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Controls on ecosystem and root respiration across a permafrost and wetland gradient in interior Alaska

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Abstract

Permafrost is common to many northern wetlands given the insulation of thick organic soil layers, although soil saturation in wetlands can lead to warmer soils and increased thaw depth. We analyzed five years of soil CO₂ fluxes along a wetland gradient that varied in permafrost and soil moisture conditions. We predicted that communities with permafrost would have reduced ecosystem respiration (ER) but greater temperature sensitivity than communities without permafrost. These predictions were partially supported. The colder communities underlain by shallow permafrost had lower ecosystem respiration (ER) than communities with greater active layer thickness. However, the apparent Q_{10} of monthly averaged ER was similar in most of the vegetation communities except the rich fen, which had smaller Q_{10} values. Across the gradient there was a negative relationship between water table position and apparent Q_{10} , showing that ER was more temperature sensitive under drier soil conditions. We explored whether root respiration could account for differences in ER between two adjacent communities (sedge marsh and rich fen), which corresponded to the highest and lowest ER, respectively. Despite differences in root respiration rates, roots contributed equally (~40%) to ER in both communities. Also, despite similar plant biomass, ER in the rich fen was positively related to root biomass, while ER in the sedge marsh appeared to be related more to vascular green area. Our results suggest that ER across this wetland gradient was temperature-limited, until conditions became so wet that respiration became oxygen-limited and influenced less by temperature. But even in sites with similar hydrology and thaw depth, ER varied significantly likely based on factors such as soil redox status and vegetation composition.

Keywords: permafrost, wetland, carbon, soil respiration, plant respiration, Q_{10} , thaw depth

1. Introduction

Wetlands represent a major land cover class in boreal and subarctic regions, occupying about 25% of the total boreal

region land area (Vitt 2006, Wieder *et al* 2006). Wetlands in the discontinuous permafrost zone range from poorly drained conifer bogs with shallow permafrost to permafrost-free inundated marshes and fens that are too wet to support trees. These wetland types could be impacted differently by climate change, particularly because of strong relationships between soil temperature, soil moisture, and active layer depth. Frozen ground impedes the drainage of surface soils,



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and thus maintains saturated conditions that reduce rates of decomposition (cf Ford and Bedford 1987, Kane *et al* 2010, Roulet and Woo 1986) and inhibit soil carbon losses through fire combustion (Trumbore and Harden 1997). In these systems, increasing thaw depth throughout the growing season regulates soil drainage but also exposes more organic carbon to decomposition.

Permafrost in interior Alaska has been showing widespread evidence of thawing (Osterkamp *et al* 2000, Jorgenson *et al* 2001). Because deep peat impedes soil drainage, changes in active layer depth in wetlands typically lead to more saturated conditions either in the form of thermokarst ponds, collapse scar bogs, or fens. Permafrost thaw in hydrologically connected uplands also can influence runoff or upwelling in wetlands, contributing to saturation. Permafrost may be particularly vulnerable to thaw where heat flow from groundwater movement maintains warmer soil conditions at depth; for example where heat can be transferred from groundwater fens to adjacent permafrost in forest margins (Racine and Walters 1994). Groundwater influences can also contribute to the maintenance of taliks or unfrozen zones in permafrost (Racine and Walters 1994). Overall, permafrost thaw related to wetlands and soil saturation in the discontinuous permafrost zone have the potential to alter soil climate, organic layer thickness, and vegetation structure, all of which are likely to influence respiration and CO₂ release from soils.

Soil water content and soil temperature interactions with thaw depth are likely to generate positive relationships between water availability and soil temperature in northern wetlands (i.e., warm and wet conditions occur with increasing thaw depth). Warming usually stimulates heterotrophic respiration and increases soil CO₂ fluxes, but can have variable effects on autotrophic respiration (cf Dorrepaal *et al* 2009, Bronson and Gower 2010, Hicks Pries *et al* 2013). More saturated soil conditions generally inhibit microbial respiration due to lack of O₂ but also could inhibit plant productivity and respiration due to reduced nutrient availability in the rooting zone. Likely as a result of these interactions, several studies have found no or weak relationships between ecosystem respiration (ER) and variation in water table position (Silvola *et al* 1996, Lafleur *et al* 2005, Dimitrov *et al* 2010).

Here we analyzed growing season ER and relationships with seasonal thaw depth, soil temperature, and soil moisture among five wetland communities that varied in permafrost and hydrologic conditions. Our measurements were collected along a physical gradient spanning from a conifer permafrost forest to an open saturated fen. Ecological gradients are useful because they capture variation in community structure associated with long-term processes along with variation in important environmental variables such as soil moisture and soil temperature (Muller 1998). Within and across wetland communities, we hypothesized that ER would be lower but more temperature sensitive in the vegetation communities with permafrost than those that lacked frozen material in the upper 1 m of soil. Given that soil saturation can occur when seasonal ice is shallow (when soil interception is constrained

by near surface ice) or when soil thaw is deeper (i.e., taliks that do not freeze due to deep water, thermokarst features that become saturated), we predicted that ER would exhibit a unimodal relationship with thaw depth across communities along the wetland gradient. Within each wetland community, we predicted that ER would show a positive relationship with depth to seasonal ice, since increasing thaw depth corresponds to warmer soil temperatures and greater unfrozen organic soil stocks.

2. Methods

2.1. Description of wetland gradient

Data were collected at the Alaskan Peatland Experiment (APEX) sites located near the Bonanza Creek Experimental Forest in Alaska (64.82°N, 147.87°W). The mean annual air temperature for the Tanana River Valley ranges from −5 to −7°C and mean annual precipitation is between 215 and 300 mm (Hinzman *et al* 2006). Our gradient is composed of five wetland communities that extend from the toe slope of an adjacent upland forest into a large fen complex (Waldrop *et al* 2012). Adjacent communities are separated by 25–50 m, including (in order from toe slope to center of the large fen complex): (1) black spruce forest underlain by permafrost with a understory dominated by feather moss and ericaceous shrubs, (2) shrub system dominated by willow (*Salix* spp.), birch (*Betula* spp.) and *Sphagnum* species (referred to as bog birch in Waldrop *et al* 2012), (3) grass tussock meadow dominated by *Calamagrostis canadensis* (referred as tussock in Waldrop *et al* 2012), (4) sedge marsh dominated by *Equisetum fluviatile* and *Carex* species with sparse *Sphagnum* and brown moss species (emergent fen in Waldrop *et al* 2012), and (5) rich fen dominated by *Equisetum fluviatile*, *Carex* species, *Potentilla palustris* and *Sphagnum* and brown mosses. Key characteristics of each community are in table 1.

2.2. Atmospheric and soil environmental variables

Air temperature, relative humidity, and precipitation data were collected at the site continuously using CR10X data loggers (Campbell Scientific Inc., Logan, UT) and are available in the Bonanza Creek LTER data archive (table 2). Soil temperatures were measured manually at 10 cm at each community during each ER flux campaign using thermistors. Soil moisture was measured continuously at various depths (5, 25, 50 cm) using CS615 and CS616 TDR soil moisture probes (Campbell Scientific Inc., Logan, UT). We calibrated the TDR probes using the method for organic soils outlined in Bourgeau-Chavez *et al* (2010). Surface soil moisture also was measured manually during each ER flux using a ThetaProbe soil moisture sensor (Delta-T Devices, Cambridge, England) inserted 10 cm vertically into the surface organic layer. During each flux measurement, we manually measured water table position in shallow wells (~1 m depth) permanently placed in the peat surface and seasonal thaw depth using tile probe inserted into the peat. Soil environmental variables were analyzed using repeated measures analysis of variance and Tukey's post hoc comparison of means (SAS Proc Mixed), with ecosystem and year as fixed effects.

Table 1. Dominant species and mean growing season soil temperature (°C) at 10 cm, soil moisture (% VMC) at 5 cm, organic soil layer depth (cm), and seasonal thaw depth (cm) for each community along the wetland gradient. Below, communities along the gradient are listed in order from the toe slope of an adjacent forest to the center of the large fen complex. A visual schematic of this wetland gradient can be found in Waldrop *et al* (2012).

	Dominant species	Soil temperature	Soil moisture	Organic layer depth	Maximum seasonal thaw depth
Black Spruce	<i>Picea mariana</i> , <i>Feather moss</i> spp.	2.8 ± 0.50	15.04 ± 3.10	21 ± 2	62.2
Shrub	<i>Salix</i> spp., <i>Betula</i> spp., <i>Sphagnum</i> spp.	3.55 ± 0.31	56.91 ± 8.25	30 ± 15	92.0
Grass	<i>Calamagrostis canadensis</i>	4.6 ± 0.58	65.95 ± 7.94	29 ± 22	120.6
Sedge marsh	<i>Equisetum fluvitile</i> , <i>Carex</i> spp., <i>Sphagnum</i> spp., <i>Brown moss</i> spp.	5.2 ± 0.40	72.17 ± 7.29	16 ± 1	>152
Rich fen	<i>Equisetum fluvitile</i> , <i>Carex</i> spp., <i>Potentilla palustris</i> , <i>Sphagnum</i> spp., <i>Brown moss</i> spp.	8.6 ± 0.22	83.88 ± 1.56	92 ± 12	>152

Table 2. Growing season (June–August) climate data from 2007–2010 for the floodplain site of the Bonanza Creek Long Term Ecological Research Program, located near our study sites. Air temperature was measured at 150 cm above the soil surface. Daily temperatures are means ± one standard error.

Year	Average daily temp (°C) ± standard error	Minimum daily temperature (°C)	Maximum daily temperature (°C)	Total precipitation (mm)
2007	15.9 ± 0.1	−1.03	28.83	93.03
2008	13.7 ± 0.1	0.15	30	105.38
2009	16.0 ± 0.1	−4.57	32.15	94.3
2010	15.3 ± 0.1	−5.33	32.92	91.38
2011	13.7 ± 0.1	−0.88	30.46	110.94

2.3. Ecosystem respiration (ER) fluxes

Ecosystem respiration of CO₂ was measured at each community from mid-May to September approximately every two weeks from 2007 to 2011. Details on the flux methods are provided in Chivers *et al* (2009). Briefly, one gas flux collar constructed of galvanized steel was permanently installed into the surface soils (~5 cm depth) of each community except at the rich fen, where three gas flux collars were installed as part of a larger experiment. Due to the lack of spatial replication within most of the community types found along the wetland gradient, the results are specific to the particular locations of each flux collar, which were installed in conditions representative of each habitat type.

At the start of each flux measurement, a clear chamber (dimensions of 0.37 m² × 26 cm deep) constructed of an aluminum frame with Teflon siding (American Durafilm, Holliston, MA) was placed on each gas flux collar. The chamber was covered with a dark shroud to block any incoming PAR. We used a PP-systems EGM-4 infrared gas analyzer (IRGA, Amesbury, Massachusetts) to measure CO₂ concentrations inside the chamber every 1.6 s for 2–3 min. Temperature, relative humidity, and PAR were recorded continuously inside the chamber using a PP-systems TRP-1 sensor attached to the inside of the chamber. A CO₂ flux (μmol CO₂ m^{−2} s^{−1}) was calculated from the slope of the linear relationship between time and the CO₂ headspace concentration.

To analyze differences in mean ER across the five communities and study years (2007–2011), we used a repeated measures analysis of variance (SAS Proc Mixed) and Tukey's post hoc comparison of means. We modeled

the dependence of ER, including both autotrophic and heterotrophic respiration, on seasonal thaw depth as:

$$ER = R_{\max} \times \exp \left[-0.5 \times \frac{(F - uR)^2}{tR^2} \right] \quad (1)$$

where ER is the observed CO₂ flux (μmol CO₂ m^{−2} s^{−1}), $R_{\max}$ is the estimated maximum ER when seasonal thaw depth is optimal for plant and heterotrophic respiration (μmol CO₂ m^{−2} s^{−1}), F is the observed thaw depth (cm), uR is the estimated optimal seasonal thaw depth for respiration (cm), and tR is an estimated measure of the width of seasonal thaw depth amplitude (cm). This nonlinear model was modified from Tuittila *et al* (2004) and here is used to examine data across communities along the gradient. The relationship between seasonal thaw depth and ER within each community was examined using linear regression models. The temperature dependence of ER was modeled as:

$$ER = A \times Q_{10}^{(T/10)} \quad (2)$$

where A is the estimated ER at 0 °C (μmol CO₂ m^{−2} s^{−1}), Q_{10} is the estimated temperature dependence of ER (unitless), and T is the observed soil temperature (°C) at 10 cm below the peat surface.

We estimated parameters from equations (1) and (2) first using instantaneous ER and environmental variables measured during the flux measurements. Parameters also were estimated using ER and environmental data averaged by month across years. All estimated parameters throughout the paper were calculated using Proc NLIN in SAS. When analyzing the temperature dependence of ER, we identified a statistical outlier for the grass community that represented a

very low ER value for a high soil moisture level (greater than 99%). This single outlier was removed from all subsequent analyses. For all linear and nonlinear analyses, we used an alpha value of 0.05 to determine significance.

2.4. Root respiration and vegetation measurements

We conducted two root experiments, the first of which was conducted in 2010. We installed five new flux collars in the rich fen and measured ER fluxes for each collar around peak biomass (mid-July) following the methods above. This was repeated daily for two weeks, after which the per cent cover of mosses and vascular vegetation was visually estimated inside each of the collars. A 10 cm × 10 cm aboveground biomass sample was randomly harvested inside each collar. We also collected vascular stem density inside each collar, and measured vascular green area (VGA) on all of the species found within the collar (m² of vascular leaf area m⁻²) following Chivers *et al* (2009). Root respiration was then measured on the three dominant vascular species (*Carex* spp., *Equisetum fluviatile*, *Potentilla palustris*) within each collar by destructively harvesting one of each species found within the collar, and picking all fine roots. The three dominant species each comprised between 20 and 40% of the total aboveground vascular biomass in all collars for both years. Fine roots were rinsed and immediately placed inside of a 5 cm diameter (0.0082 m³) aluminum root cuvette (following Burton and Pregitzer 2003) and a flux was measured using the EGM-4 infrared gas analyzer, which measured the CO₂ concentration inside of the chamber every 1.6 s until concentrations reached around 1000 parts per million (ppm). This took 5–10 min. In all cases, fluxes were linear and there was no evidence of higher respiration rates at lower headspace CO₂ concentrations (cf Burton and Pregitzer 2002). Temperatures were continuously monitored inside the cuvette, which allowed us to later standardize all fluxes to the same soil temperature. Roots were placed in a cooler and transported back to the lab where field moisture content was determined by weighing and then drying at 65 °C to a constant mass. These data allowed us to calculate root respiration for each species on a per g dry mass basis.

After root fluxes were measured in the field, three soil cores (5 cm diameter, 20 cm length) were collected from within each collar, placed in a cooler, and transported back to the lab. Cores were cut in half length-wise and half of each core was analyzed for bulk density while fine roots were separated from soil with tweezers from the other half of each core, dried to a constant mass, and weighed to obtain a measure of root biomass (g root biomass m⁻²).

We conducted this experiment as a pilot study in the rich fen in 2010. Because our analyses showed that mean ER was highest at the sedge marsh and lowest at the rich fen, we repeated this experimental design in both of these communities in 2011. For the 2011 experiment, we installed five new collars at the rich fen and also installed five collars at the sedge marsh, and repeated the methods outlined for the 2010 experiment.

Table 3. Results of a repeated measures analysis of variance (ANOVA) analyzing the fixed effects (year, community) on ecosystem respiration, soil temperature (°C at 10 cm depth), soil moisture (% volumetric moisture content (VMC)), seasonal thaw depth (cm), water table position (cm).

	Effect	df	F	P
ER	Year	4	1.74	0.1396
	Community	4	19.23	<0.0001
	Year × Community	15	2.13	0.0082
Soil temperature	Year	4	6.87	<0.0001
	Community	4	58.14	<0.0001
	Year × Community	15	5.01	<0.0001
Soil moisture	Year	4	11.98	<0.0001
	Community	4	23.68	<0.0001
	Year × Community	9	2.57	0.0077
Water table	Year	4	9.71	<0.0001
	Community	4	1.68	0.1547
	Year × Community	14	6.80	<0.0001
Seasonal thaw	Year	4	5.33	0.0004
	Community	4	20.53	<0.0001
	Year × Community	15	6.24	<0.0001

Root respiration fluxes were standardized to a g m⁻² basis using a weighted average based on species per cent cover and root biomass estimates at a collar level. Root respiration was also standardized to the average 10 cm soil temperature during flux measurements to account for differences in temperature between the soil and the chamber atmosphere (collected using thermistors). During our 2010 measurements, one collar had root respiration values that exceeded ER, and a higher variance in root respiration relative to the other collars. The studentized residual error for this measurement location was -3.30, thus we removed this data as an outlier. For all other data, we analyzed root respiration as a predictor of ER using a linear regression (SAS Proc GLM).

3. Results

3.1. Patterns in soil environment and ER across a wetland gradient

While surface soil temperature, volumetric soil moisture content, seasonal thaw depth, and water table position all varied by a community × year interaction (table 3), communities tended to differ predictably in environmental conditions. In general, soils were colder and drier in the black spruce and shrub communities and were warmer and wetter in the more open marsh and fen (table 1). Seasonal thaw depth was shallowest at the black spruce community and increased along the gradient into the rich fen. These patterns in soil conditions were consistent among sampling years with a few exceptions. The sedge marsh and rich fen had much deeper seasonal thaw depths in 2008 and 2009, when the general study region experienced a severe natural flood (Wyatt *et al* 2012), than in the other years.

Averaged across years, ER was highest in the sedge marsh and grass communities, which did not differ from one another and averaged $4.85 \pm 0.27 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. Ecosystem respiration in the black spruce, shrub, and rich fen communities did not differ from one another, and averaged

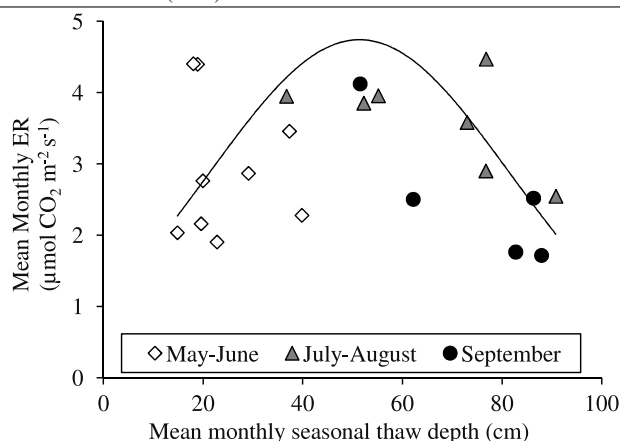


Figure 1. Effect of mean monthly thaw depth (cm below peat surface) on mean ER ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) across communities along the wetland gradient. Model line was fitted to the data using equation (1); $R^2 = 0.20$.

$2.70 \pm 0.09 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. While instantaneous ER varied by a community $\times$ year interaction (table 3), this general trend across communities was consistent in most study years. Across all vegetation community types and years, mean seasonal ER peaked in July–August (least squared mean value of $4.29 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), compared with May–June (least squared mean value of $3.15 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) or September (least squared mean value of $2.94 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$).

3.2. Effects of soil environmental variables on ER

Across communities, there was a significant unimodal relationship (following equation (1)) between soil thaw depth and instantaneous ER (not shown; $R_{\text{max}} = 3.09 \pm 0.15$, $uR = 63.33 \pm 37.97$, $tR = 171.90 \pm 117.10$, model

$p < 0.0001$, $F_{2,226} = 277.83$) as well as between soil thaw depth and ER averaged by month (figure 1; $R_{\text{max}} = 4.74 \pm 0.58$, $uR = 51.39 \pm 4.70$, $tR = 30.09 \pm 6.24$, model $p < 0.0001$, $F_{3,19} = 37.41$). Within each community, there were no significant linear relationships between frost depth and ER (figure 2).

Across all vegetation communities and years, depth to seasonal ice was positively correlated with surface soil temperature (Pearson correlation coefficient = 0.63 , $p < 0.0001$) but was not significantly correlated with water table position or soil moisture. Surface soil temperature was positively correlated with surface soil moisture content (Pearson correlation coefficient = 0.41 , $p < 0.0001$).

Instantaneous ER was more sensitive to temperature in the sedge marsh and shrub communities than the other communities (table 4). Not surprisingly, the predictive ability of these relationships declined with smaller Q_{10} values (table 4). Monthly averaged ER had lower temperature sensitivity (estimated via Q_{10}) in the rich fen than the other communities (figure 3). Estimates of A (respiration at 0°C) based on instantaneous data were highest at the grass community and lowest at the shrub and rich fen communities (table 4). While estimates of A based on monthly averaged data were similar to those reported for the instantaneous ER models, Q_{10} values from the monthly model in each community tended to be higher than those derived from instantaneous data (table 4). Mean monthly Q_{10} values increased as the mean depth to water table increased across all communities (figure 4). Mean monthly Q_{10} was not related to depth to seasonal ice ($F = 1.43$, $p = 0.28$).

3.3. Contributions of root respiration to ER

Averaged across collars, ER flux during the experimental campaigns was $0.143 \pm 0.015 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at the rich

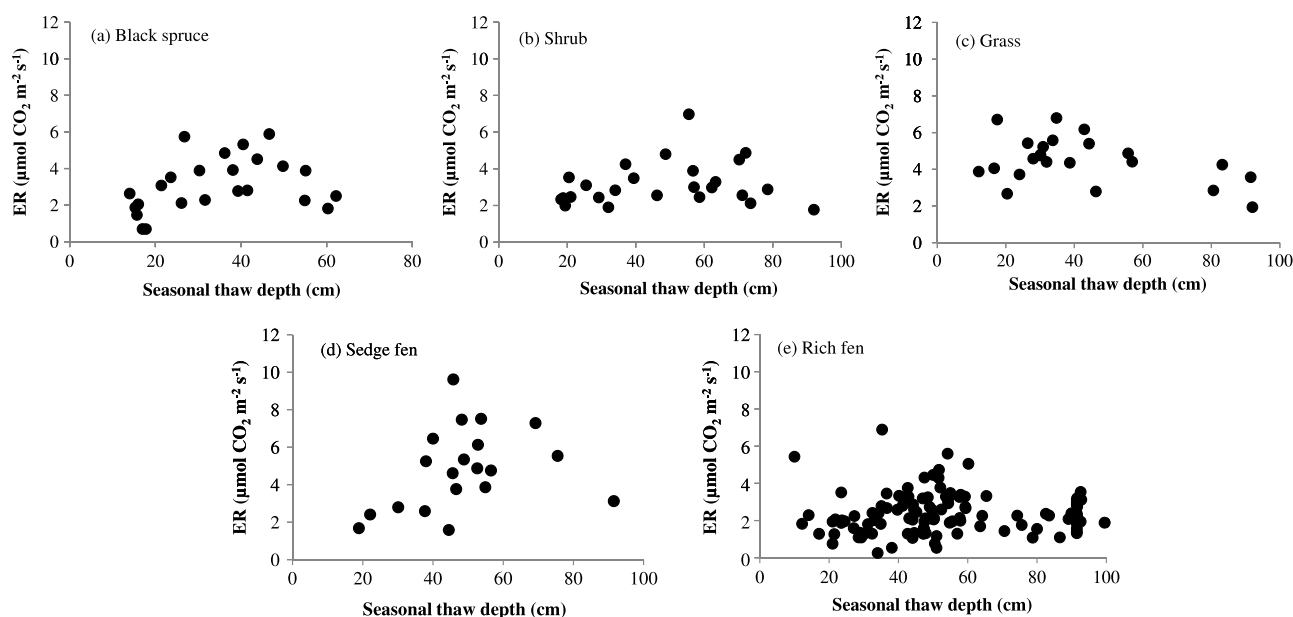


Figure 2. Effect of soil thaw depth on instantaneous ER within each wetland community.

Table 4. Results of nonlinear modeling (equation (2)) analyzing the dependence of ecosystem respiration on soil temperature. Instantaneous ER was analyzed using soil temperature at the time of flux measurements, while mean monthly ER was analyzed using mean monthly soil temperatures across the entire growing season as well as peak biomass (not possible to run at the rich fen).

	A ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	Q_{10}	$P; F_{(\text{num}, \text{den})}; R^2$
<i>Instantaneous ER</i>			
Black spruce	2.87 ± 0.41	1.28 ± 0.44	$<0.001; 59.01_{(2,23)}; 0.06$
Shrub	1.91 ± 0.37	3.88 ± 1.72	$<0.001; 133.29_{(2,24)}; 0.29$
Grass	4.26 ± 0.48	1.16 ± 0.23	$<0.001; 144.03_{(2,23)}; 0.04$
Sedge marsh	2.16 ± 0.98	4.36 ± 3.29	$<0.001; 59.83_{(2,18)}; 0.22$
Rich fen	1.78 ± 0.19	1.46 ± 0.16	$<0.001; 331.25_{(2,135)}; 0.11$
<i>Mean monthly ER</i>			
Growing season black spruce, shrub, grass, and marsh	1.96 ± 0.40	5.22 ± 2.03	$<0.0001; 218.08_{(2,18)}; 0.64$
Peak biomass (July, Aug) black spruce, shrub, grass, and marsh	2.11 ± 0.77	5.62 ± 3.70	$<0.0001; 92.80_{(2,5)}; 0.48$
Growing season rich fen	1.46 ± 0.39	1.82 ± 0.59	$0.002; 97.39_{(2,5)}; 0.53$

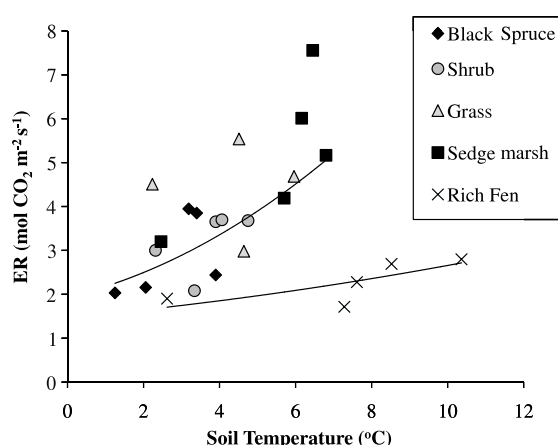


Figure 3. Effect of mean monthly temperature on mean monthly ER for all years (2007–2011) along the wetland gradient. The relationship found at the rich fen is shown as the dotted line and the relationship across the other communities combined is shown as the solid line. Lines were fitted to the data using equation (2) and modeled parameters and model significance are reported in table 4.

fen and $0.262 \pm 0.015 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at the marsh. Root fluxes averaged $0.003 \pm 0.001 \mu\text{mol CO}_2 \text{ s}^{-1} \text{ g}^{-1}$ at the rich fen and $0.004 \pm 0.0002 \mu\text{mol CO}_2 \text{ s}^{-1} \text{ g}^{-1}$ at the sedge marsh. We used root biomass (rich fen: $494.13 \pm 281.72 \text{ g dry mass m}^{-2}$; sedge marsh: $605.15 \pm 123.38 \text{ g m}^{-2}$) to scale root respiration. On a m^2 basis, mean root fluxes were $0.059 \pm 0.02 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at the rich fen and $0.095 \pm 0.007 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ at the sedge marsh. We observed no change in respiration rates as chamber CO_2 concentrations changed from ~ 400 to 1000 mg l^{-1} , which suggests little to no CO_2 acclimation effect (Burton and Pregitzer 2002).

Root respiration contributed to 40% of ER in the rich fen in both years, and 37% of ER at the marsh. In 2011, when we measured root respiration in both systems, both root respiration and ER fluxes were higher in the marsh than in the rich fen. Across both communities and years (rich fen only), root respiration ($\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) was a strong predictor of ER, explaining 60% of the variation in ER (figure 5).

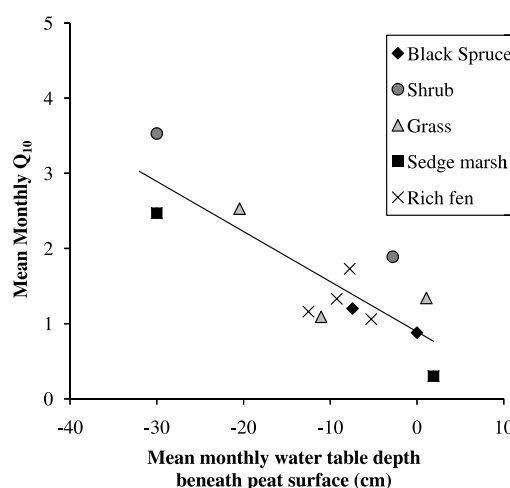


Figure 4. Effect of mean monthly water table position on mean monthly Q_{10} for all years (2007–2011) along the wetland gradient. Q_{10} was estimated using equation (2); only significant values ($p < 0.05$) are included. The linear regression across all points is described by the coefficients: intercept = 0.893 ± 0.192 , slope = -0.067 ± 0.013 , $F = 25.49$, $p = 0.0004$, $R^2 = 0.70$.

At the rich fen, soil temperature and seasonal thaw depth during our root respiration experiment (mid-July measurements only) explained 60% and 20% of the variation in ER respectively (figures 6(a) and (b)). We found that ER was not related to surface soil moisture (figure 6(c)) or water table position (not shown). The two communities differed in their relationships between ER and plant biomass. At the rich fen, there was a positive relationship between ER and root biomass, while at the sedge marsh this relationship was not significant (figure 6(d)). Conversely, there was a trend towards a positive relationship between VGA and ER at the marsh, but not at the rich fen (figure 6(e)).

4. Discussion

This study analyzes a 5-year dataset of ER across a wetland gradient of distinct vegetation communities varying

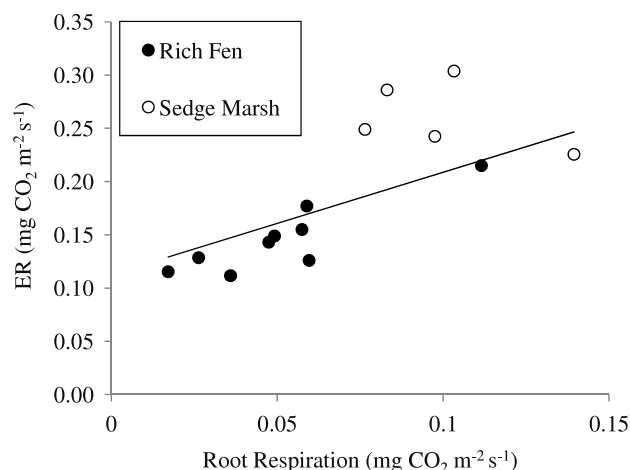


Figure 5. Relationship between ecosystem respiration and root respiration for the marsh and rich fens ($p = 0.0012$; $r^2 = 0.60$, slope = 1.44 ± 0.03 ; intercept = 0.09 ± 0.34).

in permafrost and soil moisture. Due to the lack of spatial replication within each community type (except the rich fen), we do not know how generalizable our results are to these community types in general. Because the wetland gradient encompasses environmental variation driven by long-term community assemblage, our results are likely to differ from shorter-term manipulation of environmental conditions in wetlands. For example, while short-term flooding in wetlands can enhance soil nutrient pools and stimulate ecosystem productivity, CO_2 transport, and respiration (cf Wyatt *et al* 2012), longer-term flooding and inundation often inhibits respiration due to anoxia. Overall, several of our hypotheses regarding environmental controls on ER were supported. As predicted, communities with permafrost on average had reduced ER relative to the communities without permafrost. Also as predicted, across the gradient ER peaked at intermediate soil thaw depths. Finally, because we found that mean ER and apparent Q_{10} values varied considerably between the sedge marsh and rich fen, two adjacent communities that lacked permafrost, we examined the contributions of root respiration to ER in these adjacent

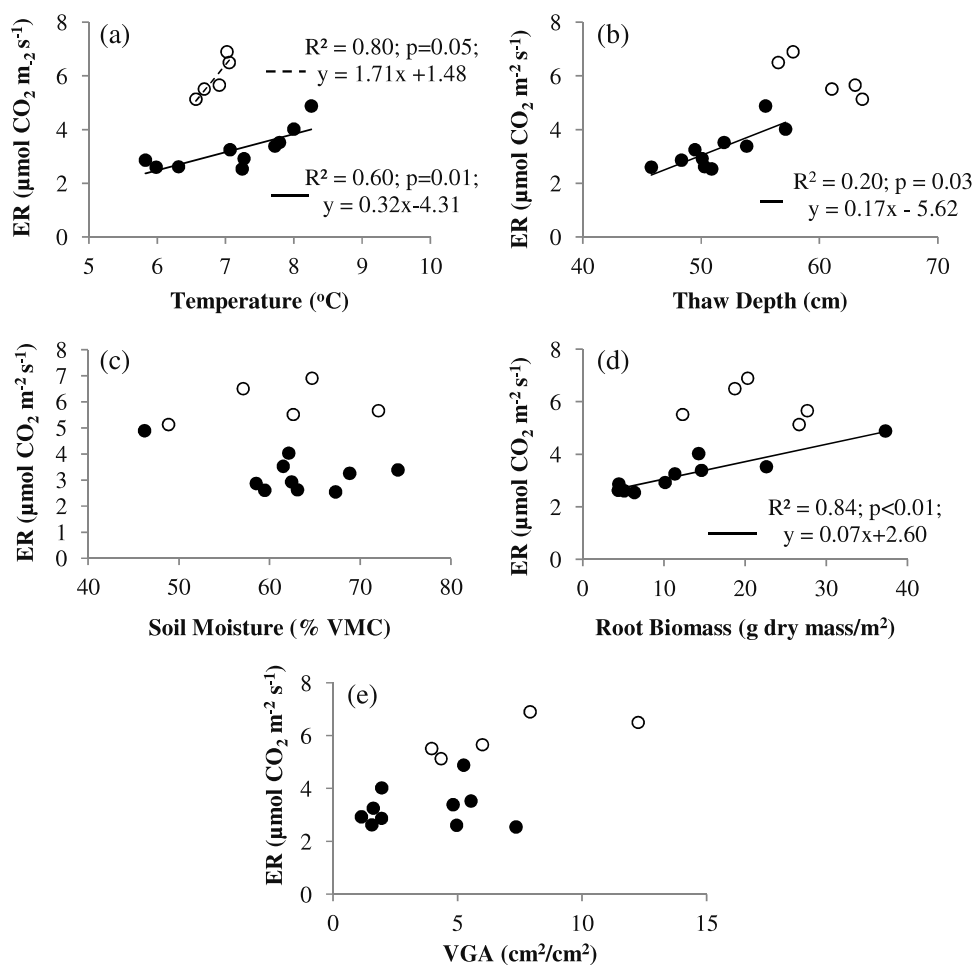


Figure 6. Relationship between ER and (a) soil temperature, (b) seasonal thaw depth, (c) soil moisture, (d) root biomass, and (e) vascular green area (VGA) at the marsh and rich fen during our root respiration experiments (mid-July). Data for the sedge marsh are shown in open circles; rich fen data are shown in closed circles. Model lines and statistics are shown only for significant relationships (dashed line for marsh, solid line for rich fen data).

systems. We found that despite differences in mean root respiration rates, root respiration contributed similarly to ER in both communities. These findings have implications for modeling C fluxes in high latitude wetlands, and are described in more detail below.

4.1. Thaw depth, soil temperature, and ecosystem respiration

We predicted that ER would peak at intermediate soil thaw depths across the wetland gradient, given that soil saturation can result from both shallow and deep soil thaw depth scenarios, potentially suppressing both heterotrophic and autotrophic respiration by limiting oxygen and nutrient availability. Our results supported this prediction, as across wetland communities we observed a unimodal relationship between soil thaw depth and ER. Estimates of uP (optimal soil thaw depth supporting maximum ER) were similar for relationships between thaw depth and instantaneous ER (63 ± 34 cm) and mean monthly ER (51 ± 4 cm; figure 1).

The presence of soil ice (seasonal ice or permafrost) also can govern ER fluxes by regulating soil temperature and access to unfrozen substrate. As a result, we predicted that within each community, there would be positive relationships between ER and soil depth. Though frost depth and soil temperature were positive correlated, we found no evidence of linear relationships between frost depth and ER within any of the communities (figure 2). Instead, within each community, the highest ER tended to occur either at intermediate or shallow soil thaw depths. Relationships between ER and soil thaw depth can be confounded by the seasonal development of vegetation, given that plant respiration (aboveground or belowground) is an important contributor to ER. Without specific data on seasonal changes in biomass or leaf area, we were not able to test how vegetation influenced ER across the gradient, and whether small ER values under deep thaw conditions were due simply to vegetation senescence. Examining the relationship between ER and soil thaw depth across three seasonal periods (figure 1) clearly shows evidence of some, but not complete, confoundment between season and thaw depth.

Finally, we predicted that permafrost communities would have lower ER but greater temperature sensitivity than communities lacking in surface permafrost. Across the gradient, the black spruce and shrub communities with shallow permafrost (maximum seasonal thaw depth of less than 1 m) had colder surface soils (between 1 and 4°C colder during the growing season) than the communities with maximum seasonal thaw depth greater than 1 m (grass, sedge marsh, and rich fen). Likely at least in part due to these differences in soil temperature, ER in the black spruce and shrub communities was lower than the other communities averaged across study years.

While both our mean ER and apparent Q_{10} values generally fall within the range of reported values for northern wetlands (Raich and Schlesinger 1992, Laffleur *et al* 2005, Bronson *et al* 2008), our results clearly show that the wetland communities diverged in the functional relationship between ER and soil temperature. Monthly ER in the black

spruce, shrub, grass, and marsh communities fell along the same relationship with soil temperature, corresponding to a gradient-wide apparent Q_{10} of 5.2 (5.6 based on mid-season data only, excluding periods of green-up or plant senescence). This Q_{10} is higher than many previous soil respiration studies, but is not atypical for boreal systems (Bronson *et al* 2008). The Q_{10} of ER was smaller in the rich fen, which could simply reflect decreasing temperature sensitivity with increasing temperatures (Lloyd and Taylor 1994). This also could indicate that other factors that co-vary with soil temperature along this gradient could be posing constraints on respiration processes. Increasing substrate quality (i.e. decreasing soil C/N/P ratios) also can result in lower temperature sensitivities due to lower activation energies for metabolic processes (Davidson and Janssens 2006). However, surface soil C/N ratios along this gradient have been shown to be lowest in the sedge marsh and not the rich fen (see Waldrop *et al* 2012; sedge marsh termed 'emergent fen' in that study), which is not consistent with the observed lower temperature sensitivity within the rich fen. Alternatively, soil saturation and anaerobiosis could reduce temperature sensitivities within the rich fen (Davidson and Janssens 2006). The rich fen had the highest soil moisture content (table 1), the shallowest average water table depth (Waldrop *et al* 2012), and the highest rates of CH₄ flux (Waldrop *et al* 2012) relative to the other vegetation communities along this gradient. These saturated and more anaerobic conditions could explain lower temperature sensitivities within the rich fen as oxygen constraints are placed on the microbial community. Moreover, we observed a strong negative relationship between water table position and apparent Q_{10} values across all communities (figure 3), showing a gradient-wide pattern of ER becoming increasingly sensitive to temperature with lower water table positions beneath the moss surface (drier). This pattern can be explained by (1) removal of anaerobic constraints on respiration as water table declines and Q_{10} increases, (2) seasonally warmer soils when water table depth is lowest and/or (3) deeper active regions of microbial activity accessing lower quality substrates and therefore producing higher apparent temperature sensitivities. These results indicate a complex interactive set of explanatory variables related to anaerobiosis, temperature, and substrate quality, but it is a complex behavior that can be captured within a simple ecosystem metric, water table depth.

Similar to trends in soil thaw depth, relationships between mean monthly ER and temperature can be influenced by the seasonal development of vegetation. However, two lines of evidence suggest that the cross-community Q_{10} value (figure 3) is robust to this seasonal confoundment. First, when we constrained our mean monthly model to periods of peak biomass (July and August; excluding periods of leaf-out and senescence), the gradient-wide Q_{10} value was not reduced (table 4). During this period, observed ER was much lower at the rich fen than at the other communities. Second, within each of the vegetation communities except the rich fen, mean monthly Q_{10} values tended to increase over time, with declines at the end of the growing season in some community types (table 5). At the rich fen, mean

Table 5. Estimates of Q_{10} (including standard errors) by month for each vegetation community type. Only significant models following equation (2) are shown.

Plot	Month	Q_{10}	SE	F	p
Black spruce	Jun	1.2	1.28	10.24	0.02
	Jul	0.88	0.4	33.14	0.0003
	Aug	5.78	6.02	31.51	0.03
Shrub	June	1.89	1	79.71	0.0001
	Aug	3.53	5.69	18.62	0.05
Grass	Jun	1.34	0.76	45.64	0.0006
	Jul	1.09	0.5	68.37	0.0001
	Aug	2.53	0.3	435.45	0.002
Sedge/Marsh	Jun	0.3	0.46	9.55	0.03
	Jul	2.47	12.22	14.54	0.01
Rich fen	Jun	1.06	0.2	115.93	0.0001
	Jul	1.73	0.36	128.37	0.0001
	Aug	1.16	0.28	125.01	0.0001
	Sept	1.33	0.57	86.9	0.0001

monthly Q_{10} varied little through the growing season, ranging from 1.1 ± 0.2 to 1.7 ± 0.4 . Averaged across all vegetation community types and years, mean seasonal Q_{10} peaked in July–August (mean $\pm$ SE of 4.9 ± 12.2), compared with May–June (of 1.2 ± 0.7) or September (of 1.3 ± 3.8).

These results have implications for modeling soil CO_2 fluxes from high latitude wetlands. We speculate from our collective results that ER was regulated by temperature across most of the wetland gradient, including all of the permafrost habitats. In the rich fen, soil conditions were warmer, likely driven by heat transfer of groundwater inputs, and temperature was less relevant to ER. This suggests that modeling CO_2 fluxes across a wide range of vegetation and permafrost conditions requires an understanding of this ‘tipping point’ where the system shifts from being mainly temperature-limited to being limited by other conditions such as oxygen.

4.2. Contributions of root respiration to ER

Ecosystem respiration is composed of both microbial and plant (above and belowground) respiration and thus to fully examine the environmental controls on ER we partitioned ER between these sources (belowground plant respiration only) within the sedge marsh and rich fen communities. While rates of plant and microbial activity are generally optimal at an intermediate level of soil moisture, these relationships may differ among these two groups such that microbial respiration may be more limited than plants at high soil moisture and plants may be more limited than microbes under dry conditions (Wickland and Neff 2007). For example, although saturated conditions can inhibit microbial respiration and also can cause plant stress due to reduced availability of oxygen and buildup of toxins in the root zone (Pezeshki 2001, Mitsch and Gosselink 2007), hydric plant adaptation has led to the development of large air spaces in the cortex of the rhizomes and roots, which allows the transport of O_2 to the roots, thus mitigating the impact of soil saturation on plant processes (Justin and Armstrong 1987, Armstrong *et al* 1991). The response of ER to changing water

availability will depend both on the response of autotrophic versus heterotrophic respiration as well as the characteristics of the vegetation community. Few studies have explicitly considered the sensitivity of these components of ER to changing moisture conditions in northern wetlands (Sulman *et al* 2012).

Our research site gave us a unique opportunity to examine variation in root respiration among different wetland communities, given that the highest and lowest mean ER was observed at the adjacent marsh and fen communities. We explored whether varying contributions of root respiration could account for these differences in ER. Our estimates of root respiration showed that root respiration was higher in the rich fen compared to the marsh ($0.003 \pm 0.0001 \mu\text{mol CO}_2 \text{ s}^{-1} \text{ g}^{-1}$ dry mass at the rich fen and $0.004 \pm 0.0002 \mu\text{mol CO}_2 \text{ s}^{-1} \text{ g}^{-1}$ dry mass at the marsh) and are slightly higher than estimates from an Alaskan lowland conifer forest (Ruess *et al* 2003). Our excised root respiration measurements may be higher than total intact root respiration rates because we selected for relatively young < 2 mm diameter roots, which have been shown to have higher respiration rates than older, larger diameter roots (Billings *et al* 1977; see Lawrence and Oechel 1983 and references therein). However, this bias would not be a strong factor in wetlands dominated by grasses and sedges, which exhibit more consistent root morphology. When root respiration is scaled to a m^2 basis, our flux estimates in the rich fen ($0.143 \pm 0.015 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) are significantly lower than the marsh ($0.262 \pm 0.015 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), and are similar to previous estimates for a boreal black spruce forest (Vogel *et al* 2005). Our experiment indicated that root respiration across the sedge marsh and rich fen communities contributed 14–62% (mean 40%) to ER. This agrees with other high latitude studies that have found that root respiration contributes approximately 40–60% of ecosystem respiration (Silvola *et al* 1996, Hanson *et al* 2000, Ruess *et al* 2003, Bond-Lamberty *et al* 2004, Griffis *et al* 2004, Crow and Wieder 2005). While fluxes of both root respiration and ER were higher at the marsh community than the rich fen, the fraction of ER that was root respiration was similar in both systems. Thus, ER fluxes in the rich fen likely are low relative to the other gradient communities because of both reduced autotrophic and heterotrophic respiration.

Despite similar levels of root biomass and VGA, we found a positive relationship between root biomass and ER at the rich fen but not the marsh. On the other hand, ER in the sedge marsh might be responding more to variation in aboveground vascular biomass than in the rich fen. Yet given the similar levels of plant biomass in the two communities, total ER in the rich fen does not appear to be constrained by low values of plant biomass, either aboveground or belowground. It seems more likely that high soil moisture is limiting both microbial respiration and plant belowground activity in the rich fen, likely through constraints on oxygen and nutrient availability.

Determining how sources of autotrophic respiration (aboveground or belowground) and heterotrophic respiration contribute to CO_2 flux or respond differently to environmental

variables is important for modeling studies predicting the fate of carbon in future scenarios with climate change. Our results show that ER in adjacent wetland communities with similar permafrost and soil moisture conditions can vary tremendously, and demonstrate different relationships with vegetation components. Direct measures of soil redox status or oxygen availability, nutrient availability, and CO₂ fluxes from different plant tissues would provide a stronger mechanistic understanding of variation in CO₂ fluxes from northern wetlands. This is particularly important given that increasing thaw depth and loss of permafrost are altering both soil environments and vegetation structure in northern wetlands.

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