JOURNAL OF GEOPHYSICAL RESEARCH, VOL. 114, G04018, doi:10.1029/2008JG000901, 2009

Response of CO_2 exchange in a tussock tundra ecosystem to permafrost thaw and thermokarst development

Jason Vogel,[1] Edward A. G. Schuur,[2] Christian Trucco,[2] and Hanna Lee[2]

Received 21 November 2008; revised 26 June 2009; accepted 3 August 2009; published 8 December 2009.

[1] Climate change in high latitudes can lead to permafrost thaw, which in ice-rich soils can result in ground subsidence, or thermokarst. In interior Alaska, we examined seasonal and annual ecosystem CO_2 exchange using static and automatic chamber measurements in three areas of a moist acidic tundra ecosystem undergoing varying degrees of permafrost thaw and thermokarst development. One site had extensive thermokarst features, and historic aerial photography indicated it was present at least 50 years prior to this study. A second site had a moderate number of thermokarst features that were known to have developed concurrently with permafrost warming that occurred 15 years prior to this study. A third site had a minimal amount of thermokarst development. The areal extent of thermokarst features reflected the seasonal thaw depth. The "extensive" site had the deepest seasonal thaw depth, and the "moderate" site had thaw depths slightly, but not significantly deeper than the site with "minimal" thermokarst development. Greater permafrost thaw corresponded to significantly greater gross primary productivity (GPP) at the moderate and extensive thaw sites as compared to the minimal thaw site. However, greater ecosystem respiration (R_{eco}) during the spring, fall, and winter resulted in the extensive thaw site being a significant net source of CO_2 to the atmosphere over 3 years, while the moderate thaw site was a CO_2 sink. The minimal thaw site was near CO_2 neutral and not significantly different from the extensive thaw site. Thus after permafrost thaw, initial periods of increased GPP and net CO_2 uptake could be offset by elevated R_{eco} during the winter, spring, and fall.

Citation: Vogel, J., E. A. G. Schuur, C. Trucco, and H. Lee (2009), Response of CO_2 exchange in a tussock tundra ecosystem to permafrost thaw and thermokarst development, *J. Geophys. Res.*, *114*, G04018, doi:10.1029/2008JG000901.

1. Introduction

[2] Air temperatures in high-latitude regions of the globe have warmed during the last century [*Serreze et al.*, 2000], which has coincided with increased permafrost temperatures [*Lachenbruch and Marshall*, 1986; *Osterkamp and Romanovsky*, 1999]. Scientists predict continued and amplified warming in northern ecosystems in response to the buildup of atmospheric greenhouse gases [*IPCC*, 2007]. Since the end of the last glacial period, atmospheric CO_2 has been transferred to northern soils because cold and saturated soil conditions slowed the microbial decomposition of soil organic matter [*Harden et al.*, 1992; *Smith et al.*, 2004]. Future warming could alter the historic role of high-latitude ecosystems in the global C cycle. The resulting accumulated soil C pool in the northern permafrost zone is roughly estimated to be 1024 Pg C when organic matter stored deep (up to 3 m) in the permafrost profile is included [*Schuur et al.*, 2008], which is equivalent to approximately 460 ppm of atmospheric CO_2. Thus with continued warming and thawing permafrost, enhanced microbial decomposition could decrease the soil C pools in permafrost and cause a significant increase in atmospheric CO_2 levels [*Davidson and Janssens*, 2006; *Schuur et al.*, 2008].

[3] An alternate hypothesis is that in addition to causing soil C loss from northern ecosystems, warming could stimulate plant growth by an amount that exceeds the rate of C loss from decomposition [*Shaver et al.*, 1992]. Increased plant growth could result from a longer growing season [*Myneni et al.*, 1998], the direct effect of warmer air and soil temperatures on photosynthetic capacity [*Marchand et al.*, 2004; *Oberbauer et al.*, 2007], and indirectly from an increase in the plant-available nutrients that are released as organic matter decomposes [*Shaver et al.*, 1992]. All of these mechanisms would result in greater annual plant photosynthesis or gross primary production (GPP) in high latitude ecosystems. Based on remotely sensed observations, GPP appears to have increased over the last several decades in arctic regions [*Goetz et al.*, 2005]. Thus, atmospheric and soil warming could, in part, offset increased soil C losses as a direct and indirect result of changes in vegetation productivity.

[4] Permafrost thawing may influence high latitude C cycling over a much longer time frame than the immediate

---

[1] School of Forest Resources and Conservation, University of Florida, Gainesville, Florida, USA.

[2] Department of Botany, University of Florida, Gainesville, Florida, USA.

0148-0227/09/2008JG000901

response of plant and microbes to changes in climate [*Walter et al.*, 2007]. In particular, permafrost thaw can lead to ground subsidence called thermokarst depressions, which form when ground ice melts and the soil subsides into the volume previously occupied by ice. Thermokarst formation can occur within 1–2 years of a climatic shift, a change in hydrology, or changes in other surface conditions [*Jorgenson et al.*, 2001, 2006]. Once formed, thermokarst features can persist from centuries to millennia, even in situations where air and permafrost temperatures have cooled to previous levels [*Vitt et al.*, 2000; *Walter et al.*, 2007]. The soil characteristics altered by thermokarst (moisture, nutrients, temperature) can also remain changed in ways that significantly alter ecosystem C cycling [*Turetsky et al.*, 2007].

[5] The effect of thermokarst on terrestrial C cycling has primarily been studied in boreal lowlands [*Wickland et al.*, 2006; *Turetsky et al.*, 2007], but thermokarst can form wherever there are ice-rich soils [*Jorgenson and Osterkamp*, 2005]. Approximately 50% of boreal and arctic permafrost is found in upland, sloped terrain [*Brown et al.*, 1998; *Yershov*, 2004], and thermokarst formation in many of these regions has proceeded rapidly in response to climate change [*Jorgenson et al.*, 2006]. In analyses of long-term soil C accumulation, scientists have reported increased C uptake with thermokarst formation in boreal lowlands [*Turetsky et al.*, 2007; *Harden et al.*, 2008]. However, as explained by *Turetsky et al.* [2007], analyses of soil C accumulation generally cannot account for ecosystem C balance when microbial activity from deep within the profile contributes to net CO_2 loss.

[6] The objective of this study was to use measurements of gas exchange to examine how permafrost thaw and thermokarst have affected ecosystem C balance in an upland tundra ecosystem. We used a natural gradient in permafrost thaw and thermokarst development that was located near a permafrost-monitoring borehole. The borehole has been visited annually for measurements of permafrost temperatures from 1985 to the present, which has allowed researchers to observe thermokarst development throughout the 1990s [*Osterkamp and Jorgenson*, 2006]. The known timeframe of thermokarst initiation and the upland research area makes the study design unique relative to other natural gradient experiments in boreal lowlands [*Turetsky et al.*, 2007]. In this study, we examine how net ecosystem exchange (NEE), ecosystem respiration (R_{eco}), and GPP respond to thermokarst and the soil environmental factors that change with this disturbance.

2. Methods

2.1. Site Description

[7] The study was conducted approximately 14 km west of Healy, Alaska at Eight Mile Lake (63° 52′ 42″N, 149°15′ 12″W), which is in the northern foothills of the Alaska Range near Denali National Park and Preserve. The mean annual temperature (1976–2005) was −1.0°C in Healy, with extreme differences between the coldest month (December, −16°C) and warmest month (July, 15°C). The total annual average precipitation was 378 mm (National Climate Data Center, NOAA). During this study (spring 2004 to winter 2006–2007), summer precipitation and air temperature were near average in 2006, but temperatures were warmer, and precipitation less, in 2004 and 2005 compared to the long-term average (Table 1). The study site was located at 700 m elevation on a gently sloping (~4%), north facing glacial terminal moraine that dates to the Early Pleistocene [*Wahrhaftig*, 1958]. An organic horizon, 0.45–0.65 m thick, covered cryoturbated mineral soil that was a mixture of glacial till (small stones and cobbles) and windblown loess. Soil organic C pools to 1 m depth averaged between 55 and 69 kg C m^{-2} across all three sites (C. Hicks, unpublished data, 2008). Permafrost was found within 1 m of the soil surface, and therefore the soils were classified in the soil order Gelisol [*Soil Survey Staff*, 1999]. Permafrost temperatures have been monitored in a 30 m deep borehole in the study area since 1985 (maximum temperature range = −0.7 to −1.2°C at 10 m) [*Osterkamp and Romanovsky*, 1999]. During this time frame, researchers recorded rapidly increasing deep permafrost temperatures (by ~0.6°C at 10 m) from 1990 until 1998, followed by a slight cooling (by ~0.2°C) between 1998 and 2004 [*Osterkamp and Jorgenson*, 2006].

Table 1. Average Temperature and Precipitation Estimates for a Long-Term Monitoring Station and the Yearly Climatic Values for the Onsite Weather Station[a]

Year	May	June	July	August	September
		Average Air Temperature[b]			
Long term	7.9	13.4	15.3	12.7	6.8
2004	10.0	15.8	16.2	14.3	1.3
2005	10.9	12.5	13.0	11.5	5.9
2006	6.9	11.0	12.6	9.2	5.9
		Cumulative Precipitation[c]			
Long term	18.8	58.2	67.6	61.2	39.6
2004	17.2	35.4	45.6	19.8	35.2
2005	11.7	20.1	66.8	21.6	25.0
2006	17.8	48.0	77.2	77.6	6.8
		Average PAR[d]			
2004	ND	472	376	298	85
2005	401	403	419	332	150
2006	437	460	382	280	249
		Average Soil Temperature[e]			
2004	ND	9.2	9.6	8.6	3.9
2005	5.8	7.8	8.5	7.9	5.4
2006	4.7	7.3	8.3	7.0	6.3

[a] Over the time period 1971–2000.
[b] Units are °C.
[c] Units are mm.
[d] Units are μmole m^{-2} s^{-1}.
[e] Units are 10 cm, °C.

[8] We selected three sites within 200 m of the borehole for our CO_2 exchange study. The sites represented differing degrees of permafrost thaw, thermokarst disturbance, and vegetation change. The sites included a 1) minimally disturbed moist acidic tundra, where the vegetation was dominated by the tussock-forming sedge *Eriophorum vaginatum* (site hereafter called "Minimal Thaw"), 2) a site adjacent to the borehole where shallow thermokarst depressions (<0.5 m deep) had increased in occurrence since 1990 ("Moderate Thaw"), and where tussock-forming sedges dominated productivity both inside and outside thermokarst, and 3) an area where deeper thermokarst depressions (0.5–1.0 m) were found ("Extensive Thaw"),

and where, based on aerial photographs from 1951, thermokarst depressions had likely been present for at least 5 decades from present. Vegetation productivity at Extensive Thaw was dominated by shrubs (*Vaccinium ulignosum*) and *Sphagnum spp.* mosses [*Schuur et al.*, 2007]. *Jorgenson and Osterkamp* [2005] developed a thermokarst classification scheme that incorporates hydrology, soil texture, soil ice content and morphology, and karst size. Out of 16 categories in this classification system, the thermokarst at the Moderate and Extensive Thaw sites were designated as ‘‘thaw slumps.’’

2.2. Climate Measurements

[9] From May 2004 to May 2007, a Campbell Scientific (Logan, UT) CR10X data logger recorded soil profile temperatures (10, 20, 30, and 40 cm from surface, n = 3) hourly at each site. For all temperature measurements, constantan-copper thermocouples and a reference thermistor were used. Water table depths were measured weekly in wells installed at each site (n = 3). The wells were 15 cm in diameter and extended from the surface to between 0.50 and 1.2 m into the soil profile. The depth of well placement resulted in the bottom 10–30 cm of pipe extending into the permafrost. For water table height, we measured the distance from the soil surface to the top of the water table. To determine the depth of water perched on the frozen soil, the depth from the soil surface to frozen soil layer was also measured immediately adjacent to the pipe. The wells were installed so that one occurred at the uppermost, the middle slope, and the deepest part of a thermokarst depression for a given site. We extrapolated water table depth from the wells to each chamber using a topographic survey [*Lee et al.*, 2009].

[10] An Onset HOBO (Bourne, MA) weather station was used to measure air temperature, photosynthetically active radiation (PAR, band length 470–940 nm), relative humidity, precipitation, and wind speed and direction at 15 s intervals. Incoming solar radiation measurements from a nearby (~4 km from site) weather station maintained by Denali National Park and Preserve were used to interpolate any gaps in our PAR using a solar radiation/PAR conversion factor derived for our site. The temperature and humidity sensor were 1.5 m above the ground surface, while the PAR, precipitation, and wind speed sensors were 2 m above the ground surface.

[11] The difference between photosynthesis and respiration equals the net exchange of CO_2. Each of these components of ecosystem CO_2 exchange was either directly measured (NEE, R_{eco}) or indirectly estimated (GPP). We used closed chambers rather than an eddy covariance tower because in our study area, permafrost thaw and thermokarst depressions occurred at a smaller spatial scale than what could be resolved with an eddy covariance footprint [*Vourlitis et al.*, 2000]. At each site, NEE was estimated at six locations spaced 8 m apart along a 40 m transect. In the summer of 2003, two square plastic bases (0.49 m^2) were cut into the soil organic layer to a depth of ~5 cm at each location. Two bases were initially used (2004–2005) so that vegetation harvests could take place within one, if needed. However, in 2006 the measurements were exclusively made on one chamber base because the fluxes from the paired bases were highly correlated with one another. The bases were subsequently used to seat a clear acrylic chamber that was 40 cm high, a height that fully accommodated the tallest plants. In 2004 and 2005, the two chamber bases in each location were treated as one replicate, for n = 6 replicates per site. At each site, the chamber bases spanned the range of microtopography created by thermokarst depressions. During measurements, a clear chamber was firmly fixed to the base, but not sealed airtight thereby minimizing the pressure differentials that can affect chamber flux measurements [*Lund et al.*, 1999]. In 2004, we only used a single chamber that was moved among chamber bases and sites; in 2005 and 2006 we used both an automated chamber system along with periodic manual measurements. Side-by-side comparisons showed no difference between the two methods for flux calculation. For the autochamber system, R_{eco} was measured only at night ($PAR < 5\ \mu mole\ m^{-2}\ s^{-1}$). For the static chamber, R_{eco} was also measured during the day time by placing an opaque cloth over the top of the chamber to stop photosynthetic uptake.

[12] For all static and autochamber measurements, air was circulated between the chamber and an infrared gas analyzer (LI-820, LICOR Corp., Lincoln, Nebraska) at 1 L min^{-1} for 1.5 min and the CO_2 concentration measured at 2 s intervals. For the static measurements, CO_2 concentrations were recorded to a Palm (Sunnyvale, CA) Tungsten C portable computing device using the software program Online (Conklin Systems, Eaton Rapids, MI). For the automated system, the LI-820 data was recorded on a Campbell Scientific CR10X at 5 s intervals. Two small fans mixed the chamber air, while air temperature and relative humidity were monitored inside the chamber with a HOBO sensor. For the static chamber measurements, PAR was measured inside the chamber with a LICOR quantum sensor attached to a LI-1400 data logger. For the automated chamber, PAR was recorded at a weather station 50–400 m from the sites. A correction factor (19% reduction) was developed for the weather station PAR to account for the effect of reduced light transmission by the Plexiglass, and light interception by the chamber support structures. In conjunction with flux measurements, the thickness of unfrozen ground or the active layer thickness (ALT) was measured once per week at each chamber base.

[13] To describe daily and weekly environmental and gas exchange variability, in 2004 we conducted static chamber measurements 5 times per week at 5 different times of day (pre-0600 LT, 0900 to noon, noon to 1500 LT, 1700 LT to 2000 LT, and after 2300 LT). Variability in incoming PAR was also created by artificially reducing PAR to 1/2 and 1/4 of ambient conditions using mesh screens placed entirely over the chamber during the midmorning and late afternoon measurements. Static chamber measurements were continued in 2005 and 2006, but in these years measurements were only conducted three times of day (approximately 0900 LT to noon, 1400 LT to 1800 LT, and after 1900 LT) because the autochamber system was collecting gas exchange measurements every 1.2 h at each individual chamber base. *Burrows et al.* [2005] compared manual and autochamber measurements and found when a warmer temperature bias in the manual chambers was accounted for, the two methods returned similar results for annual NEE. Our manual and automated chambers only differed by 1.2°C in 2005 and 2006 for daytime NEE, which was likely

why we found no difference in NEE estimated with the two techniques. The automated chamber system was moved every 7–12 days among the three sites, and in general, measured for at least 3 days in a given location. These measurement regimes generally began immediately after snowmelt (∼2–5 May) and continued until a lasting snowfall (∼25–30 September).

[14] After the first snowfall, C exchange measurements were continued on the snow surface (October 2004 to March 2005), and in snow pits dug to the soil surface (November 2005 to April 2007). Measurements using the snow surface approach were only made when the wind was calm (<0.2 m/s) because wind can evacuate CO_2 from the snow profile and result in artificially low or highly erratic efflux rates. A rectangular chamber (0.0794 m^2) on a 0.5 m pole was first pressed into the snow surface to create an imprint, then lifted ∼1 m to flush the chamber, and after 20 s placed again in the imprint. The chamber CO_2 concentration was measured for 6 min, and snow depth was measured afterwards. We used the snow pit method in 2005–2006 because it was less sensitive to wind conditions. The method followed that of *Grogan and Jonasson* [2006], where we dug snow pits that ranged between 0.15 and 0.75 m in depth. At the bottom of the pit, we left ∼5 cm of residual snow on the ground surface. Using the same approach as the surface measurements, the residual snow was used to create a seal with the edge of the chamber. In addition, the outside edge of the chamber was covered with a thin snow layer. Based on repeated measurements of efflux at 3 min intervals, we determined that after the snow pit was excavated, another 13–15 min was needed for CO_2 efflux to approach a near constant rate [*Grogan and Jonasson*, 2006]. At each site, six locations were measured adjacent to the chamber base locations (5–15 m downslope). We avoided measuring directly at the established bases in the winter because we were concerned that disturbing the snow cover would alter the soil thermal regime.

2.3. Estimates of Annual CO_2 Exchange

[15] Seasonal and annual estimates of CO_2 balance were estimated using two methods: gap filling with response functions to environmental factors, and by interpolating mean estimates between time points. For the period from June through August, a rectangular hyperbola equation was used to describe the relationships between PAR and NEE [*Thornley and Johnson*, 1990]. For R_{eco}, we used nighttime and dark chamber measurements to develop exponential relationships between R_{eco} and air (June–August) or soil temperature (winter, and June–August 2006). During spring (May) and fall (September), integrated estimates of NEE and R_{eco} were developed by interpolating fluxes between time points. R_{eco} and NEE at these times of year could not be explained with response functions, likely because plant phenology and soil conditions were changing rapidly. We defined the total growing season as being the period of May–September, but we note that snow often covered the site for the first few days of May and the last days of September. GPP was estimated as the difference between the integrated NEE and R_{eco} values.

[16] We filtered flux measurements for estimates that may have been biased by unusual environmental conditions created by the chamber, or when background conditions created erratic fluxes. When chamber air temperature exceeded 30°C, the collected data point was removed because this temperature was greater than the maximum air temperature measured at the weather station. For the remaining data, chamber air temperature warmed <1°C for 72% of all daytime NEE measurements with a maximum warming of 5.4°C. In addition, automated chamber measurements that occurred during rain, or when wind speeds exceeded >5 m s^{-1}, were also removed because the fluxes were generally erratic. No data were removed based on RH changes inside the chamber. In total, 14% of measurements were eliminated with the data filters. After screening fluxes for environmental conditions, the total number of individual NEE and R_{eco} measurements used for making integrated growing season estimates were 2,986 in 2004, 5,148 in 2005, and 7,152 in 2006.

2.4. Statistical Analysis

[17] The equation parameters for the rectangular hyperbola PAR-NEE relationships, and the exponential R_{eco}-temperature relationships were developed using the nonlinear equation feature in SAS statistical software version 9.1. The integrated May, September, growing season and annual GPP, R_{eco} and NEE were compared using a two-way analysis of variance (mixed model) with site and year as fixed effects. Tukey's HSD post hoc test was used to correct significance levels for multiple comparisons. Soil environmental variables were only statistically compared for those measurements that occurred in each pair of chamber bases (soil temperature at 10 cm, surface moisture, ALT) during the growing season, and for depth to water table. Multiple least squares linear regression was used to determine if site and a combination of soil environmental variables (ALT, average surface soil moisture, soil temperature, and depth to water table) could describe integrated growing season C exchange across sites. Selection for the maximum coefficient of variation (adjusted R^2) and Mallow's CP statistic were used for model selection [*Sokal and Rohlf*, 1995]. When a minimum CP statistic and maximum R^2 are selection criteria, the result is the best fit model with the minimum number of parameters.

3. Results

3.1. Differences in Abiotic Conditions

[18] In all years, the sites differed in the rate of active layer thickening, which describes the seasonal trend of thawing soil surface ice. Soil ice receded faster ($p < 0.001$) at Extensive and Moderate Thaw compared to Minimal until midsummer (Figure 1). Around this time, the seasonal soil ice thawed at a similar rate in both Minimal and Moderate Thaw, while Extensive Thaw continued to lose ice faster than the other two sites ($p < 0.001$). At the end of the growing season, the ALT was significantly greater ($p < 0.01$) at Extensive (78.3 ± 4.5 cm) than Minimal Thaw (68.7 ± 2.0 cm) with Moderate Thaw (70.0 ± 2.0 cm) intermediate but not significantly different from the other two sites. Soil temperature measured at 10 cm during the growing season was on average significantly greater ($p < 0.001$) across years for Moderate (9.6 ± 1.0°C) and Exten-

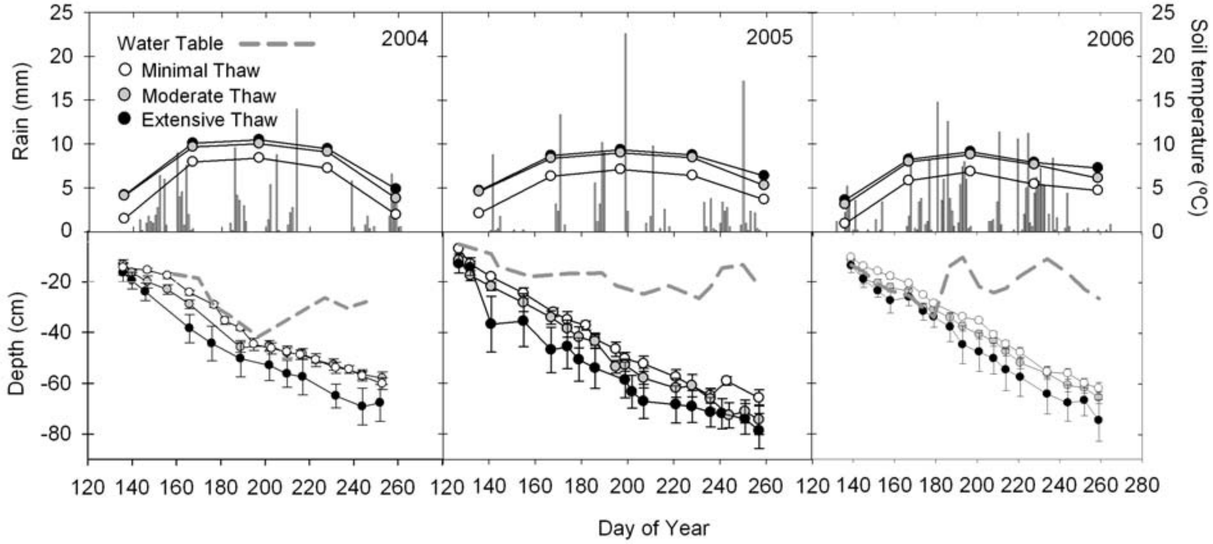

Figure 1. (top) Growing season variation in precipitation (bars) and soil temperature at 10 cm (circles) for 3 years of measurement. (bottom) Active layer thickness (circles) and the water table height (dashed line) averaged across the three sites. The trends across individual ALT measurements and monthly averages of soil temperature are represented by the black lines.

sive (8.8 ± 1.2°C) than for Minimal Thaw (7.6 ± 1.0°C) (Figure 1). The depth to the water table did not differ among sites in any year; however, there was less water on the upper parts of the thermokarst features and more pooled on the bottom of karst. This water accumulation is reflected in the difference between the ALT and water table height (Figure 1); with Extensive Thaw effectively having more free water in the soil horizon because of the greater ALT and more extensive thermokarst.

[19] During winter, the average snow depth was significantly ($p < 0.01$) greater at Extensive (27.1 ± 2.0 cm) and Moderate (27.5 ± 2.4 cm) than Minimal Thaw (21.8 ± 1.7 cm) over the 3 years of periodic measurement. In comparison to Minimal Thaw, Moderate and Extensive Thaw accumulated more snow both in the thermokarst depressions and also in undisturbed areas, likely because these two sites were somewhat closer to the ridge line of the moraine. In summary, the Extensive and Moderate Thaw sites had faster seasonal ice loss, warmer soil temperatures, and deeper snow depths than Minimal Thaw.

3.2. CO_2 Flux Response to Abiotic Factors

[20] The Extensive and Moderate Thaw sites had distinctive growing season peaks in daytime net ecosystem exchange (NEE), while the peak NEE at the Minimal Thaw site was less pronounced (Figure 2). Across all years, the average growing season daytime NEE was positive at all sites, and followed the site order: Moderate Thaw > Extensive Thaw > Minimal Thaw (1.68 ± 0.045, 1.58 ± 0.045, 1.26 ± 0.038 μmole CO_2 m^{-2} s^{-1}). The average R_{eco} for day (shaded chamber) and nighttime measurements increased across sites where Extensive Thaw < Moderate Thaw < Minimal Thaw (−2.68 ± 0.038, −2.25 ± 0.032, −1.98 ± 0.029 μmole CO_2 m^{-2} s^{-1}).

[21] NEE responded to variation in PAR, with the NEE-PAR relationship following a rectangular hyperbola equation during the June–August period (Table 2). Each of the equation parameters (GP_{max}, Alpha, R_{eco}) are related to specific features of ecosystem C dynamics. Averaged across all 3 years, the maximum photosynthetic uptake at full PAR (GP_{max}) was significantly greater at Extensive (8.2 ± 0.80 μmole CO_2 m^{-2} s^{-1})) and Moderate (7.8 ± 0.62 μmole CO_2 m^{-2} s^{-1}) than Minimal Thaw (5.67 ± 0.14 μmole CO_2 m^{-2} s^{-1}). The rate of ecosystem C uptake at low light (Alpha) was not significantly different among sites. Ecosystem respiration (R_{eco}) at the y intercept decreased from Extensive (−2.90 ± 0.19 μmole CO_2 m^{-2} s^{-1}) > Moderate (−2.55 ± 0.10 μmole CO_2 m^{-2} s^{-1}) > Minimal Thaw (−2.00 ± 0.14 μmole CO_2 m^{-2} s^{-1}).

[22] During the growing season, R_{eco} most closely followed air and soil temperature (Table 3). Although the relationships were significant ($p < 0.01$) for all chambers, air and 10 cm soil temperature explained a wide range in the total variance ($R^2 = 0.12–0.56$, Table 3). The y intercepts of the exponential relationships followed the same site order as the NEE intercept: Extensive > Moderate > Minimal Thaw (Table 3), while the exponents of the equations followed no consistent site order.

[23] For winter R_{eco}, the best fit between soil temperature and CO_2 efflux was obtained when the temperature of the entire soil profile was averaged across all soil depths (10–40 cm). There was a distinct drop in R_{eco} as the average soil temperature crossed a threshold at approximately −2°C (Figure 3). Below −2°C, R_{eco} responded exponentially to the mean temperature of the soil profile, but neither the slope nor intercept of the response curves differed among sites (Figure 3). Near −2°C, R_{eco} increased dramatically and values above this temperature could not be fit to the same response curve describing respiration below −2°C. Moreover, between −2 and 0.5°C, the relationship between R_{eco} and soil temperature was not significant for any site, possibly due to the limited temperature range. The average

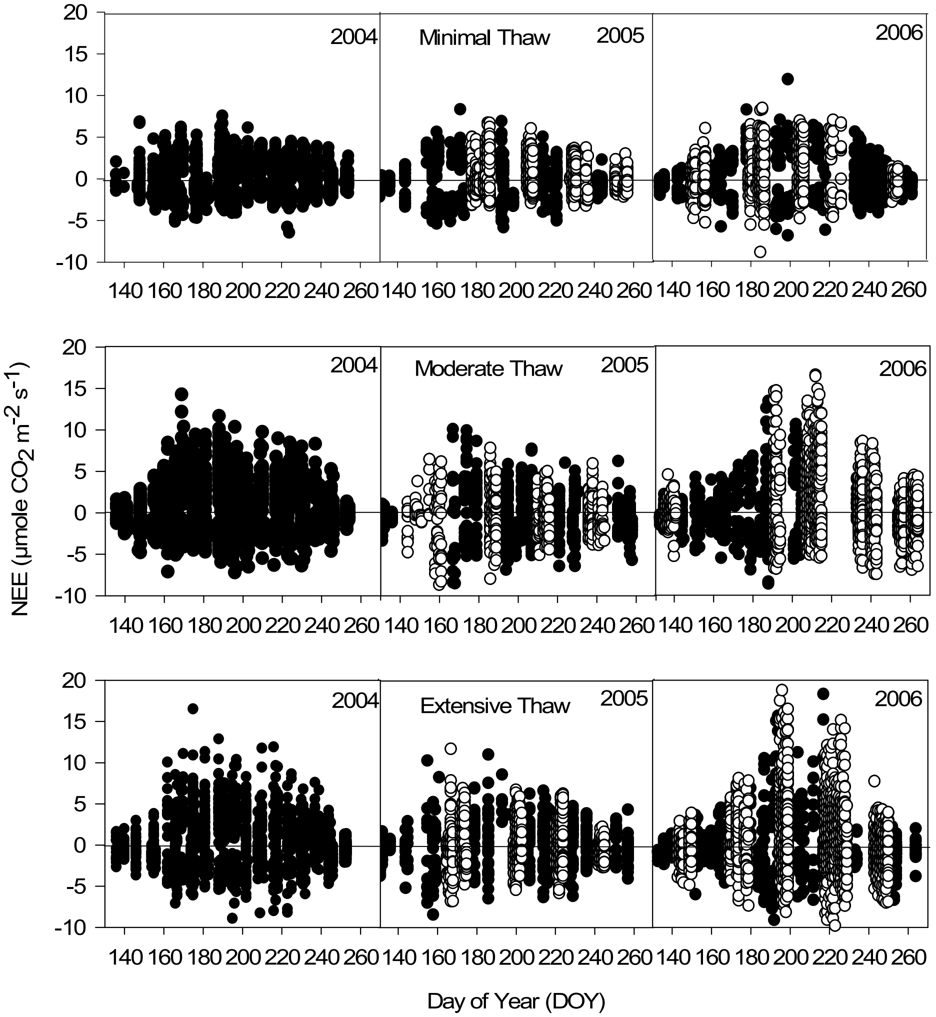

Figure 2. All net ecosystem exchange (NEE) and ecosystem respiration (R_{eco}) data collected during the growing season. Open circles are automated chamber (2005 and 2006), and closed symbols are manual chamber measurements. Negative values are C loss from the ecosystem.

(n = 45) winter R_{eco} in the −2 and 0.5°C soil temperature range was significantly greater for Extensive Thaw (0.85 ± 0.05 μmole CO_2 m^{-2} s^{-1}) than either Moderate (0.60 ± 0.06 μmole CO_2 m^{-2} s^{-1}) or Minimal Thaw (0.55 ± 0.03 μmole CO_2 m^{-2} s^{-1}). Moderate and Minimal Thaw did not differ significantly from one another. Snow depth was positively correlated to the residuals of the temperature relationship, explaining 8% of the remaining variance ($p < 0.05$, data not shown). Outliers became obvious for individual measurement areas with very deep snow cover at the Extensive Thaw site. Deep snow areas were generally the lowest points within thermokarst, where ice lenses formed from standing water. The lenses could have prevented CO_2 diffusion during the winter.

Table 2. Growing Season Light Response Curves of NEE for Three Sites With Varying Degrees[a]

Site	Year	Gp_{max}	Alpha (α)	R_{eco}	R^2	n
Minimal thaw	2004	5.38 (0.38)	0.040 (0.012)	−2.20 (0.40)	0.73	1077
Moderate thaw		7.76 (0.38)	0.052 (0.010)	−2.69 (0.39)	0.71	1174
Extensive thaw		8.72 (0.29)	0.047 (0.010)	−3.13 (0.26)	0.72	1137
Minimal thaw	2005	5.85 (0.46)	0.026 (0.006)	−2.07 (0.24)	0.64	1122
Moderate thaw		6.68 (0.22)	0.038 (0.005)	−2.50 (0.22)	0.68	1002
Extensive thaw		6.58 (0.30)	0.027 (0.005)	−2.49 (0.33)	0.69	1475
Minimal thaw	2006	5.78 (0.37)	0.040 (0.006)	−1.74 (0.29)	0.68	1111
Moderate thaw		8.81 (0.39)	0.042 (0.003)	−2.35 (0.39)	0.60	1897
Extensive thaw		9.18 (0.39)	0.073 (0.005)	−3.00 (0.22)	0.47	1868

[a] Coefficient of variation corresponds to pseudo R^2.

Table 3. Average Parameters for Exponential Response Curves That Explain the Relationship Between Growing Season Nighttime and Darkened Chamber R_{eco} and Temperature at Each Site[a]

Independent Variable/Site	Year	Intercept	Exponent	R^2	n
		Air Temperature			
Minimum thaw	2004	−1.21 (0.05)	−0.030 (0.003)	0.33	341
Moderate thaw		−1.51 (0.13)	−0.030 (0.003)	0.25	354
Extensive thaw		−1.81 (0.19)	−0.031 (0.004)	0.28	332
Minimum thaw	2005	−1.16 (0.18)	−0.048 (0.006)	0.31	329
Moderate thaw		−1.30 (0.24)	−0.054 (0.007)	0.35	335
Extensive thaw		−1.40 (0.20)	−0.050 (0.008)	0.34	402
		Soil Temperature			
Minimum thaw	2006	−1.42 (0.17)	−0.040 (0.014)	0.22	401
Moderate thaw		−2.05 (0.20)	−0.020 (0.005)	0.18	434
Extensive thaw		−2.40 (0.29)	−0.020 (0.013)	0.20	326

[a] Average parameters: mean ± stderr; Units for R_{eco} are μmole CO_2 m^{-2} s^{-1}. More negative R_{eco} values denote increasing ecosystem CO_2 loss.

3.3. Net CO_2 Balance: Seasonal and Interannual Variation

[24] In all years, the three sites were sinks of CO_2 (NEE positive) from 1 June through 31 August at an average monthly rate of 33 g CO_2-C m^{-2} (Figure 4). In general, modeled NEE peaked in June because this was the maximum point for GPP, while R_{eco} was greatest in July. This latter offset between the GPP and R_{eco} peaks occurred because, on average, 10% more PAR occurred in June than July while air and surface soil temperatures were always greatest in July (Table 1). A two-way ANOVA indicated that across years, R_{eco} and GPP were significantly greater ($p < 0.01$) at Extensive and Moderate compared to Minimal Thaw during the midgrowing season (June–August) (Table 4). During this season, the NEE of Moderate Thaw was greater than Minimal Thaw ($F = 6.00$, $p = 0.018$), with Extensive Thaw intermediate between these two sites and nominally greater than Minimal Thaw ($F = 2.81$, $p = 0.10$, Table 4). In both May and September, all sites were a source of C (NEE negative), and Extensive Thaw lost significantly ($p < 0.05$) more C than Minimal Thaw in both months (Figure 4). This occurred primarily because R_{eco} at Extensive Thaw was significantly greater than at the other two sites (Table 4), while GPP in the spring and fall was not significantly different among sites.

[25] Growing season (May–September) NEE varied significantly ($F = 8.7$, $p = 0.0032$) for Extensive Thaw across years (Figure 5a). This variation occurred for two reasons: (1) interannual changes in spring and fall NEE, and (2) the response curve parameters changed significantly among years for the equations that described growing season NEE and R_{eco} (Tables 2 and 3). For both effects, it was difficult to identify a single climatic factor that could explain these changes, likely because the study had only been ongoing for 3 years. After winter R_{eco} was included in the annual estimate (Figure 5b), annual NEE was negative for Extensive and Minimal Thaw for 2 of 3 years. Moderate Thaw remained a CO_2 sink or near neutral even after winter R_{eco} was included in the annual estimate (Table 4 and Figure 5b). Including winter R_{eco} did not increase the degree of interannual change in annual NEE.

[26] The 3 year average C uptake for Moderate Thaw was positive (25 ± 17 g CO_2-C m^{-2} yr^{-1}, $u \neq 0$, $p = 0.06$, Mixed Model ANOVA); Extensive Thaw lost a significant amount of C (-32 ± 22 g CO_2-C m^{-2} yr^{-1}, $u < 0$, $p = 0.02$), while Minimal Thaw was negative but not significantly different from C neutral (-17 ± 9 g CO_2-C, $u \neq 0$, $p = 0.22$) (Table 4). The error terms reflect the error among replicates bases at each site after 3 years of integration. The error associated with measurement methods, scaling, and interannual variation were not explicitly included in the overall error. The annual NEE of Moderate Thaw indicated it was taking up significantly greater amounts of C ($p < 0.05$) than either Extensive or Minimal Thaw, which did not differ from one another (Table 4).

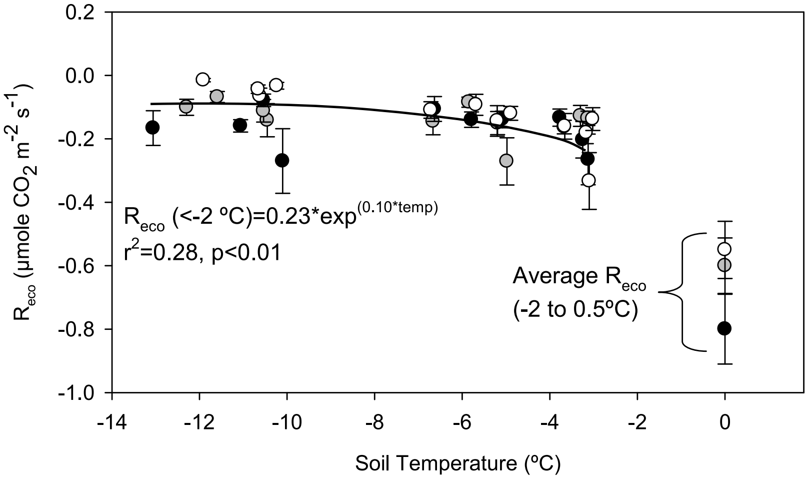

Figure 3. Response of ecosystem respiration (R_{eco}) during winter to integrated soil temperature averaged across 10, 20, 30, and 40 cm depths. Winter R_{eco} values measured between −2 and 0.5°C were not significantly related to temperature, but increased dramatically relative to respiration at colder (<2°C) temperatures. Below <2°C, R_{eco} and temperature were significantly correlated but the exponential relationships were not significantly different across sites.

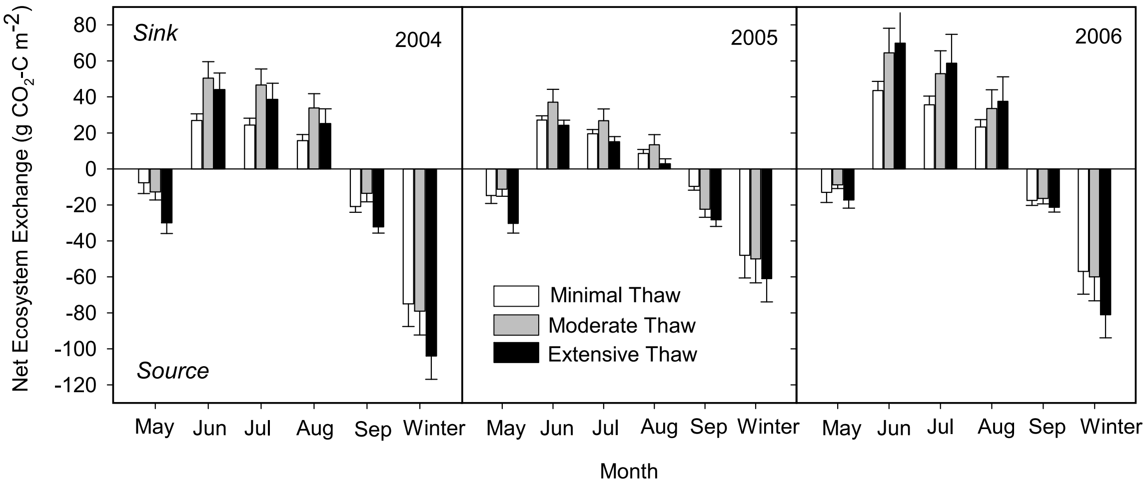

Figure 4. Modeled monthly NEE and winter R_{eco} (average ± stderr) for three sites varying in degree of permafrost thaw over 3 years of measurement.

3.4. Spatial Variability in Fluxes

[27] We examined whether the soil environmental properties that characterized a chamber base (growing season average 10 cm soil temperature and surface moisture, mean water table height, and active layer thickness) could be combined in a multiple regression to describe growing season (May–September) C exchange (GPP, NEE, R_{eco}). Across all years, ALT was selected in the model as the only soil variable that explained a significant amount of cross-site variation for the various fluxes (Figure 6). The patterns of ecosystem C cycling across sites suggests that both GPP and R_{eco} will increase with thaw, with some relationships being year specific (Figures 6a and 6b). In 2005, the GPP versus ALT relationship was significantly different ($p < 0.05$) in slope from the other 2 years, but the R_{eco} versus ALT relationships did not significantly vary among years. In 2006, NEE was also positively related to ALT (Figure 6c), but an NEE value from one Extensive Thaw chamber location was deemed to have high leverage on the regression analysis; removing this point restricted the range of observations and resulted in a nonsignificant relationship.

[28] As previously reported by *Schuur et al.* [2007], total aboveground biomass (moss plus vascular plants) was the least at Minimal Thaw (173 ± 8 g C m^{-2} yr^{-1}), and nearly identical at Extensive Thaw (233 ± 8 g C m^{-2} yr^{-1}) and Moderate Thaw (234 ± 18 g C m^{-2} yr^{-1})[*Schuur et al.*, 2007]. Trends in aboveground net primary productivity (ANPP) followed biomass, and in 2006 the biomass and ANPP values were nearly identical to 2004 estimates (2005 measurements were not made). Across sites, ANPP was significantly correlated with GPP, R_{eco}, and NEE during the 2004 and 2006 growing seasons (May–September, Figures 7a–7c). The 2 years did not differ from one another in the slope or intercept of any of the relationships.

4. Discussion

4.1. Annual CO_2 Balance

[29] With climate warming in permafrost regions, permafrost thaw and thermokarst formation is likely to accelerate [*Osterkamp*, 2007]. The primary question of this study was: How would thermokarst affect ecosystem C cycling in an upland moist acidic tundra ecosystem? We found that the greater active layer thickness (ALT) inside thermokarst depressions corresponded to greater rates of GPP and R_{eco} (Table 4 and Figures 6a and 6b). NEE, however, was generally unrelated with ALT (Figure 6c), indicating that for the growing season, GPP and R_{eco} increased proportionately with active layer thickness. However, spring, fall, and winter were critically important to site differences in C balance because GPP was minimal at those times of year, while R_{eco} continued to be greater in the thermokarst depressions at Extensive Thaw. The importance of winter and seasonal transition periods in affecting arctic C balance has been previously noted [*Oechel et al.*, 2000; *Elberling et al.*, 2008]; however our study suggests that the degree of thermokarst will accentuate the importance of these seasons.

[30] During the late fall and early winter, R_{eco} at Extensive Thaw diverged from Moderate and Minimal Thaw because of greater respiration between the soil temperatures of −2 and 0.5°C (Figure 3). The sites likely differed in how much of the soil profile remained in this temperature range because of the interaction between active layer thickness in thermokarst, subsequent water accumulation, and soil temperature. At the end of the year, water preferentially accumulated in thermokarst (Figures 1 and Figure 8), which generally causes permafrost under thermokarst to thaw longer into the winter and to a deeper point than permafrost in drier terrain [*Osterkamp*, 2005]. The depth and spatial distribution of our soil temperature probes did not allow us to directly characterize deep soil temperatures for the thermokarst at Extensive Thaw, but we note that the Extensive Thaw site had a deeper point of thaw than the other two sites in all years (Figure 1). This we presume reflected warmer soil temperatures below our probes, which likely resulted in a greater R_{eco} per degree Celsius. Previous research has demonstrated that microbial respiration increases dramatically from −2 to 0°C [*Mikan et al.*, 2002; *Panikov et al.*, 2006], possibly because there is an exponential increase in soil moisture within this temperature

Table 4. Average Growing Season, Winter and Annual GPP, R_{eco}, and NEE for Three Sites Varying in Degree of Permafrost Thaw[a]

		Spring (May)			Summer (June–August)			Fall (September)					
Site	Year[b]	GPP	R_{eco}	NEE	GPP	R_{eco}	NEE	GPP	R_{eco}	NEE	Winter (October–April) R_{eco}	Annual R_{eco}	Annual NEE
Minimal	2004	40 ± 7a	−48 ± 3a	−8 ± 6a	264 ± 16a	−197 ± 9a	67 ± 11a	23 ± 2a	−43 ± 2a	−20 ± 3a	−75 ± 12a	−362 ± 15a	−36 ± 16a
Moderate	2004	40 ± 4a	−52 ± 5ab	−13 ± 2a	371 ± 42b	−241 ± 21ab	131 ± 23b	34 ± 5a	−46 ± 4a	−13 ± 4a	−79 ± 14a	−418 ± 25b	26 ± 26b
Extensive	2004	31 ± 7a	−62 ± 5b	−31 ± 7b	391 ± 49b	−283 ± 29b	108 ± 21b	28 ± 4a	−59 ± 4b	−31 ± 2b	−104 ± 18b	−507 ± 35c	−58 ± 23a
Minimal	2005	24 ± 2a	−39 ± 2a	−15 ± 3a	260 ± 13a	−205 ± 9a	55 ± 5a	21 ± 2a	−32 ± 2a	−11 ± 2a	−48 ± 10a	−324 ± 14a	−19 ± 4a
Moderate	2005	32 ± 4a	−46 ± 4ab	−15 ± 2a	326 ± 30a	−249 ± 20ab	77 ± 19a	26 ± 3a	−46 ± 6b	−20 ± 7ab	−50 ± 11a	−390 ± 23ab	−7 ± 24a
Extensive	2005	32 ± 6a	−65 ± 7b	−33 ± 7b	319 ± 25a	−277 ± 24b	42 ± 7b	25 ± 3a	−51 ± 7b	−27 ± 5b	−61 ± 16a	−454 ± 29b	−78 ± 13b
Minimal	2006	26 ± 2a	−49 ± 4a	−23 ± 3a	273 ± 20a	−170 ± 12a	103 ± 13a	30 ± 4a	−47 ± 5a	−18 ± 5a	−57 ± 11a	−324 ± 16a	5 ± 14a
Moderate	2006	21 ± 2a	−32 ± 3ab	−11 ± 2b	369 ± 47ab	−218 ± 21ab	151 ± 35a	40 ± 3a	−63 ± 7b	−23 ± 4a	−60 ± 12a	−373 ± 24ab	57 ± 36a
Extensive	2006	24 ± 5a	−47 ± 9b	−23 ± 5a	411 ± 71b	−245 ± 35b	166 ± 39a	45 ± 9a	−67 ± 14ab	−22 ± 6a	−81 ± 17b	−440 ± 39b	40 ± 31a
Minimal	Average	30 ± 4a	−46 ± 3a	−15 ± 4a	266 ± 16a	−191 ± 10a	75 ± 10a	24 ± 3a	−41 ± 3a	−16 ± 3a	−60 ± 11a	−337 ± 15a	−17 ± 9a
Moderate	Average	31 ± 3a	−44 ± 4a	−13 ± 2a	355 ± 40b	−236 ± 21b	120 ± 26b	33 ± 4b	−52 ± 5b	−19 ± 5ab	−63 ± 12a	−394 ± 24b	25 ± 17b
Extensive	Average	29 ± 6a	−58 ± 7b	−29 ± 6b	374 ± 49b	−268 ± 30b	106 ± 22ab	32 ± 5ab	−59 ± 6b	−27 ± 4b	−82 ± 17b	−467 ± 34c	−32 ± 22a

[a] Average is ± stderr. GPP, gross primary productivity; R_{eco}, ecosystem respiration; NEE, net ecosystem exchange. Units for C exchange are g CO_2-C m^{-2}. Different letters within a column represent significant differences ($p < 0.05$) among sites within a year, or the average across years.

[b] Calendar year refers to the spring and summer. Winter includes October to December of the same calendar year, plus January to April of the following calendar year.

range [*Schimel et al.*, 2006]. At subzero temperatures, microbes respond quickly to free water [*Panikov et al.*, 2006], because water films allow microbes to maintain cell integrity [*Mikan et al.*, 2002; *Price and Sowers*, 2004], and to access dissolved organic carbon [*Michaelson and Ping*, 2003]. The combination of a deeper thaw depth and greater accumulated water inside thermokarst may have been why Extensive Thaw had greater winter R_{eco} than did the other two sites (Figure 3).

[31] This study differs from previous studies in upland tussock tundra ecosystems because we incorporated a gradient of time-since-permafrost thaw into the study design. Assuming that these sites represent a natural progression in thermokarst, the trend across sites suggests that before permafrost thaw, ecosystem C balance may be near neutral in tussock tundra (represented by our Minimal Thaw site). Then, after 15 years of thaw (represented by the Moderate Thaw site) ecosystem C uptake will increase, but with further thaw (represented by Extensive Thaw), net ecosystem C loss to the atmosphere will occur due to increases in R_{eco} that offset increases in GPP. Although our estimates of annual C balance should be viewed with some caution because of the inherent difficulties in estimating error [*Alm et al.*, 1997], modeling studies of arctic tundra have suggested that ecosystem C balance approaches equilibrium under stable climates, but that warming initially induces C loss, and as decomposition proceeds and nutrients are released, arctic tundra becomes a stronger C sink [*Waelbroeck et al.*, 1997; *Zhuang et al.*, 2001]. We began this study 13 years after permafrost thaw had started, during a phase of stable permafrost temperatures [*Osterkamp*, 2007]. Therefore, Moderate Thaw may have undergone an earlier stage of C loss, but the greater total plant canopy nitrogen of both Extensive and Moderate

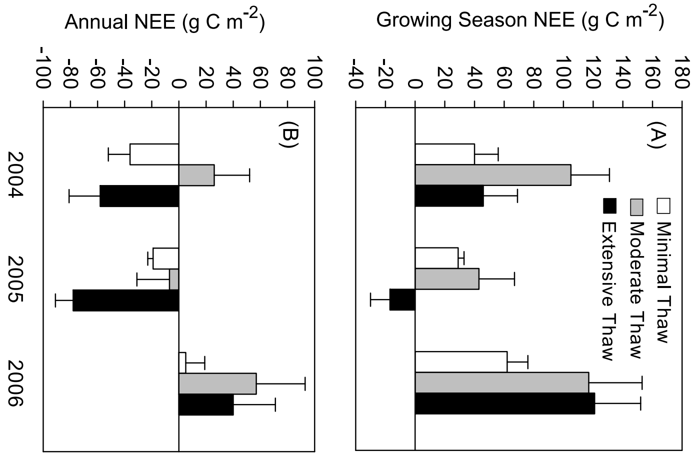

Figure 5. The NEE of the (a) growing season (May–September) and (b) annual period for 3 years of this study.

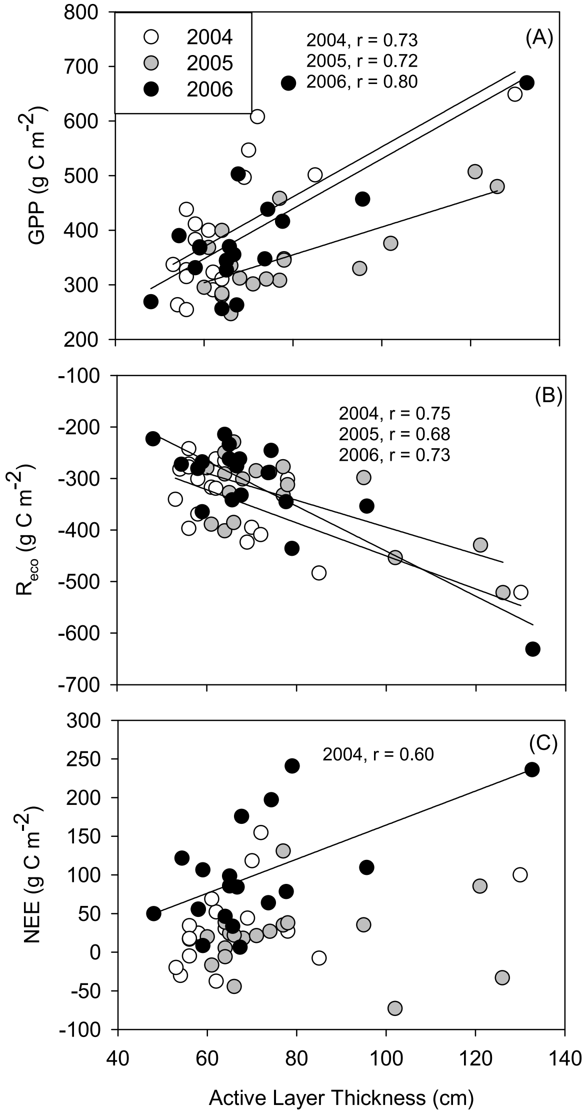

Figure 6. Relationship between active layer thickness and growing season (May–September) CO_2-C exchange. All data with an associated linear fit line and a correlation coefficient (r) have a p value that is <0.01.

Thaw than Minimal Thaw [*Schuur et al.*, 2007], suggests that these two sites have entered the phase where increased nutrient availability has increased plant photosynthesis. The difference between those two sites is that greater R_{eco} at Extensive Thaw has caused it to be a source of C (Table 4), suggesting that microbial respiration, nutrient release, and photosynthesis may have become decoupled. This decoupling may have occurred because of the deeper active layer at Extensive than Moderate Thaw and the shift in species dominance from graminoids to shrubs and nonvascular sphagnum moss species (*Sphagnum lenense*, *Sphagnum girgensohnii*) that are adapted to wetter environments (Figure 8). Shrubs are shallower rooted than graminoids [*Mack et al.*, 2004], and mosses cannot access nutrients below their intact tissues. Therefore, we hypothesize that the "deep" nutrients released at Extensive Thaw with stimulated microbial respiration had less of an effect on plant growth than at Moderate Thaw.

4.2. Intraannual Variation in CO_2 Exchange

[32] We estimated NEE for an entire annual period, which proved critical to understanding the C dynamics of this ecosystem. We found that during the midgrowing season, in most years each site was C sink (Table 4), which agrees with the many other studies conducted in high latitude ecosystems [*Alm et al.*, 1997; *Christensen et al.*, 2000; *Oechel et al.*, 2000; *Zamolodchikov and Karelin*, 2001; *Aurela et al.*, 2007; *Welker et al.*, 2004; *Rennermalm et al.*, 2005; *Kwon et al.*, 2006]. Our one instance of growing season C loss (Extensive Thaw, 2005) was caused by spring and fall C loss (Table 4), and was less than that reported by *Larsen et al.* [2007] for a heath ecosystem (-107 g CO_2-C m^{-2}) and by *Heikkinen et al.* [2002] for the growing season in a variety of tundra community types (-60 to -123 g CO_2-C m^{-2}). The spring and fall are generally periods when arctic tundra and boreal bogs lose C because GPP is low and offset by respiration [*Vourlitis et al.*, 2000; *Mertens et al.*, 2001; *Harazono et al.*, 2003; *Marchand et al.*, 2004; *Welker et al.*, 2004; *Glenn et al.*, 2006]. We also observed winter R_{eco} to cause either a significant reduction in annual C uptake, or a net loss of ecosystem C (Figure 5b); an observation that has become fairly common for northern and montane ecosystems [*Alm et al.*, 1997; *Oechel et al.*, 2000; *Zamolodchikov and Karelin*, 2001; *Aurela et al.*, 2007; *Lafleur et al.*, 2003; *Welker et al.*, 2004; *Rennermalm*

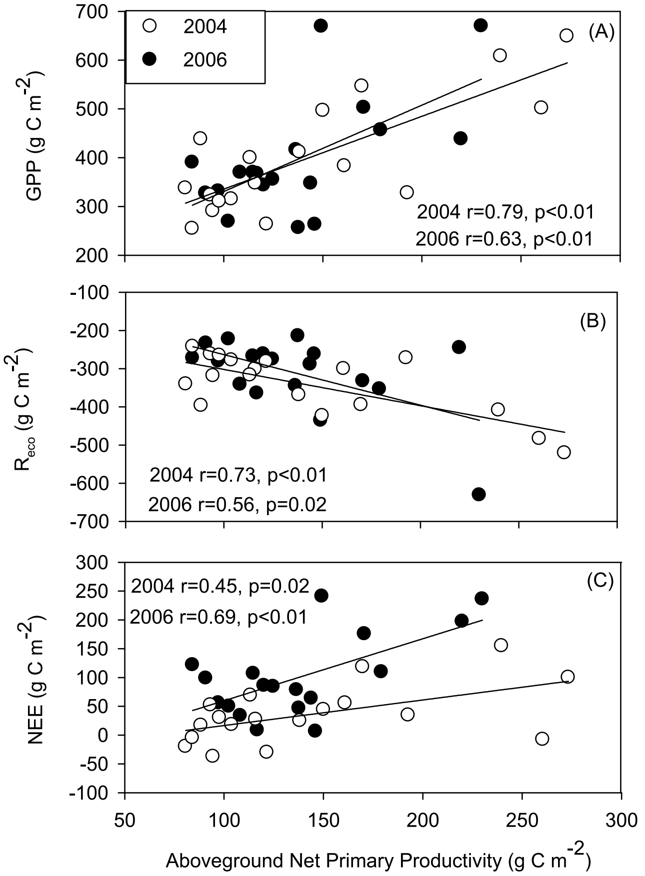

Figure 7. Relationship between aboveground net primary productivity (ANPP) and growing season (May–September) CO_2-C exchange for 2004 and 2006. ANPP was not measured in 2005.

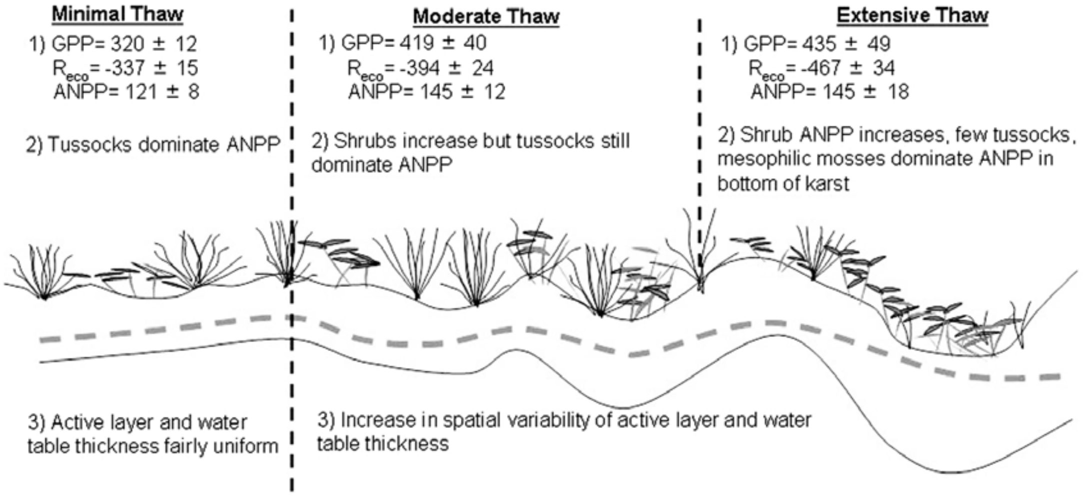

Figure 8. Summary of gross primary productivity (GPP, g CO_2-C m^{-2} yr^{-1}), ecosystem respiration (R_{eco}, g CO_2-C m^{-2} yr^{-1}), and aboveground net primary productivity (ANPP, g C m^{-2} yr^{-1}) and conceptual diagram linking these fluxes to the changes in vegetation dominance of ANPP, active layer thickness (solid line), and water table height (dashed line) with increasing occurrence of thermokarst. Note that the depth to water table is similar at the site level, but within the Extensive Thaw site, water tends to pool where the active layer thickness is the greatest.

et al., 2005; *Monson et al.*, 2006; *Nobrega and Grogan*, 2007]. Our estimates of winter respiration (−48 to −104 g CO_2-C m^{-2}, Table 4) are slightly greater than those from colder arctic and boreal regions of Alaska [*Jones et al.*, 1999; *Fahnestock et al.*, 1999; *Schimel et al.*, 2006] and boreal bogs and fens [*Aurela et al.*, 2007; *Moore et al.*, 2002; *Lafleur et al.*, 2003], but are similar to Russian tundra [*Zimov et al.*, 1996]. In contrast, studies in warmer arctic regions have found winter R_{eco} to be nearly 2x greater than our estimates [*Grogan and Jonasson*, 2006; *Elberling et al.*, 2008].

4.3. Plant Productivity and CO_2 Exchange

[33] ANPP correlated with both growing season GPP and R_{eco} across sites (Figures 6a and 6b), and ANPP better described the spatial variability of NEE than did any soil environmental variable (Figure 6c). In general, this supports the observation that in arctic ecosystems, growing season NEE is highly sensitive to GPP and ANPP [*Shaver et al.*, 2007]. In contrast, ALT only described NEE variability for 2004, despite ANPP and canopy N both generally increasing with active layer thickness [*Schuur et al.*, 2007]. Still, this result highlights that although permafrost thaw and thermokarst can correlate to ANPP, NEE may not necessarily increase with permafrost thaw.

[34] The moist acidic tussock tundra ecosystem that we studied covers a larger portion of Alaska than any other tundra type [*Epstein et al.*, 2004]. Prior studies of this ecosystem have focused on areas north of the Brooks Mountain Range [*Oechel et al.*, 2000; *Shaver et al.*, 2001; *Oberbauer et al.*, 2007]; regions that are colder than the more southerly area that we studied. The contrast in ANPP and GPP between the relatively undisturbed Minimal Thaw site, and studies from more northern regions, supports the observation that regional climate warming will increase plant productivity and GPP [*Oberbauer et al.*, 2007]. At the Minimal Thaw site, our estimate of ANPP was 32% greater than for moist acidic tundra near Toolik Lake [*Shaver et al.*, 2001; *Schuur et al.*, 2007], a proportion similar to the difference between Healy and Toolik in average July air temperatures (26%) [*Oberbauer et al.*, 2007, Table 1]. Air warming experiments in some tussock tundra communities also suggest proportional increases of GPP and ANPP with summer warming [*Chapin and Shaver*, 1996; *Oberbauer et al.*, 2007]. In contrast, ANPP at Moderate and Extensive Thaw was 75% greater than northern Alaska, suggesting that permafrost thawing, with associated changes in soil nutrients and water, could increase plant growth to a greater degree than atmospheric warming alone. However, as was discussed earlier, annual NEE decreased with relatively extensive permafrost thaw because growing season GPP could not offset increased winter, spring, and fall R_{eco}.

4.4. Flux Response to Abiotic Variables

[35] Instantaneous NEE and R_{eco} responded to PAR and temperature in a manner generally consistent with past arctic research [*Vourlitis et al.*, 2000], and similar to past studies, R_{eco} and NEE were poorly correlated in the spring and fall to the climatic variables that described growing season C exchange [*Oberbauer et al.*, 2007]. This disconnect between C exchange and climate could represent a significant difficulty in estimating future C balance [*Sitch et al.*, 2007], and different processes may be responsible for the climate-CO_2 exchange disconnect in the spring and fall. In May, the soil profile CO_2 concentration was 10–30x higher at 10 cm depth in the soil than at the soil surface [*Lee et al.*, 2006], indicating that a seasonal ice layer was likely obstructing diffusion. Ice thawing may have released pockets of soil CO_2, as evidenced by the autochambers recording periodic spikes in R_{eco} (Figure 1). This outgassing has been previously observed in the Arctic [*Harazono et al.*, 2003; *Elberling et al.*, 2008], and is a phenomenon that can sometimes make it difficult to relate R_{eco} and NEE to daily

variation in temperature or incoming radiation [*Oberbauer et al.*, 2007]. In the fall, a photosynthetic decrease linked with leaf senescence can progress independent of direct air temperature changes [*Aerts et al.*, 2006], causing the plant and microbial components of R_{eco} to become decoupled. Furthermore, peaks in air and soil temperature become offset in time (Table 1), and this temperature disconnect could result in surface and subsoil R_{eco} also being temporally disconnected from one another. Both thermokarst and undisturbed areas had relatively poor response curves at these times of year, but the relative importance of spring and fall to ecosystem CO_2 imbalance increased with the degree of permafrost thaw. Thus, linking climate and ecosystem CO_2 exchange for the spring and fall will be critical for predicting how arctic ecosystem CO_2 balance will change with warming and permafrost thaw.

5. Summary

[36] The results from this gradient study suggest that CO_2 gains after initial permafrost thaw can be reversed with enough time and thermokarst development. The reason for the net C loss was because of enhanced R_{eco} in the winter, spring, and fall in thermokarst areas, and R_{eco} was likely greater in thermokarst areas because of greater active layer thickness, which we speculate was related to warmer deep soil layers that fell within a critical temperature range (−2 to 0.5°C). A better understanding of the controls on ecosystem C flux are needed for this soil temperature range and the nonphotosynthetic season in general, because in the next century, the largest climatic changes for the Arctic are predicted for the spring, fall, and winter [*IPCC*, 2007]. For the growing season, plant primary productivity increased enough with the initial permafrost thaw to offset increased respiration, but this trend was not sustained when permafrost thaw and thermokarst development became extensive. A possible reason is that the vegetation that predominates in thermokarst areas (shrubs and mosses) are shallow rooted or nonvascular and cannot access nutrients released by microbial activity deeper in the soil horizon. Thus, further research is needed on why plant species composition changes with permafrost thaw.

[37] **Acknowledgments.** We would like to thank Terry Chapin and the personnel of BNZ-LTER for the use of equipment and laboratory space. This research is based upon work supported by NSF EAR grant 0223193 to E.A.G.S.; NASA New Investigator Award to E.A.G.S.; a NSF LTER grant 0080609 to E.A.G.S.; a NSF DEB grant 0516326 to E.A.G.S.; a DOE-NICCR grant to E.A.G.S. and J.G.V. DE-FC02-06ER64159 and an A.W. Mellon Foundation grant to E.A.G.S.

References

Aerts, R., J. H. C. Cornelissen, and E. Dorrepaal (2006), Plant performance in a warmer world: General responses of plants from cold, northern biomes and the importance of winter and spring events, *Plant Ecol.*, *182*, 65–77.

Alm, J., A. Talanov, S. Saarnio, J. Silvola, E. Ikkonen, H. Aaltonen, H. Nykanen, and P. J. Martikainen (1997), Reconstruction of the carbon balance for microsites in a boreal oligotrophic pine fen, Finland, *Oecologia*, *110*, 423–431, doi:10.1007/s004420050177.

Aurela, M., T. Riutta, T. Laurila, J. P. Tuovinen, T. Vesala, E. S. Tuittila, J. Rinne, S. Haapanala, and J. Laine (2007), CO_2 exchange of a sedge fen in southern Finland: The impact of a drought period, *Tellus, Ser. B*, *59*, 826–837.

Brown, J., O. J. Ferrians Jr., J. A. Heginbottom, and E. S. Melnikov (1998), Circum-arctic map of permafrost and ground-ice conditions, map, Natl. Snow and Ice Data Cent./World Data Cent. for Glaciol., Boulder, Colo.

Burrows, E., J. Bubier, A. Mosedale, G. Cobb, and P. Crill (2005), Net ecosystem exchange of carbon dioxide in a temperate poor fen: A comparison of automated and manual chamber techniques, *Biogeochemistry*, *76*, 21–56, doi:10.1007/s10533-004-6334-6.

Chapin, F. S., and G. R. Shaver (1996), Physiological and growth responses of arctic plants to a field experiment simulating climatic change, *Ecology*, *77*, 822–840, doi:10.2307/2265504.

Christensen, T. R., T. Friborg, M. Sommerkorn, J. Kaplan, L. Illeris, H. Soegaard, C. Nordstroem, and C. S. Jonasson (2000), Trace gas exchange in a high-arctic valley: 1. Variations in CO_2 and CH4 flux between tundra vegetation types, *Global Biogeochem. Cycles*, *14*(3), 701–713, doi:10.1029/1999GB001134.

Davidson, E. A., and I. A. Janssens (2006), Temperature sensitivity of soil carbon decomposition and feedbacks to climate change, *Nature*, *440*, 165–173, doi:10.1038/nature04514.

Elberling, B., C. Nordstrom, L. Grondahl, H. Sogaard, T. Friborg, T. R. Christensen, L. Strom, F. Marchand, and I. Nijs (2008), High-arctic soil CO_2 and CH_4 production controlled by temperature, water, freezing and snow, *Adv. Ecol. Res*, *40*, 441–472, doi:10.1016/S0065-2504(07)00019-0.

Epstein, H. E., M. P. Calef, M. D. Walker, F. S. Chapin, and A. M. Starfield (2004), Detecting changes in arctic tundra plant communities in response to warming over decadal time scales, *Global Change Biol.*, *10*, 1325–1334, doi:10.1111/j.1529-8817.2003.00810.x.

Fahnestock, J. T., M. H. Jones, and J. M. Welker (1999), Wintertime CO_2 efflux from arctic soils: Implications for annual carbon budgets, *Global Biogeochem. Cycles*, *13*, 775–779, doi:10.1029/1999GB900006.

Glenn, A. J., L. B. Flanagan, K. H. Syed, and P. J. Carlson (2006), Comparison of net ecosystem CO_2 exchange in two peatlands in western Canada with contrasting dominant vegetation, Sphagnum and Carex, *Agric. For. Meteorol.*, *140*, 115–135, doi:10.1016/j.agrformet.2006.03.020.

Goetz, S. J., A. G. Bunn, G. J. Fiske, and R. A. Houghton (2005), Satellite-observed photosynthetic trends across boreal North America associated with climate and fire disturbance, *Proc. Natl. Acad. Sci. U. S. A.*, *102*, 13,521–13,525, doi:10.1073/pnas.0506179102.

Grogan, P., and S. Jonasson (2006), Ecosystem CO_2 production during winter in a Swedish subarctic region: The relative importance of climate and vegetation type, *Global Change Biol.*, *12*, 1479–1495, doi:10.1111/j.1365-2486.2006.01184.x.

Harazono, Y., M. Mano, A. Miyata, R. C. Zulueta, and W. C. Oechel (2003), Inter-annual carbon dioxide uptake of a wet sedge tundra ecosystem in the Arctic, *Tellus, Ser. B*, *55*, 215–231.

Harden, J. W., E. T. Sundquist, R. F. Stallard, and R. K. Mark (1992), Dynamics of soil carbon during deglaciation of the Laurentide ice sheet, *Science*, *258*, 1921–1924, doi:10.1126/science.258.5090.1921.

Harden, J. W., C. C. Fuller, M. Wilmking, I. H. Meyers-Smith, S. E. Trumbore, and J. Bubier (2008), The fate of terrestrial carbon following permafrost degradation: Detecting changes over recent decades, *Proc. Ninth Int. Conf. Permafrost*, edited by D. L. Kane and K. M. Kinekl, pp. 649–653, Inst. of North. Eng., Univ. of Alaska Fairbanks, Fairbanks, Alaska.

Heikkinen, J. E. P., V. Elsakov, and P. J. Martikainen (2002), Carbon dioxide and methane dynamics and annual carbon balance in tundra wetland in NE Europe, Russia, *Global Biogeochem. Cycles*, *16*(4), 1115, doi:10.1029/2002GB001930.

IPCC (2007), Summary for policymakers, in *Climate Change 2007: Impacts, Adaptation and Vulnerability*, pp. 1–18, Cambridge Univ. Press, Cambridge, U. K.

Jones, M. H., J. T. Fahnestock, and J. M. Welker (1999), Early and late winter CO_2 efflux from arctic tundra in the Kuparuk river watershed, Alaska, USA, *Arct. Antarct. Alp. Res.*, *31*, 187–190, doi:10.2307/1552607.

Jorgenson, M. T., and T. E. Osterkamp (2005), Response of boreal ecosystems to varying modes of permafrost degradation, *Can. J. For. Res.*, *35*, 2100–2111, doi:10.1139/x05-153.

Jorgenson, M. T., C. H. Racine, J. C. Walters, and T. E. Osterkamp (2001), Permafrost degradation and ecological changes associated with a warming climate in central Alaska, *Clim. Change*, *48*, 551–579, doi:10.1023/A:1005667424292.

Jorgenson, M. T., Y. L. Shur, and E. R. Pullman (2006), Abrupt increase in permafrost degradation in arctic Alaska, *Geophys. Res. Lett.*, *33*, L02503, doi:10.1029/2005GL024960.

Kwon, H. J., W. C. Oechel, R. C. Zulueta, and S. J. Hastings (2006), Effects of climate variability on carbon sequestration among adjacent wet sedge tundra and moist tussock tundra ecosystems, *J. Geophys. Res.*, *111*, G03014, doi:10.1029/2005JG000036.

Lachenbruch, A. H., and B. V. Marshall (1986), Changing climate: Geothermal evidence from permafrost in the Alaskan Arctic, *Science*, *234*, 689–696, doi:10.1126/science.234.4777.689.

Lafleur, P. M., N. T. Roulet, J. L. Bubier, S. Frolking, and T. R. Moore (2003), Interannual variability in the peatland-atmosphere carbon dioxide exchange at an ombrotrophic bog, *Global Biogeochem. Cycles*, *7*(2), 1036, doi:10.1029/2002GB001983.

Larsen, K. S., A. Ibrom, S. Jonasson, A. Michelsen, and C. Beier (2007), Significance of cold-season respiration and photosynthesis in a subarctic heath ecosystem in northern Sweden, *Global Change Biol.*, *13*, 1498–1508, doi:10.1111/j.1365-2486.2007.01370.x.

Lee, H., E. A. G. Schuur, and J. G. Vogel (2006), Soil carbon dioxide fluxes in subarctic tundra where permafrost is thawing, *Eos Trans AGU*, *87*, Fall Meet., Suppl., Abstract GC51A-0440.

Lee, H., E. A. G. Schuur, and J. G. Vogel (2009), Soil CO_2 production in upland tundra where permafrost is thawing, *J. Geophys. Res.*, doi:10.1029/2008JG000906, in press.

Lund, C. P., W. J. Riley, L. L. Pierce, and C. B. Field (1999), The effects of chamber pressurization on soil-surface CO_2 flux and the implications for NEE measurements under elevated CO_2, *Global Change Biol.*, *5*, 269–281, doi:10.1046/j.1365-2486.1999.00218.x.

Mack, M. C., E. A. G. Schuur, M. S. Bret-Harte, G. R. Shaver, and F. S. Chapin (2004), Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization, *Nature*, *431*, 440–443, doi:10.1038/nature02887.

Marchand, F. L., I. Nijs, H. J. de Boeck, F. Kockelbergh, S. Mertens, and L. Beyens (2004), Increased turnover but little change in the carbon balance of high-arctic tundra exposed to whole growing season warming, *Arctic Ant. Alp. Res.*, *36*, 298–307, doi:10.1657/1523-0430(2004)036[0298:ITBLCI]2.0.CO;2.

Mertens, S., I. Nijs, M. Heuer, F. Kockelbergh, L. Beyens, A. Van Kerckvoorde, and I. Impens (2001), Influence of high temperature on end-of-season tundra CO_2 exchange, *Ecosystems*, *4*, 226–236, doi:10.1007/s10021-001-0006-3.

Michaelson, G. J., and C. L. Ping (2003), Soil organic carbon and CO_2 respiration at subzero temperature in soil of arctic Alaska, *J. Geophys. Res.*, *108*(D2), 8164, doi:10.1029/2001JD000920.

Mikan, C. J., J. P. Schimel, and A. P. Doyle (2002), Temperature controls of microbial respiration in arctic tundra soils above and below freezing, *Soil Biol. Biochem.*, *34*, 1785–1795, doi:10.1016/S0038-0717(02)00168-2.

Monson, R. K., D. L. Lipson, S. P. Burns, A. A. Turnipseed, A. C. Delany, M. W. Williams, and S. K. Schmidt (2006), Winter forest soil respiration controlled by climate and microbial community composition, *Nature*, *439*, 711–714, doi:10.1038/nature04555.

Moore, T. R., J. L. Bubier, S. E. Frolking, P. M. Lafleur, and N. T. Roulet (2002), Plant biomass and production and CO_2 exchange in an ombrotrophic bog, *J. Ecol.*, *90*, 25–36, doi:10.1046/j.0022-0477.2001.00633.x.

Myneni, R. B., C. J. Tucker, G. Asrar, and C. D. Keeling (1998), Interannual variations in satellite-sensed vegetation index data from 1981 to 1991, *J. Geophys. Res.*, *103*(D6), 6145–6160.

Nobrega, S., and P. Grogan (2007), Deeper snow enhances winter respiration from both plant-associated and bulk soil carbon pools in birch hummock tundra, *Ecosystems*, *10*, 419–431, doi:10.1007/s10021-007-9033-z.

Oberbauer, S. F., et al. (2007), Tundra CO_2 fluxes in response to experimental warming across latitudinal and moisture gradients, *Ecol. Monogr.*, *77*, 221–238, doi:10.1890/06-0649.

Oechel, W. C., G. L. Vourlitis, S. J. Hastings, R. C. Zulueta, L. Hinzman, and D. Kane (2000), Acclimation of ecosystem CO_2 exchange in the Alaskan Arctic in response to decadal climate warming, *Nature*, *406*, 978–981, doi:10.1038/35023137.

Osterkamp, T. E. (2005), The recent warming of permafrost in Alaska, *Global Planet. Change*, *49*(3–4), 187–202.

Osterkamp, T. E. (2007), Characteristics of the recent warming of permafrost in Alaska, *J. Geophys. Res.*, *112*, F02S02, doi:10.1029/2006JF000578.

Osterkamp, T. E., and J. C. Jorgenson (2006), Warming of permafrost in the Arctic National Wildlife Refuge, Alaska, *Permafrost Periglacial Proc.*, *17*, 65–69, doi:10.1002/ppp.538.

Osterkamp, T. E., and V. E. Romanovsky (1999), Evidence for warming and thawing of discontinuous permafrost in Alaska, *Permafrost Periglacial Proc.*, *10*, 17–37, doi:10.1002/(SICI)1099-1530(199901/03)10:1<17::AID-PPP303>3.0.CO;2-4.

Panikov, N. S., P. W. Flanagan, W. C. Oechel, M. A. Mastepanov, and T. R. Christensen (2006), Microbial activity in soils frozen to below-39 degrees C, *Soil Biol. Biochem.*, *38*, 785–794, doi:10.1016/j.soilbio.2005.07.004.

Price, P. B., and T. Sowers (2004), Temperature dependence of metabolic rates for microbial growth, maintenance, and survival, *Proc. Natl. Acad. Sci.*, *101*(13), 4631–4636.

Rennermalm, A. K., H. Soegaard, and C. Nordstroem (2005), Interannual variability in carbon dioxide exchange from a high arctic fen estimated by measurements and modeling, *Arct. Antarct. Alp. Res.*, *37*, 545–556, doi:10.1657/1523-0430(2005)037[0545:IVICDE]2.0.CO;2.

Schimel, J. P., J. Fahnestock, G. Michaelson, C. Mikan, C. L. Ping, V. E. Romanovsky, and J. Welker (2006), Cold-season production of CO_2 in arctic soils: Can laboratory and field estimates be reconciled through a simple modeling approach?, *Arct. Antarct. Alp. Res.*, *38*, 249–256, doi:10.1657/1523-0430(2006)38[249:CPOCIA]2.0.CO;2.

Schuur, E. A. G., K. G. Crummer, J. G. Vogel, and M. C. Mack (2007), Plant species composition and productivity following permafrost thaw and thermokarst in Alaskan tundra, *Ecosystems*, *10*, 280–292, doi:10.1007/s10021-007-9024-0.

Schuur, E. A. G., et al. (2008), Vulnerability of permafrost carbon to climate change: Implications for the global carbon cycle, *BioScience*, *58*(8), 701–714, doi:10.1641/B580807.

Serreze, M. C., J. E. Walsh, F. S. Chapin III, T. E. Osterkamp, M. Dyurgerov, V. E. Romanovsky, W. C. Oechel, J. Morison, T. Zhang, and R. G. Barry (2000), Observational evidence of recent changes in the northern high-latitude environment, *Clim. Change*, *46*, 159–207, doi:10.1023/A:1005504031923.

Shaver, G. R., W. D. Billings, F. S. Chapin, A. E. Giblin, K. J. Nadelhoffer, W. C. Oechel, and E. B. Rastetter (1992), Global change and the carbon balance of arctic ecosystems, *BioScience*, *42*, 433–441, doi:10.2307/1311862.

Shaver, G. R., S. M. Bret-Harte, M. H. Jones, J. Johnstone, L. Gough, J. Laundre, and F. S. Chapin (2001), Species composition interacts with fertilizer to control long-term change in tundra productivity, *Ecology*, *82*, 3163–3181.

Shaver, G. R., L. E. Street, E. B. Rastetter, M. T. Van Wijk, and M. Williams (2007), Functional convergence in regulation of net CO_2 flux in heterogeneous tundra landscapes in Alaska and Sweden, *J. Ecol.*, *95*, 802–817, doi:10.1111/j.1365-2745.2007.01259.x.

Sitch, S., A. D. McGuire, J. Kimball, N. Gedney, J. Gamon, R. Engstrom, A. Wolf, Q. Zhuang, J. Clein, and K. C. McDonald (2007), Assessing the carbon balance of circumpolar arctic tundra using remote sensing and process modeling, *Ecol. Appl.*, *17*, 213–234, doi:10.1890/1051-0761(2007)017[0213:ATCBOC]2.0.CO;2.

Smith, L. C., G. M. MacDonald, A. A. Velichko, D. W. Beilman, O. K. Borisova, K. E. Frey, K. V. Kremenetski, and Y. Sheng (2004), Siberian peatlands a net carbon sink and global methane source since the early Holocene, *Science*, *303*, 353–356, doi:10.1126/science.1090553.

Soil Survey Staff (1999), *Soil Taxonomy: A Basic System of Soil Classification for Making and Interpreting Soil Surveys. Agricultural Handbook*, vol. 436, Natl. Res. Conserv. Serv., USDA, Washington, D. C.

Sokal, R., and F. M. Rohlf (1995), *Biometry: The Principles and Practice of Statistics in Biological Research*, 3rd ed., 887 pp., W. H. Freeman, New York.

Thornley, J. H. M., and I. R. Johnson (1990), *Plant and Crop Modeling: A Mathematical Approach to Plant and Crop Physiology*, Clarendon, Oxford, U. K.

Turetsky, M. R., R. K. Wieder, D. H. Vitt, R. J. Evans, and K. D. Scott (2007), The disappearance of relict permafrost in boreal North America: Effects on peatland carbon storage and fluxes, *Global Change Biol.*, *13*, 1922–1934, doi:10.1111/j.1365-2486.2007.01381.x.

Vitt, D. H., L. A. Halsey, and S. C. Zoltai (2000), The changing landscape of Canada's western boreal forest: The current dynamics of permafrost, *Can. J. For. Res.*, *30*, 283–287, doi:10.1139/cjfr-30-2-283.

Vourlitis, G. L., W. C. Oechel, A. Hope, D. Stow, B. Boynton, J. Verfaillie, R. Zulueta, and S. J. Hastings (2000), Physiological models for scaling plot measurements of CO_2 flux across an arctic tundra landscape, *Ecol. Appl.*, *10*, 60–72.

Waelbroeck, C., P. Monfray, W. C. Oechel, S. Hastings, and G. Vourlitis (1997), The impact of permafrost thawing on the carbon dynamics of tundra, *Geophys. Res. Lett.*, *24*, 229–232, doi:10.1029/97GL00071.

Wahrhaftig, C. (1958), *Quaternary Geology of the Nenana River Valley and Adjacent Parts of the Alaska Range*, *U. S. Geol. Surv.*1–68.

Walter, K. M., M. E. Edwards, G. Grosse, S. A. Zimov, and F. S. Chapin (2007), Thermokarst lakes as a source of atmospheric CH4 during the last deglaciation, *Science*, *318*, 633–636, doi:10.1126/science.1142924.

Welker, J. M., J. T. Fahnestock, G. H. R. Henry, K. W. O'Dea, and R. A. Chimner (2004), CO_2 exchange in three Canadian high arctic ecosystems: Response to long-term experimental warming, *Global Change Biol.*, *10*, 1981–1995, doi:10.1111/j.1365-2486.2004.00857.x.

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.

Yershov, E. (2004), *General Geocryology*, 604 pp., Cambridge Univ. Press, Cambridge, U. K.

Zamolodchikov, D. G., and D. V. Karelin (2001), An empirical model of carbon fluxes in Russian tundra, *Global Change Biol.*, *7*, 147–161, doi:10.1046/j.1365-2486.2001.00380.x.

Zhuang, Q., V. E. Romanovsky, and A. D. McGuire (2001), Incorporation of a permafrost model into a large-scale ecosystem model: Evaluation of temporal and spatial scaling issues in simulating soil thermal dynamics, *J. Geophys. Res.*, *106*(33), L17403, doi:10.1029/2006GL026972.

Zimov, S. A., S. P. Davidov, Y. V. Voropaev, S. F. Prosiannikov, I. P. Semiletov, M. C. Chapin, and F. S. Chapin (1996), Siberian CO_2 efflux in winter as a CO_2 source and cause of seasonality in atmospheric CO_2, *Clim. Change*, *33*, 111–120.

H. Lee, E. A. G. Schuur, and C. Trucco, Department of Botany, University of Florida, 214 Bartram Hall, Gainesville, FL 32611, USA.

J. Vogel, School of Forest Resources and Conservation, University of Florida, 342A Newin-Ziegler, Gainesville, FL 32611, USA. (jvogel@ufl.edu)