

## Peatland responses to varying interannual moisture conditions as measured by automatic CO<sub>2</sub> chambers

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[1] Net ecosystem CO<sub>2</sub> exchange (NEE) was measured from June 2000 through October 2001 by 10 automatic chambers at a peatland in southeastern New Hampshire. The high temporal frequency of this sampling method permitted detailed examination of NEE as it varied daily and seasonally. Summer of 2001 was significantly drier than the 30-year average, while summer of 2000 was wetter than normal. Although NEE varied spatially across the peatland with differences in plant species composition and biomass, maximum CO<sub>2</sub> uptake was 30–40% larger in the drier summer in evergreen and deciduous shrub communities but the same or lower in sedge sites. Ecosystem respiration rates were 13–84% larger in the drier summer depending on plant growth form with water table and temperature as strong predictors. Ecosystem respiration was also correlated with maximum ecosystem productivity and foliar biomass suggesting that plant processes, water table, and temperature are tightly linked in their control of respiratory losses. The ratio between maximum productivity and respiration declined for evergreen shrub and sedge sites between the wet and dry summer, but increased in deciduous shrub sites. A drier climate may reduce the CO<sub>2</sub> sink function of peatlands for some growth forms and increase it for others, suggesting that ecosystem carbon and climate models should account for differences in growth form responses to climate change. It also implies that plant functional types respond on short timescales to changes in moisture, and that the transition from sedges to shrubs could occur rapidly in peatlands under a drier and warmer climate. *INDEX TERMS*: 0315 Atmospheric Composition and Structure: Biosphere/atmosphere interactions; 1615 Global Change: Biogeochemical processes (4805); 1890 Hydrology: Wetlands; 1833 Hydrology: Hydroclimatology; *KEYWORDS*: peatland, net ecosystem CO<sub>2</sub> exchange, respiration, autochamber, plant functional groups, drought

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### 1. Introduction

[2] Recent climate models and field studies have highlighted considerable uncertainty in the response of different ecosystems to climate change. Although our understanding of these responses has improved, there are still gaps in our knowledge of terrestrial ecosystem processes [Schimel *et al.*, 2001]. In one of the first coupled atmosphere-biosphere climate models, Cox *et al.* [2000] predict that changes in terrestrial ecosystem carbon cycling as a result of climate

warming will in turn contribute to increased concentrations of CO<sub>2</sub> in the atmosphere. Specifically, they predict that terrestrial ecosystems will switch from C sinks to sources in the next 50 years due to a greater increase in respiration relative to photosynthesis. This result is dependent on the long-term sensitivity of soil respiration to climate warming, a topic which is currently under debate [Melillo *et al.*, 2002; Grace and Rayment, 2000]. There is also uncertainty as to whether photosynthesis and respiration, the two components of net ecosystem exchange of CO<sub>2</sub> (NEE), will be affected equally by climate change. Recent studies have shown that plant production, temperature, and moisture are all important predictors of ecosystem respiration across

latitudinal gradients [Janssens *et al.*, 2001; Oechel *et al.*, 1995; Raich and Schlesinger, 1992]. Climate change scenarios predict both warmer and drier conditions in the northern midlatitudes [Gregory *et al.*, 1997]. Hanson and Weltzin [2000] reviewed the potential impacts of drought on forested ecosystems and concluded that significant changes to net primary production (NPP) and decomposition will occur. Wetlands were not included in their study, however, and it is likely that wetlands will respond differently to drought than upland forests.

[3] Northern peatlands have sequestered vast stores of soil carbon since deglaciation [ $\sim 100$  kg C m<sup>-2</sup>; Turunen *et al.*, 2002] and account for approximately one third of the global pool of soil carbon [Gorham, 1991]. Yet these ecosystems have low rates of production compared with upland ecosystems [Frolking *et al.*, 1998] and even lower rates of decomposition [Moore *et al.*, 1998]. Although they have been persistent long-term sinks of C, the annual rate of accumulation is extremely small [10–30 g C m<sup>-2</sup>; Turunen *et al.*, 2002; Gorham, 1991], interannual variability is high [Lafleur *et al.*, 2001a, 2001b; Griffis *et al.*, 2000] and they may switch from sinks to sources on short timescales with small changes in the moisture balance [Aurela *et al.*, 2001; Alm *et al.*, 1999; Joiner *et al.*, 1999; Shurpali *et al.*, 1995; Oechel *et al.*, 1993]. Even within peatlands, different plant communities may be sinks or sources within the same year [Waddington and Roulet, 1996]. Decomposition is sensitive to changes in the water balance because rates of CO<sub>2</sub> emission are significantly faster in the aerated portion of the peat profile above the water table [Frolking *et al.*, 2001; Whiting and Chanton, 2001; Scanlon and Moore, 2000; Silvola *et al.*, 1996a]. However, a lower water table may also enhance plant production by expanding the zone of aeration for roots. In a long-term study of drained peatlands, Laine and Minkinen [1996] found that peatlands sequester more C after long-term water table lowering because of an increase in litter and fine root production of trees. However, this result may not apply to peatlands without trees [Alm *et al.*, 1999]. When water table is included in experimental manipulations, it is often a more important control than temperature on CO<sub>2</sub> exchange [Johnson *et al.*, 1996]. Peatland carbon models indicate that changes in the water table affect both plant production and decomposition [Frolking *et al.*, 2002; Wieder, 2001; Hilbert *et al.*, 2000].

[4] Evergreen and deciduous shrubs, sedges, and mosses are common plant forms in peatlands as well as in other nutrient-poor boreal, subarctic and arctic ecosystems. Climate and ecosystem models predict that the distribution of plant functional types or growth forms will change in response to climate with an increase in deciduous species and a decrease in evergreen plant forms [Kittel *et al.*, 2000]. Other studies have shown that plant types respond differently to warming and nutrient applications through differences in CO<sub>2</sub> exchange, plant production and allocation, phenology, nutrient absorption, and litter decomposition [Shaver and Jonasson, 1999; Chapin and Shaver, 1996; Jonasson *et al.*, 1999; Hobbie, 1996]. These responses occur on a variety of timescales, however, which is important for modeling [Shaver *et al.*, 2000]. In addition, there is evidence that growth forms respond differently to changes

in the moisture balance with evergreen shrubs being more resilient to drought than sedges [Bubier *et al.*, 2003; Weltzin *et al.*, 2000; Busch and Losch, 1999; Small, 1972a, 1972b].

[5] Most chamber studies measure NEE on a weekly to biweekly timescale. In order to capture the short-term responses of peatlands to changes in temperature and precipitation, we used automatic chambers that sample every 3 hours over the diurnal cycle. Micrometeorological measurements of peatland CO<sub>2</sub> exchange show the importance of continuous measurements for understanding the C balance [Lafleur *et al.*, 2001a, 2001b, 2003]. Also, process-oriented ecosystem models require measurements with high temporal frequency for testing and validation [Frolking *et al.*, 2002]. The purposes of this study were to (1) compare NEE across a range of plant communities in two climatically different growing seasons; (2) to assess the impact of drought conditions on different plant functional types (graminoid, evergreen shrub, deciduous shrub, and *Sphagnum* moss); and (3) to measure NEE at high temporal frequency to improve our understanding of environmental controls on the exchange of CO<sub>2</sub> between peatland ecosystems and the atmosphere.

## 2. Methods

### 2.1. Site Description

[6] Sallies Fen is a mineral poor, *Sphagnum*-dominated peatland located in southeastern New Hampshire (43°12.5'N, 71°03.5'W). Gas exchange studies at this 1.7 ha fen have been ongoing since 1989 focusing on growing season exchange of CH<sub>4</sub> and CO<sub>2</sub> [e.g., Carroll and Crill, 1997; Frolking and Crill, 1994] and winter fluxes of CH<sub>4</sub> [Melloh and Crill, 1995, 1996] and CO<sub>2</sub> [Bubier *et al.*, 2002]. The fen surface is dominated primarily by *Sphagnum* mosses (e.g., *Sphagnum fallax* and *Sphagnum magellanicum*). The overall fen complex has a nutrient and hydraulic gradient of minerotrophic wet edges to an oligotrophic central area with pH ranging from 4.2 to 5.7 and peat depth ranging from 2 to 4.5 m [Melloh and Crill, 1996]. Sedges (*Carex rostrata* Stokes) dominate the plant communities in the wetter portions of the fen, while ericaceous shrubs, such as leatherleaf (*Chamaedaphne calyculata* (L.) Moench) and cranberry (*Vaccinium oxycoccus* L.) dominate the drier areas. Red maple (*Acer rubrum* L.) is common along the margins of the fen, while speckled alder (*Alnus incana* (L.) Moench ssp. *rugosa*) and highbush blueberry (*Vaccinium corymbosum* L.) are interspersed throughout the fen. Chambers were placed along plant community gradients to sample all dominant species and ranges of biomass among representative plant functional types (Table 1).

### 2.2. NEE Measurements

[7] In May 2000, 10 automatic chambers and an associated control system were installed approximately 10 m from the lagg entrance to the fen, and have been operational since June 2000. Chambers are 45.7 × 45.7 cm at the base and either 34 or 68 cm tall depending on the height of the vegetation. Each chamber is anchored at five points to wood strapping that was driven into the silt or sand below the peat surface. The chambers are attached to the control box

**Table 1.** Dominant and Codominant Vascular Plant Species, Aboveground Total and Foliar Vascular Plant Biomass ( $\text{g m}^{-2}$ ), and Average Summer Water Table Position (cm Below Peat Surface) for 2000 and 2001<sup>a</sup>

Chamber	Vascular Plant Species	Total Biomass, %	Foliar Biomass, %	Total AG Biomass	Total Foliar Biomass	Water Table (2000)	Water Table (2001)
1	<i>Carex rostrata</i>	26	62	268	110	11.1	14.0
	<i>Vaccinium oxycoccus</i>	58	17				
2	<i>Carex rostrata</i>	25	40	313	198	12.4	17.5
	<i>Chamaedaphne calyculata</i>	46	38				
	<i>Vaccinium oxycoccus</i>	19	17				
3	<i>Chamaedaphne calyculata</i>	64	74	1018	504	16.5	20.6
	<i>Vaccinium corymbosum</i>	31	22				
	<i>Carex rostrata</i>	27	39				
4	<i>Vaccinium oxycoccus</i>	29	23	238	163	14.2	18.6
	<i>Chamaedaphne calyculata</i>	33	23				
	<i>Carex rostrata</i>	24	39				
5	<i>Vaccinium oxycoccus</i>	13	11	254	151	6.2	10.1
	<i>Alnus rugosa</i>	66	54				
	<i>Chamaedaphne calyculata</i>	28	34				
7	<i>Chamaedaphne calyculata</i>	80	82	421	231	12.0	15.1
	<i>Carex rostrata</i>	7	12				
	<i>Acer rubrum</i>	11	5				
8	<i>Vaccinium oxycoccus</i>	50	45	174	94	1.2	4.8
	<i>Carex rostrata</i>	29	52				
	<i>Chamaedaphne calyculata</i>	11	3				
9	<i>Carex rostrata</i>	26	43	197	118	15.3	18.9
	<i>Chamaedaphne calyculata</i>	43	35				
	<i>Vaccinium oxycoccus</i>	16	14				
10	<i>Chamaedaphne calyculata</i>	52	46	136	71	9.3	13.3
	<i>Carex rostrata</i>	24	45				

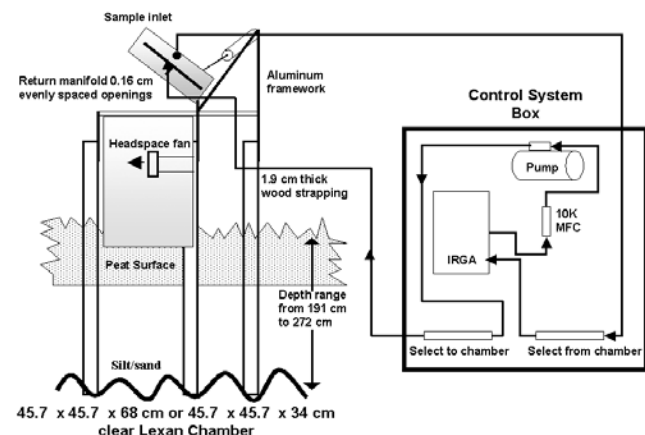
<sup>a</sup>Dominant species representing major functional plant groups include *Chamaedaphne calyculata* (leatherleaf) for evergreen shrub, *Alnus rugosa* (alder) for deciduous shrub, and *Carex rostrata* for sedge/graminoid.

sampling manifold (Action Automation, North Attleboro, MA) with 3/8" (0.95 cm) OD high density polyethylene (Read Plastics, Rockville, MD) tubing (Figure 1). Chambers are within a 20-m radius of the control box, in order to minimize the length of tubing attached to each chamber.

[8] The chambers were constructed out of 2.54 cm aluminum channel and angle, and 0.31 cm thick polycarbonate lexan at the University of New Hampshire Space Science Machine shop. The lexan lid is 15.3 cm  $\times$  45.7 cm  $\times$  45.7 cm and is motivated by a 20.3-cm stroke double-acting pneumatic cylinder (Clippard Minimatic, Cincinnati, OH). A 2.54 cm  $\times$  46 cm  $\times$  46 cm trough built into the chamber framework receives the lid during a sampling run to ensure an adequate seal. The lexan chamber walls or skirts are 40.6  $\times$  15.3 cm each and fastened below the trough framework; two skirts can be used on top of each other doubling the total chamber height above the peat surface (Figure 1; for more specific details of the system design and operation, please contact P. Crill, Complex Systems Research Center, University of New Hampshire; patrick.crill@unh.edu).

[9] The automatic CO<sub>2</sub> exchange control and analysis system at Sallies Fen is similar in design to one used by *Goulden and Crill* [1997] at a black spruce forest in central Manitoba. The chamber design is based on those used in Costa Rica studies [e.g., *Crill et al.*, 2000], although the chambers in this study are transparent and much larger to enclose a taller canopy. Line power is provided from a nearby residential house and the total consumption for the system is  $\sim$ 1.150 kW at 115 V AC. The air supply for the pneumatics is provided by a small air compressor (GAST

Manufacturing Inc., Bridgman, MI). Air from each chamber is pulled continuously by a diaphragm pump (KNF Neuberger, Inc., Trenton, NJ) through a CO<sub>2</sub> infrared gas analyzer in absolute mode (IRGA, Model 6252, LiCor, Inc., Lincoln NE). The flow through the system is controlled by a mass flow controller (MKS Instruments, Andover, MA) at 5 l m<sup>-1</sup> (Figure 1). Inflow and outflow rates were balanced in the chambers and internal pressure dynamics were examined with a micromanometer. Chamber closure produced a transitory spike of less than 10 Pa that decayed within 2 s to a condition of no detectable pressure differential between the outside and inside of the chambers.

**Figure 1.** Autochamber and control system diagram.

The pressure within the sample cell of the IRGA is a good indicator of tubing blockage. Large internal diameter tubing (0.64 cm) is used to minimize water entrainment into the airstream as well as to allow for uniform airflow back to detector [Goulden and Crill, 1997]. A 12 V brushless muffin fan (NMB, Minebea Co. Ltd., Thailand) with a flow rate of 708–1301 l min<sup>-1</sup> is used to mix the chamber head space during lid closure and to induce transverse winds that may be prevented by the high chamber walls. There were no noticeable temperature increases in the chamber after lid closure due to the internal 12 V fans.

[10] A weather tight box containing three control boards opens and closes each of the 10 chambers every 3 hours. An individual chamber is selected every 18 min. The first 9 min flushes the tubing, clearing the sample line of previous air artifacts. At 10 min the lid closes, CO<sub>2</sub> concentration is sampled every 3 s and averaged every 30 s. Since CO<sub>2</sub> within the chamber can become saturated, the initial five points (30 s mean CO<sub>2</sub> concentration × 5 = 2.5 min) of this trace are used to calculate a flux with a slope and  $r^2$  of the linear increase or decrease in CO<sub>2</sub> concentration over the sampling period. Four fluxes are calculated using the first five 30 s mean CO<sub>2</sub> concentrations, then the second five, third five, and fourth five. In choosing the best of these four fluxes, the highest  $r^2$  value determines CO<sub>2</sub> efflux and the steepest decreasing slope determines the CO<sub>2</sub> uptake. Usually, the first five 30 s means are used for the 2.5 min flux, but occasionally a subsequent set yields a stronger  $r^2$  or slope. The reason for treating CO<sub>2</sub> uptake differently from release is that plants saturate very quickly at high light and by choosing the steepest slope, we were assuring that the most accurate CO<sub>2</sub> uptake rates were chosen. At night, photosynthesis is not occurring so the highest  $r^2$  ensures that flux represents the increase in CO<sub>2</sub> concentration over time that is closest to linear. All fluxes (positive or negative) with  $r^2 < 0.87$  (minimum necessary for 95% confidence limits) were eliminated; low  $r^2$  often occurred in early morning when condensation in the chamber inhibited some light transmission. Other reasons for filtering data included pneumatic line seizure and intermittent power outages. Approximately, 17% of the measured data from June through September in both years were not included in the final filtered data set after quality checking fluxes. Data acquisition and mechanical control were performed by a CR10X data logger (Campbell Scientific, Logan, UT). The data were transferred to a SM4M storage module (Campbell Scientific, Logan, UT), which was then downloaded to a computer every 4–7 days for processing.

### 2.3. Environmental Variables

[11] Surface peat temperature and internal chamber air temperature were measured at each chamber with type-T thermocouples (Omega Engineering, Stamford, CT). Photon flux density was measured with gallium arsenide phosphide photodiode (Hamamatsu, Bridgewater, NJ) at three locations representing the range of light conditions. In addition, two quantum sensors (LiCor, Inc., Lincoln, NE) measured photosynthetically active radiation (PAR), one associated with the permanent meteorological station in the center of the fen, and the other near the automatic chamber control

system. The ancillary chamber temperatures, flows, and photon fluxes were sampled every 3 s and averaged every 9 min. The meteorological station sampled air and peat temperature at several depths (every 2 cm below the peat surface to -20 cm, then at -25, -30, -50, -70, and -90 cm), water table position, relative humidity, barometric pressure, PAR, net radiation, and precipitation every minute; hourly averages and total precipitation were recorded every hour. The position of the water table relative to the peat surface for each chamber location was determined by measuring the height of the peat surface above the water table at the nearest well using a tube-leveling device.

### 2.4. Climate

[12] Monthly and seasonal air temperature and precipitation data from Epping, NH, 16 km south of Sallie's Fen but equidistant from the coast, show that the summer of 2001 was significantly drier and slightly warmer than summer 2000 (Table 2). June through September 2001 had 277 mm of total precipitation, 74 mm less than the 30-year mean of 351 mm. By the end of July 2001, southern New Hampshire was in a moderate drought according to the Palmer Drought Index, and in severe drought by mid-September. Conversely, the same period in 2000 was 59 mm wetter than normal with 410 mm of precipitation. The largest differences occurred in July when 2000 was 71 mm wetter than normal and 2001 was 30 mm drier than normal; and in August when 2000 had close to normal precipitation, but 2001 precipitation was 42 mm lower than normal. The differences in precipitation resulted in a 10-cm lower water table in 2001 by the end of the summer. The water table in the first half of the 2001 summer, however, was 5 cm higher than in 2000. Summer 2001 was 1.1°C warmer than normal with 19.7°C average air temperature compared with 18.2°C in 2000. July of both years was cooler than the 30-year mean by more than 1°C.

### 2.5. Vegetation

[13] Aboveground biomass of vascular plants in each chamber was determined by clipping all stems and leaves aboveground in six plots with a similar range of species composition and biomass as the autochambers. Plants were separated into stems and leaves by species, then dried and weighed at 60°C for 24–48 hours. Before clipping, each stem in the clipped plots and autochambers was counted and measured for height above the peat surface. Allometric equations using stem number, stem height, and biomass were developed for each functional group and major species in the clipped plots. Aboveground vascular plant total and foliar biomass in the autochambers were predicted from these equations. Phenology measurements were made in both growing seasons by counting numbers of new and old leaves every 1–2 weeks, and measuring leaf and branch length of 3–10 plants of each major species with 5 branches per plant. Plant functional types [Chapin *et al.*, 1996a] are more useful than individual species to vegetation and climate modeling groups in order to simplify ecosystem models and to predict responses of plants to global climate change [Kittel *et al.*, 2000]. Dominant species representing major plant functional types in this study include *Chamae-*

**Table 2.** Monthly Air Temperature and Total Precipitation Data for June Through September 2000 and 2001<sup>a</sup>

	Average Maximum $T$ , °C	Average Minimum $T$ , °C	Average $T$ , °C	Departure From Normal $T$ , °C	Precipitation, mm	Departure From Normal Precipitation, mm
June 2000	24.61	12.28	18.44	0.28	86	-7
June 2001	26.67	13.17	19.89	1.72	112	19
Normal	25.50	10.89	18.17		93	
July 2000	25.33	13.28	19.28	-1.67	160	71
July 2001	26.72	13.00	19.83	-1.11	59	-30
Normal	28.11	13.78	20.94		89	
Aug. 2000	25.72	13.61	19.67	-0.22	84	2
Aug. 2001	28.78	15.50	22.17	2.28	40	-42
Normal	26.89	12.83	19.89		82	
Sept. 2000	22.06	8.89	15.50	0.17	80	-6
Sept. 2001	23.89	9.78	16.83	1.50	65	-21
Normal	22.56	8.11	15.33		86	
4 months average 2000	24.43	12.01	18.22	-0.36	410	59
4 months average 2001	26.51	12.86	19.68	1.10	277	-74
4 months normal	25.76	11.40	18.58		351	

<sup>a</sup>Data are for Epping, NH, 16 km south of Sallie's Fen, NH. Barry Keim, NH State Climatologist. Normal and departure from normal refers to the 30-year mean for the period 1970–2000.

*daphne calyculata* (leatherleaf) for evergreen shrub, *Alnus incana* ssp. *rugosa* (speckled alder) for deciduous shrub, *C. rostrata* for sedge/graminoid, and *Sphagnum* moss for peat-forming nonvascular plants. Six chambers were chosen to focus the analyses because each of these chambers was dominated by one of the main plant functional types or growth forms (evergreen or deciduous shrub, sedge, or *Sphagnum*). The other four chambers that were not analyzed in detail showed similar patterns, but were not as clearly dominated by one plant type.

## 2.6. Data Analyses

[14] The relationship between NEE and PAR was described by a rectangular hyperbola using a curve-fitting technique [Thornley and Johnson, 1990]:

$$NEE = \frac{GP_{\max} \alpha PAR}{\alpha PAR + GP_{\max}} + R, \quad (1)$$

where alpha ( $\alpha$ ) is the initial slope of the rectangular hyperbola at low light levels (also called the apparent quantum yield),  $GP_{\max}$  is the asymptotic approach to a maximum productivity at high light levels, and  $R$  is the  $y$  axis intercept (or dark respiration value,  $R < 0$ ). Since most plant communities saturate at  $PAR > 1000 \mu\text{mol photon m}^{-2} \text{s}^{-1}$ , and  $GP_{\max}$  assumes an infinite upper limit for PAR, we calculated the average rate of NEE for each chamber for  $PAR > 1000 \mu\text{mol photon m}^{-2} \text{s}^{-1}$  ( $NEE_{\max}$ ) in order to compare the maximum rates of  $\text{CO}_2$  uptake at actual maximum PAR values for each plant community. We adopted the sign convention of  $\text{CO}_2$  uptake by the ecosystem as positive and  $\text{CO}_2$  emission to the atmosphere from respiration as negative. At night, chambers measured ecosystem respiration (total of enclosed plant stems, leaves, roots, and soil microbes). Nighttime respiration was consistent with temperature corrected daytime dark chamber fluxes (E. H. Burrows et al., unpublished data, 2002).

[15] Relationships among NEE and measured environmental variables were analyzed using the statistical software JMP-IN version 4.0.3 [SAS Institute, 2001]. In an initial

analysis of the nighttime NEE data, trends in differences between years were examined by analyzing the differences in NEE of corresponding days of the 2 years. Such a pairing essentially corrects for factors that are mainly driven by seasonal fluctuation. The mean of the pairwise differences was significantly different from zero (paired  $t$ -test). Significance was further increased when correlations between adjacent daily differences was corrected for by fitting an autoregressive-moving average (ARMA) [Shumway and Stoffer, 2000, chap. 2] model to the differences. The main analysis of nighttime  $\text{CO}_2$  flux data in this paper consisted of stepwise linear regression to develop empirical models to explain the trends in nighttime respiration using water table depth, air, and peat temperature (maximum, minimum, and mean) as the explanatory variables.

## 3. Results

### 3.1. Spatial and Seasonal Variability Among Plant Functional Types

[16] Figure 2 shows the diurnal pattern and spatial variability in NEE among six autochambers representing the range of plant communities and biomass at the fen. Although there was a similar diurnal pattern among all chambers with maximum uptake occurring between 1000 and 1600 hours and maximum emission between 0000 and 0400 hours, the ranges of maximum uptake varied from 12 to 5  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  and the maximum nighttime emissions ranged from -5 to -12  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ . Differences in maximum NEE correlated with aboveground vascular plant foliar biomass in each chamber ( $r^2 = 0.79$ ;  $p < 0.05$ ), which also varied by plant species composition (Tables 1, 3, and 4). Autochambers with large evergreen (e.g., ch. 3) or deciduous (ch. 6) shrubs generally had larger rates of NEE than chambers with smaller biomass of sedge or shrub (e.g., ch. 7, 8, and 9). All chambers had a 90–100% ground cover of *Sphagnum* moss beneath the vascular plant canopy, but ch. 8 had the least amount of vascular plant biomass (Table 1), so it was labeled as primarily a *Sphagnum* chamber.

**Table 3.** Estimated July–August  $NEE_{max}$  and Respiration Rates Per Unit Foliar Biomass, Based on Flux Data and Vegetation Composition of Three Chambers (3, 4, and 6)<sup>a</sup>

Vegetation Class	$NEE_{max}$ , $\mu\text{mol g}^{-1} \text{s}^{-1}$		Respiration, $\mu\text{mol g}^{-1} \text{s}^{-1}$	
	2000	2001	2000	2001
Sedge/herb	0.045	0.046	-0.022	-0.032
Deciduous shrub	0.019	0.031	-0.011	-0.008
Evergreen shrub	0.015	0.016	-0.007	-0.015

<sup>a</sup>See text for details. These parameters were multiplied by foliar biomass (Table 1) to generate estimates for the other chambers (Figure 3). Coefficients are listed for each vegetation class and year (2000 and 2001).

[17] To explore the role of vegetation type and biomass in determining chamber NEE, and to test the replication among chambers based on their shared component vegetation, we chose one chamber dominated by each of the three main vascular plant types, deciduous shrub (ds, ch. 6), evergreen shrub (es, ch. 3), and sedge/herb (sh, ch. 4). For these three chambers, we set mean July and August NEE at high light ( $\langle NEE \rangle$ ;  $PAR > 1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) equal to the sum of a parameter times the foliar biomass,  $F$ , of each plant type, as follows:

$$\langle NEE \rangle_i = aF_{ds,i} + bF_{es,i} + cF_{sh,i}, \quad (2)$$

where the subscript  $i$  denotes the chamber, and  $a$ ,  $b$ , and  $c$  are fitted parameters ( $\mu\text{mol CO}_2 \text{ g}^{-1} \text{s}^{-1}$ ), and the  $F$ s are the foliar biomasses in chamber  $i$  ( $\text{g m}^{-2}$ ). With three chambers, this gives three equations, which were solved analytically for the three parameter values. These parameter values, representing NEE per unit foliar biomass for each vegetation type, were then applied to the other seven chambers to estimate  $\langle NEE \rangle_i$  for comparison with the field data.

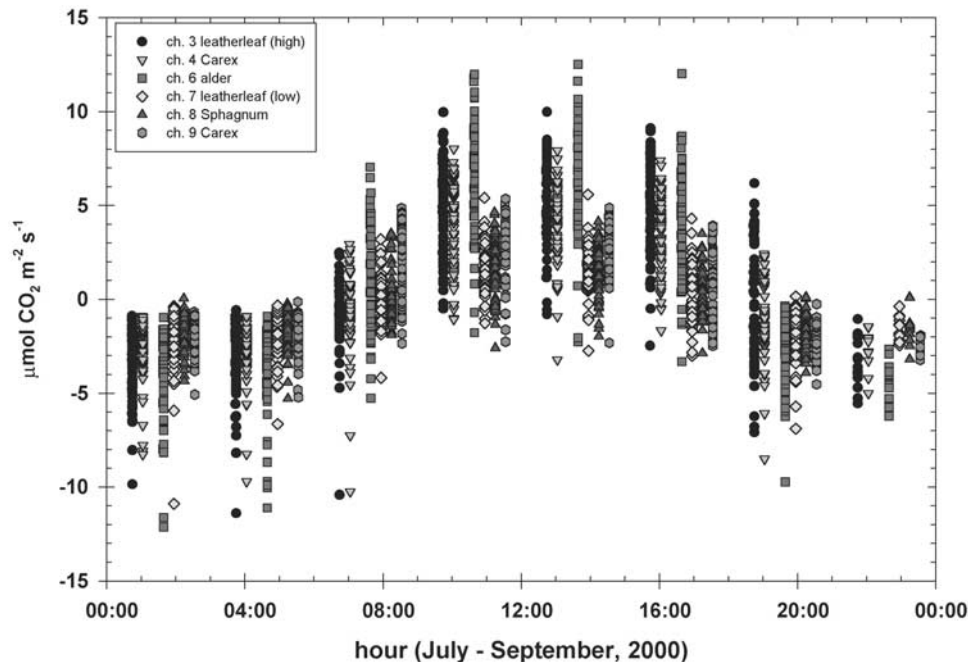
[18] Maximum NEE and respiration rates per unit biomass calculated with data from chambers 3, 4, and 6 were different for the three vegetation types (coefficients listed in Table 3). For example, maximum NEE rates for 2001 are sedge/herb =  $0.046 \mu\text{mol s}^{-1} \text{g}^{-1} >$  deciduous shrub =  $0.031 \mu\text{mol s}^{-1} \text{g}^{-1} >$  evergreen shrub =  $0.016 \mu\text{mol s}^{-1} \text{g}^{-1}$ ). This ordering of vegetation types (sedge  $>$  deciduous shrub  $>$  evergreen shrub) has also been noted for photosynthetic rates for these three growth forms [e.g., *Chapin and Shaver*, 1996; *Semikhatova et al.*, 1992; *Small*, 1972a, 1972b]. Although coefficients varied between years, the vegetation types were ranked in the same order for both maximum NEE and respiration, with the exception of 2001 respiration where evergreen shrub had a higher (more negative) coefficient than deciduous shrub (Table 3).

[19] Prediction of mean July and August 2001 chamber NEE at high light using these coefficients for different vegetation types was good for five chambers (ch. 1, 2, 8, 9,

**Table 4.** Nonlinear Parameter Estimates for  $GP_{max}$ , Alpha ( $\alpha$ ), and Nighttime Respiration by Month, and Mean Monthly Values for  $NEE_{max}$  for Chambers Representing Dominant Plant Species<sup>a</sup>

Chamber	July 2000	Aug. 2000	Sept. 2000	July 2001	Aug. 2001	Sept. 2001
<i>GP<sub>max</sub></i>						
3	14.79 (0.52)	14.59 (0.75)	15.24 (1.44)	20.66 (0.92)	25.59 (1.64)	20.79 (1.19)
4	12.51 (0.35)	10.60 (0.54)	8.26 (0.66)	13.06 (0.53)	15.93 (0.67)	12.72 (0.77)
6	15.08 (0.46)	16.31 (0.69)	12.62 (0.85)	21.29 (0.56)	23.57 (0.77)	18.71 (0.99)
7	6.84 (0.39)	5.96 (0.51)	4.18 (0.64)	7.74 (0.38)	9.59 (0.64)	7.39 (1.17)
8	6.63 (0.40)	5.56 (0.34)	2.58 (0.33)	7.34 (0.42)	9.59 (1.22)	3.37 (0.88)
9	8.58 (0.25)	6.29 (0.31)	7.59 (0.61)	9.56 (0.43)	11.52 (0.72)	6.79 (1.02)
<i>Alpha (<math>\alpha</math>)</i>						
3	0.062 (0.007)	0.048 (0.007)	0.038 (0.007)	0.080 (0.010)	0.080 (0.011)	0.074 (0.009)
4	0.041 (0.003)	0.029 (0.004)	0.055 (0.016)	0.036 (0.004)	0.045 (0.007)	0.050 (0.007)
6	0.094 (0.009)	0.082 (0.011)	0.117 (0.028)	0.084 (0.007)	0.106 (0.010)	0.084 (0.011)
7	0.016 (0.002)	0.020 (0.004)	0.021 (0.008)	0.004 (0.006)	0.053 (0.010)	0.027 (0.008)
8	0.017 (0.003)	0.015 (0.002)	0.022 (0.009)	0.019 (0.002)	0.014 (0.002)	0.013 (0.007)
9	0.059 (0.007)	0.093 (0.022)	0.026 (0.004)	0.035 (0.004)	0.034 (0.004)	0.084 (0.067)
<i>Respiration</i>						
3	-3.99 (0.19)	-3.89 (0.19)	-3.42 (0.30)	-6.35 (0.32)	-7.50 (0.40)	-4.05 (0.18)
4	-3.26 (0.13)	-2.83 (0.10)	-3.42 (0.34)	-2.62 (0.12)	-6.52 (0.29)	-4.48 (0.20)
6	-4.75 (0.19)	-4.53 (0.19)	-4.52 (0.27)	-4.45 (0.14)	-6.99 (0.17)	-4.17 (0.26)
7	-2.46 (0.13)	-2.68 (0.16)	-2.27 (0.22)	-3.30 (0.19)	-5.19 (0.26)	-5.06 (0.24)
8	-2.52 (0.13)	-2.02 (0.09)	-1.78 (0.14)	-1.47 (0.05)	-2.61 (0.09)	-3.01 (0.19)
9	-2.67 (0.07)	-2.35 (0.06)	-2.35 (0.13)	-2.70 (0.10)	-4.41 (0.15)	-2.78 (0.15)
<i>NEE<sub>max</sub></i>						
3	8.28 (0.32)	8.17 (0.36)	7.79 (0.36)	9.95 (0.37)	10.64 (0.42)	10.81 (0.67)
4	6.99 (0.13)	5.47 (0.27)	3.21 (0.46)	7.01 (0.16)	5.77 (0.17)	5.21 (0.15)
6	8.19 (0.35)	9.80 (0.45)	8.90 (0.82)	12.60 (0.39)	12.27 (0.52)	9.67 (0.63)
7	2.56 (0.14)	2.03 (0.16)	1.82 (0.28)	3.20 (0.11)	2.78 (0.19)	1.69 (0.26)
8	2.74 (0.22)	2.48 (0.21)	0.54 (0.31)	4.27 (0.11)	3.48 (0.17)	-0.12 (0.43)
9	5.35 (0.12)	4.51 (0.30)	3.36 (0.34)	5.18 (0.16)	4.29 (0.15)	5.67 (0.23)

<sup>a</sup> $NEE_{max}$  is in  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$ . Chambers 3 and 7 are dominated by leatherleaf, chamber 6 by alder, chambers 4 and 9 by sedge, and chamber 8 by *Sphagnum*. Standard errors are in parentheses. Sample size ranges from 150 to 250 for each chamber/month for  $GP_{max}$ , alpha and respiration, and from 15 to 60 for each chamber/month for  $NEE_{max}$  (defined as NEE at PAR values  $> 1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ ).



**Figure 2.** Variation in NEE of six representative autochambers by hour of day in summer 2000 based on the range of dominant plant species and biomass found at the fen. High and low refer to vascular plant biomass (see Table 1).

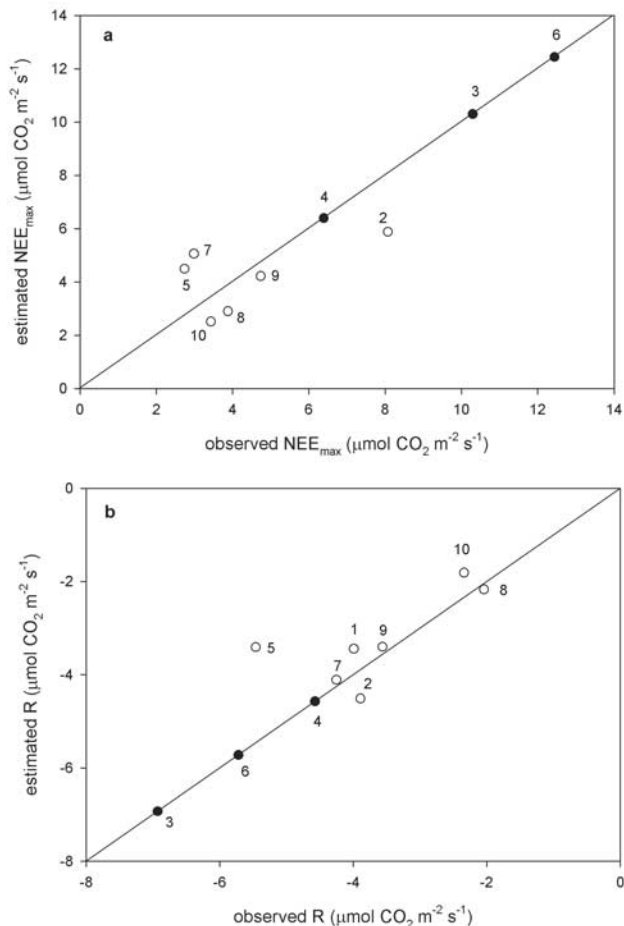
and 10) and high for two chambers (ch. 5 and 7) (Figure 3), while predicted respiration rates were good for all chambers except ch. 5. Similar results were seen for July and August 2000. This suggests that component analysis can be used to predict NEE of chambers composed of different ranges of biomass of representative vegetation types. The deviation from the 1:1 line is an indication of variability in NEE attributed to factors other than foliar biomass.

### 3.2. Differences in NEE and Respiration Between Years

[20] Not only were there differences among plant communities in their range of NEE over the diurnal cycle and across a gradient of foliar biomass, but the seasonal and interannual patterns varied as well. A comparison of NEE during two climatically different summers for each major plant community shows that each dominant vascular plant growth form (sedge, evergreen, or deciduous shrub) responded differently to varying moisture conditions. Chambers dominated by leatherleaf and alder had higher rates of CO<sub>2</sub> uptake and release during the drier summer of 2001 compared with the wetter 2000 summer (Figure 4). The relationship between NEE and PAR shows that nighttime values were significantly larger (more negative) in 2001 and that the ecosystem had higher rates of uptake at all light levels above PAR of 500 μmol photon m<sup>-2</sup> s<sup>-1</sup> (Figure 4a). Although early season rates of NEE were similar between the two summers, leatherleaf chambers showed higher rates of uptake from about day 180 until the end of the summer, and higher rates of respiration especially in the midsummer (days 180–240; Figure 4b).

[21] *Carex* showed a different pattern of maximum CO<sub>2</sub> uptake from the shrubs between years, but similar respiration patterns. Unlike the shrub-dominated chambers, there was no difference in maximum CO<sub>2</sub> uptake for *Carex* chambers between the wet and dry summers (Figure 5). The different seasonal and interannual patterns of CO<sub>2</sub> uptake among the three functional plant types reflect differences in plant physiology and adaptations to moisture or drought stress. Phenology data for the two summers show that alder produced more leaves in the drier summer (Figure 6a), while *C. rostrata* produced less green leaf tissue (Figure 6b) and fewer leaves (data not shown) in the same dry period. This compares with the NEE data showing higher rates of CO<sub>2</sub> uptake for alder, but no difference for *Carex* in the drier summer (Figures 4 and 5, and Table 4). The larger respiration rates for *Carex* in the mid-late summer of 2001 compared with summer 2000, however, correspond with a similar pattern for the shrubs, except that maximum respiration occurred later in the season (days 215–240) for *Carex* (Figure 5b). In addition to the late summer drought, the timing of root development could also explain the seasonal respiration patterns. Evergreens begin their root growth simultaneously with the onset of leaf growth, while root growth is delayed in sedges until the roots are thawed to a depth of 10–25 cm [Shaver and Kummerow, 1992].

[22] Curve fitting a rectangular hyperbola to the seasonal NEE versus PAR data (Figures 4a–5a) shows that all chambers had larger parameter estimates (GP<sub>max</sub>, α, R) on average in 2001 (Table 4). However, leatherleaf chambers showed a larger increase in α between years (chs. 3, 7) than *Carex* (chs. 4, 9) or alder (ch. 6), particularly during August



**Figure 3.** Estimated chamber (a) maximum NEE and (b) respiration based on vascular plant foliar biomass. Data from three chambers (3, 4, and 6; solid circles on the 1:1 line) were used to determine three coefficients (see Table 3) relating foliar biomass for three vegetation classes (deciduous shrub, evergreen shrub, and sedge/herb) to mean, midsummer (July and August), midday ( $\text{PAR} > 1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) NEE and respiration. These parameters were then multiplied by foliar biomass data (Table 1) to generate estimated NEE values for the other seven chambers (open circles). All points are labeled by their chamber number and data for 2001 are shown.

and September, the period when respiration was also largest for all chambers in 2001 (Table 4). All the shrub-dominated chambers had larger increases in  $\text{GP}_{\text{max}}$  in 2001 compared with the sedge-dominated chambers (Table 4).

[23] Since  $\text{GP}_{\text{max}}$  is a theoretical limit to productivity at infinitely high light, the data were analyzed using maximum NEE at  $\text{PAR} > 1000 \mu\text{mol photon m}^{-2} \text{s}^{-1}$  ( $\text{NEE}_{\text{max}}$ ), the light level at which most plants saturate, but  $< 2000 \mu\text{mol photon m}^{-2} \text{s}^{-1}$ , the approximate maximum light level observed at the fen. Paired  $t$ -tests show that  $\text{NEE}_{\text{max}}$  was significantly higher in 2001 in all chambers except in the sedge chambers (ch. 4, 9), which were not significantly different between years. Respiration was significantly larger in the drier 2001 summer for all chambers, however (Figure 7, and Table 4). Given the fact that *Carex*

produced less green leaf tissue in 2001 (Figure 6b), one would expect maximum NEE to be lower in the sedge-dominated chambers in 2001, not the same. The explanation could be that the *Carex* chambers also contained a shrub component, particularly leatherleaf (Table 1), which had higher rates of NEE in the drier summer (Figures 4 and 7).

### 3.3. Environmental Controls on Ecosystem Respiration

[24] Respiration rates were significantly larger in the drier summer for all plant functional types. Paired  $t$ -tests of the annual differences of nighttime NEE of corresponding days were highly significant for all chambers (Figure 7;  $p < 0.0001$ ). Therefore a combined analysis of all 10 chambers was conducted to examine environmental controls across the suite of plant communities. Differences between years using pairwise-differenced series and by fitting ARMA models (to further correct for correlations in daily adjacent differences) and testing the null model of a zero mean difference were highly significant ( $p < 0.0001$ ). On average, differences were negative; hence the 2001 series were significantly lower than the 2000 series, predominantly due to the drought effect between mid-July and mid-September. Residuals from the AR (1) model did not have any temporal structure. The seasonal pattern of respiration for the two summers showed that the nighttime  $\text{CO}_2$  fluxes were similar between years until around day 210, the point where the water table between the 2 years diverged (Figures 8a and 8b). Prior to that day, the 2001 water table was higher than 2000, but dropped below the 2000 levels afterward and remained lower until the end of the summer. The seasonal pattern of nighttime air temperature appeared to be similar between years.

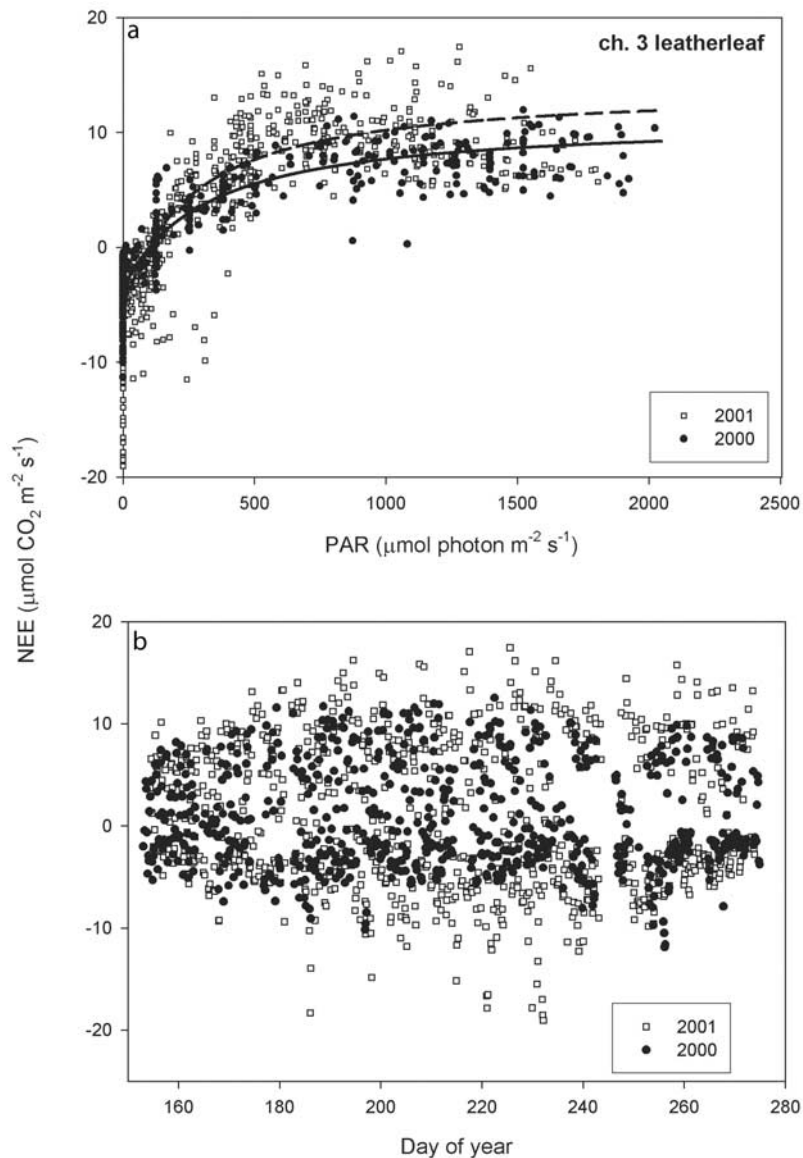
[25] Linear regressions between respiration, water table, and temperature show that both environmental factors were important in predicting nighttime  $\text{CO}_2$  flux. Stepwise linear regression using both water table and temperature (removing highly correlated variables) resulted in the following models for nighttime  $\text{CO}_2$  flux:

$$\begin{aligned} \text{Mean nighttime CO}_2 \text{ flux (2000)} &= 0.106\text{WT} \\ &- 0.266 \text{ Max Ground Temp} + 3.506 (r^2 = 0.75; p < 0.01) \end{aligned} \quad (3)$$

and

$$\begin{aligned} \text{Mean nighttime CO}_2 \text{ flux (2001)} &= 0.095\text{WT} \\ &- 0.221 \text{ Max Ground Temp} - 0.107 \text{ Mean Air Temp} \\ &+ 1.035 (r^2 = 0.75; p < 0.01). \end{aligned} \quad (4)$$

The two models are very similar with similar coefficients for both maximum ground temperature and water table; but maximum ground temperature was a stronger predictor in 2000, while maximum ground temperature plus mean air temperature was stronger in 2001. The intercept is higher in the 2000 model, reflecting the smaller fluxes in the wetter summer. But the relationships among  $\text{CO}_2$  flux, water table,



**Figure 4.** Chamber 3 (leatherleaf) (a) NEE versus PAR and (b) NEE by day of year showing larger rates of maximum NEE and respiration in 2001. This pattern is similar for alder (ch. 6).

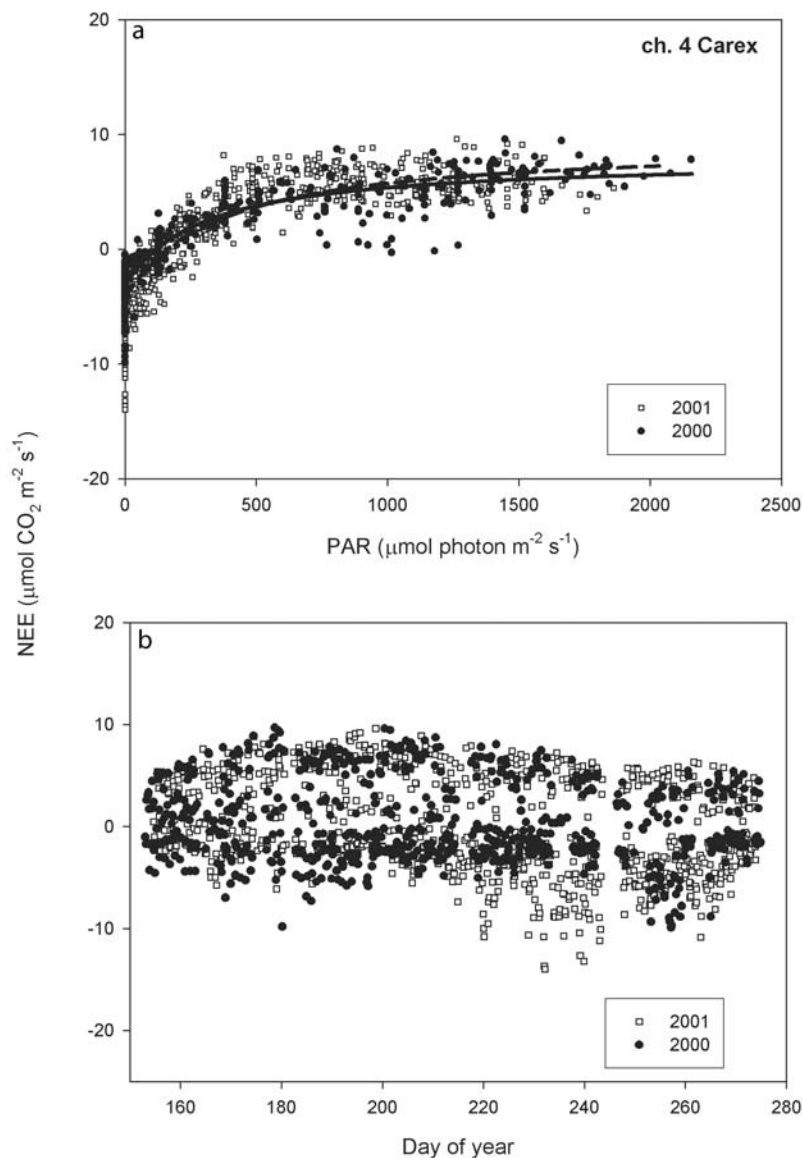
and temperature are similar for both summers in spite of different moisture conditions. Combining data for both years and fitting a combined model allowing for separate means (intercepts) yields the following:

$$\begin{aligned} \text{Mean nighttime CO}_2 \text{ flux} &= 1.948 \pm 0.558 \text{ (2000/2001)} \\ &+ 0.107\text{WT} - 0.146 \text{ Max Ground Temp} \\ &- 0.083 \text{ Mean Air Temp} \quad (r^2 = 0.75; p < 0.0001). \end{aligned} \quad (5)$$

### 3.4. Relationship Between Ecosystem Productivity and Respiration

[26] Although water table and temperature explained a significant portion of the variability in nighttime CO<sub>2</sub> flux, other factors contributed to ecosystem respiration. Since the

chambers vary in their species composition, biomass, and NEE, and various studies have shown that plant respiration is a significant component of ecosystem respiration [e.g., *Silvola et al.*, 1996a, 1996b], we examined the relationship between ecosystem productivity and respiration.  $\text{NEE}_{\text{max}}$  (NEE at PAR > 1000) was used for maximum ecosystem productivity. There are strong relationships between vascular plant foliar biomass and respiration (Figure 9a;  $r^2 = 0.71$  in 2000;  $r^2 = 0.67$  in 2001;  $p < 0.01$ ) and between mean  $\text{NEE}_{\text{max}}$  and mean respiration for both years (Figure 9b;  $r^2 = 0.83$  in 2000;  $r^2 = 0.39$  in 2001;  $p < 0.01$ ). This shows the importance of plant processes in addition to the effect of water table and temperature on respiration. However, since plant productivity ( $\text{NEE}_{\text{max}}$ ) was higher for shrub species in the drier summer, there is an interaction among water table, temperature, and plant processes. It is interesting to note



**Figure 5.** Chamber 4 (sedge) (a) NEE versus PAR and (b) NEE by day of year showing similar rates of maximum NEE between the two summers, but greater respiration rates in 2001.

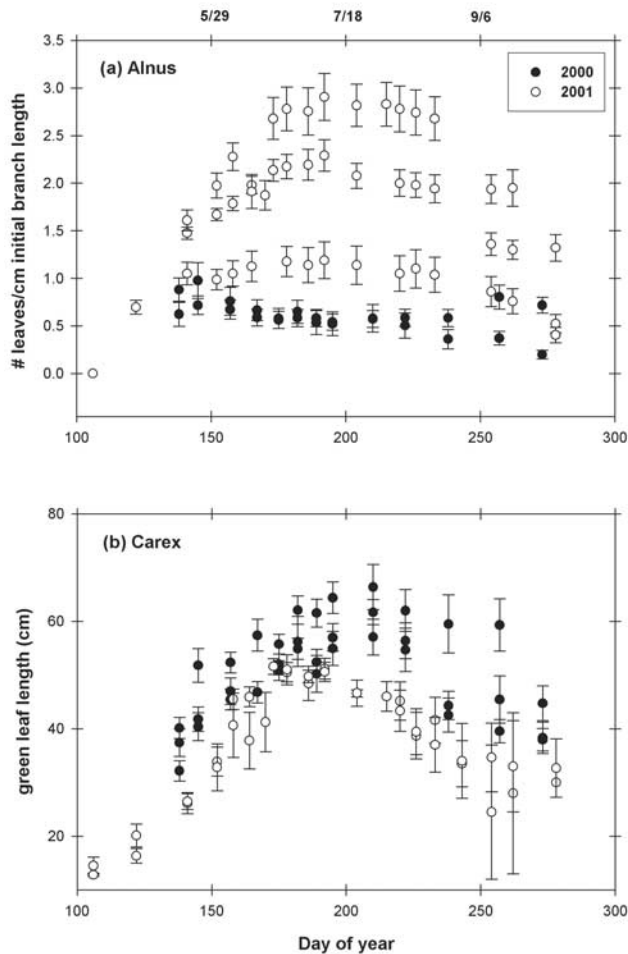
that the relationship between  $\text{NEE}_{\text{max}}$  and respiration is not as strong in the drier summer when sedges were less productive even though respiration rates were higher (Figure 9b). The differential response to drier conditions by shrubs and sedges could explain the weaker relationship in the drier year.

## 4. Discussion

### 4.1. Coupled Ecosystem and Climatic Controls on Respiration

[27] Previous studies have shown that water table is an important control on the carbon balance of peatlands both spatially and temporally [Joiner *et al.*, 1999; Alm *et al.*, 1999, 1997; Schreder *et al.*, 1998; Waddington and Roulet, 1996; Shurpali *et al.*, 1995; Oechel *et al.*, 1993]. Lowering

the water table expands the aerated portion of the peat profile, enhancing oxygen availability for microbes and plant roots. *Silvola et al.* [1996a, 1996b] predicted a 50–100% increase in respiration with 14–22 cm drop in the water table (as predicted under  $2 \times \text{CO}_2$  scenarios by *Roulet et al.* [1992]) based on field and laboratory studies in Finnish peatlands. In our study, respiration rates were on average 47% larger in the drier summer with a 10-cm lower water table, similar to the range predicted by *Silvola et al.* [1996a, 1996b]. In laboratory incubations of Canadian peat soils, respiration rates were 12–20 times greater under oxic compared with anoxic conditions [Moore and Dalva, 2001; Scanlon and Moore, 2000]. The mechanisms for these differential rates include increased microbial decomposition under aerobic conditions with enhanced activity of phenol oxidase, the enzyme responsible for degrading recalcitrant



**Figure 6.** (a) Number of *Alnus incana ssp. rugosa* (speckled alder) leaves per initial branch length. Each point represents a different plant and an average of approximately four to five branches per plant. (b) Length of green section of leaves for the sedge *Carex rostrata*. Each point represents an average of 10 plants. Error bars are standard errors.

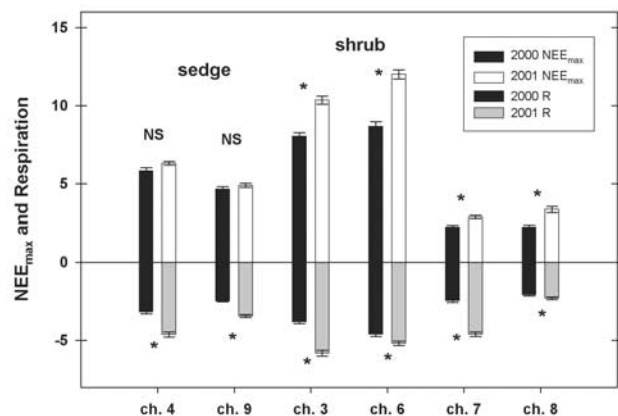
phenolic compounds in peat [Christensen *et al.*, 1998; Moore and Dalva, 1993; Freeman *et al.*, 2001], and increased N mineralization which contributes to faster decomposition of organic compounds [Updegraff *et al.*, 1995]. In addition to showing the different seasonal mean differences in respiration fluxes between years using *t*-tests (Figure 7), the high temporal frequency data in this study provided a unique opportunity to examine temporal trends within and between seasons. The significance of the difference in respiration between years was further increased when correlations between adjacent daily differences were corrected for by fitting an ARMA model.

[28] Although most studies concur that a lower water table increases soil respiration rates, there is less agreement on the effect of drier conditions on plant processes. Since the net ecosystem exchange of CO<sub>2</sub> (NEE) is the difference between uptake by plants and loss of CO<sub>2</sub> to the atmosphere by soil and plant respiration, plant responses are equally important as soils for predicting changes in the carbon

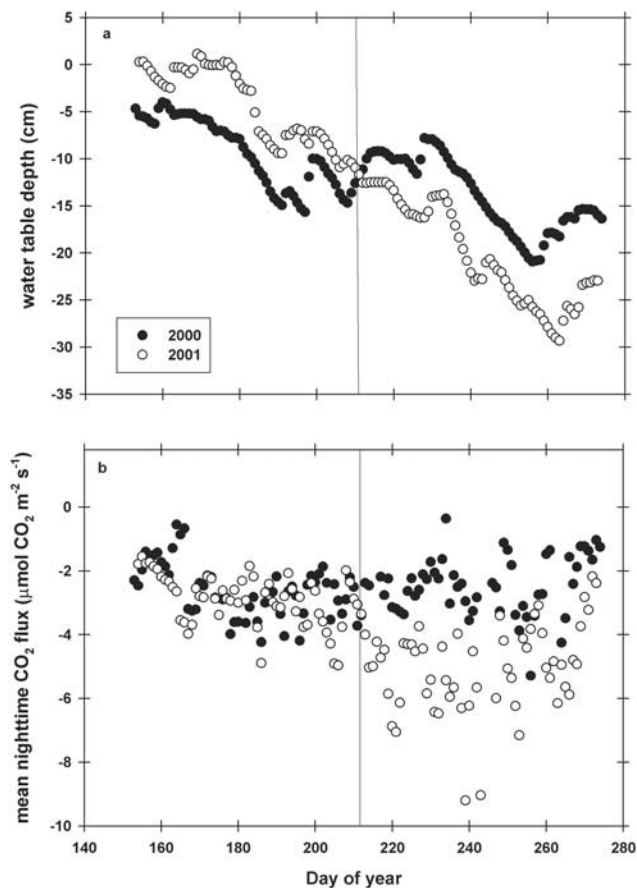
balance. For example, plant respiration can be responsible for as much as 35–90% of the ecosystem respiration in organic soils [Johnson *et al.*, 2000; Silvola *et al.*, 1996a, 1996b]. Our data show that ecosystem respiration is controlled by interactions among water table, temperature, and plant production. Ecosystem respiration rates were 53–84% larger in the evergreen shrub sites in the drier summer compared with an increase of 13% for deciduous shrub and 36–48% in the sedge sites with water table and temperature as strong predictors ( $r^2 = 0.74$ – $0.75$ ). The strong correlation between maximum CO<sub>2</sub> uptake and respiration in this study ( $r^2 = 0.39$ – $0.83$ ;  $p < 0.01$  in Figure 9b) has also been demonstrated across a suite of European forests [Janssens *et al.*, 2001]. In addition, the replicability of chamber NEE and respiration based on foliar biomass and plant functional types shows that species composition and biomass are important predictors across a range of vegetation gradients (Figure 3 and Table 3).

#### 4.2. Response of Different Plant Growth Forms to Drought

[29] Different plant functional types can alter the sink/source strength potential of peatlands. Bubier *et al.* [1999] and Bellisario *et al.* [1998] showed that sedge-dominated mineral-poor fens sequester more CO<sub>2</sub> than ericaceous shrub bogs or deciduous shrub-rich fens, because the poor fens had higher rates of photosynthesis relative to respiration. Longer term (50–100 years) rates of C accumulation in these same sites showed a comparable difference among sites [Trumbore *et al.*, 1999]. Plant growth forms vary in their maximum CO<sub>2</sub> uptake (Figure 3 and Table 3) and photosynthetic capacity per unit biomass [Chapin and Shaver, 1996; Semikhatova *et al.*, 1992] with sedges > deciduous shrubs > evergreen shrubs and they also have



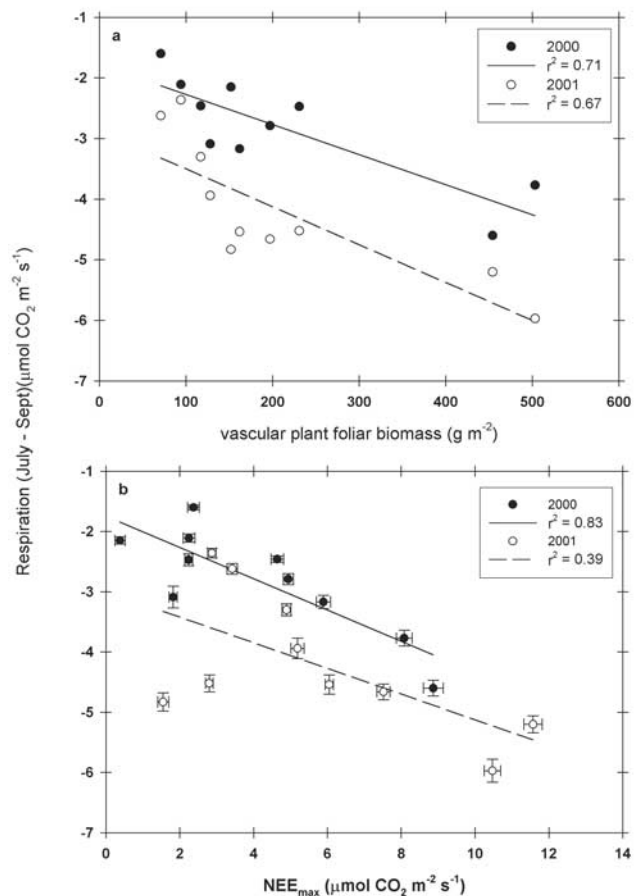
**Figure 7.** NEE<sub>max</sub> (mean summer NEE at PAR > 1000  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and nighttime respiration for ch. 3 (leatherleaf: large biomass), ch. 4 (sedge), ch. 6 (alder), ch. 7 (leatherleaf: low biomass), ch. 8 (*Sphagnum* with a small vascular plant component), and ch. 9 (sedge). Asterisks indicate significant differences ( $p < 0.05$ ) in *t*-tests. Note that the sedge-dominated chambers (4, 9) are the only ones to have similar, not larger, maximum NEE rates in the drier summer of 2001.



**Figure 8.** Nighttime (a) average water table and (b) CO<sub>2</sub> flux by day of year in 2000 and 2001.

different physiological responses to changes in the moisture balance [Busch and Losch, 1999]. In studies of interannual CO<sub>2</sub> exchange, sedge-dominated fens usually have less CO<sub>2</sub> uptake during drier years [e.g., Lafleur et al., 2001a, 2001b; Joiner et al., 1999]. For example, Griffis et al. [2000] reported that a northern Canadian fen switched from a sink to a source of CO<sub>2</sub> in a dry year primarily due to reduced rates of sedge photosynthesis early in the growing season at a critical time of plant development. In a Finnish bog with a small vascular plant component, net CO<sub>2</sub> exchange was lower in a dry summer primarily due to *Sphagnum* moss dessication [Alm et al., 1999]. In an experimental manipulation of water table in bog and fen mesocosms, rates of plant production varied with water table level with shrubs favoring drier conditions, and sedges and bryophytes favoring wetter conditions [Weltzin et al., 2000]. The fen in this study is mineral poor, *Sphagnum* dominated in the ground layer, and characterized by relative importance of both sedges and shrubs depending on spatially varying water table elevation within the fen (Table 1). Therefore we were able to compare the response of different growth forms to climate change at the same site. Evergreen and deciduous shrub sites had higher rates of maximum CO<sub>2</sub> uptake in the drier summer, while sedge sites had similar or lower rates of uptake under drier conditions (Figure 7).

[30] In general, fens have higher water tables because of a more consistent influence of mineral-rich groundwater and are dominated by sedges; bogs are usually drier and dominated by evergreen shrubs. Woody plants are not as well adapted to waterlogged conditions as sedges because their stems do not have well-developed aerenchyma for transporting oxygen to roots below the water table. As a result, sedge species have lower rates of photosynthesis under drought conditions [Busch and Losch, 1999], while ericaceous shrubs have higher rates of water potential and photosynthesis than sedges under dry conditions [Small, 1972a, 1972b]. Reductions in sedge photosynthesis have been attributed to stomatal closure [Schreader et al., 1998] and vapor pressure deficit during drought periods [Suyker et al., 1997]. Over the long term, evergreen shrubs have a competitive advantage over herbaceous plant forms in stressed conditions because they retain nutrients and moisture longer than sedges [Aerts, 1995, 1999; Chapin and Shaver, 1996; Small, 1972a, 1972b]. The widespread documentation of shrubs and trees dominating peatlands with lower water tables and sedges dominating on wetter sites supports this plant physiological difference [e.g.,



**Figure 9.** Relationship between mean summer respiration and (a) estimated aboveground vascular plant foliar biomass and (b) maximum NEE at PAR > 1000  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . Each point represents an individual chamber.

Glaser *et al.*, 1990]. In many northern peatlands, foresters have lowered the water table intentionally in order to promote tree growth. Our study shows that the transition from sedge to shrub-dominated communities could occur on very short timescales as evidenced by the rapid response of different plant forms to moisture stress. In one season of drier weather, shrubs had significantly higher rates of maximum CO<sub>2</sub> uptake and leaf production than sedges (Figures 4–7).

[31] Long-term average moisture conditions are also important in predicting the effect of a lower water table on plant production. In an eastern Canadian bog during the same 2 years as this study, sedges had significantly lower rates of photosynthesis in the drier summer of 2001, while shrubs had similar or only slightly lower rates during the same period. All sites experienced significantly higher rates of ecosystem respiration [Bubier *et al.*, 2003]. The response of sedges was similar in this study, but shrub response was different. Drought conditions enhanced shrub productivity in this study, but had little or a slightly negative effect on shrub productivity at the bog. The dominant evergreen shrub species was the same in both studies (*Chamaedaphne calyculata*; leatherleaf). The main difference between the two sites was the average water table position during seasons with more normal rainfall. Mer Bleue Bog is a dry site dominated by shrubs with a very minor sedge component (*Eriophorum vaginatum* in the drier areas and *Carex oligosperma* in the wetter margins of the peatland). The average summer water table is 25–50 cm below the peat surface at the bog [Moore *et al.*, 2002]. Sallie's Fen is dominated by sedges (primarily *C. rostrata*) with a moderate shrub component, and the average summer water table position is 10–20 cm below the peat surface. The shrubs at the bog site may have already been at the dry end of their moisture tolerance level when the drought began, while the shrubs at the fen in this study may have been at the wet end of this tolerance gradient.

[32] The different response of these two dominant plant functional types obfuscates the implications of climatic drying on the carbon balance of peatlands. Although the importance of water table and temperature for controlling soil decomposition has been shown in this and previous studies [e.g., Silvola *et al.*, 1996a, 1996b], peatland responses to climate change are still uncertain [Moore *et al.*, 1998]. Lowering the water table increases soil decomposition, but either enhances or diminishes plant production depending on the antecedent moisture conditions, the length of the drought, and plant species composition of the peatland in question. The effect on plant respiration is also unclear because of varying rates of photosynthesis in response to drought. In forested peatlands, long-term lowering the water table enhances the C sink potential [Minkinen and Laine, 1998] because of the increase in tree production relative to increases in soil decomposition. But in sedge-dominated sites, a lower water table stresses these water-adapted plants and can reduce the C sink potential by lowering rates of plant production [Griffis *et al.*, 2000]. Shrubs have higher rates of production with a lower water table (this study) as long as the water table is not too low to

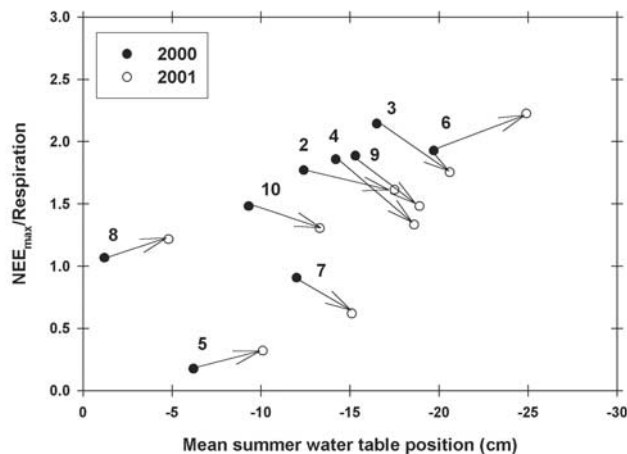
begin with, a situation which may stress even stress-adapted evergreen species [Bubier *et al.*, 2003].

[33] To examine the effect of less moisture on the relationship between productivity and respiration, we analyzed the ratio of maximum NEE to respiration as a function of water table depth (Figure 10). The ratio declined with a lower water table position for most chambers, but increased at either end of the water table gradient in the drier summer. The ratios ranged from 0.2:1 to 2.1:1 (mean = 1.5:1) in the wetter summer and from 0.3:1 to 2.2:1 (mean = 1.3:1) in the drier summer. This compares with 1.3:1 to 2.2:1 in the wet summer and 0.9:1 to 1.4:1 in the dry summer for Mer Bleue Bog [Bubier *et al.*, 2003]. Lower values are similar to those reported for European forests [1:1 to 1.4:1; Janssens *et al.*, 2001]. In sites dominated by evergreen shrubs and sedges, dry conditions appear to lower the ratio between maximum NEE and respiration (Figure 10). This same pattern was observed for evergreen shrubs and sedges at Mer Bleue Bog in Ontario [Bubier *et al.*, 2003] suggesting that drought will diminish the C sink strength of peatlands dominated by these growth forms. However, the ratio between maximum NEE and respiration for deciduous shrub (ch. 6, alder) increased during the dry summer because plant production was far greater than increases in respiration. Several field studies have shown that deciduous shrubs increase in abundance with warming and nutrient additions in the arctic [e.g., Chapin *et al.*, 1995], and that deciduous shrubs may become more dominant globally than evergreens due to their faster rates of nutrient cycling, which are enhanced under warmer and drier conditions [Kittel *et al.*, 2000]. The dominance of deciduous shrubs may also promote carbon storage because of their large allocation to woody stems that decompose slowly [Hobbie, 1996]. The ratio between maximum NEE and respiration also increased at the wettest chambers in our study.

[34] In the global terrestrial carbon budget, net releases of C are reported during warm and dry years; however, the contribution of various terrestrial ecosystem processes is still uncertain [Schimel *et al.*, 2001]. In addition, ecosystem responses to climate change occur on a variety of timescales from hours to years. Some ecosystems will become stronger C sources, while others will sequester more C [Shaver *et al.*, 2000]. We have shown that some growth forms respond positively to a drier climate and others negatively within a single peatland. This short-term CO<sub>2</sub> exchange response has longer-term implications for changes in growth form dominance, plant production and allocation, phenology, nutrient absorption, litter decomposition, and ecosystem feedbacks to climate change [Shaver and Jonasson, 1999; Chapin and Shaver, 1996; Jonasson *et al.*, 1999; Hobbie, 1996].

## 5. Conclusions

[35] This study highlights the importance of understanding interactions among plant and soil processes with climatic factors such as precipitation and temperature in predicting responses of ecosystems to climate change. The fortuitous juxtaposition of dry and wet growing seasons allowed us to study short-term responses of peatland plant communities and their associated soils to changes in moisture. The benefit



**Figure 10.** Ratio between maximum NEE (mean summer NEE at  $PAR > 1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) and mean summer nighttime respiration (sign changed to positive) for each chamber. Arrows indicate changes in ratios between wet summer of 2000 and dry summer of 2001. Most ratios declined because increases in respiration in 2001 are greater than increases in  $NEE_{\text{max}}$ . However, the ratios increase in the chamber with highest (chs. 5, 8) and lowest (ch. 6 alder) water tables because increases in  $NEE_{\text{max}}$  are greater than respiration in 2001.

of automatic NEE chambers is that we were able to capture changes in NEE as they occurred on an hourly basis and to develop more robust relationships between NEE and climatic variables. Respiration was correlated with water table, temperature, and plant production suggesting a close linking of these processes. The larger rates of shrub production and smaller rates for sedges in the drier summer suggest that the transition from sedge to shrub-dominated communities in peatlands could occur on short timescales with sustained drought of even moderate severity. This in turn has implications for nutrient and carbon cycling. The decline in ratio of  $NEE_{\text{max}}$  to respiration in the sedge and evergreen shrub sites between the wet and dry summers, but an increase in this ratio for deciduous shrub sites may increase the C sink potential of some wetlands in a drier climate and diminish it for others. Antecedent moisture conditions also play an important role in determining not only species composition, but the tendency for enhanced or diminished rates of plant production and respiration depending on the habitat conditions of different growth forms.

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