Carbon dioxide exchange in a peatland ecosystem

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Abstract. Micrometeorological measurements of carbon dioxide exchange were made in an open peatland in north central Minnesota during two growing seasons (1991 and 1992). The vegetation at the site was dominated by *Sphagnum papillosum, Scheuchzeria palustris,* and *Chamaedaphne calyculata.* The objective of the study was to examine the diurnal and seasonal variations in canopy photosynthesis (P) and develop information on the net ecosystem CO_2 exchange. The two seasons provided contrasting microclimatic conditions: as compared with 1991, the 1992 season was significantly wetter and cooler. Canopy photosynthesis was sensitive to changes in light, temperature, and moisture stress (as indicated by water table depth and atmospheric vapor pressure deficit). Under moderate conditions (temperature 18–28°C, vapor pressure deficit 0.7–1.5 kPa, and water table near the surface) during the peak growth period, midday (averaged between 1000–1400 hours) P values ranged from 0.15 to 0.24 mg m^{-2} s^{-1}. Under high-temperature (30°–34°C) and moisture stress (water table 0.16–0.23 m below the surface and vapor pressure deficit 2.2–3.0 kPa) conditions, midday P was reduced to about 0.03–0.06 mg m^{-2} s^{-1}. There was a high degree of consistency in the values of P under similar conditions in the two seasons. Seasonally integrated values of the daily net ecosystem CO_2 exchange indicated that the study site was a source of atmospheric CO_2, releasing about 71 g C m^{-2} over a 145-day period (May–October) in 1991. Over a similar period in 1992, however, this ecosystem was a sink for atmospheric CO_2 with a net accumulation of about 32 g C m^{-2}. These results are consistent with previous investigations on CO_2 exchange in other northern wetland sites during wet and dry periods.

Introduction

Peat in northern wetlands contains about one third of the total world pool of carbon [e.g., *Miller et al.,* 1983; *Gorham,* 1991]. The carbon sink/source strengths in these important ecosystems, however, are not well understood. Northern wetlands have been thought to be a net sink for atmospheric CO_2 in the past [e.g., *Oechel et al.,* 1993]. How these ecosystems will respond to future climatic perturbations is not known. Recent studies [e.g., *Tans et al.,* 1990; *Oechel et al.,* 1993] suggest a possible shift in the carbon balance of northern boreal and arctic ecosystems, from a sink to a source. However, these results can not readily be generalized to other regions.

Some information is available on carbon dioxide fluxes in arctic and subarctic peatlands [e.g., *Coyne and Kelley,* 1975; *Billings et al.,* 1982; *Armamento and Menges,* 1986; *Oechel and Billings,* 1992]. However, very little is known about the carbon dioxide exchange in peatlands in other areas. Also, most of the prior studies have used chambers and are limited to small areas. Micrometeorological techniques have been recommended for measurement of large-scale fluxes of mass and energy. These techniques allow direct, continuous, and spatially integrated fluxes and cause minimal disturbance to the microenvironment being investigated. We know of only two short-term micrometeorological measurements of carbon di-

oxide flux in northern wetlands (*Coyne and Kelley* [1975], over a wet meadow tundra in Alaska, and *Neumann et al.* [1994], above a raised open bog at Lake Kinosheo in the southern Hudson Bay lowlands). Here, we report the results of a micrometeorological study conducted during two contrasting growing seasons (mid-May to mid-October 1991 and 1992) in a peatland in north central Minnesota. The primary objective of the study was to examine the diurnal and seasonal variations in canopy photosynthesis and net ecosystem CO_2 exchange at this site.

Materials and Methods

Site

The study site, referred to as the Bog Lake Peatland, is located in the Chippewa National Forest, adjacent to the Marcell Experimental Forest (47°32'N, 93°28'W) in north central Minnesota. The vegetation is dominated by *Sphagnum papillosum,* a carpet-forming moss species. The most common emergent species are *Scheuchzeria palustris* (a triseeded arrow grass), *Carex spp.* (sedges), and *Chamaedaphne calyculata* (leather leaf). Other prevalent species include *Rhynchospora alba* (beak-rush), *Sararacenia purpurea* (pitcher plant), and 1- to 3-m tall, widely scattered *Larix laricina* (tamarack). The organic soil of the peatland consists primarily of *Sphagnum*-derived peat. The surface consists of a pattern of hummocks (microhills of 0.15–0.55 m) and hollows (microvalleys). The site provided at least 250–300 m of upwind fetch of open
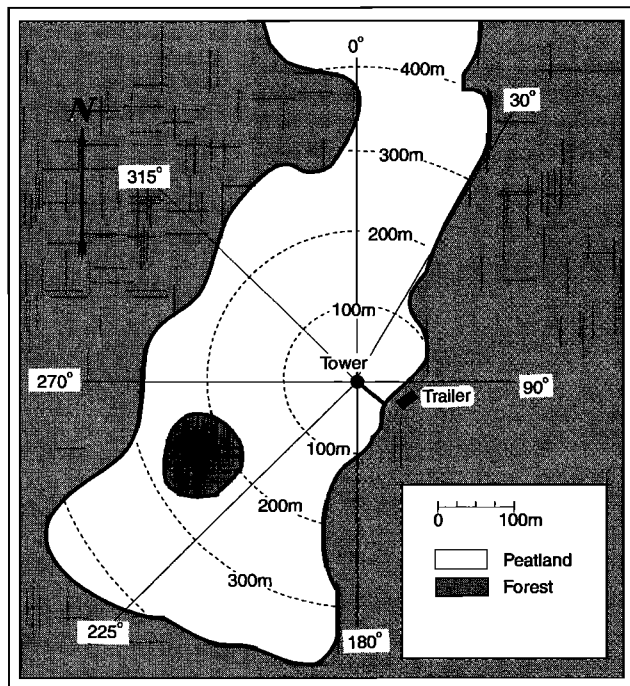
Figure 1. Map showing the area upwind of the instrument tower.

peatland from the instrument tower in the SSW through NNE (200°–390°) directions (Figure 1).

Micrometeorological Measurements

Fluxes of CO_2, latent and sensible heat, and momentum were made employing the eddy correlation technique. The eddy correlation system consisted of a closed path, differential, nondispersive, infrared CO_2 gas analyzer (model LI-6251, LI-COR Inc., Lincoln, Nebraska), one-dimensional sonic anemometers (Campbell Scientific, Logan, Utah), a three-dimensional sonic anemometer (Kaijo Denki Co., Tokyo, Japan), fine-wire thermocouples and krypton hygrometers (Campbell Scientific, Logan, Utah). The three-dimensional sonic anemometer and a fine-wire thermocouple were mounted at a height of 3.5 m above the peat surface. The rest of the instruments were mounted on a horizontal boom at a height of 2.5 m above the peat surface. Further details of the eddy correlation instruments and installation can be found in the works by *Verma* [1990], *Verma et al.* [1992], and *Suyker and Verma* [1993].

The CO_2 sensor was calibrated twice on each day of measurement. Eddy fluxes were obtained from covariances computed over 30-min averaging periods. The CO_2 flux was corrected for the variation in air density due to the transfer of water vapor following the method of *Webb et al.* [1980]. The use of metal intake tubing to draw air samples through the CO_2 sensor eliminated the need for the density correction term due to heat transfer [e.g., *Leuning and Moncrieff*, 1990]. Covariance values were corrected for the effects of tube attenuation [*Suyker and Verma*, 1993] and spatial separation of sensors [*Moore*, 1986]. The combined effect (tube attenuation and spatial sensor separation) was of the order of 10% for CO_2 flux for daytime conditions.

Supporting measurements included air temperature, humidity, horizontal wind speed, wind direction, and photosyntheti-

cally active radiation (R_p). Surface temperature was measured by an infrared thermometer (although the infrared thermometer was pointed toward an area dominated by moss, the measured values were assumed to represent the overall vegetation temperature). The daily water table position was recorded using a recording well installed near the instrument mast. The daily water table depth was measured relative to an "average" hollow surface referenced at 415.84-m altitude from the mean sea level. Peat temperature (at 0.1-m depth relative to an average hollow surface) was also monitored.

To evaluate the overall performance of the flux measurement system at a micrometeorological study site, it is worthwhile to investigate the tower footprint, examine the closure of the surface energy budget components, and develop information on aerodynamic characteristics, such as the drag coefficient. A footprint analysis [e.g., *Gash*, 1986; *Scheupp et al.*, 1990] indicated that about 90% of the measured flux at a height of 2.5 m (under neutral and unstable conditions) should be from the peatland. Results on the surface energy budget closure and drag coefficient for this site, included in the work by *Verma et al.* [1992], are typical of observations on agricultural crops and prairie vegetation in reasonably flat terrain.

Soil Surface CO_2 Measurements

A closed gas exchange system [*Norman et al.*, 1992] consisting of a 0.75 L dark chamber, attached to an infrared gas analyzer (model LI-6200, LI-COR Inc., Lincoln, Nebraska), was used to measure soil surface CO_2 flux (F_s). Details of these measurements are reported by *Kim and Verma* [1992]. An empirical relationship of the following type, developed from these measurements, was used in this study:

$$F_s = [(b_1 + b_2W)/(b_1 + 0.4b_2)]a_3a_4^{[(T-10)/10]} \quad 0 \le W \le 0.4 \text{ m}$$

(1)

where W is the water table depth (in meters), T is peat temperature (in degrees Celsius) at 0.10-m depth, b_1 is a nondimensional constant, b_2 is a constant with units of m^{-1}, a_3 is the soil surface CO_2 flux at 10°C (g m^{-2} d^{-1}), and a_4 is the temperature Q_{10} coefficient. The soil surface CO_2 flux was about 5–15 g m^{-2} d^{-1} during midseason in 1991. In 1992, when the water table was higher and air temperature substantially cooler (see the next section for details), the midseason soil CO_2 flux was smaller (4–8 g m^{-2} d^{-1}). These values of F_s include the contribution from moss dark respiration. We estimated this contribution by making soil CO_2 flux measurements at locations where the moss was clipped. Results indicated that the moss dark respiration during the midseason was about 1.5–3.0 g m^{-2} d^{-1} in 1991 and 1992.

Dark Respiration Measurements

Leaf level measurements at the study site were used to estimate the values of dark respiration of *Scheuchzeria palustris* and *Chamaedaphne calyculata*. The data were expressed by the following relationship:

dark respiration (vascular plants)

$$= R_d^r \exp \{E(T_l - 25)/[298R(T_l + 273)]\}L$$

(2)

where R_d^r is the rate of dark respiration in μmol m^{-2} s^{-1} at 25°C (1 μmol m^{-2} s^{-1} = 0.044 mg m^{-2} s^{-1}), E is the activation energy in J mol^{-1}, and T_l is the leaf temperature in degrees Celsius. Since these vascular plants grow in close proximity to

moss, T_l was approximated by the moss surface temperature measured by an infrared thermometer discussed above. R (8.314 J °K^{-1} mol^{-1}) is the gas constant. The values of R'_d and E were estimated to be 3.0 μmol m^{-2} s^{-1} and 42,884 J mol^{-1} for *Scheuchzeria palustris* and 1.9 μmol m^{-2} s^{-1} and 27,552 J mol^{-1} for *Chamaedaphne calyculata*, respectively. The term L represents the leaf area index of the vascular plants. The leaf area was measured using a hand-held leaf area meter (model LI-2000, LI-COR Inc., Lincoln, Nebraska). The value of L reached up to 0.6. This value was approximately equally partitioned between the two dominant vascular species. Moss dark respiration was estimated as described in the previous subsection.

Calculation of Canopy Photosynthesis

During daytime, F_c (the atmospheric flux measured with eddy correlation sensors) is the sum of the net uptake of CO₂ by the vegetation (or canopy photosynthesis, P) and the soil surface CO₂ flux due to microbial respiration:

$$F_c(\text{day}) = P + (1 - \alpha)R_s(\text{day}) \qquad (3)$$

The term R_s includes only the contribution from CO₂ evolution due to microbial activity in the soil and root respiration. We used an average value of 0.7 for the term α, which is the fraction of R_s due to root respiration [e.g., *Billings et al.*, 1977]. Equation (3) was used to compute canopy photosynthesis. On some days, F_c data during the early morning and late afternoon hours were missing. The missing F_c values were estimated by a canopy photosynthesis-light response relationship (5).

At night, F_c is the sum of R_s and the dark respiration (R_d) of the aboveground vegetation (vascular plants and moss):

$$F_c(\text{night}) = R_s(\text{night}) + R_d(\text{night}) \qquad (4)$$

Most of our CO₂ flux data are from daylight hours. Many nights were quite calm and did not allow accurate eddy flux measurements. The missing nighttime F_c values were estimated using the measurements of R_s and R_d in (4). A comparison of calculated and measured values, during the periods when the nighttime eddy correlation measurements were available, suggests that this approach is reasonable (Figure 2).

Results and Discussion

Microclimatic Conditions

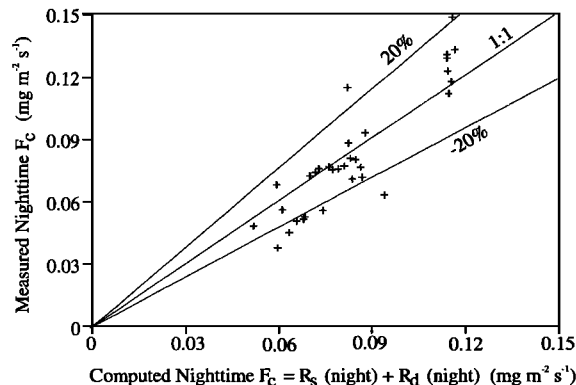The 1991 and 1992 seasons had contrasting microclimatic conditions. As compared with 1991, the 1992 season was wetter

Figure 2. Comparison of measured and calculated nighttime F_c.
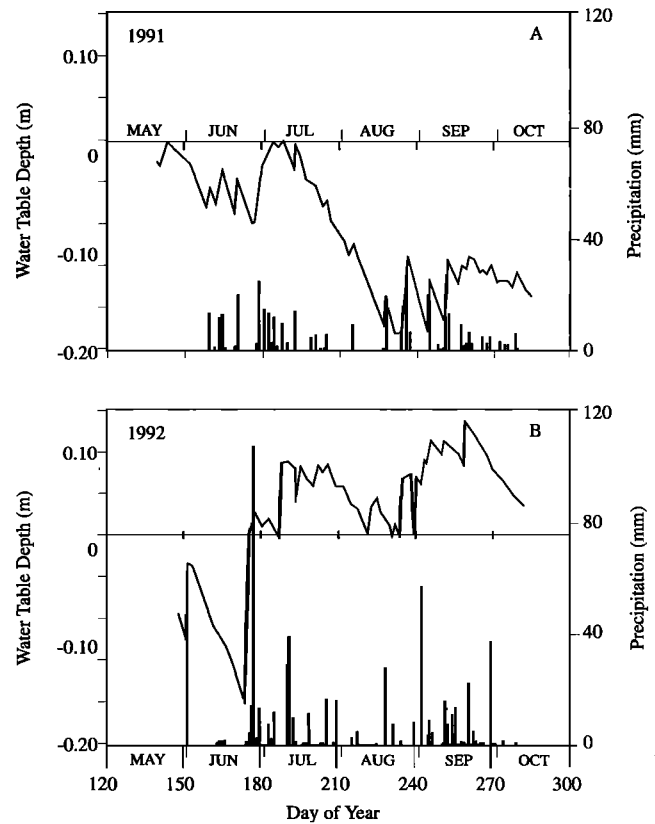
Figure 3. Seasonal distributions of precipitation and water table depth in (a) 1991 and (b) 1992. Water table depth is the distance of the water table from an average hollow surface (referenced at 415.84 m from the mean sea level). The negative value of water table depth indicates the water table position below the surface.

and cooler. The total precipitation and average temperature during May–October in 1991 were 452 mm and 14.9°C, while in 1992 these values were 642 mm and 13.4°C, respectively. The 30-year (normal) total precipitation and average temperature for the May–October period are 553 mm and 13.6°C.

The water table fluctuated within the first 0.10 m below an average hollow surface from late May until the third week of July in 1991 (Figure 3a). There was a sustained drop in the water table (from 0.08 to 0.23 m below the surface) during late July until the end of August. During the remainder of the 1991 season, the water table fluctuated between 0.14 and 0.22 m below the surface. The water table was generally above the surface during most of the 1992 season, except for a brief dry spell during late May to mid-June, when the water table declined from 0.03 to 0.20 m below the surface (Figure 3b).

Canopy Photosynthesis

Sphagnum papillosum and vascular plants such as *Scheuchzeria palustris* and *Chamaedaphne calyculata* were the dominant species contributing to canopy photosynthesis in this peatland. Chamber measurements of photosynthesis (T. J. Arkebauer, manuscript in preparation, 1995) and aboveground dry matter sampling indicated that the relative contribution of *Sphagnum papillosum* to the total canopy photosynthesis was about 50% and the remainder was contributed by vascular plants. Canopy photosynthesis in this ecosystem is affected by factors including light, temperature, moss moisture content, and atmospheric
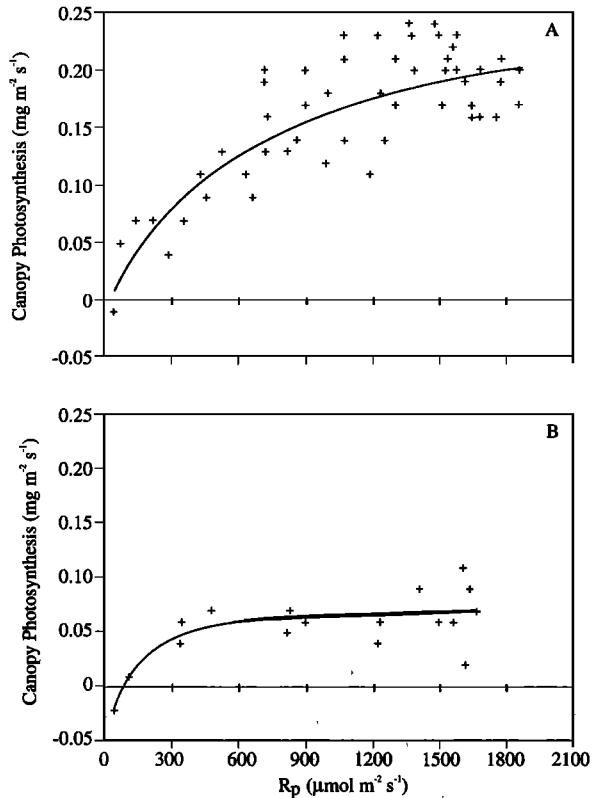
Figure 4. Canopy photosynthesis as a function of light (R_p) under (a) moderate conditions (temperature $\approx$20°–28°C, vapor pressure deficit $\approx$1.2–1.5 kPa, and water table 0.00–0.08 m below the surface) and (b) high-temperature (30°–34°C) and moisture stress (water table 0.21 m below the surface and vapor pressure deficit between 1.9 and 2.4 kPa). Data are fitted (nonlinear regression) with a rectangular hyperbolic relationship (see text for details).

vapor pressure deficit. Moss moisture content was not measured in this study. Variation in water table was used as a qualitative indicator of changes in moss moisture content.

Light response. The dependence of P on R_p is shown in Figure 4a. These measurements were from periods when temperature was moderate (20°–28°C), the water table was close to the surface (0.01–0.08 m below the surface), and vapor pressure deficit was low (1.2–1.5 kPa). Although there is some scatter in the data, a (rectangular) hyperbolic relationship between P and R_p can be seen. These data were fitted (nonlinear regression) with a relationship of the form [e.g., *Landsberg*, 1977]

$$P = a_1 a_2 (R_p - a_3)/[a_1 + a_2(R_p - a_3)] \qquad (5)$$

where a_1 is the maximum P, a_2 is the slope of the fitted curve at $P = 0$, and a_3 is the value of R_p at the light compensation point $(R^2 = 0.70)$. The values of a_1 and a_2 were 0.28 mg m^{-2} s^{-1} and 0.0004 mg CO$_2$ per μmol of R_p, respectively. The light compensation point (a_3) was estimated to be 33 μmol m^{-2} s^{-1}. *Skre and Oechel* [1981] reported values ranging from 10 to 140 μmol m^{-2} s^{-1} (at 20°C) for the light compensation point for *Sphagnum* species.

Data from periods with high temperature (30°–34°C), low water table (0.21 m below the surface, implying reduced moss moisture content), and high vapor pressure deficit (1.9–2.4

kPa) are shown in Figure 4b (a nonlinear least squares fit of these data to (5) yielded an R^2 value of 0.58). These data clearly depict the effects of high-temperature and moisture stress on photosynthesis of the peatland vegetation. Under these conditions, the value of a_1 was reduced to 0.07 mg m^{-2} s^{-1}. The coefficient a_2 remained about the same (0.0005 mg CO$_2$ per μmol of R_p). However, the value of the light compensation point (a_3) was much higher (81 μmol m^{-2} s^{-1}). A similar observation of increased light compensation point in mosses with increasing temperature has been reported by *Harley et al.* [1989]. *Oechel and Collins* [1976] reported an optimum temperature range of 10°–15°C for net photosynthesis of mosses at tundra sites. Under high-temperature and moisture stress, the moss surface tissue turns brown and presumably contains a lower percentage of photosynthetically competent cells [*Harley et al.*, 1989]. This may be a result of the gradual shrinkage of the *Sphagnum* protoplasts on removal of water from photosynthetically active cells [*Clymo and Hayward*, 1982; *Kaiser*, 1987; *Tenhunen et al.*, 1992]. Vascular plants commonly have somewhat higher optimum temperatures. T. J. Arkebauer (manuscript in preparation, 1995) found a marked decline in leaf photosynthesis for *Scheuchzeria palustris* at leaf temperatures above 30°C in a concurrent study at this site. *Limbach et al.* [1982] noted a significant reduction in net photosynthesis of three common tundra plant types (*Vaccinum vitis-idaea*, *Betula nana*, and *Carex aquatilis*) at leaf temperatures above 25°C. Temperatures ranging over 30°C were found to reduce photosynthesis of the vegetation in an open bog at Lake Kinosheo, near Ontario [*Whiting*, 1994]. The high-temperature and moisture stress (Figure 4b) therefore presumably affected the photosynthetic rates of the vascular plants also.

Diurnal variation. Shown in Figure 5 are values of P and R_p for a mostly clear day (July 23, 1991: day 205) with moderate conditions. On this day, temperature was 20°–24°C, the water table was 0.08 m below the surface, and vapor pressure deficit was 1.2–1.5 kPa. The value of P early in the morning was near zero. It increased with increasing light, and reached a peak value of 0.23 mg m^{-2} s^{-1} at about 1000 hours. Photosynthesis decreased later in the day and was 0.06 mg m^{-2} s^{-1} late in the afternoon.

The midmorning peak in P and a subsequent decline later in the day is typical at this study site for days with moderate conditions and is similar to the pattern of atmospheric CO$_2$ flux reported in previous studies (e.g., in an open bog at Lake Kinosheo in northern Ontario, Canada [*Neumann et al.*, 1994]). The decline in P after the midmorning hours could be due to a combination of several factors, such as the vegetation's light response characteristics coupled with increasing ambient temperature and vapor pressure deficit. Moss species are known to attain light saturation at low intensities [*Harley et al.*, 1989]. Data in Figure 4a indicate a tendency toward light saturation above 1200 μmol m^{-2} s^{-1}, which occurs around midmorning hours on clear days. Also, temperature and vapor pressure deficit were significantly higher (by 5°–6°C and 0.2–0.3 kPa, respectively) in the afternoon hours (Figure 5c). With higher evaporative demand in the afternoon hours, the moss surface became drier. Vascular plant gas exchange may also be affected by increases in temperature and vapor pressure deficit. Under these conditions, the midday depression of photosynthesis has been observed in other species [e.g., *Tenhunen et al.*, 1980; *Raschke and Resemann*, 1986].

The peak P rate mentioned above (0.23 mg m^{-2} s^{-1}) is similar to values observed in other wetland studies (atmo-

spheric CO_2 flux ≈ 0.18 mg m^{-2} s^{-1} in a wet meadow tundra near Barrow, Alaska [Coyne and Kelley, 1975]; 0.15 mg m^{-2} s^{-1} in an open bog at Lake Kinosheo in northern Ontario, Canada [Neumann et al., 1994]; 0.1–0.2 mg m^{-2} s^{-1} in fen and bog sites at Lake Kinosheo, Ontario, Canada [Whiting, 1994]). Considerably higher values of midday atmospheric CO_2 flux, however, have been observed in agricultural crops (1.0–2.0 mg m^{-2} s^{-1} [Anderson and Verma, 1986; Baldocchi et al., 1983; Monteith et al., 1964]), in grasslands (0.6–1.3 mg m^{-2} s^{-1} [Kim and Verma, 1990]), and in deciduous and coniferous forests (0.4–1.0 mg m^{-2} s^{-1} [Jarvis et al., 1976; Verma et al., 1986]). These differences in CO_2 fluxes can be attributed to differences in plant photosynthesis and respiration rates and soil biological activities (e.g., root respiration, decomposition of organic matter).

Seasonal variation. Midday (averaged between 1000 and 1400 hours) P during the 1991 season is plotted in Figure 6a. In the beginning of the growing season (middle to late May) the vascular canopy was just developing and the value of P was

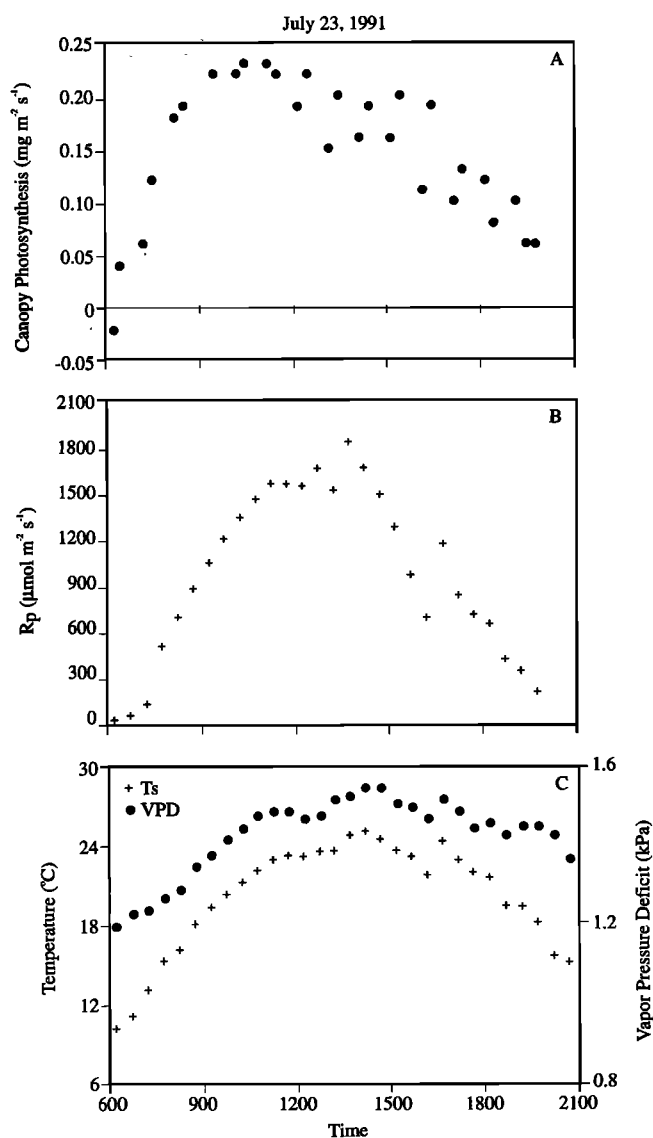Figure 6. Seasonal distributions of canopy photosynthesis in (a) 1991 and (b) 1992.

Figure 5. Daytime pattern of (a) canopy photosynthesis, (b) photosynthetically active radiation (R_p), and (c) surface temperature (degrees Celsius) and vapor pressure deficit (kPa) on July 23, 1991.
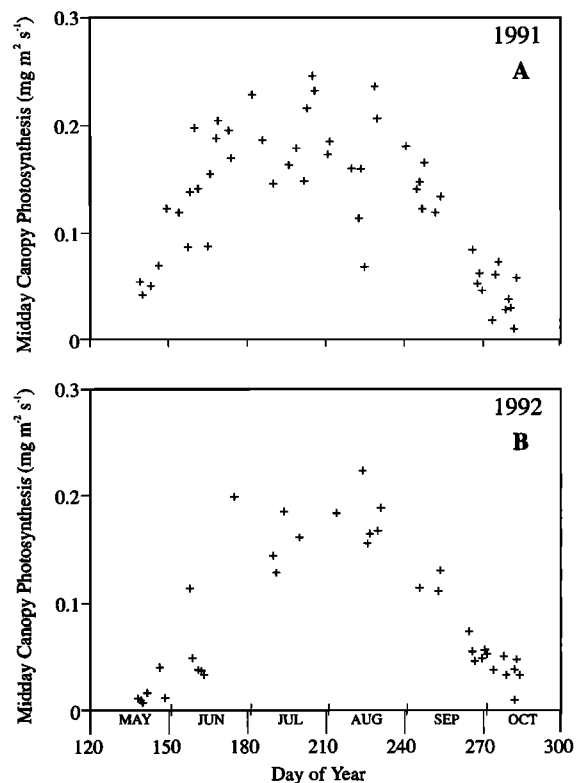
small (0.04–0.07 mg m^{-2} s^{-1}). The value of P increased to 0.12 mg m^{-2} s^{-1} during the first week of June and ranged from 0.09 to 0.24 mg m^{-2} s^{-1} during the period from the second week of June to the third week of July. During this period, temperature (22°–28°C) and vapor pressure deficit (0.8–1.2 kPa) were moderate, and the water table was close to the surface (0.00–0.07 m).

Following a peak (0.24 mg m^{-2} s^{-1}) during the third week of July, P declined to a low of 0.06 mg m^{-2} s^{-1} in the second week of August (day 227). The water table dropped continuously (from 0.08 to 0.23 m below the surface) from late July until the end of August. The reduced values of P during the second week of August were associated with high temperature (30°–34°C) and moisture stress (water table was 0.21 m below the surface, and vapor pressure deficit was between 1.9–2.4 kPa). This drop in P was followed by 20 mm of precipitation on August 16 (day 229) and moderate temperature (18°–22°C) and low vapor pressure deficit (0.7–1.0 kPa) during the third week of August. In this period, P reached 0.23 mg m^{-2} s^{-1}. The values of P declined from 0.17 mg m^{-2} s^{-1} by the end of August to 0.05 mg m^{-2} s^{-1} in late September and 0.03 mg m^{-2} s^{-1} in the second week of October.

During late May in 1992 (Figure 6b), P was low (0.01–0.04 mg m^{-2} s^{-1}). These values are similar to those observed during this period in 1991. There was a dry spell beginning in the last week of May until the second week of June. Photosynthesis declined from 0.12 mg m^{-2} s^{-1} during the first week of June to 0.03 mg m^{-2} s^{-1} during the second week of June. These small values of P (as compared with those in the corresponding period in 1991) were likely due to high-temperature (29°–30°C) and moisture stress (water table was about 0.18 m below the
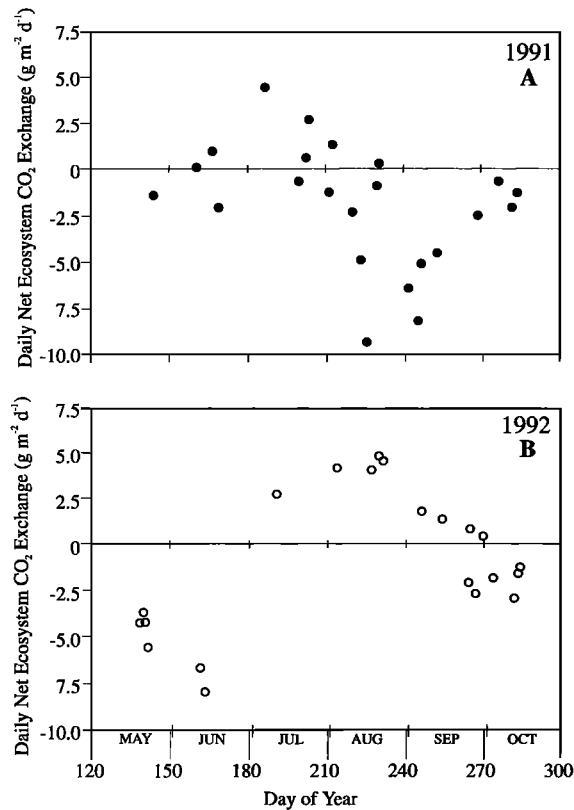
Figure 7. Seasonal distributions of daily net ecosystem CO_2 exchange in (a) 1991 and (b) 1992.

surface and vapor pressure deficit was between 2.5 and 3.0 kPa).

Ample rainfall (about 145 mm) raised the water table above the surface during the third week of June. Canopy photosynthesis increased to 0.20 mg m^{-2} s^{-1} by late June. Subsequent rainfall during the remainder of the season kept the water table at or above the surface. Canopy photosynthesis ranged from 0.13 to 0.23 mg m^{-2} s^{-1} during the period from the second week of July to the third week of August. In this period, temperature was moderate, ranging from 18° to 24°C, and vapor pressure deficit was 0.5–1.4 kPa. These values of P are comparable with those observed during the second week of June to the second week of July in 1991, when temperature, vapor pressure deficit, and water table conditions were similar. The values of P ranged from 0.13 mg m^{-2} s^{-1} in early September to 0.03 mg m^{-2} s^{-1} in mid-October.

Daily Net Ecosystem CO₂ Exchange

The net daily exchange (F) of $\overset{\cdot}{C}O_2$ between this ecosystem and the atmosphere was calculated by integrating F_c data over 24-hour periods:

$$F = F_c(\text{day}) + F_c(\text{night}) \qquad (6)$$

A positive value of F implies that the ecosystem is a sink for atmospheric CO_2. The seasonal distributions of F in 1991 and 1992 (Figure 7) indicate significant day-to-day and interannual variations.

Early season. The value of F was −1.4 g m^{-2} d^{-1} in late May 1991, and it ranged from −5.5 to −3.6 g m^{-2} d^{-1} during the same time in 1992. Peat decomposition and plant respiration exceeded canopy photosynthesis early in the season. Dur-

ing this period in 1992 the water table was lower, and peat temperature was higher, which caused greater release of soil CO_2, thus resulting in more negative values of F.

In the second week of June the value of F was 0.9 g m^{-2} d^{-1} in 1991 and −7.9 g m^{-2} d^{-1} in 1992. This difference in F was associated with the contrasting conditions that prevailed during this time in 1991 and 1992. Moderate temperature (22°–27°C), vapor pressure deficit (0.7–1.5 kPa), and high moss moisture content (water table 0.04–0.06 m below the surface) conditions favored high canopy photosynthesis and small soil CO_2 release during this period in 1991. On the other hand, higher temperature and vapor pressure deficit and lower moisture content (the water table was 0.16–0.18 m below the surface) in 1992 reduced P. In addition, the decrease in water table and high temperature resulted in a release of large amounts of soil CO_2 (about 10 g m^{-2} d^{-1}) to the atmosphere during this time in 1992.

Midseason. During the first week of July to the first week of August, temperature (18°–28°C) and vapor pressure deficit (0.8–1.2 kPa) were generally moderate in both years. The water table elevations, however, were different. The water table dropped (0.00–0.14 m) below the surface during this time in 1991 (implying continued depletion of moss moisture content and hence decreasing photosynthetic rates and increasing soil CO_2 flux). In 1992 the water table was above the surface (resulting in low rates of soil CO_2 release). Accordingly, the values of F indicated opposite trends during this period in the 2 years: F declined from 4.4 to 1.4 g m^{-2} d^{-1} in 1991 and increased from 2.8 to 4.2 g m^{-2} d^{-1} in 1992.

In 1991 the drop in the water table continued until the end of August. During the middle of August in 1991 the water table was low (0.21 m below the surface). The increased aerated depth below the surface and high temperature caused a substantially greater soil CO_2 flux (about 13 g m^{-2} d^{-1}) to the atmosphere. Also, high-temperature (30°–34°C) and moisture stress conditions resulted in a significant reduction in photosynthesis. Hence the peatland was a source of CO_2 releasing 9.2 g m^{-2} d^{-1} during this time. During the same period in 1992, however, conditions were favorable for high photosynthesis and small soil CO_2 flux. Accordingly, the peatland was a sink for CO_2 during the middle of August with a peak CO_2 uptake rate of 4.9 g m^{-2} d^{-1} in the third week of August.

Late season. The photosynthetic rate declined toward the end of the season. Soil CO_2 release also decreased. In 1991 the water table was below the surface during the period from the end of August to mid-October, and the soil CO_2 flux exceeded the uptake by canopy photosynthesis. Thus the ecosystem remained a source of atmospheric CO_2. The magnitude of F decreased toward the end of the season (F ranged from −8.1 to −2.5 g m^{-2} d^{-1} during the month of September and from −2.5 to −0.7 g m^{-2} d^{-1} during the first 2 weeks of October). In 1992, however, moisture conditions were nonlimiting, and the ecosystem was a sink until mid-September ($F \approx 1.5$ g m^{-2} d^{-1}). Toward the end of the season (mid-September to mid-October), due to rapid reduction in canopy photosynthesis, the values of F ranged from 0.4 to −2.9 g m^{-2} d^{-1}.

Seasonally integrated values. Integration of the daily net ecosystem CO_2 exchange indicated that this ecosystem released about 71 g C m^{-2} over a period of 145 days (mid-May to mid-October) in 1991. As was discussed above, moisture stress conditions prevailed during the later half of the growing season in this year, which reduced the uptake of CO_2 by the vegetation. The decrease in water table led to enhanced soil

aeration and increased release of soil CO_2. Wetlands have been reported to be possible sources of atmospheric CO_2 under moisture stress conditions. *Billings et al.* [1982] measured CO_2 exchange from intact cores from the wet coastal arctic tundra at Barrow, Alaska. They found that lowering the water table from the surface to 0.05 m below had a pronounced effect in reducing net carbon storage and concluded that greenhouse warming could change this ecosystem from a sink to a source. *Oechel et al.* [1993] made whole-ecosystem CO_2 flux measurements over five seasons at Toolik Lake, Alaska. They reported a net carbon loss to the atmosphere at all sites measured. They attributed the carbon loss at their sites to a decrease in the water table, enhanced drainage, and soil aeration. The average rate of annual CO_2 loss at their sites ranged from 34 to 156 g C m^{-2} yr^{-1}. *Whiting* [1994] found that the open bog and interior fen sites near Lake Kinosheo, Ontario, released carbon to the atmosphere at rates between 9 and 21 g C m^{-2}, respectively, over a 153-day growing season. Measurements of CO_2 exchange by *Grulke et al.* [1990] also indicated a net loss of carbon (53.4 g C m^{-2} yr^{-1}) from an upland tussock tundra site in Alaska.

The 1992 season was wetter and had conditions favorable for high photosynthesis and low rates of soil CO_2 release. Accordingly, this ecosystem was a sink for atmospheric CO_2 with a net accumulation of 32 g C m^{-2} over a 145-day period (mid-May to mid-October). Previous investigations have reported wetland sites to be sinks for CO_2 during wetter periods. *Coyne and Kelley* [1975] measured a net seasonal uptake of 40 g C m^{-2} yr^{-1} over a wet meadow tundra site in Barrow, Alaska. *Whiting* [1994] estimated a net uptake of 6 g C m^{-2} in a productive coastal fen site near Lake Kinosheo, Ontario, over a 153-day growing season. *Neumann et al.* [1994] reported an average daily net ecosystem exchange rate of 1.7 g CO_2 m^{-2} d^{-1} in an open bog at Lake Kinosheo during the month of July in 1990.

Summary and Conclusions

Carbon dioxide flux was measured during the 1991 and 1992 seasons in a Minnesota peatland. On days with moderate conditions, the canopy photosynthesis (P) data indicated a midmorning peak. The subsequent decline in P was likely associated with increasing temperature and vapor pressure deficit in the afternoon hours. The light compensation was estimated to be 33 μmol m^{-2} s^{-1} under moderate conditions. This value is consistent with those reported for similar vegetation types in northern wetlands.

During the early part of the season (late May to early June), midday P ranged from 0.01 to 0.12 mg m^{-2} s^{-1}. During the period from mid-June to mid-August, photosynthesis varied from 0.15 to 0.24 mg m^{-2} s^{-1} when temperature was moderate and the water table was close to the surface. Under high-temperature and moisture stress conditions, P declined to 0.03–0.06 mg m^{-2} s^{-1}. Toward the end of the season (late September to mid-October), canopy photosynthesis decreased to small values (0.03–0.05 mg m^{-2} s^{-1}).

The daily net CO_2 exchange showed significant day-to-day and year-to-year variations. During most of the 1992 season, moisture conditions were nonlimiting, and temperatures were moderate. Accordingly, canopy photosynthesis was high, soil CO_2 flux was small, and this ecosystem was a sink for atmospheric CO_2. Because of high temperatures and a low water table in the 1991 season, photosynthetic rates were low, and large amounts of soil CO_2 were emitted; hence the ecosystem

was a source of atmospheric CO_2. These results indicate that the predicted higher temperature and lower water table elevations, due to greenhouse warming [e.g., *Gorham*, 1991], could significantly affect the net ecosystem CO_2 exchange in northern wetlands and, consequently, change them from sinks to sources of atmospheric CO_2.

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