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

Ben Bond-Lamberty¹, A. Peyton Smith², Vanessa Bailey²

¹Joint Global Change Research Institute, DOE Pacific Northwest National Laboratory, College Park, MD USA
²Biological Sciences Division, Pacific Northwest National Laboratory, Richland, WA USA

Correspondence to: Ben Bond-Lamberty (bondlamberty@pnnl.gov)

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 CO₂ and CH₄ 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
chemical characteristics of the cores. Gravimetric water content was $0.31 \pm 0.12$
(unsaid) at the beginning of the incubation; cores at field moisture were unchanged
at the end, but drought cores had declined to $0.06 \pm 0.04$. 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 $\text{CH}_4$ fluxes. The cumulative
production of $\text{C}$ from $\text{CO}_2$ was over six orders of magnitudes higher than that from
$\text{CH}_4$. 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;
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 (CH₄) or carbon dioxide
(CO₂)—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-intensive 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 CO₂, and under some conditions of CH₄
(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
aerobic and anaerobic microbial activity; and (iii) core CH$_4$ fluxes would be sensitive only to temperature, as no anaerobic conditions were imposed on the 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 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 permafrost) 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 Richland, WA within 48-72 hours of collection.

2.2 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 included two incubation temperatures of 4 and 20 °C, following the protocol of a number of previous boreal incubation studies (Treat et al., 2015). Within each temperature there were 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 N, and bulk density. Subsamples were collected and stored at -20 °C for dissolved organic carbon measurements or air-dried for soil C and N (see below).

On 18 August 2015 cores were placed into one of two growth chambers (Conviron Control Systems BDW80, 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 (CH$_4$ and CO$_2$) emissions 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 had a 200 µm mesh screen fit to the base and 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 CH$_4$ and CO$_2$ 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 CO$_2$ conditions and instrument stability.
The incubation experiment concluded on 9 December 2015, following the final CO\textsubscript{2} and CH\textsubscript{4} 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 calculated 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.

2.3 Data and statistical analysis

For each measurement of each sample throughout the 100-day incubation (i.e., each gas, core, and date/time), we used the rise in gas concentrations to calculate a flux rate in ppm s\textsuperscript{-1} (CO\textsubscript{2}) or ppb s\textsuperscript{-1} (CH\textsubscript{4}), 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). Each core's respiration flux ($F$) was then calculated as

$$F = \frac{\delta c V P_a}{\delta t M RT}$$

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 ($8.3 \times 10^{-3} \text{ m}^3 \text{kPa mol}^{-1} \text{K}^{-1}$) and $T$ the chamber air temperature (K) at time of measurement. The final respiration rate was expressed on a dry soil mass basis ($\mu g \text{ C g soil}^{-1} \text{ day}^{-1}$).

Anomalous data were excluded based on their gas fluxes being more than 5 (for $\text{CO}_2$) or 10 (for $\text{CH}_4$) 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 ($+0.1 \mu g \text{ C g}^{-1} \text{ day}^{-1}$) to ensure all positive fluxes, following Treat et al. 2015) transformation. Soil core was treated as
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 $\frac{F_2^{10}}{F_1} (\frac{T_2}{T_1})$ 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
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⁻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. CH₄ rates ranged from 0.00 ng C g⁻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, 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). 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.
Colman and Schimel (2014). The interaction between water content and percent N was also highly significant (P < 0.001), with high-N cores having little relationship between water content and CO$_2$ flux (data not shown).

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 CH$_4$ fluxes.

The cumulative production of C from CO$_2$ (Figure 4) was over six orders of magnitude higher than that from CH$_4$, with CO$_2$/CH$_4$ 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 CO$_2$ evolved was highly affected by temperature (P = 0.003), and "field moisture" cores emitted significantly more CO$_2$ than the other two moisture treatments at both temperatures (P < 0.001 for both, with no significant interactive effect). There was no difference between fluxes from the 20 °C "drought" and "controlled drought" treatments (P = 0.377). "Drought" cores' cumulative production was 73% (4 °C) and 52% (20 °C) lower than the cores kept at field moisture. Neither temperature (P = 0.200) nor moisture treatment (mean P = 0.975) was a significant factor in predicting cumulative CH$_4$ fluxes.

The cumulative flux numbers above result in CO$_2$ temperature sensitivity (Q$_{10}$) values of 1.3 and 1.9 for the field moisture and drought treatments, respectively; the corresponding Q$_{10}$ values based on cumulative CH$_4$ were 1.2 and 1.3. Computing Q$_{10}$ values based on fluxes normalized by water filled pore space changed these values only slightly: to 1.2 and 1.7 for CO$_2$, respectively, and 1.1 and 1.2 for CH$_4$. 


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$^{-1}$ 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$_2$
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 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. 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.
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 73% (4 °C) and 52% (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 were low (all less than 2.0, even when controlling for changes in soil moisture), but not unprecedented in comparison to a wide range of other laboratory soil incubations (Hamdi et al., 2013). Observed surface CO₂ fluxes at this range exhibited a Q₁₀ of 5.1 ± 1.4 over a temperature range of 3.5-15 °C (personal communication, C. Anderson); these surface fluxes were measured over multiple months and include root respiration, however, confounding any direct comparison. It is also important to note that while increased temperature does not always drive C mineralization rates in forest mineral soils (Giardina and Ryan, 2000), it is linked with increases in soil moisture content can lead to changes in microbial community structure and GHG fluxes (Xue et al., 2016).

More surprisingly, Q₁₀ values were lower in the drought treatment cores, a mathematical consequence of the fact that drought restricted CO₂ respiration more at 4 than at 20 °C. There is evidence that climate warming changes the microbial
decay dynamics of soil organic C compounds generally considered to be stable (Frey et al., 2013; Bond-Lamberty et al., 2016a). Unlike surface soils, active layer soils, which store large quantities of soil C (Mueller et al., 2015), are not subject to abundant inputs of fresh C from vegetation, so the starting quality of the native soil C in active layer soils may be older, more microbially processed, and dominated by more stable "heavy" organic C (Karlsson et al., 2011). Thus, it is not surprising that these more stable C compounds would be metabolized by processes that have been reported to be less temperature-sensitive.

We observed very low but positive CH$_4$ production from these upland mineral soils. This is contrast to many field studies that have observed CH$_4$ uptake (oxidation) in dry boreal sites (Matson et al., 2009; Schaufler et al., 2010). Anoxic microsites in soil can however provide enough CH$_4$ production to balance low-level consumption in otherwise aerobic soils (Kammann et al., 2009). In addition, our results are broadly consistent with data from 65 studies summarized by Olefeldt et al. (2013), who found that CH$_4$ emissions were more sensitive to soil temperature in wetter ecosystems; it would have been a surprise if the little methanogenic activity in our upland, well-drained soils was temperature-sensitive at all. Methane was also a far smaller C flux than CO$_2$ from these soils, in particular at higher temperatures (as CO$_2$ was responsive to temperature, but CH$_4$ was not). This is true more generally: for example, Treat et al. found a median CO$_2$:CH$_4$ production ratio of 387 for boreal sites, far lower than (but consistent with) our observed ratios of several million. Thus we see little opportunity for CH$_4$ to be a significant contributor to these upland
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 CO₂ and CH₄ 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 CO₂ 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 (R² = 0.84)
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
are a serious possibility in this low-precipitation ecosystem (Barber et al., 2000). In addition, the soils here are not surface layer soils (where the majority of microbial activity and C mineralization of labile C takes place); taking them out of depth (where they are less exposed to O₂, for example) may significantly change the abiotic conditions to which the microbial community is adapted. However, focusing on the active layer provides crucial information about the potential loss of C from these soils, a risk that needs to be well understood as permafrost degradation leads to expansions in the depth of the active layer across the Arctic.

5 Conclusions

In this laboratory experiment, we found that CO₂ fluxes were strongly influenced by temperature and water content, and correlated with soil C and N, while CH₄ fluxes were much smaller and not sensitive to temperature or water content in these well-drained mineral soils. This suggests that understanding how soil moisture might change with spatially variable permafrost degradation, how soil biota will respond to these changes, and how models should treat soil organic matter decomposition with respect to multiple and interacting drivers are all critical areas of research going forward. Further controlled field and laboratory studies, ideally tightly integrated with modeling experiments, are critical to understand GHG emission dynamics from high-latitude soils.

Acknowledgments

We are grateful to Jamie Hollingsworth for information about, and facilitating access to, the Caribou Poker Creeks Research Watershed Long-Term Ecological Research

19
site. This research was supported by the Office of Science of the U.S. Department of Energy as part of the Terrestrial Ecosystem Sciences Program. The Pacific Northwest National Laboratory is operated for DOE by Battelle Memorial Institute under contract DE-AC05-76RL01830.

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.

References


Barber, V. A., Juday, G. P., and Finney, B. P.: Reduced growth of Alaskan white spruce
in the twentieth century from temperature-induced drought stress, Nature, 435

Bieniek, P. A., Walsh, J. E., Thoman, R. L., and Bhatt, U. S.: Using climate divisions to

Bond-Lamberty, B., Wang, C., and Gower, S. T.: Spatiotemporal measurement and

444 browning and soil respiration at high northern latitudes, PLoS ONE, 7,
445 e50441, 10.1371/journal.pone.0050441, 2012.

447 A., Smith, J. L., and Bailey, V. L.: Soil respiration and bacterial structure and
448 function after 17 years of a reciprocal soil transplant experiment, PLoS ONE,
449 11, e0150599, 10.1371/journal.pone.0150599, 2016a.

Bond-Lamberty, B., Smith, A. P., and Bailey, V. L.: Running an open experiment:
451 transparency and reproducibility in soil and ecosystem science, Environ. Res.

Colman, B. P., and Schimel, J. P.: Drivers of microbial respiration and net N
454 mineralization at the continental scale, Soil Biol Biochem, 60, 65-76,

Davidson, E. A., and Janssens, I. A.: Temperature sensitivity of soil carbon
457 decomposition and feedbacks to climate change, Nature, 440, 165-173,


Giardina, C. P., and Ryan, M. G.: Evidence that decomposition rates of organic carbon
in mineral soil do not vary with temperature, Nature, 404, 858-861,
10.1038/35009076, 2000.

Hamdi, S., Moyano, F. E., Sall, S., Bernoux, M., and Chevallier, T.: Synthesis analysis of
the temperature sensitivity of soil respiration from laboratory studies in
relation to incubation methods and soil conditions, Soil Biol. Biochem., 58,

Hashimoto, S., Carvalhais, N., Ito, A., Migliavacca, M., Nishina, K., and Reichstein, M.:
Global spatiotemporal distribution of soil respiration modeled using a global

Helbig, M., Pappas, C., and Sonnentag, O.: Permafrost thaw and wildfire: Equally
important drivers of boreal tree cover changes in the Taiga Plains, Canada,

Griffith, B., Hollister, R. D., Hope, A., Huntington, H. P., Jensen, A. M., Jia, G. J.,
Jorgenson, T., Kane, D. L., Klein, D. R., Kofinas, G., Lynch, A. H., Lloyd, A. H.,
McGuire, A. D., Nelson, F. E., Oechel, W. C., Osterkamp, T. E., Racine, C. H.,
Romanovsky, V. E., Stone, R. S., Stow, D. A., Sturm, M., Tweedie, C. E., Vourlitis,
and Yoshikawa, K.: Evidence and implications of recent climate change in
northern Alaska and other Arctic regions, Climatic Change, 72, 251-298,

IPCC: Working Group I contribution to the IPCC Fifth Assessment Report Climate


Zhang, Y., Wolfe, S. A., Morse, P. D., Olthof, I., and Fraser, R. H.: Spatiotemporal

Table 1. Linear mixed-effects model parameters, testing effects of temperature (°C), gravimetric water content (unitless), 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); a colon (";") indicates an interaction. 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.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
<th>SE</th>
<th>DF</th>
<th>T</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>1.713</td>
<td>0.354</td>
<td>1153</td>
<td>4.839</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Temperature</td>
<td>0.046</td>
<td>0.020</td>
<td>26</td>
<td>2.336</td>
<td>0.027</td>
</tr>
<tr>
<td>WC_gravimetric</td>
<td>3.496</td>
<td>1.052</td>
<td>1153</td>
<td>3.322</td>
<td>0.001</td>
</tr>
<tr>
<td>N_percent</td>
<td>37.976</td>
<td>6.810</td>
<td>26</td>
<td>5.576</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Temperature:WC_gravimetric</td>
<td>0.116</td>
<td>0.061</td>
<td>1153</td>
<td>1.905</td>
<td>0.057</td>
</tr>
<tr>
<td>Temperature:N_percent</td>
<td>-0.507</td>
<td>0.300</td>
<td>26</td>
<td>-1.690</td>
<td>0.103</td>
</tr>
<tr>
<td>WC_gravimetric:N_percent</td>
<td>-37.347</td>
<td>8.425</td>
<td>1153</td>
<td>-4.433</td>
<td>&lt; 0.001</td>
</tr>
</tbody>
</table>
Table 2. Linear mixed-effects model parameters, testing effects of temperature (°C), gravimetric water content (unitless), soil N (%), and dissolved organic carbon (DOC, mg kg$^{-1}$) on log-transformed, individual core CH$_4$ fluxes (+0.1 µg C g C$^{-1}$ day$^{-1}$); a colon (":") indicates an interaction. 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.

<table>
<thead>
<tr>
<th></th>
<th>Value</th>
<th>SE</th>
<th>DF</th>
<th>T</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>1.713</td>
<td>0.354</td>
<td>1153</td>
<td>4.839</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Temperature</td>
<td>0.046</td>
<td>0.020</td>
<td>26</td>
<td>2.336</td>
<td>0.027</td>
</tr>
<tr>
<td>WC_gravimetric</td>
<td>3.496</td>
<td>1.052</td>
<td>1153</td>
<td>3.322</td>
<td>0.001</td>
</tr>
<tr>
<td>N_percent</td>
<td>37.976</td>
<td>6.810</td>
<td>26</td>
<td>5.576</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Temperature:WC_gravimetric</td>
<td>0.116</td>
<td>0.061</td>
<td>1153</td>
<td>1.905</td>
<td>0.057</td>
</tr>
<tr>
<td>Temperature:N_percent</td>
<td>-0.507</td>
<td>0.300</td>
<td>26</td>
<td>-1.690</td>
<td>0.103</td>
</tr>
<tr>
<td>WC_gravimetric:N_percent</td>
<td>-37.347</td>
<td>8.425</td>
<td>1153</td>
<td>-4.433</td>
<td>&lt; 0.001</td>
</tr>
</tbody>
</table>
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. Mass-normalized CO$_2$ fluxes over the 100-day incubation, by temperature (4 and 20 °C, rows) and treatment (field moisture, drought, and controlled drought; columns). Error bars show core-to-core standard deviation. The "controlled drought" treatment, for 20 °C only, was meant to dry cores at roughly the same rate as the drought cores at 4 °C.
Figure 3. Mass-normalized CH$_4$ fluxes over the 100-day incubation, by temperature (4 and 20 °C, rows) and treatment (field moisture, drought, and controlled drought; columns). Error bars show core-to-core standard deviation. The "controlled drought" treatment, for 20 °C only, was meant to dry cores at roughly the same rate as the drought cores at 4 °C.
Figure 4. Cumulative C fluxes (mg g C⁻¹) over the incubation, by gas (CH₄ and CO₂, top and bottom panels respectively) and treatment (columns). Letters within a panel indicate significant differences based on Tukey's HSD.