soil temperature. Soegaard and Nordstroem (1999) used an R_{10} value of 1.6 μmol CO$_2$ m^{-2} s^{-1} for the same site in 1996. This R_{10} value was used in the simulation presented here. In the simulations, the modeled top-layer soil temperature (0–10 cm) was used as T_{soil}.

NPP, which was modeled with MOSES, is the sum of the plant assimilation uptake of carbon dioxide and the losses of carbon dioxide through dark, growth, and maintenance respiration. We chose to neglect the growth and maintenance respiration terms modeled by MOSES because Lloyd and Taylor (1994) incorporated root respiration in their model and we considered the stem and leaf respiration to be directly recycled by plant assimilation during daytime (recall that growth and maintenance respiration can be split up in leaf, stem, and root respiration). This modeling strategy is similar to that used by Soegaard and Nordstroem (1999).

Forcing Data and Model Parameters

Air temperature, air humidity, wind speed, incoming solar radiation, net radiation, and precipitation data were taken from the measurement station in Rylekæret, when available. Gaps were filled by using data from the two meteorological stations 3 km south of Rylekæret (the ZERO stations described above). In 1998, there were concurrent gaps in the data from Rylekæret and the ZERO stations. In these cases, data from Daneborg (DMI, 2000) 30 km east were used. In 1996, measurements in Rylekæret ended around day 226. For the remainder of that season, data from the ZERO mast was used.

Model parameter values used in the simulations are listed in Table 2 and include saturated hydraulic conductivity, saturated hydraulic suction, Clapp-Hornberger's B constant (e.g., Cox et al., 1999), soil-moisture content at the wilting point, at the critical point, and at saturation, heat capacity, and heat conductivity. Letts et al.'s (2000) summary of peat-soil characteristics was used to determine saturated hydraulic conductivity, saturated hydraulic suction, the Clapp-Hornberger's B constant, soil-moisture content at the wilting point, critical point, and saturation. Heat capacity and heat conductivity were calculated on the basis of organic content according to the method described in Williams and Smith (1989) and Campbell and Norman (1998).

Model parameters for the leaf-level carbon dioxide model were taken from Cox et al. (1999), except for the parameters that were calibrated for this particular site by Soegaard and Nordstroem (1999). These site-specific parameters are listed in Table 3 and include peak maximum Rubisco capacity (V_{cmax}), quantum efficiency, constants in the equation for the photosynthetic rate determined by removal of assimilates, and two coupling factors relating the three potential rates to the gross carbon dioxide assimilation of the leaf.

Initial values for canopy-intercepted water content, snow depth, surface temperature, height of the canopy, and soil-moisture content and soil temperatures for the four soil layers were determined for the model start at day 182. Day 182 is after the snow-cover end date for all years; we therefore assumed that no canopy water content or snow cover were present at this time. The canopy height was fixed to 0.1 m, and the soil was assumed to be saturated. The temperature distribution with depth was estimated by using the soil-temperature profile measured at the ZERO masts separately for each year.

Results

ENVIRONMENTAL CONDITIONS

Air temperatures over the 4-yr period (1996–1999) were 1.7°C, 5.1°C, and 4.0°C in June, July, and August, respectively (Table 4). Compared to the 4-yr mean, 1996 was warmer than normal, and 1999 was colder than normal. The monthly mean net radiation was 69 W m^{-2}, 121 W m^{-2}, and 82 W m^{-2} for June, July, and August, respectively. Net radiation was above normal in 1996 and below normal in 1998 and 1999. The monthly mean solar radiation was 282 W m^{-2}, 213 W m^{-2}, and 128 W m^{-2} in June, July, and August,

TABLE 4

Monthly climate anomalies and mean values.

	June	July	August	JJA
TEMPERATURE				
Mean value (°C)	1.7	5.1	4.0	
1996 anomaly	0.12	0.47	0.32	0.91
1997 anomaly	0.88	−1.38	0.62	0.12
1998 anomaly	−0.47	0.21	0.79	0.53
1999 anomaly	−0.47	0.7	−1.7	−1.47
INCOMING SOLAR RADIATION				
Mean value (W m^{-2})	282	213	128	
1996 anomaly	47.6	−3.5	−38.8	5.3
1997 anomaly	−56.6	−7.7	22.6	−41.7
1998 anomaly	−5.7	−13	−16	−34.7
1999 anomaly	9.9	24.2	32.2	66.3
NET RADIATION				
Mean value (W m^{-2})	69	121	82	
1996 anomaly	32	1.9	37.8	71.7
1997 anomaly	15.1	−3.4	−9.6	2.1
1998 anomaly	−20.3	−5.7	−22.2	−48.2
1999 anomaly	−28.3	7.3	−6	−27

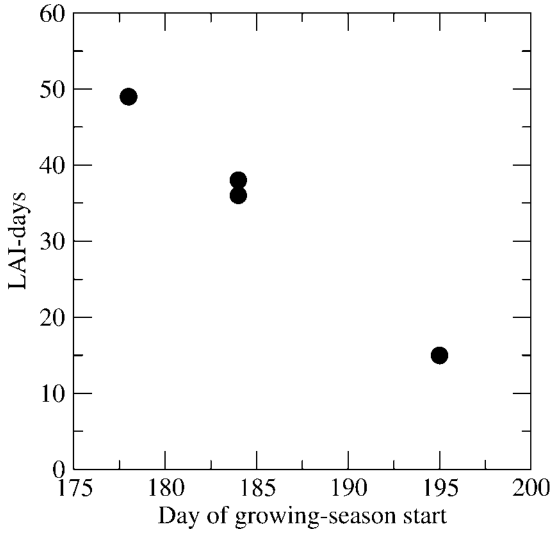

FIGURE 4. Leaf area index days (sum of daily growing-season LAI) against day of growing-season start during the period 1996–1999.

respectively. In 1999, the Zackenberg area received more incoming solar radiation than normal, and in 1997 and 1998, it received less than normal. The total amount of summer precipitation varied significantly from year to year. In 1998, the total summer precipitation was 112 mm; in 1996, it was only 11 mm. The summer precipitation was 45 mm in 1997 and 35 mm in 1999.

Early-summer snow depth (i.e., June 1st), snow-cover end date, and growing-season start (defined as the first day of nonzero LAI) and growing-season length (defined as number of days with nonzero LAI) varied significantly from year to year; 1996 and 1999 were the two extremes (Table 1). In 1996, the early-summer snow depth was shallow, the snow-cover end date and growing-season start were early, and the growing-season length was the longest of the four years. In 1999, the greatest early-summer snow depth, the latest snow-cover end date and growing-season start, and the shortest growing-season length were observed. It is notable that although the snow-cover end date and the growing-season start varied by as much as 11 and 17 d, respectively, over the 4-yr period, the growing-season end date only varied by 3 d. The small variability in growing-season end date is a result of forcing LAI to become zero at day 245 in 1998 and 1999. However, if other means were available to determine the growing-season end, the same observation of small variability in that date would most likely occur, because the same pattern is repeated for the measured sink-season start and end (defined as the start and end of the period of negative daily NEE). The start of the sink season varied by as much as 19 d, whereas the end of the sink season varied only by as much as 5 d (Table 1).

The leaf development showed a large interannual variability. The peak of the leaf area index was highest and occurred earliest in 1996 (Fig. 3). In 1999 the peak LAI was about half the peak LAI in 1996, and it occurred ~20 d later. The LAI peaks in 1997 and 1998 were intermediate. We computed "LAI-days" as an analogue to degree-days; i.e., we added up the daily LAI values over the growing season. We found that the LAI-day totals were considerable higher in 1996 than in 1999 (49 vs. 15, respectively). Furthermore, LAI-day totals showed a linear relationship with the growing-season start date (Fig. 4).

EVALUATING MODEL MODIFICATIONS AND SOIL-RESPIRATION MODEL

Net ecosystem carbon dioxide exchange was modeled by adding a soil-respiration model to MOSES. The soil-respiration model result was validated against literature data because the eddy covariance measurements do not resolve net assimilation and soil respiration separately. Modeled midday respiration fluxes in 1998 varied between 1 and 3 μmol CO_2 m^{-2} s^{-1} throughout the season. This range is lower than the 4.9 μmol CO_2 m^{-2} s^{-1} for tundra vegetation reported by Buchmann and Schulze (1999), but consistent with the midday average respiration of 1.6 μmol CO_2 m^{-2} s^{-1} measured by Christensen et al. (2000) from the same site (the value was computed as the average

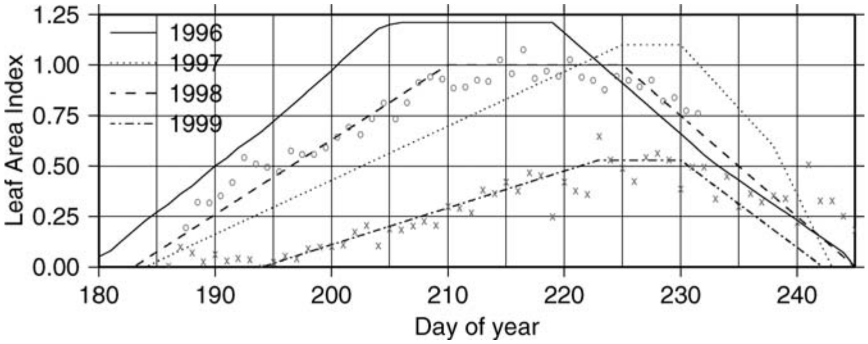

FIGURE 3. Leaf area index from 1996 to 1999. The crosses and circles represent the LAI calculated from the ratio of R_{NIR} and R_{PAR} for 1999 and 1998, respectively.

of continuous fen measurements given in Table 1 of Christensen et al., 2000).

The introduction of a constant heat-advection term in the energy balance improved the modeled surface and soil temperature for the 1998 data set for which it was tested. The heat-advection term was introduced to adjust for the requirement of energy-balance closure in MOSES. Owing to heat advection associated with lateral runoff (Soegaard et al., 2000), the in situ measurements of latent, sensible, and ground heat flux do not add up to the measured net radiation. Therefore, MOSES overestimated the latent, sensible, and ground heat fluxes by forcing them to add up to the measured net radiation. As an end result, the soil temperature in 1998 was overestimated on average by 2.3°C, and the surface temperature in 1998 was underestimated on average by 3°C over the season. By running the model with varying constants for the heat-advection term (in the interval 10–35 W m^{-2}), a best fit of 10 W m^{-2} was found. With the constant heat-advection term, the modeled topsoil temperature and surface-temperature deviations were reduced to 0.1°C and –1°C, respectively.

The modeled NEE in 1999 was unsatisfactory with the default setup, as the total sink-season NEE was only modeled as 56% of the measured value (–28 g C m^{-2} vs. –50 g C m^{-2}). In the period 1996–1999, the modeled daytime leaf assimilation was typically constrained by the Rubisco capacity; therefore, we expected the modeled NEE to be highly dependent on the maximum Rubisco capacity (V_{cmax}.) A sensitivity test revealed that our anticipation was indeed the case (Fig. 5). Instead of using a constant V_{cmax} of 50 μmol CO_2 m^{-2} s^{-1} for all years, we found the best-fit V_{cmax} for each year. The best fit was found by running the model for each year with the peak V_{cmax} varying between 50 and 100 μmol CO_2 m^{-2} s^{-1} and then comparing the model data with half-hourly measurements from the growing-season start until day 220. Day 220 was chosen so that the senescent decline in V_{cmax} would not affect the best fit. This procedure confirmed that using a constant of 50 μmol CO_2 m^{-2} s^{-1} was the best fit for 1996, but that the best-fit V_{cmax} for 1997–1999 deviated from this value. In 1997, the best fit was 52 μmol CO_2 m^{-2} s^{-1}. In 1998 it was 56 μmol CO_2 m^{-2} s^{-1}. In 1999 it was 86 μmol CO_2 m^{-2} s^{-1} and thus considerably higher than the other three years.

The model performance with the addition of a soil-respiration model, constant heat sink, and an interannually varying best-fit peak V_{cmax} value was evaluated by comparing the modeled NEE with half-hourly measurements (Fig. 6). The correlation coefficients were 0.77, 0.95, 0.90, and 0.81 for 1996, 1997, 1998, and 1999, respectively.

The model's ability to estimate the summer sink strength was evaluated by comparing the modeled and measured sink-season NEE for 1997 and 1999 (the two years with a complete measurement series). In 1997, the modeled NEE was 133% of the measured NEE. In 1999, the modeled NEE was 106% of the measured NEE.

INTERANNUAL VARIABILITY OF NEE

Combing model and measurement results showed that there was a large interannual variability in the sink-season NEE between 1996 and 1999. The strongest uptake took place in 1996, when the model showed an uptake of –123 g C m^{-2} (recall that negative NEE = uptake of carbon dioxide). Measurement showed that 1999 was the weakest sink with an uptake of only –50 g C m^{-2}, followed by that of 1997 with an uptake of –63 g C m^{-2}. Intermediate CO_2 uptake took place in 1998, where the model predicted an NEE of –88 g C m^{-2}.

The effect of using generalized LAI and V_{cmax} data was investigated by replacing the seasonally and interannually varying LAI and V_{cmax} data with constant values representing the 4-yr mean. The mean LAI was 0.73, and the mean V_{cmax} was 63 μmol CO_2 m^{-2} s^{-1}. Not representing the seasonal and interannual variation in LAI and V_{cmax} resulted in poor modeling of the seasonal variation of NEE (Fig. 7). The early- and late-season NEE was overestimated for all years. This overestimation was especially problematic in 1999 when the modeled net assimilation started 25 d too early. As a result, the modeled sink-season NEE in 1999 was 244% of the measured value compared to only 106% when seasonally and interannually varying LAI and V_{cmax} data were used. In 1997, the sink-season NEE was overestimated by 163% compared to 133% when using seasonally and interannually varying LAI and V_{cmax}. In 1996 and 1998, the early- and late-season overestimation was compensated by an underestimation of peak season fluxes, and the net difference between using constant LAI and V_{cmax} values and using seasonally varying LAI and V_{cmax} values was negligible. The net difference was 4–9 g C m^{-2} compared to 18–49 g C m^{-2} in 1997 and 1999.

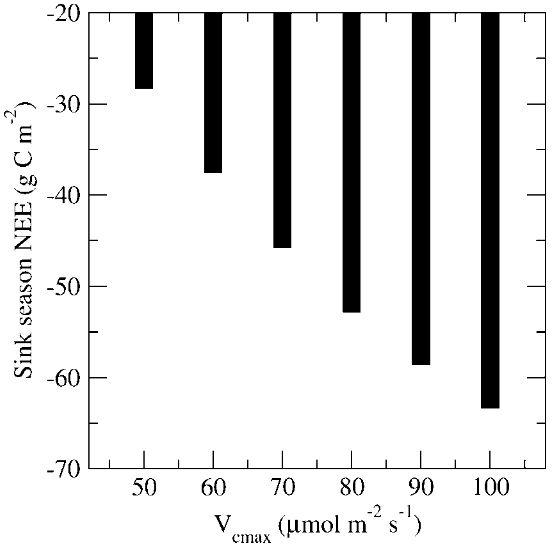

FIGURE 5. Modeled sink-season net ecosystem exchange against maximum Rubisco capacity for the growing season in 1999.

The seasonal variation of LAI is important because it scales photosynthesis from leaf to canopy level (equation 1). In the transition from spring to summer, the meteorological conditions might allow leaf photosynthesis in the model; however, because there is no leaf development and LAI is zero, the canopy photosynthesis will also be zero. When LAI increases over the growing season, more leaves develop, and the canopy photosynthesis increases. During the senescence, reducing LAI will limit the photosynthesis. The leaf photosynthetic capacity is to a large extent determined by V_{cmax}, which also has a seasonal variation. To separate the impact of seasonally varying V_{cmax} from LAI, a simulation using the peak V_{cmax} as a constant throughout the growing season was compared with simulations that let V_{cmax} decline in the senescent period. In 1997 the growing-season sink was overestimated by 21 g C m^{-2}; without the temporal variation in V_{cmax}, the 1997 senescent fluxes were overestimated by an additional 18 g C m^{-2}. During the other years, the effect of a constant V_{cmax} was also to increase the total growing-season NEE. However, the overestimation was less than that of 1997. In 1996, the sink-season NEE was increased by 5 g C m^{-2}, in 1998 by 1 g C m^{-2}, and in 1999 by 3 g C m^{-2}.

To investigate the importance of meteorological forcing vs. LAI and V_{cmax} input data in controlling sink-season NEE, 16 model simulations were set up with interchanging meteorological forcing, initial conditions, and LAI and V_{cmax} data. The model was run four times with meteorological forcings and initial conditions for a specific year; each run had a new set of LAI and V_{cmax} data representing the conditions for 1996, 1997, 1998, or 1999. Figure 8 shows the sink-season NEE

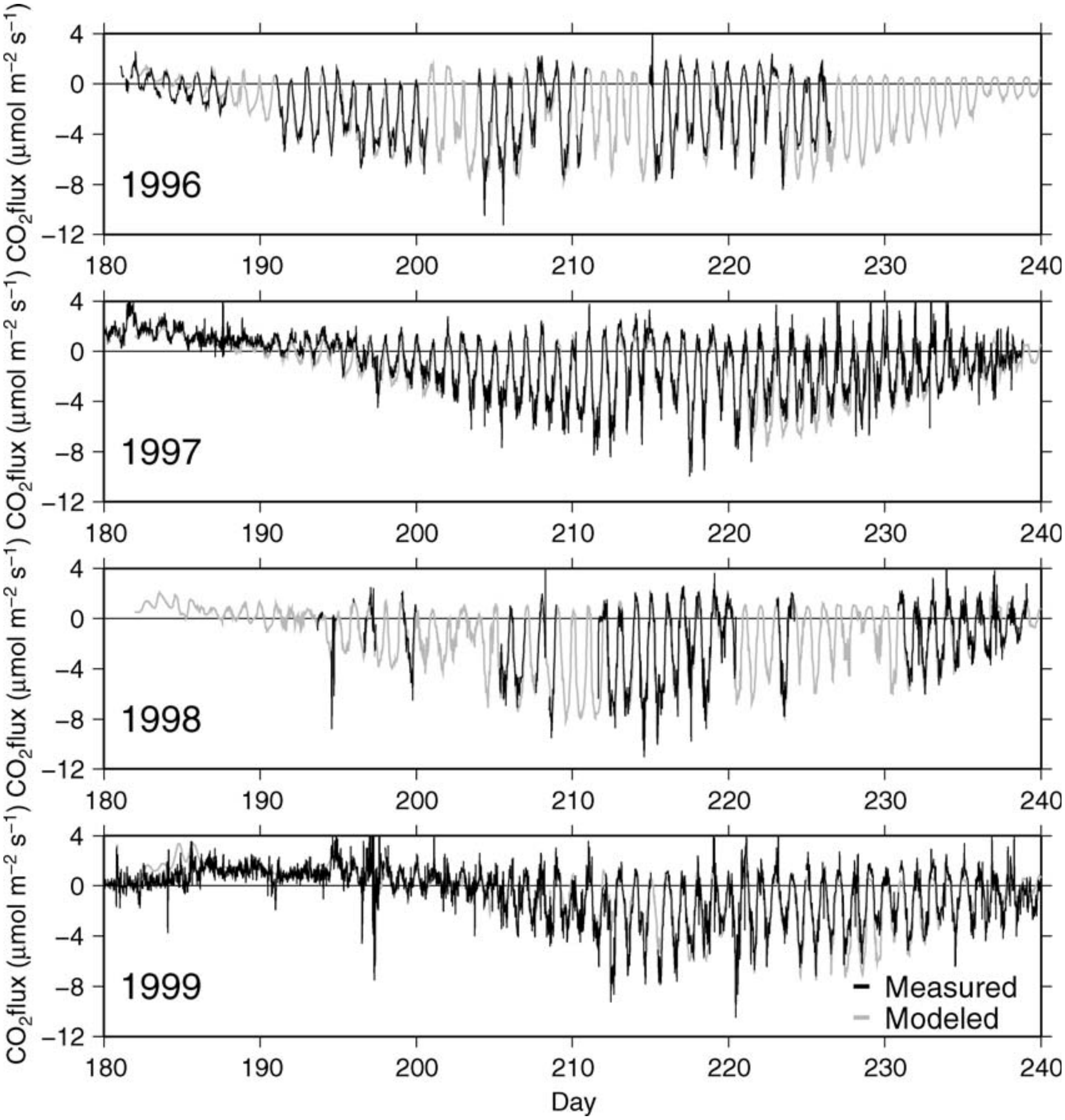

FIGURE 6. Half-hourly modeled and measured carbon dioxide fluxes during the period 1996–1999. The solid black lines show the measured data, the gray lines show the modeled flux.

against LAI-days (the sum of daily growing-season LAI). This figure indicates a linear relationship between LAI-days and sink-season NEE. A large number of LAI-days resulted in strong sinks, and a small number of LAI-days resulted in weak sinks. The different meteorological forcing data caused a span between the highest and lowest sink strength for a given value of LAI-days. On average, the span in NEE was 35 C m^{-2}. Regardless of which LAI and V_{cmax} data set was used, the meteorological forcing data from 1999 always resulted in the strongest sink, and the meteorological forcing data from 1998 always resulted in the weakest. Figure 9 show a different representation of the same simulation where NEE is plotted against the year from which the meteorological forcing data was taken. This figure shows no pattern between sink-season NEE and the year of meteorological forcing. The span between the highest and lowest NEE for a particular year was 78 C m^{-2}, more than double the span observed in Figure 8.

Discussion and Conclusions

This study shows that there is a large interannual variability in summertime net ecosystem carbon dioxide exchange in a high arctic fen; the sink-season NEE ranges from –50 g C m^{-2} to –123 g C m^{-2}. The interannual fluctuations in summertime NEE from a high arctic polar desert in Svalbard were much smaller, only ±5 g C m^{-2} over a 2-yr measurement period (Lloyd, 2001b). The differences between the two ecosystem types (i.e., a fen and a polar desert) probably explain the great differences in net ecosystem exchange. Studies made in the arctic and boreal ecosystem show interannual variability similar to that of this study. The summer NEE (May–September) at a wet sedge ecosystem at Barrow, Alaska, varied between –161 g C m^{-2} and –104 g C m^{-2} over two consecutive years (Harazono et al., 2003). At a boreal peatland, the NEE varied from –71 g C m^{-2} one year to 32 g C m^{-2} the following year (Shurpauli et al., 1995). Another 4-yr data series from the boreal region shows that the summer NEE varied between –52 g C m^{-2} and –94 g C m^{-2} (Lafleur et al., 2003).

Studies of boreal and arctic ecosystems indicate that wetness and temperature are important factors in determining the summertime NEE. Wet summers are often associated with strong sinks of carbon dioxide, whereas dry summers are associated with weak sinks and are sometimes even sources of carbon dioxide (e.g., Lafleur et al., 2003; Shurpauli et al., 1995). Harazono et al. (2003) showed that with similar

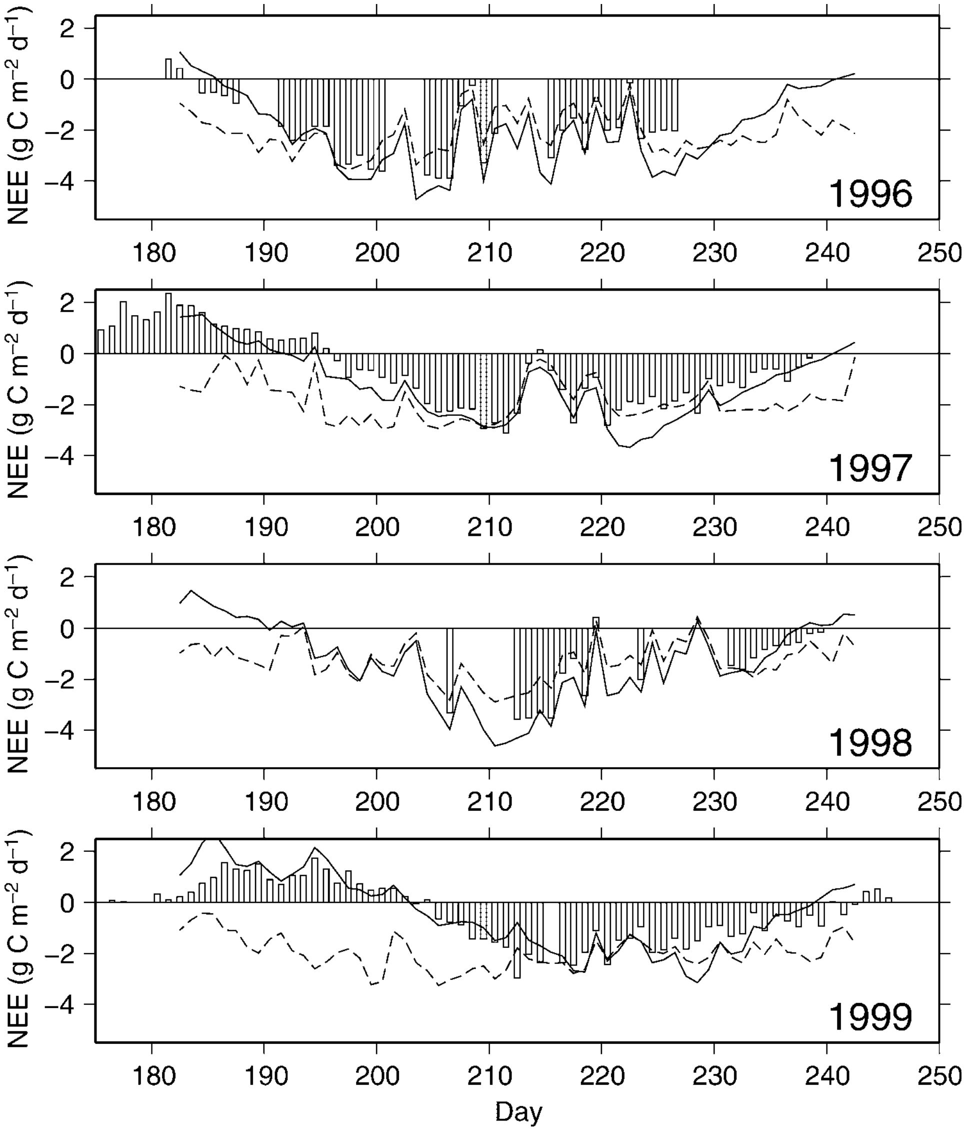

FIGURE 7. Daily net ecosystem exchange during the period 1996–1999. The bars represent measurements. The solid line shows the modeled NEE based on a leaf area index and V_{cmax} that varied individually for each year. The dashed line shows the modeled NEE based on a constant LAI and V_{cmax} where the values of LAI and V_{cmax} are the average values from the 4-yr period.

wetness conditions, low air temperatures and high solar radiation after spring thaw resulted in strong carbon dioxide sinks whereas high air temperatures and low solar radiation resulted in weak carbon dioxide sinks. Our study seems to contradict previous findings. The strongest sink occurred in the driest and warmest of the four years (1996). The wet year (1998) had an intermediate uptake of carbon dioxide, and the coldest year (1999) had the weakest sink. However, our simulations indicate that LAI was more important in determining NEE than the climate conditions. We demonstrated a linear relationship between NEE and the number of LAI-days: a large number of LAI-days resulted in a large carbon dioxide uptake, and a small number of LAI-days resulted in a small carbon dioxide uptake. There was no similar relationship between meteorological forcing and sink-season NEE, and the NEE variability caused by different meteorological forcing data sets was much less than the variability caused by different LAI and V_{cmax} data sets. However, the meteorological forcings had a secondary control on sink-season NEE. Model results using the meteorological conditions in 1998 consistently resulted in the weakest NEE sinks regardless which LAI and V_{cmax} data set was used, whereas the model results using the meteorological conditions in 1999 always resulted in the strongest NEE sink.

We showed that the LAI development was dependent on the day of growing-season start. Although the start of the growing season was highly variable between 1996 and 1999, the end of the growing season and the end of the sink season occurred on almost the same day over the 4 yr. Thus, the earlier the growing-season start, the longer the growing season becomes. This relationship provides a greater potential for leaf-area development because photosynthesis will take place over a longer period of time. The start of the growing season in turn appears to be determined by the snow-cover end date. Our study shows that years with an early snow-cover end date also have an early growing-season start, whereas years with a late snow-cover end date have a late growing-season start. Meteorological conditions between snow-cover end date and growing-season start will be important in controlling when plant development can occur. However, the snow-cover end date will be a primary controlling factor because plant development will not take place under snow-covered ground.

In conclusion, our study indicates that the leaf area index is the primary control of the summertime NEE sink and that LAI itself is highly dependent the snow-cover end date and growing-season start. Thus, the summertime NEE is also controlled by the snow-cover end date and the growing-season start. This further indicates that climate conditions in the winter and spring may be more important than summer climate in controlling the net ecosystem fluxes of carbon dioxide from this high arctic fen. This is because the winter and spring precipitation controls the snow thickness and the spring temperatures

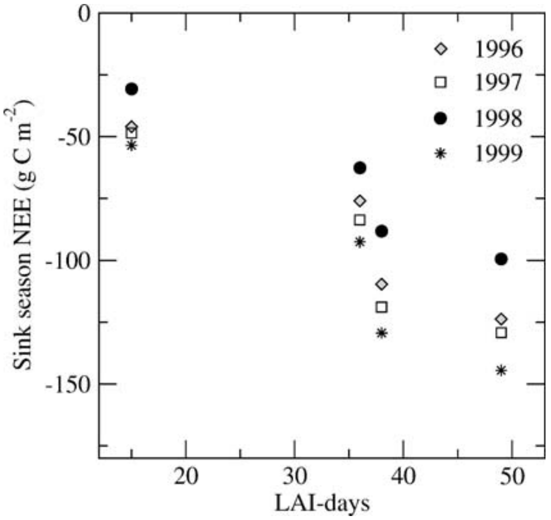

FIGURE 8. Modeled sink-season net ecosystem exchange against leaf area index days (sum of daily growing-season LAI) during the period 1996–1999. The forcing and initial data have been kept fixed for each year and have each been used in four runs with varying LAI and V_{cmax}. The LAI and V_{cmax} conditions have varied according to the conditions for 1996 (LAI-days of 49), 1997 (LAI-days of 36), 1998 (LAI-days of 38), and 1999 (LAI-days of 15).

control the rate at which the snow pack melts in the spring. Our observations of the growing-season start controlling summertime sink strength are in accordance with several other studies. A snow-removal study showed that earlier snow-free conditions lead to greater carbon dioxide assimilation in the arctic ecosystem (Oberbauer et al., 1998). Goulden et al. (1996) found that the growing-season length was important in controlling annual carbon dioxide flux. Myneni et al. (1997) suggested that increased growing-season length could explain the observed increases in plant productivity in the northern latitudes between 1981 to 1991.

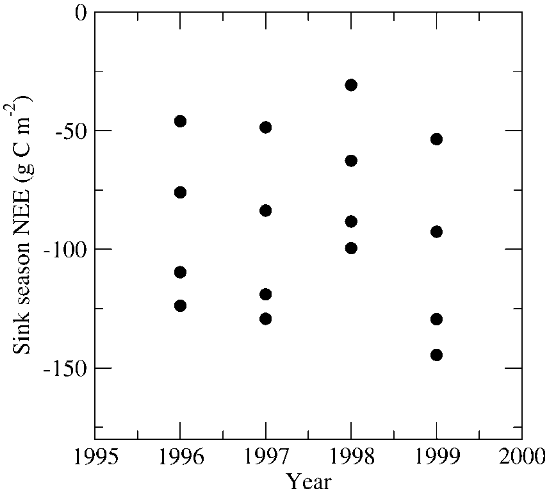

FIGURE 9. Modeled sink-season net ecosystem exchange against year. The forcing and initial data have been kept fixed for each year and have each been used in four runs with varying LAI and V_{cmax}. Each circle represent a model run with LAI and V_{cmax} conditions from 1996 (LAI-days of 49), 1997 (LAI-days of 36), 1998 (LAI-days of 38), or 1999 (LAI-days of 15).

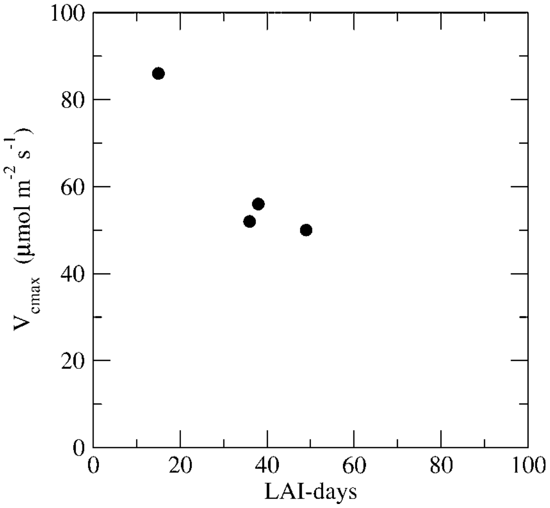

FIGURE 10. Peak V_{cmax} against LAI-days (sum of daily growing-season LAI) during the period 1996–1999.

Successful modeling of net ecosystem carbon dioxide exchange is based on good estimates of net primary production and soil respiration. In the arctic summer, NEE is the sum of soil respiration and net primary production. Because soil respiration and net primary production have opposite signs, the NEE is typically much smaller than the two magnitudes. Small modeling errors of soil respiration and net primary production will be magnified in the NEE estimate and may lead to incorrect conclusions regarding whether the ecosystem acts as a net sink or source of carbon dioxide. Accurate estimates of both components become very important in the estimation of NEE. Arctic soil respiration has a strong temperature dependence, as expressed in Lloyd and Taylor's equation (equation 5). The successful application of this equation depends on precise soil-temperature estimates. The present study demonstrates that modeling soil respiration can be achieved by using MOSES and that modeling soil and surface temperatures benefited from adding a heat-advection term to the surface energy balance.

MOSES simulated half-hourly fluxes well and made good predictions of the sink-season NEE. Although meteorological data can be obtained from meteorological stations or reanalysis, data determining LAI and V_{cmax} might be a greater challenge. The measurements of PAR and NIR that we used to determine leaf area index for the 4-yr period typically are not available. Using generalized values of LAI and V_{cmax} would greatly simplify the modeling task. However, our study showed that seasonal and interannually varying LAI and V_{cmax} were very important in determining the fluxes. Not representing the variability in LAI and V_{cmax} could result in large errors. Today, data from the NASA Earth Observing System (EOS) MODIS sensor offer geometrically rectified and atmospherically corrected biophysical data, free of charge, suitable for processing in a geographic information system (GIS). This opportunity opens up the possibility of determining seasonally varying parameters like LAI through remote sensing. However, determining V_{cmax} without a fitting procedure remains a challenge. We found a linear relationship between peak V_{cmax} and the number of LAI-days (Fig. 10) that we think could alleviate the need for finding V_{cmax} by fitting. We hypothesize that the plant nitrogen availability and allocation explain the linear relationship between V_{cmax} and accumulated LAI. Arctic ecosystems are typically nitrogen limited, partly owing to permafrost (Hobbie et al., 2002). Because of the limited nitrogen availability in the soil, the leaf nitrogen concentration and therefore the Rubisco capacity (Nijs et al., 1995) can be assumed to be low when the leaf nitrogen is diluted by a large number of leaves (S. Jonasson, 2005, personal communication). This statement implies that the high LAI in 1996 resulted in a reduction of leaf nitrogen concentration, leading to a lower photosynthetic efficiency, whereas the low LAI in 1999 has a higher nitrogen concentration and thus a greater photosynthetic efficiency.

Our study does not answer the question of whether high arctic ecosystems are still a sink of carbon dioxide. Soegaard and Nordstroem (1999) estimated the wintertime soil respiration to be 41.7 g C m^{-2} for the same study site in 1996. For the same site, but in 1997, Nordstroem et al. (2001) estimated the wintertime respiration to be between 30 g C m^{-2} and 38 g C m^{-2}. Under the assumption that this range of values is representative for all the years studied, none of the years between 1996 and 1999 were a source of carbon dioxide to the atmosphere. Although the strength of the sink was reduced over the period 1996–1999, four years of data are insufficient to determine trends caused, for example, by climate change. Furthermore, the method of estimating annual fluxes is extremely simplified. Elberling (2003) demonstrated the complexity of wintertime respiration in the Arctic, and Lafleur et al. (2003) showed that fall and wintertime net ecosystem carbon dioxide exchange shows large interannual variability (27 g C m^{-2} to 49 g C m^{-2}). Because sensor problems and the inaccessibility in wintertime makes it challenging to perform year-round measurements in the Arctic, a model like MOSES may provide a useful tool in future attempts to characterize the wintertime fluxes.

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