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

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Abstract

Rapid climatic changes, rising air temperatures, and increased fires are expected to drive permafrost degradation and alter soil carbon (C) cycling in many high-latitude ecosystems. How these soils will respond to changes in their temperature, moisture, and overlying vegetation is highly uncertain, but critical to understand given the large soil C stocks in these regions. We used a laboratory experiment to examine how temperature and moisture control CO_2 and CH_4 emissions from mineral soils sampled from the bottom of the annual active layer, i.e. directly above permafrost, in an Alaskan boreal forest. Gas emissions from thirty cores, subjected to two temperatures and either field moisture conditions or experimental drought, were tracked over a 100-day incubation; we also measured a variety of physical and

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chemical characteristics of the cores. Gravimetric water content was 0.31 ± 0.12 (unitless) at the beginning of the incubation; cores at field moisture were unchanged at the end, but drought cores had declined to 0.06 ± 0.04. Carbon dioxide fluxes were strongly influenced by incubation chamber temperature, core water content, and percent soil nitrogen, and had a temperature sensitivity (Q_{10}) of 1.3 and 1.9 for the field moisture and drought treatments, respectively. Methane emissions were most strongly correlated with percent nitrogen, but neither temperature nor water content was a significant first-order predictor of CH_4 fluxes. The cumulative production of C from CO_2 was over six orders of magnitudes higher than that from CH_4. These results suggest that deep active-layer soils may be much more sensitive to changes in moisture than to temperature, a critical factor as discontinuous permafrost melts in interior Alaska. Deep but unfrozen high-latitude soils have been shown to be strongly affected by long-term experimental warming, and these results provide insight into their future dynamics and feedback potential with future climate change.

1 Introduction

High latitude ecosystems are being subjected to rapid changes in climate (IPCC, 2013) and increases in fire frequency and intensity (Kasischke et al., 2010), notably in northwestern North America and Alaska (Hinzman et al., 2005; Ju and Masek, 2016). This will have a wide variety of ecosystem effects (Alexander and Mack, 2016): in particular, rising temperatures and increasing fire will likely result in permafrost degradation (Pastick et al., 2015; Zhang et al., 2015; Genet et al., 2013;

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Helbig et al., 2016) and changes in soil temperature, with subsequent hydrology changes that will influence soil greenhouse gas (GHG) fluxes to the atmosphere. Such fluxes are a large component of the global C cycle and, because of the high C stocks of northern soils (Tarnocai et al., 2009), could result in a significant and positive climate feedback (Treat et al., 2015; Koven et al., 2011; Schaefer et al., 2014).

The magnitude, timing, and form-in particular as methane (CH_4) or carbon dioxide (CO_2)-of such any such 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 and succession dynamics (for example, thermal insulation by mosses) promote permafrost resilience to even large temperature changes (Jorgenson et al., 2010; Turetsky et al., 2012). Such dynamics may however be disrupted by increased fire disturbance, particularly with more-intense fires (Johnstone et al., 2010; Genet et al., 2013). 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; Karhu et al., 2014), 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. Laboratory incubations, field observations, and meta-analyses have documented increased fluxes of CO_2, and under some conditions of CH_4

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(Olefeldt et al., 2013), with rising temperature (Davidson and Janssens, 2006; Hashimoto et al., 2015; Treat et al., 2015). Greenhouse gas (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 CO_2 emissions but increase those of CH_4 (Treat et al., 2015; Treat et al., 2014), and such interactions are critical to examine in the course of long-term incubation experiments (Elberling et al., 2013). Decadal warming and drying trends in Alaska (Bieniek et al., 2014) may counteract these effects, however. A critical question, then, is how the structure, chemistry, and microbial communities of current active-layer soils will respond to almost-certain temperature and moisture changes in the future (Xue et al., 2016).

The goal of this study was to examine how temperature and moisture control GHG (CO_2 and CH_4) 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 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 structural properties of these soils following a 100-day incubation at different temperatures, subjecting some cores to drying treatments. We hypothesized that (i) CO_2 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-CO_2 than cores incubated at 4˚C, due to increased

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86 aerobic and anaerobic microbial activity; and (iii) core CH_4 fluxes would be sensitive
87 only to temperature, as no anaerobic conditions were imposed on the cores.

88 ## 2 Methods

89 ### *2.1 Field sampling*

90 The field component of this research took place in Caribou-Poker Creeks Research
91 Watershed (CPCRW), part of the Bonanza Creek LTER
92 (http://www.lter.uaf.edu/research/study-sites-cpcrw). CPCRW is located in the
93 Yukon-Tanana Uplands northeast of Fairbanks, AK, a part of the boreal forest that
94 has seen strong increases in air temperature and forest browning (Ju and Masek,
95 2016) over several decades. Annual average air temperature is -2.5 °C, and annual
96 average precipitation 400 mm (Petrone et al., 2006). The watershed's lowlands and
97 north-facing slopes are dominated by black spruce (*Picea mariana* (Mill.) BSP),
98 feathermoss (*Pleurozium schreberi* and others), and *Sphagnum* spp.; the drier south
99 slopes tend to be deciduous with a mixture of trembling aspen (*Populus tremuloides*
100 Michx.), paper birch (*Betula neoalaskana*), and patches of alder (*Alnus crispa*).

101 We sampled soils from a southeast slope (65.1620 °N, 147.4874 °W) at CPCRW, in a
102 60 m transition zone between lowland *Picea mariana* and upland *Betula*
103 *neoalaskana*, with significant white spruce (*Picea glauca*) presence as well. Stand
104 density in this transition zone was 4060 ± 2310 trees ha^{-1}, with basal area of 27.9 ±
105 7.0 m^2 ha^{-1}. The forest was at least 90 years old (cf. Morishita et al., 2014) according
106 to tree rings taken at the stem base of several of the largest white spruce. The soil is

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107 characterized as a poorly-drained silt loam, and on average had ~20 cm of organic
108 material over the mineral soil.

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

115 *2.2 Laboratory incubation*

116 In the lab, the soil cores were stored at 4 °C for several days until they were weighed
117 and prepared for incubation. At that point (11-12 August 2015), three fragmented
118 or otherwise damaged cores were discarded, and the remaining cores were
119 randomly assigned to one of six groups (N=6 in each group). These included two
120 incubation temperatures of 4 and 20 °C, following the protocol of a number of
121 previous boreal incubation studies (Treat et al., 2015). Within each temperature
122 there were two moisture treatments: one in which soil moisture was maintained at
123 field conditions (~28% moisture by volume), and a drought treatment in which no
124 water was added and cores were allowed to dry down to ~5% moisture by volume.
125 The fifth group was a 20 °C "controlled drought" one, in which water was added so
126 that these cores' moisture status would close match those of the 4 °C "drought"
127 cores, which we anticipated would dry more slowly than their 20 °C counterparts.
128 The final 6-core group was used for destructive, pre-incubation measurements

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129 including moisture content, pH, soil carbon and N, and bulk density. Subsamples
130 were collected and stored at -20 °C for dissolved organic carbon measurements or
131 air-dried for soil C and N (see below).

132 On 18 August 2015 cores were placed into one of two growth chambers (Conviron
133 Control Systems BDW80, Winnipeg, Canada) maintained at 4 and 20 °C
134 temperatures and 70% relative humidity and allowed to equilibrate for two weeks.
135 Starting on 31 August 2015 we measured the cores' mass and GHG (CH_4 and CO_2)
136 emissions four times in the first week, then twice per week for the first month, and
137 then once per week for the rest of the 100-day incubation. Throughout the
138 incubation, cores had a 200 µm mesh screen fit to the base and were mounted on
139 porous ceramic plates (Soil Moisture Equipment Corp., Santa Barbara, CA, USA) so
140 that, when the plates were placed in contact with water, water would move up into
141 the cores via capillary action. The "drought" cores were mounted on dry plates, but
142 not allowed to drop below 5% water content. When necessary, cores received
143 additional wetting from the top to maintain their water status at the desired level.

144 For each measurement, a six-core treatment group was connected to a Picarro
145 A0311 multiplexer that was in turn connected to a Picarro G2301 GHG Analyzer
146 (Picarro Inc., Santa Clara, CA, USA). Dry CH_4 and CO_2 concentrations were monitored
147 for 2 minutes, and this was repeated 2-3 times before moving on to a new treatment
148 group. Cores were weighed immediately after gas measurements. Ambient air was
149 measured between treatment groups, and before starting measurements in a
150 chamber, as a check on ambient CO_2 conditions and instrument stability.

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151 The incubation experiment concluded on 9 December 2015, following the final CO_2
152 and CH_4 readings. Each soil core was maintained at the treatment-dependent
153 temperature and moisture content (by mass) until removed for destructive
154 sampling, December 14-18, 2015. Sub-samples were collected and composited
155 throughout each soil core for dissolved organic carbon analysis (110 ± 24 g dry
156 mass equivalent) and dry-mass calculations (~28 g each). The remaining core
157 material was air-dried and separated into particles (>2 mm diameter) and soil (≤2
158 mm) using a U.S. Standard Test Sieve No. 10 (Fisherbrand, Pittsburg, PA, USA). The
159 dry mass and volume of soil were used in calculations of gravimetric and volumetric
160 soil moisture content, respectively (Gardner, 1986). Soil volume was calculated as
161 the total core volume minus the volume of particles >2 mm diameter, with the latter
162 determined by water displacement. Air-dried soil and sub-samples stored at -20 °C
163 were sent to the Agricultural and Environmental Services Laboratory at the
164 University of Georgia Extension in February 2016 for total C, N, and dissolved
165 organic C. Samples were combusted in an oxygen atmosphere at 1350 °C, and
166 measured for gaseous C and N using a Elementar Vario Max CNS. DOC was measured
167 using a Shimadzu 5000 TOC Analyzer.

168 *2.3 Data and statistical analysis*

169 For each measurement of each sample throughout the 100-day incubation (i.e., each
170 gas, core, and date/time), we used the rise in gas concentrations to calculate a flux
171 rate in ppm s^{-1} (CO_2) or ppb s^{-1} (CH_4), a linear rate of change ($\delta c/\delta t$) based on the
172 concentration rise from a minimum (up to 10 seconds after measurement began) to

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a maximum (at 10-45 seconds). Each core's respiration flux (F) was then calculated as $F = \frac{\delta c}{\delta t}\frac{V}{M}\frac{P_a}{RT}$ where V is the core-specific system volume, M the core dry mass as determined at the end of the incubation, P_a atmospheric pressure (101 kPa; the incubation chambers were ~120 m a.s.l.), R the universal gas constant (8.3 x 10^{-3} m^3 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}).

Anomalous data were excluded based on their gas fluxes being more than 5 (for CO_2) or 10 (for CH_4) 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 (CV) of fluxes from any core on a single day exceeded 140%, a value chosen based on the distribution of CVs across all cores, the entire core was 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.

The effects of temperature, gravimetric water content, percent C, percent N, 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 (CO_2 or CH_4 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. Soil core was treated as

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a random effect in the model. We then 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 evaluated with a post-hoc Tukey Honest Significant Differences test. Temperature sensitivity (Q_{10}) was calculated for each gas and treatment as $\frac{F_2}{F_1}^{\left(\frac{10}{T_2-T_1}\right)}$ where F_1 and F_2 are the cumulative gas fluxes (mg C g C^{-1}) at temperatures T_1 and T_2 (°C), respectively.

All data analysis and statistics were performed using 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., 2016b) 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*].

3 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

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kg^{-1}. Carbon content was 1.20% ± 1.19%, while N content was 0.06% ± 0.06%. Mean C:N was 20.7. Neither temperature nor moisture treatment exerted any significant effect on these highly variable 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 across all cores. Water filled pore space, assuming a particle density of 2.65 g cm^{-3}, was 22-65% over all cores, moisture treatments, and temperatures.

Carbon dioxide fluxes 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) over the 100 days. CH_4 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 variability over the course of the incubation (**Figures 2 and 3**). In the linear mixed-effects model, CO_2 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**). Percent C and percent N were highly correlated ($r = 0.99$) for these cores. Because percent N was a slightly stronger predictor, it was retained in the model while percent C was excluded; cf.

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238 Colman and Schimel (2014). The interaction between water content and percent N
239 was also highly significant ($P < 0.001$), with high-N cores having little relationship
240 between water content and CO_2 flux (data not shown).

241 Methane fluxes were most strongly correlated with percent N, while water content
242 exhibited significant interactions with percent N and DOC (**Table 2**). Neither
243 temperature nor water content was a significant first-order predictor of CH_4 fluxes.

244 The cumulative production of C from CO_2 (**Figure 4**) was over six order of
245 magnitudes higher than that from CH_4, with CO_2:CH_4 C ratios ranging from 1.4
246 million in the 4 °C "Field moisture" treatment, to 6.2 million in the 20 °C "Field
247 moisture" treatment. Cumulative CO_2 evolved was highly affected by temperature ($P = 0.003$), and "field moisture" cores emitted significantly more CO_2 than the other
249 two moisture treatments at both temperatures ($P < 0.001$ for both, with no
250 significant interactive effect). There was no difference between fluxes from the 20 °C
251 "drought" and "controlled drought" treatments ($P = 0.377$). "Drought" cores'
252 cumulative production was 73% (4 °C) and 52% (20 °C) lower than the cores kept at
253 field moisture. Neither temperature ($P = 0.200$) nor moisture treatment (mean $P =$
254 0.975) was a significant factor in predicting cumulative CH_4 fluxes.

255 The cumulative flux numbers above result in CO_2 temperature sensitivity (Q_{10})
256 values of 1.3 and 1.9 for the field moisture and drought treatments, respectively; the
257 corresponding Q_{10} values based on cumulative CH_4 were 1.2 and 1.3. Computing Q_{10}
258 values based on fluxes normalized by water filled pore space changed these values
259 only slightly: to 1.2 and 1.7 for CO_2, respectively, and 1.1 and 1.2 for CH_4.

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4 Discussion

Rises in boreal air temperatures, and unpredictable precipitation changes, will warm and dry many soils, increase vegetation stress (Ju and Masek, 2016; Barber et al., 2000), degrade permafrost and deepen the active layer (Schuur et al., 2015), with uncertain consequences for soil dynamics and GHG fluxes. In this laboratory experiment we found that CO_2, but not CH_4, fluxes from these oxic active-layer mineral soils were sensitive to temperature and, in particular, moisture.

Several studies have measured microbial respiration and GHG fluxes from soils very close to our study site. Morishita et al. (2014) quantified gas fluxes in the field at CPCRW and nearby forests, and found CO_2 production to be correlated with both temperature and moisture, consistent with our results They found however that CH_4 uptake (no emissions were observed) was driven by temperature only. Waldrop et al. (2010) incubated active-layer and permafrost soils from *Picea mariana* sites near Fairbanks, AK, under varied temperature and aerobic conditions, observing Q_{10} 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) and fundamental biokinetics (Davidson and Janssens, 2006). Waldrop et al. (2010) also observed flux rates of 0.001-0.10 μmol CH_4 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 CH_4 emissions), and ~1-5 μg C-CO_2 hr^{-1} g^{-1} (~2000-10000 μg C g C^{-1} day^{-1}), considerably higher than the CO_2 rates observed from our cores. In an incubation of active-layer Alaskan permafrost peats, Treat et al. (2014) found CO_2

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and CH_4 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-CO_2 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 CO_2 rates of 47 (all mineral soils) and 101 (for 20-100 cm soils) μg C-CO_2 g C^{-1} day^{-1}, somewhat lower than our aerobic incubation results. The response of soil biota to stresses such as drought tends to differ between soil types and organisms, but be broadly similar across biomes and climatic conditions (Manzoni et al., 2012), making such comparisons between useful, in spite of significant ecological and climatic differences of studies collected by meta-analyses such as Treat et al. (2015).

4.1 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 enhance the production of extracellular enzymes, increase enzyme activities, and enhance desorption 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, that is itself driven by increases in high-latitude temperatures, vapor pressure deficit, and potentially precipitation changes.

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303 Our results suggest that moisture limitation could exert a large effect on CO_2
304 production for deep active-layer soils (**Figure 4**): "drought" cores' cumulative
305 production was 73% (4 °C) and 52% (20 °C) lower than the cores kept at field
306 moisture. This effect was highly significant, and suggests that moisture limitations
307 could exert a significant constraint on deep active-layer soils as they slowly warm.
308 Such moisture constraints are thought to be already exerting effects on vegetation
309 and soil fluxes at large scales (Ju and Masek, 2016; Bond-Lamberty et al., 2012), but
310 our understanding of the interactive effects involved is poor.

311 In contrast, the temperature sensitivities observed in this experiment were low (all
312 less than 2.0, even when controlling for changes in soil moisture), but not
313 unprecedented in comparison to a wide range of other laboratory soil incubations
314 (Hamdi et al., 2013). Observed surface CO_2 fluxes at this range exhibited a Q_{10} of 5.1
315 ± 1.4 over a temperature range of 3.5-15 °C (personal communication, C. Anderson);
316 these surface fluxes were measured over multiple months and include root
317 respiration, however, confounding any direct comparison. It is also important to
318 note that while increased temperature does not always drive C mineralization rates
319 in forest mineral soils (Giardina and Ryan, 2000), it is linked with increases in soil
320 moisture content can lead to changes in microbial community structure and GHG
321 fluxes (Xue et al., 2016).

322 More surprisingly, Q_{10} values were lower in the drought treatment cores, a
323 mathematical consequence of the fact that drought restricted CO_2 respiration more
324 at 4 than at 20 °C. There is evidence that climate warming changes the microbial

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325 decay dynamics of soil organic C compounds generally considered to be stable (Frey
326 et al., 2013; Bond-Lamberty et al., 2016a). Unlike surface soils, active layer soils,
327 which store large quantities of soil C (Mueller et al., 2015), are not subject to
328 abundant inputs of fresh C from vegetation, so the starting quality of the native soil
329 C in active layer soils may be older, more microbially processed, and dominated by
330 more stable "heavy" organic C (Karlsson et al., 2011). Thus, it is not surprising that
331 these more stable C compounds would be metabolized by processes that have been
332 reported to be less temperature-sensitive.

333 We observed very low but positive CH_4 production from these upland mineral soils.
334 This is contrast to many field studies that have observed CH_4 uptake (oxidation) in
335 dry boreal sites (Matson et al., 2009; Schaufler et al., 2010). Anoxic microsites in soil
336 can however provide enough CH_4 production to balance low-level consumption in
337 otherwise aerobic soils (Kammann et al., 2009). In addition, our results are broadly
338 consistent with data from 65 studies summarized by Olefeldt et al. (2013), who
339 found that CH_4 emissions were more sensitive to soil temperature in wetter
340 ecosystems; it would have been a surprise if the little methanogenic activity in our
341 upland, well-drained soils was temperature-sensitive at all. Methane was also a far
342 smaller C flux than CO_2 from these soils, in particular at higher temperatures (as CO_2
343 was responsive to temperature, but CH_4 was not). This is true more generally: for
344 example, Treat et al. found a median CO_2:CH_4 production ratio of 387 for boreal
345 sites, far lower than (but consistent with) our observed ratios of several million.
346 Thus we see little opportunity for CH_4 to be a significant contributor to these upland

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soils' C fluxes and climate feedback risk, even accounting for the stronger radiative forcing of this gas.

4.2 Soil nitrogen

Somewhat unexpectedly, percent soil N was very significantly and positively correlated with both CO_2 and CH_4 fluxes (**Tables 1 and 2**). N interacts with microbial respiration via a number of complex, interactive, and still unclear mechanisms (Luo and Zhou, 2006), including reductions in belowground plant allocation, shifts in energy source or population of the saprotrophic community (Saiya-Cork et al., 2002) that leave it less capable of decomposing recalcitrant compounds, and perhaps abiotic stabilization mechanisms (Janssens et al., 2010). Meta-analyses have generally shown negative to neutral effects of N deposition on microbial biomass (Treseder, 2008) and respiration (Ramirez et al., 2012), and total soil respiration across ecosystems and biomes (Janssens et al., 2010; Zhou et al., 2014). These effect are likely due to several one or more mechanisms involving soil pH, ligninase enzymes, and phenol oxidase activity (Luo and Zhou, 2006).

These conclusions have generally come from examining the effect of anthropogenic N deposition or experimental N amendments. Individual studies, including this one, have however observed positive correlations between ambient soil N and microbial respiration. For example, Weiss et al. (2015) found CO_2 production from Siberian Yedoma permafrost samples to be correlated with both percent C and N, consistent with our active-layer results (**Table 1**). In an incubation of 84 North American soils, Colman and Schimel found that percent C and percent N were highly (R^2 = 0.84)

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correlated and that the former was a significant predictor of microbial respiration--similar to our findings (C to N correlation of 0.99), except that percent N out-predicted percent C in this study. *In situ* respiration rates have also been shown to be negatively correlated with C:N at large spatial scales (Allaire et al., 2012). Percent C and N both varied widely in our soil cores, even though they were collected within tens of meters of each other, suggesting that active-layer SOC response to temperature and moisture may also be highly spatially variable, even in a visually uniform boreal forest. Spatially explicit analyses of soil properties, temperatures (Bond-Lamberty et al., 2005), and respiration (Allaire et al., 2012) are likely necessary to accurately constrain and predict soil fluxes in this ecosystem.

4.3 Limitations and weaknesses

There were weaknesses in our approach and experimental design that should be considered. Laboratory experiments offer precise control, but lack the *in situ* nature of field manipulations (Sistla et al., 2013), raising uncertainties to what degree their results can be extrapolated. They also have more specific weaknesses, for example in what can be inferred about temperature sensitivity (Podrebarac et al., 2016; Hamdi et al., 2013). Nonetheless, the controlled environments of incubations provide an important way to elucidate the key mechanisms controlling GHG from high-latitude soils (Schuur et al., 2015).

We focused on an experimental drought, rather than flooding, because of the well-drained nature of the field site: it is unlikely that the mid-slope forest we sampled in will ever suffer from thermokarst or excessive soil moisture, but too-dry conditions

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391 are a serious possibility in this low-precipitation ecosystem (Barber et al., 2000). In
392 addition, the soils here are not surface layer soils (where the majority of microbial
393 activity and C mineralization of labile C takes place); taking them out of depth
394 (where they are less exposed to O_2, for example) may significantly change the
395 abiotic conditions to which the microbial community is adapted. However, focusing
396 on the active layer provides crucial information about the potential loss of C from
397 these soils, a risk that needs to be well understood as permafrost degradation leads
398 to expansions in the depth of the active layer across the Arctic.

399 ## 5 Conclusions

400 In this laboratory experiment, we found that CO_2 fluxes were strongly influenced by
401 temperature and water content, and correlated with soil C and N, while CH_4 fluxes
402 were much smaller and not sensitive to temperature or water content in these well-
403 drained mineral soils. This suggests that understanding how soil moisture might
404 change with spatially variable permafrost degradation, how soil biota will respond
405 to these changes, and how models should treat soil organic matter decomposition
406 with respect to multiple and interacting drivers are all critical areas of research
407 going forward. Further controlled field and laboratory studies, ideally tightly
408 integrated with modeling experiments, are critical to understand GHG emission
409 dynamics from high-latitude soils.

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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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649 **Table 1.** Linear mixed-effects model parameters, testing effects of temperature (°C),
650 gravimetric water content (unitless), soil C (%), soil N (%), and dissolved organic
651 carbon (mg kg^{-1}) on individual core CO_2 fluxes (+0.1 µg C g C^{-1} day^{-1}); a colon (":")
652 indicates an interaction. Dependent variable has units of log(µg C g C^{-1} day^{-1}).
653 Columns include parameter value; standard error (SE); degrees of freedom (DF); T
654 statistic; and P value.

	Value	SE	DF	T	P
(Intercept)	1.713	0.354	1153	4.839	< 0.001
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	< 0.001
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	< 0.001

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657 **Table 2.** Linear mixed-effects model parameters, testing effects of temperature (°C),
658 gravimetric water content (unitless), soil N (%),and dissolved organic carbon (DOC,
659 mg kg^{-1}) on log-transformed, individual core CH_4 fluxes (+0.1 µg C g C^{-1} day^{-1}); a
660 colon (":") indicates an interaction. Dependent variable has units of log(µg C g C^{-1}
661 day^{-1}). Columns include parameter value; standard error (SE); degrees of freedom
662 (DF); T statistic; and P value.

	Value	SE	DF	T	P
(Intercept)	1.713	0.354	1153	4.839	< 0.001
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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	< 0.001

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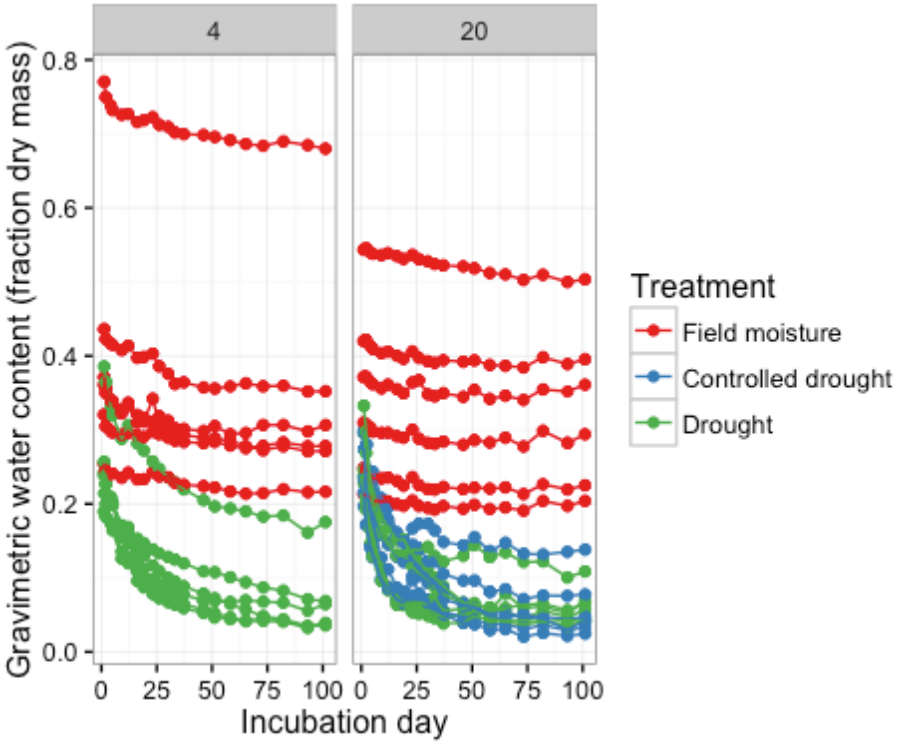
665 **Figure 1.** Core water content across the course of the incubation experiment by

666 temperature (left panel 4 °C, right panel 20 °C) and treatment.



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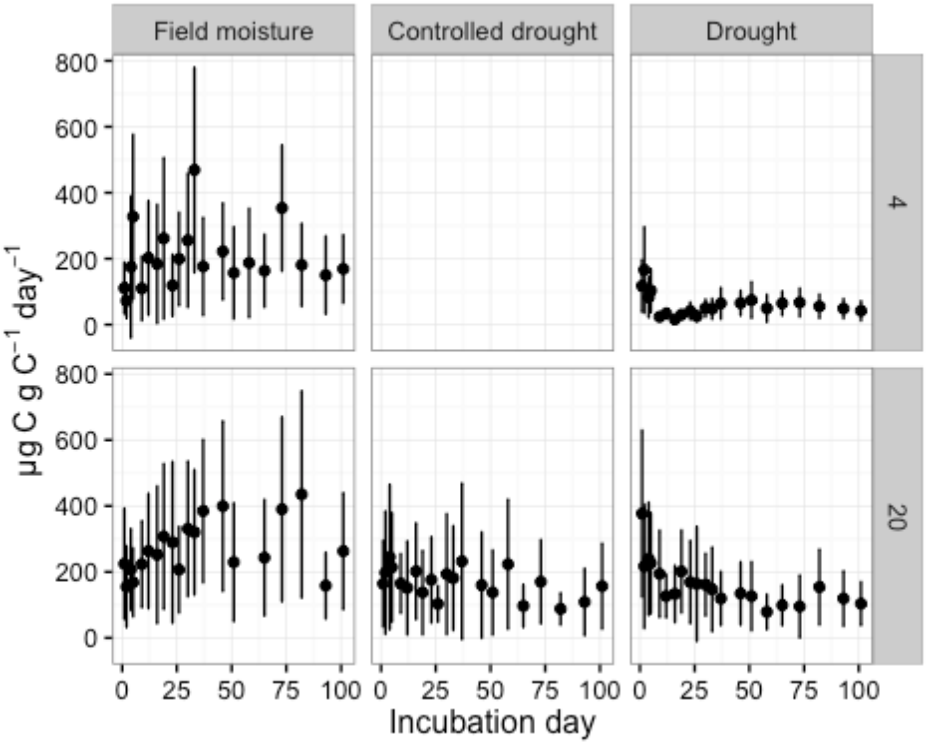
669 **Figure 2.** Mass-normalized CO_2 fluxes over the 100-day incubation, by temperature
670 (4 and 20 °C, rows) and treatment (field moisture, drought, and controlled drought;
671 columns). Error bars show core-to-core standard deviation. The "controlled
672 drought" treatment, for 20 °C only, was meant to dry cores at roughly the same rate
673 as the drought cores at 4 °C.



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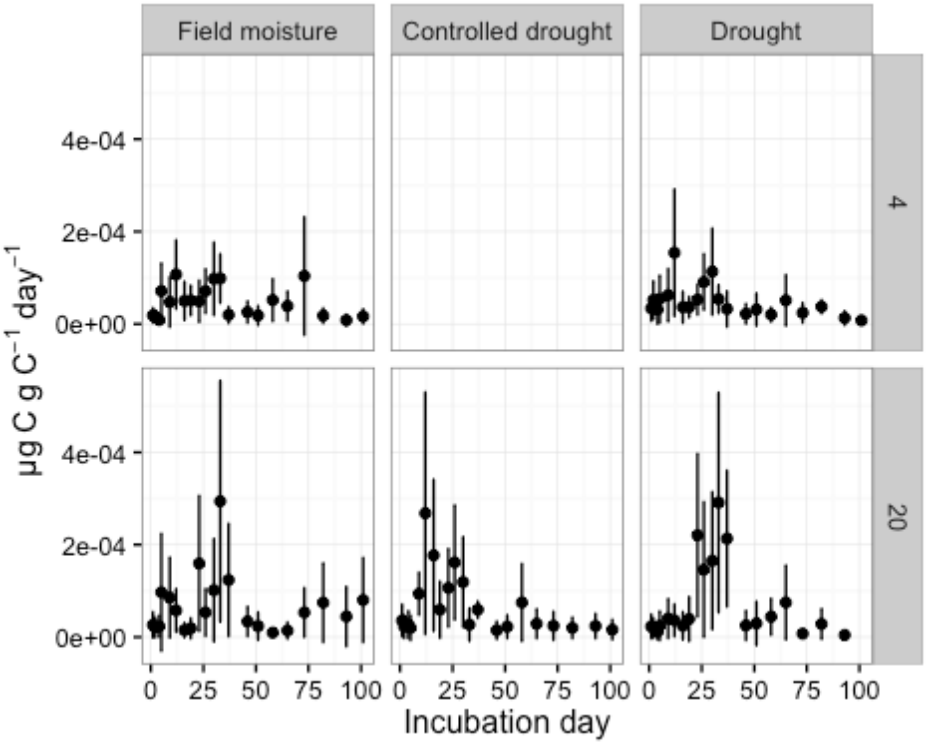
676 **Figure 3.** Mass-normalized CH_4 fluxes over the 100-day incubation, by temperature
677 (4 and 20 °C, rows) and treatment (field moisture, drought, and controlled drought;
678 columns). Error bars show core-to-core standard deviation. The "controlled
679 drought" treatment, for 20 °C only, was meant to dry cores at roughly the same rate
680 as the drought cores at 4 °C.



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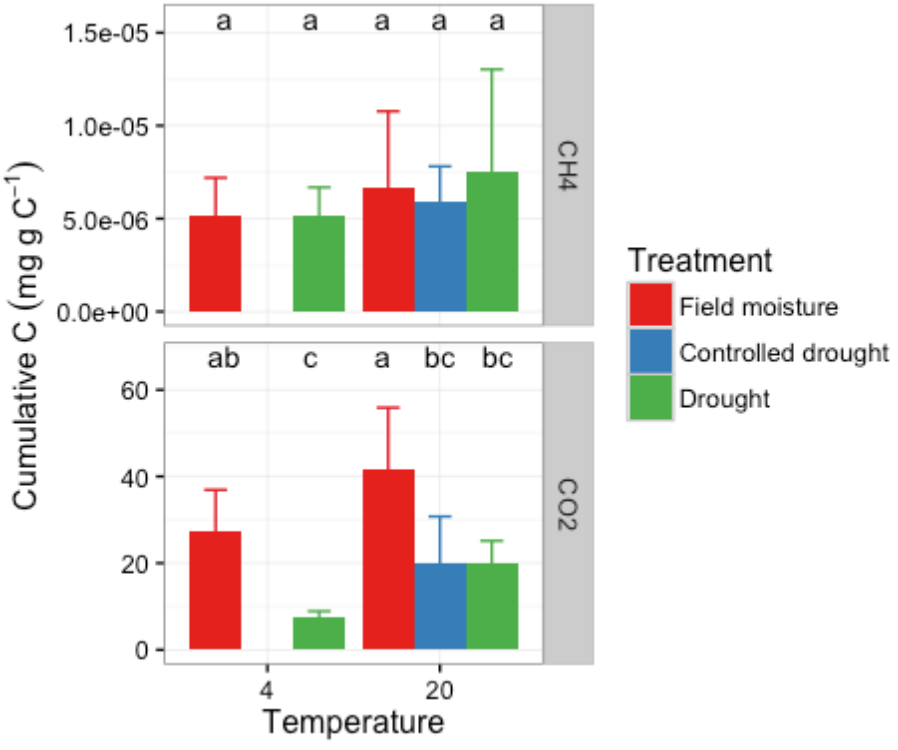
683 **Figure 4.** Cumulative C fluxes (mg g C^{-1}) over the incubation, by gas (CH_4 and CO_2,
684 top and bottom panels respectively) and treatment (columns). Letters within a
685 panel indicate significant differences based on Tukey's HSD.



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