JOURNAL OF GEOPHYSICAL RESEARCH, VOL. 111, G02011, doi:10.1029/2005JG000099, 2006

Effects of permafrost melting on CO_2 and CH_4 exchange of a poorly drained black spruce lowland

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Received 7 September 2005; revised 8 February 2006; accepted 22 February 2006; published 2 June 2006.

[1] Permafrost melting is occurring in areas of the boreal forest region where large amounts of carbon (C) are stored in organic soils. We measured soil respiration, net CO_2 flux, and net CH_4 flux during May–September 2003 and March 2004 in a black spruce lowland in interior Alaska to better understand how permafrost thaw in poorly drained landscapes affects land-atmosphere CO_2 and CH_4 exchange. Sites included peat soils underlain by permafrost at ~0.4 m depth (permafrost plateau, PP), four thermokarst wetlands (TW) having no permafrost in the upper 2.2 m, and peat soils bordering the thermokarst wetlands having permafrost at ~0.5 m depth (thermokarst edges, TE). Soil respiration rates were not significantly different among the sites, and 5-cm soil temperature explained 50–91% of the seasonal variability in soil respiration within the sites. Groundcover vegetation photosynthesis (calculated as net CO_2 minus soil respiration) was significantly different among the sites (TW > TE > PP), which can be partly attributed to the difference in photosynthetically active radiation reaching the ground at each site type. Methane emission rates were 15 to 28 times greater from TW than from TE and PP. We modeled annual soil respiration and groundcover vegetation photosynthesis using soil temperature and radiation data, and CH_4 flux by linear interpolation. We estimated all sites as net C gas sources to the atmosphere (not including tree CO_2 uptake at PP and TE), although the ranges in estimates when accounting for errors were large enough that TE and TW may have been net C sinks.

Citation: Wickland, K. P., R. G. Striegl, J. C. Neff, and T. Sachs (2006), Effects of permafrost melting on CO_2 and CH_4 exchange of a poorly drained black spruce lowland, *J. Geophys. Res.*, *111*, G02011, doi:10.1029/2005JG000099.

1. Introduction

[2] The boreal forest biome covers the circumpolar region between ~50°N and 70°N, including large parts of North America and Eurasia [*Van Cleve and Dyrness*, 1983]. It occupies approximately 25% of the world's forested land surface [*Whittaker and Likens*, 1975], and boreal soils contain about one third of the world's soil organic carbon [*Post et al.*, 1982; *Billings*, 1987; *Gorham*, 1991]. Many regions of the boreal forest are underlain by discontinuous permafrost, where 50–90% of the area is frozen [*Brown et al.*, 1997]. Permafrost soils contain a considerable amount of organic carbon [*Billings*, 1987], and have important impacts on local hydrology [*Quinton and Marsh*, 1999]. There is evidence that temperatures of discontinuous permafrost have warmed during recent decades, approaching or surpassing the melting point in some areas. Permafrost temperatures in areas of Alaska increased up to 1.5°C from the late 1980s to the mid 1990s [*Osterkamp and Romanovsky*, 1999], and rates of permafrost thawing in boreal Canada have accelerated significantly since the mid-twentieth century [*Payette et al.*, 2004; *Camill*, 2005]. This warming is in response to increased air temperatures as well as to changes in the timing and depth of snow cover [*Osterkamp and Romanovsky*, 1999]. A major concern regarding thawing permafrost is the release of stored soil carbon to the atmosphere as carbon dioxide (CO_2) through increased decomposition upon thaw [*Shaver et al.*, 1992; *Oechel et al.*, 1993; *Goulden et al.*, 1998; *Smith et al.*, 2004]. Mobilization of this carbon could have important repercussions for global climate if it adds to atmospheric CO_2 concentrations [*Intergovernmental Panel on Climate Change* (*IPCC*), 1996].

[3] Permafrost melting will result in increased decomposition of soil organic matter and CO_2 release to the atmosphere if soils become drier as permafrost melts, making conditions for aerobic decomposition more favorable. However, permafrost thaw does not exclusively result in drier soils. The drainage condition of an area, as determined by local hydrology, topography, and geology, will largely dictate how permafrost thaw affects soil moisture condi-

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0148-0227/06/2005JG000099$09.00

tions. Permafrost thaw in well-drained areas such as hillslopes may lead to drier soils, while thaw in poorly drained areas can result in wetter soils. The most dramatic change in soil moisture conditions occurs where thawing of ice-rich permafrost in poorly drained landscapes results in areas of ground subsidence, or thermokarst [*Osterkamp et al.*, 2000; *Camill et al.*, 2001]. The ground may sink more than a meter and become saturated or have standing water, forming thermokarst ponds or collapse scar bogs/fens. The flooded area undergoes significant vegetation change as trees die and wetland vegetation such as *Carex* and *Sphagnum* mosses become established [*Camill et al.*, 2001; *Jorgenson et al.*, 2001]. Methane (CH_4) emissions produced from anaerobic decomposition may increase in areas where permafrost thaw results in significantly wetter soils [*Turetsky et al.*, 2002]. A significant increase in CH_4 release from these soils could also affect global climate, particularly because it is a powerful greenhouse gas [*IPCC*, 1996].

[4] Information regarding the effects of permafrost thaw on carbon (C) cycling in poorly drained landscapes where thermokarst wetlands form is limited to a small number of studies that focus primarily on organic matter (OM) accumulation rates and on CH_4 fluxes. These studies present evidence that thermokarst wetlands have greater OM accumulation rates over hundreds of years and emit greater amounts of CH_4 when compared to poorly drained permafrost soils. Organic matter accumulation rates in collapse bogs increased by 60–100% over 100–200 years in peatlands of Alberta and Manitoba, Canada [*Turetsky et al.*, 2000; *Camill et al.*, 2001], and by 50–200% over 1200 years in collapse wetlands in Northwest Territories, Canada [*Robinson and Moore*, 1999, 2000]. *Camill et al.* [2001] attribute greater accumulation rates in thermokarst wetlands to higher net primary productivity (NPP) of *Sphagnum* moss and *Carex*, and to slower decomposition rates induced by peat burial and recalcitrant peat chemistry. The response of C accumulation rates to thermokarst formation in peatlands studied by *Robinson and Moore* [1999, 2000] varied depending on the hydrology of the wetlands. Collapse bogs had 72% greater mean C accumulation rate over 1200 years than permafrost soils, but collapse fens had a statistically similar mean C accumulation rate as permafrost soils. Methane emissions from collapse wetlands formed by permafrost thaw were significantly higher than the surrounding permafrost soils in peatlands in Canada [*Bubier et al.*, 1995a; *Liblik et al.*, 1997; *Turetsky et al.*, 2002], Alaska [*Moosavi et al.*, 1996], and Sweden [*Christensen et al.*, 2004]. The single study in which CO_2 fluxes were measured [*Turetsky et al.*, 2002] reported that soil respiration rates were 60% higher at thermokarst wetlands than surrounding permafrost soils. *Bubier et al.* [1998] measured CO_2 exchange (net and gross) of a collapse bog and a collapse poor fen within a peatland complex underlain by discontinuous permafrost in Manitoba, Canada, but did not include permafrost soils. Soil respiration of permafrost soils at the same site measured two years earlier during May–September 1994 [*Savage et al.*, 1997] averaged 8.33 mmol CO_2 m^{-2} hr^{-1}, compared with a July–August 1996 mean of 8.78 and 11.52 mmol CO_2 m^{-2} hr^{-1} at the collapse bog and poor fen [*Bubier et al.*, 1998].

[5] These studies indicate that permafrost thaw in poorly drained systems commonly results in the formation of thermokarst wetlands that may have greater C accumulation rates and CH_4 emissions than permafrost soils. However, there is a need for additional information on how thermokarst wetland formation affects the magnitude and seasonality of CO_2 and CH_4 fluxes and the factors that control these processes, especially considering that further climate warming is expected to cause widespread permafrost thaw [*Stendel and Christensen*, 2002; *Camill*, 2005]. We studied C dynamics in four thermokarst wetlands and surrounding areas underlain by permafrost in interior Alaska by measuring gross CO_2 (soil respiration) fluxes, net CO_2 fluxes, net CH_4 fluxes, and ancillary data over a complete growing season and under snow cover. Our main objectives were to quantify seasonal C gas exchange of thermokarst wetlands and permafrost soils, and to identify the dominant controls on C gas fluxes.

2. Site Description

[6] The study site (64°41.773′N, 148°19.263′W) is located about 32 km southwest of Fairbanks, Alaska, and is adjacent to the Bonanza Creek Experimental Forest, which is part of the Long Term Ecological Research (LTER) program. It is a poorly drained lowland on level terrain near the Tanana River at ~120 m elevation. Permafrost is present at approximately 0.4 m depth, and organic soils extend to approximately 0.9 m depth. Active layer soils are generally saturated a few centimeters above the seasonal ice depth, which increases through the growing season. Stunted black spruce ((*Picea mariana* Mill.) B.S.P.) up to 130-years old are scattered across the site, interspersed with a small number of tamarack (*Larix laricina* (Du Roi) K. Koch). Mean height and diameter at breast height (dbh) of the black spruce trees are 3.7 m (range = 1.8–8.0 m) and 14.5 cm (range = 6.0–32.0 cm), respectively. Black spruce tree basal area is 8.7 m^2 ha^{-1}. Other vegetation includes shrubs such as narrow-leaf labrador tea (*Ledum decumbens* (Ait.) Small), dwarf arctic birch (*Betula nana* L.), leatherleaf (*Chamaedaphne calyculata* (L.) Moench), cloudberry (*Rubus chamaemorus* L.), bog cranberry (*Vaccinium vitis-idaea* L.), bog blueberry (*Vaccinium uliginosum* L.), and small bog cranberry (*Vaccinium oxycoccus* L.); herbaceous species such as sheathed cotton grass (*Eriophorum vaginatum* L.) and other various grasses; and mosses including *Aulacomnium turgidum* (Wahlenb.) Schwaegr., *Pleurozium schreberi* (Brid.) Mitt., *Hylocomium splendens* (Hedw.) B.S.G., *Sphagnum angustifolium* (Russow) C. Jens., *Sphagnum magellanicum* Brid., and *Sphagnum fuscum* (Schimp.) Klinggr.

[7] Isolated thermokarst features have formed within the lowland where permafrost has melted (Figure 1). In these areas the ground surface is 0.5–1 m lower than the surrounding forest and there is standing water in many places. The thermokarst wetland complex does not have surface water inlets or outlets, and continuous ponding suggests that groundwater drainage is poor. There are standing dead black spruce and tamarack trees in the thermokarst wetlands, and there are live leaning trees at the wetland edges. No permafrost is present to a depth of at least 2.2 m. Vegetation in these wetlands includes *Carex* spp., tall cotton grass (*Eriophorum angustifolium* Honckeny), marsh cinquefoil (*Potentilla palustris* (L.) Scop.),

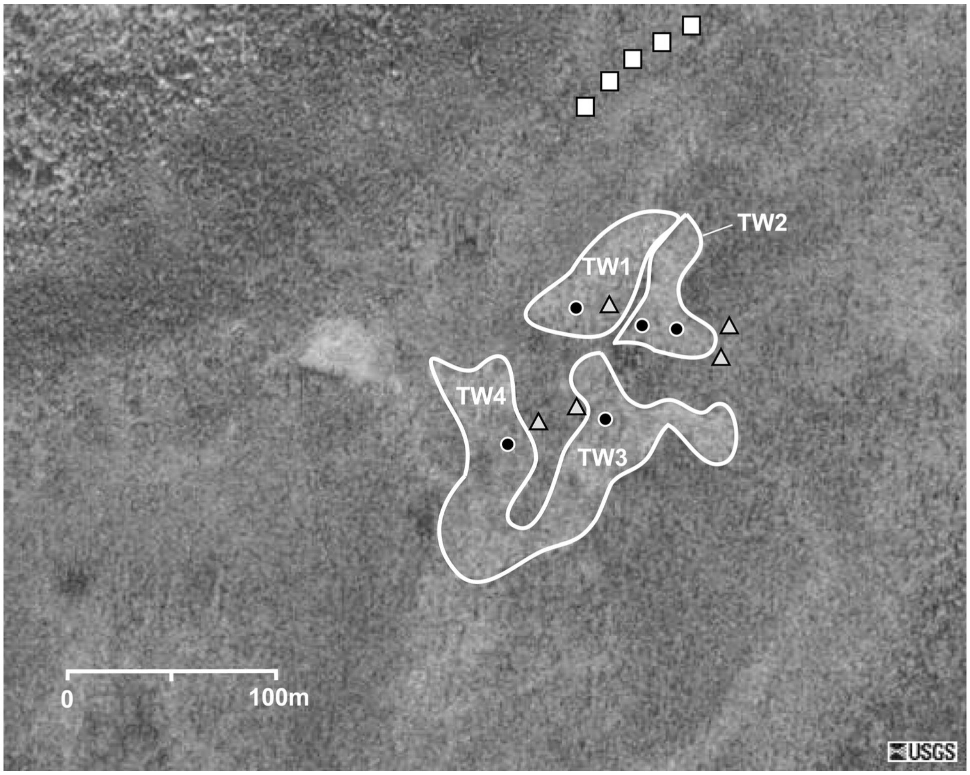

Figure 1. Aerial photo (1-m resolution) and map of study site. The symbols mark measurement locations (circles, Thermokarst Wetlands, TW; triangles, Thermokarst Edges, TE; squares, Permafrost Plateau, PP). The four thermokarst wetlands are outlined in white and labeled. The TE site within TW 1 is located on a small island that has not collapsed.

Sphagnum riparium Ångstr., *S. fuscum, S. angustifolium*, and *S. magellanicum*. The water table was within the upper 0.05 m of the vegetation surface at all the thermokarst wetland sampling locations during the study period, and surface water pH ranged from 5.0 to 5.6 during the season. One of the wetlands (TW2, Figure 1) has only a few standing dead trees and has established dwarf arctic birch shrubs, while the other three wetlands have a large number of standing dead trees, no dwarf arctic birch shrubs, and areas of open water.

[8] Aerial photographs of the area suggest that these wetlands may have formed within the last 30–40 years and are expanding in area. This concurs with an estimated warming of permafrost in the late 1960s and early 1970s modeled for a site in Bonanza Creek LTER using mean annual soil and permafrost temperatures from 1950–1996 [*Osterkamp and Romanovsky*, 1999]. Examination of tree rings and compression wood formation in cores obtained from live leaning trees at the edge of one of the wetlands show that these particular trees began leaning in 1992–1993 (J. Lukas, personal communication, 2003). The areas bordering the thermokarst wetlands are underlain by permafrost and the ground has not subsided, but the soils are generally drier than the permafrost plateau soils, likely due to local drainage into the wetlands. *Lloyd et al.* [2003] described the same phenomenon at a site near Seward Peninsula, Alaska where soils bordering thaw ponds were significantly drier than level tundra.

[9] Fifteen locations for flux measurements were established among three different site types designated as permafrost plateau (PP), thermokarst wetland (TW), and edges of the thermokarst wetlands (TE) (Figure 1). Each site type was represented by five sampling locations where 0.10-m-tall, 0.37-m-inner-diameter flux chamber collars were inserted approximately 0.05 m into the soil in early May 2003.

3. Methods

3.1. Active Layer Thickness, Soil and Air Temperatures, Soil Moisture, and PAR

[10] We measured the depth to ice (active layer thickness) at every flux measurement location whenever gas flux was measured by driving a steel rod into the soil at three locations within 1 m of each chamber collar. Depth to ice could be measured to a maximum of 2.2 m, the length of our longest rod. Air temperature and 5 cm, 10 cm, and 15 cm soil temperatures were measured at every location when we measured gas flux using a Fluke digital thermometer equipped with a 30-cm-long temperature probe. Hourly soil temperature at 5 cm below the vegetation surface was continuously recorded using data loggers installed in May 2003 at one sampling location each for PP, TE, and TW. Soil was collected from the upper 5 cm (immediately beneath the live vegetation) at PP and TE flux measurement sites for volumetric soil moisture content on several dates in 2003.

[11] Photosynthetically active radiation (PAR) was measured at each chamber collar immediately before and after net CO_2 flux chamber measurements using a LI-COR Quantum sensor and a LI-250 Light Meter placed next to each chamber. Ground PAR measurements were discontinued after 8 August owing to equipment malfunction. Missing PAR data were estimated using average hourly PAR measured at a weather station operated by the Bonanza Creek LTER located ~3 km east of the study site (see http://www.lter.uaf.edu). The relationship between ground PAR at each site type and LTER weather station PAR (hereafter referred to as "LTER PAR") during 16 May to 8 August was used to adjust LTER PAR to approximate ground PAR on subsequent dates. The adjustment factors are as follows: PP ground PAR = 0.52 * LTER PAR; TE ground PAR = 0.68 * LTER PAR; TW ground PAR = 0.98 * LTER PAR.

3.2. Gas Flux Measurements

[12] We measured gross CO_2 flux (soil respiration) and net CO_2 flux (soil respiration minus photosynthesis) weekly to biweekly at the sampling sites during May–September 2003. We measured CH_4 flux biweekly at the TW and TE sites during May–September 2003, and biweekly at the PP sites during July–September 2003. Fluxes were measured between 1000 and 1600 local time. We also measured soil respiration under snow once in March 2004. 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 were 0.20 m tall with a 0.37-m inner diameter, had sample ports fitted with three-way stopcocks, and had a coiled aluminum tube (1.6-mm inside diameter) installed through the sidewall for pressure equalization. Soil respiration was measured using an opaque chamber constructed of polyvinyl chloride (PVC), and net CO_2 flux and CH_4 flux were measured using a clear PVC and Lexan chamber. Trees and large shrubs at PP and TE sites were not included in gas flux measurements.

[13] Gas fluxes were measured by placing the chamber onto the PVC collars installed in the soil, sealing the interface with a rubber gasket, and measuring the change in CO_2 or CH_4 concentration. Chamber CO_2 concentration was measured by circulating chamber air through a 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 internal pump circulated air at a maximum rate of 0.3 L min^{-1}. An additional pump circulated the chamber air at 3 L min^{-1}. Beginning at time zero, CO_2 concentrations were recorded at 15-s intervals for 5 min for both soil respiration and net CO_2 flux measurements. Methane concentrations were measured by collecting 12-mL chamber air samples through a top sample port every 4 min for 16 min using a syringe, and immediately transferring the sample to a 10-mL serum bottle that was previously flushed with N_2 gas, sealed with a butyl rubber septum, and evacuated. The serum bottle samples were analyzed for CH_4 on a gas chromatograph (GC) within 1 month of collection. The Hewlett-Packard 5890 Series II GC had a 2-m 100–120 mesh Porapak-N column, a flame ionization detector, nitrogen carrier gas, and an oven temperature of 40°C. Calibration tables were constructed using CH_4 standards that bracketed the sample concentrations, and chromatographic data were integrated using a Hewlett-Packard 3365 Series II ChemStation computer program.

[14] The net rate of gas emission or consumption was determined by

$$J = (dC/dt)h, \tag{1}$$

where J is flux (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 regression of gas concentration with time as time approaches zero [*Rolston*, 1993; *Healy et al.*, 1996]. Slopes of regressions had r^2 of at least 0.95 for CO_2 fluxes and 0.90 for CH_4 fluxes.

3.3. Pore Water CO_2 and CH_4 Concentrations

[15] We collected soil pore water at various depths in the thermokarst wetlands on 2 July and 1 August 2003 using a 60-mL syringe attached to a stainless steel probe (3-mm inner diameter) that had slotted openings at the end. Immediately after the pore water was collected, 15 mL of the sample was injected through a 15-mm diameter Whatman GF/A syringe filter into a 37-mL sealed serum bottle containing nitrogen gas and 2 g KCl as an inhibitor of microbial activity [*Striegl et al.*, 2001]. CO_2 in the equilibrated headspace of the serum bottles was analyzed by injecting four 0.5-mL replicates of each sample into a nitrogen carrier stream passing through a LI-COR 6252 infrared CO_2 analyzer. Three mL of equilibrated headspace was injected into the GC for CH_4 analysis. Dissolved CO_2 and CH_4 concentrations were calculated using known CO_2 [*Plummer and Busenberg*, 1982] and CH_4 [*Yamamoto et al.*, 1976] equilibrium constants adjusted for field temperature and pressure.

3.4. Statistical Analyses

[16] We used nonparametric statistics to check for significant differences within and among the three site types for active layer thickness, soil moisture content, and gas fluxes, which had nonnormal distributions (Mann-Whitney U and Kruskall-Wallis analysis of variance of rank tests, $\alpha = 0.05$, p-values are listed when significant [*Judd and McClelland*, 1989]).

4. Results

4.1. Active Layer Thickness

[17] The active layer thickness was greatest at the TW sites on all dates in 2003 (Figure 2). The PP sites had a slightly shallower active layer than the TE sites on almost every date, but the difference is not statistically significant. Maximum active layer thickness was 0.41 ± 0.03 m (30 August) at the PP sites, and 0.46 ± 0.04 m (29 September) at the TE sites. Active layer thickness was somewhat greater at the TW sites than at the other sites during May–June, while in July and August it was much greater as the seasonal ice layer thawed completely in the wetlands. This seasonal ice layer extended to about 0.60 m depth at all the TW sites, and there was no detectable ice between 0.60 and 2.20 m (we do not know whether there is permafrost deeper than 2.20 m).

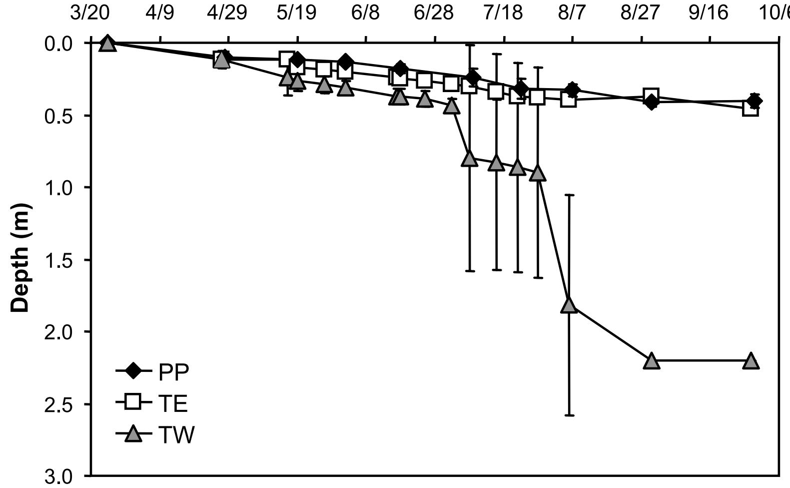

Figure 2. Active layer thickness, 2003–2004. Each point is the mean (±1 standard deviation) of five measurements (exceptions are 16 May, when there were two measurements at TE and TW; and 30 August, when there was one measurement at TE). Measurements on 25 March were made in 2004.

4.2. Soil Moisture

[18] The mean volumetric soil moisture content (vol/vol) at the PP sites (0.48 ± 0.19, n = 16) was significantly greater than at the TE sites (0.34 ± 0.20, n = 21; Mann-Whitney U test, p-value < 0.05).

4.3. Soil Respiration

[19] Soil respiration at PP, TE, and TW followed a seasonal pattern, with minimum measured fluxes occurring in March–May and September, and maximum fluxes occurring in July (Figures 3a–3c; a positive value indicates a flux

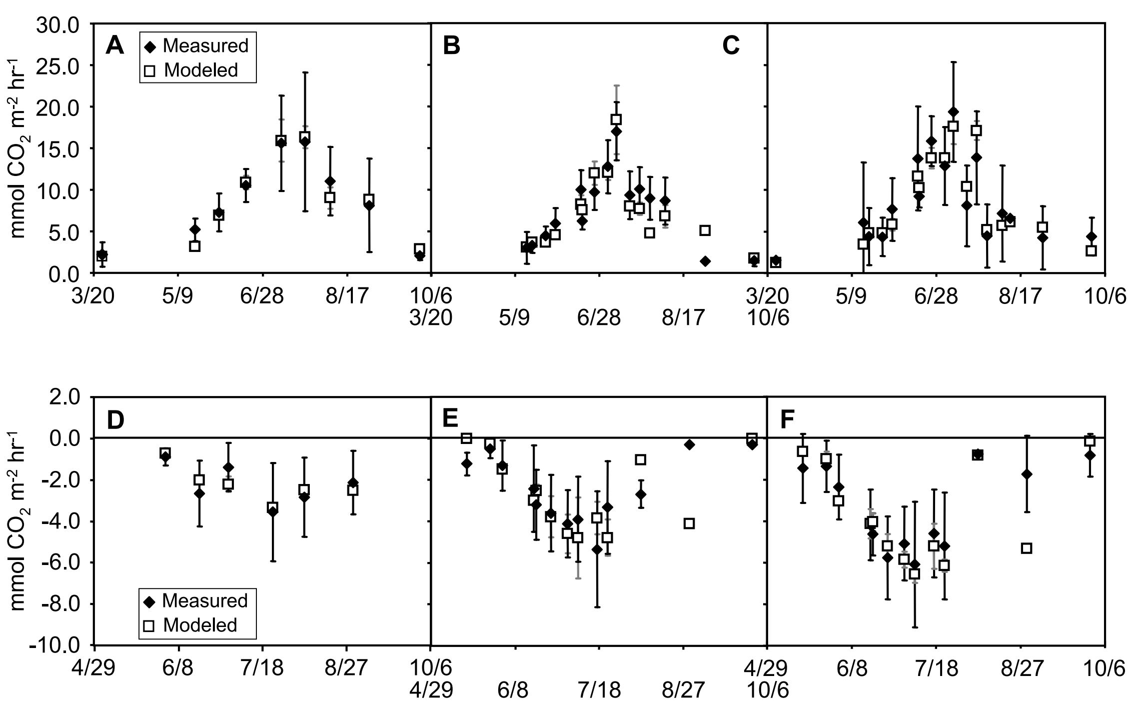

Figure 3. Measured and modeled soil respiration, 2003–2004 (measurements on 25 March were made in 2004), at (a) PP, (b) TE, and (c) TW; and measured and modeled photosynthesis, 2003, at (d) PP, (e) TE, and (f) TW. Each point is the mean ±1 standard deviation of four to five measurements or modeled fluxes (the following dates had one or two measurements due to logistical reasons: 16 May (TW and TE), 7 August (TW and TE), 30 August (TW and TE), and 28 September (TE)). Photosynthesis is calculated as the difference between soil respiration and net CO_2 flux (data not shown). A positive value is a flux to the atmosphere.

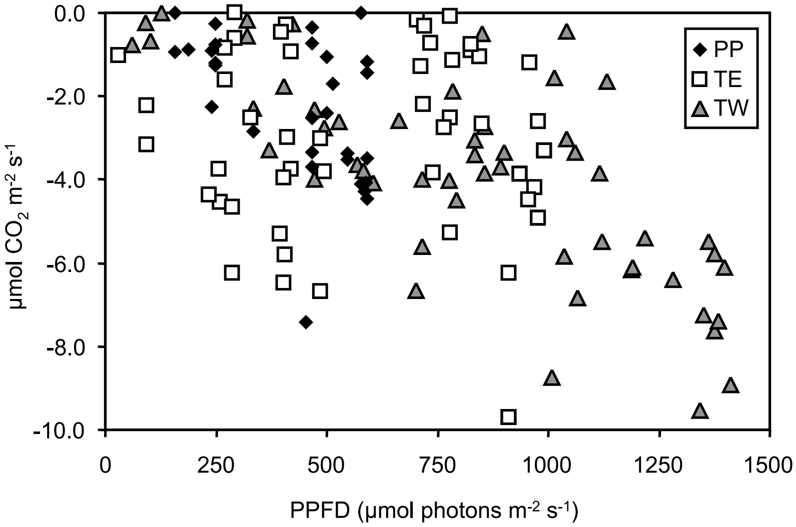

Figure 4. Photosynthesis (calculated as soil respiration minus net CO_2 flux) versus photosynthetic photon flux density (PPFD). Each point represents one chamber measurement.

to the atmosphere). Although there is some difference in respiration among sites for certain times of the measurement period, overall PP, TE, and TW fluxes are not significantly different from each other. The means of the individual chamber measurements (±1 standard deviation) at each of the sites for May 2003 to March 2004 were: PP = 9.07 ± 6.21 mmol CO_2 m^{-2} hr^{-1} (n = 41); TE = 8.24 ± 4.54 mmol CO_2 m^{-2} hr^{-1} (n = 65); and TW = 9.25 ± 6.21 mmol CO_2 m^{-2} hr^{-1} (n = 70).

4.4. Net CO_2 Fluxes and Groundcover Vegetation Photosynthesis

[20] The PP sites were mean net CO_2 sources to the atmosphere on all measurement dates, while the TW sites were mean net CO_2 sinks on most measurement dates (data not shown; net CO_2 flux measurements pertain only to the ground surface as they do not include CO_2 uptake by trees and large shrubs). The TE sites were mean net CO_2 sinks except in early to mid-June and in late August to September. The net CO_2 fluxes were significantly greater (more net CO_2 uptake) at the TE and TW sites than at the PP sites (Mann-Whitney U test, p-values = 0.001, <0.0001) over the entire measurement period. Net CO_2 fluxes at the TE and TW sites were not significantly different from each other. The means of the individual net CO_2 flux chamber measurements (±1 standard deviation) at each of the sites for May–September 2003 were: PP = 3.48 ± 5.44 mmol CO_2 m^{-2} hr^{-1} (n = 29); TE = −1.71 ± 7.23 mmol CO_2 m^{-2} hr^{-1} (n = 49); and TW = −3.22 ± 4.90 mmol CO_2 m^{-2} hr^{-1} (n = 54). The variation among the sites is primarily a result of differences in photosynthesis, as there was no significant difference in soil respiration rates.

[21] Photosynthesis of groundcover vegetation (net CO_2 minus soil respiration) was significantly different among the three sites (Kruskal-Wallis test, p-value = 0.025; Figures 3d–3f). CO_2 uptake was greatest at the TW sites, with peak rates in late June and early July (peak mean photosynthesis = −21.9 ± 10.9 mmol CO_2 m^{-2} hr^{-1} on 8 July 2003). Peak mean photosynthesis for the other sites were: PP = −12.8 ± 8.5 mmol CO_2 m^{-2} hr^{-1} (7/22/03), and TE = −19.2 ± 10.0 mmol CO_2 m^{-2} hr^{-1} (16 July 2003). Mean photosynthesis (±1 standard deviation) calculated from flux measurements during May–September 2003 were: PP = −7.93 ± 6.35 mmol CO_2 m^{-2} hr^{-1} (n = 29); TE = −10.7 ± 7.80 mmol CO_2 m^{-2} hr^{-1} (n = 49); and TW = −14.2 ± 9.10 mmol CO_2 m^{-2} hr^{-1} (n = 50). The difference in groundcover vegetation photosynthesis among the sites may be attributed in part to differences in PAR reaching the ground at each site (Figure 4). The presence of trees reduces light penetration at the PP sites, and to a lesser extent at the TE sites.

4.5. CH_4 Fluxes

[22] The means of the individual CH_4 flux chamber measurements (±1 standard deviation; Figure 5) for May–September 2003 were: PP = 0.016 ± 0.028 mmol CH_4 m^{-2} hr^{-1}(n = 16); TE = 0.030 ± 0.026 mmol CH_4 m^{-2} hr^{-1} (n = 34); and TW = 0.45 ± 0.33 mmol CH_4 m^{-2} hr^{-1} (n = 37). There was no significant difference between fluxes at the PP and TE sites, which emitted small amounts of CH_4 throughout the season. The PP sites were a small net sink of CH_4 on one measurement date. Methane fluxes were significantly greater at the TW sites (Mann-Whitney U test, p-value < 0.0001). The CH_4 emission rates were highly variable among the individual TW sites, and in fact there is a significant difference among them (Kruskal-Wallis test, p-value < 0.0001). Methane emissions from TW#2 (mean = 0.72 ± 0.32 mmol CH_4 m^{-2} hr^{-1}) were significantly greater than from TW 1, 3, and 4 (mean = 0.24 ± 0.10 mmol CH_4 m^{-2} hr^{-1}; Mann-Whitney U test, p-values = 0.001 to 0.008).

4.6. Controls of CO_2 and CH_4 Fluxes

[23] Soil respiration at the PP, TE, and TW sites was positively correlated with hourly 5-cm temperature, accounting for 50–90% of the variability in flux (Figures 6a–6c). The flux-temperature relationship exhibited a seasonal shift at the TW and TE sites, with soil respiration responding more strongly to soil temperature from spring through mid-July than in late July through fall. A record rainfall event of almost 100 mm during 26–28 July

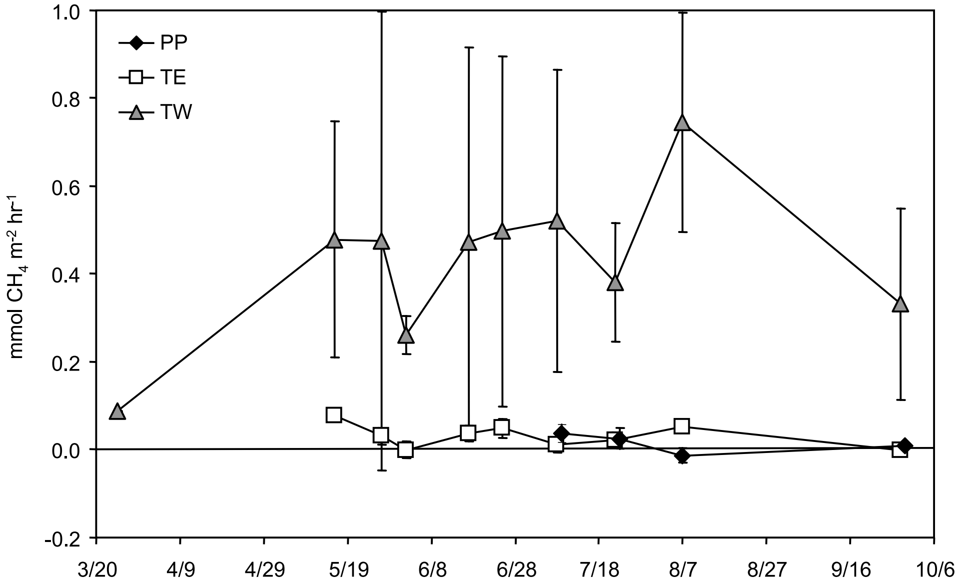

Figure 5. CH_4 flux, 2003–2004 (measurements on 25 March were made in 2004). Each point is the mean (±1 standard deviation) of four to five measurements (the following dates had two to three measurements at TE and TW owing to logistical reasons: 16 May, 2 June, and 7 August. On 28 September two measurements were made at TE and PP). A positive value is a flux to the atmosphere.

2003 flooded much of the study area, which may have had a dampening effect on respiration. A seasonal shift in the flux-temperature relationship was not evident at the PP sites, where a single exponential relationship was maintained throughout the study period. Soil respiration responded most strongly to soil temperature at PP (Q_{10} = 4.2), followed by TE ("early" Q_{10} = 3.8, "late" Q_{10} = 3.3) and TW ("early" Q_{10} = 3.4, "late" Q_{10} = 1.8).

[24] Soil respiration and active layer thickness at the PP and TE sites covaried during the season. From spring thaw through early July, there was a linear increase in soil respiration with increasing active layer thickness at both PP and TE. After mid-July active layer thickness continued to increase, but soil respiration steadily decreased. Methane flux was not significantly correlated with soil temperature or soil moisture at any of the site types.

4.7. Pore Water CO_2 and CH_4 Concentrations at TW Sites

[25] Concentrations of dissolved CO_2 and CH_4 in pore waters collected from the four thermokarst wetlands are listed in Table 1. In general the highest dissolved CO_2 and CH_4 concentrations were measured between 0.5 and 1.2 m depth. TW 1 peak CO_2 and CH_4 concentrations were 3–4.5 and 1.5–2.5 times greater than TW 2–4, respectively. Shallow dissolved gas concentrations (0.05–0.2 m) were 2–4.5 times greater at TW 2 than at the other wetlands. Dissolved CH_4 concentrations declined sharply between 0.4 m and 0.2 m at all sites (68–85% reduction) except at TW 2, where they remained high at shallow depths. The higher CH_4 concentrations at shallow depths at TW 2 are consistent with the significantly higher CH_4 fluxes measured there.

[26] High gas concentrations at depth indicate that biological decomposition is occurring throughout the profile. However, it is unlikely that these deep gases contribute significantly to diffusive flux across the wetland-air interface because gas diffusion is extremely slow in water. To evaluate the potential diffusion rate of dissolved CO_2 and CH_4 through the saturated wetland peat, we calculated one-dimensional diffusion through the water column using a form of Fick's first law modified for diffusion in porous media [*Striegl*, 1993],

$$J = -D_C \theta (dC/dz), \qquad (2)$$

where J is flux (mmol m^{-2} t^{-1}), D_C is the diffusion constant of CO_2 or CH_4 through water at ambient temperature and pressure (m^2 d^{-1}), θ is porosity, and dC/dz is the measured concentration gradient of CO_2 or CH_4 (mmol m^{-3} m^{-1}). We used the portion of the profiles having increasing concentration with depth (generally 0.1–0.5 m), and $D_C = 1.69 * 10^{-4}$ m^2 d^{-1} for CO_2 and CH_4 [*Perry*, 1963]. Even if it is assumed that $\theta = 1$, and not a more realistic 0.83–0.93 [*Letts et al.*, 2000], mean diffusive fluxes within the wetland peat on 1 August 2003 were only 0.06 ± 0.06 mmol CO_2 m^{-2} hr^{-1} and 0.02 ± 0.01 mmol CH_4 m^{-2} hr^{-1}. This suggests that only a small amount of the measured gas flux (4–7%) across the air-water/vegetation interface could come from gas diffusion through deep peat. Therefore biological production of CO_2 and CH_4 at shallow depths and/or modes of gas transport through the peat profile other than diffusion (i.e., ebullition, plant transport) are responsible for the fluxes measured at the surface.

4.8. Estimated Annual C Gas Exchange

[27] We estimated annual CO_2 gas exchange at the surface at each site type by modeling hourly soil respiration and groundcover photosynthesis using the 5-cm soil temperature records and the LTER PAR record for 2003.

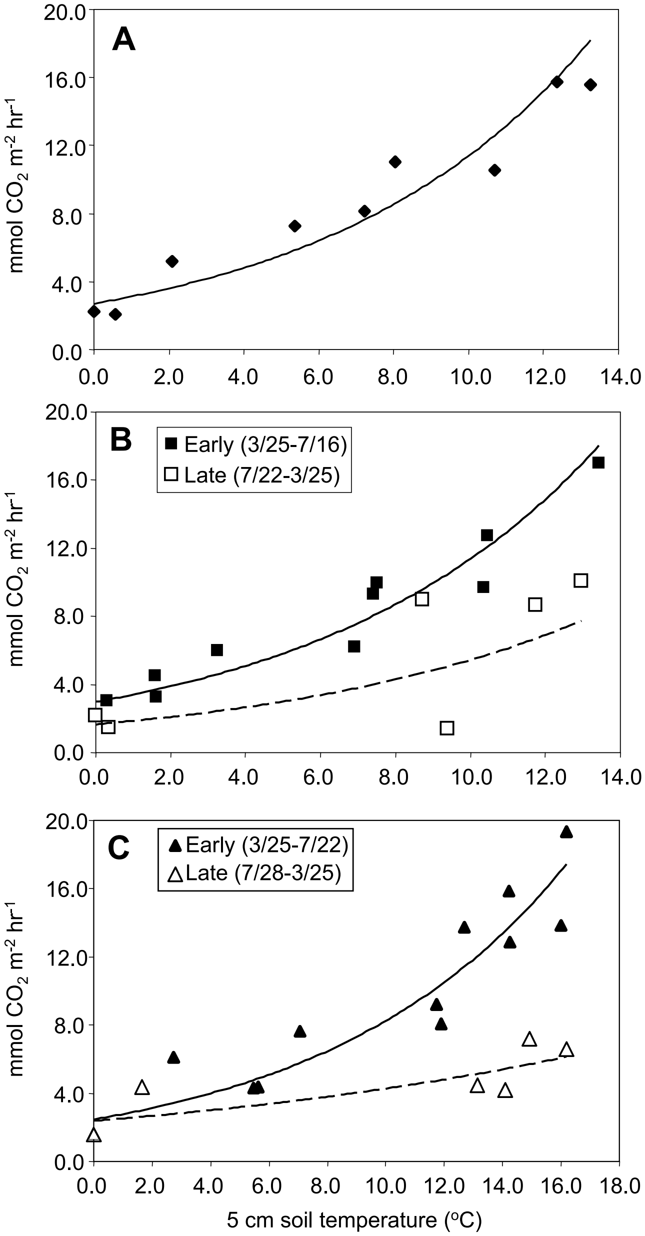

Figure 6. (a–c) Soil respiration versus 5-cm soil temperature at (a) PP, (b) TE, and (c) TW. The equations, r^2 values, and standard errors are: (Figure 6a) $y = 2.7021e^{0.1439x}$, $r^2 = 0.90$ SE = 1.21; (Figure 6b) Early: $y = 2.971e^{0.1342x}$, $r^2 = 0.91$, SE = 1.44; Late: $y = 1.6545e^{0.1191x}$, $r^2 = 0.50$, SE = 3.08, (Figure 6c) Early: $y = 2.4586e^{0.121x}$, $r^2 = 0.85$, SE = 2.34; Late: $y = 2.3774e^{0.0587x}$, $r^2 = 0.60$, SE = 1.43.

Missing portions of the soil temperature record (when data loggers were not installed) were reconstructed using the relationship between 5-cm soil temperature at the sites and 5-cm soil temperature measured at the LTER weather station. We applied the soil respiration-temperature equations for each site type (Figure 6) to the 5-cm soil temperature records to calculate hourly soil respiration, and summed the values for an annual estimate. We modeled hourly groundcover vegetation photosynthesis at each site by applying a rectangular hyperbola equation relating photosynthesis and radiation [*Thornley and Johnson*, 1990] to the site-adjusted LTER PAR record,

$$P = (\alpha Q P_{\max}/\alpha Q + P_{\max})^{*} T/T_{\max}, \qquad (3)$$

where P = gross photosynthesis (μmol CO_2 m^{-2} s^{-1}), α = apparent quantum yield (μmol CO_2 μmol^{-1} photons), Q = photosynthetic photon flux density (PPFD; μmol photons m^{-2} s^{-1}), $P_{\max}$ = maximum rate of photosynthesis at saturating light, T = 5-day running mean of 5-cm soil temperature, and $T_{\max} = T$ when $P_{\max}$ was measured ($T_{\max}$ was set to equal one when $T > T_{\max}$). This equation is commonly used to model photosynthesis, and the parameter values for α and $P_{\max}$ are often determined using photosynthesis or net CO_2 and PAR measured at a study site [*Ruimy et al.*, 1995]. We did not have enough flux measurements to accurately determine the parameter values for each site type, so we used a range of parameter values determined by *Frolking et al.* [1998] specific to northern peatlands. For each site type we modeled hourly photosynthesis using parameters for "bogs" (α = 0.017, $P_{\max}$ = 5.2), "poor fens" (α = 0.024, $P_{\max}$ = 11.5), and "all peatlands" (α = 0.020, $P_{\max}$ = 9.2) [*Frolking et al.*, 1998]. We estimated annual groundcover vegetation photosynthesis by summing the hourly fluxes for 19 April to 14 October 2003, assuming that no photosynthesis occurred when mean daily surface temperatures were below 0°C (determined from LTER weather station data).

[28] The modeled fluxes are compared to measured fluxes in Figures 3a–3f. Photosynthesis at the PP sites was best described by the "bogs" parameter values, while photosynthesis at the TW and TE sites was best described by the parameter values for "all peatlands." The modeled soil respiration and photosynthesis fluxes were not significantly different from the measured fluxes at any of the sites. The annual estimates of soil respiration and groundcover photosynthesis for each site type are listed in Table 2. The upper and lower ranges for soil respiration were calculated by adding or subtracting one standard error determined for the corresponding flux-temperature relationship, and the ranges for photosynthesis are the modeled maximum and minimum fluxes determined using the three sets of parameter values from *Frolking et al.* [1998].

Table 1. Dissolved CO_2 and CH_4 Concentrations in Pore Waters Collected From TW Sites[a]

Date	Depth, m	TW1		TW2		TW3		TW4	
		P_{CO2}	P_{CH4}	P_{CO2}	P_{CH4}	P_{CO2}	P_{CH4}	P_{CO2}	P_{CH4}
2 July	0.05	4.2	0.25	2.7	0.18	4.0	0.13	1.9	0.066
2 July	0.15	3.0	0.23	4.7	0.56	3.7	0.25	2.4	0.26
1 August	0.1	3.1	0.044	4.7	0.88	2.1	0.20	2.2	0.051
1 August	0.2	4.1	0.32	4.3	1.0	2.2	0.18	2.5	0.057
1 August	0.4	9.2	1.0	7.7	1.3	1.6	0.99	2.9	0.38
1 August	0.5	8.6	1.0	8.3	1.6	4.1	1.4	2.3	0.75
1 August	0.6	9.6	0.86	7.6	1.6	4.7	1.4	5.5	1.7
1 August	0.7	23	2.5	7.4	1.6	7.3	1.7	…	…
1 August	0.8	33	3.0	5.4	1.1	1.8	0.49	8.0	1.9
1 August	0.9	31	3.3	4.9	1.0	1.6	0.13	8.1	2.3
1 August	1.0	22	2.8	7.4	2.2	2.1	0.24	7.3	1.3
1 August	1.1	…	…	7.2	1.4	…	…	…	…
1 August	1.2	11	1.1	…	…	…	…	8.3	1.7

[a]All concentrations are in $mmol^{-1}$.

Table 2. Annual Modeled CO_2 and CH_4 Fluxes[a]

	PP	TE	TW
Respiration	35.9	31.5	33.9
Range	25.3 to 46.5	17.1 to 50.9	19.7 to 51.0
Photosynthesis	−9.9	−15.6	−22.7
Range	−9.9 to −16.6	−10.8 to −19.0	−15.3 to −27.8
Net CH_4	0.2	0.2	2.6
Range	0.1 to 0.2	0.1 to 0.4	1.4 to 3.5

[a]All values are mol m^{-2} yr^{-1}. Annual respiration and photosynthesis were modeled, and annual CH_4 exchange was calculated by summing linearly interpolated values between measurements.

[29] We estimated annual CH_4 exchange at each site type by linear interpolation of the measured fluxes, assuming that mean midday fluxes approximated daily means. We applied CH_4 flux measurements made at the TW sites in March 2004 to 1 January to 24 March and 30 September to 31 December, and applied a flux of 0.017 mmol CH_4 m^{-2} hr^{-1} at the PP and TE sites for those time periods based on winter CH_4 flux measurements by *Wickland et al.* [1999] in snow-covered subalpine soils. Although this is not an ideal method for estimating annual flux, it is the best method in the absence of a significant relationship with an environmental variable such as temperature or water table. The annual estimates are in Table 2, with upper and lower ranges determined by linear interpolation of individual site fluxes.

5. Discussion

5.1. CO_2 Exchange

[30] The main source of soil respiration (root plus heterotrophic respiration) during the measurement period at all the sites is likely the surface peat (upper 10 cm). The significant positive relationships between 5-cm temperature and soil respiration are evidence of this. Even though the active layer is deep at the TW sites, the amount of CO_2 diffusing through the saturated peat only accounted for a maximum of 4% of the CO_2 flux measured at the surface. The existence of high concentrations of CO_2 and CH_4 down to 1.2 m depths in the TW sites confirms that decomposition is occurring at depth [*Clymo*, 1984], but at very slow rates compared to surficial soil respiration. Factors that are often identified as contributing to slow decomposition rates of deep organic matter include low O_2 availability in saturated soils, low temperatures, and substrate recalcitrance [*Schlesinger*, 1977; *Clymo*, 1984; *Yavitt et al.*, 1987].

[31] Soil respiration rates at the TW sites (mean = 9.25 mmol CO_2 m^{-2} hr^{-1}) are similar to respiration measured by *Bubier et al.* [1998] (collapse bog July–August mean = 8.78 mmol CO_2 m^{-2} hr^{-1}, collapse fen July–August mean = 11.52 mmol CO_2 m^{-2} hr^{-1}). They are 1 to 2 orders of magnitude greater than what *Turetsky et al.* [2002] measured (collapse wetland mean = 0.11 mmol CO_2 m^{-2} hr^{-1}), which may be owing to differences in chamber measurement technique. Mean soil respiration rates at the TE sites (8.24 mmol CO_2 m^{-2} hr^{-1}) and the PP sites (9.07 mmol CO_2 m^{-2} hr^{-1}) are comparable to mean respiration at a Manitoba black spruce forest and a black spruce palsa during May–September (7.58 mmol CO_2 m^{-2} hr^{-1} [*Moosavi and Crill*, 1997], 8.33 mmol CO_2 m^{-2} hr^{-1} [*Savage et al.*, 1997]). Soil respiration at the permafrost soils was more responsive to temperature (PP Q_{10} = 4.2) compared to soil respiration of thermokarst wetlands (TW Q_{10} = 1.8–3.4). The Q_{10}s that we measured are similar to the range measured by *Bubier et al.* [1998] for a collapse bog, a collapse poor fen, and intermediate and rich fens (Q_{10} = 3.0–4.1). The seasonal shift in the soil respiration-temperature relationships at the TE and TW sites suggest that variables other than soil temperature were limiting respiration late in the season.

[32] Our annual estimate of soil respiration was slightly greater at PP than at TW (35.9 vs. 33.9 mol C m^{-2} yr^{-1}), despite the TW sites having an active layer five times thicker than the PP sites. We can account for differences in root respiration by assuming that ~55% of the total respiration from the PP sites is autotrophic (root respiration = 54–56% of total soil respiration in a Canada black spruce forest [*Uchida et al.*, 1998; *Ruess et al.*, 2003]), and that ~40% of the total soil respiration at the TW sites is autotrophic (root respiration = 35–45% of total peatland respiration [*Silvola et al.*, 1996]). The resulting estimate of heterotrophic respiration is somewhat higher at the TW sites than at the PP sites (20.3 versus 16.2 mol C m^{-2} yr^{-1}). Normalizing heterotrophic respiration to active layer thickness suggests that decomposition rates per unit of thawed soil are 4 times faster at the PP sites than at the TW sites (36 versus 9 mol C m^{-3} yr^{-1}).

[33] The difference in the amount of light reaching groundcover vegetation, as well as variations in moss types and moisture availability are likely responsible for the differences in photosynthesis and net CO_2 exchange between the sites. *Sphagnum* mosses have greater average NPP than feathermosses [*Bisbee et al.*, 2001], which may explain in part why mean photosynthesis was significantly greater at the TW sites. In addition any *Sphagnum* present at the PP and TE sites may have been moisture-limited because *Sphagnum* moss photosynthesis is highly sensitive to moisture [*Silvola*, 1991; *Williams and Flanagan*, 1996; *McNeil and Waddington*, 2003]. *Tuittila et al.* [2004] measured the optimum water table level for photosynthesis by *S. angustifolium* as −12 cm, with decreased photosynthesis at lower water table levels. Peak photosynthesis at the TW sites (−21.9 mmol CO_2 m^{-2} hr^{-1}) was comparable to maximum photosynthesis rates of −18.2 and −23.0 mmol CO_2 m^{-2} hr^{-1} measured by *Bubier et al.* [1998] at a collapse bog and a collapse fen.

5.2. CH_4 Exchange

[34] Thermokarst development substantially increases CH_4 emissions from these ecosystems. Mean CH_4 fluxes for all sites were similar to those measured by *Bubier et al.* [1995a] (0.015–0.050 mmol CH_4 m^{-2} hr^{-1} at peat plateaus, 0.16–0.28 mmol CH_4 m^{-2} hr^{-1} at open bogs and poor fens), *Moosavi et al.* [1996] (0.11–1.06 mmol CH_4 m^{-2} hr^{-1} at wetland sites), *Liblik et al.* [1997] (−0.003 mmol CH_4 m^{-2} hr^{-1} at permafrost peat, 0.55 mmol CH_4 m^{-2} hr^{-1} at a collapse bog), and *Savage et al.* [1997] (−0.0007 mmol CH_4 m^{-2} hr^{-1} at a palsa). The mean CH_4 emission rate was about 20 times greater from the thermokarst wetlands than at the edge and permafrost plateau sites. Similar increases have been documented in other studies: *Turetsky et al.* [2002] measured a 30-fold increase and *Bubier et al.*

[1995a] measured up to a 19-fold increase between permafrost peat and collapse wetlands. *Moosavi et al.* [1996] and *Liblik et al.* [1997] measured >100-fold increases in CH_4 emissions at their study sites. At a larger landscape scale, *Christensen et al.* [2004] calculated that changes in hydrology and vegetation caused by permafrost thawing in a poorly drained area of Sweden have led to 22–66% increases in CH_4 emissions over 30 years.

[35] Methane flux was not significantly correlated with soil temperature or soil moisture at any of the site types. *Bubier et al.* [1995a] and *Liblik et al.* [1997] found that within-site temporal variability of CH_4 flux from collapse wetlands was only weakly related to temperature and to water table position. In contrast, *Moosavi et al.* [1996] measured a significant exponential relationship between shallow soil temperature and CH_4 flux from their wetland sites over two years. Diffusive CH_4 flux from deep peat at the TW sites accounted for a maximum of 7% of the measured CH_4 flux, indicating that shallow CH_4 production was responsible for the majority of CH_4 flux at the surface, and/or that ebullitive transport of deep (>0.1 m) CH_4 to the surface occurred [*Christensen et al.*, 2003; *Rosenberry et al.*, 2003; *Glaser et al.*, 2004]. All individual CH_4 chamber measurements at the wetlands exhibited steady increases of CH_4 concentration with time, suggesting that episodic ebullitive transport did not occur during our measurements. However, this does not exclude the possibility that ebullitive transport was occurring, as *Baird et al.* [2004] found that both regular and episodic ebullition patterns occur in peat.

[36] Methane flux was significantly higher at TW 2 than at the other TW sites. Dissolved CH_4 concentrations were about equal at 0.6–0.7 m depth in all four wetland sites suggesting that deep CH_4 production rates are similar. The steep reduction in dissolved CH_4 concentrations in the upper 0.05–0.20 m on both sampling dates at TW 1, 3, and 4 may be a result of high CH_4 oxidation rates relative to CH_4 production. *Moosavi and Crill* [1998] determined that arctic wet sedge communities in Alaska oxidized up to ~80% of gross CH_4 production, but that oxidation was highly variable (0–80% oxidation) both spatially and temporally. All TW sites had vascular vegetation, which is known to enhance CH_4 transport through potential oxidation zones [*Dacey and Klug*, 1979; *Whiting and Chanton*, 1992]. *Bubier et al.* [1995a, 1995b] found that certain moss species were associated with higher CH_4 flux as they were good indicators of mean water table position, but the wetlands in this study were fairly similar with regards to moss species and to water table position through the season. The main difference between the wetlands is that TW 2 appears to be an older wetland based on the almost total absence of standing dead trees, no open water, and the establishment of dwarf birch shrubs.

5.3. Estimated Annual C Gas Exchange

[37] Our modeled estimates of annual soil respiration agree with estimates in black spruce forests of Saskatchewan by *O'Connell et al.* [2003] of 26.6 and 47.0 mol C m^{-2} yr^{-1}, and by *Swanson and Flanagan* [2001] of 33.0 mol C m^{-2} for May–October. *Ruess et al.* [2003] estimated a larger growing season soil respiration term of 41.7–52.0 mol C m^{-2} (May–September 1999) at floodplain black spruce forest sites located within 8 km of our sites; while *Schlentner and Van Cleve* [1985] reported a 2-year growing season average soil respiration of 30.7 mol C m^{-2} yr^{-1} for upland and floodplain black spruce stands located in the same vicinity. Our groundcover vegetation photosynthesis estimates agree with estimates by *Swanson and Flanagan* [2001], who modeled gross photosynthetic uptake as −26.0 and −9.0 mol C m^{-2} for *Sphagnum* and feather moss communities, respectively, during May–October.

[38] On the basis of our modeling results of soil respiration and groundcover vegetation photosynthesis we estimated that all sites were net C sources to the atmosphere during 2003 (PP = 26.2, TE = 16.1, TW = 13.8 mol C m^{-2} yr^{-1}). However, the range in our estimates was large enough that the TE and TW sites may have been net C sinks (TE = −1.8, TW = −6.7 mol C m^{-2} yr^{-1}). In addition, our estimates do not include CO_2 uptake by black spruce and large shrubs at the PP and TE sites. *Ruess et al.* [2003] measured mean aboveground and belowground annual NPP of black spruce trees and shrubs as 391 g biomass m^{-2} yr^{-1} at three sites having similar tree basal areas to ours (11.2–11.9 m^2 ha^{-1}; this study = 8.7 m^2 ha^{-1}). Assuming biomass is 50% C [*Gower et al.*, 1997], we can estimate that 16.3 mol C m^{-2} yr^{-1} was assimilated to biomass at those sites. If we assume that annual black spruce and shrub NPP from *Ruess et al.* [2003] is applicable to our study site, the PP and TE sites could have been net C sinks of up to −7.5 and −18.1 mol C m^{-2} yr^{-1}, respectively. There were no live trees in any of the thermokarst wetlands to offset the net C loss that we calculated.

[39] Our annual C gas exchange estimates are comparable to those measured by *Heikkinen et al.* [2004] of 1.3 and 2.3 mol C m^{-2} 100 d^{-1} loss to the atmosphere (June–September) from *Sphagnum* peat plateau and a thermokarst lake in the discontinuous permafrost zone of eastern Russia, respectively. *O'Connell et al.* [2003] measured a net loss of 10.7 ± 1.2 mol C m^{-2} yr^{-1} from a poorly drained black spruce-*Sphagnum* forest, and *Swanson and Flanagan* [2001] estimated a C loss at the forest floor of 21.3 mol C m^{-2} from May–October. Net ecosystem C exchange estimates often have large terms of uncertainty because the difference between production and decomposition is small, and standard errors in estimates can span the range of net C source and sink [*Bubier et al.*, 1999]. Our annual C gas exchange estimates fall under this category. A term we did not include in our C exchange estimates was DOC/POC transfer into and out of the system, which can be significant in some areas undergoing permafrost degradation [*Malmer et al.*, 2005]. Our poorly drained sites did not have any surface water inputs or outputs; thus we do not expect that DOC/POC export is significant.

[40] The Global Warming Potential (GWP) of CH_4 equals 62 on a 20-year time horizon, meaning that on a per mass basis the relative radiative forcing of CH_4 is 62 times greater than that of CO_2 when integrated over 20 years [*IPCC*, 1996, 2001]. The GWP of CH_4 declines on longer timescales due to differences in lifetime between CH_4 and CO_2 in the atmosphere (GWP = 23, 100-yr horizon; GWP = 7, 500-yr horizon [*IPCC*, 2001]). Therefore, in terms of greenhouse gases, a system that emits CH_4 may contribute to the greenhouse effect even if it is removing CO_2 from the atmosphere [*Whiting and Chanton*, 2001; *Friborg et al.*, 2003]. The GWP (20-year horizon) of the annual CH_4 and

net CO_2 exchange of a system can be calculated by multiplying the mass of CH_4 emitted by 62, and adding that to the net mass of CO_2 consumed (or emitted). If the sum is negative, then the emissions have a net negative radiative forcing on the climate. A positive value indicates that the emissions exert a positive net radiative forcing over that time horizon. Our annual estimate of CH_4 (42 g CH_4 m^{-2} yr^{-1}) and net CO_2 (607 g CO_2 m^{-2} yr^{-1}) exchange at the thermokarst wetlands have a GWP = 3211 (20-year horizon). The CH_4 emissions continue to exert positive radiative forcing on longer timescales (GWP = 1573, 100 years; GWP = 901, 500 years). *Friborg et al.* [2003] calculated that the GWP of annual CH_4 and CO_2 exchange at Siberian wetlands equaled 1216 (20-year horizon) and 202 (100-year horizon). Annual CH_4 emission from the TW sites was about 1.6 times greater than from the Siberian wetlands of *Friborg et al.* [2003]. If we assume that net CO_2 exchange at the permafrost and edge sites in our study was 9.9 and −0.2 mol C m^{-2} yr^{-1} after accounting for tree NPP, then GWP = 634 and 190 (20-year horizon), 509 and 65 (100-year horizon), and 458 and 14 (500-year horizon).

[41] The GWP values stated here consider the annual emissions as a single pulse emission rather than as a continuous sustained emission. *Frolking et al.* [2006] conclude that under the scenario of sustained CH_4 emission and C sequestration in peatlands, the radiative forcing of CH_4 emissions on climate diminishes after about 50 years and that C sequestration then has a net cooling impact lasting thousands of years. Even under this scenario, however, significant increases in CH_4 emissions and only small changes in CO_2 uptake as a result of large-scale thermokarst wetland formation [*Camill*, 2005; *Jorgenson et al.*, 2006] may have significant short-term impact on climate as radiative forcing will respond more rapidly to changes in CH_4 fluxes than to changes in CO_2 fluxes [*Frolking et al.*, 2006].

6. Conclusions

[42] The formation of thermokarst wetlands upon localized permafrost melting in a poorly drained forest resulted in a 13-fold increase in estimated annual CH_4 emission. Soil respiration was not significantly different between permafrost soils and wetlands, but the wetlands had greater groundcover vegetation photosynthesis. Shallow soils appeared to be the main source of CO_2 and CH_4 emissions at all sites, even at the thermokarst wetlands where the active layer was >2 m. Shallow soil temperature explained between 50 and 91% of the variation in respiration of permafrost soils, and 60–85% of the variation in wetland soil respiration. Methane emissions were not significantly related to soil temperature or soil moisture at any of the sites, and were variable among the wetlands. The potential impact of increased CH_4 emissions from the thermokarst wetlands on climate may far outweigh the magnitude of increased CO_2 uptake, especially when considering widespread thermokarst wetland formation.

[43] **Acknowledgments.** We thank J. Harden for her assistance in locating the field site and her input on study design, J. Hollingsworth of the Bonanza Creek LTER for logistical support for winter sampling, B. Charlton of Bonanza Creek LTER and the Boreal Ecology Cooperative Research Unit for providing LTER weather station data, J. Lukas for dendrochronology analyses, M. Turetsky for assistance with moss species identification, and the following people for assistance with field measurements: Z. Frederick, P. Schuster, D. Fernandez, A. Ivanova, M. Dornblaser, M. Walvoord, and M.J. Baedecker. We would also like to thank J. Vogel, L. Chasar, T. Moore, and two anonymous reviewers for their comments, which helped to greatly improve this paper. The use of brand names does not constitute endorsement by the U.S. Geological Survey.

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