

Seven-year trends of CO₂ exchange in a tundra ecosystem affected by long-term permafrost thaw

Christian Trucco,¹ Edward A. G. Schuur,¹ Susan M. Natali,¹ E. Fay Belshe,¹ Rosvel Bracho,¹ and Jason Vogel²

Received 11 November 2011; revised 12 May 2012; accepted 20 May 2012; published 29 June 2012.

[1] Arctic warming has led to permafrost degradation and ground subsidence, created as a result of ground ice melting. Frozen soil organic matter that thaws can increase carbon (C) emissions to the atmosphere, but this can be offset in part by increases in plant growth. The balance of plant and microbial processes, and how this balance changes through time, determines how permafrost ecosystems influence future climate change via the C cycle. This study addressed this question both on short (interannual) and longer (decadal) time periods by measuring C fluxes over a seven-year period at three sites representing a gradient of time since permafrost thaw. All three sites were upland tundra ecosystems located in Interior Alaska but differed in the extent of permafrost thaw and ground subsidence. Results showed an increasing growing season (May – September) trend in gross primary productivity (GPP), net ecosystem exchange (NEE), aboveground net primary productivity (ANPP), and annual NEE at all sites over the seven year study period from 2004 to 2010, but no change in annual and growing season ecosystem respiration (R_{eco}). These trends appeared to most closely follow increases in the depth to permafrost that occurred over the same time period. During the seven-year period, sites with more permafrost degradation had significantly greater GPP compared to where degradation was least, but also greater growing season R_{eco} . Adding in winter R_{eco} decreased, in part, the summer C sink and left only the site with the most permafrost degradation C neutral, with the other sites still C sinks. Annual C balance was strongly dependent on winter R_{eco} , which, compared to the growing season, was relatively data-poor due to extreme environmental conditions. As a result, we cannot yet conclude whether the increased NEE in the growing season is truly sustained on an annual basis. If it turns out that winter measurements shown here are an underestimate, we may indeed find these systems are already losing net C to the atmosphere.

Citation: Trucco, C., E. A. G. Schuur, S. M. Natali, E. F. Belshe, R. Bracho, and J. Vogel (2012), Seven-year trends of CO₂ exchange in a tundra ecosystem affected by long-term permafrost thaw, *J. Geophys. Res.*, 117, G02031, doi:10.1029/2011JG001907.

1. Introduction

[2] Permafrost (perennially frozen ground) regions, which underlie about 24% of the northern hemisphere land surface, are an important component of the global carbon (C) cycle because they store an estimated 50% of the belowground global organic soil C pool [Schuur *et al.*, 2008; Zhang *et al.*, 1999]. About 1672 Pg C, roughly equivalent to twice the amount of C in the atmosphere, is currently sequestered in the permafrost zone in the form of organic soil C [Intergovernmental Panel on Climate Change, 2007; Post

et al., 1982; Schuur *et al.*, 2008; Tarnocai *et al.*, 2009; Zimov *et al.*, 2006a]. Increasing air temperature during the past century has caused permafrost in regions of the arctic and subarctic to warm and become susceptible to thaw [Burn and Smith, 1993; Osterkamp, 2007; Osterkamp and Romanovsky, 1999; Romanovsky *et al.*, 2010]. This susceptibility is especially pronounced in the subarctic region, where permafrost temperatures are already near thaw and as a result, small changes in surface temperature are expected to cause irreversible permafrost degradation [Åkerman and Johansson, 2008; Jorgenson and Osterkamp, 2005; Lawrence and Slater, 2005; Lawrence *et al.*, 2008; Osterkamp and Romanovsky, 1999]. Enhanced warming in northern latitude has the potential to shift this region substantially from its current state.

[3] Changes in arctic and subarctic permafrost are already in evidence in the form of landscape disturbances called thermokarst [Jorgenson and Osterkamp, 2005; Osterkamp and Romanovsky, 1999; Schuur *et al.*, 2007]. Thermokarst refers to ground subsidence that results from thawing of ice-

¹Biology Department, University of Florida, Gainesville, Florida, USA.

²Department of Ecosystem Science and Management, Texas A&M University, College Station, Texas, USA.

Corresponding author: E. A. G. Schuur, Biology Department, University of Florida, 220 Bartram Hall, Gainesville, FL 32611, USA. (tschuur@ufl.edu)

©2012. American Geophysical Union. All Rights Reserved.
10.1029/2011JG001907

rich permafrost soils. Upon thaw, the soil surface collapses into the volume previously occupied by ice within the soil profile. Ground subsidence as a result of increasing temperature has a secondary effect on the surface hydrology and soil moisture of ecosystems [Jorgenson *et al.*, 2001; McNamara *et al.*, 1998; Schuur *et al.*, 2007; Yoshikawa and Hinzman, 2003]. In the summer months, water perched on the permafrost surface is channeled toward subsided areas, creating saturated areas, while at the same time causing drying in nearby unsubsided areas [Jorgenson and Osterkamp, 2005]. During the winter months, thermokarst can accumulate more snow, further insulating soils from cold winter air temperature [Hinkel and Hurd, 2006; Natali *et al.*, 2011; Nowinski *et al.*, 2010; Walker *et al.*, 1999]. These internal feedbacks via water and snow can cause permafrost ground to degrade at an accelerated pace as compared to the direct effect of changing regional temperature alone [Hinkel and Hurd, 2006; Seppälä, 1994].

[4] These physical changes in soil temperature and moisture that accompany permafrost thaw have important biological consequences that can feedback to climate change via changes in the C cycle. Thawing of organic C enhances microbial metabolism and hence increases ecosystem respiration of C to the atmosphere [Dutta *et al.*, 2006; Hobbie *et al.*, 2002; Mack *et al.*, 2004]. Indeed, laboratory [Dutta *et al.*, 2006; Zimov *et al.*, 2006b] and field measurements [Schuur *et al.*, 2009; Nowinski *et al.*, 2010] have documented the release of millennial-aged C metabolized by microbes after permafrost soil C has thawed. Increases in heterotrophic respiration can be offset, at least in part, by uptake of C by plants during the growing season. This increase in plant C uptake can happen in response to increased nutrients that are released from decomposing organic matter. Over time, in response to warmer conditions, shifting plant species composition, including increasing shrub abundance with larger biomass, will be an important ecosystem C pool offsetting C release. However, continued microbial activity during the long winter months, even at low rates, can result in the net release of C, either as CO₂ and/or CH₄, to the atmosphere causing a positive feedback to climate warming [Vogel *et al.*, 2009]. The net response of plant and soil processes determine whether, on an annual basis, permafrost ecosystems gain or lose C in exchange with the atmosphere.

[5] The objective of this study was to understand how permafrost thaw altered ecosystem C cycling over long (decadal) time scales and how short-term (annual) variation in environmental conditions altered ecosystem C balance. In order to understand these differing time scales, we compared C dynamics among three sites arrayed across a naturally degrading permafrost gradient in an upland tussock tundra ecosystem [Schuur *et al.*, 2009]. Our study area has experienced differential amounts of permafrost degradation over the last 50 years, which has caused ground subsidence and subsequent alteration of surface hydrology and ground temperatures [Osterkamp, 2007; Osterkamp and Romanovsky, 1999; Schuur *et al.*, 2007].

[6] We measured components of ecosystem C cycle—specifically, ecosystem respiration (R_{eco}), gross primary productivity (GPP) and net ecosystem exchange (NEE)—across three sites that differed in the amount of permafrost degradation and the degree of ground subsidence. Measurements across the three thaw gradient sites provided insight

into decadal scale changes induced by permafrost thaw. Because interannual variation in C balance is substantial at any particular site, we made these measurements over a seven-year period to determine annual trends in these fluxes. Along with growing season C fluxes, we also quantified soil respiration with direct measurements over three winters, and combined these measurements with continual ground temperature measurements to estimate annual C exchange for the study period. We then determined how variation in C fluxes, both annual (seven-year record) and decadal (thaw gradient), were controlled by environmental variables such as photosynthetically active radiation (PAR), air and soil temperature, water table levels, and thickness of the active layer. This seven year data record made across the permafrost thaw gradient representing decades of change in this ecosystem allows us to understand both the short- and long-term influence of permafrost degradation in a tundra ecosystem and how these changes might be expected to feedback to global C cycling and climate change.

2. Methods

2.1. Site Description

[7] The study was conducted within the Eight Mile Lake (EML) watershed, west of Healy, Alaska, USA (63°52'42.1"N, 149°15'12"W, 700 m.a.s.l.) [Lee *et al.*, 2010; Schuur *et al.*, 2007; Schuur *et al.*, 2009; Vogel *et al.*, 2009], located within the discontinuous permafrost zone. The 30-year mean annual air temperature is −1°C, with a growing season (May–Sept) mean air temperature of 11.2°C. Average cumulative precipitation is 378 mm annually with 245 mm during the growing season. The watershed is bounded by glacial moraines dating from the early Pleistocene [Wahrhaftig, 1958]. The study site lies on a gentle north-facing (<5°) slope, where permafrost is thawing, and as a result, ground subsidence has occurred. Three sites within 1 km of each other representing a gradient of permafrost degradation were sited in the EML watershed, one of which is adjacent to a permafrost borehole installed in 1985. Ground temperature has been observed to increase since the borehole was installed [Osterkamp and Romanovsky, 1999; Osterkamp *et al.*, 2009]. The first site, hereafter called Minimal Thaw, had the least permafrost degradation, with little or no defined subsidence. Vegetation at this site is typical moist acidic tundra dominated by the tussock-forming sedge *Eriophorum vaginatum*, dwarf shrubs, and an understory of moss and lichen [Schuur *et al.*, 2007]. The second site, hereafter called Moderate Thaw, had some subsidence and a deeper active layer. This site was co-located with the borehole; active thawing was observed starting in 1990. Shrubs, graminoids, and mosses were abundant at Moderate Thaw, and productivity was relatively high. The third site on the gradient, hereafter called Extensive Thaw, had even deeper subsidence and the deepest active layer of all three sites. Thawing at this site is thought to have initiated several decades prior to Moderate Thaw based on aerial photography [Osterkamp and Romanovsky, 1999]. The plant community at Extensive Thaw was dominated by shrubs and hydrophilic mosses, with a significant decrease in abundance of graminoid tussocks. The redistribution of surface water caused by subsidence created both saturated areas where the water table was at or near the soil surface and adjacent dry patches that had not

subsided and were covered with dead moss and had lower vascular plant biomass. The redistribution of surface water started to become evident at Moderate Thaw and was widespread at Extensive Thaw.

2.2. Ecosystem Carbon Fluxes

[8] Net ecosystem exchange (NEE) is the net gain or loss of C, measured as CO₂, by an ecosystem within a given time interval. This exchange is the balance of two opposing processes: ecosystem C uptake by primary producers (gross primary production, GPP) and ecosystem respiration losses (R_{eco}) (autotrophic, R_a, plus heterotrophic, R_h):

$$NEE = (GPP - R_a) - R_h \quad (1)$$

where (GPP-R_a) is net primary production (NPP). Both NEE and R_{eco} can be measured; GPP is estimated as the difference between the two measured fluxes. We used the convention that positive values of NEE indicate net C uptake by the ecosystem.

[9] We measured NEE and R_{eco} using a combination of static (manual) and automated chamber systems (70 × 70 × 40 cm) during seven continuous growing seasons (from 2004 through 2010) as described in Vogel *et al.* [2009]. For both static and autochambers, air was circulated through an infrared gas analyzer to measure CO₂ concentration. Static chambers were used in 2004 and 2009–2010. Weekly static measurements were taken concurrently (within four hours) at the three sites, starting soon after snowmelt (3–6 May) and continuing until the end of the growing season around the third or fourth week of September for a total of ~400 individual flux measurements per year. The automated system consisted of chambers that measured continuously at each site (n = 6/site) and was moved among the three sites on a sub-weekly basis from 2005 through 2008, for a total of ~7000 individual measurements per year. Simultaneous static chamber measurements were performed at the other two sites that did not have the autochamber system at that particular time. For the static chamber, R_{eco} was measured during the daytime by covering the chamber with a reflective material that prevented light from getting inside the chamber. Autochamber R_{eco} was estimated based on nighttime measurements.

2.3. Environmental Variables

[10] An Onset HOBO weather station (Bourne, MA) was located at the study site measuring photosynthetically active radiation (PAR), air temperature, relative humidity, precipitation, atmospheric pressure, and wind speed and direction. The station was maintained year-round for the duration of the study. This data stream was gap-filled over short periods when necessary using Remote Automated Weather Station (RAWS, Western Regional Climate Center, Stampede station) located in Denali National Park.

[11] Soil temperature was measured at multiple depths in the soil profile at a single reference location using type T thermocouples controlled by a CR10X data logger (Campbell Scientific, Logan, Utah). Soil temperature at 10 cm depth was used for comparisons across the seven-year period. Thaw depth was measured weekly throughout the growing season

using a thin metal rod pushed through the unfrozen soil until it hit the ice surface. Three measurements were taken around each base used for CO₂ flux measurements and reported as site average thaw depth. Maximum seasonal thaw depth (equivalent to active layer depth; ALD) occurs in late season and was determined by averaging the last two weeks of measurements in September. The water table was measured weekly throughout the growing season, but starting in June, using three wells installed at each site. Water table depth is reported as the distance from the soil surface to the surface of the water table.

2.4. Carbon Fluxes

[12] Instantaneous C fluxes were calculated as the change in CO₂ concentration inside the measurement chamber over the 2-min measurement interval [Vogel *et al.*, 2009]. Data were filtered to eliminate spurious values resulting from erratic fluctuations in CO₂ concentration. We avoided chamber overheating (inside temp >30°C), windy (speed >5 m s⁻¹) and rainy conditions. Gaps in the flux data during the leaf-out period of June, July, and August were filled as follows: First, if PAR was >5 μmol m⁻² s⁻¹, NEE was gap-filled using parameters obtained by fitting measured NEE at each chamber to PAR through a non-rectangular hyperbola:

$$NEE = \frac{(\alpha * PAR * Fc_{max})}{[(\alpha * PAR) + Fc_{max}]} - R_d \quad (2)$$

[13] Here, α is the initial linear slope of the light response curve (quantum yield, μmol CO₂ m⁻² s⁻¹), Fc_{max} is maximum photosynthesis (μmol CO₂ m⁻² s⁻¹) at light saturation, and R_d is dark ecosystem respiration (e.g., NEE at PAR = 0). Parameters for equation (2) were obtained for individual chamber bases across all three sites. Second, if PAR was <5 μmol m⁻² s⁻¹, NEE was gap-filled using parameters relating NEE at night, plus dark static chamber measurements (R_{eco}), to air temperature (T_a) from each chamber using an exponential relationship:

$$R_{eco} = R * \exp^{\beta * T_a} \quad (3)$$

[14] Here, R is basal respiration and β is the rate of respiration change. May and September NEE parameters for equation (2) could not be determined (with the exception of 2008 and May of 2007) because these months represent changing periods of leaf out and senescence. Therefore, interpolated values of NEE were estimated using average measured day and night NEE values and multiplying those values by the duration of day and night.

[15] Last, GPP was calculated as the difference between NEE and R_{eco}:

$$GPP = NEE - R_{eco} \quad (4)$$

These measured and gap-filled C fluxes were then combined into monthly, growing season, and annual averaged C fluxes for each site across the seven-year period. Growing season was defined as May 1–September 30 to keep the number

Table 1. Average Growing Season Photosynthetically Active Radiation (PAR), Air Temperature, Soil Temperature, and Cumulative PAR and Precipitation From the Eight Mile Lake, AK Weather Station

Year	Cumulative PAR ($\mu\text{mol m}^{-2}$)	Average PAR ($\mu\text{mol m}^{-2} \text{sec}^{-1}$)	Precipitation (mm)	Air Temp ($^{\circ}\text{C}$)	Soil Temp ^a ($^{\circ}\text{C}$)
2004	–	332	153	11.5	6.7
2005	3767	341	145	10.8	7.2
2006	3906	354	227	9.1	6.8
2007	4116	375	331	10.3	7.0
2008	3935	357	346	8.1	5.9
2009	4147	376	178	9.7	6.8
2010	3919	356	182	9.8	7.7

^aSoil temperature at 10 cm depth, from Minimal Thaw only.

of days constant so that observed changes were a result of changes in fluxes, not in growing season length.

[16] Winter C fluxes were estimated as in *Vogel et al.* [2009], using the integrated temperature of the soil profile to model winter C flux in the form:

$$R_{\text{eco}}(< -2^{\circ}\text{C}) = 0.23 * \exp^{(0.10 * T_s)} \quad (5)$$

Here, T_s is the integrated soil temperature averaged across 10, 20, 30 and 40 cm. The model was used for integrated T_s ranging from -2°C and colder. Due to limited wintertime sampling and low fluxes, the parameters for the exponential equation did not differ among the three sites; therefore a single model (equation (5); $R^2 = 0.28$, $p < 0.01$) was developed and used across all sites. This relationship between soil temperature and measured winter fluxes did not hold when soil temperature was between -2°C and 0.5°C because of the water/ice phase change. For integrated soil temperatures warmer than -2°C the average C flux was used. These fluxes were measured at each site during the winters of 2004 through 2006.

2.5. Plant Productivity Measurements

[17] We quantified above ground net primary production (ANPP) as an independent way to assess ecosystem C uptake by plants and to understand the effects of permafrost disturbance on plant growth. We estimated ANPP by measuring plant biomass at the height of the growing season in late July using point-intercept methods [*Schuur et al.*, 2007; *Shaver et al.*, 2001; *Walker*, 1996]. Vascular plant ANPP was determined using a 70×70 cm point frame with 64 evenly spaced intersecting points [*Walker*, 1996], within the same frame used for flux measurements. At each grid point a metal rod (1 mm diameter) was placed vertically through the plant canopy. We recorded species identity and tissue type (leaf, stem, or fruit) for every plant that touched the rod ('hits'). We applied allometric growth equations developed for this site to the average number of point-frame 'hits' per plot [*Schuur et al.*, 2007]. Moss ANPP was estimated using a cranked-wire method [*Clymo*, 1970], where moss vertical growth was directly measured over the growing season. These values were converted to moss biomass using allometric equations that were developed from off-plot destructive harvests and applied to the moss area within each flux chamber base

[*Schuur et al.*, 2007]. These methods were conducted in all years of the study with the exception of 2005 and 2010.

2.6. Statistical Analysis

[18] All environmental and C flux variables were analyzed using repeated measures analyses of variance (RM ANOVA, SAS 9.0) with site as a fixed effect and year (random) as the repeated factor. All data were tested for normality using Kolmogorov-Smirnov test and by assessing normal probability plots. Data that did not show normal distributions were transformed and then re-tested to ensure normality. We treated year as a categorical variable to examine variation among sites and years, and we also tested for linear trends across the seven-year sampling period by using RM ANOVA with year as a continuous linear variable. Multiple comparisons were obtained by the least squares means (Tukey's HSD) method for treatment, year, and treatment differences within each measurement year. Because this test corrects for multiple comparisons and is conservative, we show differences both at $P < 0.05$ and $P < 0.1$. We did not perform a RM ANOVA on winter C flux because winter respiration in the later years of this study (2007–2009) was not measured directly, but rather, was modeled based on earlier measurements and soil temperature at a central location at EML. As a result we were only able to obtain a single winter R_{eco} value for each year. The error bars for winter respiration represent an estimate based on the spatial error from the first three years of direct winter measurements at each site, which we extended to subsequent modeled years. Statistical results (F and P values) for all RM ANOVAs can be found in Table S1 in the auxiliary material.¹

[19] We explored the relationships among C fluxes (NEE, GPP, R_{eco}) and abiotic factors using mixed effect multiple linear regressions. We incorporated a random effect of year because we knew from the RM ANOVA that C fluxes varied among years. All potential explanatory variables were selected a priori, centered, and scaled to allow for comparison among variables with different units [*Schielzeth*, 2010]. We gap filled one year (2004) of missing data for water table depth using its seven-year mean. All models were fit using the *nmlme* package (J. Pinheiro, D. Bates, S. DebRoy, and D. Sarkar, *nmlme*: Linear and nonlinear mixed effects models. R package version 3.1-97, 2010) using restricted maximum likelihood in R (R Core Development Team 2010). We used single linear regressions to further examine those abiotic factors that were significant drivers of C fluxes, based on the multiple regression models.

3. Results

3.1. Environmental Variation

[20] During the time period of this study (2004–2010), growing season precipitation at EML ranged from 145 to 346 mm (Table 1). Average growing season air temperature ranged from 8.1°C to 11.5°C , while cumulative growing season PAR varied $\sim 10\%$ among years. Lower cumulative PAR did not reflect higher precipitation for some of the years; for instance, 2010 received about half the growing season precipitation of 2008, but experienced the same cumulative

¹Auxiliary materials are available in the HTML. doi:10.1029/2011JG001907.

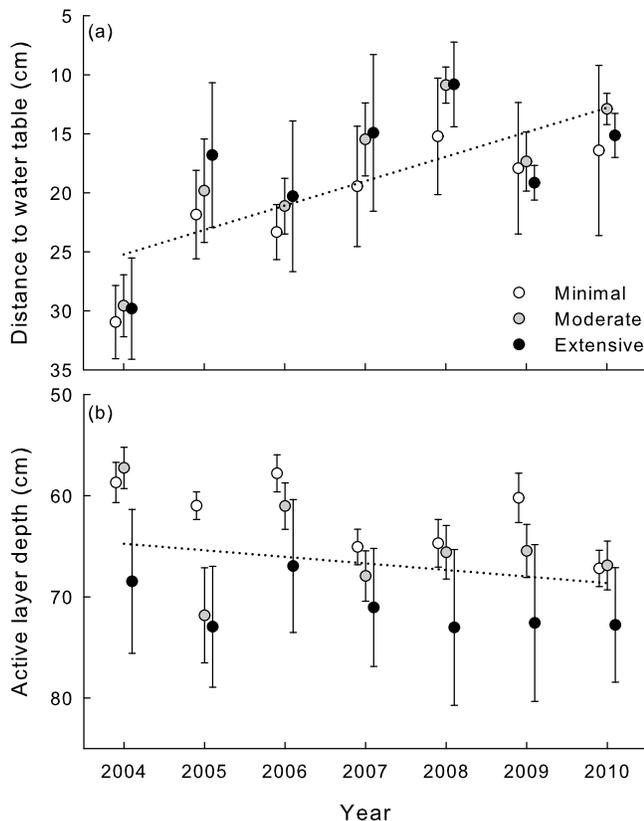


Figure 1. Growing season (a) average distance to water table (June – September) and (b) active layer depth measured at three sites varying in degree of permafrost thaw (September). Dotted line represents the significant linear trend in water table ($P < 0.01$) and active layer depths ($P = 0.01$) at all sites across the seven-year measurement interval. Significant annual site differences are reported in Table S2.

PAR ($3919 \mu\text{mol m}^{-2}$ and $3935 \mu\text{mol m}^{-2}$, respectively; Table 1). There was a trend of warmer years being drier and cooler years being wetter, with the exception of 2007, which was warmer and wetter, making the pattern non-significant across the study period ($P > 0.1$).

[21] In most years, water table distance was greater (i.e., drier) at Minimal Thaw than at Moderate or Extensive Thaw (Figure 1a and Table S2), but site differences were not statistically significant ($P = 0.27$). Water table depth varied among years ($P < 0.01$), with deeper and shallower water tables during the drier and wetter years, respectively (Table 1 and Figure 1a). Across sites, there was a trend of increasingly wetter conditions (i.e., shallower water table) through the measurement period ($P < 0.01$). This trend was influenced by the deepest water table depth in 2004; when 2004 water table depth was removed from the linear model, the trend was weaker ($P = 0.15$).

[22] Average ALD across the seven-year study period was greatest in Extensive Thaw (71 ± 7) compared to Moderate (65 ± 2) or Minimal Thaw (62 ± 2). However, site differences were not significant ($P = 0.31$) due to high within-site variability, especially at Extensive and Moderate Thaw sites (Figure 1b and Tables S1 and S2). There was significant variation in ALD among years ($P < 0.001$), largely driven

by variation in the initial years of the data set when 2004 had some of the shallowest ALDs and 2005 had some of the deepest (Figure 1b and Table S2). Some of the interannual variation in ALD was caused by a trend of increasing ALD through the time period of this study ($P < 0.001$). The rate of increase in ALD (0.7 cm yr^{-1}) did not vary among sites ($P = 0.55$), which demonstrates that permafrost thaw continues at all three sites along this thaw gradient. As with ALD, average growing season thaw depth was greatest at Extensive Thaw ($48 \pm 5 \text{ cm}$), followed by Moderate (42 ± 2) and Minimal Thaw (40 ± 1), but differences were not significant ($P = 0.54$). There was a significant trend of decreasing average thaw depth across the measurement period as a result of lower seasonal averages in the later years of this study (Tables S1 and S2). Together this suggests that early season thaw slowed over the seven-year record, but more rapid thaw in the late growing season caused an overall deeper thaw depth over the seven-year record.

3.2. Ecosystem Carbon Fluxes

3.2.1. Growing Season

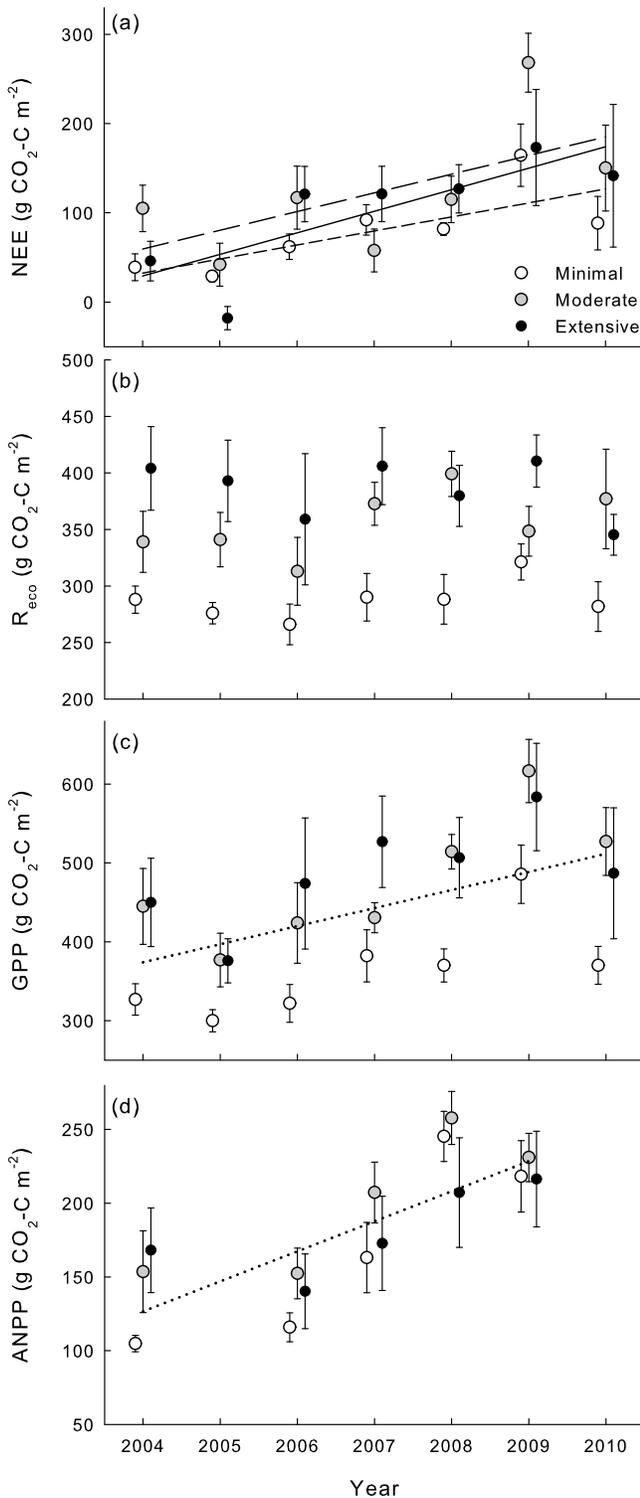
[23] All three sites were net growing season C sinks (positive NEE) during most years of this study (Figure 2a). Average growing season NEE across the study period was greatest at Moderate Thaw ($122 \pm 30 \text{ g C m}^{-2}$), followed by Extensive ($102 \pm 34 \text{ g C m}^{-2}$) and Minimal Thaw ($80 \pm 14 \text{ g C m}^{-2}$) (Figure 3a and Table S3). While average growing season NEE was not significantly different among sites ($P = 0.55$), there was a significant site \times year interaction ($P < 0.001$) as a result of site differences in 2004 and 2005. In 2004, Moderate Thaw took up twice as much C during the growing season as Extensive and Minimal Thaw, while in 2005 Extensive Thaw was a growing season C source (Figure 2a and Table S3). There was significant variation in NEE among years ($P < 0.01$) and a linear trend of increasing NEE ($P = 0.03$), indicating that the sites became stronger growing season C sinks from 2004 through 2010 (Figure 2a). The rate of NEE increase varied among sites ($P = 0.04$). The increase in growing season NEE was twofold higher in Extensive Thaw ($24.8 \text{ g CO}_2\text{-C m}^{-2} \text{ yr}^{-1}$) compared to Minimal Thaw ($12.2 \text{ g CO}_2\text{-C m}^{-2} \text{ yr}^{-1}$). The increase in NEE at Moderate Thaw was intermediate between these two sites ($20.3 \text{ g CO}_2\text{-C m}^{-2} \text{ yr}^{-1}$).

[24] Unlike growing season NEE, growing season R_{eco} did vary among sites ($P = 0.01$; Figures 2b and 3a). Growing season R_{eco} was lower in Minimal than both Extensive ($P = 0.01$) and Moderate Thaw ($P = 0.08$). There was also a significant site \times time interaction ($P = 0.03$); as with R_{eco} averaged across years, Minimal Thaw had significantly lower R_{eco} rates than the other sites in all years (Table S3). While there was significant annual variation in growing season R_{eco} ($P < 0.01$; Figure 2b), we did not detect a linear trend in R_{eco} across the measurement interval ($P = 0.92$).

[25] As with R_{eco} , there were significant differences in GPP among sites ($P = 0.07$; Figures 2c and 3a), with lower GPP in Minimal Thaw ($364 \pm 15 \text{ g CO}_2\text{-C m}^{-2} \text{ yr}^{-1}$) compared to Extensive thaw ($484 \pm 59 \text{ g CO}_2\text{-C m}^{-2} \text{ yr}^{-1}$) and Moderate Thaw ($475 \pm 30 \text{ g CO}_2\text{-C m}^{-2} \text{ yr}^{-1}$; $P < 0.05$). There was also a significant site \times time interaction ($P = 0.02$), primarily driven by significantly lower GPP in Minimal Thaw compared to the other sites in 2007 and 2008

(Table S3). Across sites, GPP varied among years ($P < 0.01$), with the lowest values in 2005 and highest values in 2009 (Figure 2c). There was a significant linear increase in GPP with time ($23.8 \text{ g CO}_2\text{-C m}^{-2} \text{ yr}^{-1}$; $P = 0.02$), which did not differ among sites ($P = 0.41$).

[26] While there were site-level differences in gross CO_2 uptake (GPP), average ANPP during the measurement period did not differ measurably among sites ($P = 0.74$; Figure 2d).



There was a significant site \times time interaction ($F = 2.38$, $P = 0.027$); however, this was a result of site differences in a single year, 2004, when ANPP at Minimal Thaw was significantly lower than Extensive Thaw ($P = 0.05$; Table S2). Across sites, ANPP varied among years ($P < 0.01$), and there was a significant linear increase in ANPP of $20.36 \text{ g C m}^{-2} \text{ yr}^{-1}$ ($P < 0.01$).

3.2.2. Winter Respiration and Annual NEE

[27] Extensive Thaw winter R_{eco} ranged from 61 to $104 \text{ g CO}_2\text{-C m}^{-2}$, which was about 40% higher than values at Moderate (49 to $79 \text{ g CO}_2\text{-C m}^{-2}$) and Minimal Thaw (45 to $75 \text{ g CO}_2\text{-C m}^{-2}$) (Figures 3b and 4a). Winter R_{eco} contributed about 15% to annual growing season R_{eco} fluxes. Annual R_{eco} at Extensive Thaw was 35% higher than Minimal Thaw and 15% higher than Moderate Thaw ($P < 0.01$; Figures 3b and 4b and Table S3). These site differences were similar to R_{eco} patterns observed both during the growing season (Figure 2b) and winter (Figure 4a). Annual R_{eco} varied among years ($P < 0.01$) but we did not detect a linear trend in R_{eco} with time ($P = 0.74$).

[28] Winter respiration had an important effect on annual C exchange for all three sites, where some years went from a C sink in the growing season (Figure 2a) to annual C neutral or even C sources (Figure 4c). Minimal and Extensive Thaw sites were C sources the first two years of the data set, but then remained sinks for the remaining years (Figure 4c and Table S3). Averaged across all years, Extensive Thaw was C neutral ($P = 0.25$), while Moderate and Minimal Thaw were C sinks ($P < 0.05$; Figure 3b). Average annual NEE did not differ significantly among sites ($P = 0.41$), but there was a significant site \times time interaction ($P < 0.01$) driven by higher CO_2 losses in Extensive Thaw compared to the other sites in 2004 and 2005 (Table S3). Annual NEE varied among years ($P < 0.01$), in part due a linear trend in NEE ($P < 0.01$; Figure 4c), which increased from 2004 to 2009 at a rate of $31.4 \text{ g CO}_2\text{-C m}^{-2} \text{ yr}^{-1}$ for all sites.

3.3. Carbon Response to Environmental Factors

[29] Active layer depth stood out as the most important explanatory environmental variable for growing season C fluxes based on significance level and the magnitude of the scaled parameter estimate ($P < 0.01$; Table 2). Active layer is an integrated measurement of ground heat flux and incorporates site variables such as temperature, moisture, and soil properties as well as local factors such as surface hydrology/water movement. As expected, ANPP was also significantly related to GPP and NEE ($P < 0.01$; Table 2), but not to R_{eco}

Figure 2. Cumulative growing season (May–September) (a) net ecosystem exchange (NEE), (b) ecosystem respiration (R_{eco}), (c) gross primary productivity (GPP), and (d) above-ground net primary productivity (ANPP) measured at three sites varying in degree of permafrost thaw. Lines represent linear change in CO_2 flux across the measurement interval. The increase in NEE ($P = 0.03$) varied significantly among sites (site \times time, $P = 0.04$, short dashed = Minimal Thaw, long dashed = Moderate Thaw, solid line = Extensive Thaw), while the linear increase in GPP ($P = 0.02$) and ANPP ($P < 0.01$) did not differ among sites. There was no significant linear trend for R_{eco} ($P = 0.92$). Significant annual site differences are reported in Table S3.

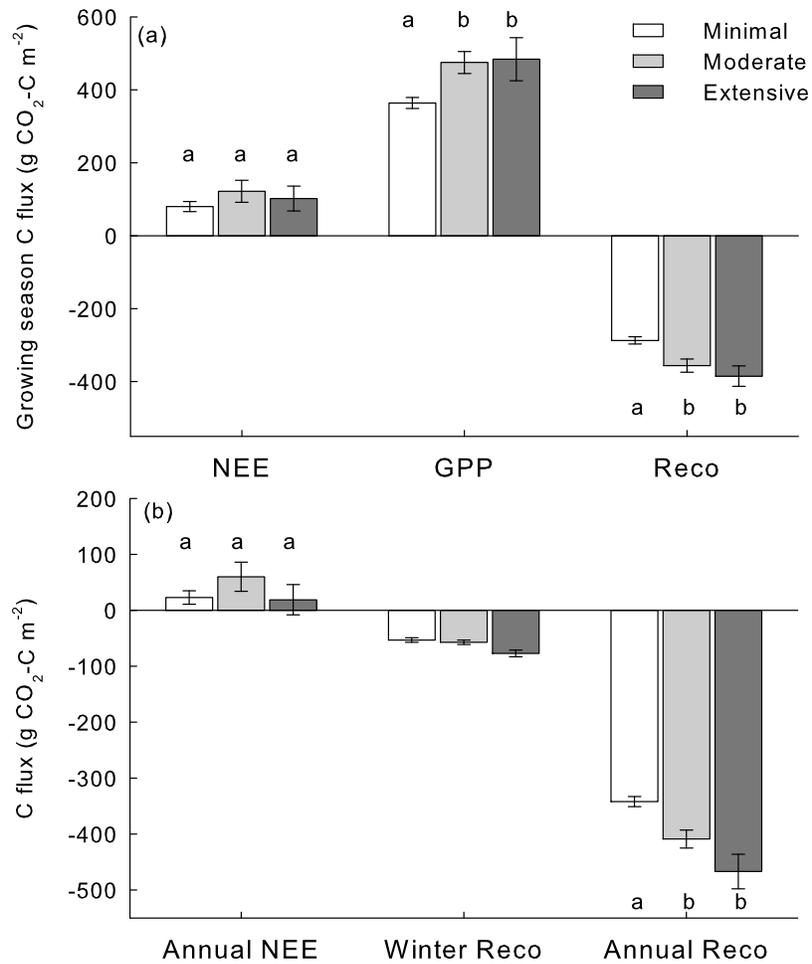


Figure 3. Average (a) growing season (May – September) net ecosystem exchange (NEE), ecosystem respiration (R_{eco}) and gross primary productivity (GPP) and (b) annual NEE, annual R_{eco} and winter R_{eco} for three sites varying in degrees of permafrost thaw, measured from 2004 through 2010. Different letters represent significant difference among sites. Bars above the zero-line represent a CO_2 sink, and those below represent a source of CO_2 to the atmosphere.

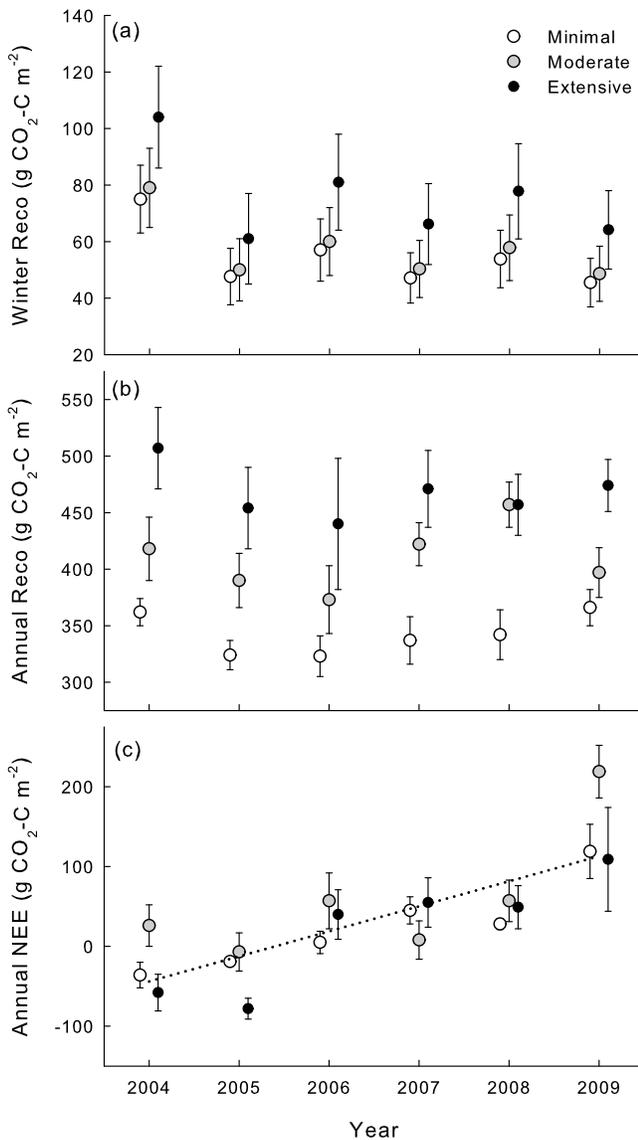


Figure 4. Cumulative (a) winter R_{eco} (October – April), (b) annual R_{eco} , and (c) annual NEE measured during six consecutive years at three sites varying in degree of permafrost thaw. Dotted line represents the linear trend in annual NEE ($P < 0.01$). R_{eco} did not change linearly during the measurement interval ($P = 0.31$). Significant annual site differences are reported in Table S3.

($P = 0.36$). Sites intercepts varied significantly for GPP, R_{eco} and NEE, and removing the intercepts increased the residual variance and AIC. This indicated there are other unmeasured factors that vary with site that are influencing C fluxes. Based on these results, we further investigated the relationship between growing season C exchange and ALD (Figure 5). Across sites, growing season NEE, GPP and R_{eco} all increased with increasing ALD ($P < 0.01$ for all sites, $R^2 = 0.13, 0.31$ and 0.24 for NEE, GPP and R_{eco} , respectively), indicating an increase in C fluxes across sites as permafrost degrades. This pattern was detectable with the wide range of ALDs provided by the full range of chamber bases across sites on the thaw gradient.

4. Discussion

[30] The objective of this study was to understand the effect of permafrost degradation on ecosystem C balance in upland tundra observed both over a seven-year time period (interannual time scale) and across a permafrost thaw gradient (decadal time scale). We observed increasing permafrost degradation during the study period, which was detected as increased ALD. This matched our permafrost thaw gradient observation of deeper ALD in sites with a longer history of thaw and ground subsidence. Permafrost degradation that occurred at both annual and decadal time scales was correlated with increased plant productivity. However, while R_{eco} was higher with decadal-scale permafrost degradation at Moderate and Extensive Thaw, annual increases in ALD did not result in detectable increases in R_{eco} , perhaps as a consequence of increased soil saturation (decreased water table depth). As a result, summer C exchange (NEE), which did not differ among sites, also increased during the seven-year study period. While all sites were C sinks during the growing season, winter respiration, in part, offset summer C uptake. However, despite the important role of winter R_{eco} in determining whether the system acted as an annual net C source or sink, C exchange during the winter period is the least well-characterized component of annual C balance. Based on the winter measurements calculated here, sites with low and intermediate levels of permafrost thaw (Minimal and Moderate Thaw) acted as annual net C sinks, while the site with most thaw (Extensive) was C neutral on an annual basis. The relative patterns across the thaw gradient roughly matched previous observations for the first three years of the study [Schuur *et al.*, 2009; Vogel *et al.*, 2009]. However, the increasing sink strength during the seven-year measurement interval shifted the most thawed site from a C source to C neutral, and shifted the least thawed site from C neutral to a C sink.

[31] Differences in C fluxes across sites reflect physical and chemical changes in the soil environment that accompany permafrost thaw, as well as longer-term ecological shifts in plant and microbial communities [Natali *et al.*, 2012; Oberbauer *et al.*, 2007; Schuur *et al.*, 2007; Jonasson *et al.*, 1999]. As a result of these abiotic and biotic changes, sites more affected by permafrost thaw and ground subsidence (Extensive and Moderate Thaw) had higher GPP compared to the site that was least affected (Minimal Thaw). Differences in GPP among sites were explained, in part, by variation in ALD, which was greatest at Extensive Thaw, an area that has been thawing for more than 50 years, and lowest at Minimal Thaw. Greater ALD is an integrated measurement that reflects a larger volume of seasonally thawed soil where microbial and plant activity is expected to increase in response to higher temperature and nutrient availability [Lee *et al.*, 2010; Natali *et al.*, 2012; Osterkamp *et al.*, 2009; Schuur *et al.*, 2007; Vogel *et al.*, 2009]. Interestingly, average thaw depth decreased across the seven-year period even as ALD increased. This is possibly due to slower early season thaw rates followed by greater late season thaw rates that led ultimately to a deeper seasonal thaw.

[32] While ALD was an important environmental driver of C uptake, site differences beyond those explained by ALD also contributed to variation in GPP. One key factor that likely affected GPP rates was plant community composition

Table 2. Mixed Model Parameter Estimates, Standard Errors (SE) and P-Values (P) for GPP, R_{eco} , and NEE^a

Variables	NEE			Ln GPP			Reco		
	Estimate	SE	P	Estimate	SE	P	Estimate	SE	P
Min (intercept)	87.048	24.749	0.001	2.5779	0.0274	0.000	300.784	10.234	0.000
Mod (intercept)	122.022	23.902	0.000	2.6586	0.0264	0.000	354.183	9.827	0.000
Ext (intercept)	94.704	23.875	0.000	2.6427	0.0264	0.000	373.131	9.971	0.000
ANPP	28.799	8.541	0.001	0.0311	0.0095	0.001	6.037	6.529	0.357
ALD	23.711	7.946	0.004	0.0445	0.0088	0.000	28.108	6.526	0.000
Precipitation	-10.934	28.632	0.718	-0.0081	0.0316	0.807	3.516	8.227	0.687
DWT	7.728	16.734	0.645	-0.0199	0.0186	0.286	-10.912	7.138	0.129
Air Temp	-28.476	27.661	0.351	-0.0193	0.0305	0.554	7.249	7.615	0.385
Random std dev	54.915			0.061			7.012		
Residual std dev	71.10			0.079			59.8		

^aCentered and standardized explanatory variables included in the model: site (Min = Minimal Thaw, Mod = Moderate Thaw, Ext = Extensive Thaw), ANPP = Aboveground net primary productivity ($\text{g C m}^{-2} \text{ yr}^{-1}$), ALD = maximum active layer depth (cm); precipitation = cumulative growing season (GS) precipitation (mm), DWT = average GS distance to water table (cm); Air temp = average GS air temperature ($^{\circ}\text{C}$). All explanatory variables were centered and scaled before analysis, and GPP was log transformed for normality.

differences among sites. Thermokarst formation has led to a shift in plant community composition and structure, where shrubs are most abundant in Extensive and Moderate Thaw, while tussock-forming sedges dominate in Minimal Thaw [Schuur *et al.*, 2007]. This shift in the plant community toward increased shrub abundance has been documented in other tundra locations in Alaska although not necessarily linked specifically to ground subsidence [Epstein *et al.*, 2004; Sturm *et al.*, 2001; Tape *et al.*, 2006]. The shift in plant community composition at EML appears to have taken decades, consistent with vegetation changes elsewhere in the arctic [Epstein *et al.*, 2004]. Against this backdrop of plant composition shifts across the different sites at the EML thaw gradient, the increasing trend of GPP and ANPP over the seven-year study period was not associated with changes in plant community composition, but rather an increase in plant productivity of the existing communities (Table S4). The observed increase in ANPP at the permafrost thaw gradient is in line with observations of increased plant biomass in the arctic over the past few decades [Hill and Henry, 2011; Hudson and Henry, 2009]. One possible mechanism for higher GPP and ANPP with increased thaw depth is an increase in ecosystem N availability as a result of thawing and decomposition of previously frozen organic matter [Chapin and Shaver, 1996; Natali *et al.*, 2012; Schuur *et al.*, 2007; Shaver *et al.*, 2001]. In particular, for moist acidic tundra, N availability is considered to be a much more important driver of NPP and plant composition as compared to temperature alone [Chapin *et al.*, 1995]. This is consistent with the observation that interannual variation in temperature was not a significant explanatory variable of GPP. Of course, ALD is an integrated measurement of ground heat flux, so warmer soils, a longer growing season, and easier access to water reflected in the shallower water table across the seven-year record could all have contributed to greater plant performance.

[33] As with GPP, growing season R_{eco} was also strongly controlled by ALD, and this was in large part determined by the variation in ALD across sites. Minimal Thaw had lower growing season R_{eco} than Extensive and Moderate Thaw across the seven-year period, corresponding to shallower ALD at that site. The positive relationship between ALD and growing season R_{eco} across sites could have resulted, at least in part, from increased thaw of previously frozen organic

matter and decomposition of old C stored at depth in the permafrost surface [Goulden *et al.*, 1998; Nowinski *et al.*, 2010; Schuur *et al.*, 2007, 2009]. The pattern of increasing respiration with thawing permafrost that was observed across our permafrost thaw gradient sites mirrors trends found in other permafrost ecosystem types [Goulden *et al.*, 1998]. In contrast to GPP, growing season R_{eco} did not show an influence of plants as reflected by ANPP. Increased respiration potentially caused by increased plant biomass and productivity might have been offset by changes in heterotrophic respiration, that together with plant respiration, comprise R_{eco} .

[34] In contrast to site-level difference in R_{eco} , there was no directional trend in growing season R_{eco} over the study period, which was surprising since the increase in ALD during the seven-year study represents an additional $\sim 3 \text{ kg m}^{-2}$ of thawed organic C (based on measured deep soil bulk density of $\sim 0.46 \text{ g cm}^{-3}$ and C concentration of $\sim 13.2\%$) [Hicks Pries *et al.*, 2012] available to microbial decomposers. Also, based on the relationship across sites, we expected increased ALD to stimulate respiration. However, during this same time period while ALD increased, water table depth decreased (i.e., wetter soils). As a result, decomposition of additional thawed C at the base of the active layer may have been limited by anoxic soil conditions. However, the decrease in water table depth may be transient over decades because the water table position is primarily determined by the permafrost surface, so that further thawing may move the water table deeper in the profile and, ultimately, exposed gravel layers may drain the water table entirely [Yoshikawa and Hinzman, 2003]. In fact both the Moderate and Extensive Thaw sites show obvious changes in surface hydrology, suggesting that interannual variation in water table may act quite differently than decadal scale water table shifts. In this upland tundra site, we did not detect a relationship between water table depth and R_{eco} , as has been found in lowland tundra and peat ecosystems [Bellisario *et al.*, 1998; Bubier *et al.*, 2003; Dunn *et al.*, 2007]. However, the water table wells at our site were not paired directly with CO_2 flux bases, making a detailed analysis of this relationship difficult. This decoupling of measurements, combined with high spatial variability in water table depth caused by permafrost degradation, may have masked an overall relationship between R_{eco} and water table.

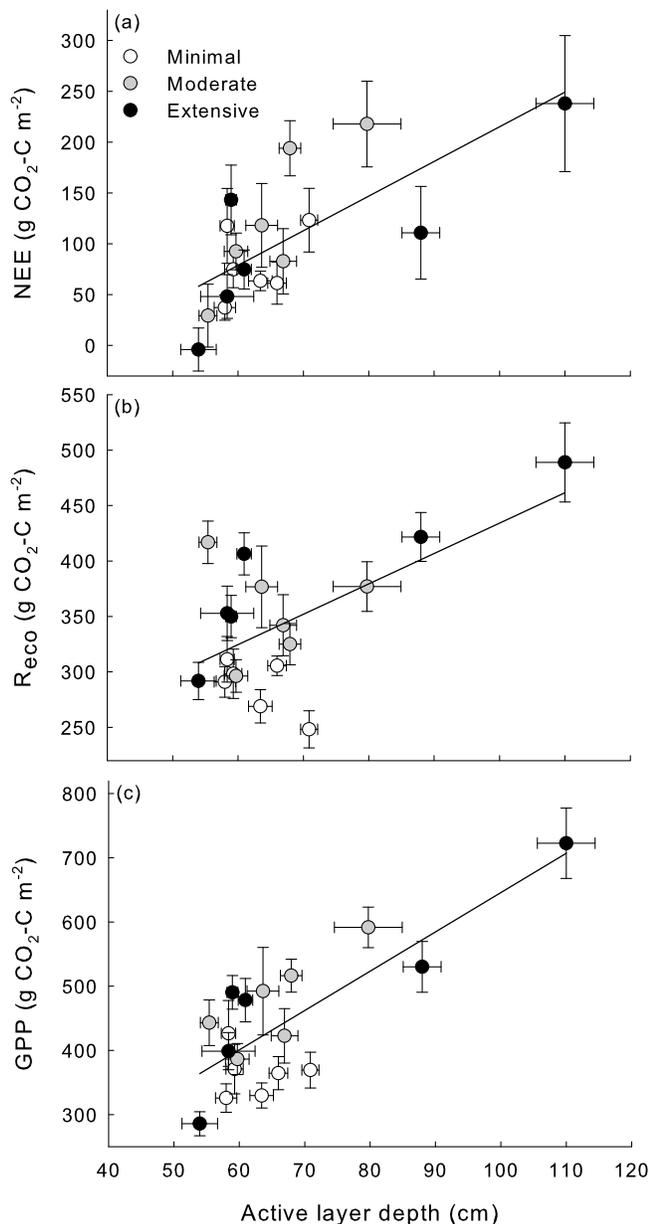


Figure 5. Relationship between active layer depth and growing season (May – September) (a) net ecosystem exchange (NEE), (b) ecosystem respiration (R_{eco}), and (c) gross primary productivity (GPP). Each point represents one CO_2 flux base averaged across the measurement interval. The regression line is fit through all data points ($P < 0.01$ for all).

[35] The combination of increasing GPP along with stable R_{eco} produced an increasing trend of NEE over the duration of the study period, both for the growing season and annually. Within the growing season, all sites acted as C sinks with the exception of 2005, when Extensive Thaw was a C source. Other studies have shown similar results in different permafrost ecosystems, where the strength of growing season NEE has increased in recent years [Oechel et al., 2000; Huemmrich et al., 2010; Ueyama et al., 2012]. In these studies, a combination of plant acclimation to

warmer temperatures, changes in position of the water table, and temperature sensitivity of GPP seemed to play an important role in dictating the fate of net C exchange.

[36] Winter R_{eco} plays a key role in determining annual C balance. While rates of winter respiration are low relative to the growing season, because of the extended length of the snow covered period in this region, winter C fluxes contributed $\sim 15\%$ to annual R_{eco} . The loss of C during the winter shifted the overall direction of NEE from a C sink to source in some years, similar to previous studies [Fahnestock et al., 1999; Vogel et al., 2009]. Extensive Thaw had a higher winter respiration rate than both Moderate and Minimal Thaw, which likely resulted from differences in ALD, water content, snow depth and soil temperature [Vogel et al., 2009]. Our results suggest that as ALD increases, winter respiration will play an increasingly important role in the annual C budget of northern tundra. Our results are in agreement with other studies that have shown higher winter R_{eco} due to warmer soil temperatures and higher snow accumulation [Fahnestock et al., 1999; Natali et al., 2011; Nobrega and Grogan, 2007]. Winter flux estimates from the EML thaw gradient ($45\text{--}104 \text{ g CO}_2\text{-C m}^{-2}$) fell within the range of reported values for other tundra sites ($20\text{--}240 \text{ g CO}_2\text{-C m}^{-2}$) [Grogan and Chapin, 1999; Fahnestock et al., 1999; Oechel et al., 2000; Sullivan et al., 2008; Welker et al., 2000]. Based on our method of calculating winter respiration, we are likely conservatively estimating flux for both Moderate and the Extensive Thaw. This is supported by observations of winter R_{eco} at EML based on new data from eddy covariance measurements (E. F. Belshe et al., unpublished data, 2010) that are greater than the plot-level estimates reported here. If we apply these higher winter R_{eco} estimates to the gradient data presented in our study, then all three sites would be net sources of CO_2 to the atmosphere, rather than net sinks (Minimal and Moderate Thaw) or C neutral (Extensive Thaw). The shift in annual C balance that can result from winter flux uncertainties highlights the importance of focusing future research efforts on obtaining accurate estimates of wintertime respiration in permafrost ecosystems.

[37] In conclusion, effects of permafrost degradation on ecosystem C fluxes on both annual and decadal timescales mirrored each other in many ways, but with a few important differences. Across the thaw gradient, we observed that with an intermediate level of thawing (i.e., Moderate Thaw), plant C uptake increased more than C loss from plant and microbial respiration (Figure 3). However, with additional permafrost thaw (i.e., Extensive Thaw), C losses increased and offset, in part, increased plant uptake. This offset at Extensive Thaw led to an annual NEE that was not statistically different from the Moderate Thaw site, but the Moderate Thaw site was statistically an annual C sink, whereas the Extensive Thaw site was not. Through our seven years of observations we also observed an increase in plant C uptake that accompanied increased permafrost thaw; however, ecosystem respiration remained relatively constant. We suggest that the lack of response of respiration to permafrost thaw on an interannual timescale could be due to water logging in the deep soils, as suggested by the trend of decreasing water table depth across the measurement interval. Only when the thaw depth varied across a bigger range, as it did across sites where it appears to have altered surface hydrology, could we detect

a relationship with thaw. Finally, our interpretation of thawing permafrost effects on annual C balance is highly dependent on the winter period when respiration estimates are not well characterized. As a result, we cannot yet conclude whether the increased NEE in the growing season is truly sustained on an annual basis. If it turns out that winter measurements shown here are an underestimate, we may indeed find these systems are already losing net C to the atmosphere.

[38] **Acknowledgments.** This work was made possible by assistance from A. Baron Lopez, K. G. Crummer, D. DeRaps, and the researchers and technicians of Bonanza Creek LTER. This work was funded by grants to EAGS including: NASA New Investigator Program, NSF CAREER Program, NSF Bonanza Creek LTER Program, Department of Energy NICCR Program, and National Park Inventory and Monitoring Program.

References

- Åkerman, H. J., and M. Johansson (2008), Thawing permafrost and thicker active layers in sub-arctic Sweden, *Permafrost Periglacial Processes*, *19*(3), 279–292, doi:10.1002/ppp.626.
- Bellisario, L. M., T. R. Moore, and J. L. Bubier (1998), Net ecosystem CO₂ exchange in a boreal peatland, northern Manitoba, *Ecoscience*, *5*, 534–541.
- Bubier, J. L., G. Bhatia, T. R. Moore, N. T. Roulet, and P. M. Lafleur (2003), Spatial and temporal variability in growing-season net ecosystem C dioxide exchange at a large peatland in Ontario, Canada, *Ecosystems*, *6*, 353–367.
- Burn, C. R., and M. W. Smith (1993), Issues in Canadian permafrost research, *Prog. Phys. Geogr.*, *17*(2), 156–172, doi:10.1177/030913339301700204.
- Chapin, F. S., and G. R. Shaver (1996), Physiological and growth responses of arctic plants to a field experiment simulating climatic change, *Ecology*, *77*(3), 822–840, doi:10.2307/2265504.
- Chapin, F. S., G. R. Shaver, A. E. Giblin, K. J. Nadelhoffer, and J. A. Laundre (1995), Responses of arctic tundra to experimental and observed changes in climate, *Ecology*, *76*, 694–711, doi:10.2307/1939337.
- Clymo, R. S. (1970), Growth of *Sphagnum*—Methods of measurement, *J. Ecol.*, *58*(1), 13–49, doi:10.2307/2258168.
- Dunn, A. L., C. C. Barford, S. C. Wofsy, M. L. Goulden, and B. C. Daube (2007), A long-term record of C exchange in a boreal black spruce forest: Means, responses to interannual variability, and decadal trends, *Global Change Biol.*, *13*, 577–590, doi:10.1111/j.1365-2486.2006.01221.x.
- Dutta, K., E. A. G. Schuur, J. C. Neff, and S. A. Zimov (2006), Potential C release from permafrost soils of northeastern Siberia, *Global Change Biol.*, *12*(12), 2336–2351, doi:10.1111/j.1365-2486.2006.01259.x.
- 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 CO₂ efflux from arctic soils: Implications for annual C budgets, *Global Biogeochem. Cycles*, *13*, 775–779, doi:10.1029/1999GB900006.
- Goulden, M. L., et al. (1998), Sensitivity of boreal forest C balance to soil thaw, *Science*, *279*, 214–217, doi:10.1126/science.279.5348.214.
- Grogan, P., and F. S. Chapin (1999), Arctic soil respiration: Effects of climate and vegetation depend on season, *Ecosystems*, *2*, 451–459, doi:10.1007/s100219900093.
- Hicks Pries, C. E., E. A. G. Schuur, and K. G. Crummer (2012), Holocene C stocks and C accumulation rates altered in soils undergoing permafrost thaw, *Ecosystems*, *15*, 162–173, doi:10.1007/s10021-011-9500-4.
- Hill, G. B., and G. H. R. Henry (2011), Responses of High Arctic wet sedge tundra to climate warming since 1980, *Global Change Biol.*, *17*, 276–287, doi:10.1111/j.1365-2486.2010.02244.x.
- Hinkel, K. M., and J. K. Hurd (2006), Permafrost destabilization and thermokarst following snow fence installation, Barrow, Alaska, USA, *Arct. Antarct. Alp. Res.*, *38*(4), 530–539, doi:10.1657/1523-0430(2006)38[530:PDATFS]2.0.CO;2.
- Hobbie, S. E., K. J. Nadelhoffer, and P. Hogberg (2002), A synthesis: The role of nutrients as constraints on C balances in boreal and arctic regions, *Plant Soil*, *242*(1), 163–170, doi:10.1023/A:1019670731128.
- Hudson, J. M. G., and G. H. R. Henry (2009), Increased plant biomass in a High Arctic heath community from 1981 to 2008, *Ecology*, *90*, 2657–2663, doi:10.1890/09-0102.1.
- Huemrich, K. F., G. Kinoshita, J. A. Gamon, S. Houston, H. Kwon, and W. C. Oechel (2010), Tundra carbon balance under varying temperature and moisture regimes, *J. Geophys. Res.*, *115*, G00102, doi:10.1029/2009JG001237. [Printed 116(G4), 2011.]
- Intergovernmental Panel on Climate Change (2007), *Climate Change 2007: The Physical Science Basis*, Cambridge Univ. Press, Cambridge, U. K.
- Jonasson, S., A. Michelsen, I. K. Schmidt, and E. V. Nielsen (1999), Responses in microbes and plants to changed temperature, nutrient, and light regimes in the arctic, *Ecology*, *80*(6), 1828–1843, doi:10.1890/0012-9658(1999)080[1828:RIMAPT]2.0.CO;2.
- Jorgenson, M. T., and T. E. Osterkamp (2005), Response of boreal ecosystems to varying modes of permafrost degradation, *Can. J. For. Res.*, *35*(9), 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*(4), 551–579, doi:10.1023/A:1005667424292.
- Lawrence, D. M., and A. G. Slater (2005), A projection of severe near-surface permafrost degradation during the 21st century, *Geophys. Res. Lett.*, *32*, L24401, doi:10.1029/2005GL025080.
- Lawrence, D. M., A. G. Slater, R. A. Tomas, M. M. Holland, and C. Deser (2008), Accelerated Arctic land warming and permafrost degradation during rapid sea ice loss, *Geophys. Res. Lett.*, *35*, L11506, doi:10.1029/2008GL033985.
- Lee, H., E. A. G. Schuur, and J. G. Vogel (2010), Soil CO₂ production in upland tundra where permafrost is thawing, *J. Geophys. Res.*, *115*, G01009, doi:10.1029/2008JG000906.
- Mack, M. C., E. A. G. Schuur, M. S. Bret-Harte, G. R. Shaver, and F. S. Chapin (2004), Ecosystem C storage in arctic tundra reduced by long-term nutrient fertilization, *Nature*, *431*(7007), 440–443, doi:10.1038/nature02887.
- McNamara, J. P., D. L. Kane, and L. D. Hinzman (1998), An analysis of streamflow hydrology in the Kuparuk River basin, Arctic Alaska: A nested watershed approach, *J. Hydrol.*, *206*(1–2), 39–57, doi:10.1016/S0022-1694(98)00083-3.
- Natali, S. M., E. A. G. Schuur, C. Trucco, C. E. Hicks Pries, K. G. Crummer, and A. F. Baron Lopez (2011), Effects of experimental warming of air, soil and permafrost on C balance in Alaskan tundra, *Global Change Biol.*, *17*(3), 1394–1407, doi:10.1111/j.1365-2486.2010.02303.x.
- Natali, S. M., E. A. G. Schuur, and R. L. Rubin (2012), Increased plant productivity in Alaskan tundra as a result of experimental warming of soil and permafrost, *J. Ecol.*, *100*, 488–498, doi:10.1111/j.1365-2745.2011.01925.x.
- Nobrega, S., and P. Grogan (2007), Deeper snow enhances winter respiration from both plant-associated and bulk soil C pools in birch hummock tundra, *Ecosystems*, *10*, 419–431, doi:10.1007/s10021-007-9033-z.
- Nowinski, N. S., L. Taneva, S. E. Trumbore, and J. M. Welker (2010), Decomposition of old organic matter as a result of deeper active layers in a snow depth manipulation experiment, *Oecologia*, *163*(3), 785–792, doi:10.1007/s00442-009-1556-x.
- Oberbauer, S. F., et al. (2007), Tundra CO₂ 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 CO₂ exchange in the Alaskan Arctic in response to decadal climate warming, *Nature*, *406*, 978–981, doi:10.1038/35023137.
- 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 V. E. Romanovsky (1999), Evidence for warming and thawing of discontinuous permafrost in Alaska, *Permafrost Periglacial Processes*, *10*(1), 17–37, doi:10.1002/(SIC)1099-1530(199901/03)10:1<17::AID-PPP303>3.0.CO;2-4.
- Osterkamp, T. E., M. T. Jorgenson, E. A. G. Schuur, Y. L. Shur, M. Z. Kanevskiy, J. G. Vogel, and V. E. Tumskey (2009), Physical and ecological changes associated with warming permafrost and thermokarst in interior Alaska, *Permafrost Periglacial Processes*, *20*(3), 235–256, doi:10.1002/ppp.656.
- Post, W. M., W. R. Emanuel, P. J. Zinke, and A. G. Stangenberger (1982), Soil C pools and world life zones, *Nature*, *298*(5870), 156–159, doi:10.1038/298156a0.
- Romanovsky, V. E., et al. (2010), Thermal state of permafrost in Russia, *Permafrost Periglacial Processes*, *21*, 136–155, doi:10.1002/ppp.683.
- Schielzeth, H. (2010), Simple means to improve the interpretability of regression coefficients, *Methods Ecol. Evol.*, *1*, 103–113.
- 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*(2), 280–292, doi:10.1007/s10021-007-9024-0.
- Schuur, E. A. G., et al. (2008), Vulnerability of permafrost C to climate change: Implications for the global C cycle, *BioScience*, *58*(8), 701–714, doi:10.1641/B580807.

- Schuur, E. A. G., J. G. Vogel, K. G. Crummer, H. Lee, J. O. Sickman, and T. E. Osterkamp (2009), The effect of permafrost thaw on old C release and net C exchange from tundra, *Nature*, *459*(7246), 556–559, doi:10.1038/nature08031.
- Seppälä, M. (1994), Snow depth controls palsa growth, *Permafrost Periglacial Processes*, *5*(4), 283–288, doi:10.1002/ppp.3430050407.
- 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*(11), 3163–3181, doi:10.1890/0012-9658(2001)082[3163:SCIWFT]2.0.CO;2.
- Sturm, M., C. Racine, and K. Tape (2001), Climate change—Increasing shrub abundance in the Arctic, *Nature*, *411*, 546–547, doi:10.1038/35079180.
- Sullivan, P. F., J. M. Welker, S. J. T. Arens, and B. Sveinbjörnsson (2008), Continuous estimates of CO₂ efflux from arctic and boreal soils during the snow-covered season in Alaska, *J. Geophys. Res.*, *113*, G04009, doi:10.1029/2008JG000715.
- Tape, K., M. Sturm, and C. Racine (2006), The evidence for shrub expansion in northern Alaska and the Pan-Arctic, *Global Change Biol.*, *12*, 686–702, doi:10.1111/j.1365-2486.2006.01128.x.
- Tarnocai, C., J. G. Canadell, E. A. G. Schuur, P. Kuhry, G. Mazhitova, and S. Zimov (2009), Soil organic carbon pools in the northern circumpolar permafrost region, *Global Biogeochem. Cycles*, *23*, GB2023, doi:10.1029/2008GB003327.
- Ueyama, M., H. Iwata, Y. Harazono, E. S. Euskirchen, W. C. Oechel, and D. Zona (2012), Growing season and spatial variations of carbon fluxes of arctic and boreal ecosystems in Alaska, *Ecol. Appl.*, in press.
- Vogel, J., E. A. G. Schuur, C. Trucco, and H. Lee (2009), Response of CO₂ exchange in a tussock tundra ecosystem to permafrost thaw and thermokarst development, *J. Geophys. Res.*, *114*, G04018, doi:10.1029/2008JG000901.
- Wahrhaftig, C. (1958), Quaternary geology of the Nenana river valley and adjacent parts of the Alaska range, *U.S. Geol. Surv. Prof. Pap.*, *293*, 1–68.
- Walker, M. D. (1996), Community baseline measurements for ITEX studies, in *International Tundra Experiment (ITEX) Manual*, edited by U. Molau and P. Mølgaard, pp. 39–41, Dan. Polar Cent., Copenhagen.
- Walker, M. D., et al. (1999), Long-term experimental manipulation of winter snow regime and summer temperature in arctic and alpine tundra, *Hydrol. Processes*, *13*(14–15), 2315–2330, doi:10.1002/(SICI)1099-1085(199910)13:14/15<2315::AID-HYP888>3.0.CO;2-A.
- Welker, J. M., J. T. Fahnestock, and M. H. Jones (2000), Annual CO₂ flux in dry and moist Arctic tundra: Field responses to increases in summer temperatures and winter snowdepth, *Clim. Change*, *44*, 139–150, doi:10.1023/A:1005555012742.
- Yoshikawa, K., and L. D. Hinzman (2003), Shrinking thermokarst ponds and groundwater dynamics in discontinuous permafrost near Council, Alaska, *Permafrost Periglacial Processes*, *14*(2), 151–160, doi:10.1002/ppp.451.
- Zhang, T., R. Barry, K. Knowles, J. Heginbottom, and J. Brown (1999), Statistics and characteristics of permafrost and ground-ice distribution in the Northern Hemisphere, *Polar Geogr.*, *23*, 132–154, doi:10.1080/10889379909377670.
- Zimov, S. A., E. A. G. Schuur, and F. S. Chapin III (2006a), Permafrost in the global carbon budget, *Science*, *312*, 1612–1613.
- Zimov, S. A., S. P. Davydov, G. M. Zimova, A. I. Davydova, E. A. G. Schuur, K. Dutta, and F. S. Chapin III (2006b), Permafrost carbon: Stock and decomposability of a globally significant carbon pool, *Geophys. Res. Lett.*, *33*, L20502, doi:10.1029/2006GL027484.