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Increased CO₂ loss from vegetated drained lake tundra ecosystems due to flooding

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[1] Tundra ecosystems are especially sensitive to climate change, which is particularly rapid in high northern latitudes resulting in significant alterations in temperature and soil moisture. Numerous studies have demonstrated that soil drying increases the respiration loss from wet Arctic tundra. And, warming and drying of tundra soils are assumed to increase CO₂ emissions from the Arctic. However, in this water table manipulation experiment (i.e., flooding experiment), we show that flooding of wet tundra can also lead to increased CO₂ loss. Standing water increased heat conduction into the soil, leading to higher soil temperature, deeper thaw and, surprisingly, to higher CO₂ loss in the most anaerobic of the experimental areas. The study site is located in a drained lake basin, and the soils are characterized by wetter conditions than upland tundra. In experimentally flooded areas, high wind speeds (greater than $\sim 4 \text{ m s}^{-1}$) increased CO₂ emission rates, sometimes overwhelming the photosynthetic uptake, even during daytime. This suggests that CO₂ efflux from C rich soils and surface waters can be limited by surface exchange processes. The comparison of the CO₂ and CH₄ emission in an anaerobic soil incubation experiment showed that in this ecosystem, CO₂ production is an order of magnitude higher than CH₄ production. Future increases in surface water ponding, linked to surface subsidence and thermokarst erosion, and concomitant increases in soil warming, can increase net C efflux from these arctic ecosystems.

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1. Introduction

[2] Recent estimates indicate that the total organic carbon in the upper 3 m of northern circumpolar permafrost-affected soils is $\sim 1024 \text{ Pg C}$, and $\sim 1672 \text{ Pg C}$ if yedoma and deltaic deposits are included [Schuur *et al.*, 2008; Tarnocai *et al.*, 2009]. This is much greater than previously reported and corresponds to $\sim 30\text{--}50\%$ of the global belowground organic carbon pool [Schuur *et al.*, 2008; Kuhry *et al.*, 2009; Tarnocai *et al.*, 2009]. Of this 1672 Pg C, 277 Pg C are present in northern circumpolar peatlands [Schuur *et al.*, 2008]. There is significant potential for this soil carbon to be released into the atmosphere as CO₂ or CH₄ in response

to changes in hydrology and soil temperature [Billings *et al.*, 1982; Peterson *et al.*, 1984; Oechel *et al.*, 1998; Schuur *et al.*, 2008; Frank *et al.*, 2010; Hayes *et al.*, 2011].

[3] Drying of wet anaerobic areas of northern peatlands increases rates of soil respiration and is therefore thought to increase net CO₂ emissions [Billings *et al.*, 1982; Peterson *et al.*, 1984; Oechel *et al.*, 1998; Olivas *et al.*, 2010; Flanagan and Syed, 2011]. A decrease in the water table generally increases oxygen diffusion into soils, leading to more aerobic conditions, and consequently increases decomposition, peat degradation, and CO₂ loss to the atmosphere [Billings *et al.*, 1982; Peterson *et al.*, 1984; Oechel *et al.*, 1998]. Conversely, a rise in the water table generally slows the diffusion of oxygen into the peat, limits aerobic microbial activity and decomposition rates, consequently decreasing CO₂ loss or increasing CO₂ sink [Billings *et al.*, 1982; Peterson *et al.*, 1984; Oechel *et al.*, 1998; Chivers *et al.*, 2009].

[4] As a result of predicted and observed decrease of soil moisture in large part of the Arctic [Oechel *et al.*, 2000; Hinzman *et al.*, 2005], the majority of the carbon flux studies in the Arctic have mostly focused on the impacts of decreased soil moisture [Billings *et al.*, 1982; Peterson *et al.*, 1984; Oechel *et al.*, 1998; Merbold *et al.*, 2009]. However, the impact of climate change over the Arctic is very complex, and increasing wetness in extensive tundra regions overlying

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continuous permafrost has also been reported [Smith *et al.*, 2005; Jorgenson *et al.*, 2006] due to topographic effects, subsidence, and ponding. In particular the total lake area has increased by more than 10% and the number of lakes by almost 5% in Siberia [Smith *et al.*, 2005]. Additionally, ice wedge degradation observed in Alaska could affect 10–30% of arctic lowland landscapes [Jorgenson *et al.*, 2006].

[5] Recent model simulations forecast an increase in precipitation, largely offset by an increase in evapotranspiration, with a small increase in soil moisture of 1% in 2041/2050, and of 3% in 2091/2100 [Wisser *et al.*, 2011]. An increase in soil water content would be expected to decrease aerobic respiration and increase anaerobic respiration. Since aerobic respiration is generally more rapid than anaerobic respiration, the net effect is assumed to be a decreasing of the rate of CO₂ loss from the biosphere to the atmosphere. Conversely, CH₄ release, mostly produced and emitted under anaerobic conditions, should increase under increased wetness [Harriss *et al.*, 1982]. Therefore, it is important to quantify the relevance of CH₄ emission compared to CO₂ with change in moisture conditions.

[6] The majority of the carbon fluxes studies generally used chamber measurements or laboratory incubations of tundra soil cores, and have shown increasing CO₂ emissions as soil moisture decreases and/or temperature increases [Billings *et al.*, 1982; Peterson *et al.*, 1984; Oechel *et al.*, 1998; Chivers *et al.*, 2009; Huemmrich *et al.*, 2010; Olivas *et al.*, 2010]. Past field manipulations [Oechel *et al.*, 1998; Strack *et al.*, 2006] of the water table have mainly been performed at small spatial scales that may not adequately capture the spatial complexity of the processes driving carbon dynamics in the Arctic. Understanding the impact of the water table on carbon exchange in field experiments is challenging, as many of the key soil environmental variables (e.g., soil temperature and thaw depth) co-vary with changes in soil moisture [Oechel *et al.*, 1998; Zona *et al.*, 2009]. For example the water table generally decreases as summer progresses. During much of this period, temperatures, active layer depth, and evapotranspiration often increase; solar radiation (after the summer solstice) decreases, and plant phenology varies [Oechel *et al.*, 1998; Zona *et al.*, 2009].

[7] To better address the impact of the hydrological changes on spatial and temporal variability in greenhouse gas emissions from the Arctic, we performed a water table manipulation over a total of ~27 ha (i.e., flooding of 9 ha) of tundra, representing the largest manipulative experiment in the Arctic. In this study, we flooded an area of ca. 9 ha (a third of the entire manipulation site of 27 ha) to determine the interaction of water table with CO₂ and CH₄ fluxes to better understand the controls on current fluxes and to better predict future CO₂ and CH₄ fluxes under a changing climate.

[8] The use of eddy covariance (EC) in this study to measure greenhouse gas fluxes minimized the surface disturbance, including pressure, airflow, and temperature alterations over water surfaces that occur with chamber measurements [Wanninkhof, 1992; Bain *et al.*, 2005]. This is the first manipulation experiment in a vegetated drained lake basin, a dominant land feature in the Arctic Coastal Plain in northern Alaska, accounting for up to ~50% and, together with lakes, up to ~70% of the land surface on the wet coastal plain [Hinkel *et al.*, 2005].

[9] The main goal of this experiment was to understand the impact of water table change on the net CO₂ fluxes from this arctic tundra ecosystem. We hypothesized that an increase in the water table would increase net CO₂ uptake from this tundra ecosystem and that this would largely be the result of decreased oxygen penetration (and aerobic respiration) in the soil under elevated water tables and/or flooding. In order to estimate the importance of the different anaerobic respiratory processes (occurring under flooded conditions) we performed laboratory anaerobic soil incubations to compare the CO₂ and CH₄ production in anoxic conditions. Under these conditions, we were able to avoid any confounding effects of CH₄ oxidation (e.g., into CO₂), a complication of ecosystem scale manipulations. We hypothesized that methanogenesis under anoxic conditions was higher than CO₂ respiration, and would contribute significantly to the carbon loss from this ecosystem.

2. Material and Methods

2.1. Study Site

[10] The study site is located about 10 km east of the town of Barrow, Alaska, in a vegetated drained lake basin. The vegetated drained lake basin chosen for this study (1.6 km long and about 0.4 km wide at the widest point) was divided into three sections separated by two dikes (Figure 1). These dikes were built from water impermeable, interlocking rigid plastic barriers inserted in trenches dug in the frozen soil during the spring of 2007. The original experimental plan was that the north section would be subjected to flooding, the central section drained (reduced water table) and the south section left as a control. For technical reasons, the drainage was not successful, and the drainage of the central section resulted in water levels equivalent to the control area in the south. As a result, the central and southern portions were both considered as control areas. Here we focused on the increase in water table and flooding of the north section and compared the effect of flooding to background controls in the center and south. These three sites are indicated as North, Central and South sites here after. As the drainage did not effectively decrease the water table of the Central section, this manipulation experiment will be referred to mostly as a flooding (e.g., increase in water table above the surface) experiment. The vegetated drained lake presented a very variable microtopography and significant polygon development, mostly in the North site, a less variable microtopography in the Central, while the South site presented fairly homogenous microtopography (Figure 2). Data prior to the start of the manipulation (summer 2005 and 2006) were used as baseline years to estimate possible differences among the three sections before the water table change. For more information about the site refer to Zona *et al.* [2009].

2.2. Water and Thaw Depth Measurements

[11] Thaw depth was recorded using a graduated metal rod. Thaw depth measurements were performed weekly in the three manipulation sites every 10 m (from 10 m to 200 m upwind from the EC towers); in summer 2006 they were performed independently with two sampling schemes: at 12 locations in the first 200 m from the EC tower, and at 20 locations every 10 m in the first 200 m from the eddy towers across the boardwalks shown in Figure 1. In summer 2008

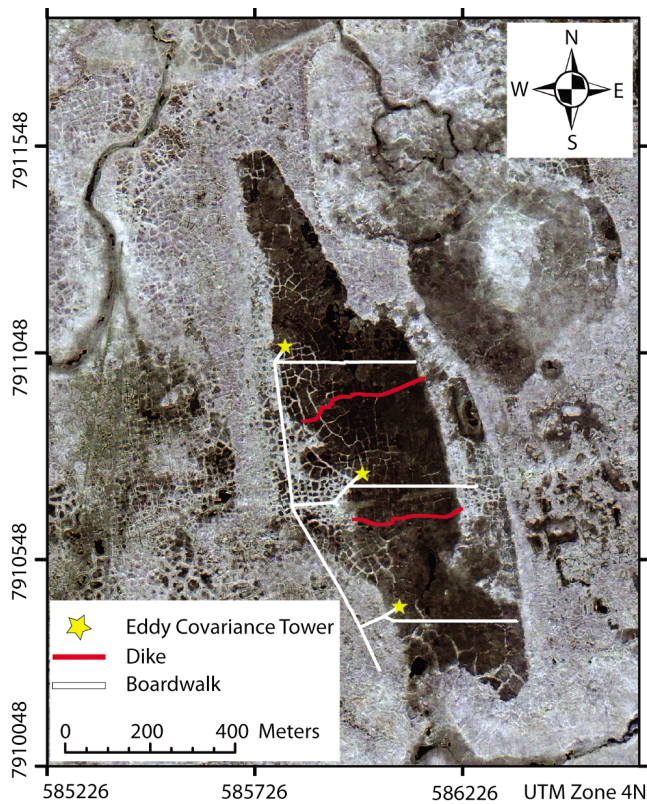


Figure 1. Site of the water manipulation experiment. Indicated are the locations of the three eddy-covariance towers, used to measure CO₂ fluxes, the location of the dikes, and of the boardwalks used to access the sites to perform manual measurements (water table, thaw depth, soil temperature). The water table was increased in the North site, while the Central and the South presented similar water tables during the manipulation experiment.

thaw depth measurements were recorded weekly across these 200 m transects every 4 m with alternating sampling schemes starting from either 0 or 2 m from the eddy covariance tower, and the total number of sampling points was 51 per week, see Figure 2.

[12] Water table measurements were manually recorded weekly, using 12 PVC pipes with diameter of 2.5 cm and holes every cm permanently inserted into the ground at the end of summer 2005 in each of the sites. Water table measurements during most part of the summer 2006 by *Olivas et al.* [2010] were made inside their experimental collars, that while appropriate to reflect the environment inside their sampling area, were not appropriate to estimate the water table over the treatment or over the footprint of the eddy covariance towers and therefore are not used here. Additional measurements outside of the chambers' collars were performed in six locations in the first 200 m from the towers on the 24 August 2006 (Figure 2). We noticed that this sampling intensity could not capture the complex microtopography of the eddy covariance tower footprint particularly in the North section (Figure 2), so we installed additional PVC pipes at the end of the following summer (wells were placed every 2 m and sampled every 4 m, alternating each week by starting from either 0 or 2 m from the eddy covariance tower, for a

total number of 51 sampling points per week, see Figure 2). This allowed a more intense spatial sampling of the water table in summer 2008. The difference in average water table calculated with the two sampling schemes (12 points and 51 points) was confirmed by the comparison of the average water table level with these two sampling schemes in 2008 (see results). For these reasons the water table of 2006 and 2007 were not used in the statistical analysis.

[13] The flooding of the North site was initiated in summer 2007, but was only successfully achieved in summer 2008. In summer 2007 and 2008, water was pumped from the Central site into the North site, increasing the water table above the surface (defined here as the top of the green moss layer) for the entire summer. In summer 2008 water was also pumped from a nearby lake (Cake Eater) into the North site. Water pumping from the Central to the North site started in June and ended in mid-July, while the water pumping from Cake Eater Lake started on 10 July and ended on 26 August 2008.

2.3. Eddy Covariance Measurements

[14] Three eddy-covariance towers (N 71°17'11.80"N 156°36'12.23"W, C 71°17'1.71"N 156°35'54.77"W and S 71°16'51.17"N 156°35'47.28"W) for the measurements of net CO₂ (NEE), H₂O vapor, and heat flux, were installed in July 2005 at ~1.6 m above the surface in three adjacent sites of the vegetated drained lake (North, Central, and South, each of about 9 ha, Figure 1). Measuring CO₂ fluxes by eddy-covariance allowed the evaluation of the impact of wind on gas exchange over flooded tundra, which is a not possible using chamber-based measurement. As the eddy covariance and meteorological towers were installed in June–July 2005, some of the data were available only from July 2005, while for the following years data for the entire summer season were collected. Flux data from summer season 2005, 2006, 2007, and 2008 were subjected to a u^* (defined as $\sqrt{|u'w'|}$) filter of 0.1 m s⁻¹. The eddy covariance baseline data (2005, 2006) and manipulation data (2007, 2008) were filtered to include only wind directions from the experimental areas (between 330° and 180°). About 50% of the all data (before filtering) was from a wind direction between 50° and 180°. The energy budget closure ($R_n - G = H + LE$) and the comparison of the co-spectra of $w'T'$, $w'CO_2'$, $w'H_2O'$, $w'CH_4'$ [*Kaimal et al.*, 1972] were used to estimate the quality of the data as already reported by *Zona et al.* [2009]. More details on the instruments, calibrations, data processing, are given elsewhere [*Zona et al.*, 2009].

[15] Two footprint models were applied to the data [*Hsieh et al.*, 2000; *Kljun et al.*, 2004]. Both of them showed that the majority of the fluxes were coming from the first 60–80 m upwind from the towers. These footprint analyses estimated that the footprint of the three towers peaked at ~25 m, and that 90% of the fluxes were coming from the first 60–70 m in front of the towers [*Kljun et al.*, 2004]. The North and Central EC towers were ~350 m apart; the Central and South towers were ~300 m apart. The distances of the towers from the dikes were all more than 100 m (see Figure 1). The footprints of all the EC towers were shorter than the distances from dikes, and consequently (once filtered by wind direction, see previous paragraph) the

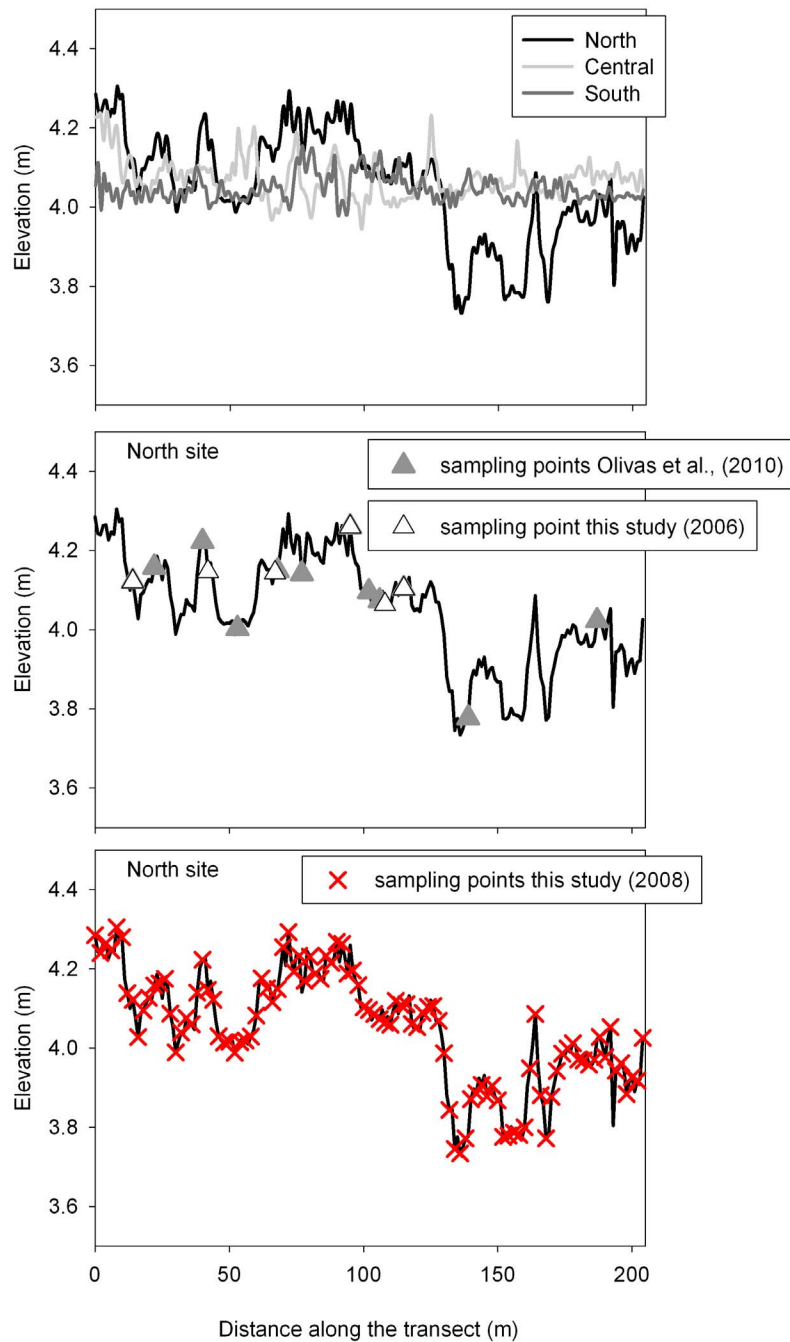


Figure 2. (top) Elevation above the sea level across the three sampling transects in the North, Central, and South sites and sampling intensity of (middle) water table and thaw depth in the North site in summer 2006–2007 and (bottom) water table, thaw depth, and manually recorded soil temperature in summer 2008.

towers measured fluxes only from their treatment areas. Data were gapfilled to estimate the net C uptake during the summer season using the standard online gap-filling used in Fluxnet <http://www.bgc-jena.mpg.de/bgc-mdi/html/eddyproc/EddyInputForm.html> [Reichstein et al., 2005; Lasslop et al., 2010] as applied previously to the Arctic [Merbold et al., 2009]. This gapfilling procedure should be further tested for arctic environments, but this analysis goes beyond the scope of this paper. Apart from the

calculation of the seasonal net C uptake, non gapfilled data were used for the analysis presented in this paper. Only data for the growing season (defined here as date of snowmelt, usually mid June until the time in which the ecosystem was no longer a net C sink, and NEE was approximately zero or slightly positive, usually at the end of August) are presented here. As previously mentioned, data from the Central site (with similar water table to the South,

Table 1. Soil Properties by Profile^a

Depth (cm)	Bulk Density (g cm ⁻³)	Organic Matter Content (g g ⁻¹)	Organic C (kg m ⁻² layer ⁻¹)	Soluble Organic C (g m ⁻² layer ⁻¹)	Acid-Extractable Fe (g m ⁻² layer ⁻¹)
0–10	0.062 ± 0.006	0.901 ± 0.012	2.47 ± 0.24	3.49 ± 0.83	102.8 ± 23.1
10–20	0.317 ± 0.125	0.641 ± 0.111	3.05 ± 0.58	4.13 ± 0.27	187.6 ± 56.0
20–30	0.402 ± 0.084	0.338 ± 0.051	4.49 ± 0.57	3.88 ± 0.05	406.4 ± 74.7
30–40	0.424 ± 0.126	0.258 ± 0.053	3.35 ± 0.41	4.03 ± 0.59	410.8 ± 90.3
40–50	0.380 ± 0.040	0.175 ± 0.011	2.89 ± 0.20	5.54 ± 0.53	520.4 ± 109.0

^aNine replicates: three from the South, two from Central, four from North site; dissolved organic C data and the data in the 40–50 cm were only from the North site. Displayed are averages and standard deviations.

the control site) were assumed to be equivalent to an additional control site.

2.4. Ecosystem Respiration Calculation

[16] Ecosystem respiration (ER) was calculated using the intercept parameter (y_0) of the light response curve for PAR < 200 μ mol m⁻² s⁻¹, approximated as linear, for daily intervals during summer 2005, 2006, 2007, and 2008. Only data from July and August were used, as June in the high Arctic is characterized by fairly high radiation at “night” making regression of NEE and PAR problematic. Only days with sufficient data (e.g., >8 points) to provide regressions of NEE on PAR resulting in a $p < 0.05$, were used to estimate respiration rates. The ER estimated with this linear model was compared to direct measurements of respiration using opaque chambers [Zona *et al.*, 2011a], see results. Detailed investigation of the environmental controls on ER and chamber measurements is provided by Zona *et al.* [2011a].

2.5. Environmental Variables

[17] Micrometeorological variables were recorded continuously at each manipulation site. These variables included: 1) soil moisture at three depths: 0–30 cm, 0–10 cm, 20–30 cm, in five different locations; 2) soil temperature in nine locations at six different depths: at surface, 1 cm, 5 cm, 10 cm, 20 cm and 30 cm below surface; 3) air temperature and RH at three different heights: 0.46, 1.6 and 2.95 m above the ground; 4) solar radiation, photosynthetic active radiation (PAR), and net radiation at 1.5 m above the surface; 5) soil heat flux at 2 cm below the surface at five different locations; and 6) precipitation 20–30 cm above the ground in one location. A more detailed description of the instruments is provided by Zona *et al.* [2009], and details on the spatial heterogeneity of some of these environmental variables is discussed by Zona *et al.* [2011a].

[18] Considering the large heterogeneity in the landscape we also measured soil temperature manually in summer 2008 (at 5 cm below the surface) weekly in the first 200 m from the eddy towers, every ~4 m from the eddy towers (with an alternating sampling scheme starting from either 0 or 2 m from the tower, for a total number of 51 sampling points per week, see Figure 2). As the time required to complete each transect was more than 3 h, each site (North, Central, and South) was measured on a consecutive day during each week, limiting the temporal overlap of these measurements, and possibly biasing their comparison. As previously mentioned, the same sampling scheme was applied to thaw depth and water table, but their variation

over three consecutive days was much less than the temperature variation, limiting this bias.

2.6. Soil Organic Carbon and Anaerobic Soil Respiration in Different Soil Layers

[19] Characteristics for the soil profile were determined from nine frozen soil cores (7.75 cm diameter, 50 cm deep) collected from the three sites during March 2008, displayed in Table 1. Bulk density, organic matter content, soluble organic carbon (extracted in 0.5 M K₂SO₄), and acid extractable Fe (1 N H₂SO₄, 24 h), were measured in these soil cores subdivided into 10 cm layers (from surface to 50 cm depth). Soil organic matter was measured by loss on combustion, and soil carbon was estimated by assuming a carbon content of 43.9% for the organic matter [Brown, 1967]. Dissolved organic C and Fe were analyzed colorimetrically as described previously [Lipson *et al.*, 2010]. For the anaerobic soil incubation experiment, a frozen core from the North site was cut into three sections (0–15, 15–30 cm, and 30–50 cm layers), and each layer was then subdivided longitudinally into four strips. The strips were placed into mason jars equipped with septa in the lids, flushed with high purity nitrogen for two minutes, and allowed to thaw at 4°C. After thawing, jars were again flushed with nitrogen to remove gases trapped in the frozen core. Headspace samples were collected after 24 h and CO₂ and CH₄ analyzed by gas chromatography. Repeatedly over the course of 56 days (after 1, 24, 28, 35, 42, 56 days from the start of the incubation), the headspace was re-flushed with nitrogen, and resampled 24 h later (so that the respiration rates were calculated over the last 24 h period).

[20] Soluble organic carbon was measured in K₂SO₄ extracts (0.05M) using a colorimetric assay [Bartlett and Ross, 1988], Fe was measured in 1 N H₂SO₄ extracts, using 1,10-phenanthroline [Analytical Methods Committee, 1978]. Acid-extractable Fe increased in the mineral layers, but significant mineral forms of Fe also exist in the organic layers. Based on differential extraction techniques, these minerals include easily reducible oxyhydroxides such as ferrihydrite, other reducible Fe oxides such as goethite, the reduced Fe mineral, siderite, the mixed valence mineral, magnetite, and primary minerals such as biotite in the deeper layers [Lipson *et al.*, 2010]. Other details of the soils are given elsewhere [Brown *et al.*, 1980; Bockheim *et al.*, 2004].

2.7. Oxidation Reduction Potential

[21] The oxidation reduction potential (ORP) measures the tendency of a chemical species to acquire electrons (e.g., and be reduced), and consequently provides information on the reactions (methanogenesis vs methane oxidation) more

likely to occur. ORP measurements were performed to estimate the effect of the water table manipulation on the oxidative status of the soils, and the most probable respiratory mechanisms (e.g., anaerobic versus aerobic respiration) occurring in this experimental site. ORP measurements were made on 12 July 2008 with a Thermo-Orion (Waltham, MA) electrode (with internal Ag/AgCl reference electrode), and portable multimeter. Measurements were taken at 5, 10 and 15 cm depths at 0, 50, 150, 200, 250, and 300 m from the eddy tower across the three transects in the North, Central, and South experimental sites. According to a general classification, the following ORP values are connected to the following soil conditions: >300 mV aerobic/oxidized, 100–300 mV moderately reduced; –100 to +100 mV Reduced, <–100 mV highly reduced [Reddy and De Laune, 2008].

2.8. Statistical Analyses

[22] To estimate the significance in the differences in respiration rates among the three sites, we performed a two-way ANOVA and Least Square Means post-hoc test with treatment (e.g., data from 2005 and 2006 were assembled together into ‘before treatment’ and data from 2007 and 2008 were assembled together into an ‘after treatment’ group), site, and their two-way interaction as fixed effects. Date and date squared were added as continuous covariates to control for temporal variation. In order to take the temporal autocorrelation into account, we included year (nested within treatment) as random effect and implemented an autoregressive correlation of the first order, in combination with Kenward Rogers approximation of the denominator degrees of freedom and standard errors of the parameter estimates.

[23] As described in the Methods section, we only tested the differences in water level among the sites in summer 2008 when there was an adequate spatial sampling intensity (weekly at 51 locations, Figure 2) using a one-way ANOVA and Least Square Means post-hoc test. As depth of thaw and the manually recorded soil temperature could be affected by water table we also tested the significance in the difference among the three sites only in 2008 sites using a one-way ANOVA and Least Square Means post-hoc test.

3. Results and Discussion

3.1. Water Table, Precipitation, and Precipitation-Potential Evapotranspiration

[24] The precipitation was 67, 62, 14, and 58 mm in the summers (from end of snowmelt to end of August) of 2005, 2006, 2007, and 2008. The moss water content measured during the entire summer season 2006, showed water saturation, or near saturation [Zona *et al.*, 2011b]. Three of the summers investigated here showed similar P-PET values (–98, –60, –90 mm, in 2005, 2006, and 2008), and consequently probably similar water content in the moss layer, while summer 2007 presented P-PET of –192 mm.

[25] As water table measurements were not performed in summer 2005, we assume that the three areas had similar water table depths as the three sites are very close, and no dikes or other disturbances had been imposed on the landscape at that time. The three sites showed similar water table depths at the end of summer 2006 (24 August), 4 ± 2 cm (mean \pm SE) below the surface in the North, 1 ± 2 cm

below the surface in the Central, and 0 ± 1 cm in the South. In summer 2007 the North section presented at end of the season (25 August) water table of 12 ± 1 (mean \pm SE) cm below the surface, the Central of 11 ± 1 cm below the surface and the South sections 19 ± 1 cm below the surface. As previously mentioned, during these two summers (2006–2007) the water table measurements were only performed in few points not representative of the complex microtopography, particularly of the North section (Figure 2). A comparison of the water table levels with the two sampling schemes ($n = 12$ and $n = 51$, see Figure 2) in 2008 showed that the less intense spatial sampling underestimated the water table by about 5 cm in the North section at the end of August 2008. The well developed polygons and variable microtopography in the North section (Figure 2) led to partial flooding even in summer 2007: the lowest elevation sampling point of *Olivas et al.* [2010] (Figure 2) was flooded for the entire summer 2007 (water table was 4 cm above the surface on the 25 August 2007). Therefore flooded areas were formed with the experimental increase in the water table in the North site even in summer 2007. The water table measured with the two sampling schemes in the Central and South sites were comparable with only 1 cm difference at the end of August 2008.

[26] During summer 2008, when water pumping was fully implemented (see materials and methods for details), the North site (flooded area) had a water table on average 6 ± 3 cm ($n = 51$) above the surface for the entire duration of the experiment (Figure 3), while at the Central (slightly drained) and South (control) sites the average water table was 3 ± 2 cm below surface and 2 ± 2 cm below surface. The one-way ANOVA (and the Least Squares Means post-hoc test) showed that in the end of the 2008 season water table was significantly higher in the North site than in the Central ($p < 0.001$) and in the South ($p < 0.001$) sites. The water table was not significantly different between the Central and South sites in summer 2008.

3.2. Snowmelt and Thaw Depth

[27] Usually snowmelt during this experiment occurred in the second week of June. In summer 2005 the eddy covariance and meteorological towers were established after the snowmelt. In summer 2006, the snowmelt occurred on 13 June, in summer 2007 on 10–11 June, and in summer 2008 on 12 June. The maximum thaw depth, measured at the end of the growing season was also very similar among the three sites in the baseline years (2005 and 2006). At the end of August 2005 the thaw depth was on average 31 ± 5 cm, 31 ± 3 cm, 30 ± 3 cm in the North, Central, and South sites. At the end of August 2006 the thaw depth, measured with two sampling frequencies ($n = 12$, and $n = 20$ locations, with the second sampling scheme reported here in parenthesis) was on average 29 ± 2 (29 ± 4), 30 ± 3 (31 ± 2), and 30 ± 3 cm (31 ± 3) below the surface in the North, Central, and South sites. At end of summer 2007 (2 September) the thaw depth ($n = 12$) was on average 32 ± 2 , 32 ± 1 , and 26 ± 2 cm in the North, Central, and South. At the end of August 2008, thaw depth ($n = 51$) was 34 ± 5 in North, 28 ± 2 in Central, and 29 ± 2 in South area. The one-way ANOVA (and the Least Squares Means post-hoc test) showed that thaw depth at the end of summer 2008 was significantly different between the North and the Central

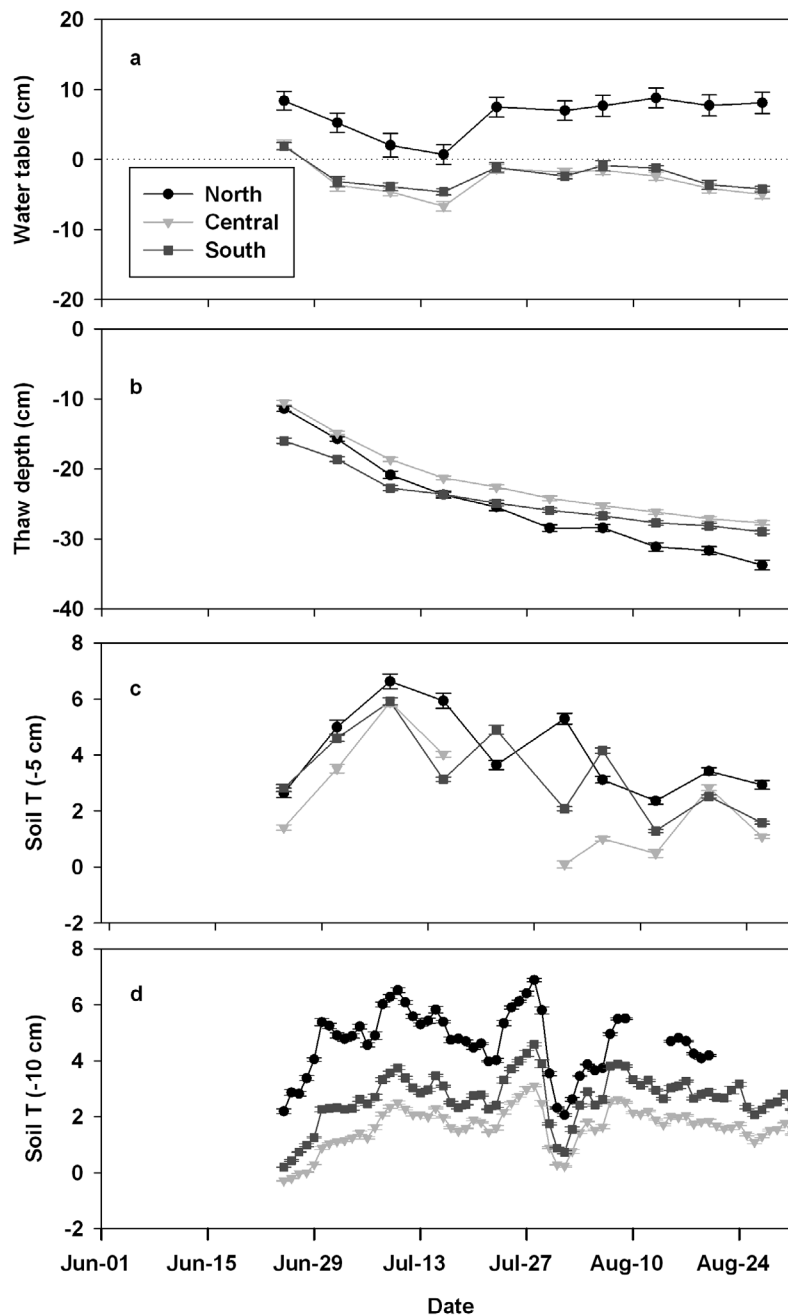


Figure 3. (a) Water table, (b) thaw depth (cm from surface), (c) soil temperature ($^{\circ}\text{C}$) manually collected weekly at 5 cm below surface across the transects, and (d) soil temperature ($^{\circ}\text{C}$) continuously recorded at 10 cm below surface in proximity of the eddy towers, in the three manipulation areas (North, Central, and South) during the growing season 2008. Water pumping from the Central to the North site started on 8 June and ended on 17 July 2008, from Cake Eater Lake the pumping started on 10 July and ended on 26 August 2008. Notice the increase in depth of thaw in the North (flooded) area after 15 July. Water table, thaw depth, and manually collected soil T (5 cm depth) values are mean and standard error of 51 measurements.

site (p -value < 0.001) and between the North and the South site ($p < 0.001$); thaw depth at the end of summer 2008 was not different between the Central and South sites.

3.3. Air and Soil Temperature

[28] Air temperature was on average $3.3 \pm 3.8^{\circ}\text{C}$ from 12 June to 31 August 2005, $3.3 \pm 3.6^{\circ}\text{C}$ from 13 June 2006

to 31 August 2006, $5.3 \pm 3.7^{\circ}\text{C}$ from 10 June to 31 August 2007, $3.9 \pm 2.8^{\circ}\text{C}$ from 13 June to 31 August 2008 in the North, Central, and South sites. Soil temperatures (at 10 cm below surface) were on average $4.5 \pm 2.2^{\circ}\text{C}$, $4.1 \pm 2.4^{\circ}\text{C}$, and $4.0 \pm 2.1^{\circ}\text{C}$ from 29 July to 31 August 2005 in the North, Central, and South sites. The average soil temperature (continuously recorded in proximity of the tower at

10 cm depth), from 13 June to 31 August 2006 was $3.2 \pm 2.0^\circ\text{C}$, $4.1 \pm 2.0^\circ\text{C}$, and $3.9 \pm 1.9^\circ\text{C}$ at 10 cm depth in the North, Central, and South sites. During summer 2007, average soil temperature was $4.7 \pm 3.1^\circ\text{C}$, $4.6 \pm 3.1^\circ\text{C}$, and $5.8 \pm 3^\circ\text{C}$ in the North, Central, and South site, in summer 2008 average soil temperature was $3.9 \pm 2^\circ\text{C}$ in the North site (from 13 June to 20 August), $1.3 \pm 1.1^\circ\text{C}$ in the Central site, and $2.2 \pm 1.5^\circ\text{C}$ in the South site from 13 June to 31 August. The soil temperature (at 5 cm depth) manually recorded weekly in 51 locations in the three transects in 2008 (Figure 2), confirmed that the temperature in the North site was statistically higher than the temperature in both the Central ($p < 0.001$) and South sites ($p < 0.001$) (one-way ANOVA and the Least Squares Means post-hoc test). The soil temperature in the Central site was significantly lower than the South site ($p < 0.001$).

[29] The high heat capacity of the standing water and the larger thermal conductivity of the saturated moss layer conducted more heat into the soil [Hinzman *et al.*, 1991] and led to deeper thaw and a higher soil temperature in the flooded area in summer 2008 (Figures 3b–3d). In the Central and South sites, with subsurface water tables, the lower water content of the moss layer increased the thermal insulation, and reduced heat conduction to deeper soil layers, leading to lower soil temperature and shallower thaw (Figure 3).

3.4. CO₂ Fluxes Following Water Table Change

[30] Energy balance closure ($R_n - G = H + LE$) were 91%, 92%, and 94% in summer 2005 for the North, Central, and South site respectively; in summer 2006, they were 91%, 86%, and 88% for the three sites; in summer 2007, they were 90% for the North, 88% for the Central site, and 94% for the South site; in summer 2008 they were 88%, 85%, and 89% for the North, Central, and South site. In the summers of 2005 and 2006, before the start of the manipulation, the three areas demonstrated similar respiration rates, while the respiration during the manipulation years (2007, and 2008) was occasionally much higher in the North site (Figure 4). The three sites showed some variability in respiration rates but none of them showed respiration rates constantly higher than the others in the baseline years of 2005 and 2006, or as high as the peak respiration rates in the North site in 2007, and 2008 (Figure 4). ER estimated by the linear model presented a reasonable comparison ($R^2 = 0.53$ and p -value < 0.001) with ER measured with chambers in the Central site [Zona *et al.*, 2011a] for the first 100 m from the eddy tower. The seasonally averaged ER estimated by chambers for the Central site in summer 2008 was 0.53 ± 0.06 (mean \pm SE) $\text{gC m}^{-2} \text{d}^{-1}$, about 20% lower than the ER estimated using the linear model of the eddy covariance ($0.42 \pm 0.03 \text{ gC m}^{-2} \text{d}^{-1}$). Even if the linear model was underestimating the respiration rates, we selected it as it was more conservative.

[31] The statistical analysis (two-way ANOVA two and Least Square Means post-hoc test with year, site, and their two-way interaction as fixed effects) performed on the ER before the increase in water table (2005, and 2006) and after the increase in water table (2007 and 2008) showed that the respiration rates from the North site were not statistically different from any of the sites before or after the water treatment. The small data set available for the statistical

analysis (together with the fact that the peak CO₂ emission in the North site only occurred in few days in both 2007 and 2008, see Figure 4) probably led to this result.

[32] The net C uptake during the growing season 2006 was 84, 46, and 51 g C m^{-2} in the North, Central, and South site (from 12 June to 31 August 2006). In summer 2007, the net C uptake was 34, 73, and 59 g C m^{-2} in the North, Central, and South site. During summer 2008 the North site presented a net C uptake of 10 g C m^{-2} , while the Central, and South site C uptake was 30 g C m^{-2} and 14 g C m^{-2} . This showed that in the baseline year 2006 the North site presented the highest C uptake while in both 2007 and 2008 the lowest.

3.5. Effect of Wind on CO₂ Flux

[33] Higher winds speeds, i.e., those above $\sim 4 \text{ m s}^{-1}$ increased CO₂ efflux during summer 2007 and 2008 in the North site (Figure 5). High winds increased the CO₂ emissions significantly, sometimes overwhelming photosynthetic uptake during daytime (Figure 6). The enhanced emission observed with high winds mostly occurred during August when the thaw was deeper (Figure 3) and the wind was higher (Figure 6). The effect of wind speed on CO₂ loss was more evident in the nighttime data that approximated ER (half-hour averaged CO₂ flux data with $\text{PAR} \leq 10 \mu\text{mol m}^{-2} \text{s}^{-1}$, see Figure 5). This CO₂ flux data filtered for $\text{PAR} \leq 10 \mu\text{mol m}^{-2} \text{s}^{-1}$, allowed selecting nighttime ER, instead of calculating respiration by extrapolating the light regression curves, providing a better temporal resolution of CO₂ fluxes and wind speed.

[34] The observed increase in CO₂ emission with an increase in wind speed was in agreement with the quadratic dependence of gas exchange on wind speed found over large water bodies [Wanninkhof, 1992]. This quadratic dependence of gas transfer implied that low solubility gas bubbles may have a significant impact on CO₂ fluxes [Huebert *et al.*, 2010]. Wind had a larger impact on CO₂ loss in the North area later in the season (3 to 31 August, see Figure 6), probably due to the increase in the depth of thaw at the end of July ($23 \pm 2 \text{ cm}$ below surface at the end of July 2007, and $28 \pm 4 \text{ cm}$ below surface at the end of July 2008). During the 2008 flooding, the higher soil temperature in the North site (Figure 3) contributed to higher CO₂ production later in the season (mostly August). Overall, the increase in water table, lead to the peak CO₂ release in the North site during both summer 2007 and 2008. The escape of CO₂ mostly occurred with high wind conditions, leading to a time lag between CO₂ production, diffusion into the water, and subsequent release to the atmosphere. To estimate this time lag we performed a simple calculation. The highest $p\text{CO}_2$ values found in the soil in the North section of this experiment during the growing season was about 10% at 20 cm (K. Nakamoto, unpublished data, 2006), which using Henry's law translates into about 7.4 mM in the soil solution. Consequently, assuming that 5 cm of permafrost thawed and released this amount of CO₂, this would represent 1.63 $\text{mg CO}_2 \text{ per cm}^2$. The ER values usually observed (with the exception of the large peak release in mid August) were up to about 1 $\text{gC m}^{-2} \text{d}^{-1}$ or 0.37 $\text{mgCO}_2 \text{ cm}^{-2} \text{d}^{-1}$, and consequently it would have required about 4.4 days for this CO₂ to be released into the atmosphere. If we used the diffusion rates for CO₂ in water,

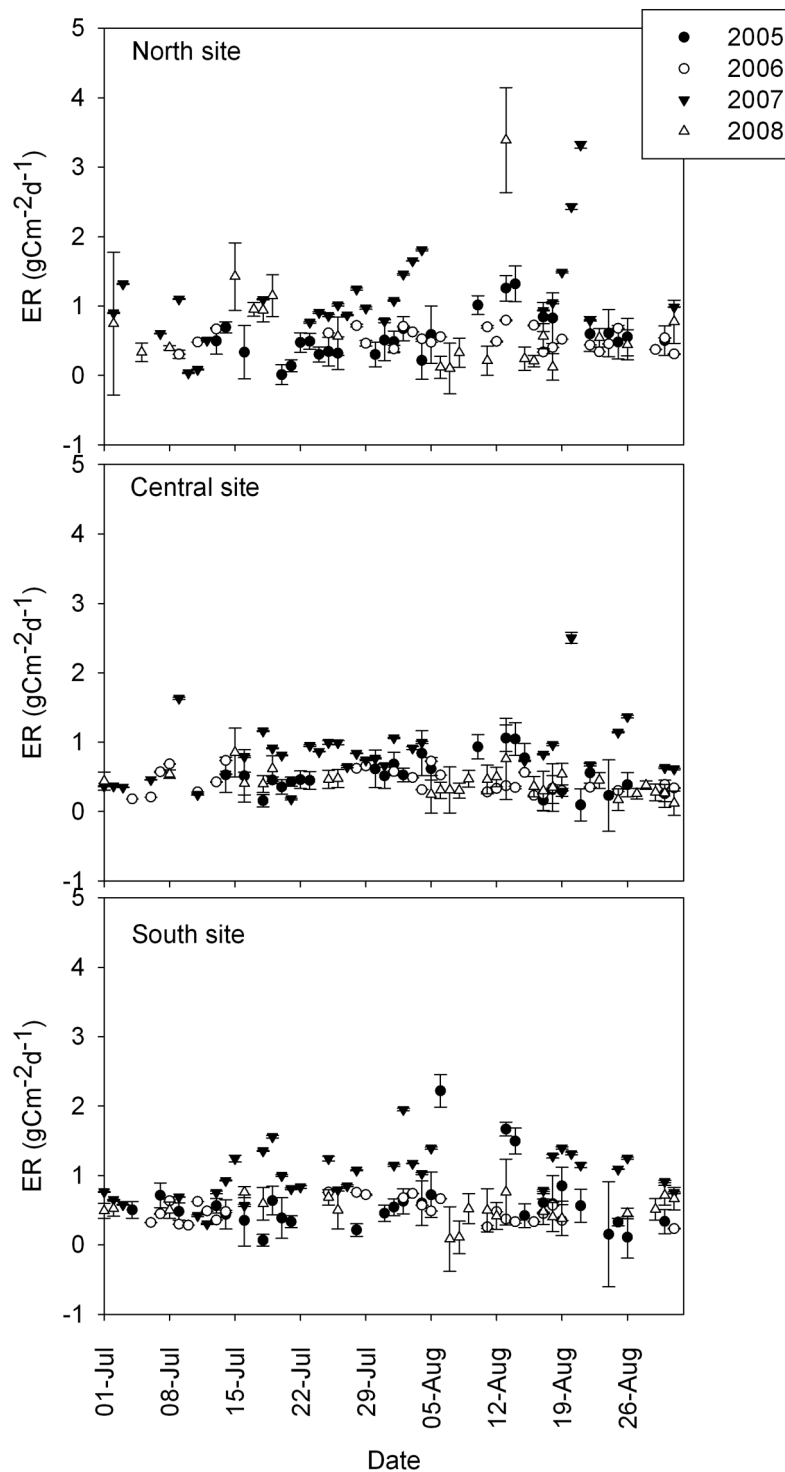


Figure 4. Ecosystem respiration, ER ($\text{g CO}_2\text{-C m}^{-2} \text{d}^{-1}$) in the three sites (North, Central, and South) calculated using the intercept parameter (y_0) of the light response curve (for CO_2 fluxes filtered for $u^* > 0.1 \text{ m s}^{-1}$ for $\text{PAR} < 200 \mu \text{ mol m}^{-2} \text{ s}^{-1}$), approximated as linear, for daily intervals during the growing season in 2005, 2006, 2007, and 2008.

the escape would be much slower: calculated rates based on concentration gradients and diffusion constants were an order of magnitude lower than measured flux rates (data not shown). In this case, it could take almost the entire summer for released CO_2 to reach the surface. Unfortunately,

dissolved CO_2 was not measured in summer 2007 and 2008, but the following summer (2009) it showed rather constant values in the pore water [Lipson *et al.*, 2012]. It appears likely that CO_2 was released from the soil by other means such as bubbles, cracks, and roots, rather than by

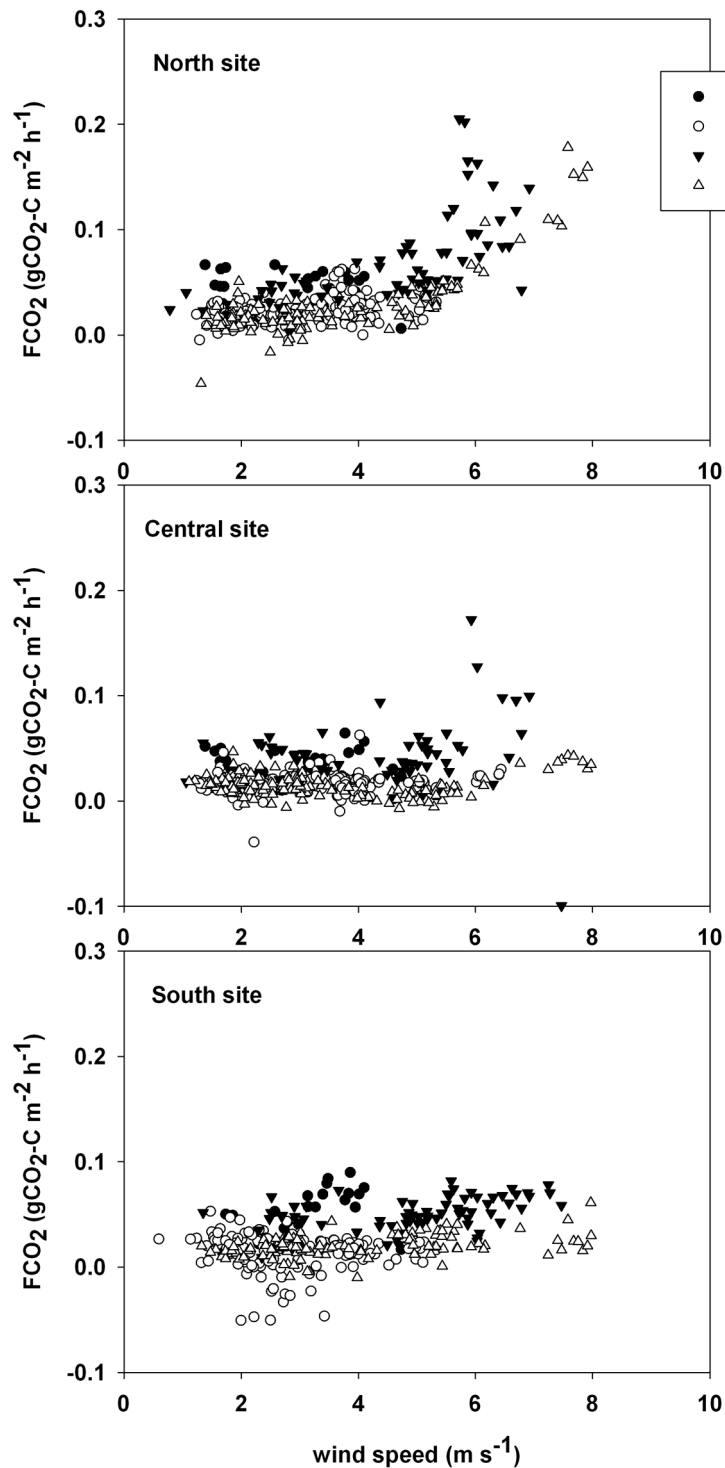


Figure 5. (a) Half-hour averaged nighttime CO₂ fluxes (filtered for $u^* > 0.1 \text{ m s}^{-1}$ and $\text{PAR} < 10 \mu \text{ mol m}^{-2} \text{ s}^{-1}$) and half-hour averaged wind speed (measured by the sonic anemometer, m s^{-1}) in the North, Central, and South sites in 2005–2008. In 2005, the regression between nighttime CO₂ fluxes and the mean wind speed resulted in R^2 values of 0.022 (p-value = 0.76), 0.022 (p-value = 0.74), and 0.18 (p-value = 0.11) for the North, Central, and South sites; in summer 2006, in R^2 values of 0.15 (p-value < 0.001), 0.019 (p-value = 0.25), and 0.053 (p-value = 0.023) for the North, Central, and South site; in summer 2007, in R^2 of 0.45 (p-value < 0.001) in the North, R^2 of 0.05 (p-value = 0.22) in the Central, R^2 of 0.21 (p-value < 0.001) in the South; in summer 2008 in R^2 of 0.84 (p-value < 0.001) in the North, R^2 of 0.35 (p-value < 0.001) in the Central, R^2 of 0.18 (p-value < 0.001) in the South site.

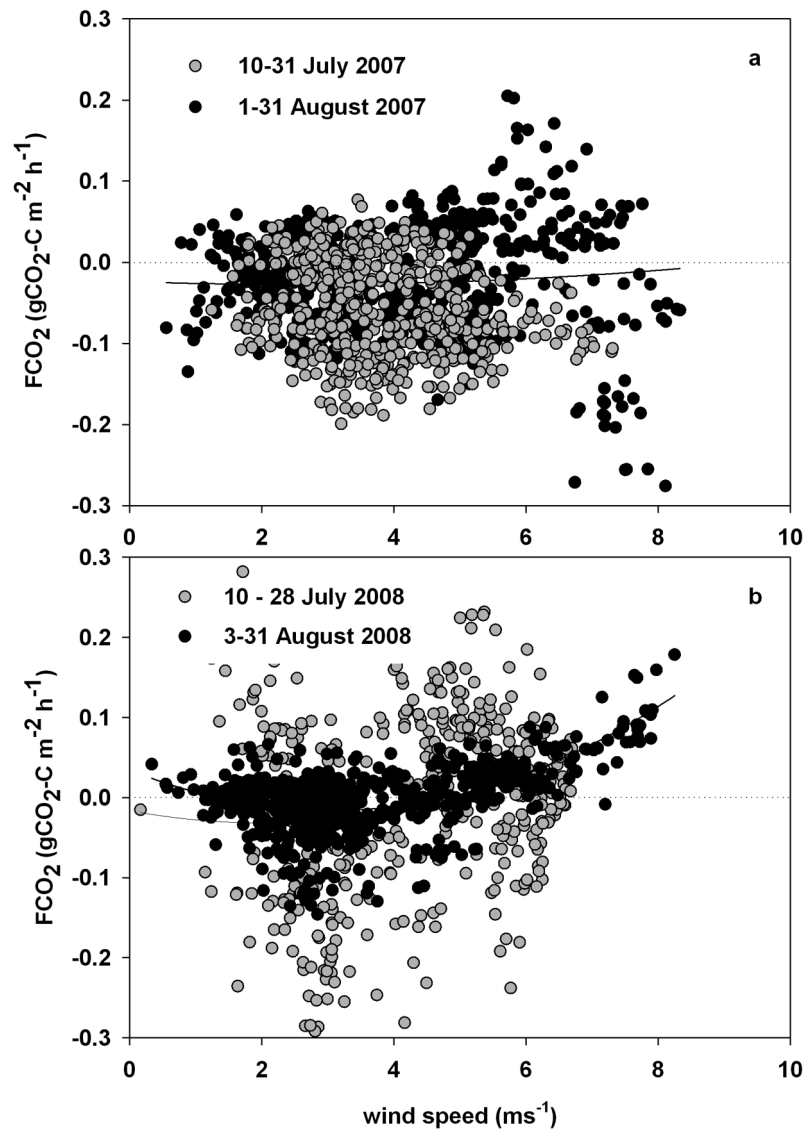


Figure 6. Half-hour averaged CO₂ fluxes (filtered for $u^* > 0.1 \text{ m s}^{-1}$) and half-hour averaged wind speed (measured by the sonic anemometer) in the North site in summer 2007 and 2008. The R^2 for the period 10–31 July 2007 was 0.05 (p-value < 0.001), and for the period 1–31 August 2007 R^2 was 0.03 (p-value < 0.001); the R^2 for the period 10 to 28 July 2008 was 0.05 (p-value < 0.001), and for the period 3 to 31 August R^2 was 0.40 (p-value < 0.001). Displayed are the regression lines during August (2007 and 2008).

diffusion through the soil alone, leading to a much faster release, before dissolving in the water. Therefore, wind can speed CO₂ release rates by three processes: 1) increasing the rate of release of CO₂ from the subsurface soil, 2) mixing in the water column, and 3) increased surface exchange. The first two of these effects most likely are more important as CO₂ production rates increase with deeper thaw and warmer soil temperatures and as a result, more bubbles are formed to be release by the indirect effects of wind [Huebert *et al.*, 2010].

[35] This strong dependence of nighttime CO₂ emission on wind speed was only observed in the summer 2007 and 2008 in the North site (e.g., the site with increased water table, and flooded microsites) (Figure 5) and it was much weaker in the Central and South sites. The baseline years

(2005–2006), before the increase in water table in the North site, CO₂ fluxes and the wind speed presented very low correlation coefficients in any of the sites. In 2005, the regression (polynomial fit, $f = y_0 + a*x + b*x^2$) between nighttime CO₂ fluxes, and the mean wind speed resulted in R^2 values of 0.022 (p-value = 0.76), 0.022 (p-value = 0.74), and 0.18 (p-value = 0.11) for the North, Central, and South sites; in summer 2006, this correlation presented R^2 values of 0.15 (p-value < 0.001), 0.019 (p-value = 0.25), and 0.053 (p-value = 0.023) for the North, Central, and South site; in summer 2007 this correlation resulted in R^2 of 0.45 (p-value < 0.001) in the North, R^2 of 0.05 (p-value = 0.22) in the Central, R^2 of 0.21 (p-value < 0.001) in the South site; in summer 2008 this correlation presented R^2 of 0.84 (p-value < 0.001) in the North, R^2 of 0.35 (p-value < 0.001)

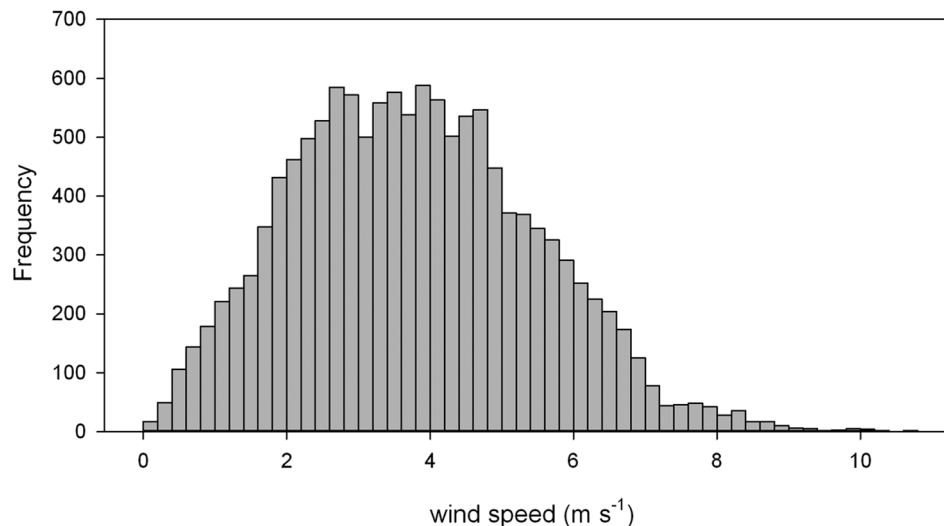


Figure 7. Frequency of half-hourly average wind speed measurements (m s^{-1}) at 1.6 m above the ground during the study period (2005–2008).

in the Central, R^2 of 0.18 (p -value < 0.001) in the South site.

[36] The low correlation between nighttime CO₂ flux and mean wind speed in the pre-treatment years (2005, and 2006) in any of the sites, and in the Central and South site in treatment years (2007 and 2008), together with the higher correlation in the North in the treatment years, indicated that the observed sensitivity of rates of CO₂ emission to wind speed in the North site was the result of the increase in water table. These results are in agreement with previous studies that showed a strong dependence of gas exchange on wind speed over water bodies [Fan *et al.*, 1992; Wille *et al.*, 2008] and high greenhouse gas emissions from boreal lakes [Vesala *et al.*, 2006; Jackowicz-Korczyński *et al.*, 2010] and from small ponds and cracks in wet tundra [Spott, 2003]. Even if the landscape was not entirely flooded in summer 2007, the very variable microtopography of the North site and the significant polygon development (Figure 2) probably led to flooded microsites.

[37] Nighttime CO₂ fluxes from the flooded area in summer 2008 were not significantly correlated with air or soil temperature, and increase in wind speed was also not driven by an increase in air or soil temperature (usually connected to increase in atmospheric turbulence). The correlations between wind speed and soil temperature in the flooded site (from 12 June to 31 August 2008, at the surface, and at 1 cm, 5 cm, 10 cm, 20 cm, and 30 cm below surface) or between wind speed and air temperature were either not significant or presented very low explanatory power (R^2). The lack of a significant correlation between the soil temperature and CO₂ flux was probably connected to the time lag between the production of CO₂ and its emission from the flooded area. As shown in the histogram of the wind speed for the three summers (Figure 7) this site is located in a fairly windy environment. Consequently, the inclusion of wind speed in models of CO₂ emissions could be highly relevant to accurately simulate CO₂ fluxes where surface water, ponds, and lakes are major components of the land cover [Hinkel *et al.*, 2005].

[38] A contemporary study [Olivas *et al.*, 2010], that measured CO₂ fluxes using chambers instead of eddy covariance, showed different pattern to that shown here (e.g., lowest respiration in the North site with the highest water table). This result is most likely due to the fact that chambers experience quite different winds compared to nature, and there appears to be a clear positive effect of wind speed on CO₂ loss from this ecosystem when the landscape was flooded as in 2007 and 2008 (Figure 5). This effect was not captured by chambers, which isolate the surface from the winds. In non-flooded areas, respiration rates estimated by chambers measurements were fairly comparable with the estimates from the eddy covariance (see previous sections).

3.6. Anaerobic Soil Incubations and Soil Characterization

[39] Anaerobic CO₂ production, measured in different soil layers at our manipulation site, was considerable even in deeper soil layers (Figure 8). In these areas, deeper soil layers produced the highest CO₂ emissions, though methanogenesis appeared to become substrate-limited more quickly in the deepest layer (as shown by the decrease in CH₄ emission with time in the 30–50 cm layer, Figure 8). The one-way ANOVA and Fisher's Least-Significant-Difference Test of the entire anaerobic soil incubations data set showed that the CO₂ and CH₄ emissions among the three layers (Figure 8) were not significantly different. This higher CO₂ production in the deepest soil layer (30–50 cm) could have contributed to the observed ecosystem scale-CO₂ loss from the North site later in the season (Figures 4 and 6) when thaw depth was greatest. Overall, this laboratory incubation showed that sufficient substrate and electron acceptors exist in these soils to sustain high levels of anaerobic respiration for at least two months (Figure 8). The sustained respiration rates under anoxic conditions showed that these microbial communities were dominated by anaerobes (Figure 8). In the North site the waterlogged soils and the generally anaerobic conditions led to fairly low oxidation reduction potential (ORP) (below about 100 mV in all

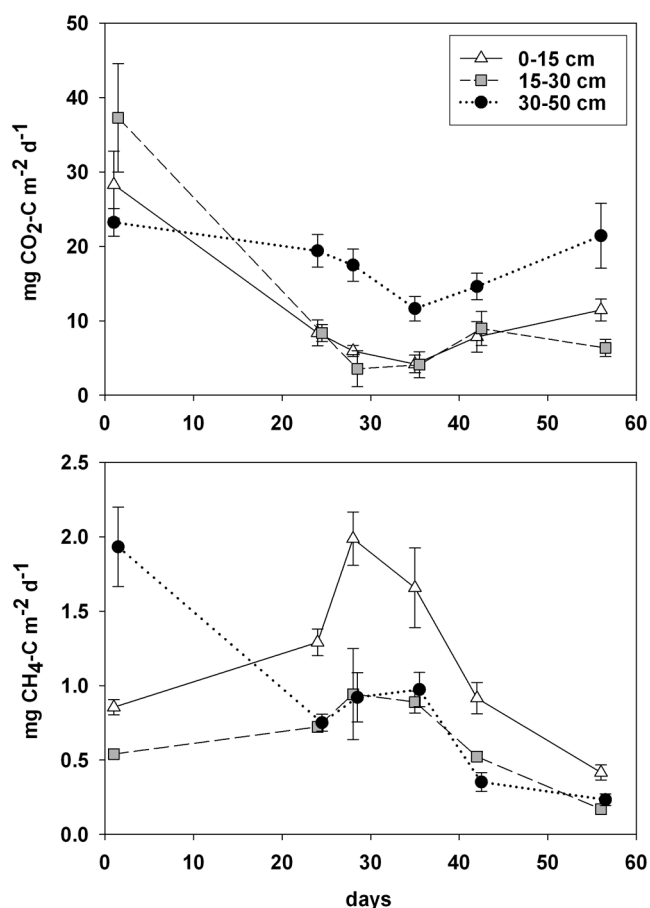


Figure 8. Rates of CO₂ and CH₄ production in long-term laboratory incubations at 4°C. Containers were flushed with N₂ gas 24 h before each measurement. Displayed are means and standard errors of six replicates. Values were converted to m² basis for comparative purposes. Data derive from laboratory experiments on soil cores from the North site (including plant roots) sampled during March 2008.

the measured soil layers from 5 to 15 cm depth) supporting anaerobic respiration as the dominant processes producing CO₂ in the flooded site. The anaerobic nature of the environment is due to the combination of the low surface elevation of these vegetated drained lakes relative to the watershed boundaries and the presence of continuous permafrost which prevents water drainage. This results in generally wetter and more anaerobic soils [Lipson *et al.*, 2010] in these vegetated drained lake basins. Anaerobic respiration (e.g., using alternative electron acceptors such as Fe(III) and humic substances instead of O₂) can contribute greatly to CO₂ flux under such conditions. The anoxic conditions of soils greatly increases the importance of anaerobic respiration [Cervantes *et al.*, 2000; Lovley *et al.*, 1996; Nevin and Lovley, 2002; Lipson *et al.*, 2010, 2012].

[40] As shown in Figure 8 the relative CO₂ emissions were much higher than the CH₄ emissions (CO₂:CH₄ ratio was on average 13:1, 20:1, 19:1 in the three soil layers 0–15, 15–30, 30–50 cm). Lipson *et al.* [2012] showed even higher CO₂:CH₄ ratios (with ratios of 46:1–572:1 dissolved in soil pore water and 42:1–890:1 evolved in anaerobic incubations).

Clearly, a much larger CO₂ than CH₄ production occurred even under anaerobic conditions. Consequently, the complete oxidation of CH₄ would only slightly increase the total CO₂ emission (on average of ~7%). This much higher CO₂ emission than CH₄ emission (Figure 8) is in agreement with our previous study in this location [Zona *et al.*, 2009]. Moreover, flooding decreased the oxic surface layer, leading to less oxidation, further confirming the dominant role of anaerobic CO₂ respiration to the carbon loss from this ecosystem during this manipulation experiment. This is consistent with an environment rich in alternative electron acceptors such as Fe(III) and humic substances [Lipson *et al.*, 2010].

[41] High concentrations of Fe were found in the soils at this manipulation site (Table 1) and the deeper thaw provided more contact with the iron-rich mineral layer which is found at depth (Table 1) [Lipson *et al.*, 2010]. The deeper thaw in the North site made previously frozen soil layers, rich in organic carbon (Table 1), available for microbial decomposition.

3.7. Importance of Anaerobic CO₂ Loss

[42] Overall, we believe that the wind most likely only facilitated the exchange of CO₂ produced previously and stored either in the water column, or possibly as bubbles in the soil beneath the water surface. The lag between CO₂ production, movement through the soil and into the water above the soil surface and then emission into the atmosphere [Elberling *et al.*, 2008] could explain at least some of the observed lack of short-term correlation between CO₂ effluxes (filtered for PAR ≤ 10 μmol m⁻² s⁻¹) and soil or air temperature at the North area.

[43] The oxidation reduction potentials (ORP) in the flooded site (always below about 100 mV in all the measured soil layers from 5 to 15 cm depths) were too low for aerobic respiration to occur below the water table level proving that other were responsible for CO₂ production [Kappler *et al.*, 2004; Lipson *et al.*, 2010]. Reduction of Fe and humic acids were proved to be major respiratory pathways in this and other similar ecosystems [Roden and Wetzel, 1996; Lipson *et al.*, 2010, 2012; Zhang *et al.*, 1999; Heitmann *et al.*, 2007] and could play an important role in the observed higher CO₂ production in anaerobic conditions at our site [Lipson *et al.*, 2010, 2012]. The deeper thaw in the North site made available more Fe from the mineral layer (Table 1), and possibly increased the production of CO₂ by the Fe(III) reduction pathway [Lipson *et al.*, 2010]. The microbial communities in these drained lakes appear well-adapted to anaerobic conditions (Figure 8), and this pathway should be considered as a potential source of CO₂ from thawing permafrost. Little information is currently available about the potential role of exocellular electron transport [Lovley *et al.*, 1996; Nevin and Lovley, 2002; Stams *et al.*, 2006] in arctic peat soils, and the role of Fe and humic substances as electron acceptors has not yet been fully integrated into an understanding of carbon cycling in Arctic soils [Lipson *et al.*, 2010, 2012]. Overall, the increase in water table in summer 2007 and 2008 led to the higher CO₂ emission in the North site, thereby suggesting that anaerobic respiration could be a very relevant process for the increased carbon loss.

[44] A lack of oxygen limits microbial activity not only directly but also indirectly by inhibiting the activity of enzymes breaking down organic matter [Freeman *et al.*, 2001] thereby limiting the substrate supply for anaerobic microbial metabolism [Freeman *et al.*, 2001]. However, the results of this study suggest that the new availability of carbon previously frozen, and thereby “trapped” in deeper soils layers in this ecosystem (Table 1), overcomes this supply limitation, and contributes, together with the higher soil temperature, to the higher respiration rates observed despite anaerobic conditions. As a consequence, the assumption that anaerobic conditions in peatlands could prevent the release into the atmosphere of the large amount of carbon stored in the soils [Billings *et al.*, 1982; Oechel *et al.*, 1998; Freeman *et al.*, 2001] is not necessarily valid. Wetter conditions can lead to increased thermal conductivity and higher soil temperatures and/or greater depth of thaw. The thawing of deeper, previously permanently frozen soil layers and the increase in soil temperature connected with climate change [Grosse *et al.*, 2011; Lee *et al.*, 2011; Wisser *et al.*, 2011] could significantly increase the loss of CO₂ to the atmosphere even under completely anaerobic conditions. Waterlogged half-bog soils are particularly sensitive to increases in temperature, as their soil carbon is at a less advanced decomposition stage than carbon in drier soils; it is therefore more vulnerable to decomposition [Douglas and Tedrow, 1959]. This soil organic carbon is distributed through the soil profile through cryoturbation before being decomposed, and it is also found in significant quantities in the permafrost layer [Michaelson *et al.*, 1996; Bockheim, 2007; Waldrop *et al.*, 2010]. The comparison of the CO₂ and CH₄ emission in the soil incubation experiment confirmed that in this ecosystem, even under anaerobic conditions, CO₂ production remains much higher than CH₄ production.

[45] Widespread warming of permafrost in the Arctic has been reported [Brown and Romanovsky, 2008; Kuhry *et al.*, 2009]. Increased active-layer thickness [Brown *et al.*, 2000] and permafrost degradation [Sannel and Kuhry, 2011], already occurring in the southern limit of the permafrost zone [Brown and Romanovsky, 2008], are leading to thawing of previously frozen organic carbon and increase microbial aerobic decomposition. Both these processes could result in a considerable increase in CO₂ emissions to the atmosphere from Arctic soils due to the large carbon stored in the soils [Schuur *et al.*, 2008; Tarnocai *et al.*, 2009], the rate of change, and the susceptibility to climate change of these systems. The large majority of the soil carbon pool is in fact present in perennially frozen soils, and the near-surface permafrost is among the most vulnerable to thawing [Tarnocai *et al.*, 2009].

[46] Increased wetness [Smith *et al.*, 2005] and subsidence due to thawing, including ice wedge degradation [Jorgenson *et al.*, 2006; Sannel and Kuhry, 2011], lead to flooding of wet tundra ecosystems. Newly flooded areas are potential emitters of CO₂, including by the processes reported here. Moreover, considering the extent of water bodies (lakes and ponds) in the Arctic tundra, wind speed could have a dominant, yet not yet fully quantified, impact on the CO₂ loss from these flooded areas. Importantly, as the C loss was connected to increase in wind speed, and could not be captured by chamber measurements, it is important to carefully choose the methodology used to measure gas exchange in

these flooded ecosystems. Furthermore, the effect of wind should be included in atmospheric analyses of the regional carbon balance from the Arctic. This is particularly important, as global climate models project the strongest warming by the end of the 21st century to be in northern latitudes, with up to 7 to 8°C of warming in these regions [Intergovernmental Panel on Climate Change (IPCC), 2007]. These models also predict an increase in total precipitation into the 21st century due to increases in atmospheric moisture with rising temperatures [IPCC, 2007; Wisser *et al.*, 2011]. This implies that many areas of the Arctic will be warmer and wetter. The inclusion of environmental drivers such as wind, in the models of the carbon exchange from the Arctic could greatly improve the temporal precision of carbon loss from this ecosystem.

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