Vegetation height and other controls of spatial variability in methane emissions from the Arctic coastal tundra at Barrow, Alaska

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[1] We conducted measurements of methane (CH4) emission and ecosystem respiration on >200 points across the Arctic coastal tundra near Barrow, Alaska, United States, in July 2007 and August 2008. This site contains broad diversity in tundra microtopography, including polygonal tundra, thaw lakes, and drained lake basins. In 2007, we surveyed CH4 emissions across this landscape, and found that soil water content was the strongest control of methane emission rate, such that emission rates rose exponentially with water content. However, there was considerable residual variation in CH4 emission in the wettest soils (>80% volumetric water content) where CH4 emissions were highest. A statistical analysis of possible soil and plant controls on CH4 emission rates from these wet soils revealed that vegetation height (especially of Carex aquatilis) was the best predictor, with ecosystem respiration and permafrost depth as significant copredictors. To evaluate whether plant height served as a proxy for aboveground plant biomass, or gross primary production, we conducted a survey of CH4 emission rates from wet, Carex-dominated sites in 2008, coincidently measuring these candidate predictors. Surprisingly, vegetation height remained the best predictor of CH4 emission rates, with CH4 emissions rising exponentially with vegetation height. We hypothesize that taller plants have more extensive root systems that both stimulate more methanogenesis and conduct more pore water CH4 to the atmosphere. We anticipate that the magnitude of the climate change–CH4 feedback in the Arctic Coastal Plain will strongly depend on how permafrost thaw alters the ecology of Carex aquatilis.


1. Introduction

[2] Methane (CH4) is a potent greenhouse gas [Denman et al., 2007] whose atmospheric concentrations rose persistently through the late 20th century, then surprisingly stabilized from 2000 until 2007, only to rise again after 2007 [Dlugokencky et al., 2009]. Several studies [Fletcher et al., 2004; Bousquet et al., 2006] have sought to identify shifts in source and/or sink strengths that led to the stabilization, but the mechanism remains unresolved, thus exposing weaknesses in our understanding of CH4 biogeochemistry. Despite success at balancing a temporally static global CH4 budget [Denman et al., 2007], our inability to explain dynamics in methane’s accumulation rate indicates that we are not yet ready to generate the century-scale predictions of CH4 accumulations that are of increasing interest for policy planning [Meehl et al., 2007].

[3] Freshwater wetlands are the largest source of CH4 to the atmosphere, with northern high-latitude (>45°N) wetlands accounting for 22–50% of the wetland sources [Zhuang et al., 2004; Denman et al., 2007]. The Arctic tundra makes the largest contribution to this region’s emissions because of moderate emission per unit area combined with a very large surface area [Zhuang et al., 2004]. There is additional interest in CH4 emissions from Arctic tundra because anthropogenic climate change is expected to warm Arctic systems more than any other ecosystem, thus enhancing CH4 emissions and inducing an important positive feedback [Callaghan et al., 2004]. Elevated CH4 emission from the Arctic has already been invoked to explain the anomalous growth rates in

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atmospheric CH$_4$ during 2007 [Dlugokencky et al., 2009], an unusually warm year in the Arctic.

[4] The net exchange of CH$_4$ from the tundra surface arises from the balance between CH$_4$ production (methanogenesis) in anoxic zones and soil CH$_4$ consumption (methanotrophy) in oxic zones. Methanogenesis can be limited either by the supply of substrates (i.e., acetate and H$_2$), or by the redox conditions that determine the relative amounts of energy flow through methanogenic versus nonmethanogenic pathways [von Fischer and Hedin, 2007]. Although temperature has a strong, direct effect on the metabolic rates of methanogens [Conrad, 1989], it also affects the thermodynamics of both methanogenesis and the fermentative processes that generate acetate and H$_2$ [Kotsyurbenko, 2005] and so rates and pathways of methanogenesis are highly temperature sensitive. Soil water and permafrost depth influence rates of methane production to the extent that these properties alter the soil temperature and redox status.

[5] Methanotrophic bacteria in the aerobic layers that typically overlie zones of methanogenesis can consume methane prior to release [Whalen and Reeburgh, 1990a, 1990b]. However, the impact of methanotrophy on net CH$_4$ emission depends strongly on the transport pathway that CH$_4$ takes to the atmosphere. High rates of methanotrophy are associated with diffusive transport of CH$_4$ through soils from deeper anoxic regions up to the atmosphere [Whalen and Reeburgh, 1990a, 1990b]. In contrast, plants can conduct CH$_4$ from deeper, anoxic zones to the atmosphere via aerenchyma (i.e., gas conducting tissues), thus bypassing the oxic layers and reducing the effects of methanotrophy [Bartlett et al., 1992; Torn and Chapin, 1993; King et al., 1998; Juutinen et al., 2003]. Ebulition is thought to have very little associated methanotrophy because the bubbles move quickly from anoxic zones to the atmosphere [Walter et al., 2006]. Cumulatively, these interacting processes cause net CH$_4$ exchange rates to respond to biological and physical factors that vary both spatially (e.g., landform, climatic zone and associated plant community) and temporally (e.g., seasonally, interannually).

[6] To quantify temporal variability, studies have employed high-frequency flux measurements on the subarctic and Arctic tundra, using eddy covariance (EC) methods [Fan et al., 1992; Friberg et al., 2008; Sachs et al., 2008; Zona et al., 2009], flux gradient methods [Harazono et al., 2006], or repeated flux chamber measurements [Whalen and Reeburgh, 1988; Mastepanov et al., 2008]. These temporally intensive studies have proven invaluable for developing annual or growing season budgets of CH$_4$ emission, and the EC towers have done so at multihectare spatial scales. But the improved temporal resolution comes at the expense of spatial resolution: EC studies are, by design, spatially integrated flux measurements, and automated chambers are necessarily fixed in place and limited in coverage. High spatial resolution is important because heterogeneity in the microtopography, hydrology and plant community over the tundra landscape drives extreme spatial variability in CH$_4$ emission rates [Morrissette and Livingston, 1992; Kutzbach et al., 2004; Riutta et al., 2007]. Reconciling top-down measurements (eddy covariance) with bottom-up measurements (flux chambers) is not simply a matter of producing flux values that are in reasonable agreement, but it also requires explaining how environmental and biological controls on the plot level could cumulatively account for the controls at the regional level. In other words, mechanisms underlying the spatial variability of fluxes at the microtopographic (flux chamber) scale should help explain the mechanisms underlying the temporal variability measured at the landscape (eddy tower) scale.

[7] A potential resolution of this problem of scale comes from the general observation that CH$_4$ emissions from northern wetlands tend to be lognormally distributed [e.g., Harriss et al., 1985]. Thus the spatially integrated CH$_4$ emission rate observed at tower and larger scales is influenced strongly by the upper tail of the emission distribution. We propose that small-scale studies should focus on finding points on the landscape that are capable of high emission rates, and then more closely examine the factors that control variability within that landscape type. Our research thus addresses the questions: (1) What parts of the tundra landscape are capable of high CH$_4$ emission rates? and (2) What factors control variation in CH$_4$ emissions in those areas?

[8] We address these questions using a large number of point observations of CH$_4$ emission rates from the Arctic coastal tundra at Barrow, Alaska, United States. In evaluating the first question, we address the hypothesis that soil moisture variation constrains the envelope of emission rates: dry sites have only low emission rates while wet sites can have low or high rates. There is support for this hypothesis from diverse ecosystems [e.g., Morrissette and Livingston, 1992; von Fischer and Hedin, 2007] and so we anticipate soil moisture will provide a useful means for identifying sites with high potential for emission. However, there is far greater uncertainty associated with the second question and so we evaluate four hypotheses. First, following the work of Whiting and Chanton [1993], we examine the hypothesis that greater ecosystem carbon flow (ecosystem respiration, gross primary production or net ecosystem exchange) induces higher rates of CH$_4$ emission. Second, we test the hypothesis that methane emissions vary with plant species composition because plant species differ in properties associated with CH$_4$ production and transport. Third, we hypothesize that edaphic properties of the tundra (permafrost depth, temperature, water table depth), as physiological controls of methanogenic and methanotrophic bacteria, are important ecosystem-scale controls of CH$_4$ emission rates [e.g., Morrissette and Livingston, 1992]. And finally, we examine the potential for plant architecture (plant height or aboveground biomass) to drive variation in CH$_4$ emissions.

[9] Overall, we seek to explain variation in CH$_4$ emissions in terms of macroscopic ecosystem properties that can be used for subsequent efforts to generate scaled-up estimates of regional CH$_4$ emissions. Our work complements the Barrow Biocomplexity Experiment that initiated a large-scale water table manipulation to simulate permafrost thaw. By examining patterns in emission in the adjacent nonmanipulated tundra, our study complements the work of Zona et al. [2009] who describe the short-term (1 year) response to treatment.

[10] Our approach is unique among studies of spatial variation in Arctic CH$_4$ emissions in the way we collect and analyze environmental covariate data. Instead of using an approach that is categorical in its treatment of the polygonal tundra surface (i.e., polygon center, rim, trough, etc.), we focus on the edaphic and vegetative properties as they vary continuously across the study site, guided by the notion that
efforts to scale-up and to develop improved mechanistic models of tundra CH$_4$ emission will benefit from using these continuously varying predictors. This approach allows us to use ANCOVA to simultaneously test the importance of a suite of covarying predictors.

2. Site Description

[11] Research was conducted at the Barrow Environmental Observatory (BEO, 71°17′N, 156°37′W), a 7466 acre reserve located ~6 km east of the town of Barrow, Alaska, United States. The BEO is on the Barrow Peninsula, the northernmost extent of the Alaskan Arctic Coastal Plain. The topography of the region is characterized by low relief and poor drainage [Brown et al., 1980]. On the Barrow Peninsula, lakes cover 22% and drained thaw lake basins (young, medium, old and ancient) cover 50% of the surface [Hinkel et al., 2003]. As basins age, patterned ground develops as a consequence of tundra heaving by ice wedges, and north of 71°15′N, about 65% of the land cover is polygonal tundra, including high-centered and low flat-centered polygons that can range from a few meters to more than 30 m in diameter [Brown et al., 1980].

[12] The bioclimatic zone of the region is sedge/grass and moss wetland tundra, which occupies 101,000 km$^2$ of land in the Arctic [CAFM-Team, 2003]. The dominant vegetation includes Carex aquatilis, Eriophorum russeolum, Eriophorum angustifolium, Dupontia fisheri, Arctophila fulva, various bryophytes and lichens, and some dwarf dicotyledonous plants [Brown et al., 1980; Billings et al., 1982].

[13] Winters are long and cold, with freezing temperatures for 9 months of the year [Brown et al., 1980]. In the Barrow area, the 30 year (1971–2000) annual average temperature is −12.1°C, precipitation is 10.6 cm, and snowfall is 74.2 cm (http://www.nws.noaa.gov/climate/). The average depth of maximum seasonal thaw (active layer) ranges from 35 to 40 cm [Nelson et al., 1998; Hinkel et al., 2003]. Because of poor drainage and cold, moist conditions, organic matter has accumulated in the soils and the permafrost [Brown et al., 1980].

3. Methods

[14] We measured fluxes of CH$_4$ and CO$_2$ during two sampling campaigns: 14–23 July 2007 and 1–9 August 2008. During the first campaign (2007), we surveyed the polygonal tundra and drained lake surfaces with 248 flux chamber measurements over 155 unique points on the landscape surface. Following the landscape sampling suggestion of Irvine et al. [2007], we used a clustered sampling strategy, distributing the 155 points over a 45 ha study area in 13 widely dispersed clusters. The 10 to 15 points in each cluster were spaced over a ca. 10 m × 10 m area to characterize heterogeneity at this finer spatial scale. Clusters were spaced between 20 m and 250 m apart to sample variability at larger spatial scales.

[15] Included in the 2007 observational campaign was a small experiment to determine the importance of acetate supply on CH$_4$ emission rates. The second campaign (2008) targeted sites dominated by Carex aquatilis on inundated terrestrial surfaces and thaw lake margins. In the 2008 campaign, we measured CH$_4$ and CO$_2$ fluxes 143 times from 82 unique locations. None of our samples were taken from areas that were experimentally manipulated as part of the Barrow Biocomplexity project.

[16] There has previously been little work to evaluate temporal variability in CH$_4$ emissions using manual flux chambers. We examined variability over two timescales that were tractable within our study. In 2007, we conducted a 48 h (8 h interval) study to characterize diurnal patterns, and in 2008 we made measures on a 6 h timescale (30 min interval) to examine emission patterns during changing weather conditions.

[17] In both campaigns, we measured CH$_4$ and CO$_2$ fluxes using a field-deployed Los Gatos High Precision CH$_4$/CO$_2$/H$_2$O analyzer. Gas concentrations are measured at 1 Hz with typical precisions better than 2 ppb/500 ppb/500 ppm, respectively. We relied upon the factory-supplied calibration algorithm for all analyses, but validated performance daily against CO$_2$ and CH$_4$ standards brought to the site in 40L Tedlar bags. Gas fluxes reported here were corrected for water vapor dilution using the instrument algorithm that calculates the mixing ratio of CH$_4$ and CO$_2$ for dry air. To measure fluxes, closed chambers were placed over the soil surface using incubation times of 3–5 min. Two pieces of 9 m-long polyethylene tubing (6.35 mm OD, 3.175 mm ID) connected the chamber headspace and the analyzer, and air was recirculated using an internal pump at 500 mL/min. The instrument was powered using a 12 V car battery and DC–AC power inverter.

[18] Chamber bases were opaque PVC and were inserted into the tundra surface ~24 h before measurement to a depth of 8 ± 2 cm to maintain vertical gradients in gas concentrations during measurement. Throughout the text, we refer to the location of each chamber base as a “point” on the landscape. Chamber lids were round, 20 cm inside diameter, and vented following Livingston and Hutchinson [1995]. They sealed against the chamber base with a narrow strip of self-adhesive closed-cell weather stripping. When used to measure ecosystem respiration, the chamber lids were opaque PVC, but we used clear acrylic chamber lids when measuring photosynthetic activity. To quantify the total system volume, we measured the height of each chamber above the soil or water surface each time we measured gas flux.

[19] During the flux measurement phase, we excluded data from the first 90 s while air in the chamber headspace, tubing and analyzer equilibrated. After this equilibration period, CH$_4$ concentrations generally rose linearly with time (>98% of observations). Because the data appeared in real time at 1 Hz on the instrument screen, we were able to immediately identify and repeat any flux measures where we observed anomalous trends in gas concentrations over time (e.g., due to ebullition events, <2% of observations). With opaque chambers, CO$_2$ concentrations also rose linearly with time, but with clear chambers, the CO$_2$ concentrations could fall asymptotically. To reduce the effect of this nonlinearity on clear-chamber CO$_2$ fluxes, we shortened the sampling period from 5 min with opaque chambers to 3 min with clear chambers. Fluxes were calculated based on linear regression of the gas concentration change with time, and the data were constrained to periods of linear concentration change. Gross primary production (GPP) was calculated from net ecosystem
CO₂ exchange (NEE) in clear chambers and ecosystem respiration from opaque chambers.

[20] Associated with every chamber flux measurement, we recorded edaphic and biological properties of the tundra. We measured permafrost depth using a 1.5 mm diameter metal rod. Soil moisture over the top 12 cm was determined using a Campbell Hydrosense handheld TDR probe, with three replicate measures per chamber. A Digisense digital thermometer indicated temperature of the landscape surface (i.e., soil temperature in well-drained areas or water temperature in inundated areas) integrated over the top 10 cm. We determined water table depth to the nearest 0.5 cm, if it was shallower than 10 cm below the soil surface. Each chamber was geolocated, using high-precision GPS.

[21] To characterize the ground cover at each chamber point, we recorded the vegetation composition based on basal cover. Some organisms were taxonomically resolved to species level (Arctophila fulva, Carex aquatilis, Dupontia fisheri), others to genus (Eriophorum, Poa, Salix), and some more coarsely (bryophytes, lichens and “other forbs”). Included in this ground cover characterization was the percent cover by litter/bare ground, and cover by standing water. We did not sample from stands of vegetation that showed any signs of herbivory (e.g., damage to leaf tips).

[22] We also measured the maximum vegetation height at each point. Vegetation height was determined as the height of the tallest leaves, to the nearest 0.5 cm. Height was measured from the soil or water surface.

[23] During the 2007 campaign, we conducted an acetate addition experiment to determine the degree to which acetate was limiting for CH₄ emissions. Previous work using ¹⁴C-labeled CO₂ additions to tundra plants [King and Reeburgh, 2002] found that ¹⁴C-labeled CH₄ was produced within 24 h, indicating very rapid turnover of soil C pools in the production of CH₄. We sought to add sufficient acetate so that if all the methyl groups in the added acetate were converted to CH₄ and emitted over 24 h, it would lead to an added 50 mg CH₃C m⁻² d⁻¹ in emissions. Thus we dissolved sufficient sodium acetate into deoxygenated distilled water, and injected 5 mL of the acetate solution into each of 12 points in the tundra encircled by our chamber bases. The injections were made via a 2 mm OD cannulus to the middle of the thawed active layer: 10 cm depth. We used two types of controls for this experiment: one set received acetate-free deoxygenated water, and another set was not manipulated. Replication was 4 chambers per treatment. We measured CO₂ and CH₄ fluxes from under opaque lids 1 day prior to the experiment, and every 6 to 8 h for the next 36 h.

[24] During the 2008 campaign, we added measures of CO₂ dynamics under illuminated conditions to quantify gross primary production (GPP), and net ecosystem exchange (NEE) using a chamber lid that was transparent to visible light. To eliminate the variability induced by variation in solar radiation, we controlled light levels to the clear chambers using an external light box that completely covered the chamber and delivered an average 460 μE m⁻² s⁻¹ of photosynthetically active radiation (PAR) to vegetation within the chamber. This light level was typical of the conditions during our sampling period (95% of samples between 250 and 850 μE m⁻² s⁻¹), and it allowed us to standardize our measures of GPP despite variable environmental conditions. Heating of the chamber by the light box was <2°C during the 3 min incubation period. At the end of the measurements, we harvested all biomass above the soil or sediment interface, dried it at 70°C overnight, and weighed it to 0.01g.

[25] The 2007 growing season was warmer and drier than 2008 (D. Zona, personal communication, 2010; data from EC tower and weather station at study site). From 12 June to 31 August 2007, the average air temperature was 5.8°C and total precipitation was 15.4 mm, while the same period in 2008 saw air temperatures of 3.4°C and 41 mm precipitation. These differences were reflected in the weather during each campaign. The 2007 campaign period saw average air temperatures of 6.4°C and no precipitation, while average air temperatures over the 2008 campaign were 2.7°C and precipitation was 6.7 mm.

[26] All data were tabulated, and mathematical manipulations conducted in Excel 2007. Regression, ANOVA and ANCOVA calculations were conducted in JMP 7.0.1. Spatial statistical results were computed in R. Significant results were reported for p < 0.05.

4. Results

4.1. Characterization of Site

[27] We observed a distinct correlation structure among measures of edaphic and vegetative properties in the 2007 campaign. Soil temperature was positively correlated with permafrost depth (r² = 0.046, p < 0.0001) and with soil water content (r² = 0.29, p < 0.0001), while soil moisture was positively correlated with permafrost depth (r² = 0.26, p < 0.0001). Thus, dry parts of the tundra were cold with shallow permafrost, while wetter parts were warmer and had deeper permafrost (i.e., a thicker active layer). This correlation structure was also present in the 2008 survey, but weaker because we sampled a narrower range of soil moisture conditions.

[28] The vegetative cover from the 2007 survey revealed dominance by bryophytes across the landscape (overall average 39% basal cover, averaged over all sampling points), with additional coverage by Carex aquatilis (14%), Eriophorum (4.7%), other forbs (1.4%), lichens (1.1%), Luzula (0.96%), Dupontia fisheri (0.18%), Salix (0.49%) and Poa spp. (0.17%). Although an exhaustive analysis of plant ecology falls outside the scope of this paper, we did find patterns in distribution associated with soil water content. As we illustrate in Table 1, some species showed distinct distribution patterns, with Luzula, lichens, Salix, Dupontia, Poa and other forbs constrained to drier sites, while Arctophila was found only in deeper standing water. Eriophorum cover was greatest at sites with intermediate moisture. Bryophyte cover declined with increasing soil moisture. Carex cover was highly variable, and showed no correlation in percent cover with soil moisture.

4.2. Characterization of Gas Fluxes

[29] Our 2007 survey of 157 points on the BEO landscape identified a wide range of CH₄ exchange rates, from weak rates of CH₄ uptake (n = 5, strongest was −0.3 mg CH₄-C m⁻² d⁻¹) to very high rates of emission, up to 179 mg CH₄-C m⁻² d⁻¹. One anomalous point on the landscape (discussed in greater detail below) emitted CH₄ at exceptionally high rates. Excluding this anomaly and points subject to experimental manipulation, the mean of our observed CH₄ emission rate
was 33 ± 33 mg CH₄·C m⁻² d⁻¹ (mean ± standard deviation). Ecosystem respiration rates from this same set of points averaged 1.39 ± 0.78 g CO₂·C m⁻² d⁻¹. Soil temperatures averaged 3.3 ± 2.1°C, permafrost depth averaged 23 ± 5.1 cm, volumetric water content averaged 77 ± 21%, and vegetation height averaged 17.3 ± 8.1 cm.

[30] Our 2008 survey, which focused on 44 inundated points dominated by Carex aquatilis, had higher CH₄ emission rates (58 ± 37 mg CH₄·C m⁻² d⁻¹), but a similar range (3.4 to 167 mg CH₄·C m⁻² d⁻¹). Ecosystem respiration from these points averaged 0.76 ± 0.29 g CO₂·C m⁻² d⁻¹, GPP averaged −4.2 ± 2.6 g CO₂·C m⁻² d⁻¹, and NEE averaged −3.5 ± 2.4 g CO₂·C m⁻² d⁻¹ (negative signs indicate net uptake from the atmosphere). Soil temperatures were slightly warmer, 4.7 ± 2.0°C. Water table depth averaged 9.8 cm deep, but ranged from 1.5 cm below the surface to 37 cm deep. Permafrost was also deeper, 38 ± 12 cm.

[31] Repeated measures of some points indicate that both CH₄ and CO₂ flux rates are stable over hours to days (Figure 1). In 2007, repeated observation of 5 chambers over 48 h (n = 5 observations per chamber) revealed that the coefficient of variation (ratio of mean to temporal standard deviation) averaged 16%. To evaluate the importance of climatic factors for regulating this temporal variation, we repeated observation of 5 different points between 10 A.M. and 5 P.M. (n = 10 observations per point) on 9 August 2008. Over this time, local conditions transitioned from overcast and still to clear and breezy, and the CH₄ emission rates increased. However, the magnitude of temporal variation was similar in magnitude to the 2007 data, with an average coefficient of variation of 18%. A statistical model of this 2008 data, considering point ID (i.e., which chamber was being measured), wind speed, air temperature and PAR explained 74% of the variation in the log of CH₄ emission rates, but only point ID and wind speed were significant predictors (p < 0.0001 and p < 0.003, respectively; all other p > 0.16). However, because this set of measures was conducted at the end of our 2008 campaign, we did not learn the importance of wind speed, and therefore did not measure wind speed at any other times during the campaign.

[32] Despite this general evidence for stability in gas emission rates, we found one extreme outlier area with very high spatial and temporal variability during our 2007 campaign. This point fell on an area of relatively dry polygonal tundra (57% volumetric water content) dominated by bryophytes. On 17 July, successive flux measures at a single point within 1.5 h yielded extremely high emission rates of 825 and 1153 mg CH₄·C m⁻² d⁻¹. Three days later, on 20 July, we installed additional chamber bases ca. 50 cm to the north, south and west of the original point. The original outlier point had fallen to 117 mg CH₄·C m⁻² d⁻¹, and the three other points were much lower (9, 11 and 64 mg CH₄·C m⁻² d⁻¹ at S, W and N, respectively).

Table 1. Soil, Vegetation, and Trace Gas Properties Observed on the Barrow Environmental Observatory, July 2007a

<table>
<thead>
<tr>
<th>Property</th>
<th>Dry</th>
<th>Moist</th>
<th>Wet</th>
<th>Flooded</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of samples</td>
<td>19</td>
<td>50</td>
<td>44</td>
<td>44</td>
</tr>
<tr>
<td>Proportion of samples (%)</td>
<td>12</td>
<td>32</td>
<td>28</td>
<td>28</td>
</tr>
<tr>
<td>Temperature (°C)</td>
<td>1.9 (1.7)</td>
<td>2.0 (0.81)</td>
<td>3.8 (1.34)</td>
<td>4.6 (1.81)</td>
</tr>
<tr>
<td>Permafrost depth (cm)</td>
<td>21 (6.0)</td>
<td>20 (2.3)</td>
<td>23 (3.9)</td>
<td>29 (2.0)</td>
</tr>
<tr>
<td>Volumetric water content (%)</td>
<td>34 (13)</td>
<td>67 (13)</td>
<td>86 (6.3)</td>
<td>95 (2)</td>
</tr>
<tr>
<td>Bryophytes (%)</td>
<td>74 (35)</td>
<td>76 (39)</td>
<td>27 (40)</td>
<td>0.6 (2.4)</td>
</tr>
<tr>
<td>Carex (%)</td>
<td>13 (16)</td>
<td>15 (14)</td>
<td>16 (12)</td>
<td>11 (10)</td>
</tr>
<tr>
<td>Eriophorum (%)</td>
<td>1 (4)</td>
<td>7 (9)</td>
<td>7 (12)</td>
<td>0.7 (1.3)</td>
</tr>
<tr>
<td>Other forbs (%)</td>
<td>7.9 (12)</td>
<td>0.4 (1.2)</td>
<td>1.0 (4.6)</td>
<td>0.4 (1.0)</td>
</tr>
<tr>
<td>Lichens (%)</td>
<td>9.8 (19)</td>
<td>0.04 (0.28)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Lužula (%)</td>
<td>8.7 (23)</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Salix (%)</td>
<td>4.4 (15)</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Dupontia (%)</td>
<td>0.3 (1.2)</td>
<td>0.5 (1.7)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Poa (%)</td>
<td>1 (5)</td>
<td>0.1 (0.8)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Arotophila (%)</td>
<td>0</td>
<td>0.22 (1.0)</td>
<td>1.4 (6.2)</td>
<td>2.8 (7.0)</td>
</tr>
<tr>
<td>Litter or bare (%)</td>
<td>4.1 (9.2)</td>
<td>25 (50)</td>
<td>68 (38)</td>
<td>33 (39)</td>
</tr>
<tr>
<td>Standing water (%)</td>
<td>0</td>
<td>0</td>
<td>0.1 (0.8)</td>
<td>67 (39)</td>
</tr>
<tr>
<td>Vegetation height (cm)</td>
<td>9.7 (4.3)</td>
<td>15 (3.7)</td>
<td>18 (8.0)</td>
<td>25 (5.1)</td>
</tr>
<tr>
<td>CH₄ emission (mg CH₄·C m⁻² d⁻¹)</td>
<td>3.1 (6.7)</td>
<td>15 (13)</td>
<td>37 (32)</td>
<td>63 (34)</td>
</tr>
<tr>
<td>Ecosystem respiration (g CO₂·C m⁻² d⁻¹)</td>
<td>1.2 (0.53)</td>
<td>1.4 (0.70)</td>
<td>1.8 (0.85)</td>
<td>1.1 (0.65)</td>
</tr>
</tbody>
</table>

aCategories are based on field evaluation of soil properties (see section 3). Values are mean (standard deviation); methane emission rates were not log-transformed for these descriptive statistics. Total number of points observed is equal to 155.

Figure 1. Temporal stability of CH₄ emission rates during tests in 2007 and 2008. Each symbol is from the repeated observation of one point on the tundra landscape. Symbols show mean observed CH₄ emission rates, and error bars are 1 SD of the repeated observation. The n = 6 for each point in 2007, and n = 10 for each point in 2008.
N and W, respectively). But on 23 July, the emission rates from the southern point increased to 491 mg CH$_4$-C m$^{-2}$ d$^{-1}$, while emissions from the other points remained essentially unchanged. We returned to these points again in 2008, but found that emissions from all four points were typical of dry polygonal tundra (<5 mg CH$_4$-C m$^{-2}$ d$^{-1}$). Results from this set of points were so extreme and anomalous that we have excluded them from other analyses.

[33] Our experimental acetate addition in 2007 did not elicit an increase in methane emissions over a 48 h period. A 2-way ANOVA for repeated measures found no significant difference in methane emission rates between control plots, plots with added deoxygenated water, and plots with added acetate plus deoxygenated water (p > 0.15).

4.3. The 2007 Campaign: Spatial Variation in CH$_4$ Emission Rates

[34] Methane emission rates in our 2007 survey had a strongly nonnormal frequency distribution, with a long positive tail. The residuals from all statistical analyses retained this tail, thus invalidating the assumption of normality that underlay our analyses. Log-transformation normalized the distribution and the residuals, and so we used log-transformations for all statistical tests associated with CH$_4$ emission rates. Rates of ecosystem respiration from the 2007 survey showed a much smaller coefficient of variation (55%, as opposed to 100% for CH$_4$ emissions), and the rates were approximately normally distributed; we did not transform rates of CO$_2$ exchange.

[35] Our analysis of spatial statistics in CH$_4$ emission and ecosystem respiration rates generated variograms of gas flux semivariance versus mean distance between sampling points. These plots revealed no spatial autocorrelation among data points, indicating that further statistical analyses need not incorporate a spatial model. We thus treat all chambers as independent observations.

[36] We observed a strong exponential relationship between water content and CH$_4$ emissions that explained 59% of variation in log CH$_4$ emission rates (Figure 2). However, soil moisture was only a strong explanatory variable when considering the breadth of soil moisture and CH$_4$ emission rates encountered at the landscape scale; soil moisture explained little variance in CH$_4$ emission from wet and flooded soils where most CH$_4$ is emitted ($r^2 = 0.19$ for soils >80% VWC).

[37] Rates of CH$_4$ emission from soils with >80% VWC were significantly correlated with water table, permafrost depth, vegetation height, water content, temperature and bryophyte cover ($r^2$ values were 26%, 24%, 20%, 19%, 15% and 12%, respectively, for correlation with log CH$_4$ emission rate; all p < 0.001). Other properties, including ecosystem respiration rates, and cover by Arctophila, Eriophorum, Carex and dead/bare ground, were not significant (all p > 0.3).

[38] To evaluate which factor(s) best explained variation in CH$_4$ emissions above 80% VWC, we conducted a multi-factor ANCOVA, using predictors that included soil properties and vegetation information for categories represented under these wet conditions. This analysis revealed that maximum vegetation height, ecosystem respiration and permafrost depth were all significant predictors of log CH$_4$ emissions from wet soils (Figure 3). Thus, the greatest rates of CH$_4$ emission came from areas with tall vegetation, high rates of ecosystem respiration, and deep permafrost. Vegetation height was a relatively uniform property for Eriophorum-dominated sites, but it was highly variable for Carex-dominated sites; Eriophorum typically grew to about 10 cm, while Carex could range from 5 to 35 cm (Table 1). When the predictive power of volumetric water content (Figure 2) and this ANCOVA were combined, they explained 68% of the variation in log CH$_4$ emissions.

4.4. The 2008 campaign: CH$_4$ Emission From Flooded, Carex-Dominated Sites

[39] Although vegetation height was a strong predictor of CH$_4$ emission rates, we hypothesized that the relationship was not mechanistic, but instead vegetation height was a proxy for aboveground biomass, gross primary production (GPP) and/or net ecosystem CO$_2$ exchange (NEE). To test these hypotheses, we returned to the study area in 2008 and sampled flooded, Carex-dominated sites, using a combination of opaque and clear chambers to quantify GPP and NEE. A comparison of CH$_4$ emission rates using clear and opaque chambers revealed a strong correlation between the paired chamber types ($r^2 = 0.92$) with no evidence of bias between the two: the slope of the relationship not different from one (p > 0.50) and the intercept was not different from zero (p > 0.49).

[40] We found that maximum vegetation height was significantly correlated with aboveground biomass ($r^2 = 0.40$, p < 0.0001), GPP ($r^2 = 0.22$, p = 0.0013), NEE ($r^2 = 0.23$, p = 0.0008), ecosystem respiration ($r^2 = 0.25$, p < 0.0001), and soil temperature ($r^2 = 0.18$, p < 0.0001). However, a multi-factor ANCOVA using those predictors (Figure 4) identified maximum vegetation height as the best predictor of methane emission rates (p = 0.0008), with basal coverage of Carex as a significant secondary predictor (p = 0.047).

[41] In a more detailed analysis of the relationship between methane emissions rate and vegetation height, we compared the predictive power of linear, quadratic and exponential
Based on Akaike’s Information Criterion (AIC [Burnham and Anderson, 2002]), the exponential model had superior explanatory power ($r^2 = 0.44$) as compared to the linear and quadratic models (both $r^2 = 0.31$).

Finally, we examined the relative importance of water table depth, soil temperature and permafrost depth for explaining variation in vegetation height in waterlogged soils. This analysis identified different controls, depending on the year (Figure 6). For the 2007 data (constrained to soils >80% VWC) water table depth was the only significant predictor, while in 2008, temperature was the only significant predictor.

5. Discussion
Despite the high spatial variability that we observed in CH$_4$ emissions, our tests of temporal stability (Figure 1) indicate that individual point observations are representative...
of rates over at least hours to days. Although our study examines spatial patterns during 10 day periods of the growing season, other studies from this area [Rhew et al., 2007; Zona et al., 2009] have found peak CH₄ emission rates during the July and August periods when our work was conducted. This timing suggests that the peak growing season is an important time period for the annual CH₄ emission budget, and therefore controls on emission during this time period are likely to be important for emissions at an annual timescale.

[44] The rates of CH₄ emission that we observed (33 ± 33 mg CH₄-C m⁻² d⁻¹ in 2007) are consistent with measurements previously reported for the Alaskan Arctic and subarctic tundra. For example, Morrissey and Livingston [1992] reported average CH₄ emissions from the Arctic Coastal Plain in July/August 1987 of 8.6, 33.2, 59.1 mg CH₄-C m⁻² d⁻¹ for sites with the water table below the surface, at the surface, and above the surface, respectively. Also on the North Slope, Sebacher et al. [1986] report emissions in August 1984 of 89.3 and 3.7 mg CH₄-C m⁻² d⁻¹ for “wet coastal tundra” and “moist coastal tundra,” respectively. At “moist” and “wet” coastal tundra sites along the Alaskan Haul Road on the North Slope in 1987, Whalen and Reeburgh [1990a, 1990b] found mean fluxes of 23 and 68 mg CH₄-C m⁻² d⁻¹. Our observations are also comparable to emission rates from the Siberian Arctic and subarctic tundra. In the Siberian sub-Arctic, Heyer et al. [2002] found a similar range of August CH₄ emissions, with an average 147 mg CH₄-C m⁻² d⁻¹ emitted from flooded Carex-dominated areas, to 3.2 mg CH₄-C m⁻² d⁻¹ emitted from drier polygonal tundra. Work in polygonal tundra of the Siberian Arctic by Kutzbach et al. [2004] found an average 28 mg CH₄-C m⁻² d⁻¹ emitted from wet low-centered polygons, and 3.2 mg CH₄-C m⁻² d⁻¹ from the drier polygon rims.

[45] Like other studies, we found soil saturation or water level as the dominant predictor of spatial variation in CH₄ emissions. This general trend of increasing CH₄ emissions with soil saturation (water table height) has been observed, for example, in Sweden [Svensson and Rosswall, 1984; Alaska [Sebacher et al., 1986; Barillet et al., 1992; Morrissey and Livingston, 1992; Christensen, 1993], and Siberia [Wagner et al., 2003]. The importance of soil moisture as a predictor is consistent with redox control of mineralization pathways [von Fischer and Hedin, 2007]; oxygen diffusion from the atmosphere into the soil decreases as soil pores become water-filled, and so methanogenic mineralization pathways become more important in wetter soils. Drier, more oxygenated soils also exhibit greater rates of CH₄ oxidation [von Fischer and Hedin, 2007; Whalen and Reeburgh, 1990a, 1990b]. In addition, the wetter soils that we sampled were typically warmer than drier soils, further increasing methane production and emission rates.

[46] Our observation of the plume that emitted CH₄ at >1100 mg CH₄-C m⁻² d⁻¹ was novel among recent studies of terrestrial CH₄ emission. Without the real-time instrument, we would have likely discarded this data point as a methodological error. But because we were able to resample the anomaly, we could verify the rates and survey its areal extent. Although this single point comprised 0.6% of the land surface surveyed, it contributed a very large proportion of the total CH₄ emission from the study area; including this point in determination of the average CH₄ emission rate would raise it by 20%, from 33 to 40 mg CH₄-C m⁻² d⁻¹. Our decision to exclude the point from analysis is based on its statistical anomalousness and high leverage, and also because we hypothesize that the emitted CH₄ is thermogenic (fossil fuel-derived) and not biogenic. Such thermogenic CH₄ seeps...
are known to exist in this area [Nisbet, 1989], and controls on such fossil fuel sources are outside the primary scope of this paper. Future studies should evaluate the commonness of such points across the landscape.

[47] Our measures of CH$_4$ emission from waterlogged soils revealed the strong, significant correlations with temperature and water table depth that other studies have found, but when analyzed together in ANCOVA, these predictors proved to be less important than vegetation height. To our knowledge, this is the first study to find that vegetation height is a stronger predictor of emission than basal coverage, aboveground biomass or measures of carbon flow (e.g., GPP, NEE). A number of studies have found basal coverage of Carex and Eriophorum to be important predictors of CH$_4$ emission rates from northern wetlands [Joossson et al., 1999; Juutinen et al., 2003; Strom et al., 2003; Kutzbach et al., 2004]. And widely cited work by Whiting and Chanton [1993] identified both NEE and aboveground biomass as important predictors of CH$_4$ emission across a wide range of Arctic, temperate and subtropical wetlands. But these other studies have not compared the relative explanatory power of height, biomass and C flow. We do not believe that height itself is mechanismically related to emission, but instead hypothesize that it is correlated with other features of the plant-microbe-gas system that were not measured in this study.

[48] There are a number of possible explanations for why plant height better predicts CH$_4$ emission rates than biomass or C flow. Height is a relatively easy property to measure that is temporally stable and it may be correlated with an aspect of C flow that is temporally variable at the scale that we sampled. However, we expected aboveground biomass to predict C flow better than height because we anticipated that biomass would be less plastic and would better integrate the long-term C flow. This suggests that height is allometrically related to the key control(s). We propose three hypotheses to explain this allometric relationship. First, we hypothesize that taller plants have greater capacity to transport CH$_4$ to the atmosphere because they more completely vascularize the tundra. Second, we hypothesize that taller plants are more deeply rooted, and that deeper allocation of belowground biomass leads to a greater fraction of C flow being allocated to methanogenic pathways (i.e., a greater “methanogenic fraction” [von Fischer and Hedin, 2007]). Third, we hypothesize that taller plants supply more labile C belowground than do shorter plants, thus stimulating more CH$_4$ production. Because we do not yet understand which of these mechanisms underlies the correlation between height and emission rates, it is difficult to anticipate its limitations (e.g., variation over the growing season). However, it seems plausible that height sets an upper bound on CH$_4$ emission rate by its effects on gas transport, and/or CH$_4$ production rates.

[49] Given the importance of plant height for predicting spatial variation in CH$_4$ emissions, there is pressing need to understand how global climate change will affect the distribution and growth of Carex aquatilis across the Arctic coastal tundra. Results of our analysis into controls on Carex height (Figure 6) are ambiguous, suggesting that the correlated properties of water table depth and temperature are both important determinants. We observe the tallest individuals in the littoral zone of thaw lakes, and in the deeper troughs that drained the polygonal parts of the tundra where the water table is high, sediments are warm and permafrost is deep. However, it remains unclear what property of these sites is most important for determining plant height. Carex aquatilis is known to have distinct ecotypes that differ physiologically over spatial scales <1 m [Shaver et al., 1979]. In a study of genetic versus environmental controls on Carex aquatilis size, Chapin and Chapin [1981] found that size differences among plants had a strong genetic basis. These findings suggest that the timescales of growth response resulting from environmental change may be constrained by rates of seed dispersal and clonal spread. To account for these slower changes in plant ecology, studies in the Arctic coastal tundra that manipulate environmental variables to elicit a response in CH$_4$ emission rates should sustain the experimental treatment long enough to allow the plant community to reach a new steady state. Likewise, changes in Arctic CH$_4$ emission rates may lag global change due to plant ecology effects. Future studies should evaluate the timescales over which these changes take place.

[50] Finally, there are two key implications of the lognormal distribution of CH$_4$ emission rates observed here and elsewhere. First, as we point out in the introduction, a lognormal distribution in emission rates indicates that the arithmetic mean emission rate from a region will be heavily influenced by “hot spots” on the landscape that lie along the tail of the distribution. In this study, we identified such hot spots occurring on inundated parts of the tundra where tall Carex aquatilis plants grow. As future studies attempt to predict the strength of Arctic CH$_4$ emissions as an amplifier of global change, these studies should focus on dynamics that shape the spatial and temporal frequency distributions of these hot spots, and the mechanisms that determine CH$_4$ emission rates from these points. Second, the presence of a lognormal distribution in the rates reveals that emission rates are nonlinearly related to environmental conditions. Mathematically, this relationship arises from the log-transformation of data to fit the assumptions of models like ANCOVA. As a result of this transformation, the statistical model indicates that CH$_4$ emission rate is exponentially related to its controls. Such an exponential relationship is clear in the univariate regressions presented in Figures 2 and 5. The consequence for global change is that linear changes in the Arctic environment are likely to have nonlinear effects on CH$_4$ emission rates. Depending on how Arctic permafrost thaw affects the distribution and growth of plants like Carex aquatilis, these nonlinear responses could indicate a very strong feedback between climate change and Arctic CH$_4$ emissions.

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