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Carbon gas exchange at a southern Rocky Mountain wetland, 1996-1998

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Abstract. Carbon dioxide (CO_2) and methane (CH_4) exchange between the atmosphere and a subalpine wetland located in Rocky Mountain National Park, Colorado, at 3200 m elevation were measured during 1996-1998. Respiration, net CO_2 flux, and CH_4 flux were measured using the closed chamber method during snow-free periods and using gas diffusion calculations during snow-covered periods. The ranges of measured flux were 1.2-526 mmol CO_2 m^{-2} d^{-1} (respiration), -1056-100 mmol CO_2 m^{-2} d^{-1} (net CO_2 exchange), and 0.1-36.8 mmol CH_4 m^{-2} d^{-1} (a positive value represents efflux to the atmosphere). Respiration and CH_4 emission were significantly correlated with 5 cm soil temperature. Annual respiration and CH_4 emission were modeled by applying the flux-temperature relationships to a continuous soil temperature record during 1996-1998. Gross photosynthesis was modeled using a hyperbolic equation relating gross photosynthesis, photon flux density, and soil temperature. Modeled annual flux estimates indicate that the wetland was a net source of carbon gas to the atmosphere each of the three years: 8.9 mol C m^{-2} yr^{-1} in 1996, 9.5 mol C m^{-2} yr^{-1} in 1997, and 9.6 mol C m^{-2} yr^{-1} in 1998. This contrasts with the long-term carbon accumulation of ~0.7 mol m^{-2} yr^{-1} determined from ^{14}C analyses of a peat core collected from the wetland.

1. Introduction

Incomplete decomposition of organic material results in the accumulation of carbon and nutrients in most wetlands. Wetlands gain a large amount of their carbon autotrophically from atmospheric CO_2, and they lose much of it back to the atmosphere as CO_2 and CH_4 emissions derived from decomposition and respiration. There is concern that changes in climate, such as warmer temperatures or decreased precipitation, may accelerate decomposition rates in some wetlands, causing them to become net sources of carbon to the atmosphere [*Gorham*, 1991; *Oechel et al.*, 1995]. Carbon cycling in northern, high-latitude wetlands has been a focus of recent research because these wetlands store about one third of the total global soil carbon pool [*Gorham*, 1991] and because the carbon balance of these wetlands appears to be sensitive to small changes in climate [*Oechel et al.*, 1995; *Carroll and Crill*, 1997; *Oechel et al.*, 1998; *Alm et al.*, 1999; *Soegaard and Nordstroem*, 1999]. Carbon cycling in high-altitude wetlands may also be sensitive to minor climate variations. *Baron et al.* [2000] modeled the response of an alpine-subalpine watershed to different climate change scenarios and found that changes in the winter and spring climate, such as snow accumulation and the timing of snowmelt, could have a significant impact on hydrology and vegetation dynamics. Short- or long-term changes in temperature and/or precipitation could invoke changes in the carbon balance of high-altitude wetlands similar to that predicted in high-latitude wetlands. During the past century, the European Alps experienced an increase of 2°C in minimum temperatures and a somewhat smaller increase in maximum temperatures [*Haeberli and Beniston*, 1998], and recent melting of Rocky Mountain glaciers is well documented [*Hall et al.*, 1994; *Fagre*, 1998]. Climate records at Niwot Ridge, Colorado (3750 m altitude, 30 km south of the study wetland), indicate trends of increased precipitation and decreased solar radiation in the Colorado Front Range, but no significant trend in temperature from 1951 to 1994 [*Williams et al.*, 1996]. The precipitation and solar radiation trends are consistent with climate change predictions simulated by the nested regional MM4 model under 2 x CO_2 scenarios [*Giorgi et al.*, 1994; *Williams et al.*, 1996]. However, the model also predicts an increase in annual temperatures. General circulation models predict an increase in summer and winter temperatures and slight changes in precipitation in both the Alps [*Haeberli and Beniston*, 1998] and in the southern Rocky Mountains [*Baron et al.*, 2000] if greenhouse gas concentrations continue to increase.

An accurate estimate of the global extent of mountain wetlands does not exist, but there are certain geomorphic characteristics that favor the formation of wetlands in mountainous regions, primarily in high mountain valleys and in intermountain basins [*Windell et al.*, 1986]. In mountain

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valleys, remnant glaciers and late-melting snow maintain spring, seep, and snowbed wetlands at the base of boulder and talus fields. Wetlands form next to streams that overflow and in remnant lakes and ponds. Intermountain basins are large, flat valleys between mountain ranges that can contain extensive wetlands along rivers and streams, in oxbow lakes, and in areas with a shallow water table maintained by aquifers, frequent flooding, or impermeable bedrock [*Windell et al.*, 1986].

There are relatively few studies of carbon cycling in high-elevation wetlands, which are commonly in remote locations that are difficult to access. CH_4 emissions during snow-free periods were significantly correlated with soil temperature in an Appalachian peatland [*Yavitt et al.*, 1988], in five lake-associated Colorado wetlands [*Smith and Lewis*, 1992], and in the Colorado subalpine wetland in this study [*Wickland et al.*, 1999]. Soil moisture [*Sebacher et al.*, 1986; *Mosier et al.*, 1993] and substrate quality [*Yavitt et al.*, 1988; *Smith and Lewis*, 1992] can also control CH_4 emissions. CO_2 and CH_4 are emitted through the snowpack during winter and may be significant to the carbon balance of seasonally snow-covered wetlands [*Sommerfeld et al.*, 1996; *Mast et al.*, 1998; *Wickland et al.*, 1999]. These studies contribute to the understanding of carbon cycling processes in high-elevation wetlands, but they focus on one process and/or only take place during snow-free or snow-covered periods. In order to improve the understanding of carbon cycling in high-elevation wetlands, we measured CO_2 and CH_4 fluxes at a subalpine wetland for 3 years, including snow-covered periods. We developed simple models for respiration, photosynthesis, and CH_4 emission from our data and calculated annual carbon gas exchange for each of the 3 years. Historical carbon accumulation was estimated from a peat core collected from the wetland to compare to the present annual carbon exchange we measured and modeled.

2. Site Description

The study site is located in the Loch Vale watershed in Rocky Mountain National Park, Colorado. Ecosystem studies in Loch Vale began in the early 1980s, and the watershed is one of five sites in the U.S. Geological Survey's Water, Energy, and Biogeochemical Budgets (WEBB) program (http://water.usgs.gov/nrp/webb). Loch Vale watershed is immediately east of the Continental Divide, having elevations ranging from 3050 to 4025 m (Figure 1). The majority of the watershed consists of rock outcrop and talus slopes, while vegetated areas make up 18% of the watershed [*Arthur*, 1992]. The climate is characterized by long, cold winters and 3-4 month snow-free periods. Mean daily air temperatures (1983-1990) range from -6.0°C in the winter to 13.7°C in the summer, and average annual precipitation is ~100 cm yr^{-1}, with up to 70% falling as snow during October through May [*Baron*, 1992]. The most important annual hydrologic event is spring snowmelt, when more than 60% of the annual streamflow occurs [*Mast et al.*, 1995].

The 0.4 ha wetland is located at 40°17'25"N, 105°39'58"W, at an elevation of 3200 m, and ~6 km from the nearest road (Figure 1). It is bordered by a steep talus slope to the north and by streams to the south and east. Englemann spruce (*Picea engelmannii* Pargy) and subalpine fir (*Abies lasiocarpa* Hook) forest surrounds the wetland, extending to ~3400 m elevation. An avalanche swept through the site on January 30, 1996, and destroyed part of the forest adjacent to the wetland, depositing debris from the felled trees in the wetland. The wetland slopes slightly downward (<1°) from the west and receives ~10 hours of direct sunlight per day during the summer months. Vegetation is dominated by *Carex aquatilis* Wahl. and *Eleocharis quinqueflora* Lightf. The sediments are peaty with 64-88% organic content in the upper 10 cm [*Wickland et al.*, 1999]. During 1996-1998 the water table was always at or above the sediment surface, averaging 3 cm above the sediment surface during the snow-free season. Three measurement sites were established along a ~45 m transect spanning the wetland (Figure 1). The three sites were chosen to represent the entire wetland, and had similar vegetation composition, but varied slightly in sediment organic matter content and water table height.

3. Methods

3.1. Local Climate

A weather station located on the southeastern edge of the wetland (Figure 1) was equipped with dataloggers that recorded continuous hourly measurements of air temperature and soil temperature at 1 and 5 cm depths using permanently installed thermistors. During snow-free periods, soil temperature was also measured at 5 and 10 cm depths using a Fluke digital thermometer at each site during snow-free periods concurrent with flux measurements. Mean hourly total solar radiation was measured using an Epply PSP Precision Pyranometer located at the weather station. Precipitation data were acquired from the National Atmospheric Deposition Program/National Trends Network (NADP/NTN) weather station in Loch Vale, located ~0.3 km southeast of the wetland (40°17'16"N, 105°39'46"W, 3159 m elevation) (http://nadp.sws.uiuc.edu/nadpdata/).

3.2. Gas Flux Measurements

CO_2 and CH_4 fluxes were measured weekly during the snow-free periods of 1996-1998. Gas fluxes were measured one time per sample day at each of the three sites, usually between 1000 and 1500 (MST). Negative flux (gross photosynthesis) indicates a transfer of atmospheric CO_2 to the wetland, while positive flux indicates a loss of CO_2 or CH_4 from the wetland. Measurements were made using the closed chamber technique, in which the change in CO_2 or CH_4 concentration in a chamber placed on the soil surface was measured over time [*Healy et al.*, 1996]. The cylindrical chambers used in 1996 were 0.20 m tall with an inner diameter of 0.19 m. In 1997 and 1998, larger chambers were used (0.20 m tall, 0.37 m inner diameter). The chambers had sample ports fitted with three-way stopcocks, a coiled aluminum tube (1.6 mm inside diameter) installed through the sidewall for pressure equalization, and a 12-volt CPU fan to increase chamber air circulation. Plastic skirts were attached around the chamber bottoms and weighted with sand-filled nylon stockings to prevent gas exchange between the chamber and the atmosphere during measurements.

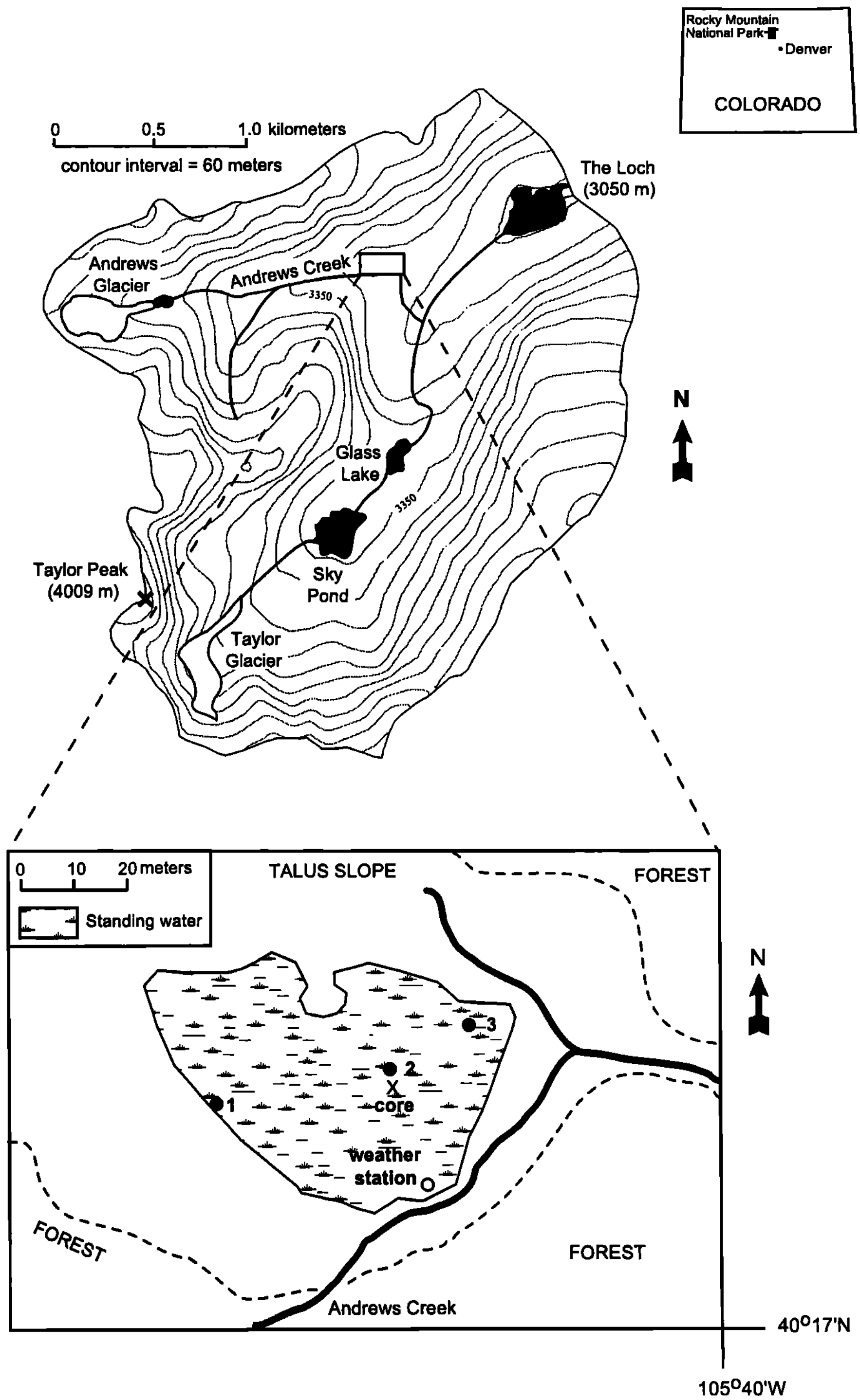

Figure 1. Map of Loch Vale Watershed, Rocky Mountain National Park, Colorado, and study site. Flux measurement locations are represented by a solid circle; the sediment core was collected where indicated. The dotted line represents the forest boundary.

Gross CO_2 flux (microbial respiration plus plant respiration, hereafter called "respiration") was measured using an opaque chamber constructed of polyvinyl chloride (PVC). Net CO_2 flux (respiration plus gross photosynthesis) and CH_4 flux were measured using a chamber constructed of clear PVC and Lexan. CO_2 concentration was measured continuously for 5 min by circulating chamber air through a PP Systems EGM-1 portable infrared gas analyzer (IRGA), which pulled air from the top center of the chamber and returned the air through a sidewall sample port. The IRGA was calibrated in the field using 350 and 2030 ppm CO_2 standards. CH_4 concentration was measured by collecting chamber air samples through a second top-center sample port at 2-min intervals for 8 min using gas-tight 20 mL nylon syringes. The samples were analyzed in the laboratory on a gas chromatograph (GC) within 32 hours of collection. The Chrompack model 438A GC had a 2 m 80-100 mesh Porapak-N column, a flame ionization detector, nitrogen carrier gas, and an oven temperature of 40°C. Calibration tables were constructed using four CH_4 standards (0.49, 1.80, 21.1, and 604 ppm), and chromatographic data were integrated using a Hewlett-Packard 3365 Series II ChemStation computer program.

The rate of gas emission or consumption was determined by

$$J=(dC/dt)h, \qquad (1)$$

where J is flux across the water surface (mol m^{-2} t^{-1}), C is the concentration of gas in the chamber at ambient temperature and pressure (mol m^{-3}), t is time, h is chamber height (m), and dC/dt is the slope of the linear regression of gas concentration on time as time approaches zero [*Rolston*, 1993; *Healy et al.*, 1996]. All regressions for flux measurements reported here have $r^2 \geq 0.95$. Gas fluxes are reported as mmol m^{-2} d^{-1} (multiply by 0.0116 to convert to μmol m^{-2} s^{-1}).

Winter emissions through snow were measured monthly at each of the three sites from January through April 1996, in March 1997, and in March and April 1998. During the snowmelt period (May and June 1996-1998), flux measurements were made weekly or twice monthly. Gas fluxes through snow were calculated using the measured CO_2 and CH_4 concentration gradients in the snowpack and physical properties of the snowpack [*Mast et al.*, 1998]. Snowpack gases were sampled through a 3.5 m long stainless steel probe (3 mm inner diameter) that was inserted to different depths in the snowpack. The IRGA was attached to the end of the probe to measure CO_2 concentration, and gas samples were collected through the probe in 20 mL nylon syringes for CH_4 analysis on the GC. Gas concentrations were measured at the air-snow interface, at 10-40 cm intervals within the snowpack, and near the snow-water/sediment interface. Snow density was measured at 10 cm intervals along a vertical face of one snowpit dug at the wetland using a 1 L stainless steel cutter, and snow temperature was measured every 10 cm along the snowpit face [*Mast et al.*, 1998]. Detailed information on how gas flux was calculated and examples of measured gas concentration gradients are given by *Mast et al.* [1998].

3.3. Biomass Measurements

Aboveground plant biomass was measured each year for comparison with annual gross photosynthesis measurements. Belowground biomass was not measured but was estimated using values from the literature. Aboveground biomass was measured weekly or bimonthly when gas flux was measured in 1997 and 1998. Two 0.3 m^2 plots were randomly selected in the wetland for harvest, one between sites 1 and 2 and the other between sites 2 and 3, so as not to disturb the flux measurement sites. Live biomass was clipped at the sediment surface and collected, then oven-dried for 24-48 hours at 100°C and weighed. Biomass values were averaged for each sample date. Plant height above the sediment surface was measured at each sample site weekly or bimonthly in 1996, 1997, and 1998. Six plants were measured for height (three *Carex* and three *Eleocharis*) at each site, which were then averaged for each date. Aboveground biomass during 1996 was calculated from plant height measurements using the relationship between biomass and plant height during 1997-1998:

$$\text{Biomass}=(0.092 \times \text{height}^2)+(5.42 \times \text{height}),\ r^2=0.94. \qquad (2)$$

3.4. Long-Term Carbon Accumulation

The historical rate of carbon accumulation was determined from a peat core from the center of the wetland near site 2 in 1996. A 5 cm diameter Livingston piston corer was used to extract peat from the entire soil profile (160 cm). The soil core was frozen until analysis for organic matter content. Subsamples of the core were taken at 5 cm intervals and oven dried at 100°C for 24 hours then weighed. Organic matter content was determined using the loss-on-ignition method by baking the soils at 450°C for 24 hours, then reweighing the samples. Radiocarbon dates were determined on a subsample of peat from 67 cm depth and a wood fragment from 138-155 cm depth in the profile by the Radiocarbon Laboratory at the Desert Research Institute, Las Vegas, Nevada, using the benzene-conversion method (H. Haas, written communication, 1997).

4. Results

4.1. Temperature and Precipitation

Mean daily air temperatures and mean daily soil temperatures at 5 cm depth recorded continuously at the wetland weather station are shown in Figure 2 (soil temperatures are missing for 22 days in 1997). Midday soil temperatures measured at 5 cm depth at the three sites were generally slightly greater than at the weather station (site temperature=0.93 x weather station temp+3.6, r^2=0.84). Wetland soil temperatures averaged 0.2°C in winter, increased rapidly immediately after the snow melted, peaked during July and August, then dropped in September and October. While the seasonal patterns are consistent each year, the onset of snowmelt and absolute air and soil temperatures varied among years (Figure 2). Annual precipitation amounts recorded at the NADP/NTN weather station were 138 cm (1996), 126 cm (1997), and 99 cm (1998). Maximum snow depths at the wetland were 300 cm (1996), 255 cm (1997), and 193 cm (1998). In 1996 and 1997 snowmelt was relatively homogenous across the wetland, and all three sites were snow-free by late June. Decreased precipitation and warmer temperatures during the winter of 1997-1998 resulted in a relatively small snowpack and an earlier snowmelt. Snow was partially melted in early June when a series of cold days occurred, resulting in uneven melting in the wetland so that sites 1 and 2 were snow-free about 10 days earlier than site 3.

4.2. Gas Fluxes

CO_2 and CH_4 fluxes during 1996-1998 exhibited a distinct seasonal pattern (Figures 3 and 4). Gross photosynthesis

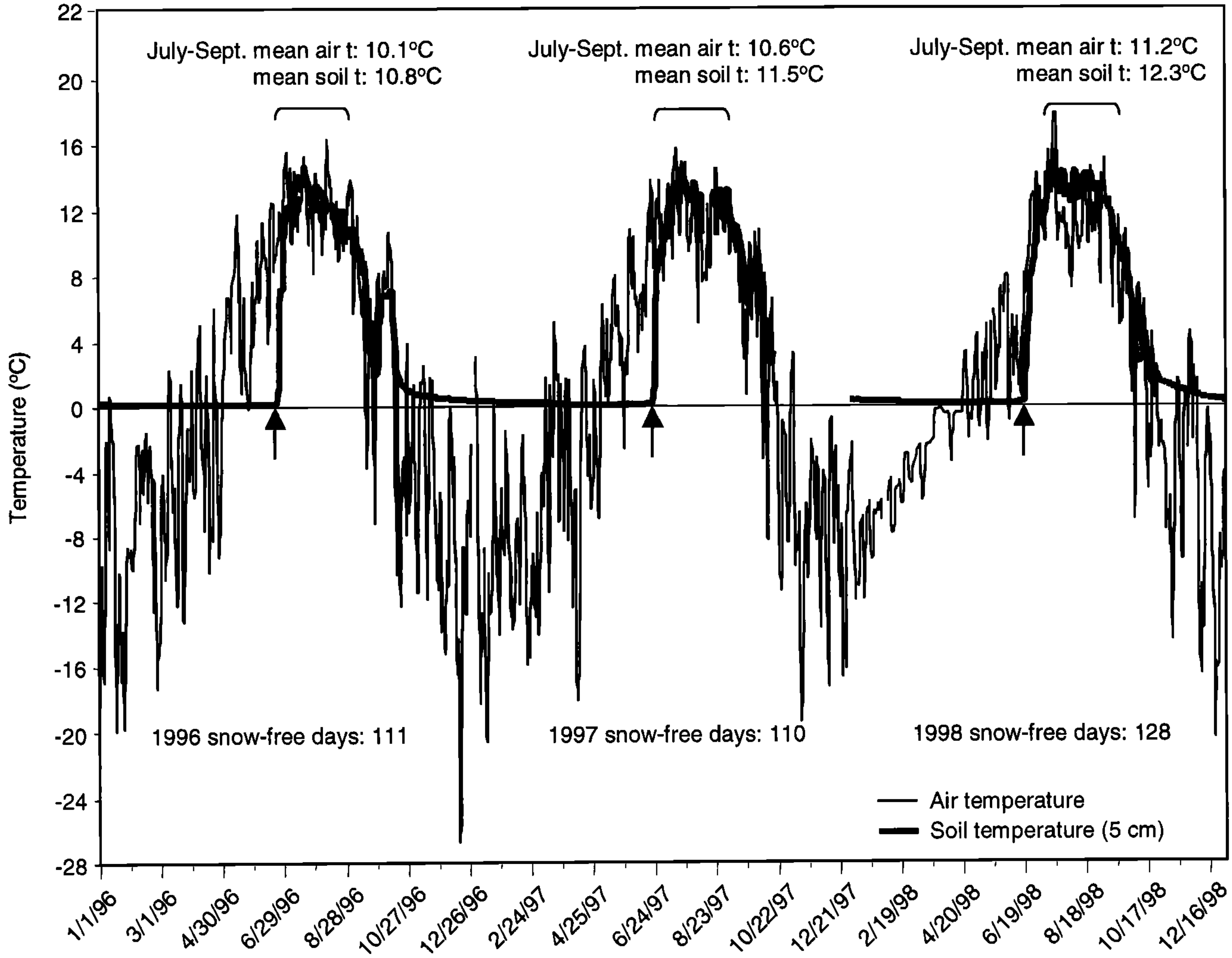

Figure 2. Daily mean air and 5 cm soil temperatures recorded at the weather station, 1996-1998.

(hereafter called "photosynthesis") is calculated as the difference between net CO_2 (clear chamber) and respired CO_2 (dark chamber) fluxes. CO_2 and CH_4 were emitted through the snowpack on all measurement dates. A small increase in CO_2 and CH_4 flux was seen every year at the onset of spring snowmelt. As soon as the wetland was snow-free, soil temperatures rose and CO_2 and CH_4 emission rates increased sharply. Photosynthesis also increased immediately after the wetland was snow-free as plants grew rapidly.

When describing gas fluxes, "individual chambers" include fluxes measured at each site, and "transect mean" designates the mean of the fluxes measured at the three sites on a given sample day. Respiration at individual chambers ranged from 10.4 to 526 mmol m^{-2} d^{-1} during snow-free periods, and from 1.2 to 258 mmol m^{-2} d^{-1} during snow-covered periods, 1996-1998. Transect means ranged from 3.3 ± 0.8 (mean ± SD, n=3) to 452 ± 70.8 mmol m^{-2} d^{-1}, with coefficients of variation (SD/mean) averaging 0.40 among chambers for all measurement days. The range of net CO_2 emission at individual chambers during the snow-free period was –1056 to 100 mmol m^{-2} d^{-1}, and the transect means ranged from –734 ± 280 to 40.0 ± 16.1 mmol m^{-2} d^{-1} (average coefficient of variation=2.8). Photosynthesis at individual chambers ranged from –1322 to –14.9 mmol m^{-2} d^{-1}, and transect means ranged from –1049 ± 236 to –47.4 ± 26.3 mmol m^{-2} d^{-1} (average coefficient of variation=0.30). CH_4 emissions at individual chambers ranged from 1.35 to 36.8 mmol m^{-2} d^{-1} during snow-free periods and from 0.1 to 13.2 mmol m^{-2} d^{-1} during snow-covered periods. Transect means ranged from 0.8 ± 0.5 to 29.0 ± 7.2 mmol m^{-2} d^{-1}, with coefficients of variation averaging 0.46 among chambers for all measurement days.

Total annual (calendar year) emissions at each of the three measurement sites were calculated by assuming that the measured CO_2 and CH_4 fluxes were representative of daily mean emission and by linear interpolation between sampling dates and assuming a 12-hour photoperiod for photosynthesis (Table 1). Annual emissions were also calculated by the linear interpolation of the mean transect fluxes on each measurement date (Table 1) for comparison with individual sites. The annual estimates of respiration, photosynthesis, and CH_4 exchange at each of the three sites indicate small variability of flux (2-20%) among sites within years. The wetland was a net

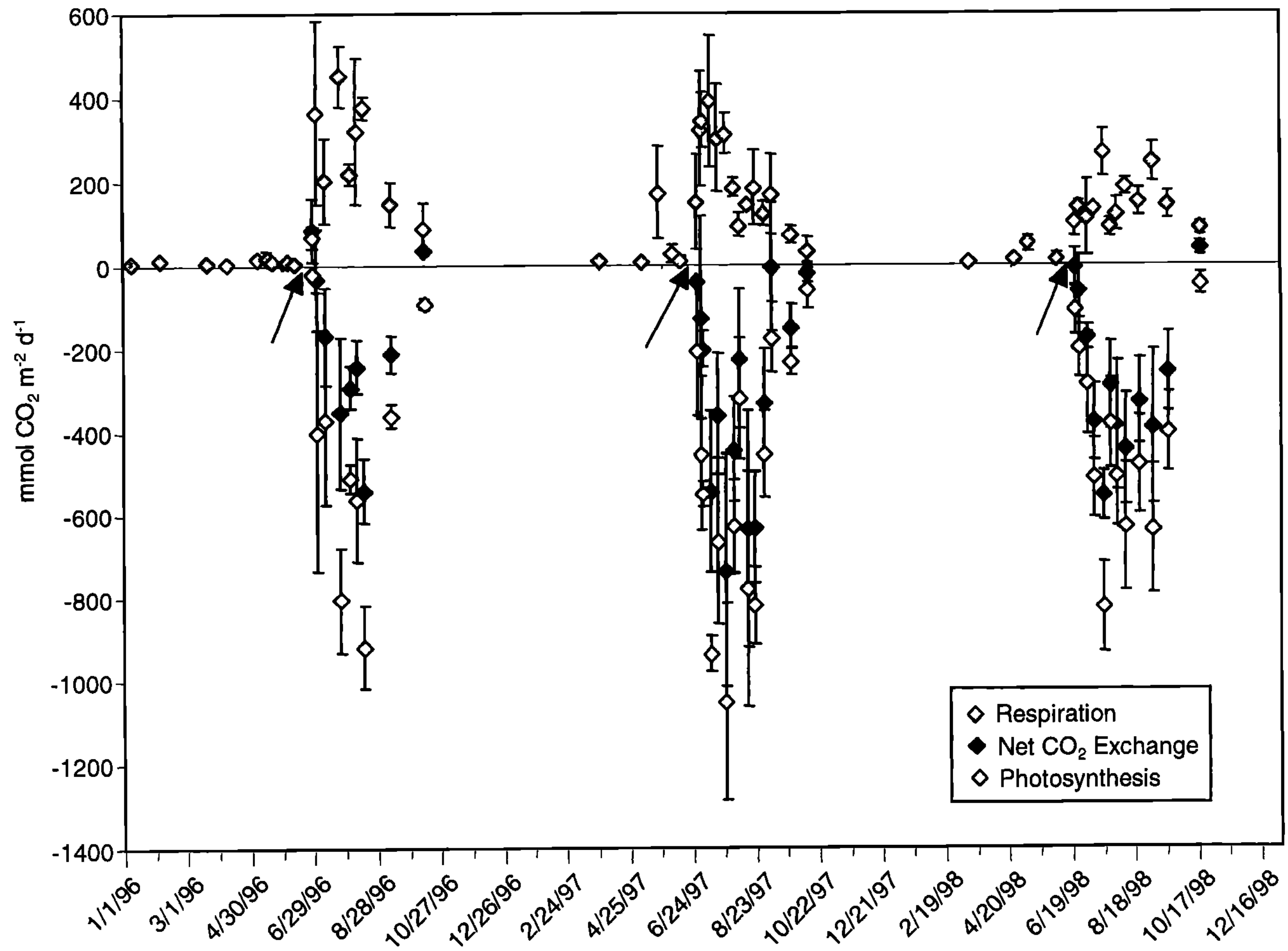

Figure 3. Mean CO_2 flux measurements, 1996-1998. Photosynthesis is the difference between respiration and net CO_2. Each point represents the mean of three measurements; the error bars are +/- one standard deviation.

source of carbon to the atmosphere each year based on the linear interpolation results.

4.2.1. Flux-temperature relationships. The mean transect respiration and CH_4 fluxes measured on each date during 1996-1998 are significantly correlated with 5 cm soil temperatures (Figures 5 and 6). The means of the measured site temperatures were used during the snow-free periods, and a temperature of 0.2°C was assumed during snow-covered periods. CO_2 flux increased exponentially with increasing soil temperature. Average winter CO_2 flux for each year was used instead of the mean winter fluxes on each date because a more realistic Q_{10} value was generated (Q_{10}=2.6 versus 5.0; Q_{10} is the change in respiration rate over a 10°C range in soil temperature) [*Raich and Schlesinger, 1992*]. The resulting equation is

$$\text{Respiration}=31.4\, e^{(0.1271 \times \text{temperature})},\ r^2=0.70. \quad (3)$$

To examine variability among sites, the CO_2 flux-temperature relationship was also determined at each site (Table 2). The equations did not differ greatly from each other or from (3). The best fit linear regressions of the log-transformed fluxes versus soil temperature at each site and the mean transect fluxes versus soil temperature were all within the same 95% confidence interval. It appears that the large seasonal variability outweighs the spatial variability across the wetland. The strongest relationship between CO_2 flux and soil temperature resulted from the mean transect data on each sampling date. Soil temperature and water table height were slightly different between sites, but upon analysis it appears that these differences did not consistently affect flux magnitude.

CH_4 flux was best described by regression analysis when the mean transect fluxes were divided into two time periods: winter through snowmelt (November to June 30) and the snow-free season to winter (July 1 to November). The annual averages of the winter CH_4 fluxes were used to represent winter values, for the same reason given for the CO_2 flux-temperature regression. CH_4 flux had a hysteretic relationship with soil temperature, in which flux increased linearly with increasing soil temperature from winter through snowmelt, then decreased exponentially with temperature as the growing season progressed into winter. The equations are

$$\text{Winter-June } CH_4 \text{ flux}=(1.40 \times \text{temperature})+3.55,\ r^2=0.85 \quad (4)$$

$$\text{July-winter } CH_4 \text{ flux}=3.12e^{(0.1065 \times \text{temperature})},\ r^2=0.84. \quad (5)$$

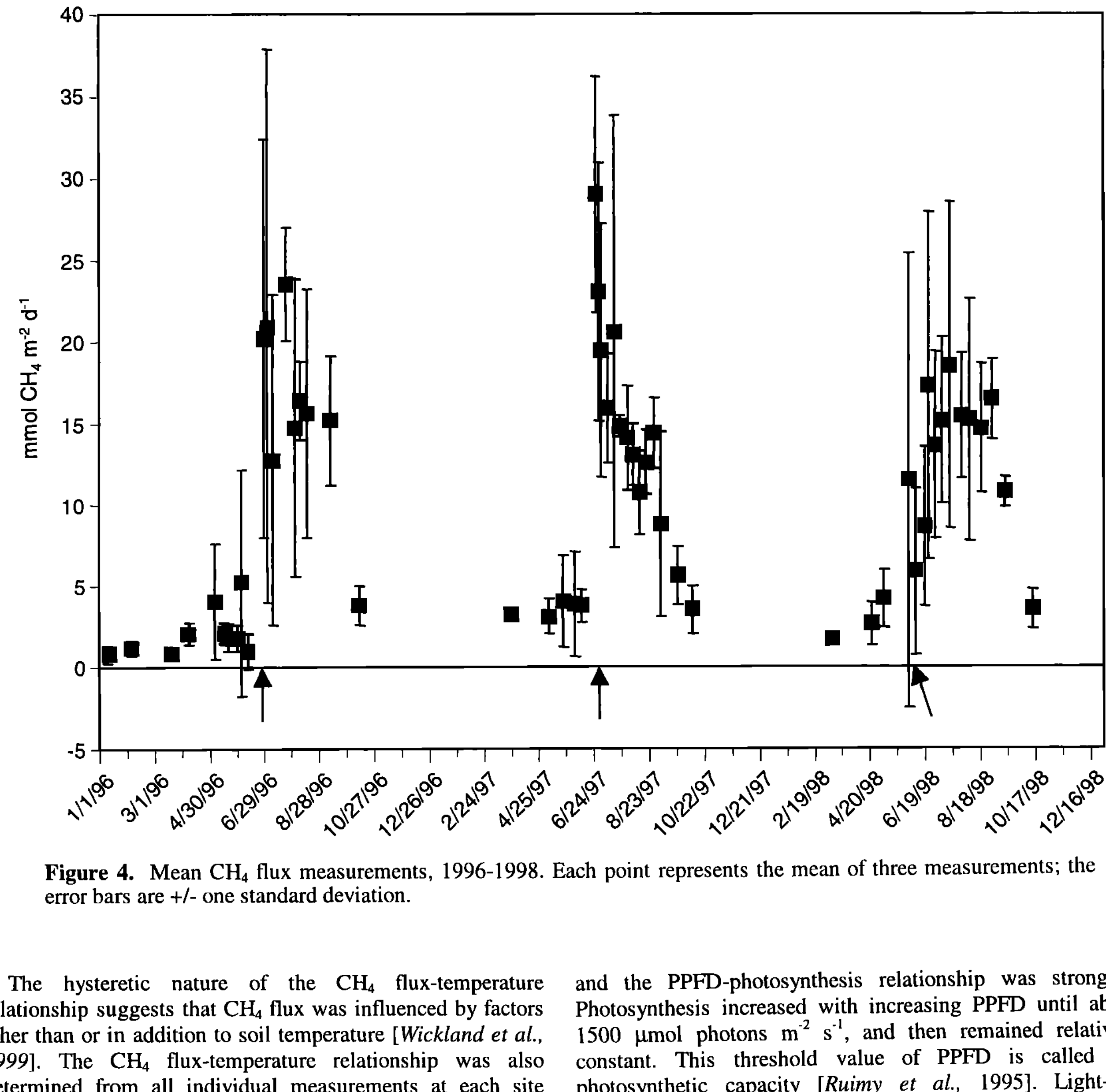

Figure 4. Mean CH_4 flux measurements, 1996-1998. Each point represents the mean of three measurements; the error bars are +/- one standard deviation.

The hysteretic nature of the CH_4 flux-temperature relationship suggests that CH_4 flux was influenced by factors other than or in addition to soil temperature [*Wickland et al., 1999*]. The CH_4 flux-temperature relationship was also determined from all individual measurements at each site (Table 2). As was the case for respiration, the resulting equations did not differ appreciably from (4) and (5) (linear regressions of log-transformed fluxes versus soil temperature within the same 95% confidence interval). The strongest CH_4 flux-temperature relationship, when considering the entire year, resulted from the mean transect flux data.

4.2.2. Flux-PAR relationship. Photosynthesis depends on the amount of photosynthetically active radiation (PAR) received by the plant and other environmental variables. Hourly total radiation measured at the wetland weather station was converted to PAR assuming PAR accounts for 48% of total solar radiation [*Ruimy et al.*, 1995]. PAR values (W m^{-2}) were then converted to units of photosynthetic photon flux density (PPFD) (μmol m^{-2} s^{-1}) by multiplying by 4.6 [*Ruimy et al.*, 1995]. The relationship between all individual chamber measurements during 1996-1998 and PPFD is shown in Figure 7. The solid symbols represent measurements during the months of July and August, after plants were established and the PPFD-photosynthesis relationship was strongest. Photosynthesis increased with increasing PPFD until about 1500 μmol photons m^{-2} s^{-1}, and then remained relatively constant. This threshold value of PPFD is called the photosynthetic capacity [*Ruimy et al.*, 1995]. Light-use efficiency (photosynthesis/PPFD) during the early and late portions of the growing season was not as great as during the middle of the season. This was probably due to cold air temperatures and to small leaf area index early in the season and plant senescence late in the season [*Jones*, 1983; *Carroll and Crill*, 1997].

4.3. Aboveground Biomass

The peak measured aboveground biomass and plant height for each year is listed in Table 3. Peak biomass and peak plant height were similar in 1996 and 1997, while in 1998 there was a noticeable decrease in aboveground biomass production and average plant height. Assuming that the aboveground biomass is 45% carbon [*Thormann and Bayley*, 1997], the peak aboveground biomass numbers translate to 8.3 mol C m^{-2} in 1996, 8.2 mol C m^{-2} in 1997, and 4.8 mol C m^{-2} in 1998. Ratios of aboveground biomass carbon to total biomass carbon measured at other wetlands with similar vegetation in

Table 1. Annual Flux Estimates Calculated by Linear Interpolation of Fluxes Between Measurement Dates for Sites 1, 2, 3, and the Mean Annual Fluxes of the Three Sites

Site	Year	Respiration	Photosynthesis	CH_4 Emission	Carbon Imbalance
1	1996	22.6	-22.5	1.9	2.0
2	1996	36.0	-25.8	2.8	13.0
3	1996	35.3	-23.9	2.1	13.5
Mean	1996	31.3	-24.1	2.3	9.5
1	1997	23.9	-29.0	2.1	-3.0
2	1997	30.5	-23.9	2.4	9.0
3	1997	24.7	-22.1	2.5	5.1
Mean	1997	26.4	-25.0	2.3	3.7
1	1998	25.2	-26.9	2.1	0.4
2	1998	23.5	-26.2	2.4	-0.3
3	1998	28.3	-25.2	2.3	5.4
Mean	1998	25.7	-26.1	2.3	1.8

Estimates are given in mol C m^{-2} yr^{-1}.

Rocky Mountain National Park averaged 0.44 [*Chimner*, 2000]. This ratio was applied to the measured peak aboveground biomass from each year to calculate belowground biomass. Total annual net primary production (the sum of aboveground and belowground biomass) was 19.0 mol C m^{-2} in 1996, 18.7 mol C m^{-2} in 1997, and 11.0 mol C m^{-2} in 1998. Although the growing season was longer and warmer in 1998 than in the two previous years and annual photosynthesis estimated by linear interpolation was greater in 1997 and 1998 than in 1996 (Table 1), aboveground plant production was ~40% less. The reason for this is unclear. The period of cold temperatures in June 1998 after portions of the wetland were snow-free was probably a factor. *Soukupova* [1988] observed that over 3 years the maximum tiller heights

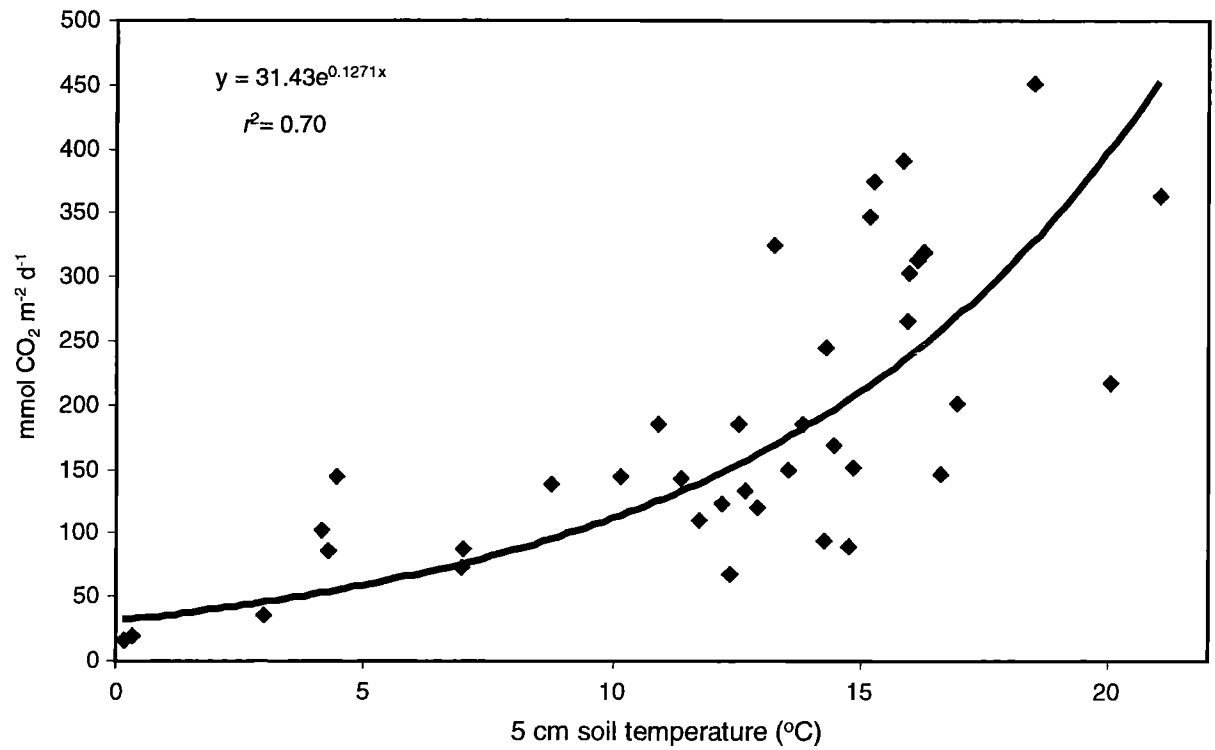

Figure 5. Mean respiration flux versus mean 5 cm soil temperature at flux measurement sites, 1996-1998.

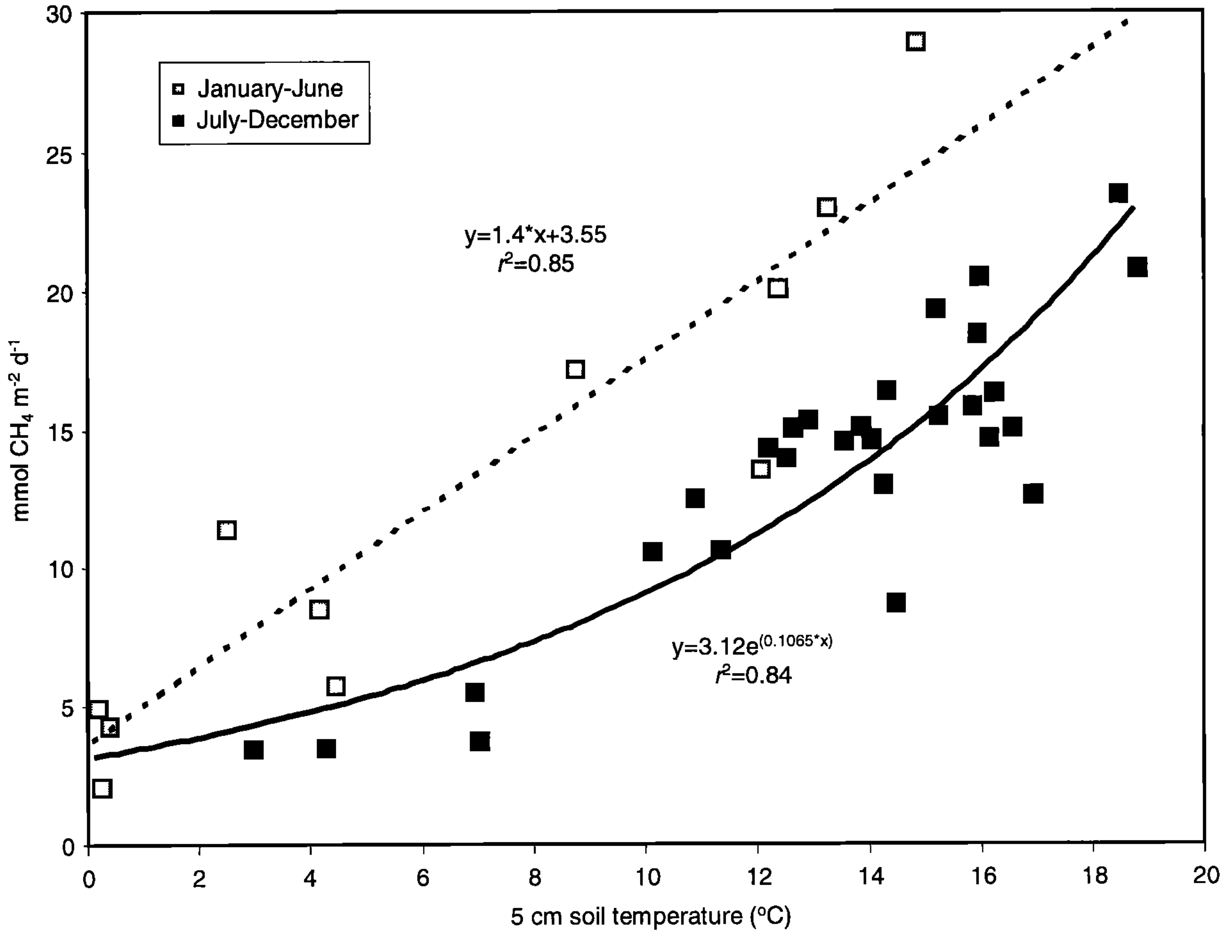

Figure 6. Mean CH_4 flux versus mean 5 cm soil temperature at flux measurement sites, 1996-1998. The linear equation represents the relationship between CH_4 emission and temperature before and immediately after snowmelt (January-June), and the exponential equation represents the relationship between emission and temperature from July to December.

of two wetland *Carex* species in the Czech Republic reflected the temperature course during spring and early summer, with the shortest shoots occurring in a year with a cold spring.

4.4. Flux Models

4.4.1. Respiration and CH_4 emission models. The relationships between 5 cm soil temperature and CO_2 and CH_4 fluxes (equations (3), (4), (5)) were used to estimate fluxes at the wetland during 1996-1998. This approach captured the variability in soil temperature, and thus in CO_2 and CH_4 flux, that the linear interpolation method could not account for. The hourly soil temperature record at the wetland weather station was used to reconstruct a 5 cm site temperature record for the snow-free period. For 22 days in 1997, no soil temperature record was available at the weather station, so temperature data from another weather station located on drier soils next to the wetland were used to calculate the site temperatures. During snow-covered periods, when soil temperatures at the sites were not measured, the 5 cm temperatures recorded at the weather station were used.

Table 2. Regression Equations for Respiration and CH_4 Flux on 5 cm Soil Temperature at the Three Measurement Sites

Site	Respiration-Temperature Relationship	r^2	CH_4 Flux- Temperature Relationship (Winter-June)	r^2	CH_4 Flux- Temperature Relationship (July-Winter)	r^2
1	$y=28.6e^{(0.1263t)}$	0.54	$y=1.07t+1.46$	0.61	$y=2.7e^{(0.1008t)}$	0.56
2	$y=36.4e^{(0.1105t)}$	0.42	$y=1.44t+4.21$	0.81	$y=2.8e^{(0.1175t)}$	0.86
3	$y=34.6e^{(0.1169t)}$	0.66	$y=1.88t+3.74$	0.84	$y=2.4e^{(0.1163t)}$	0.63
Transect means	Equation (3)	0.70	Equation (4)	0.85	Equation (5)	0.84

y=CO_2 or CH_4 flux, mmol m^{-2} d^{-1}, t=5 cm soil temperature (°C).

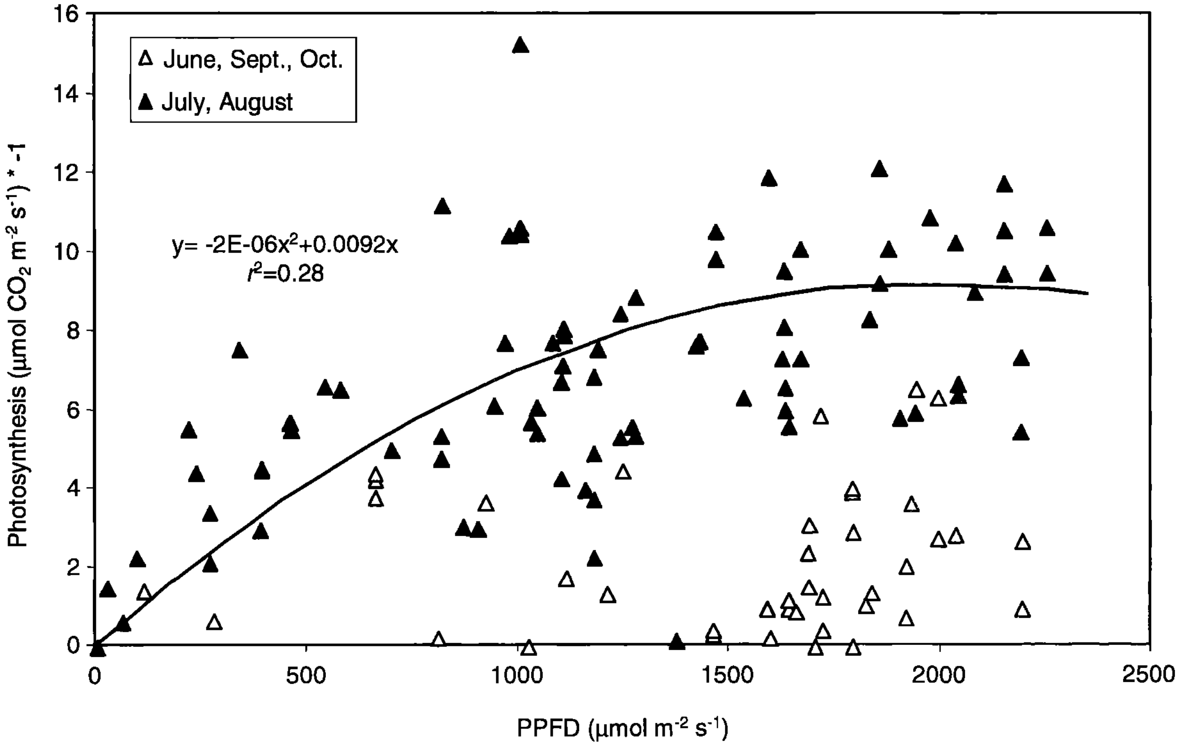

Figure 7. Photosynthesis (x -1) versus photosynthetic photon flux density (PPFD), 1996-1998. The line is the relationship between photosynthesis and PPFD during July and August.

Equation (3) and flux-temperature equations for each site (Table 2) were applied to the reconstructed hourly 5 cm temperature record during 1996-1998, and the values were summed to calculate respiration at the wetland (Table 4). The modeled fluxes ranged from 31.9 to 342 mmol CO_2 m^{-2} d^{-1} and averaged 126 ± 90.8 mmol CO_2 m^{-2} d^{-1}, compared to the measured fluxes which ranged from 3.30 to 452 mmol CO_2 m^{-2} d^{-1} and averaged 136 ± 123 mmol CO_2 m^{-2} d^{-1} (Figure 8a). Analysis of variance (ANOVA) results indicated that there was no significant difference between the measured and modeled CO_2 fluxes (F=0.21, F_{crit}=3.9, p=0.65, df=107). CO_2 emission through the snowpack accounted for 27% of the annual CO_2 emission at the wetland.

Annual CH_4 emission from the wetland was modeled by applying (4) to the reconstructed soil temperature record during November through June of each year, and applying (5) during July through October of each year. Modeled CH_4 flux ranged from 3.70 to 24.3 mmol CH_4 m^{-2} d^{-1} and averaged 10.7 ± 6.60 mmol CH_4 m^{-2} d^{-1}. Measured flux ranged from 0.80 to 29.0 mmol CH_4 m^{-2} d^{-1} and averaged 10.6 ± 7.40 mmol CH_4 m^{-2} d^{-1} (Figure 8b). There was no significant difference between the measured and modeled CH_4 fluxes (ANOVA, F=0.01, F_{crit}=3.9, p=0.92, df=105). Table 4 lists the modeled annual CH_4 emissions from the wetland and from each site. CH_4 emission through the snowpack accounted for 30-35% of the total annual CH_4 emission at the wetland.

Table 3. Aboveground Primary Production

Year	Peak Aboveground Biomass, g m^{-2}	Peak Plant Height, cm
1996	220.8	33.0
1997	218.1	29.4
1998	127.5	24.0

4.4.2. Photosynthesis model. Hourly photosynthesis was modeled using a rectangular hyperbola equation relating photosynthesis and radiation [*Thornley and Johnson*, 1990]:

$$P=(\alpha Q P_{max} \,/\, \alpha Q + P_{max})\; T/T_{max}, \qquad (7)$$

where P=gross photosynthesis (μmol CO_2 m^{-2} s^{-1}), α=apparent quantum yield (μmol CO_2 $umol^{-1}$ photons), Q=PPFD (μmol photons m^{-2} s^{-1}), P_{max}=the maximum rate of photosynthesis at saturating light (μmol CO_2 m^{-2} s^{-1}), T=the 5 day running mean of 5 cm soil temperature, and T_{max}=the 5 day running mean of 5 cm soil temperature when P_{max} was measured. This equation has been commonly used in the literature to model photosynthesis [*Ruimy et al.*, 1995; *Frolking et al.*, 1998; *Bubier et al.*, 1999]. All individual photosynthesis measurements were used to determine α (-0.0157 umol CO_2 $umol^{-1}$ photons), which is the initial slope of the regression of photosynthesis on PPFD (Figure 7) and P_{max} (-12.57 umol CO_2 m^{-2} s^{-1}). The value of α determined from the data is less than the value determined for a C3 leaf at atmospheric CO_2 concentration (-0.05 umol CO_2 $umol^{-1}$ photons) [*Ehleringer and Pearcy*, 1983], but it is within the range of values published for northern peatlands (-0.007 to -0.029 umol CO_2 $umol^{-1}$ photons) [*Frolking et al.*, 1998; *Bubier et al.*, 1999]. The value for P_{max} is also within the range published for northern peatlands (-4.0 to -19.8 umol CO_2 m^{-2} s^{-1}) [*Frolking et al.*, 1998]. The temperature term is included to impose a

Table 4. Modeled Annual Flux Estimates Using the Equations Relating CO_2 Flux and CH_4 Flux to Soil Temperature

Site	Year	Respiration	Photosynthesis	CH_4 Emission	Carbon Imbalance
1	1996	26.1	-22.6	1.9	5.4
2	1996	30.1	-22.6	2.5	10.0
3	1996	28.7	-22.6	2.1	8.2
Transect means	1996	29.0	-22.6	2.5	8.9
1	1997	26.5	-22.4	1.9	6.0
2	1997	30.6	-22.4	2.5	10.7
3	1997	29.2	-22.4	2.1	8.9
Transect means	1997	29.4	-22.4	2.5	9.5
1	1998	28.6	-24.9	2.1	5.8
2	1998	32.5	-24.9	2.8	10.4
3	1998	31.2	-24.9	2.4	8.7
Transect means	1998	31.7	-24.9	2.8	9.6

Equations (3), (4), and (5) were used to calculate the annual flux estimates listed as Transect means. The equations from Table 2 were used to calculate the annual flux estimates at the individual sites. Estimates are given in mol C m^{-2} yr^{-1}.

seasonality on the predicted photosynthesis [*Bubier et al.*, 1999]. If T was greater than T_{max}, the ratio was set to equal one.

The modeled photosynthesis rates ranged from -0.010 to -9.30 μmol CO_2 m^{-2} s^{-1}, averaging -5.80 ± 2.40 μmol CO_2 m^{-2} s^{-1}. The measured photosynthesis rates ranged from 0 to -15.3 μmol CO_2 m^{-2} s^{-1}, averaging -5.30 ± 3.40 μmol CO_2 m^{-2} s^{-1}. The model generally over predicted small fluxes and under predicted large fluxes (Figure 8c). *Bubier et al.* [1999] noted a similar trend when using a comparable model. The measured and modeled photosynthesis values were not significantly different from each other (ANOVA, F=2.2, F_{crit}=3.9, p=0.14, df=122). The photosynthesis model was run for the entire snow-free period of each year to calculate annual photosynthesis at the wetland (Table 4). The model predicted similar estimates in 1996 and 1997 and about a 10% increase in 1998. Part of this increase was due to the longer snow-free period in 1998. The modeled annual estimates are large enough to account for the annual measured aboveground plus the calculated belowground primary production. The modeled estimates were less than the linear interpolation estimates for all years. This is not surprising because the linear interpolation estimate was based upon the assumption that photosynthesis was constant during an entire 12-period, while the model takes into account variations in PPFD and temperature.

4.4.3. Modeled carbon balance. Carbon imbalance as predicted by the gas flux models is listed in Table 4. The wetland was a net source of carbon to the atmosphere at all three sites during the 3 years, according to the results of the models. Linear interpolation results suggest this difference is even smaller (Table 1). When the growing seasons are examined, the modeled carbon uptake and loss from the wetland are essentially in balance (<1 mol C m^{-2} difference). Predicted carbon imbalances for individual sites were within one standard deviation of the carbon imbalance calculated for the transect.

4.5. Long-Term Carbon Accumulation

The wetland formed ~7100 years ago according to radiocarbon dating, not long after the start of a warm dry period that lasted from ~7500 to 3800 years before present [*Richmond*, 1974]. During that time glaciers retreated, treeline was higher, and the summers were probably longer [*Richmond*, 1974]. The climate cooled ~3800 years ago and small glaciers, such as Andrews Glacier (Figure 1), formed [*Richmond*, 1974]. In the center of the wetland, the peat is 160 cm thick, is interspersed with mineral layers, and is underlain by coarse sand. Radiocarbon dates of peat material and a wood fragment (H. Haas, written communication, 1997) indicate that sediment has accumulated at a rate of 0.19 - 0.28 mm yr^{-1}. This is within the range of sediment accumulation rates observed in other Colorado Front Range wetlands of 0.19 - 0.45 mm yr^{-1} [*Pennak*, 1963].

The rate of carbon accumulation in the wetland was calculated from the organic matter content of the peat, assuming that the dry bulk density over the entire profile was the same as the average bulk density of sediment from 5 to 15 cm and the radiocarbon dates. The organic carbon content of the peat was assumed to be 58% of the organic matter content, according to the Van Bemmelen Factor [*Nelson and Sommers*, 1982]. Over the entire profile, the average organic carbon accumulation rate was 0.66 mol C m^{-2} yr^{-1} for 7100 years at this location in the wetland. The accumulation rate for the upper half of the profile was apparently faster, ~1.07 mol C m^{-2} yr^{-1} for 2400 years. The increased rate of carbon accumulation in the upper part of the profile may be a result of decreased decomposition during the cool period of 3800 years

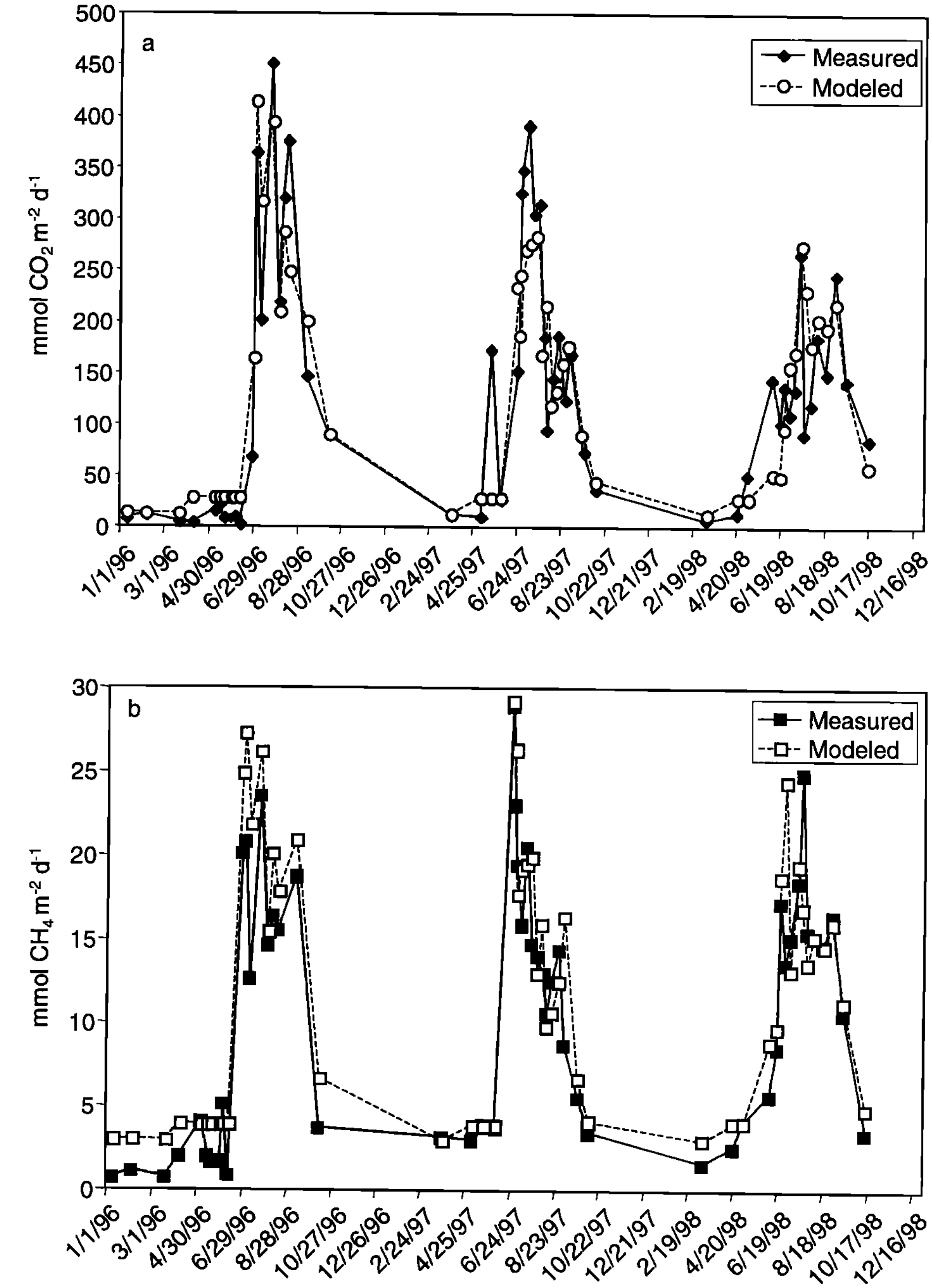

Figure 8. Measured and modeled (a) respiration, (b) CH_4 flux, and (c) photosynthesis, 1996-1998. The line in (c) represents a one to one relationship.

ago to the present. Specific rates of accumulation for the past several decades are not known.

5. Discussion

Although the wetland has accumulated carbon for the past 7100 years, we measured a net carbon flux from the wetland to the atmosphere during 1996-1998. This was not expected. One possible explanation may be that decreased solar radiation in combination with no change in temperature for the Colorado Front Range since the 1950s [*Williams et al.*, 1996] has caused a shift toward decreased primary production, with decomposition unaffected. It is not unusual, however, for a wetland to have large interannual variability in its carbon balance and even be a carbon source between periods of carbon gain [*Shurpali et al.*, 1995; *Joiner et al.*, 1999].

CO_2 and CH_4 emitted through the snowpack each year were a significant portion of the annual emissions and were even more important when considering the carbon balance. According to our model results, the wetland was essentially in balance during the growing seasons but was a net carbon source on an annual basis when the winter fluxes were included. Soil heterotrophic activity a under snowpack in alpine and subalpine sites in Wyoming mineralized 20-50% of yearly aboveground primary production [*Sommerfeld et al.*,

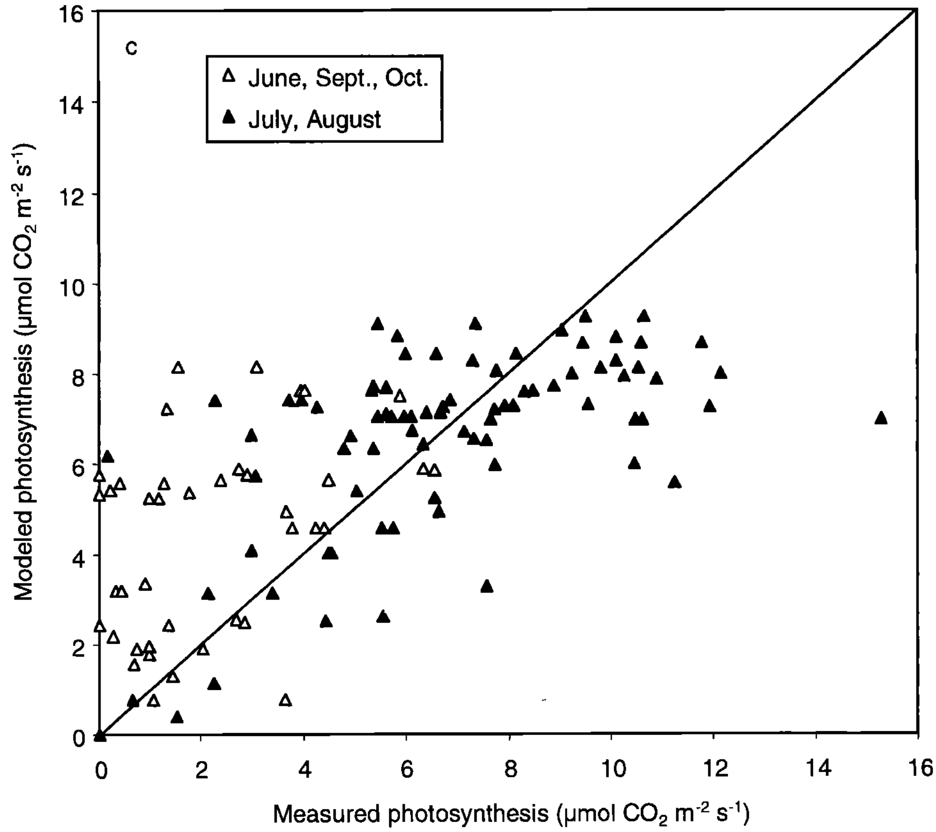

Figure 8. (continued)

1996]. CO_2 and CH_4 emissions continued through the winter because the snowpack acted as an insulating layer from cold air temperatures, preventing the soil from freezing. Microbial activity can continue at temperatures even slightly below freezing, so the timing and amount of snow accumulation is important in determining winter fluxes [*Brooks et al.*, 1997].

The amount of carbon lost annually to the atmosphere at the study wetland is within the range of losses observed at other wetlands. *Whiting* [1994] measured losses of 0.75 mol CO_2 m^{-2} and 1.75 mol CO_2 m^{-2} from a bog and a fen in Ontario during the growing season (153 days); *Shurpali et al.* [1995] measured a loss of 5.91 mol CO_2 m^{-2} during the growing season (145 days) from a Minnesota peatland during a relatively dry year; a New Hampshire wetland lost 12.1 mol C m^{-2} during 9 months one year [*Carroll and Crill*, 1997]; *Alm et al.* [1999] measured losses of 0.33 to 13.1 mol C m^{-2} yr^{-1} from a Finland bog; and a Manitoba wetland lost 2.56 mol CO_2 m^{-2} during the growing season (124 days)[*Joiner et al.*, 1999].

Carbon inputs and outputs other than CO_2 and CH_4 exchange were not measured. Additional carbon sources and sinks include hydrologic transport of dissolved and particulate carbon, grazing and waste deposition by elk, and litter input from avalanche debris. Dissolved organic carbon (DOC) may be very significant to a wetland's carbon balance [*Johnson et al.*, 1996; *Waddington and Roulet*, 1997] or be almost insignificant [*Carroll and Crill*, 1997]. The greatest potential of DOC transport through the wetland probably occurs during spring snowmelt [*Bachmann*, 1994]. Inputs of DOC from the dilute snowpack or from snowmelt run-off are probably not significant because the area above the wetland is mostly unvegetated or has thin soils. Loss of DOC from the wetland may be more significant. *Denning et al.* [1991] observed increased levels of DOC and nutrients in Loch Vale streams at the beginning of snowmelt, indicating a flush of soil solution into the surface water. Grazing and waste deposition by elk at the wetland were assumed to be insignificant compared to carbon gas exchange. In the winter of 1996, portions of spruce and fir trees were deposited in the wetland by an avalanche, which would provide substrates for soil heterotrophic activity. The carbon content of the woody debris was not determined.

Respiration and CH_4 emission were both significantly correlated with soil temperature. While this is not a new finding [*Yavitt et al.*, 1987; *Moore and Knowles*, 1990; *Raich and Schlesinger*, 1992; *Bubier et al.*, 1995], it is encouraging that the response to soil temperature was consistent spatially and temporally during the 3 year study period. The exponential relationship between respiration and soil temperature results from the combined response of microbial and plant respiration to temperature. Microbial respiration may account for more CO_2 emission early in the snow-free season, while plant respiration may contribute more as the growing season advances and biomass increases. However, it is difficult to separate the two sources of CO_2 [*Striegl and Wickland*, 1998].

CH_4 emission was significantly correlated with soil temperature during the entire snow-free season, but it changed from a linear relationship immediately after snowmelt to an exponential relationship as the growing season progressed. This may have been due to additional influencing factors such as substrate limitation of CH_4 production and/or increased CH_4 oxidation. Substrates from plant litter deposited the previous fall and not utilized during the winter may be consumed within days after complete snowmelt, resulting in the limitation of methanogenesis by substrate quality or availability later in the growing season [*Valentine et al.*, 1994]. It is also likely that methanotrophy increased during summer, consuming a large fraction of the CH_4 before reaching the atmosphere. Oxygen diffusing out of plant roots into the soil creates conditions favorable for methanotrophs [*Gerard and Chanton*, 1993; *Watson et al.*, 1997]. This may offset methanogenesis supported by plants root exudates probably supported methanogenesis, therefore reducing CH_4 emission.

The consistent flux-temperature relationships observed here may in part be due to the lack of water table height as a factor within and between years. During all snow-free periods there was standing water, and water table height did not exhibit large fluctuations. Water table height can be an important factor in determining the magnitude and direction of net CO_2 and CH_4 fluxes [*Moore and Roulet*, 1993; *Johnson et al.*, 1996; *Oechel et al.*, 1998; *Alm et al.*, 1999]. When the water table drops below the sediment surface, there is typically an increase in respiration from aerobic decomposition and a decrease in CH_4 emissions. If the aerobic layer is large enough, the soil may become a net CH_4 consumer. Several studies that report a net carbon loss from wetlands attribute the loss to low water table levels [*Shurpali et al.*, 1995; *Johnson et al.*, 1996; *Carroll and Crill*, 1997; *Oechel et al.*, 1998; *Alm et al.*, 1999; *Joiner et al.*, 1999]. A drop in the water table below the surface at the wetland would have probably resulted in an increased loss of carbon. Unsaturated areas surrounding the wetland exhibited much smaller CH_4 emissions or CH_4 consumption and respiration fluxes that were up to 5 times as large as those measured at the wetland [*Wickland et al.*, 1999; K.P. Wickland, unpublished data, 1998].

Photosynthesis was modeled using a simple equation that took into account only radiation and soil temperature. The decreased aboveground biomass in 1998 suggests that less photosynthesis occurred that year than in 1996 and 1997. However, our model did not capture this. The decreased biomass in 1998 may be the result of a number of things: nutrient limitation [*Chapin*, 1981; *Chapin and Oechel*, 1983; *Shaver et al.*, 1998], plant life cycles [*Callaghan*, 1976; *Bernard*, 1990], or possibly reduced growth caused by exposure to freezing temperatures early in the growing season [*Sakai and Larcher*, 1987].

High-altitude wetlands are commonly remote and difficult to access and therefore are difficult ecosystems to study. Our objective in relating flux to easily measured environmental variables such as soil temperature and radiation was to develop simple equations for the purpose of predicting carbon exchange when flux measurements are not available or not feasible. Variability in flux associated with processes unrelated to soil temperature or radiation is not captured by these simple equations. The applicability of our models to other high-altitude wetlands is a subject of further study.

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