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 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

20   chemical characteristics of the cores. Gravimetric water content was 0.31 ± 0.12

21   (unitless) at the beginning of the incubation; cores at field moisture were unchanged

22   at the end, but drought cores had declined to 0.06 ± 0.04. Daily CO_2 fluxes were

23   positively correlated with incubation chamber temperature, core water content, and

24   percent soil nitrogen, and had a temperature sensitivity (Q_{10}) of 1.3 and 1.9 for the

25   field moisture and drought treatments, respectively. Daily CH_4 emissions were most

26   strongly correlated with percent nitrogen, but neither temperature nor water

27   content was a significant first-order predictor of CH_4 fluxes. The cumulative

28   production of C from CO_2 was over six orders of magnitudes higher than that from

29   CH_4; cumulative CO_2 was correlated with incubation temperature and moisture

30   treatment, with drought cores producing 52% - 73% lower C. Cumulative CH_4

31   production was unaffected by any treatment. These results suggest that deep active-

32   layer soils may be sensitive to changes in soil moisture under aerobic conditions, a

33   critical factor as discontinuous permafrost thaws in interior Alaska. Deep but

34   unfrozen high-latitude soils have been shown to be strongly affected by long-term

35   experimental warming, and these results provide insight into their future dynamics

36   and feedback potential with future climate change.

37   **1 Introduction**

38   High latitude ecosystems are being subjected to rapid changes in climate (IPCC,

39   2013) and increases in fire frequency and intensity (Kasischke et al., 2010), notably

40   in northwestern North America and Alaska (Hinzman et al., 2005; Ju and Masek,

41   2016). This will have a wide variety of ecosystem effects (Alexander and Mack,

42 2016): in particular, rising temperatures and increasing fire will likely result in

43 changes in soil temperature and permafrost degradation (Pastick et al., 2015; Zhang

44 et al., 2015; Genet et al., 2013; Helbig et al., 2016), with subsequent hydrology

45 changes that will influence soil greenhouse gas (GHG) fluxes to the atmosphere

46 (Schädel et al., 2014). Such fluxes are a large component of the global C cycle and

47 could result in a significant and positive climate feedback (Treat et al., 2015; Koven

48 et al., 2011; Schaefer et al., 2014).

49 The magnitude, timing, and form-in particular as methane (CH_4) or carbon dioxide

50 (CO_2)-of such any such feedback remain highly uncertain (Schuur et al., 2015).

51 While northern soils hold enormous quantities of potentially mineralizable soil

52 organic carbon (SOC) (Hugelius et al., 2014), vegetation and succession dynamics

53 (for example, thermal insulation by mosses) promote permafrost resilience to even

54 large temperature changes (Jorgenson et al., 2010; Turetsky et al., 2012). Vegetation

55 type also influences SOC quality and quantity, with microbial communities (Högberg

56 et al., 2007), soil respiration (Raich and Tufekcioglu, 2000), and SOC all linked to

57 aboveground factors such as woody versus nonwoody stems, deciduous versus

58 evergreen canopies, and the presence of nitrogen-fixing plants. A number of factors

59 may however disrupt these these feedbacks between vegetation type, ground cover,

60 permafrost, and SOC stability. Climate changes, in particular regional warming and

61 drying, cause vegetation stress (Ju and Masek, 2016; Barber et al., 2000) and

62 increased mortality. Conversely, increasing plant productivity in some regions can

63 stimulate the decomposition of older SOC (Hartley et al., 2012). Climate also drives

64 fire regime changes, and ecosystem disruption is particularly likely after intense

65   fires (Johnstone et al., 2010; Genet et al., 2013). Even absent disturbance, the

66   stability of SOC is highly uncertain, as it depends on soil temperature and moisture,

67   the ages of and ratio between the carbon (C) and nitrogen (N) pools (Weiss et al.,

68   2015; Karhu et al., 2014), and its protection (whether by organomineral sorption,

69   chemical lability, or physical location) from competent microorganisms, enzymes,

70   and resources (Bailey et al., 2012; Schmidt et al., 2011).

71   Temperature and moisture typically have strong and often interactive influences on

72   soil GHG emissions. Laboratory incubations, field observations, and meta-analyses

73   have documented changing greenhouse gas (GHG) fluxes with rising temperature

74   (Olefeldt et al., 2013; Davidson and Janssens, 2006; Hashimoto et al., 2015; Treat et

75   al., 2015). GHG responses to wetting and thawing dynamics exhibit substantial

76   variability between studies, probably due to differences in soil type, antecedent

77   conditions, phase changes, experimental protocols, etc. (Kim et al., 2012). The

78   anaerobic conditions common following permafrost thaw are expected to lower CO_2

79   emissions but increase those of CH_4 (Treat et al., 2015; Treat et al., 2014), but

80   emissions from aerobic soils will likely dominate the permafrost C feedback

81   (Schädel et al., 2016). Decadal warming and drying trends in Alaska (Bieniek et al.,

82   2014) thus seem likely to increase GHG emissions from soils, and laboratory

83   incubation experiments are critical to understand these dynamics (Elberling et al.,

84   2013).

85   Most previous studies have focused on surface soils or permafrost soils, neglecting

86   deep active-layer soils that were identified as subject to strong effects from a two-

87 decade warming experiment in the Alaskan Arctic (Sistla et al., 2013). Such deeper

88 soils have particular characteristics distinguishing them from both shallow active

89 layer soils and underlying permafrost: they are most affected by interannual

90 variability in thaw depth, potentially flipping the C source/sink status of entire

91 ecosystems (Goulden et al., 1998; Harden et al., 2012); they are subject to distinctive

92 freeze-thaw, cryoturbation, and microbial dynamics, which are likely to change their

93 sensitivity to climate change and feedback potential (Schuur et al., 2008); and they

94 are known to pose particular problems for accurate modeling of high-latitude

95 carbon dynamics (Nicolsky et al., 2007). These soils are likely to be a highly

96 important contributor to future climate feedbacks, with modeling studies suggesting

97 that one-third of 21st century climate-induced carbon loss may originate from

98 seasonally frozen soil carbon (Koven et al., 2015).

99 The goal of this study was to examine how temperature and moisture control GHG

100 (CO_2 and CH_4) emissions from soils sampled from the bottom of the annual active

101 layer–i.e., directly above permafrost–in an Alaskan boreal forest. We also aimed to

102 characterize the chemical and structural properties of these soils following a 100-

103 day incubation at different temperatures, subjecting some cores to drying

104 treatments. We hypothesized that (i) CO_2 would be the dominant pathway for C loss

105 in these largely aerobic soils; (ii) soils maintained at field moisture and high (20°C)

106 temperature would lose more C-CO_2 than cores incubated at 4°C, due to increased

107 aerobic and anaerobic microbial activity; and (iii) core CH_4 fluxes would be small

108 and sensitive only to temperature, as no anaerobic conditions were imposed on the

109 cores.

2 Methods

2.1 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 is -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* (Mill.) BSP), feathermoss (*Pleurozium schreberi* and others), and *Sphagnum* spp.; the drier south slopes tend to be deciduous with a mixture of trembling aspen (*Populus tremuloides* Michx.), 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* and upland *Betula neoalaskana*, with significant white spruce (*Picea glauca*) presence as well. Stand density in this transition zone was 4060 ± 2310 trees ha^{-1}, with basal area of 27.9 ± 7.0 m^2 ha^{-1}. The forest was at least 90 years old (cf. Morishita et al., 2014) according to tree cores taken at the 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.

131 Thirty-nine soil cores, each 30 cm high by 7.5 cm wide, were taken using a soil

132 recovery augur (AMS Inc., American Falls, ID) on 3-5 August 2015. We sampled from

133 the bottom (within 0-2 cm of permafrost) of the active layer, which averaged 80 cm

134 depth. Sample points were randomly located in the transition zone described above,

135 and separated by 2-5 m. Cores were kept cool in the field before being packed in dry

136 ice and shipped to Richland, WA within 48-72 hours of collection.

137 **2.2 Laboratory incubation**

138 In the lab, the soil cores were stored at 4 °C for several days until they were weighed

139 and prepared for incubation. At that point (11-12 August 2015), three fragmented

140 or otherwise damaged cores were discarded, and the remaining cores were

141 randomly assigned to one of six groups (N=6 in each group). These included two

142 incubation temperatures of 4 and 20 °C, following the protocol of a number of

143 previous boreal incubation studies (Treat et al., 2015). Within each temperature

144 there were two moisture treatments: one in which soil moisture was maintained at

145 field conditions (~28% moisture by volume), and a drought treatment in which no

146 water was added and cores were allowed to dry down to ~5% moisture by volume.

147 The fifth group was a 20 °C "controlled drought" one, in which water was added so

148 that these cores' moisture status would close match those of the 4 °C "drought"

149 cores, which we anticipated would dry more slowly than their 20 °C counterparts.

150 The final 6-core group was used for destructive, pre-incubation measurements

151 including moisture content, pH, soil carbon and N, and bulk density. Subsamples

152   were collected and stored at -20 °C for dissolved organic carbon measurements or

153   air-dried for soil C and N (see below).

154   On 18 August 2015 cores were placed into one of two growth chambers (Conviron

155   Control Systems BDW80, Winnipeg, Canada) maintained at 4 and 20 °C

156   temperatures and 70% relative humidity and allowed to equilibrate for two weeks.

157   Starting on 31 August 2015 we measured the cores' mass and GHG emissions four

158   times in the first week, then twice per week for the first month, and then once per

159   week for the rest of the 100-day incubation. Throughout the incubation, cores had a

160   200 μm mesh screen fit to the base and were mounted on porous ceramic plates

161   (Soil Moisture Equipment Corp., Santa Barbara, CA, USA) so that, when the plates

162   were placed in contact with water, water would move up into the cores via capillary

163   action. The "drought" cores were mounted on dry plates, but not allowed to drop

164   below 5% water content. After each flux measurement, cores received additional

165   wetting from the top to maintain their desired water status.

166   For each measurement, a six-core treatment group was connected to a Picarro

167   A0311 multiplexer that was in turn connected to a Picarro G2301 GHG Analyzer

168   (Picarro Inc., Santa Clara, CA, USA). Dry CH_4 and CO_2 concentrations were monitored

169   for 2 minutes, and this was repeated 2-3 times before moving on to a new treatment

170   group. Cores were weighed immediately after gas measurements. Ambient air was

171   measured between treatment groups, and before starting measurements in a

172   chamber, as a check on ambient CO_2 conditions and instrument stability.

173 The incubation experiment concluded on 9 December 2015, following the final CO_2

174 and CH_4 readings. Each soil core was maintained at the treatment-dependent

175 temperature and moisture content (by mass) until removed for destructive

176 sampling, December 14-18, 2015. Sub-samples were collected and composited

177 throughout each soil core for dissolved organic carbon analysis (110 ± 24 g dry

178 mass equivalent) and dry-mass calculations (~28 g each). The remaining core

179 material was air-dried and separated into particles (>2 mm diameter) and soil (≤2

180 mm) using a U.S. Standard Test Sieve No. 10 (Fisherbrand, Pittsburg, PA, USA). The

181 dry mass and volume of soil were used in calculations of gravimetric and volumetric

182 soil moisture content, respectively (Gardner, 1986). Soil volume was calculated as

183 the total core volume minus the volume of particles >2 mm diameter, with the latter

184 determined by water displacement. Air-dried soil and sub-samples stored at -20 °C

185 were sent to the Agricultural and Environmental Services Laboratory at the

186 University of Georgia Extension in February 2016 for total C, N, and dissolved

187 organic carbon (DOC). Samples were combusted in an oxygen atmosphere at 1350

188 °C, and measured for gaseous C and N using an Elementar Vario Max CNS

189 (Langenselbold, Germany). DOC was measured using a Shimadzu 5000 TOC

190 Analyzer (Columbia, Maryland, USA).

191 **2.3 Data and statistical analysis**

192 For each measurement of each sample throughout the 100-day incubation (i.e., each

193 gas, core, and date/time), we used the rise in gas concentrations to calculate a flux

194 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

195   concentration rise from a minimum (up to 10 seconds after measurement began) to

196   a maximum (at 10-45 seconds). Each core's respiration flux (F) was then calculated

197   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

198   determined at the end of the incubation, P_a atmospheric pressure (101 kPa; the

199   incubation chambers were ~120 m a.s.l.), R the universal gas constant (8.3×10^{-3} m^3

200   kPa mol^{-1} K^{-1}) and T the chamber air temperature (K) at time of measurement. The

201   final respiration rate was expressed on a soil C basis (µg or ng C g C^{-1} day^{-1}).

202   Anomalous data were excluded based on their gas fluxes being more than 5 (for

203   CO_2) or 10 (for CH_4) mean absolute deviations (Davies and Gather, 1993) from the

204   treatment mean within a 10-day period, for a given treatment and temperature. We

205   excluded 172 of 2686 (6.4%) measurements for this reason. If the coefficient of

206   variability (CV) of fluxes from any core on a single day exceeded 140%, a value

207   chosen based on the distribution of CVs across all cores, the entire core was

208   excluded for that day (90 data points, 3.4%). Other data (4.8%) were removed

209   because of known instrument problems, e.g. the analyzer was left running after

210   leaving a chamber. The final number of valid flux samples from the 100-day

211   incubation was 2198.

212   The effects of temperature, gravimetric water content, percent C, percent N, and

213   DOC concentration on instantaneous gas fluxes were evaluated using a linear mixed-

214   effects model fit by the R function *lme* in the R 'nlme' package, version 3.1.128.

215   Because the dependent variable (CO_2 or CH_4 flux) was non-normally distributed, it

216   was transformed using a natural-logarithm (+0.1 µg C g C^{-1} day^{-1} to ensure all

217   positive fluxes, following Treat et al. 2015) transformation. Soil core was treated as

218   a random effect in the model. We then performed stepwise model selection by

219   Akaike's information criterion (AIC) using the *stepAIC* function in the R 'MASS'

220   package, version 7.3.45. A linear mixed-effects model was also used to evaluate the

221   effect of treatment on core water content.

222   Cumulative respiration for each core and gas was calculated by linearly

223   interpolating flux rates between measurement dates and summing respired C over

224   the entire incubation. The effect of temperature and treatment (drought, controlled

225   drought, or field moisture conditions) on cumulative gas fluxes was evaluated with a

226   post-hoc Tukey Honest Significant Differences test. Temperature sensitivity (Q_{10})

227   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

228   cumulative gas fluxes (mg C g C^{-1}) at temperatures T_1 and T_2 (°C), respectively.

229   All data analysis and statistics were performed using R version 3.3.1 (2016-06-21)

230   (R Development Core Team, 2016). This experiment was run as an 'open

231   experiment' (Bond-Lamberty et al., 2016b) with all analysis code, data (from raw

232   instrument data to final summaries), diagnostics, etc., available at

233   https://github.com/bpbond/cpcrw_incubation. The summarized flux data backing

234   the main results have been archived under the Digital Object Identifier

235   10.6084/m9.figshare.4240436.v1.

3 Results

236

237   The 30 experimental cores had a bulk density of 1.00 ± 0.18 (mean $\pm$ sd) g cm^{-3}.

238   Large (>2 mm) particles, primarily schist, comprised $41\% \pm 11\%$ of the cores' total

239   mass. Soil ($\leq$2 mm) dry mass was 886 ± 154 g. Sample DOC was 157.93 ± 55.74 mg

240   kg^{-1}. Carbon content was $1.20\% \pm 1.19\%$, while N content was $0.06\% \pm 0.06\%$. Mean

241   C:N was 20.7. Neither temperature nor moisture treatment exerted any significant

242   effect (P > 0.1 for all) on these highly variable properties (**Table 1**).

243   Gravimetric water content was 0.31 ± 0.12 (min 0.19, max 0.77) at the beginning of

244   the incubation (**Figure 1**). "Field moisture" cores were on average unchanged (0.33

245    $\pm$ 0.13) at the end of the incubation, but both the drought treatments, which did not

246   differ from each other in their effect on gravimetric water content (P = 0.880), had

247   declined to 0.06 ± 0.04. Volumetric water content values ranged from 0.29 ± 0.05

248   (min 0.23, max 0.43) at the beginning of the experiment to 0.15 ± 0.11 (min 0.03,

249   max 0.38) at the end across all cores. Water filled pore space, assuming a particle

250   density of 2.65 g cm^{-3}, was 22-65% over all cores, moisture treatments, and

251   temperatures.

252   Carbon dioxide fluxes during the incubation ranged from 1.1 µg C g C^{-1} day^{-1} to a

253   maximum of 5245.1 µg C g C^{-1} day^{-1}, with a mean of 248.9 µg C g C^{-1} day^{-1} over the

254   100 days. CH$_4$ rates ranged from 0.00 ng C g C^{-1} day^{-1} to a maximum of 1.31 ng C g C^{-1}

255   day^{-1}, with a mean of 0.06 ng C g C^{-1} day^{-1}. These means conceal considerable

256   variability over the course of the incubation (**Table 1, Figures 2 and 3**).

257   In the linear mixed-effects model (AIC = 2992.6), instantaneous CO_2 flux was

258   positively correlated with incubation chamber temperature, core gravimetric water

259   content, and percent soil N (all P < 0.05, and the latter two P < 0.001; **Table 2**).

260   Temperature sensitivity decreased significantly (P < 0.001) over the course of the

261   incubation, while moisture sensitivity was unaffected by time. Percent C and percent

262   N were highly correlated (r = 0.99) for these cores. Because percent N was a slightly

263   stronger predictor, it was retained in the model while percent C was excluded; cf.

264   Colman and Schimel (2014). The interaction between water content and percent N

265   was also highly significant (P < 0.001), although cores with N > 0.2% exhibited little

266   relationship between water content and CO_2 flux (data not shown). Instantaneous

267   CH_4 fluxes were positively correlated with percent N, while water content exhibited

268   significant interactions with percent N and DOC as a predictor (**Table A1**). This

269   model had little predictive power (AIC = -10879.2), however, and neither

270   temperature nor water content was a significant first-order predictor of CH_4 fluxes.

271   The cumulative production of C from CO_2 (**Figure 4**) was over six order of

272   magnitudes higher than that from CH_4, with CO_2:CH_4 C ratios ranging from 1.4

273   million in the 4 °C "Field moisture" treatment, to 6.2 million in the 20 °C "Field

274   moisture" treatment. Cumulative CO_2 evolved was highly affected by temperature (P

275   = 0.003), and "field moisture" cores emitted significantly more CO_2 than the other

276   two moisture treatments at both temperatures (P < 0.001 for both, with no

277   significant interactive effect). There was no difference between fluxes from the 20 °C

278   "drought" and "controlled drought" treatments (P = 0.377). "Drought" cores'

279   cumulative production was 73% (4 °C) and 52% (20 °C) lower than the cores kept at

280   field moisture. Neither temperature (P = 0.200) nor moisture treatment (mean P =

281   0.975) was a significant factor in predicting cumulative CH_4 fluxes.

282   The cumulative flux numbers above result in CO_2 temperature sensitivity (Q_{10})

283   values of 1.3 and 1.9 for the field moisture and drought treatments, respectively; the

284   corresponding Q_{10} values based on cumulative CH_4 were 1.2 and 1.3. Computing Q_{10}

285   values based on fluxes normalized by water filled pore space changed these values

286   only slightly: to 1.2 and 1.7 for CO_2, for the field moisture and drought treatments

287   respectively, and 1.1 and 1.2 for CH_4.

288   **4 Discussion**

289   Rises in boreal air temperatures, and unpredictable precipitation changes, will

290   change fire disturbance regimes, warm and dry many soils, increase vegetation

291   stress, degrade permafrost, and deepen the active layer (Schuur et al., 2015), all

292   with uncertain consequences for soil dynamics and GHG fluxes. In this laboratory

293   experiment we found that CO_2, but not CH_4, fluxes from these oxic active-layer

294   mineral soils were sensitive to temperature and, in particular, moisture.

295   A number of studies have measured microbial respiration and GHG fluxes very close

296   to our study site. Morishita et al. (2014) quantified GHG fluxes at CPCRW and nearby

297   forests, and found CO_2 production to be correlated with both temperature and

298   moisture in upland Cryosols, consistent with our results. Waldrop et al. (2010)

299   incubated active-layer and permafrost soils from *Picea mariana* sites near

300   Fairbanks, AK, observing aerobic Q_{10} values of 9.0 (active layer) and 2.3

301   (permafrost) from -5 to 5 °C, and flux rates of 0.001-0.10 μmol CH_4 day^{-1} g^{-1}

302   (~0.001-0.133 ng C g C^{-1} day^{-1}), and ~1-5 µg C-CO_2 hr^{-1} g^{-1} (~2000-10000 µg C g C^{-1}

303   day^{-1}), considerably higher than the CO_2 rates observed here. During the first 100

304   days of an incubation of Fairbanks-area 0-10 cm mineral soils, Neff and Hooper

305   (2002) observed fluxes of ~55-409 µg C-CO_2 g C^{-1} day^{-1}, in line with the results here,

306   while Wickland and Neff (2008) reported that temperature and moisture exhibited

307   interactive effects, of similar magnitude, on decomposition in *P. mariana* soils.

308   A number of synthesis studies have documented dynamics and C feedback potential

309   of Arctic and boreal soils more generally; comparing to these results is useful

310   because although the response of soil biota to stresses such as drought tends to

311   differ between soil types, organisms, and vegetation, it is often broadly similar

312   across biomes and climatic conditions (Manzoni et al., 2012). Using two meta-

313   analyses of aerobic and anaerobic permafrost soil incubations, Schädel et al. (2016)

314   showed that C release was highly sensitive to temperature, and that soils released

315   far more (220-520%) C under aerobic conditions. Our incubation was fully aerobic,

316   but its results are consistent with the conclusion that respiration in the form of CO_2

317   is likely to dominate the high latitude C feedback, and that aerobic soils, and the

318   conditions under which currently waterlogged soils may drain, deserve particular

319   attention. In terms of absolute flux rates, Treat et al. (2015) reported mean CO_2

320   rates of 47 (all mineral soils) and 101 (for 20-100 cm soils) µg C-CO_2 g C^{-1} day^{-1} from

321   a pan-Arctic synthesis of anaerobic soil incubations, somewhat lower than our

322   aerobic incubation results. Treat et al. (2014) also found CO_2 and CH_4 emissions to

323   be strongly correlated with temperature and moisture based on an incubation of

324   Alaskan peats. Whether climate change makes northern regions wetter or driers is

325   thus a critical factor affecting the quantity and form of C release.

326   The drought treatment imposed in this experiment reduced soil C fluxes by 52% -

327   73%. The importance of this result depends, in part, on the spatial extent and

328   intensity of precipitation changes across the boreal and Arctic this century. There is

329   a detectable anthropogenic influence in high latitude precipitation changes (Wan et

330   al., 2015), but these changes are inconsistent: drier and warmer conditions in boreal

331   Eurasia (Buermann et al., 2014), for example, but growing season length increases

332   in interior Alaska with no increase in precipitation (Wendler and Shulski, 2009).

333   This spatial variability will interact with permafrost thaw dynamics to produce a

334   complex patchwork of soil moisture changes (Zhang et al., 2012; Watts et al., 2012).

335   The high uncertainty in this area makes it all the more important to understand the

336   interactive effects of soil moisture and temperature on decomposition and GHG

337   emissions (Sierra et al., 2015).

338   We observed very low but positive CH_4 production from these upland mineral soils.

339   This is contrast to many field studies that have observed CH_4 uptake (oxidation) in

340   dry boreal sites (Matson et al., 2009; Schaufler et al., 2010). Anoxic microsites in soil

341   can however provide enough CH_4 production to balance low-level consumption in

342   otherwise aerobic soils (Kammann et al., 2009). In addition, our results are broadly

343   consistent with data from 65 studies summarized by Olefeldt et al. (2013), who

344   found that CH_4 emissions were more sensitive to soil temperature in wetter

345   ecosystems; it would have been a surprise if the little methanogenic activity in our

346   upland, well-drained soils was temperature-sensitive at all. Methane was also a far

347   smaller C flux than CO_2 from these soils, in particular at higher temperatures (as CO_2

348   was responsive to temperature, but CH_4 was not). This is true more generally: for

349   example, Treat et al. found a median CO_2:CH_4 production ratio of 387 for anaerobic

350   incubations of boreal soils. This is naturally far lower than our observed aerobic

351   (and thus high-CO_2) ratios, but nonetheless consistent with them. Thus we see little

352   opportunity for CH_4 to be a significant contributor to these upland soils' C fluxes and

353   climate feedback risk, even accounting for the 25x stronger radiative forcing of this

354   gas over a 100-year time horizon (Lee et al., 2012).

355   **4.1 Temperature versus moisture sensitivity for cumulative emissions**

356   The cumulative GHG fluxes (**Figure 4**) integrate the entire 100-day incubation,

357   eliminating the day-to-day variability of instantaneous fluxes and are thus more

358   generalizable. Our results suggest that moisture limitation could exert a large effect

359   on CO_2 production for deep active-layer soils: "drought" cores' cumulative

360   production was 73% (4 °C) and 52% (20 °C) lower than the cores kept at field

361   moisture. This effect was highly significant, and suggests that moisture limitations

362   could exert a significant constraint on deep active-layer soils as they slowly warm.

363   Such moisture constraints are thought to be already exerting effects on vegetation

364   and soil fluxes at large scales (Ju and Masek, 2016; Bond-Lamberty et al., 2012), but

365   our understanding of the interactive effects involved is poor.

366   The Q_{10} values observed in this experiment were low (all less than 2.0, even when

367   controlling for changes in soil moisture). Temperature sensitivities of ~2 are more

368 typical (Dutta et al., 2006; Schädel et al., 2016), although the temperature sensitivity

369 of C release can change over time of incubation (Dutta et al., 2006) and vary

370 between soil fractions cycling over different time horizons (Karhu et al., 2010;

371 Schädel et al., 2014). Observed surface CO_2 fluxes at this CPCRW site exhibited a Q_{10}

372 of 5.1 ± 1.4 over a temperature range of 3.5-15 °C (personal communication, C.

373 Anderson); these surface fluxes were measured over multiple months and include

374 root respiration, however, preventing any direct comparison. While increased

375 temperature does not always drive C mineralization rates in forest mineral soils

376 (Giardina and Ryan, 2000), it is linked with increases in soil moisture content can

377 lead to changes in microbial community structure and GHG fluxes (Xue et al., 2016).

378 Interestingly, Q_{10} values were lower in the drought treatment cores, a mathematical

379 consequence of the fact that drought restricted CO_2 respiration more at 4 °C than at

380 20 °C. There is evidence that climate warming changes the microbial decay

381 dynamics of soil organic C compounds generally considered to be stable (Frey et al.,

382 2013; Bond-Lamberty et al., 2016a). Conditions such as drought can change the

383 amount and quality of DOC available to microbes (1999), but we observed no DOC

384 changes between treatments here. Deep active layer soils store large quantities of

385 soil C (Mueller et al., 2015) but are not subject to abundant inputs of fresh C from

386 vegetation, so the starting quality of the native soil C in active layer soils is older,

387 more microbially processed, and dominated by more stable "heavy" organic C

388 (Karlsson et al., 2011). Thus, it may not be surprising that these more stable C

389 compounds would be metabolized by processes that have been reported to be less

390 temperature-sensitive.

4.2 Soil nitrogen

391

392 Somewhat unexpectedly, percent soil N was very significantly and positively

393 correlated with both CO_2 and CH_4 fluxes (**Tables 2 and 3**). Nitrogen interacts with

394 microbial respiration via a number of complex, interactive, and still unclear

395 mechanisms (Luo and Zhou, 2006), including reductions in belowground plant

396 allocation, shifts in energy source or population of the saprotrophic community

397 (Saiya-Cork et al., 2002) that leave it less capable of decomposing recalcitrant

398 compounds, and perhaps abiotic stabilization mechanisms (Janssens et al., 2010).

399 Meta-analyses have generally shown negative to neutral effects of N deposition on

400 microbial biomass (Treseder, 2008) and respiration (Ramirez et al., 2012), and total

401 soil respiration across ecosystems and biomes (Janssens et al., 2010; Zhou et al.,

402 2014). These effect are likely due to several one or more mechanisms involving soil

403 pH, ligninase enzymes, and phenol oxidase activity (Luo and Zhou, 2006), and

404 incubation results examining N effects can be highly variable (Lavoie et al., 2011;

405 Sistla et al., 2012). Some studies have however observed positive correlations

406 between ambient soil N and microbial respiration. For example, Weiss et al. (2015)

407 found CO_2 production from Siberian Yedoma permafrost samples to be correlated

408 with both percent C and N, consistent with our active-layer results (**Table 2**).

409 The C:N ratio was not a significant predictor of GHG fluxes in this study, although

410 this ratio has been found to be important in meta-analyses (Sistla et al., 2012;

411 Schädel et al., 2014). *In situ* respiration rates have also been shown to be negatively

412 correlated with C:N at large spatial scales (Allaire et al., 2012). Percent C and N both

413   varied widely in our soil cores (**Table 1**), and were highly correlated with each

414   other, even though the cores were collected within tens of meters of each other. This

415   suggests that active-layer SOC response to temperature and moisture may also be

416   highly spatially variable, even in a mixed-species boreal forest that we expected, *a*

417   *priori*, to provide spatial variation in litter and SOC quality (Fierer et al., 2005).

418   Spatially explicit analyses of soil biochemistry, temperatures (Bond-Lamberty et al.,

419   2005), and respiration (Allaire et al., 2012) are likely necessary to accurately

420   constrain and predict soil fluxes in this ecosystem.

421   **4.3 Limitations and weaknesses**

422   There were weaknesses in our approach and experimental design that should be

423   considered. Laboratory experiments offer precise control, but lack the *in situ* nature

424   of field manipulations (Sistla et al., 2013), raising uncertainties to what degree their

425   results can be extrapolated. Soils isolated during incubation may, for example,

426   underestimate temperature sensitivity of respiration (Podrebarac et al., 2016) or

427   exhibit lag effects (Treat et al., 2015). It should also be noted that our 100-day

428   incubation was not long enough to observe slowly-cycling soil fractions, which may

429   vary in their response to experimental manipulation (Karhu et al., 2010).

430   Nonetheless, the controlled environments of incubations provide an important way

431   to elucidate the key mechanisms controlling GHG from high-latitude soils (Schuur et

432   al., 2015).

433   The soils studied here were from an upland, mixed conifer-deciduous boreal forest,

434   and care needs to be taken before drawing regional inferences, or about other

435   ecosystem types. We focused on an experimental drought, rather than flooding,

436   because of the well-drained nature of the field site: it is unlikely that the mid-slope

437   forest we sampled in will ever suffer from thermokarst or excessive soil moisture,

438   but too-dry conditions are a serious possibility in this relatively low-precipitation

439   ecosystem (Barber et al., 2000).

440   Finally, the soils here are not surface layer soils (where the majority of microbial

441   activity and C mineralization of labile C takes place); removing them from *in situ*

442   conditions (where they are less exposed to O_2, for example) may significantly

443   change the abiotic conditions to which the microbial community is adapted.

444   However, focusing on the active layer provides crucial information about the

445   potential loss of C from these soils, a risk that needs to be well understood as

446   permafrost degradation leads to expansions in the depth of the active layer across

447   the Arctic.

448   **5 Conclusions**

449   In this laboratory experiment, we found that CO_2 fluxes were strongly influenced by

450   temperature and water content, and correlated with soil C and N, while CH_4 fluxes

451   were much smaller and not sensitive to temperature or water content in these well-

452   drained mineral soils. These results add to a growing body of Arctic permafrost and

453   active layer incubation literature, and underscore the importance of understanding

454   moisture effects on CO_2 fluxes in particular. How soil moisture might change with

455   spatially variable permafrost degradation, how soil biota will respond to these

456   changes, and how models should treat soil organic matter decomposition with

457 respect to multiple and interacting drivers are all critical areas of research going

458 forward. Further controlled field and laboratory studies, ideally tightly integrated

459 with modeling experiments, are important to understand GHG emission dynamics

460 from high-latitude soils.

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468 **Author contributions**

469 B.B.-L., A.P.S., and V.L.B. designed this experiment. B.B.-L. and A.P.S. performed field

470 sampling, and A.P.S. led the laboratory incubation and analyses. B.B.-L. wrote the

471 manuscript, with contributions from all authors.

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 Table 1. Summary of dissolved organic carbon (DOC), percent C, percent N, bulk

788 density (BD), and CO_2 and CH_4 fluxes by treatment. The "Field moisture" and

789 "Drought" columns summarize (mean ± s.d.) 12 cores, combining two groups of N=6

790 at each incubation temperature, while the "Controlled drought" and "Pre-

791 incubation" columns are N=6.

Variable	Field moisture	Controlled drought	Drought	Pre-incubation
DOC (mg kg^{-1})	173.62 ± 46.67	165.68 ± 66.46	154.60 ± 57.15	125.43 ± 49.07
C (%)	1.67 ± 1.60	0.87 ± 0.50	0.76 ± 0.60	1.44 ± 1.32
N (%)	0.08 ± 0.08	0.04 ± 0.03	0.03 ± 0.03	0.07 ± 0.06
BD (g cm^{-3})	0.89 ± 0.18	1.06 ± 0.17	1.08 ± 0.14	1.13 ± 0.29
CO2 (µg C g C^{-1} day^{-1})	456.40 ± 543.91	159.77 ± 116.41	97.03 ± 96.38	-
CH4 (ng C g C^{-1} day^{-1})	0.10 ± 0.00	0.10 ± 0.00	0.10 ± 0.00	-

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793

794   **Table 2.** Linear mixed-effects model parameters, testing effects of temperature (°C),

795   gravimetric water content (unitless), soil C (%), soil N (%), and dissolved organic

796   carbon (mg kg^{-1}) on individual core CO_2 fluxes (+0.1 µg C g C^{-1} day^{-1}); a colon (":")

797   indicates an interaction. Dependent variable has units of log(µg C g C^{-1} day^{-1}).

798   Columns include parameter value; standard error (SE); degrees of freedom (DF); T

799   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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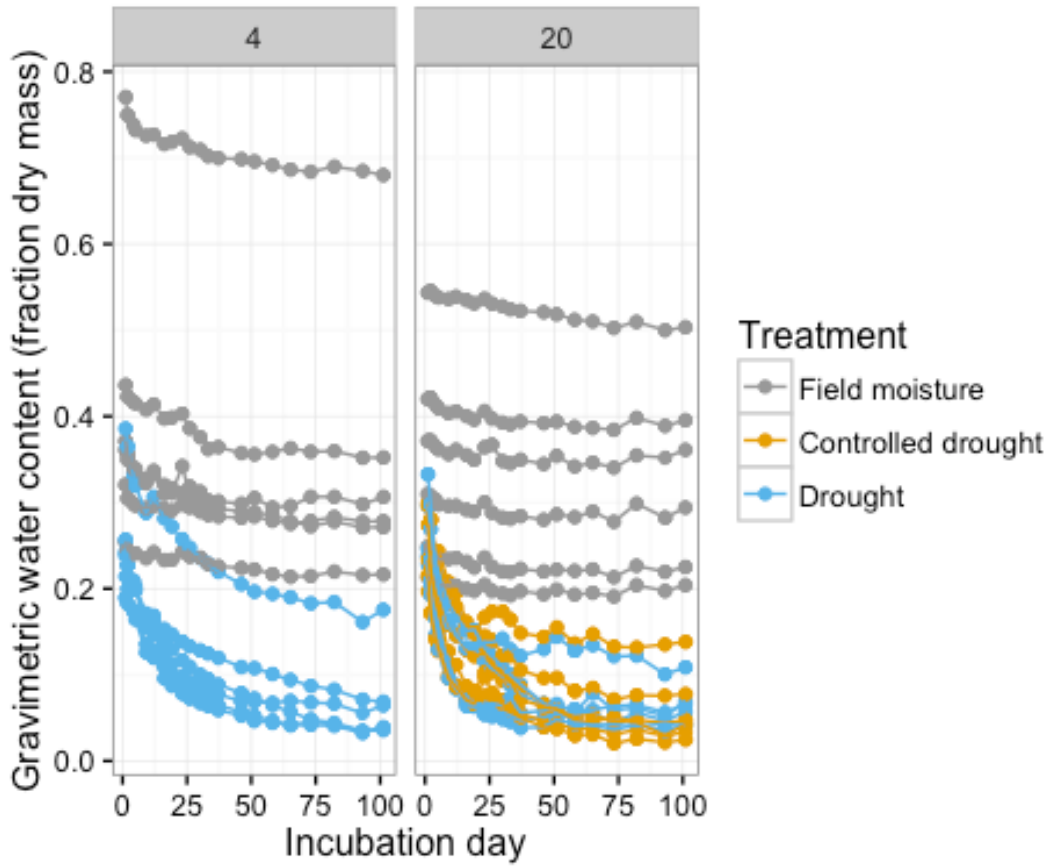
802   **Figure 1.** Core water content across the course of the incubation experiment by

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

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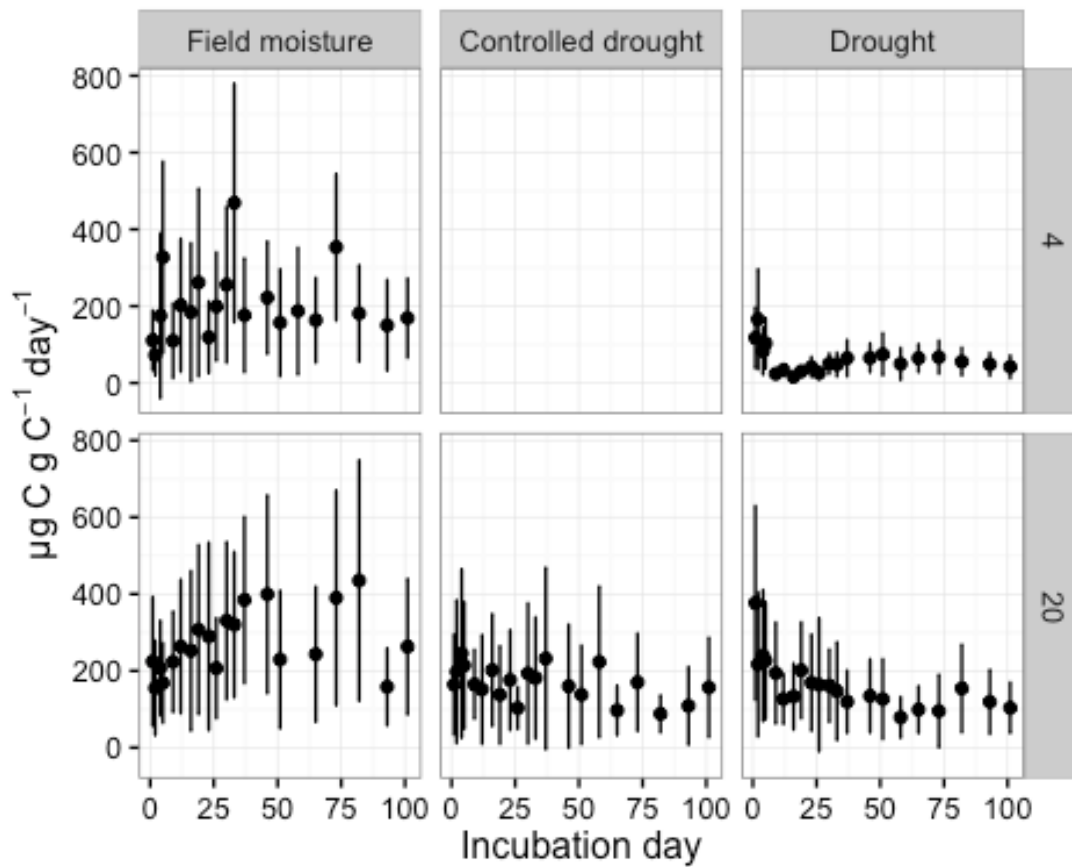
806   **Figure 2.** Mass-normalized CO_2 fluxes over the 100-day incubation, by temperature

807   (4 and 20 °C, rows) and treatment (field moisture, drought, and controlled drought;

808   columns). Error bars show core-to-core standard deviation. The "controlled

809   drought" treatment, for 20 °C only, was meant to dry cores at roughly the same rate

810   as the drought cores at 4 °C.

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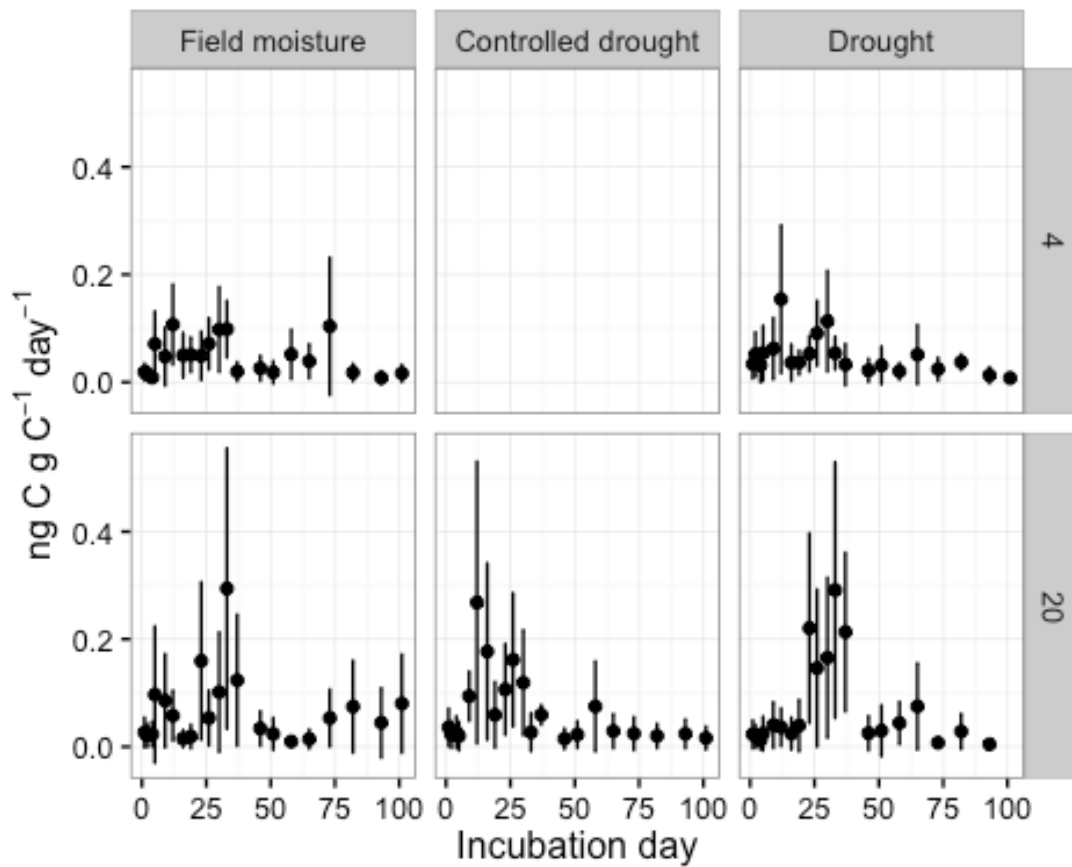
813 **Figure 3.** Mass-normalized CH$_4$ fluxes over the 100-day incubation, by temperature

814 (4 and 20 °C, rows) and treatment (field moisture, drought, and controlled drought;

815 columns). Error bars show core-to-core standard deviation. The "controlled

816 drought" treatment, for 20 °C only, was meant to dry cores at roughly the same rate

817 as the drought cores at 4 °C.

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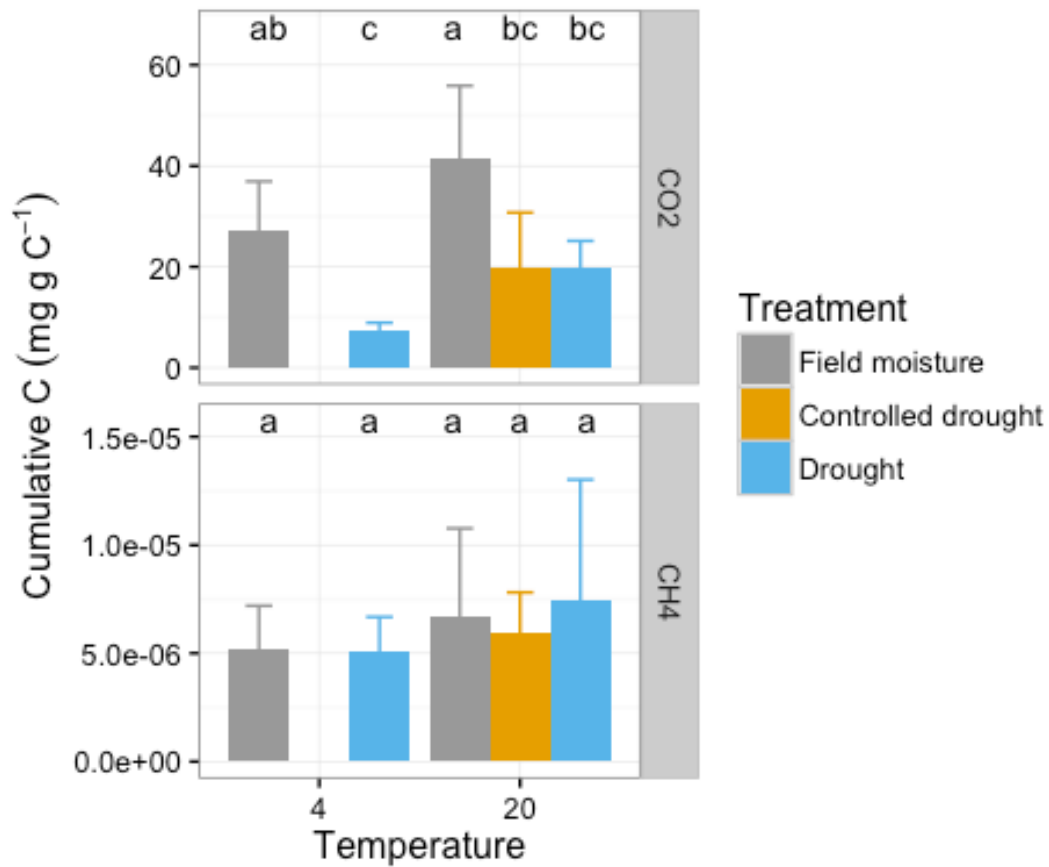
820 **Figure 4.** Cumulative mass-normalized C fluxes (mg g C^{-1}) over the incubation, by

821 gas (CO_2 and CH_4, top and bottom panels respectively), treatment (columns), and

822 temperatures (x-axis, °C). Letters within a panel indicate significant differences

823 based on Tukey's HSD.

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826 **Table A1.** Linear mixed-effects model parameters, testing effects of temperature

827 (°C), gravimetric water content (unitless), soil N (%),and dissolved organic carbon

828 (DOC, mg kg^{-1}) on log-transformed, individual core CH$_4$ fluxes (+0.1 µg C g C^{-1} day^{-1});

829 a colon (":") indicates an interaction. Dependent variable has units of log(µg C g C^{-1}

830 day^{-1}). Columns include parameter value; standard error (SE); degrees of freedom

831 (DF); T statistic; and P value.

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