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CO_2 and CH_4 flux between a boreal beaver pond and the atmosphere

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Abstract. The surface-atmospheric exchange of CO_2 and CH_4 was measured continuously using the flux gradient approach from a beaver pond in the northern study area of the Boreal Ecosystem-Atmosphere Study between May 22 and September 19, 1994. The beaver pond was a large source of CO_2 and CH_4 for the entire study period. The half-hourly mean flux of CO_2 and CH_4 ranged from −0.498 to 1.135 mg CO_2 m^{-2} s^{-1} and from −0.805 to 37.5 μg CH_4 m^{-2} s^{-1}, respectively, while the seasonal mean fluxes were 0.072 ± 0.095 mg CO_2 m^{-2} s^{-1} and 1.26 ± 1.87 μg CH_4 m^{-2} s^{-1}. The beaver pond rarely took up CO_2. There was a large flux of both gases during the daytime. This increase is related to the transfer of the gases rather than to specific controls on production. The total efflux of CO_2 and $CH_4$for the 120 days of the study was 678 g CO_2 m^{-2} and 11.3 g CH_4 m^{-2}, or 183 and 8.4 g C m^{-2}, respectively. When the measurements ceased, the sediment temperatures were >10°C, so it is reasonable to expect that the fluxes of CO_2 and CH_4 continued into the late fall. This indicates that the beaver pond released more than 200 g C m^{-2} yr^{-1}.

Introduction

The landscape of the boreal biome comprises a mixture of land surface types. These include spruce, pine and aspen forests, wetlands, and lakes. Most of the wetlands in the boreal region are peatlands [*Polyscience*, 1988], but beaver ponds, a particular type of shallow open water wetlands can account for between 5 and 10% of all wetlands [*Roulet et al.*, 1992]. Previous studies have indicated that beaver ponds and their associated wetlands are large sources for methane [CH_4] [e.g., *Ford and Naiman*, 1988; *Yavitt et al.*, 1990; *Roulet et al.*, 1992; *Yavitt et al.*, 1992; *Bubier et al.*, 1993]. Measurements show that heterotrophic sediment respiration in beaver ponds is large [*Naiman et al.*, 1986, 1988] suggesting that the efflux of CO_2 may also be large. Because beaver ponds appear to be a large source located among ecosystems such as forests [*Schimel et al.*, 1994] and peatlands [*Gorham*, 1995] that are thought to be sinks for carbon, beaver ponds may play a disproportionately important role in the regional scale carbon exchange, even though they represent a small fraction of the landscape.

The role beaver ponds play in the boreal biome carbon exchange is determined by the fluxes of CO_2 and CH_4 and the areal extent of the beaver ponds. There are no continuous measurements of either CO_2 or CH_4 from beaver ponds reported in the literature. Measurements using enclosures and surface water concentrations in conjunction with the thin film boundary layer model show that beaver ponds can emit between 2 and 75 g CH_4 m^{-2} yr^{-1} (see review by *Moore and Roulet* [1995]). There are no comparable measurements for the flux of CO_2 from beaver pond, but annual rates of sediment respiration of between 30 and 70 g C m^{-2} yr^{-1} (110 and 260 g CO_2 m^{-2} yr^{-1}) have been reported [*Naiman et al.*, 1986, 1988]. There is also a dearth of information on the areal extent of beaver ponds. Estimates of the percent coverage of specific areas of the boreal region by beaver ponds range from <2% [*Roulet et al.*, 1992; *Bubier et al.*, 1994] to >10% [*Naiman et al.*, 1988; *Johnston and Naiman*, 1990; *Johnston*, 1994]. Beaver populations are presently about 10% of the population that is believed to have existed prior to the heavy exploitation by Europeans in the 18th and 19th centuries [*Naiman et al.*, 1988].

The objectives of the overall study of beaver ponds in the northern study area (NSA) of the Boreal Ecosystem-Atmosphere Study (BOREAS) were to (1) continuously measure the flux of CO_2 and CH_4 from one beaver pond using micrometeorological techniques, (2) determine the processes that control the flux of carbon gases from beaver ponds, and (3) estimate the potential impact of beaver ponds in the boreal carbon budget by conducting a survey of many beaver ponds and develop a technique using some of the remote sensing done during BOREAS to compute the areal extent of beaver ponds. The purpose of the present paper is to report the results of our continuous measurements of CO_2 and CH_4 fluxes made during the ice-free season of the 1994 field campaign of BOREAS.

Study Site

The measurement of the CO_2 and CH_4 flux took place in a 5 ha beaver pond located in the NSA of BOREAS (55°55′N; 98°01′W; military grid reference 614887). The pond depths range from 0.25 to 2.2 m, but most of the pond is 0.5 to 1.0 m deep. The pond surface has three distinct cover types (Figure 1). A 75 m long open water area spanned the width of the pond from the dam to near the location of the tower base. This represents 25% of the area of the pond. Approximately 10% of the surface of the pond was covered with peat islands. The remaining pond area was sparsely covered with emergent vegetation (primarily *Carex aquatilis*, *Calamagrostis canadensis*, and *Potenilla paustris*) and submergent vegetation, primarily

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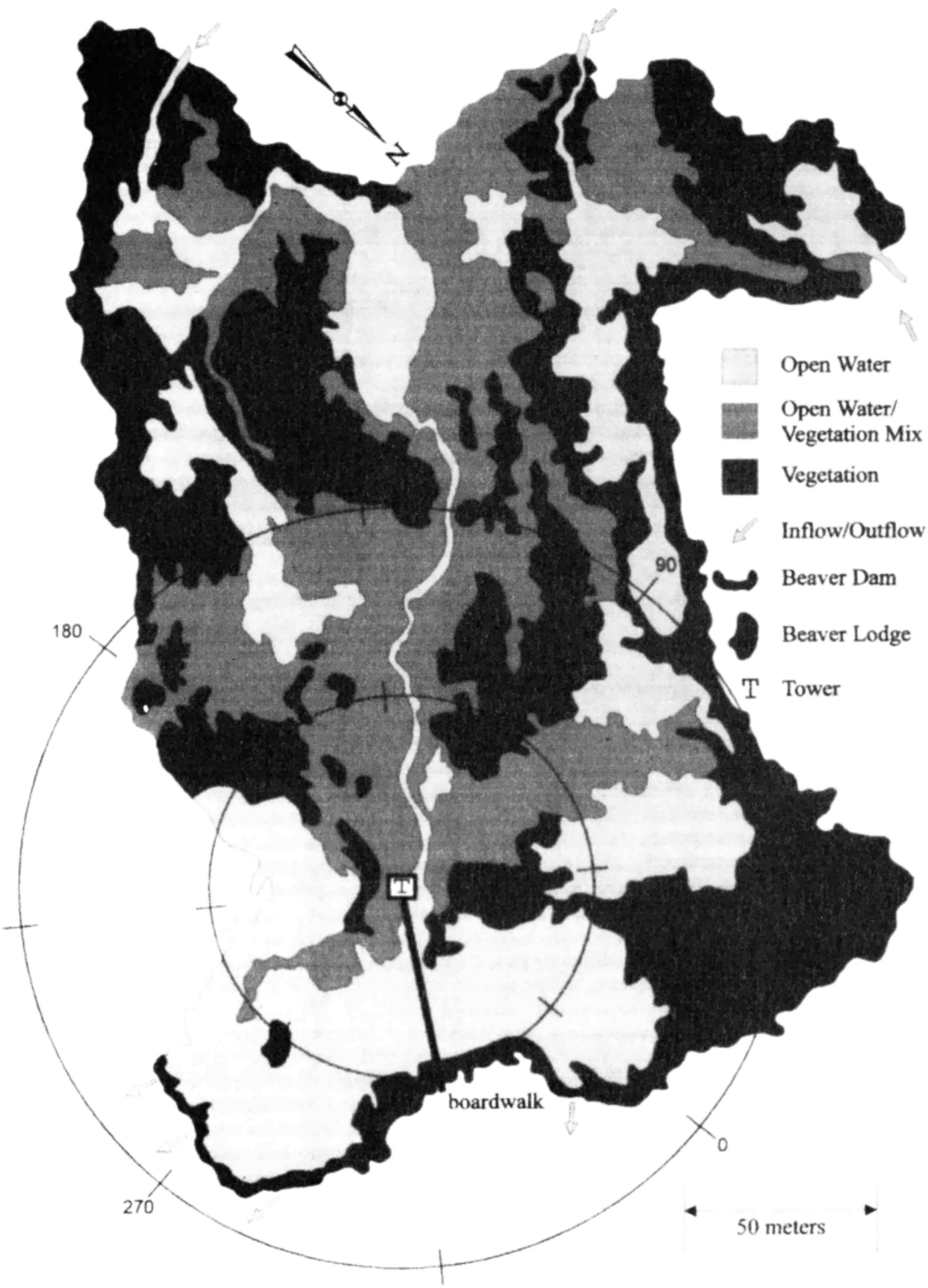

Figure 1. Distribution of cover types in the beaver pond. The location of the boardwalk and tower platform is shown.

Utricularia sps. (*U. vulgarius*, *U. cornata*, *U. intermedia*). The bulk density, nitrogen and carbon content of the sediments of the beaver pond, ranged from 93 to 105 kg m^{-3}, 1.3 to 1.4%, and 24.0 to 26.8%, respectively, for the upper 0.4 m, and from 292 to 509 kg m^{-3}, 0.8 to 1.1%, and 14.6 to 19.8% respectively, for sediments between 0.5 and 0.75 m (J. Harden, personal communication, 1995). The high carbon contents and very low bulk densities suggest that the beaver pond is an impounded riparian peatland.

Measurements and Methods

The measurements of the CO_2 flux began on May 22 and continued until September 19. The measurement of the CH_4

began on June 23. There were several short periods (<1 day) when measurements were suspended for instrument maintenance or for occasional problems. There were no measurements of CH_4 between July 15 and July 24 because of a generator failure.

The fluxes of both gases were computed by using the flux-gradient technique [*Fowler and Duyzer*, 1989; *Lenschow*, 1995]:

$$F_{CO_2} = K_m \, \delta\rho_{CO_2}/\delta z \tag{1}$$

where K_m is the transfer coefficient for CO_2, ρ_{CO_2} is the density of CO_2, and z is the height above the pond surface. The transfer coefficient was computed as $K_m = u_* \, k \, z$, where u_* is the friction velocity (determined from the slope of the slope of the wind profile: $u_* = k \, [(u_2 - u_1)/\ln(z_2/z_1)]$), k is von Karman's constant, and z is elevation. The transfer coefficient was then corrected for stability [*Dyer and Hicks*, 1970]. Wind speed was measured by using Young cup anemometers (stall speed of 0.2 m s^{-1}) at four heights: 0.25, 0.50, 1.00, and 1.50 m. The actual height of the wind sensors was determined for each half hour from continuous measurements of the elevation of the water level of the pond (±0.5 mm).

The concentration of CO_2 in air was measured using a LICOR 6250 infrared gas analyzer (IRGA) at 0.25 and 1.00 m above the surface. A continuous airflow (5 L min^{-1}) was drawn into a baffle for each elevation to equilibrate pressure, and then a subsample was drawn through the IRGA from each baffle at 1 L min^{-1} for 30 s. For the first 15 s no concentrations were measured as the new sample flushed the sample lines and the IRGA. In the last 15 s of a sample period the concentrations were measured every 12 Hz. A mean concentration for a given height was computed on the basis of a sample size of 75 obtained over the 15 s period. The IRGA was calibrated with a reference gas of a known concentration. Concentrations were resolved to ±40 ppbv. A profile was obtained every minute, and mean half-hour gradients were computed on the basis of 30 concentrations from each level. A half-hour averaging time is long enough to remove the bias produced by large magnitude, short duration fluctuations in the concentrations of CO_2 or CH_4 at one of the intakes but short enough to be in generally constant boundary condition.

CH_4 concentrations were determined for the same heights using a Shimadzu Mini II gas chromatograph equipped with a flame ionization detector. Samples were drawn continuously from 0.25 and 1.00 m at a flow rate of 2 L min^{-1}. A sample was injected into the gas chromatograph (GC) using an automated 1 ml sample loop from each level separated with a sample of a reference gas. The reproducibility between reference gas measurements was ±4 ppbv. To cycle through the two levels and a reference gas took ~6 min. Every half hour a mean concentration gradient was computed on the basis of five discrete concentrations from each level.

Photosynthetically active radiation, wind direction, air pressure, and water level were measured every minute to compute half-hour means. Water column (0.1, 0.2, 0.5) and sediment temperatures (0.01, 0.1, 0.2, 0.3, 0.5, and 1.0 m) were measured by using referenced thermocouples. Oxygen concentrations and redox potentials were obtained by a Hydrolab sensor. During most of the study period this sensor was stationary, recording dissolved O_2 at 0.9 m depth. At other times profiles of O_2 and temperature were obtained by using the same sensor.

All measurements with the exception of the O_2 concentration profiles were obtained at a tower platform positioned in the center of the beaver pond. The platform was erected to support a 2.5 m tower. Access to the tower was via a floating boardwalk. The wind fetch was limiting for flux measurements in two wind sectors. A 20° swath from 10° to 30°N was occupied by the boardwalk and obstructed by the tower (fetch = 55 m). At the section between 120° and 160° the distance to shore was <50 m. In all other directions the fetch ≥90 m. The fluxes obtained from the restricted fetch were not used in the analysis of the mean half-hourly or temporally integrated gas exchanges. The O_2 measurements were obtained in the open water area near the main dam of the pond. This was the deepest portion of the beaver pond.

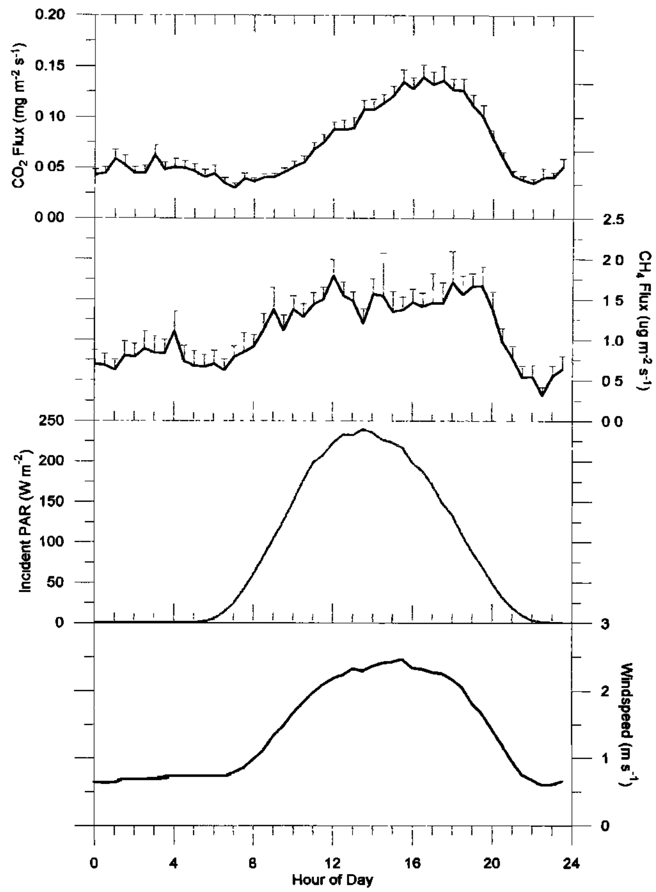

Figure 2. Diurnal pattern of mean half-hourly CO_2 and CH_4 flux, photosynthetically active radiation (PAR), and wind speed for the beaver pond for the period May 22 to September 19, 1994. Standard errors for the CO_2 and CH_4 flux are indicated.

Results and Discussion

Mean Diurnal and Daily CO_2 and CH_4 Fluxes

The seasonal mean half-hourly CO_2 and CH_4 fluxes for the entire study period were 0.072 ± 0.095 mg CO_2 m^{-2} s^{-1} and 1.26 ± 1.87 μg CH_4 m^{-2} s^{-1}, respectively. The maximum and minimum CO_2 fluxes observed were −0.498 and 1.135 mg CO_2 m^{-2} s^{-1}. The maximum and minimum CH_4 fluxes were −0.05 and 37.5 μg CH_4 m^{-2} s^{-1}.

There was a diurnal pattern to both the CO_2 and the CH_4 flux (Figure 2). The sample period mean half-hour flux of CO_2 was always positive, i.e., to the atmosphere. The diurnal pattern is closely related to the pattern in wind speed. The small-

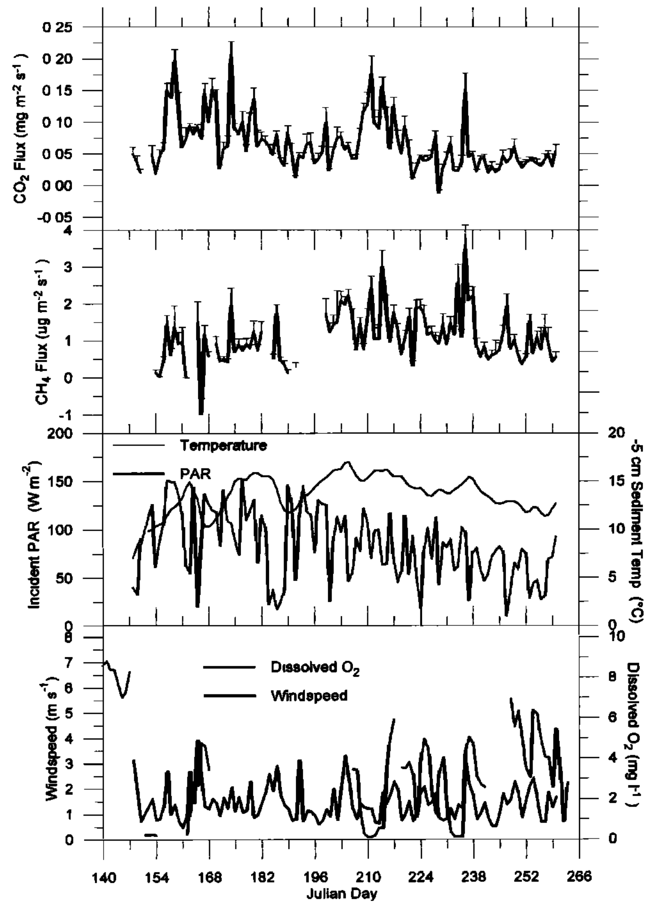

Figure 3. Seasonal pattern of mean daily CO_2 and CH_4 flux, PAR, sediment temperature, dissolved oxygen, and wind speed for the beaver pond for the period May 22 to September 19, 1996. Standard errors of the daily means are indicated for the CO_2 and CH_4 flux.

est flux was observed at dawn and sunset which corresponded to the minima in mean wind speed. CH_4 had generally the same pattern as CO_2. However, the amplitude of the diurnal change in CH_4 flux was not so great, nor did it follow the pattern of wind speed as closely as that of CO_2 (Figure 2).

The daily mean flux of CO_2 ranged from slightly <0.0 to >0.20 mg CO_2 m^{-2} s^{-1} (Figure 3). There was only one day (230) during the entire study period when a net uptake of CO_2 was observed; all of the other days the beaver pond was a net source of CO_2. The pattern of mean daily CO_2 flux appears to be related to the pattern of sediment temperatures. The broad pattern of greater fluxes earlier in the summer and a slight general decrease to early September is similar to the pattern in sediment temperature. There is also a higher-frequency pattern of change in CO_2 associated with changes in sediment temperature. Local peaks in CO_2 and sediment temperatures are synchronous around days 161-162, 175-180, 205-212, and 233-234. There are day-to-day variations in CO_2 flux that appear related to variations in the dissolved O_2 concentrations. Unfortunately, the record of O_2 concentrations is not complete. The dissolved O_2 concentrations at 0.9 m depth ranged from >6 to near 0 mg L^{-1}, but most of the time, the concentration varied between 1.5 and 4 mg L^{-1}.

The mean daily CH_4 flux ranged from −0.05 to 3.2 μg CH_4 m^{-2} s^{-1} (−4.1 to 276.5 mg CH_4 m^{-2} d^{-1}). As with the CO_2, there was a broad seasonal pattern to the mean daily CH_4 flux (Figure 3). The flux increased through the season to a period of peak fluxes around days 210–214 and another peak between 234 and 238. The first period of peak fluxes corresponds to the maximum daily mean sediment temperature (>17°C), while the second period corresponds to a second local maximum sediment temperature (>15°C). The maximum fluxes also correspond to a transition from a lower to a much higher wind speed.

Relationship Between Fluxes and Beaver Pond Environment

The seasonal patterns indicate that there is an association between the CO_2 and the CH_4 flux and several environmental factors related to the production, consumption, and therefore transport of the gases. The association between the gas fluxes and the environmental factors was examined by using the nonparametric Spearman correlation because many variables were not normally distributed.

The half-hourly flux of CO_2 was strongly correlated with wind speed (Table 1). The transfer of CO_2 across the air-water interface is a function mixing rate of the water surface to resupply CO_2, which is a function of wind drag. Both the mixing of the water and the turbulent transfer of air away from the air-water interface are a function of wind speed and atmospheric stability [*Denmead and Freney*, 1992]. The half-hourly flux is weakly correlated with photosynthetically active radiation (PAR), deeper sediment temperatures, and air pressure. The relationship between the CO_2 flux and the PAR exists since both variables follow the same diurnal pattern (see Figure 2). CO_2 could be causally linked to PAR due to the photosynthetic fixation of CO_2, but the CO_2 flux is always positive and higher during the day, indicating that the mechanical exchange dominates biological fixation. Wind is also strongly correlated with the CH_4 flux, and there is a strong correlation between the flux of CO_2 and CH_4, providing further evidence that mechanical exchange dominates biological processes. There are weaker positive correlations between PAR and sediment temperatures with the CH_4 flux. The correlation between sediment temperatures and CH_4 fluxes is reasonable,

Table 1. Spearman Correlation Coefficients for Half-Hourly Mean Flux of CO_2 and CH_4 Versus Various Environmental Variables

Independent Variable	CO_2 Flux	*N*	CH_4 Flux	*N*
CH_4 flux	0.544	3728	···	···
Air pressure	−0.128	5157	−0.189	3811
Wind speed	0.603	5157	0.531	3811
PAR	0.393	5157	0.273	3811
Underwater PAR	0.385	5157	0.260	3811
Dissolved O_2	−0.047	2436	−0.089	2063
Redox	−0.113	2436	−0.039	2063
Sediment temperature, m				
0.01	0.098	5154	0.202	3809
0.05	0.092	5154	0.218	3809
0.10	0.082	5154	0.227	3809
0.20	0.055	5154	0.223	3809
0.40	−0.043	5154	0.193	3809
0.75	−0.210	5154	0.014	3809
1.50	−0.174	5154	0.044	3809

PAR, photosynthetically active radiation.

given that the rate of microbial activity is controlled, in part, by temperature.

The interaction among variables which could either directly or indirectly control the flux of CO_2 and CH_4 from the beaver pond are numerous. In order to reduce the number of possible interactions the data set was divided into nighttime and daytime fluxes, and the mean daily flux for each of these periods was then examined against the environmental variables for the corresponding time period (Table 2). The logic behind this was to try and reduce the counteracting tendencies of carbon fixation and sediment respiration during periods of measurable PAR. The mean nighttime CO_2 flux was more strongly correlated with wind speed than it was when all the half-hourly data were used. Nighttime CO_2 was also correlated positively, though weakly, with dissolved O_2 and negatively correlated with air pressure. The correlations with sediment temperature were very weak. In contrast with the nighttime correlations the mean daytime CO_2 flux was not correlated with wind speed but was negatively correlated with dissolved O_2 and redox potential. The relationship with O_2 is expected, since a decrease in O_2 should be associated with an increase in CO_2 production, as O_2 is consumed during respiration. The positive correlations between sediment temperature and CO_2 is also expected, but it should be noted that these correlations become negative at depth. An examination of the propagation of the daily temperature wave with depth indicates that the peak temperature becomes progressively later in the day with increasing depth. This leads to the CO_2 flux and temperature of the deeper sediments being out of phase.

The daytime CH_4 flux was strongly correlated with sediment temperatures and negatively correlated with dissolved O_2 in the open water (Table 2). The nighttime CH_4 was strongly correlated with the CO_2, but this correlation arises because both fluxes correlate with wind speed, which determines K_m. The relationship between the daytime CO_2 and the CH_4 flux is much more subtle, but both fluxes are weakly correlated with wind speed during the day, again suggesting that the association between CO_2 and CH_4 fluxes is due to their covariance with transport phenomena.

The difficulty obtaining clear relationships has much to do with competing processes. Since the beaver pond is a net CO_2 source, the sediment respiration exceeds the photosynthetic fixation of CO_2. The role of photosynthetic fixation can be seen by examining the magnitude of the CO_2 flux with wind direction. The lowest positive CO_2 flux is in wind sectors with vegetated islands, or limited fetch which may be influenced by land adjacent to the beaver pond (Figure 4). The flux is greater from areas with sparse vegetation and open water. In areas that are more heavily vegetated, carbon fixation by the plants should partially offset the CO_2 produced by sediment respiration, leading to a reduced positive net ecosystem exchange. However, fixation is seldom sufficient to completely compensate for respiration; therefore no wind sector has a net carbon uptake. There is also likely some CO_2 fixation in the open water areas by phytoplankton, but this amount is probably quite low since the phytoplankton biomass is believed to be low. A single chlorophyll *a* concentration in early September was determined to be 4.3 mg L^{-1}, indicating the pond is fairly oligotrophic [*Wetzel*, 1983].

Table 2. Spearman Correlation Coefficients Describing Association Between Mean Daytime and Nighttime CO_2 or Mean Daytime CH_4 Flux and Mean Day or Nighttime Environmental Indicators

Independent Variable	Night CO_2	*N*	Day CO_2	*N*	Day CH_4	*N*
Mean CH_4 flux	0.862	86	0.226	93	···	···
Air pressure	−0.269	110	−0.001	112	−0.172	93
Wind speed	0.785	110	0.086	112	0.139	93
PAR	···	···	0.510	112	−0.102	93
Underwater PAR	···	···	0.162	112	−0.255	93
Dissolved O_2	0.154	53	−0.220	57	−0.227	53
Redox	0.077	53	−0.310	57	−0.070	53
Sediment temperature, m						
0.01	0.032	110	0.308	112	0.486	93
0.05	0.037	110	0.266	112	0.500	93
0.10	0.053	110	0.228	112	0.501	93
0.20	0.084	110	0.139	112	0.510	93
0.40	0.076	110	−0.139	112	0.440	93
0.75	···	···	−0.474	112	0.140	93
1.50	0.014	110	−0.398	112	0.210	93

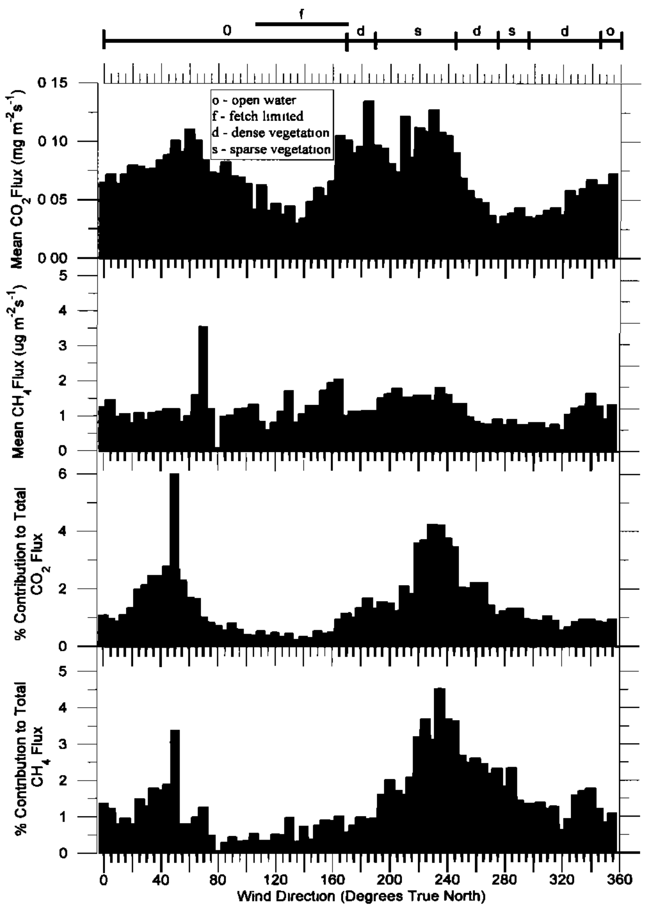

Figure 4. Mean daily flux of CO_2 and CH_4 and the percent contribution to the total spatially integrated flux for 10° wind sectors over the beaver pond. The *x* axis is annotated according to whether the sector is predominantly open water, sparse vegetation, or dense vegetation on peat islands. The notion *f* means the fluxes may be influenced by fluxes from the land adjacent to the beaver pond.

Integrated Seasonal CO_2 and CH_4 Exchange

The half-hourly flux for periods of good wind fetch were integrated for May 22 to September 19 for CO_2 and June 23 to September 19 for CH_4 (Table 3). There were relatively few half

Table 3. Time-Integrated Net Flux of CO_2 and CH_4 for the Study Period, Referred to as t in units, From May 22 to September 19, 1994

Gas	g m^{-2} t^{-1}	g C m^{-2} t^{-1}	CO_2: CH_4 (g C)
CO_2	677.9	183.0	21.8
CH_4	11.3	8.4	

hours of missing CO_2 flux with the exception of days 149–151, but there were two periods when the measurements of the CH_4 flux were interrupted (days 162–164 and 191–198). For these periods the missing flux was interpolated between the periods of measurements assuming a linear change with time. Examining the time series of both the CO_2 and CH_4 flux, they clearly do not change linearly with time; however, the interpolated fluxes fall in the midrange of the fluxes observed during the summer.

The total flux of CO_2 and CH_4 is large. The ratio of CO_2 to CH_4 flux is 21. The global warming potential (GWP) for CH_4 is 54 times more than that of CO_2; therefore beaver ponds would play a more important role in greenhouse gases through CH_4 than CO_2. However, beaver ponds are a very unique ecosystem in that they contribute positive fluxes of both CO_2 and CH_4. Most northern wetlands are sinks for CO_2 [*Gorham*, 1995] and sources for CH_4.

There are few data with which to compare the fluxes observed in this study. *Moore and Roulet* [1995] reviewed the flux data of CH_4 from beaver ponds and found it ranged from 2 to 75 g CH_4 m^{-2} yr^{-1}, with a mean and median flux from the 13 ponds of 36.6 and 13.8 g CH_4 m^{-2} yr^{-1}. Therefore the beaver pond in the present study is near the median value for boreal ponds. However, in comparison to the CH_4 flux from other northern wetland types [*Bartlett and Harriss*, 1993], the study pond is a large emitter. There are no comparable data for CO_2 flux from beaver ponds. The fluxes observed in the present study are 3 to 4 times larger than the heterotrophic respiration observed by *Naiman et al.* [1988], but it should be noted that we measured the net flux of CO_2 at the surface of the beaver pond, not sediment respiration. Presumably, the sediment respiration that supports the large CO_2 flux at the air-water interface is substantially larger than the flux, as there is evidence suggesting that there is some CO_2 uptake by the pond vegetation. It is interesting to note that the amount of carbon emitted as CO_2 is of the same magnitude (2–10 g CO_2 m^{-2} d^{-1}) of that respired from peat soil [*Kim and Verma*, 1992; *Whiting et al.*, 1992, 1994; *Waddington and Roulet*, 1996].

The total amount of carbon emitted to the atmosphere from the beaver pond during the study period was 191 g C m^{-2}. When the measurements ceased, the sediment temperatures were still above 5°C and the pond remained ice free for at least another month. If it is assumed the gas fluxes decrease linearly from September 19 to zero flux one month later, this would add another 20 g C m^{-2} and bring the total carbon source to 210 g C m^{-2}. Beaver ponds are located among forests and peatlands in the boreal biome, which are generally believed to be carbon sinks. *Gorham* [1991] estimates that the sink for carbon in northern peatlands, similar to the peatlands in the NSA of BOREAS, is between 20 and 30 g C m^{-2} yr^{-1}. There are no observations available yet on the areal extent of beaver ponds in the NSA, but *Roulet et al.* [1992] estimated that beaver ponds made up 7 to 10% of the wetland area in the low boreal region of Ontario. If beaver ponds represent 10% of the NSA wetland area, the carbon they emit can easily offset the carbon accumulation in the peatlands. Early indications of the CO_2 flux from the upland forests of the NSA suggest that they are a small sink, retaining no more than 50 g C m^{-2} yr^{-1} (D. Fitzgarrald and M. Goulden, personal communication, 1995). If beaver ponds represent more than 1% of the NSA area, they could also offset much of the upland forest sink for carbon. The determination of the absolute role of beaver ponds in the NSA carbon balance requires an estimation of beaver pond areal extent. This estimation is the subject of ongoing remote sensing investigations of BOREAS.

Conclusions

On the basis of the observations of this study, the study beaver pond is a large source of both CO_2 and CH_4 to the atmosphere. This result is particularly significant given that beaver ponds in the boreal biome are interspersed among ecosystems that are believed to be carbon sinks. The flux of CO_2 is believed to be supported by heterotrophic respiration of the sediments, and the CH_4 flux is sustained by the difference between methanogenesis in the sediments and CH_4 oxidation at the sediment-water interface and in the water column.

A readily available source of carbon is required to sustain such a large gaseous efflux. There are three potential sources of carbon: dissolved organic carbon input from the adjacent ecosystems, particulate carbon input from adjacent ecosystems actively transported to the pond by the beavers themselves, and/or respiration of the sediments of the pond. The dissolved organic input to the beaver pond is almost equal to the export of DOC from the pond (T. R. Moore, personal communication, 1995) and therefore does not represent a net source. An adult beaver can bring 1 t of woody plant material into a pond per year [*Nisbet*, 1989]. There were two adult beavers in the study pond representing a potential input of 2 tonnes. Assuming that 50% of the mass of a tree is organic carbon, then a 1 tonne or 1×10^6 g C yr^{-1} source per year is possible. Most of this input, however, is woody biomass, which is extremely difficult to decompose. The fresh, leaf biomass of trees usually represents less than 10% of the total tree biomass [*Schlesinger*, 1991]; therefore beavers might have introduced $\approx 1 \times 10^5$ g C yr^{-1} to the pond. Dividing the efflux of carbon measured from the study point into this potential input of carbon indicates the pond would need to be smaller than 470 m^2 in area. The beaver pond is in fact 50,000 m^2 in area, hence it is very unlikely that even a small proportion of the net efflux of carbon is supported from the actual activity of the beavers. Furthermore, beavers do not distribute the material they bring into the pond evenly: it either goes to the lodge to be used as food or to the dam to be used as building material. The far more probable source of carbon is from the beaver pond sediments which likely comprise a former riparian peatland given their high organic content. In a study of landscape conversion by beavers in northern Minnesota, *Johnston* [1994] found that over 70% of the sites flooded by beavers were peatlands or other types of wetlands prior to impoundment.

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