

CONTROLS ON ECOSYSTEM RESPIRATION OF CARBON DIOXIDE ACROSS A  
BOREAL WETLAND GRADIENT IN INTERIOR ALASKA

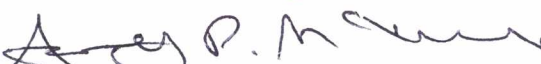
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CONTROLS ON ECOSYSTEM RESPIRATION OF CARBON DIOXIDE ACROSS A  
BOREAL WETLAND GRADIENT IN INTERIOR ALASKA

A  
THESIS

Presented to the Faculty  
of the University of Alaska Fairbanks

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**Abstract**

Permafrost and organic soil layers are common to most wetlands in interior Alaska, where wetlands have functioned as important long-term soil carbon sinks. Boreal wetlands are diverse in both vegetation and nutrient cycling, ranging from nutrient-poor bogs to nutrient- and vascular-rich fens. The goals of my study were to quantify growing season ecosystem respiration (ER) along a gradient of vegetation and permafrost in a boreal wetland complex, and to evaluate the main abiotic and biotic variables that regulate CO<sub>2</sub> release from boreal soils. Highest ER and root respiration were observed at a sedge/forb community and lowest ER and root respiration were observed at a neighboring rich fen community, even though the two fens had similar estimates of root biomass and vascular green area. Root respiration also contributed approximately 40% to ER at both fens. These results support the conclusion that high soil moisture and low redox potential may be limiting both heterotrophic and autotrophic respiration at the rich fen. This study suggests that interactions among soil environmental variables are important drivers of ER. Also, vegetation and its response to soil environment determines contributions from aboveground (leaves and shoots) and belowground (roots and moss) components, which vary among wetland gradient communities.

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## I. Introduction

### Introduction to Boreal Wetlands

The boreal forest region covers 18.5 million km<sup>2</sup> of the earth's surface across interior Alaska, Canada, Scandinavia, Russia, and parts of Mongolia and China. Wetlands, which are ecosystems with either permanently or seasonally flooded soils, represent a major boreal land cover class, occupying about 25% of the total boreal land area (Vitt 2006; Wieder and Vitt 2006). According to the Canadian wetland classification system, boreal wetlands include swamps, marshes, open water wetlands, bogs, and fens (Zoltai and Vitt 1995), with bogs and fens representing the most common boreal wetland types. These wetland types vary in hydrologic regime, water chemistry, and/or mineral material, all of which interact to control vegetation functional type and cover (Zoltai and Vitt 1995). Bogs and fens are peatlands, which are defined as wetlands that have accumulated more than 40 cm of peat. In general, peat accumulates in northern wetlands because plant primary productivity exceeds decomposition and other losses of soil organic matter such as fire combustion (Sharitz and Pennings 2006; Trumbore and Harden 1997). In general, the accumulation of peat in boreal wetlands is thought to be due primarily to slow decomposition rates that occur with cold, anoxic soil conditions (Sharitz and Pennings 2006). However, the poor organic matter quality of some peatland vegetation, particularly mosses, also contributes to peat accumulation rates (Turetsky et al. 2010).

While bogs and fens both accumulate peat, they vary in vegetation structure, productivity, and nutrient cycling. Bogs typically are nutrient poor, ombrotrophic systems that receive the majority of their nutrients through precipitation and dry fall (Sharitz and Pennings 2006). Bogs usually are dominated by *Sphagnum spp.*, which create acidity and inhibit nutrient availability due to their high cation exchange capacity. In North America, bogs often contain a sparse to moderate tree canopy, typically black spruce (*Picea mariana*). Fens often have higher nutrient availability than bogs, given that they are minerotrophic systems that receive nutrients through groundwater or surface flow in contact with mineral soils (Sharitz and Pennings 2006). Fens are very diverse,

and can be acidic with *Sphagnum* groundcover (poor fens) or alkaline with brown moss groundcover (rich fens). Fens also can be open (no trees) or forested, usually with black spruce or tamarack (*Larix laricina*).

Both in large wetland complexes in river floodplains across interior Alaska or in small valley bottom wetlands, vegetation composition is strongly regulated by the presence or absence of permafrost (Camill 1999). Frozen ground impedes the drainage of surface soils, and thus maintains saturated conditions that reduce rates of decomposition (Dingman and Koutz 1974; Ford and Bedford 1987; Kane et al. 2010; Roulet and Woo 1986). Permafrost in interior Alaska has been showing widespread evidence of thawing over the past few decades. Studies on the Tanana Flats in interior Alaska indicate that the extent of totally degraded permafrost has increased from 39 to 47% between 1949 and 1995 (Jorgenson et al. 2001). While this estimate is high compared to most other areas in central Alaska, similar rates of thaw have been noted in other isolated lowland areas such as the Innoko and Nowitna lowlands (Jorgenson et al. 2001; Osterkamp et al. 2000). Changes in hydrology associated with permafrost thaw, both in the wetlands themselves as well as in adjacent or hydrologically connected uplands, are influencing runoff into and drainage within Alaskan wetlands (Jorgenson and Osterkamp 2005). This has the potential to influence vegetation structure and both plant and soil processes such as ecosystem respiration (ER).

### **Ecosystem Respiration and Its Role in Peatland Function**

Ecosystem respiration is the process by which carbon dioxide (CO<sub>2</sub>) is released from a peatland. The balance between net C uptake and ER represents net ecosystem exchange (NEE), and determines whether an ecosystem is serving as a sink or source of CO<sub>2</sub>. There are two main sources of peatland ER (Charman 2002): microbial decomposition (heterotrophic respiration) and plant respiration (autotrophic respiration, which can include moss, leaf, stem, and root respiration). Studies have shown that a number of

variables regulate ER, including soil temperature, the type of vegetation present, the depth of the water table and/or soil moisture, and the seasonal thaw depth (Blodau 2002).

Ecosystem respiration has been shown to increase with temperature (Raich 1992; Silvola et al. 1996) in warming experiments (Chivers et al. 2009; Dorrepaal et al. 2009) and gradient studies (Myers-Smith et al. 2007). The  $Q_{10}$  values (i.e., the increase in soil  $CO_2$  production for each  $10^\circ C$  increase) of ER in peatlands tend to range from 2-3, but vary with peat depth and location (Blodau 2002). This suggests that warming will stimulate plant and microbial activity, and thereby increase the autotrophic and heterotrophic components of ER (Davidson et al. 2000). Increases in temperature also have been shown to increase vascular green area (VGA) and rates of photosynthesis in some studies (Wilson et al. 2006), but not in others (Chivers et al. 2009). Thus, whether warming will stimulate aboveground autotrophic respiration associated with photosynthesis responses is unclear.

ER is also sensitive to soil moisture and the depth of the water table, which both determine the availability of the oxygen ( $O_2$ ) in the peat column. As peat plateaus underlain with surface permafrost transition into collapse scar fens or bogs, soil moisture and water table position typically increase with inundation (Halsey et al. 1995; Turetsky and Wieder 2002; Turetsky et al. 2000). This decreases the availability of  $O_2$  and inhibits decomposition, as other electron acceptors such as sulfate (through sulfate reduction) and iron (through iron reduction) are less efficient than  $O_2$  (Wieder and Vitt 2006). While laboratory incubations of peat in general show higher soil  $CO_2$  fluxes with drier conditions (Lafleur et al. 2005), results from field studies are not consistent. Silvola et al. (1996) found that declining water table positions (i.e., drier conditions) increased soil  $CO_2$  flux, but that soil  $CO_2$  flux became less sensitive to change in water table below a water table position of 30 cm beneath the moss surface. Bubier et al. (1998) found that water table position was not a significant predictor of ER for daily fluxes, but became more important when predicting seasonal variation in monthly averaged ER. Some of this discrepancy could be because soil moisture and water table position are not always

correlated in peat soils. *Sphagnum* species, which are the main contributors to peat-formation in many boreal peatlands, rely on capillary transport to move water up from the water table to the surface of the moss where they photosynthesize (Strack and Price 2009). Certain species of *Sphagnum* are able to increase capillary rise by growing in tighter colonies, and therefore are able to maintain higher moisture as water tables are drawn down (Hayward and Clymo 1982; Strack and Price 2009; Titus and Wagner 1984). Thus, *Sphagnum* may create moist soil conditions and anaerobic hotspots for microbial activity even during drought periods, at least until the water table falls below the zone of capillary force and *Sphagnum* are no longer able to wick water upwards.

In most high latitude ecosystems, including wetlands, seasonal thaw depth is an important control on ER through its influence on both water table and soil temperature. The seasonal thaw depth is the portion of the soil profile above the permafrost that thaws and re-freezes annually (Hinzman et al. 2006). If soils become drier as the surface soil thaws in the summer due to increased sub-surface drainage (Hinzman et al. 2006), then ER will increase as more soil carbon is available for aerobic decomposition. The autotrophic component of ER may also increase in this situation, as plant productivity overall may increase with a greater rooting zone. In general, shallow thaw depths lead to colder and more saturated surface soils (Wickland et al. 2006) inhibiting both heterotrophic and autotrophic respiration. Thus, seasonal thaw depth in some ecosystems may be important to ER in the spring and early summer, but may become less important later in the growing season when other variables such as soil moisture become the primary determinant of ER (Wickland et al. 2006).

## **II. Brief Rationale for this Study**

Between 40-60% of the landscape in interior Alaska has poorly drained soils (Harden et al. 2001; Myers-Smith et al. 2007) and most of these soils are underlain by discontinuous permafrost (Hinzman et al. 2006). Permafrost temperatures in interior Alaska between the late 1980s and early 1990s have increased by 1.5 °C (Osterkamp & Romanovsky 1999; Myers-Smith et al. 2007) and evidence of permafrost thaw is being observed across

the landscape (Osterkamp & Romanovsky 1999). Both in areas with fairly stable permafrost and in areas without any surface permafrost, warming associated with climate change is expected to increase seasonal thaw depth (Goulden et al. 1998). As seasonal thaw depth increases, heterogeneity of soil processes will also increase and this will have implications for the carbon cycle.

Ecosystem respiration is influenced by a variety of biotic and abiotic factors, including the availability of O<sub>2</sub> in the soil, depth of the water table, the microbial activity present, soil temperature, type of vegetation present, and nutrients available for biological uptake (Blodau 2002). To examine how climate change is likely to alter ecosystem CO<sub>2</sub> release, previous studies have used experiments in the field (Chivers et al. 2009; Oechel et al. 1998; Updegraff et al. 2001) or in controlled laboratory conditions (Lafleur et al. 2005; Turetsky 2004; Wickland and Neff 2007) to manipulate one or more climate factors affecting plant respiration and/or decomposition. A limitation of such manipulations is they tend to implement treatments representing rapid and often drastic changes in climate rather than a gradual process of climate change (i.e, changed climate versus climate change). Studies with measurements conducted over seasons to years also emphasize fast ecosystem responses over slower processes such as succession (Fukami 2005; Muller 1998). Here I use an alternative approach, which is to examine controls on ER along an ecological gradient spanning variation in permafrost and vegetation characteristics from black spruce forest to wetter fen communities. 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).

### **III. Goals, Objectives, and Hypotheses:**

The overall goals of this study were to quantify growing season ecosystem respiration fluxes along a gradient of vegetation and permafrost in a boreal wetland complex, and to

evaluate the strength of factors that affect soil CO<sub>2</sub> release. I addressed the following objectives and hypotheses:

***Objective 1:*** Compare growing season ecosystem respiration among five communities along a vegetation gradient in the context of abiotic controls (soil temperature and seasonal thaw depth).

***Hypotheses:***

- i. Mean ER will primarily be responsive to variation in soil temperatures along the gradient regardless of variation in other variables such as soil moisture because decomposition and root respiration are both sensitive to changes in soil temperature. Thus, ER will be lowest in the cold lowland black spruce forest and highest in the warmer fen communities.
- ii. Communities with deeper seasonal thaw will have higher ER because of relationships between thaw depth and temperature, and because greater thaw depths expose more soil carbon to decomposition. Thus, ER will be lowest in the cold lowland black spruce forest and highest in the more thawed fen communities, and will vary as a function of total unfrozen organic soil depth.

***Objective 2:*** Evaluate the importance of root respiration to ecosystem respiration. To accomplish this objective, I performed an experiment to measure the importance of root respiration to total soil CO<sub>2</sub> flux in the communities along the gradient with the highest and lowest ER.

***Hypothesis:***

- i. Root respiration will be higher in warmer communities with greater seasonal thaw depth for root growth because root respiration is sensitive to changes in soil temperature.

**IV. Methods****Description of Study Site and the Gradient Design**

Data for this study were collected at the Alaskan Peatland Experiment (APEX) sites located near the Bonanza Creek Experimental Forest approximately 35 km southwest of Fairbanks, Alaska, USA (64.82 °N, 147.87 °W) on the Tanana river floodplain (Chivers et al. 2009). The mean annual air temperature for the Tanana River Valley ranges from -5 °C to -7 °C and mean annual precipitation is between 215 and 300 mm (Hinzman et al. 2006).

Sampling was conducted along a soil thermal/soil moisture vegetation gradient that spans a spectrum of vegetation, permafrost, and organic soil conditions. The gradient is composed of five communities that extend from the toe slope of the adjacent uplands to wetland ecosystems. The gradient is hydrologically connected to ground water flow that runs from the uplands towards the nearby Tanana River. The five communities include:

**Black spruce:** A black spruce-dominated forest with *Sphagnum* and feather moss species in the ground layer. The organic layer depth is  $21 \pm 2$  cm (Waldrop et al. 2012). The surface soil is relatively dry with percent volumetric moisture content (VMC) of  $15.04 \pm 3.10$  and cold in temperature with an average soil temperature at 10 cm of  $2.8 \pm 0.50$  °C (Table 1.1). The maximum seasonal thaw depth is 62.2 cm (Table 1.1).



**Table 1.1** Dominant species and mean soil temperature (°C) at 10 cm, soil moisture (% VMC) at 5 cm, and seasonal thaw depth (cm) for each community along the wetland gradient.

	Dominant Species	Soil Temperature	Soil Moisture	Maximum Seasonal Thaw Depth
<b>Black Spruce</b>	<i>Picea mariana</i> , <i>Sphagnum spp.</i> , <i>Feather moss spp.</i>	2.8±0.50	15.04±3.10	62.2
<b>Shrub</b>	<i>Salix spp.</i> , <i>Betula spp.</i> , <i>Sphagnum spp.</i>	3.55±0.31	56.91±8.25	92.0
<b>Grass</b>	<i>Calamagrostis canadensis</i>	4.6±0.58	65.95±7.94	120.6
<b>Sedge/Forb Fen</b>	<i>Equisetum fluvitile</i> , <i>Carex spp.</i> , <i>Sphagnum spp.</i> , <i>Brown moss spp.</i>	5.2±0.40	72.17±7.29	>152
<b>Rich Fen</b>	<i>Equisetum fluvitile</i> , <i>Carex spp.</i> , <i>Potentilla polustris</i> , <i>Sphagnum spp.</i> , <i>Brown moss spp.</i>	8.6±0.22	83.88±1.56	>152

Shrub: A shrub-dominated ecosystem with willow (*Salix spp.*), birch (*Betula spp.*) and Sphagnum moss species (Table 1.1). The organic layer depth is  $30 \pm 15$  cm (Waldrop et al. 2012). In comparison to the black spruce community, this ecosystem has warmer (average soil temperature at 10 cm of  $3.55 \pm 0.31$  °C) and wetter (average percent VMC of  $56.91 \pm 8.25$ ; Table 1.1) soils. The maximum seasonal thaw depth is 92.0 cm (Table 1.1).

Grass: A tussock grass (*Calamagrostis canadensis*) dominated ecosystem (Table 1.1). The organic layer depth between tussocks is  $29 \pm 22$  cm (Waldrop et al. 2012). This plot has warmer and wetter soils than the shrub ecosystem with an average soil temperature at

10 cm of  $4.6 \pm 0.58$  °C and an average percent VMC of  $65.95 \pm 7.94$  (Table 1.1). The maximum seasonal thaw depth is 120.6 cm (Table 1.1).

Sedge/Forb Fen: A sedge and forb fen dominated by *Equisetum* (*Equisetum fluvitile*) and *Carex* species as well as *Sphagnum* and brown moss species (Table 1.1). The organic layer depth is  $16 \pm 1$  cm (Waldrop et al. 2012). This plot has warmer and wetter soils than the grass ecosystem with an average soil temperature at 10 cm of  $5.2 \pm 0.40$  °C and an average percent VMC of  $72.17 \pm 7.29$  (Table 1.1). The maximum seasonal thaw depth is greater than 152 cm (Table 1.1).

Rich Fen: An open rich fen dominated by *Equisetum* (*Equisetum fluvitile*), *Carex* species, and *Potentilla* (*Potentilla polustris*) as well as *Sphagnum* and brown mosses (Table 1.1). The organic layer depth is  $92 \pm 12$  cm (Waldrop et al. 2012). Soil temperature is warmer and soil moisture is higher in general than at the forb/sedge ecosystem with an average soil temperature at 10 cm of  $8.6 \pm 0.22$  °C and an average percent VMC of  $83.88 \pm 1.56$  (Table 1.1). The maximum seasonal thaw depth is greater than 152 cm (Table 1.1).

#### **Atmospheric and Soil Environmental Variables:**

Air temperature, relative humidity, and precipitation data were collected at the APEX sites continuously using CR10X data loggers (Campbell Scientific Inc., Logan, UT) and are available in the Bonanza Creek LTER data archive (Table 1.2).

**Table 1.2** Growing season (June-August) climate data from 2007-2010 for the floodplain of the Bonanza Creek Long Term Ecological Research Program. Air temperature was measured at 150 cm above the soil surface.

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

At each community, soil environmental variables were measured either continuously or manually during measurements of ER fluxes. Soil temperatures were measured at each community continuously using temperature thermistors at various depths in the soil profile (0 cm, 2 cm, 10 cm, and 25 cm depth below the surface) and logged using CR10X data loggers (Campbell Scientific Inc., Logan, UT). Soil temperatures were also measured manually at 10 cm concurrently with each ecosystem respiration flux using manual temperature thermistors. Soil moisture was measured continuously at each plot at various depths (5 cm, 25 cm, 50 cm) using CS615 and CS616 TDR soil moisture probes (Campbell Scientific Inc., Logan, UT). I calibrated the TDR probes using the method for organic soils outlined in Bourgeau-Chavez et al. (2010). Surface soil moisture also was measured manually concurrently with each ecosystem respiration flux using a ThetaProbe soil moisture sensor (Delta-T Devices, Cambridge, England) inserted 10 cm vertically into the surface organic layer. Water table was measured manually at each community with each flux using shallow wells placed in the peat surface. Seasonal thaw depth was measured by inserting a tile probe into the peat each time a flux was measured.

Analysis of soil environmental variables across ecosystems and years at the gradient was conducted using a repeated measures analysis of variance and Tukey's post hoc comparison of means (SAS Proc Mixed).

## Ecosystem Respiration Fluxes

Ecosystem respiration fluxes were measured at each community along the gradient during the growing season (May to September) approximately every two weeks from 2007-2011. One gas flux collar (constructed of galvanized steel) was permanently installed into the surface soils of each community except at the rich fen, where three gas flux collars were installed. At the start of each gas flux measurement, a clear gas flux chamber constructed of a 0.31cm aluminum frame with Teflon siding (American Durafilm, Holliston, MA) was placed on each gas flux collar. The chamber had an area of 0.3721 m<sup>2</sup> and a volume of 0.277 m<sup>3</sup> (226.981L), and a removable Lexan top to allow the chamber to be flushed between flux measurements. The chamber was covered with a dark shroud to block any PAR from entering the chamber (Chivers et al. 2009). I used a PP-systems EGM-4 infrared gas analyzer (IRGA, Amesbury, Massachusetts) to measure CO<sub>2</sub> concentrations inside the chamber every 1.6 seconds for 2-3 minutes (Chivers et al. 2009). After each 2-3 minute flux, the chamber was removed from the collar for several minutes to allow headspace conditions to return to ambient concentrations before beginning the next flux. Temperature, relative humidity, and PAR were recorded continuously during flux measurements inside the chamber using a PP-systems TRP-1 sensor attached to the inside of the chamber. A CO<sub>2</sub> flux (μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>) was calculated from the slope of the linear relationship between time and the CO<sub>2</sub> headspace concentration.

To analyze differences in mean ER across the spruce, shrub, grass, forb/sedge, and rich fen communities and across study years (2007-2011), I used a repeated measures analysis of variance (ANOVA) and Tukey's post hoc comparison of means (SAS Proc Mixed). The unimodal dependence of ER, including both autotrophic and heterotrophic respiration, on seasonal thaw depth (F) was modeled as:

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

where  $R_{\max}$  is maximum ER when seasonal thaw depth is optimal for plant and heterotrophic respiration,  $uR$  is the optimal seasonal thaw depth for respiration (modification from Chivers et al. 2009), and  $tR$  is a measure of the width of seasonal thaw depth amplitude (Chivers et al. 2009; Tuittila et al. 2004). The temperature dependence of ER was modeled as:

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

where  $A$  is the ER at 0 °C,  $Q_{10}$  is the temperature dependence of ER, and  $T$  is the soil temperature at 10 cm below the peat surface (Chivers et al. 2009). Proc NLIN in SAS was used from each community along the gradient to model ER.

### **Root Respiration Fluxes and Aboveground Vegetation Measurements**

To determine the contribution of root respiration to ecosystem respiration, two root experiments were conducted during the 2010 and 2011 field seasons. The first experiment was conducted in 2010 in the rich fen. I installed five ER flux collars at this community and measured ER fluxes for each collar following the methods outlined above (Ecosystem Respiration Fluxes). This was repeated daily for a two-week period. At the end of the 2-week flux campaign, the percent cover of mosses and vascular vegetation was visually estimated inside each of the collars. A 10 cm x 10 cm aboveground biomass sample was randomly harvested inside each collar. I also collected stem density inside each collar, and measured leaf area on all of the species found within the collar to measure vascular green area (VGA; m<sup>2</sup> of vascular leaf area/m<sup>2</sup>). Root respiration was then measured on the three dominant vascular species (*Carex*, *Equisetum*, *Potentilla*) within each collar by destructively harvesting the plants and picking all fine roots. Fine roots were placed inside of a 5-cm diameter root cuvette (Burton et al. 2002) and a flux was measured using the EGM-4 infrared gas analyzer, which measured the CO<sub>2</sub> concentration inside of the chamber every 1.6 seconds until concentrations reached

around 500 parts per million (ppm). This took 5-10 minutes. I also collected temperature data from inside the cuvette to standardize all fluxes to the same soil temperature. Roots were then placed in a cooler and transported back to the lab where they were weighed under field moisture, dried at 65 °C for 24 - 48 hours, and then reweighed to determine the moisture content.

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. Once back in the lab, cores were cut in half length-wise. Half of the core was analyzed for bulk density and the other half of the core was picked of all fine roots to obtain a root biomass (g biomass/m<sup>2</sup>) estimate. A soil profile description (USGS protocol; <http://carbon.wr.usgs.gov/protocols.html>) also was conducted on each of the cores. Soil horizons were described as live moss, dead moss fibric, mesic, and humic organic soil horizons. Root abundance (mean roots per square decimeter) and decomposition of plant materials in the soil were also noted. I conducted this experiment as a pilot study in the rich fen in 2010. Because my analyses showed that among the five communities, mean ER estimates were highest at the forb/sedge fen and lowest at the rich fen, I repeated this experimental design in both of these communities in 2011. For the 2011 experiment, I installed five new collars at the rich fen and also installed five collars at the sedge/forb fen, and repeated the methods outlined for the 2010 experiment.

Root respiration fluxes were standardized to a g/m<sup>2</sup> basis by using root biomass estimates from the soil cores collected within each flux collar. Root respiration was also standardized to the average soil temperature during flux measurements to account for differences in temperature between the soil (collected at 10 cm using temperature thermistors) and the chamber (collected using a temperature thermistor in the chamber). I analyzed root respiration as a predictor of ER using a linear regression (SAS Proc Glim).

## V. Results

### Soil Environmental Variables along the Gradient

I analyzed the effects of community, year, and a community x year interaction on soil temperature (10 cm depth), soil moisture, seasonal thaw depth, and water table position.

All environmental variables varied by a community x year interaction (Table 1.3).

**Table 1.3** Results of a repeated measures analysis of variance (ANOVA) analyzing the effects of year, community, and year x community interactions on ecosystem respiration, soil temperature, soil moisture, water table depth, and seasonal thaw depth along the gradient.

	Effect	df	<i>F</i>	<i>P</i>
ER	Year	4	1.74	0.1396
	Community	4	19.23	<0.0001
	Year x Community	15	2.13	0.0082
Soil Temperature	Year	4	6.87	<0.0001
	Community	4	58.14	<0.0001
	Year x Community	15	5.01	<0.0001
Soil Moisture	Year	4	11.98	<0.0001
	Community	4	23.68	<0.0001
	Year x Community	9	2.57	0.0077
Water Table	Year	4	9.71	<0.0001
	Community	4	1.68	0.1547
	Year x Community	14	6.80	<0.0001
Seasonal Thaw	Year	4	5.33	0.0004
	Community	4	20.53	<0.0001
	Year x Community	15	6.24	<0.0001

In general, soils were colder and drier in the black spruce and shrub communities and were warmer and wetter in the open fen communities. These general patterns in soil conditions across the gradient were consistent among sampling years with only a few exceptions. For example, in 2011, the shrub community had warmer surface soils than

the grass community. Across most study years, seasonal thaw depth was shallowest at the black spruce community and increased in depth along the gradient into the more open fen communities. In 2008 and 2009, when the general study region experienced a severe natural flood, the sedge/forb and rich fen communities had much deeper seasonal thaw depths compared to the other years.

Across all communities and years, soil temperature was positively correlated with seasonal thaw depth, soil moisture, and water table position (Table 1.4).

**Table 1.4** Results of correlation analyses among environmental predictors across all communities as well as for each community. Only significant results ( $p < 0.05$ ) are shown along with an indication of whether the correlation was positive (+) or negative (-) and an  $R^2$  value.

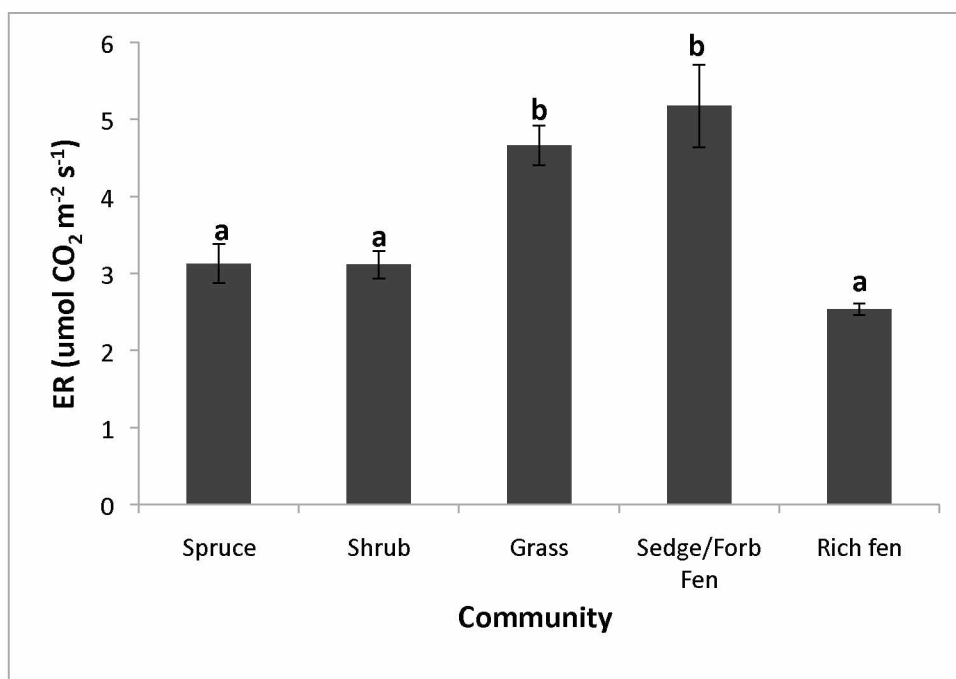
	Seasonal thaw	Soil temperature	Soil moisture	Water table
Seasonal thaw				
Soil temperature	All (+), 0.38; Shrub (+), 0.17; Sedge/forb (+), 0.32; Rich fen (+), 0.40			
Soil moisture	Black spruce(-), 0.35; Shrub (-), 0.42; Grass (-), 0.28; Sedge/forb (-), 0.27;	All (+), 0.17; Rich fen (+), 0.11		
Water Table	Shrub (-), 0.42; Grass (-), 0.50; Sedge/forb (-), 0.35; Rich fen (+), 0.19	All (+), 0.06; Sedge/forb (-), 0.31; Rich fen (+), 0.30	All (+), 0.30; Shrub (+), 0.22 ; Grass (+), 0.52; Sedge/forb (+), 0.72; Rich fen (+), 0.52	



In the rich fen and the shrub, grass, and sedge/forb communities, surface soil moisture was positively correlated with water table position (Table 1.4). However, water table and soil temperature were negatively correlated at the sedge/forb community (Table 1.4).

### Ecosystem Respiration

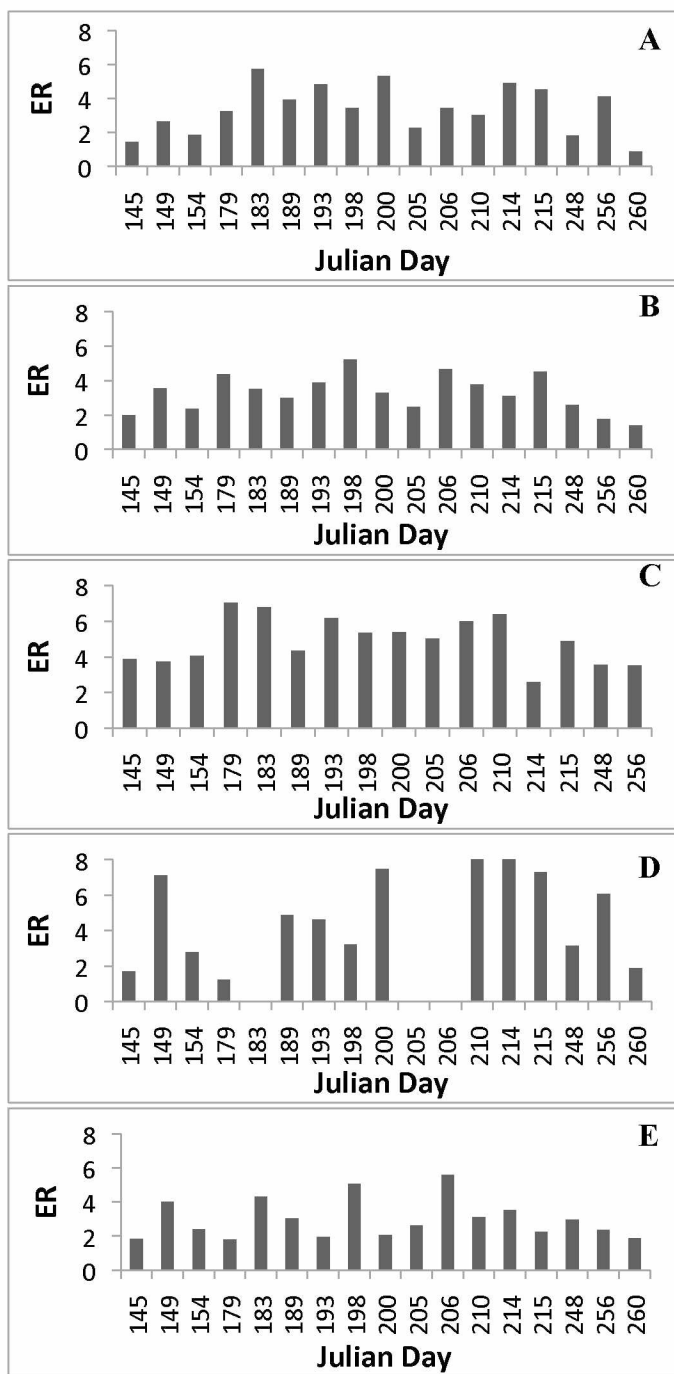
I analyzed the effects of community, year, and a community x year interaction on instantaneous ER. Instantaneous ER varied by a community x year interaction (Table 1.3). Averaged across all sampling years, ER was higher in the forb/sedge and grass communities than in the rich fen, black spruce, and shrub communities (Figure 1.1).



**Figure 1.1** Mean ecosystem respiration ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) for each community along the gradient from 2007-2011. Data are means  $\pm$  1 SE.

In general, ER was highest in the sedge/forb fen, and lowest in the rich fen. Across study years, the black spruce community had higher ER on average than the shrub community in 2009 and 2010, but this pattern was reversed in the other study years. Across years, the black spruce, shrub, grass, sedge/forb, and rich fen communities had coefficients of variation in ER of 45%, 33%, 32%, 53%, and 45% respectively. So while the forb/sedge community had the highest mean ER fluxes across years, fluxes in this community also had the highest interannual variation relative to the other four communities.

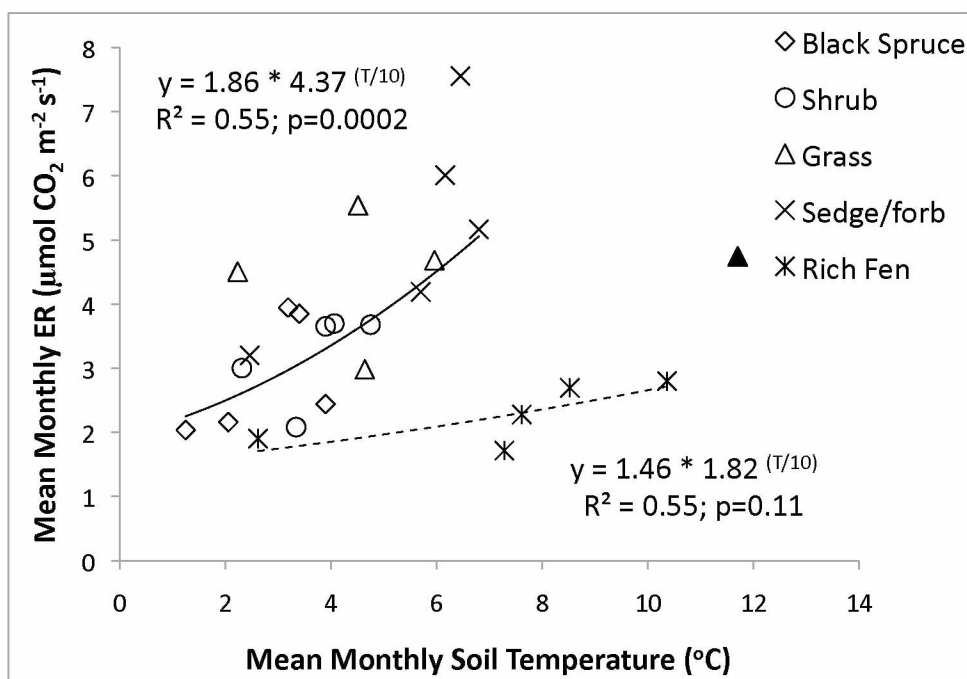
Across communities, ER generally was highest during peak biomass when thaw depth and soil temperature were also at maximum (in late July around Julian day 210) (Figure 1.2).



**Figure 1.2:** Daily ecosystem respiration ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) averaged across years (2007-2011) at five communities as a function of Julian Day. **A.** black spruce, **B.** shrub, **C.** grass, **D.** sedge/forb, **E.** rich fen.

The sedge/forb community, however, seemed to have a maximum ER a few days later than the other communities.

Across communities, mean monthly ER increased with mean monthly temperature, though there were differences in how the five communities responded to temperature. Data from the black spruce, shrub, grass, and sedge/forb fen communities appeared to follow a single exponential relationship between mean monthly ER and soil temperature (Figure 1.3).



**Figure 1.3:** Non-linear relationships between mean monthly temperature and mean monthly ER for all years measured (2007-2011) along the wetland gradient. The relationship found at the rich fen only is shown as the dotted line and the relationship across the other communities is shown as the solid line. The grass outlier is depicted as the shaded in triangle. Lines were fitted to the data using equation 2.

On the other hand, there was a non-significant nonlinear relationship between mean monthly ER and mean monthly temperature in the rich fen (Figure 1.3).

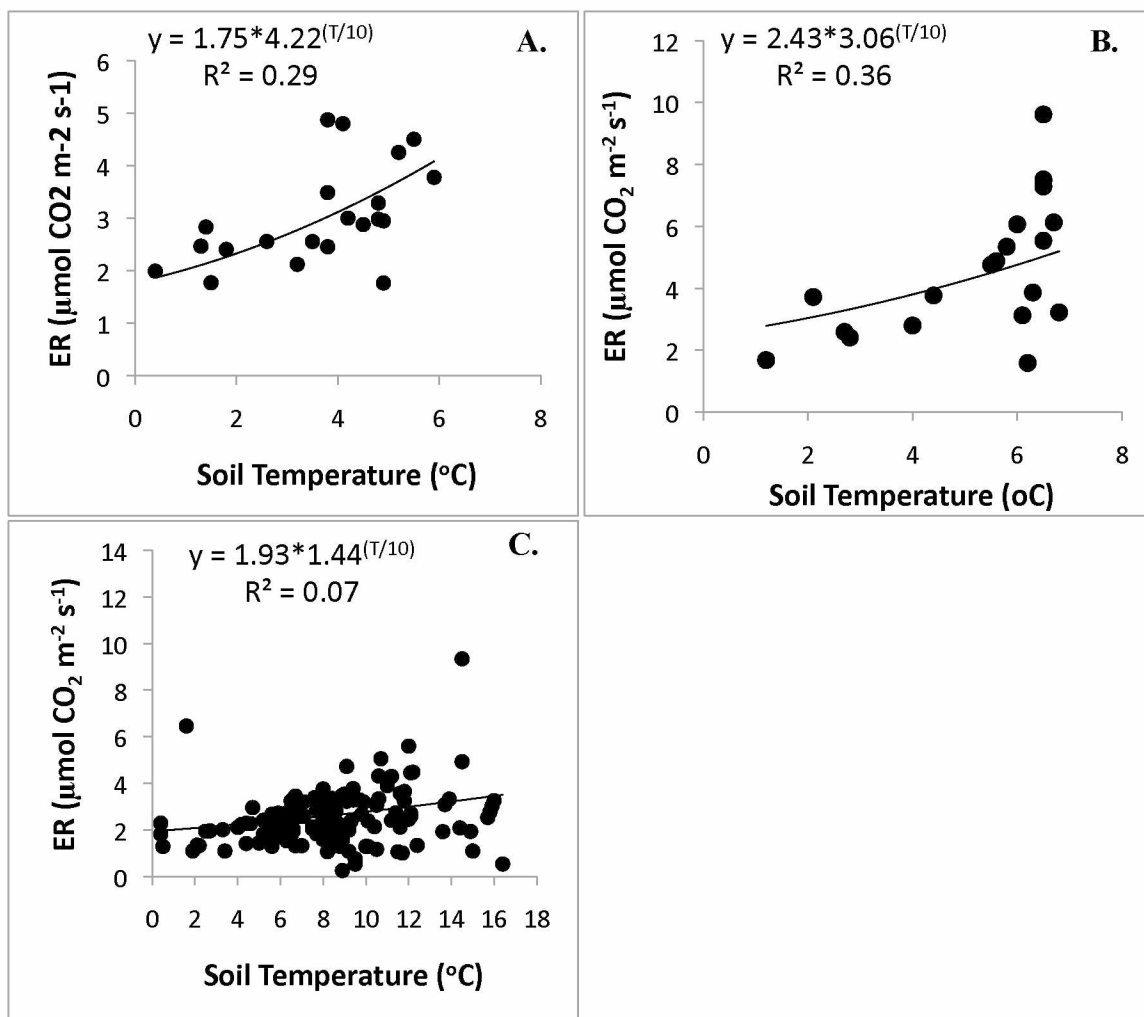
The difference in slopes among these two functional relationships suggests that ER in the rich fen was less sensitive to variation in monthly temperature than the other four communities. I identified an outlier for the grass community that represented a very low ER value for high soil moisture levels (greater than 99%). This outlier was removed from the analysis portrayed in Figure 1.3.

I found few relationships between instantaneous ER and environmental variables among the five communities. There were significant exponential relationships between instantaneous ER and soil temperature at the shrub and sedge/forb communities (Table 1.5; Figure 1.4).

**Table 1.5** Results of non-linear models analyzing the dependence of ecosystem respiration on seasonal thaw depth and soil temperature at 10 cm (equations 1 and 2).

	$R_{\max}$ ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )	$uR$ (cm)	$tR$ (cm)	$p$	$A$ ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )	$Q_{10}$	$p$
Black Spruce	3.87±0.37	41.50±2.65	19.41±3.13	0.13	2.52±0.52	1.32±0.77	0.42
Shrub	3.48±0.34	51.08±4.92	36.34±8.28	<b>0.03</b>	1.75±0.34	4.22±1.95	<b>0.01</b>
Grass	DNC	DNC	DNC	DNC	4.47±0.57	0.88±0.24	0.23
Forb/Sedge	6.28±0.95	78.77±16.99	36.97±11.9	0.96	2.43±0.94	3.06±2.13	<b>0.001</b>
Rich Fen	3.09±0.33	162.9±132.9	193.6±176.1	0.66	1.93±0.17	1.44±0.13	<b>0.002</b>

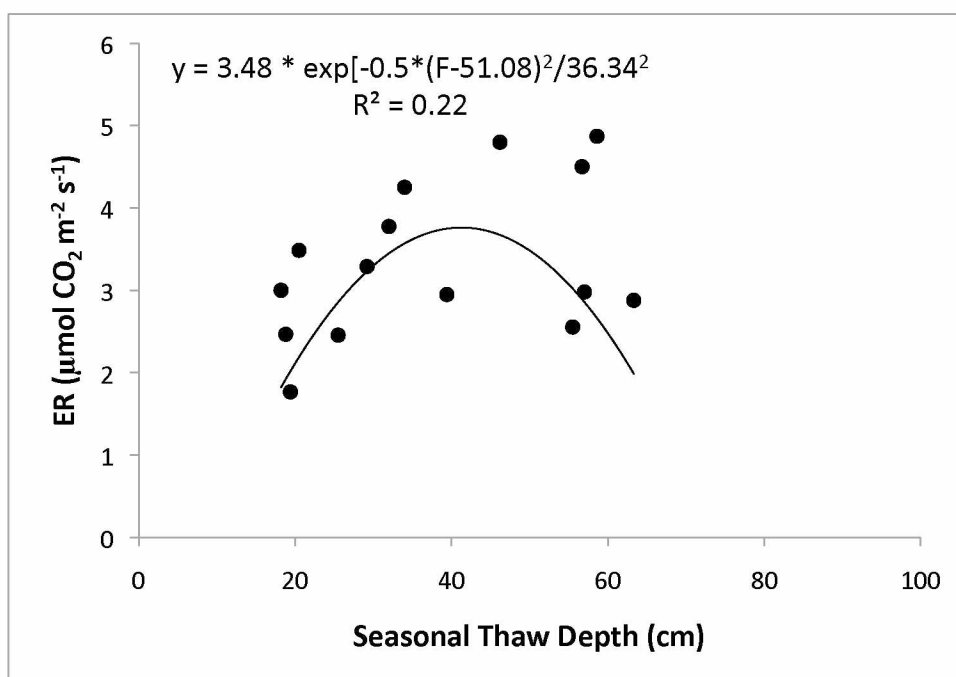
\*Significant relationships in bold.



**Figure 1.4:** Relationships between instantaneous estimates of ecosystem respiration ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) from chamber measurements and soil temperature ( $^{\circ}\text{C}$ ) at the time of chamber measurement for the **A.** shrub and **B.** sedge/forb, and **C.** rich fen communities. All lines fitted to the data using equation 2.

I also found a very weak significant exponential relationship between instantaneous ER and soil temperature and the rich fen (Table 1.5; Figure 1.4). The rich fen had a lower slope, indicating a lower sensitivity to soil temperature relative to the shrub community, which is in agreement with my analysis of monthly fluxes.

There were few relationships between instantaneous ER and soil thaw depth (Table 1.5). I observed a significant relationship only at the shrub community. This relationship was quadratic, suggesting that ER peaked at a thaw depth of approximately 40 cm beneath the moss surface (Figure 1.5).



**Figure 1.5:** Relationship between seasonal thaw depth (cm below peat surface) and instantaneous estimates of ecosystem respiration ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) at the shrub community. Line was fitted to the data using equation 1.

### Contributions of Root Respiration to ER

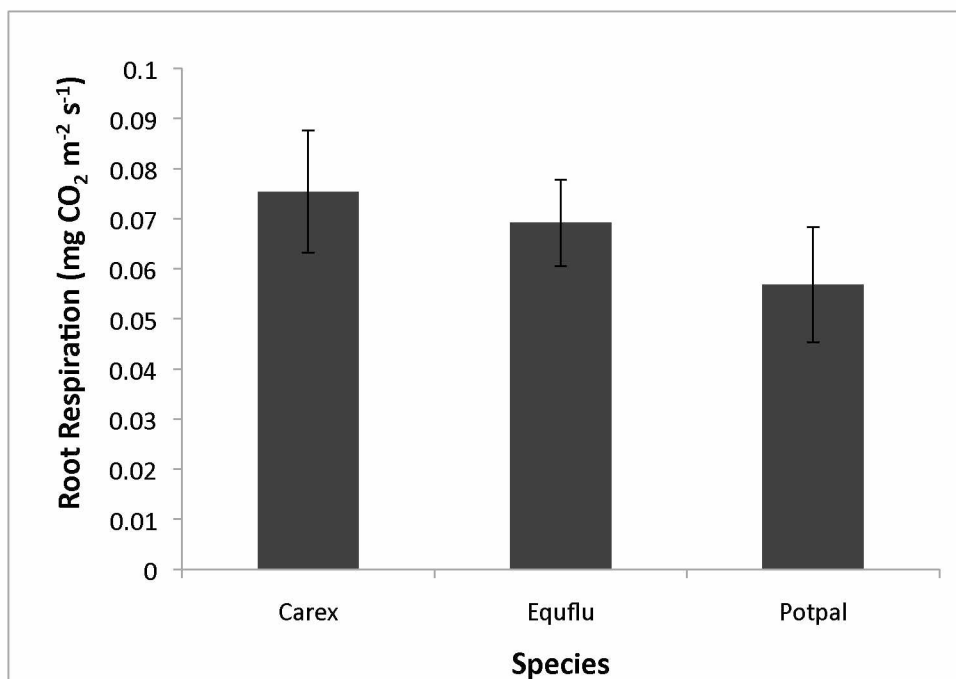
I analyzed the contributions of root respiration to ER at the sedge/forb and rich fen communities by measuring ER and root respiration rates in the same gas flux collars during peak biomass. ER fluxes averaged by collar during the experimental campaigns ranged from 0.112-0.215  $\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  at the rich fen and ranged from 0.225-0.304  $\text{mg}$

$\text{CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  at the sedge/forb fen. Averaged across collars, mean ER flux ( $\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) was  $0.143 \pm 0.015$  at the rich fen and  $0.262 \pm 0.015$  at the sedge/forb fen.

Mean root fluxes ( $\mu\text{mol s}^{-1} \text{ g}^{-1}$ ) were  $0.003 \pm 0.001$  at the rich fen and  $0.004 \pm 0.00002$  at the sedge/forb fen. Average root biomass was  $494.13 \pm 281.72 \text{ kg/m}^2$  at the rich fen and  $605.15 \pm 123.38 \text{ kg/m}^2$  at the sedge/forb fen. I used these root biomass data to scale root respiration fluxes to a  $\text{m}^2$  basis. Mean root fluxes ( $\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) were  $0.059 \pm 0.02$  at the rich fen and  $0.095 \pm 0.007$  at the sedge/forb fen.

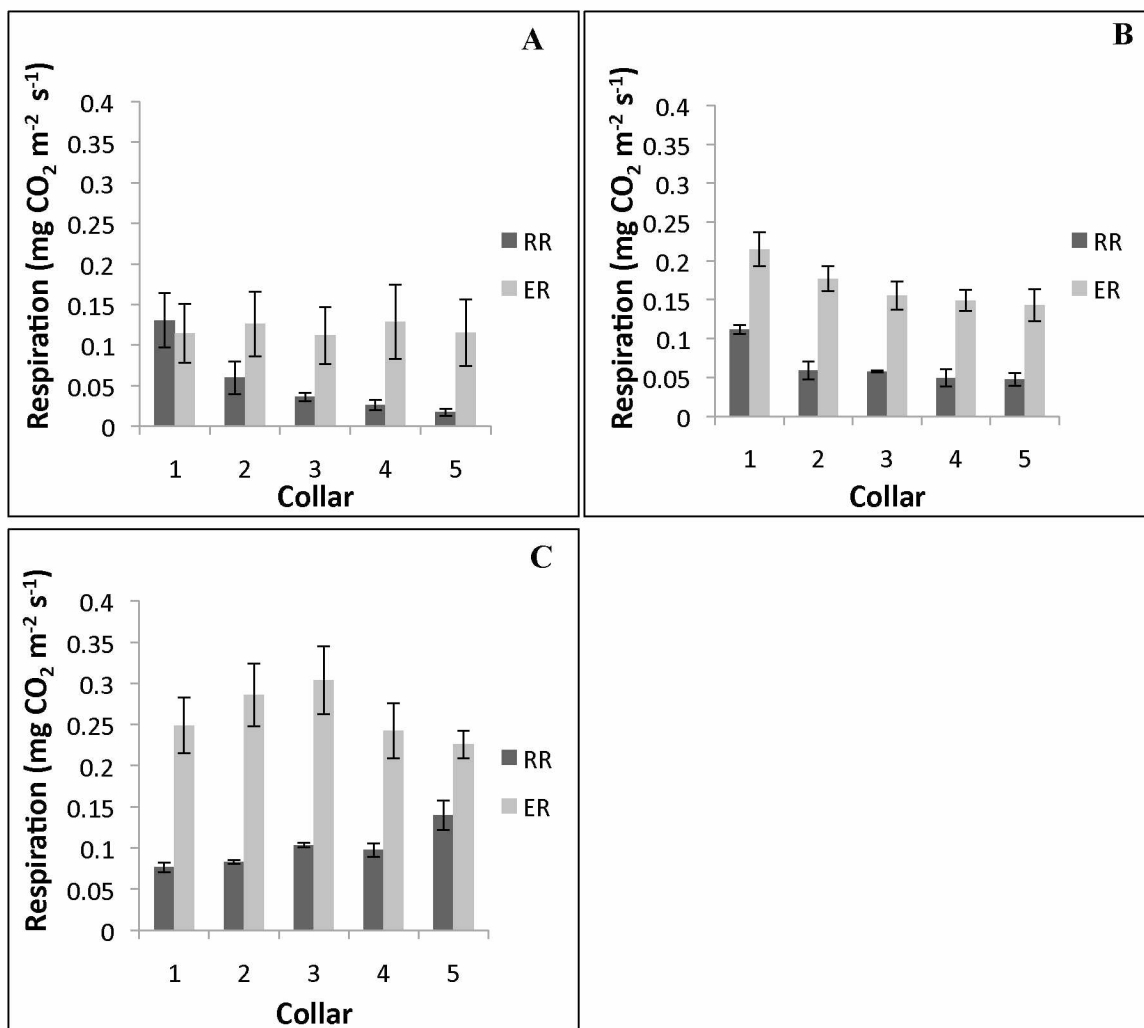
On a per  $\text{m}^2$  scale, root respiration did not vary significantly among dominant vascular species, however in general, *Carex spp.* tended to have higher respiration than *Potentilla polustris* (Figure 1.6)





**Figure 1.6:** Mean root respiration rates ( $\text{mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) between dominant species at the rich fen and sedge/forb fen. Dominant species include *Carex spp.* (Carex), *Equisetum fluvitile* (Equflu), and *Potentilla palustris* (Potpal). Data are means  $\pm$  1 SE.

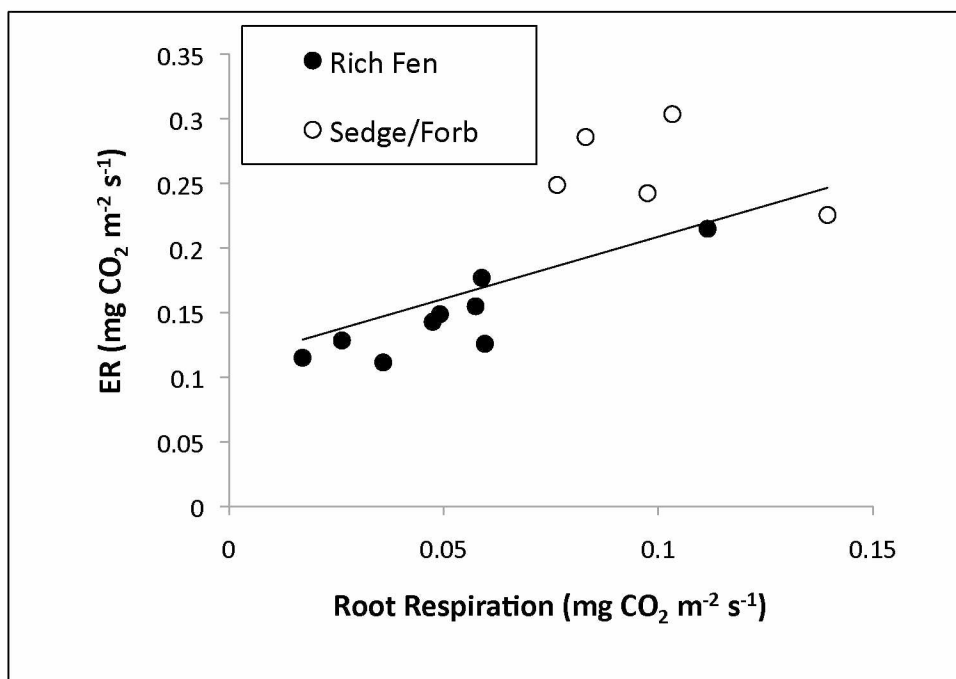
At the rich fen in 2010, root respiration ranged from 14% to over 100% of ER across gas flux collars (Figure 1.7 A).



**Figure 1.7:** Mean root respiration and ecosystem respiration **A.** at the rich fen in 2010, **B.** at the rich fen in 2011, and **C.** at the sedge/forb fen in 2011. Standard error is represented with error bars.

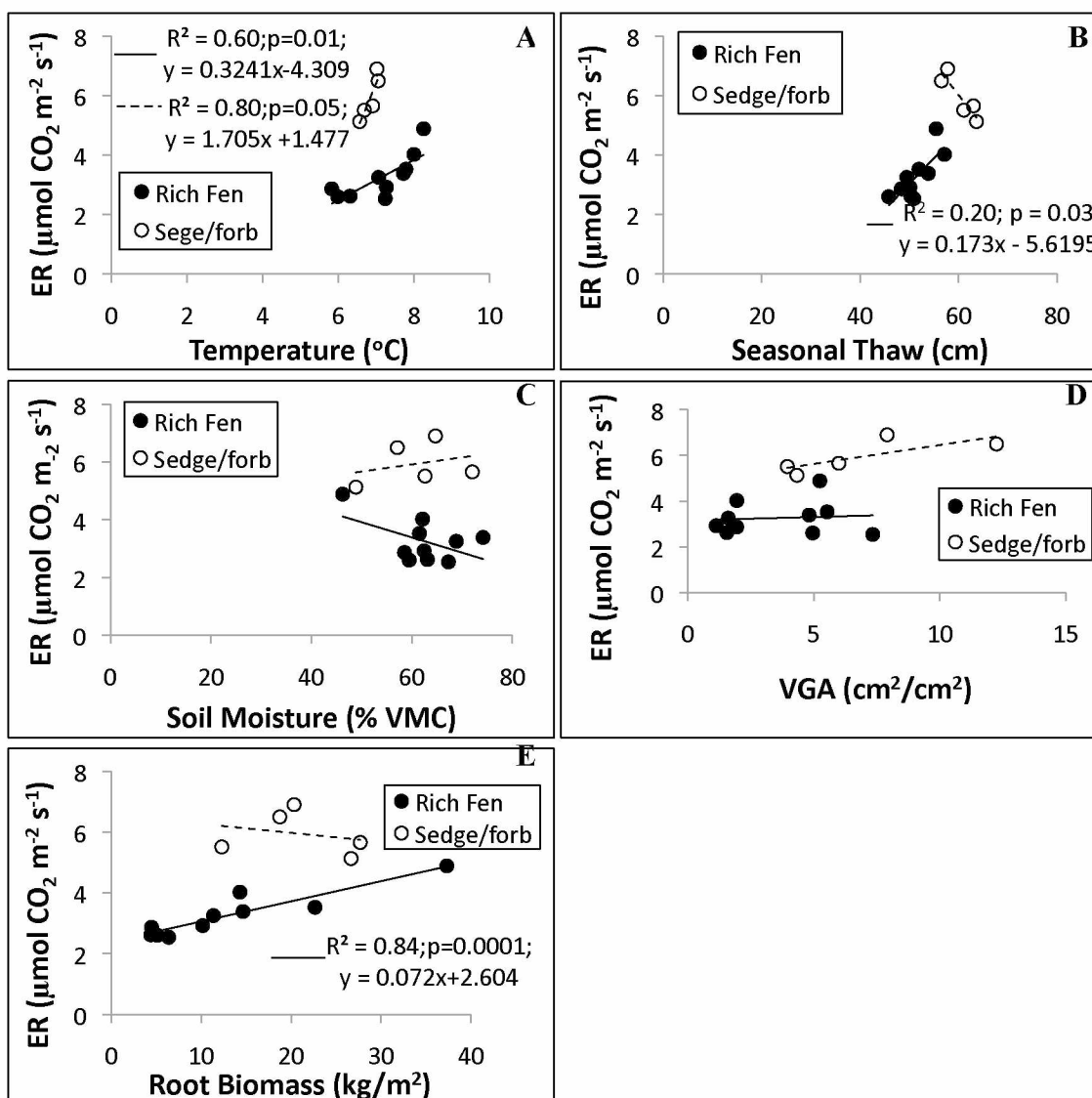
The collar where root respiration exceeded ecosystem respiration had a higher variance in root respiration relative to the other collars. Excluding that collar, root respiration contributed 14-47% to ER at the rich fen in 2010, and on average across collars contributed 39% of ER. At the rich fen in 2011, root respiration contributed 33-52% to ER fluxes (Figure 1.7B), and on average across collars contributed 39% of ER.

Similarly, at the sedge/forb community in 2011, root respiration contributed 29-62% to ER fluxes (Figure 1.7C), on average across collars contributing to 37% of ER. In 2011, both root respiration and ER fluxes were higher in the forb/sedge community than in the rich fen. Across both communities and years (rich fen only), root respiration explained 60% of the variation in ER ( $p = 0.0012$ ,  $F = 17.85$ , num df = 1, den df = 12; Figure 1.8).



**Figure 1.8:** Relationship between ecosystem respiration and root respiration for 2010 and 2011. Root respiration was a significant predictor of ecosystem respiration ( $p=0.0012$ ;  $r^2=0.60$ ,  $y = 0.9607x + 0.1128$ ).

I analyzed the effects of soil temperature, seasonal thaw depth, root biomass, and VGA on ER at both fen communities using data from the root partitioning experiment. At the rich fen, soil temperature and seasonal thaw depth explained 60% and 20% of the variation in ER respectively (Figure 1.9 A,B).



**Figure 1.9** Relationships between ecosystem respiration and **A.** soil temperature, **B.** seasonal thaw depth, **C.** soil moisture, **D.** vascular green area, and **E.** root biomass at the root respiration experimental communities. Statistics of the regression lines are reported for the significant relationships only.

I found that ER was not significantly related to soil moisture (Figure 1.9C). 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/forb fen this relationship was not significant (Figure 1.9E). However, there was a trend towards a positive relationship between VGA and ER at the sedge/forb community, but not at the rich fen (Figure 1.9D).

## **VI. Discussion**

### **Patterns of Ecosystem Respiration along the Wetland Gradient**

Boreal wetlands represent a wide range of wetland types, ranging from forested permafrost wetlands to inundated fens, all of which could be impacted differently by climate change and/or permafrost thaw.

My goals for this study were to quantify growing season ecosystem respiration fluxes along a gradient of vegetation and permafrost in a boreal wetland complex, and to evaluate the factors that affect soil CO<sub>2</sub> release. I used a gradient design for my study because I wanted to capture the variation in ER associated with different vegetation communities and soil along a wide range of wetland conditions. The five communities examined in my study varied with respect to active layer depth, peat thickness, and dominant plant species, including the presence/absence of trees and shrubs. I examined 5 years of ER data along with environmental variables in each of the communities. While an experimental design would have allowed me to examine the effects of an individual variable such as soil temperature on ER, the gradient design used in this study allowed me to explore a wide variation in ER that occurs naturally with both seasonal and interannual variation among the diverse wetland conditions along the gradient.

Overall, I expected the presence of seasonal ice and permafrost to govern ER fluxes through controls on soil temperature. Therefore, I hypothesized that ER would be lowest in the cold lowland black spruce community and highest in the warmer fen communities. Temperature is expected to stimulate both microbial and plant respiration. If soils are warmer and microbial activity increases, then more plant available nitrogen should be available through mineralization, which would stimulate plant growth and respiration

(Flanagan and Syed 2011; Kirschbaum 1995). My hypotheses were partially supported. In general, the black spruce and shrub communities with surface permafrost (maximum seasonal thaw depth of less than one meter) were colder than the communities with maximum seasonal thaw depth greater than one meter (grass, sedge/forb, and rich fen). During the growing season, the surface soils in the black spruce and shrub communities were between 1 and 4 °C colder than the grass, sedge/forb, and rich fen communities. Likely as a result of these differences in soil temperature, I found that ER in the black spruce and shrub communities was lower than the other communities averaged together. Since the rich fen lacks surface permafrost and had the highest surface soil temperatures, I expected that this community would have high ER, similar to the grass and sedge/forb communities. Surprisingly, this was not the case as I found that the rich fen had the lowest average ER relative to the four communities along the gradient.

I found only weak relationships between instantaneous ER and soil temperature at three of the five communities. These three communities were also the communities with the highest  $Q_{10}$  values, which indicates that they are the most temperature sensitive. However, the rich fen had the weakest relationship with instantaneous ER and soil temperature and had the lowest  $Q_{10}$  out of these three significant communities, which indicates that ER of the rich fen is not very responsive to soil temperature.

I found a strong relationship between mean monthly ER and mean monthly soil temperature among the communities along the gradient except for the rich fen (Figure 1.3). Monthly ER in the black spruce, shrub, grass, and sedge/forb communities appeared to have similar dependence on soil temperature, with a  $Q_{10}$  of 4.37. However, monthly ER in the rich fen had a non-significant dependence on soil temperature, with a  $Q_{10}$  of only 1.82. This suggests that ER in the rich fen is much less sensitive to soil temperature than the other communities. This is surprising, given that I anticipated that the communities without surface permafrost (upper one meter of soil) might respond more similarly to one another than to the colder black spruce and shrub communities. However, these results suggest that the rich fen is different from the rest of the gradient.

Because the exponential relationships between temperature and ER are qualitatively different between the rich fen and the other communities, I hypothesized that interactions between soil moisture and temperature were governing both instantaneous and mean monthly ER at the rich fen. I found a strong relationship between soil temperature and soil moisture ( $p < 0.0001$ ;  $F = 31.91$ ; num df = 1, den df = 159;  $R^2 = 0.17$ ) indicating that soils become warmer under wetter conditions. This suggests that there is the potential for soil moisture and soil temperature to interact to drive ER, yet I found no evidence of such interaction as a significant control on monthly or instantaneous ER. Differences in monthly soil moisture between the rich fen and the other communities did not explain the qualitative difference in the relationships of monthly ER with monthly soil temperature. However, it should be noted that surface soil moisture tends to be higher in the rich fen than in the other communities (Table 1.3). Thus, it is possible that the soil moisture in the rich fen is high enough to suppress microbial respiration in comparison to the other communities.

Increasing seasonal thaw depth should expose more carbon to decomposition. Thus I expected to see a strong relationship between thaw depth and ER. Therefore, I had hypothesized that ER would be lowest in the cold black spruce communities and highest in the warmer fen communities because of the shallower seasonal thaw depth of the colder communities and the deeper seasonal thaw depth of the warmer communities. My hypothesis was only partially supported. My results indicated that communities with surface permafrost had lower mean ER fluxes than the communities without surface permafrost, except for the rich fen that had low ER despite the deeper seasonal thaw depth. I found no significant relationship between mean monthly ER and mean monthly thaw depth across the communities. Also, surprisingly, only the shrub community showed a significant relationship between instantaneous ER and thaw depth. This relationship was not linear as predicted, but was quadratic. Perhaps ER was responding to seasonal thaw depth earlier in the season, and other soil variables became more important later in the season. Other soil variables could have also been more important to

ER at the other communities, which could be why I saw no relationships between ER and seasonal thaw depth at any of the other communities.

### **The Role of Roots in Ecosystem Respiration of CO<sub>2</sub>**

One potential reason for weak relationships between environmental variables and respiration is the potential strong contribution of root respiration to total CO<sub>2</sub> flux from wetlands. Saturated conditions create low O<sub>2</sub> availability for roots, so wetland plants have developed mechanisms for gas exchange. This adaptation has led to the development of large air spaces in the cortex of the rhizomes and roots which allow the transport of O<sub>2</sub> to the roots (Armstrong et al. 1991; Justin and Armstrong 1987; Thomas et al. 1996). If hydric plants continue to grow under wet conditions, then this could lead to high root respiration despite decreases in microbial respiration. Therefore, my second objective was to evaluate the importance of root respiration to ecosystem respiration.

Root respiration (R<sub>r</sub>) has been estimated by others to contribute between 40% and 56% of total soil respiration in lowland black spruce forests in interior Alaska (Bond-Lamberty et al. 2004; Hanson et al. 2000; Ruess et al. 2003). Research also has indicated that R<sub>r</sub> can account for as little as 10% to as much as 90% of soil respiration depending on the time of year it is measured (Hansen et al. 2006).

A previous study conducted in a lowland black spruce forest measured R<sub>r</sub> averaging  $0.0019 \pm 0.0001 \mu\text{mol CO}_2 \text{ s}^{-1} \text{ g}^{-1}$  of fine root dry mass (Ruess et al. 2003). Estimates of R<sub>r</sub> from my study were higher, averaging  $0.003 \pm 0.0001 \mu\text{mol CO}_2 \text{ s}^{-1} \text{ g}^{-1}$  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 sedge/forb fen. However, when scaled to a m<sup>2</sup> basis, another study conducted in a lowland black spruce forest reported R<sub>r</sub> averaging  $0.264 \pm 0.10 \text{ mg CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  (Vogel et al. 2005). While this literature value is higher than estimates of R<sub>r</sub> I made for the rich fen ( $0.143 \pm 0.015 \text{ mg}$



CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>), they are similar to the estimates I made for the sedge/forb fen (0.262 ± 0.015 mg CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>).

My results indicated that R<sub>r</sub> across two fen communities contributed between 14-62% to ER across collars and could account for about 40% of ER in the two fen communities. While fluxes of both R<sub>r</sub> and ER were higher at the sedge/forb community than the rich fen, R<sub>r</sub> contributed similarly to ER in these two systems. These results suggest that root respiration does not play a stronger role in contributing to ER in the rich fen, and thus cannot explain why ER fluxes in the rich fen are lower on average than in the other communities.

My results, however, do suggest that aboveground versus belowground plant tissues might contribute differently to ER in the two fen communities. I found a positive relationship between root biomass and ER at the rich fen but not the sedge/forb fen. In contrast, while not significant possibly because of my small sample size, there was a trend towards a positive relationship between VGA and ER at the sedge/forb fen but not at the rich fen. These results suggest that ER at the rich fen is more sensitive to variation in root biomass while ER in the sedge/forb fen is sensitive to variation in aboveground green biomass. However, the two fen communities had similar levels of root biomass and VGA. Thus, while my study suggests that ER at the rich fen is more sensitive to root biomass than aboveground biomass, my results do not support the conclusion that ER in this community is constrained by low values of plant biomass (either aboveground or belowground) relative to the other communities. These results may support my earlier conclusion that high soil moisture and low redox potential may be limiting ER at the rich fen. Low oxygen availability would influence microbial respiration but also would limit plant belowground activity. This may be why ER in the rich fen is more sensitive to variation in root biomass than in the sedge/forb fen. I did not directly measure redox status across my communities. An improved understanding of how both plants and microbes respond to changes in redox status along the gradient might help to clarify the patterns in ER observed in this study.

Above and belowground plant biomass varies in northern wetlands depending on environmental conditions such as water table position (Moore et al. 2002). A lowering of the water table will increase aboveground biomass and encourage deeper root growth (Moore et al. 2002; Murphy and Moore 2010). My results suggest that greater plant allocation to belowground tissues with a lowering of the water table may have a greater effect on ER in the rich fen community than in the sedge/forb fen.

Determining the source of autotrophic respiration (leaf, stem, moss, or root) is important for modeling studies predicting the fate of carbon in future scenarios with climate change. Current models partition respiration into leaf, stem, and root components (Euskirchen et al. 2009) because the rates of carbon release from these parts of the plant can be different. My study showed that ER is not only governed by soil environmental variables such as soil temperature and seasonal thaw depth, but is also driven by changes in vegetation. My results highlighted the fact that the importance of above- and belowground plant biomass to ER may also differ among neighboring wetland communities. A better understanding of vascular plant, moss, and soil respiration in relation to biomass, and how each component contributes to ER would help ecosystem and climate models make better predictions of wetland carbon fluxes to the atmosphere under changing climate and permafrost conditions.

### **Study Limitations and Ideas for Future Research**

One of the goals of my study was to quantify growing season ecosystem respiration (ER) fluxes along a wetland gradient that encompassed a wide range of vegetation, soil, and climatic variables. My analyses evaluated the importance of soil temperature, soil moisture, seasonal thaw depth, and vegetation to explaining the variability in ER both across the gradient as well as within each of the five communities along the gradient. The gradient design in this study has several limitations. First, using a gradient design to look at how soil environmental variables, such as soil temperature and soil moisture, drive ER fluxes is difficult because they often cannot be isolated very easily from one

another. In particular, I found that soil temperature was correlated with seasonal thaw depth, soil moisture and water table across all gradient communities. Seasonal thaw depth was also correlated with soil moisture and water table depth at most of the communities. These complicated interactions made it difficult to tease out the importance of specific environmental variables with my study design.

Another limitation to my gradient design is the lack of replication of gas flux collars within each community. Each community along the gradient contained one CO<sub>2</sub> flux collar and while these collars were measured at repeated intervals, they were not replicated spatially. The rich fen was the only community that had replicated collars (n=3). While the collar locations were carefully selected to represent typical vegetation and soil characteristics for each community, I cannot test whether or not the collars truly are representative. At the black spruce and shrub communities, the collars were placed in between trees and large shrubs, which is typical of soil CO<sub>2</sub> flux studies but nonetheless means that my measurements do not include respiration from aboveground biomass of large plants. Another limitation is that I have only measured along one gradient. This is a problem because I cannot extrapolate my results to other locations other than the communities I've included in my design. It would be interesting to see if the patterns I observed in this study were similar to other wetland gradients or in other locations.

To determine the contribution of root respiration to ER, I conducted my root respiration experiment during peak biomass. I did not examine the seasonal response of roots and how this could affect root contributions to ER. A previous study has shown that root respiration is a dominant driver of soil respiration during the summer months, while heterotrophic respiration is a dominant driver of soil respiration in the winter, spring, and fall months in the boreal forest when plants are dormant or coming into/out of dormancy (Gaumont-Guay et al. 2008). Thus, my data should be taken as maximum root respiration values, and likely represent the greatest seasonal contributions of root respiration to ER at both fen communities. Despite this, I still observed higher root respiration rates at the sedge/forb fen than at the rich fen.

Root respiration was quantified by placing excised roots from the soil into a root cuvette to measure a flux (Burton and Pregitzer 2003). A limitation to this technique is that respiration is being measured from roots that have been excised instead of roots that are still connected to the plant in the soil. However, my study, and other studies (Burton et al. 2002; Ruess et al. 2003) have found that roots continue to respire immediately after being excised. Another limitation of this methodology is that root activity is temperature sensitive (Boone et al. 1998; Burton et al. 2002; Ruess et al. 2003) and the fact that temperature was higher in the cuvette than in the soil by about 10-15 °C might be important in estimating root respiration. However, to account for the changes in temperature, I standardized all of the root fluxes to the temperature of the soil during the flux measurement. Other studies have used root exclusion experiments and subtracted the flux rate of the soil with roots from the flux rate of the soil without roots (Vogel and Valentine 2005). This method seems to provide a fairly reasonable estimation of root respiration by subtraction, but does not allow for calculation of root respiration and ER fluxes in the same locations. Also, plant and soil interactions might affect heterotrophic respiration, which would affect estimates of microbial versus root respiration.

## **VII. Conclusions**

The analysis of five years of ER data across a wetland gradient showed that in general, the communities underlain by surface permafrost were colder and tended to have low ER relative to communities without surface permafrost. However, I also found that the warmest community (rich fen) with the greatest thaw depth corresponded to the lowest ER fluxes along the gradient. This result cannot be explained by simple interactions between soil temperature and moisture, but I speculated that high soil moisture levels and low redox potential remains a possible explanation for the low ER fluxes in the rich fen. I also measured ER in the two fen communities, corresponding to the highest (sedge/forb fen) and lowest (rich fen) ER across the gradient, to explore whether variation in the

contributions of root respiration to ER could be a possible explanation for the low ER fluxes in the rich fen. My results indicated that root respiration contributed similarly to ER at both fens, and was equivalent to about 40% of ER on average in each community. ER in the sedge/forb fen appeared to be more sensitive to variation in VGA while ER in the rich fen was more sensitive to root biomass. Determining the sources of CO<sub>2</sub> flux from plants and soils, and how they each respond to changes in soil oxygen availability and redox, may help in understanding how CO<sub>2</sub> fluxes from wetlands to the atmosphere will be affected by climate change and associated shifts in permafrost, soil climate, and vegetation.

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