Temperature and moisture effects on greenhouse gas emissions from deep active-layer boreal soils

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#### Abstract

High latitude ecosystems are being subjected to rapid climatic changes, with rising air temperatures and fires expected to drive permafrost degradation and soil carbon (C) cycle changes. How these soils' greenhouse gas emissions will respond to changes in temperature, moisture, and vegetation is highly uncertain. We used a laboratory experiment to examine how temperature and moisture control CO2 and CH4 emissions from soils sampled from the bottom of the annual active layer in an Alaskan boreal forest. Gas emissions were measured from thirty cores, subjected to two temperatures and either field moisture conditions or drought, over a 100-day incubation. TODO...

#### Introduction

High latitude ecosystems are being subjected to rapid changes in climate (IPCC, 2013) and fire occurrence and intensity (Kasischke et al., 2010). This has a wide variety of effects on ecosystems and society, notably in northwestern North America and Alaska (Hinzman et al., 2005; Ju and Masek, 2016). In particular, rising temperatures and increasing fire will result in permafrost degradation (Pastick et al., 2015; Zhang et al., 2015) and changes in soil temperature and hydrology that are expected to increase soil greenhouse gas (GHG) fluxes to the atmosphere, promoting a positive climate feedback (Treat et al., 2015; Koven et al., 2011).

The magnitude, timing, and form-in particular as methane (CH4) or carbon dioxide (CO2)-of such a feedback remain highly uncertain (Schuur et al., 2015). While northern soils hold enormous quantities (Tarnocai et al., 2009) of potentially mineralizable soil organic carbon (SOC), vegetation succession dynamics promote permafrost resilience to even large temperature changes (Jorgenson et al., 2010). Such dynamics may however be disrupted by increased fire disturbance (Johnstone et al., 2010). In addition, the stability of SOC is itself highly uncertain, as it depends on soil temperature and moisture, the ages of and ratio between the carbon (C) and nitrogen (N) pools (Weiss et al., 2015), and its protection from competent microorganisms, enzymes, and resources (Bailey et al., 2012), whether by organomineral sorption, chemical lability, or physical location (Schmidt et al., 2011).

Temperature and moisture typically have strong and often interactive influences on soil GHG emissions. A long literature of laboratory incubations, field observations, and meta-analyses has documented increased CO2 fluxes with rising temperature (Davidson and Janssens, 2006; Hashimoto et al., 2015; Treat et al., 2015). GHG responses to wetting and thawing dynamics are much less certain, with substantial variability between studies (Kim et al., 2012). The anaerobic conditions common following permafrost thaw are expected to lower CO2 emissions but increase those of CH4 (Treat et al., 2015; Treat et al., 2014), and interact with soil temperature effects in long-term incubations (Elberling et al., 2013). More uniformly across the landscape, however, decadal warming, and perhaps drying, trends in Alaska (Bieniek et al., 2014) will work to counteract these effects, with uncertain consequences for the carbon cycle and climate system.

The goal of this study was to examine how temperature and moisture control C loss and GHG (CO2 and CH4) emissions from soils sampled from the bottom of the annual active layer--i.e., directly above permafrost--in an Alaskan boreal forest. Most previous studies have focused on surface soils or permafrost soils, neglecting deep active-layer soils that experience fluctuating temperature and, especially, moisture conditions. Such deep but unfrozen soils were identified as subject to strong effects from a two-decade warming experiment in the Alaskan Arctic (Sistla et al., 2013). We also aimed to characterize the chemical and biological properties of these soils as they were subjected to a 100-day incubation at different temperatures, subjecting some cores to drying treatments. We hypothesized that (i) CO2 would be the dominant pathway for C loss in these largely aerobic soils; (ii) soils maintained at field moisture and high temperature would lose more C-CO2 than cores incubated at 4˚C, due to increased aerobic and anaerobic microbial activity; and (iii) core CH4 fluxes would be sensitive only to temperature, as no anaerobic conditions were planned for the cores.

#### Methods

**Field sampling**

The field component of this research took place in Caribou-Poker Creeks Research Watershed (CPCRW), part of the Bonanza Creek LTER (<http://www.lter.uaf.edu/research/study-sites-cpcrw>). CPCRW is located in the Yukon-Tanana Uplands northeast of Fairbanks, AK, a part of the boreal forest that has seen strong increases in air temperature and forest browning (Ju and Masek, 2016) over several decades. Annual average air temperature was -2.5 °C, and annual average precipitation 400 mm (Petrone et al., 2006). The watershed's lowlands and north-facing slopes are dominated by black spruce (*Picea mariana*), feathermoss (*Pleurozium schreberi* and others), and *Sphagnum* spp.; the drier south slopes tend to be deciduous with a mixture of quaking aspen (*Populus tremuloides*), paper birch (*Betula neoalaskana*), and patches of alder (*Alnus crispa*).

We sampled soils from a southeast slope (65.1620 °N, 147.4874 °W) at CPCRW, in a 60 m transition zone between lowland *Picea mariana* Mill BSP. and upland *Betula neoalaskana*, with significant white spruce (*Picea glauca*) presence. Stand density in this transition zone was 4060 ± 2310 trees ha-1, with basal area of 27.9 ± 7.0 m2 ha-1. The forest was at least 90 years old (cf. Morishita et al., 2014) according to tree rings taken at the stem base of several of the largest white spruce. The soil is characterized as a poorly-drained silt loam, and on average had ~20 cm of organic material over the mineral soil.

Thirty-nine soil cores, each 30 cm high by 7.5 cm wide, were taken using a soil recovery augur (AMS Inc., American Falls, ID) on 3-5 August 2015. We sampled from the bottom (within 0-2 cm) of the active layer, which averaged 80 cm depth. Sample points were randomly located in the transition zone described above, and separated by 2-5 m. Cores were kept cool in the field before being packed in dry ice and shipped to the lab in Richland, WA within 48-72 hours of collection.

**Laboratory incubation**

In the lab, the soil cores were stored at 4 °C for several days until they were weighed and prepared for incubation. At that point (11-12 August 2015), three fragmented or otherwise damaged cores were discarded, and the remaining cores were randomly assigned to one of six groups (N=6 in each group). These groups included two incubation temperatures (4 and 20 °C), each with two moisture treatments: one in which soil moisture was maintained at field conditions (~28% moisture by volume), and a drought treatment in which no water was added and cores were allowed to dry down to ~5% moisture by volume. The fifth group was a 20 °C "controlled drought" one, in which water was added so that these cores' moisture status would close match those of the 4 °C "drought" cores, which we anticipated would dry more slowly than their 20 °C counterparts. The final 6-core group was used for destructive, pre-incubation measurements including moisture content, pH, soil carbon and nitrogen, and bulk density. Subsamples were collected and stored at -20 °C for dissolved organic carbon measurements.

On 18 August 2015 cores were placed into one of two growth chambers (Conviron CMP6050 Control Systems, Winnipeg, Canada) maintained at 4 and 20 °C temperatures and 70% relative humidity and allowed to equilibrate for two weeks. Starting on 31 August 2015 we measured the cores' mass and GHG (CH4 and CO2) evolution four times in the first week, then twice per week for the first month, and then once per week for the rest of the 100-day incubation. Throughout the incubation, cores were mounted on porous ceramic plates (Soil Moisture Equipment Corp., Santa Barbara, CA, USA) so that, when the plates were placed in contact with water, water would move up into the cores via capillary action. The "drought" cores were mounted on dry plates, but not allowed to drop below 5% water content. When necessary, cores received additional wetting from the top to maintain their water status at the desired level.

For each measurement, a six-core treatment group was connected to a Picarro A0311 multiplexer that was in turn connected to a Picarro G2301 GHG Analyzer (Picarro Inc., Santa Clara, CA, USA). Dry CH4 and CO2 concentrations were monitored for 2 minutes, and this was repeated 2-3 times before moving on to a new treatment group. Cores were weighed immediately after gas measurements. Ambient air was measured between treatment groups, and before starting measurements in a chamber, as a check on ambient CO2 conditions and instrument stability.

The incubation experiment concluded on 9 December 2015, following the final CO2 and CH4 readings. Each soil core was maintained at the treatment-dependent temperature and moisture content (by mass) until removed for destructive sampling, December 14-18, 2015. Sub-samples were collected and composited throughout each soil core for dissolved organic carbon analysis (110 ± 24 g dry mass equivalent) and dry-mass calculations (~28 g each). The remaining core material was air-dried and separated into particles (>2 mm diameter) and soil (≤2 mm) using a U.S. Standard Test Sieve No. 10 (Fisherbrand, Pittsburg, PA, USA). The dry mass and volume of soil were used in calculations of gravimetric and volumetric soil moisture content, respectively (Gardner, 1986). Soil volume was caclulated as the total core volume minus the volume of particles >2 mm diameter, with the latter determined by water displacement. Air-dried soil and sub-samples stored at -20 °C were sent to the Agricultural and Environmental Services Laboratory at the University of Georgia Extension in February 2016 for total C, N, and dissolved organic C. Samples were combusted in an oxygen atmosphere at 1350 °C, and measured for gaseous C and N using a Elementar Vario Max CNS. DOC was measured using a Shimadzu 5000 TOC Analyzer.

**Data and statistical analysis**

At each GHG measurement, we measured the rise in gas concentrations, considering this as the flux rate in ppm s-1 (CO2) or ppb s-1 (CH4). The GHG concentration measurements for each sample (i.e., each gas, core, and date/time) were used to calculate a linear rate of change (δc/δt), based on the concentration rise from a minimum (up to 10 seconds after measurement began) to a maximum (at 10-45 seconds). This value was calculated for each sample, i.e. each individual core measurement throughout the 100-day incubation.

Anomalous data were excluded based on their gas fluxes being more than 5 (for CO2) or 10 (for CH4) mean absolute deviations (Davies and Gather, 1993) from the treatment mean within a 10-day period, for a given treatment and temperature. We excluded 172 of 2686 (6.4%) measurements for this reason. If the coefficient of variability of fluxes from any core on a single day exceeded 140%, the entire core was also excluded for that day (90 data points, 3.4%). Other data (4.8%) were removed because of known instrument problems, e.g. the analyzer was left running after leaving a chamber. The final number of valid flux samples from the 100-day incubation was 2198.

Each core’s respiration flux (*F*) was calculated following e.g. Steduto et al. (2002) as where *V* is the core-specific system volume, *M* the core dry mass as determined at the end of the incubation, *Pa* atmospheric pressure (101 kPa; the incubation chambers were ~120 m a.s.l.), *R* the universal gas constant (8.3 x 10-3 m3 kPa mol-1 K-1) and *T* the chamber air temperature (K) at time of measurement. The final respiration rate was expressed on a dry soil mass basis (µg C g soil-1 day-1).

The effects of temperature, gravimetric water content, C percent, N percent, and DOC concentration on instantaneous gas fluxes were evaluated using a linear mixed-effects model fit by the R function *lme* in the R 'nlme' package, version 3.1.126. Because the dependent variable (CO2 or CH4 flux) was non-normally distributed, it was transformed using a natural-logarithm (+0.1 µg C g C-1 day-1 to ensure all positive fluxes, following Treat et al. 2015) transformation. Core number was treated as a random effect in the model. We then used performed stepwise model selection by Akaike's information criterion (AIC) using the *stepAIC* function in the R 'MASS' package, version 7.3.45. A linear mixed-effects model was also used to evaluate the effect of treatment on core water content.

Cumulative respiration for each core and gas was calculated by linearly interpolating flux rates between measurement dates and summing respired C over the entire incubation. The effect of temperature and treatment (drought, controlled drought, or field moisture conditions) on cumulative gas fluxes was evaluted with a post-hoc Tukey Honest Significant Differences test. Temperature sensitivity (Q10) was calculated for each gas and treatment as where *F1* and *F2* are the cumulative gas fluxes (mg C) at temperatures *T1* and *T2* (°C), respectively.

All data analysis and statistics were performed using R version R version 3.2.4 (2016-03-10) (R Development Core Team, 2016). This experiment was run as an "open experiment" (Bond-Lamberty et al., 2016) with all analysis code, data (from raw instrument data to final summaries), diagnostics, etc., available at <https://github.com/bpbond/cpcrw_incubation>. The summarized flux data backing the main results have been archived at [DOI to be filled in on acceptance].

#### Results

The 30 experimental cores had a bulk density of 1.00 ± 0.18 (mean ± sd) g cm-3. Large (>2 mm) particles, primarily schist, comprised 41% ± 11% of the cores' total mass. Soil (≤2 mm) dry mass was 886 ± 154 g. Sample DOC was 157.93 ± 55.74 mg kg-1. Carbon content was 1.20% ± 1.19%, while N content was 0.06% ± 0.06%. Neither temperature was treatment exerted any significant effect on these properties (P > 0.1 for all).

Gravimetric water content was 0.31 ± 0.12 (min 0.19, max 0.77) at the beginning of the incubation (**Figure 1**). "Field moisture" cores were on average unchanged (0.33 ± 0.13) at the end of the incubation, but both the drought treatments, which did not differ from each other in their effect on gravimetric water content (P = 0.880), had declined to 0.06 ± 0.04. Volumetric water content values ranged from 0.29 ± 0.05 (min 0.23, max 0.43) at the beginning of the experiment to 0.15 ± 0.11 (min 0.03, max 0.38) at the end. Water filled pore space, assuming a particle density of 2.65 g cm-3, was 22-65%.

After removal of known problematic data, and exclusion of statistical outliers, CO2 flux rates measured during the incubation ranged from 1.1 µg C g C-1 day-1 (1.7 µg C g soil-1 day-1) to a maximum of 5245.1 (1251.31), with a mean of 248.9 (174.1). CH4 rates ranged from 0.00 ng C g C-1 day-1 (0.00 ng C g soil-1 day-1) to a maximum of 1.31 (0.768), with a mean of 0.06 (0.06).

These means conceal considerable variablility over the course of the incubation (**Figures 2 and 3**). In the linear mixed-effects model, CO2 was strongly influenced by incubation chamber temperature, core gravimetric water content, and percent soil N (all P < 0.05, and the latter two P < 0.001; **Table 1**). (Note that percent C and percent N were highly correlated (r ≥ 0.98) for these cores. Because percent N was a slightlyl stronger predictor, it was retained in the model while percent C was excluded.) The interaction between water content and soil N was also highly significant (P < 0.001), with high-N cores having little relationship between water content and CO2 flux (data not shown). "Drought" cores' cumulative production was 66% (4 °C) and 47% (20 °C) lower than the cores kept at field moisture.

Methane fluxes were most strongly correlated with percent N, while water content exhibited significant interactions with percent N and DOC (**Table 2**). Neither temperature nor water content was a significant first-order predictor of CH4 fluxes, however.

The cumulative production of C from CO2 was over six order of magnitudes higher than that from CH4, with CO2:CH4 C ratios ranging from 1.4 million in the 4 °C "Field moisture" treatment, to 6.2 million in the 20 °C "Field moisture" treatment. Cumulative CO2 evolved was highly affected by temperature (P < 0.001), and "field moisture" cores emitted significantly more CO2 than the other two treatments at both temperatures (P < 0.001 for both). There was no difference between the 20 °C "drought" and "controlled drought" treatments (P = 0.336). Neither temperature (P = 0.261) nor treatment (mean P = 0.853) was a significant factor in predicting cumulative CH4 fluxes.

The cumulative flux numbers above result in CO2 temperature sensitivity (Q10) values of 1.4 and 1.8 for the field moisture and drought treatments, respectively; the corresponding Q10 values based on cumulative CH4 were 1.2 and 1.2. Computing Q10s based on fluxes normalized by water filled pore space changed these values only slightly: to 1.3 and 1.7 for CO2, respectively, and 1.1 and 1.1 for CH4.

#### Discussion

**Importance and context**

Rises in boreal air temperatures, and unpredictable precipitation changes, will warm and dry many soils, increase vegetation stress (Ju and Masek, 2016), degrade permafrost and deepen the active layer (Schuur et al., 2015). The resulting changes in the soil carbon cycle may already be visible (Bond-Lamberty et al., 2012) but are highly uncertain going forward, increasing the need for controlled laboratory studies of GHG emission dynamics from high-latitude soils.

**Previous results**

Several studies have measured microbial respiration and GHG fluxes from soils very close to our study site. Morishita et al. (2014) measured gas fluxes in the field at CPCRW and nearby forests, and found CO2 production to be correlated with both temperature and moisture, consistent with our results They found however that CH4 uptake (no emissions were observed) was driven by temperature only. Waldrop et al. (2010) incubated active-layer and permafrost soils from near Fairbanks, AK, under varied temperature and aerobic conditions, observing Q10 values of 9.0 (active layer) and 2.3 (permafrost) from -5 to 5 °C; these values are higher than we observed, consistent with the lower temperature range (Hamdi et al., 2013). Waldrop et al. (2010) observed flux rates of 0.001-0.10 µmol CH4 day-1 g-1 (~0.001-0.133 ng C g C-1 day-1), differing by orders of magnitude between sites (but roughly similar to our observed CH4 emissions), and ~1-5 µg C-CO2 hr-1 g-1 (~2000-10000 µg C g C-1 day-1), considerably higher than the CO2 rates observed from our cores. In an incubation of active-layer Alaskan permafrost peats, Treat et al. (2014) found CO2 and CH4 emissions to be strongly correlated with temperature and moisture. Finally, during the first 100 days of a year-long incubation of Fairbanks-area 0-10 cm mineral soils, Neff and Hooper (2002) observed fluxes of ~55-409 µg C-CO2 g C-1 day-1, in line with the results here.

More generally, in a pan-Arctic synthesis of anaerobic soil incubations, Treat et al. (2015) reported mean CO2 rates of 47 (all mineral soils) and 101 (for 20-100 cm soils) µg C-CO2 g C-1 day-1, somewhat lower than our aerobic incubation results. Weiss et al. (2015) found CO2 production from Yedoma permafrost samples to be correlated with both percent C and N, consistent with our results (**Table 1**). TODO.

**Temperature versus moisture sensitivity**

Warming usually increases soil GHG fluxes, for example at depth in a long-term Arctic tundra experiment (Sistla et al., 2013), as increased temperatures increment enzyme kinetics, enhance the production of extracellular enzymes, and enhance desorptions rates of organic matter from minerals. A key question, for both experimentalists and modelers (Falloon et al., 2011), is to what degree such soils' emissions could by constrained by their moisture status--in particular, limited by low soil moisture driven by increases in high-latitude temperatures, vapor pressure deficit, and potentially precipitation changes.

Our results suggest that moisture limitation could exert a large effect on CO2 production for deep active-layer soils (**Figure 4**): "drought" cores' cumulative production was 66% (4 °C) and 47% (20 °C) lower than the cores kept at field moisture. This effect was highly significant, and suggests that moisture limitations could exert a significant constraint on deep active-layer soils as they slowly warm. Such moisture constraints are thought to be already exerting effects on vegetation and soil fluxes at large scales (Ju and Masek, 2016; Bond-Lamberty et al., 2012), but our understanding of the interactive effects involved is poor.

In contrast, the temperature sensitivities observed in this experiment are low (all less than 2.0, even when controlling for changes in soil moisture). Such values are not unprecedented in comparison to a wide range of other laboratory soil incubations (Hamdi et al., 2013). It is important to note, however, that even if increased temperature alone may not always drive C mineralization rates in forest-mineral soils (Giardina and Ryan, 2000), but it is frequently linked with increases in soil moisture content can lead to changes in microbial community structure, amplifying GHG fluxes (Xue et al, 2016). TODO: PEYTON - WHAT IS THIS CITATION?

**Methane**

We observed very low, but consistently positive, CH4 production from these unsaturated mineral soils. This is contrast to many field studies, e.g. Schaufler et al. (2010) who found consistent CH4 uptake (oxidation) in dry conditions at a boreal site.

Treat et al. found a median CO2:CH4 production ratios of 387 for boreal sites, far lower than (but consistent with) our observed ratios of several million.

**Limitations and weaknesses**

Incubation experiments can only go so far though...

Laboratory soil incubations have weaknesses, for example in what can be inferred about temperature sensitivity (Podrebarac et al., 2016; Hamdi et al., 2013), but their controlled environments provide an important way to elucidate the key mechanisms controlling GHG from high-latitude soils (Schuur et al., 2015).

these are not surface layer soils (where majority of microbial activity and C mineralization of labile C takes place) and that taking them out of depth (where they are not exposed to O2 as readily, etc.) for our laboratory incubation may differ from in situ CO2/CH4 production.

Necessity of integrated lab-field-modeling experiments...

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#### Author contributions

B.B.-L., A.P.S., and V.L.B. designed this experiment. B.B.-L. and A.P.S. performed field sampling, and A.P.S. led the laboratory incubation and analyses. B.B.-L. wrote the manuscript, with contributions from all authors.

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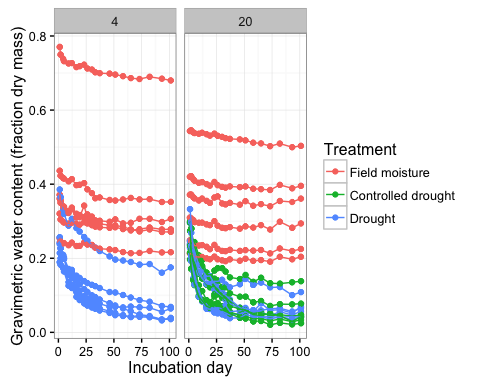
**Table 1.** Linear mixed-effects model parameters, testing effects of gravimetric water content (unitless), temperature (°C), soil C (%), soil N (%), and dissolved organic carbon (mg kg-1) on individual core CO2 fluxes (+0.1 µg C g C-1 day-1). Dependent variable has units of log(µg C g C-1 day-1). Columns include parameter value; standard error (SE); degrees of freedom (DF); T statistic; and P value.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  | Value | SE | DF | T | P |
| (Intercept) | 1.713 | 0.354 | 1153 | 4.839 | 0.000 |
| Temperature | 0.046 | 0.020 | 26 | 2.336 | 0.027 |
| WC\_gravimetric | 3.496 | 1.052 | 1153 | 3.322 | 0.001 |
| N\_percent | 37.976 | 6.810 | 26 | 5.576 | 0.000 |
| Temperature:WC\_gravimetric | 0.116 | 0.061 | 1153 | 1.905 | 0.057 |
| Temperature:N\_percent | -0.507 | 0.300 | 26 | -1.690 | 0.103 |
| WC\_gravimetric:N\_percent | -37.347 | 8.425 | 1153 | -4.433 | 0.000 |

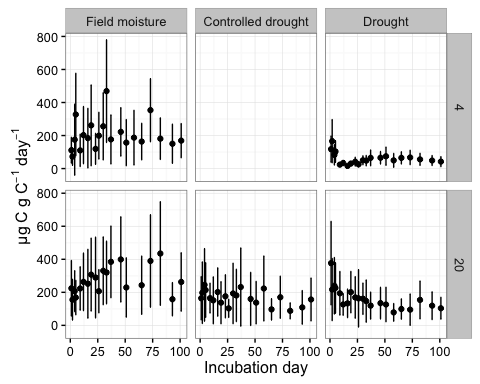
**Table 2.** Linear mixed-effects model parameters, testing effects of gravimetric water content (unitless), temperature (°C), soil C (%), soil N (%), and dissolved organic carbon (mg kg-1) on log-transformed, individual core CH4 fluxes (+0.1 µg C g C-1 day-1). Dependent variable has units of log(µg C g C-1 day-1). Columns include parameter value; standard error (SE); degrees of freedom (DF); T statistic; and P value.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  | Value | SE | DF | T | P |
| (Intercept) | -2.302 | 0.000 | 978 | -6163.334 | 0.000 |
| Temperature | 0.000 | 0.000 | 26 | 1.999 | 0.056 |
| WC\_gravimetric | -0.001 | 0.002 | 978 | -0.849 | 0.396 |
| N\_percent | 0.014 | 0.004 | 26 | 3.645 | 0.001 |
| DOC\_mg\_kg | 0.000 | 0.000 | 26 | -2.041 | 0.052 |
| Temperature:WC\_gravimetric | 0.000 | 0.000 | 978 | -1.657 | 0.098 |
| WC\_gravimetric:N\_percent | -0.015 | 0.007 | 978 | -2.287 | 0.022 |
| WC\_gravimetric:DOC\_mg\_kg | 0.000 | 0.000 | 978 | 2.437 | 0.015 |

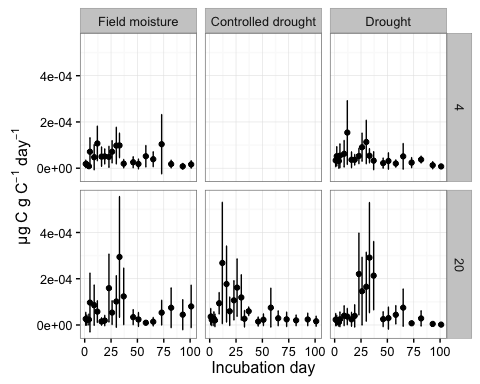
**Figure 1.** Core water content across the course of the incubation experiment by temperature (left panel 4 °C, right panel 20 °C) and treatment.



**Figure 2.** A faceted (Temperature ~ Treatment) plot showing normalized CO2 flux means and errors by incubation time.



**Figure 3.** A faceted (Temperature ~ Treatment) plot showing normalized CH4 flux means and errors by incubation time.



**Figure 4.** Cumulative fluxes over the incubation.

