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Response of CO_2 and CH_4 emissions from Arctic tundra soils to a multifactorial manipulation of water table, temperature and thaw depth

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Abstract

Significant uncertainties persist concerning how Arctic soil tundra carbon emission responds to environmental changes. In this study, 24 cores were sampled from drier (high centre polygons and rims) and wetter (low centre polygons and troughs) permafrost tundra ecosystems. We examined how soil CO_2 and CH_4 fluxes responded to laboratory-based manipulations of soil temperature (and associated thaw depth) and water table depth, representing current and projected conditions in the Arctic. Similar soil CO_2 respiration rates occurred in both the drier and the wetter sites, suggesting that a significant proportion of soil CO_2 emission occurs via anaerobic respiration under water-saturated conditions in these Arctic tundra ecosystems. In the absence of vegetation, soil CO_2 respiration rates decreased sharply within the first 7 weeks of the experiment, while CH_4 emissions remained stable for the entire 26 weeks of the experiment. These patterns suggest that soil CO_2 emission is more related to plant input than CH_4 production and emission. The stable and substantial CH_4 emission observed over the entire course of the experiment suggests that temperature limitations, rather than labile carbon limitations, play a predominant role in CH_4 production in deeper soil layers. This is likely due to the presence of a substantial source of labile carbon in these carbon-rich soils. The small soil temperature difference (a median difference of 1 °C) and a more substantial thaw depth difference (a median difference of 6 cm) between the high and low temperature treatments resulted in a non-significant difference between soil CO_2 and CH_4 emissions. Although hydrology continued to be the primary factor influencing CH_4 emissions, these emissions remained low in the drier ecosystem, even with a water table at the surface. This result suggests the potential absence of a methanogenic microbial community in high-centre polygon and rim ecosystems. Overall, our results suggest that the temperature increases reported for these Arctic regions are not responsible for increases in carbon losses. Instead, it is the changes in hydrology that exert significant control over soil CO_2 and CH_4 emissions.

1. Introduction

The Arctic has undergone exceptional warming of roughly 1 °C per decade over the past three decades (Christensen 2013, Rantanen *et al* 2022). While the global average surface temperature is predicted to rise between 1.8 °C–4.0 °C by 2100 (Collins *et al* 2013), Arctic surface temperatures could rise by as much as 5 °C in summer and 13 °C in late fall by the end of the century (Overland *et al* 2014). The Arctic is also experiencing increased precipitation (both rainfall and snowfall) (Min *et al* 2008, Collins *et al* 2013, Bintanja

and Selten 2014). These climate changes are expected to have major effects on the greenhouse gas (GHG) fluxes (e.g. carbon dioxide (CO_2) and methane (CH_4)) from northern wetlands (Billings *et al* 1982, Oechel *et al* 1998, Deslippe *et al* 2012). Rises in temperature and the associated increase in the depth of the seasonally thawed soil layer (i.e. thaw depth) stimulates microbial degradation of the large carbon stocks in Arctic soils (Shiklomanov *et al* 2010, Schuur *et al* 2013, 2015). Soil hydrological status is also critical for predicting CO_2 and CH_4 emissions: lower soil moisture and more oxic soils are primarily associated with CO_2 emission, while more saturated soils are associated with anaerobic CO_2 and CH_4 emissions (Treat *et al* 2015). Despite several decades of research on the patterns and controls of GHG emissions from tundra ecosystems (Whalen and Reeburgh 1992, Christensen *et al* 2000, Walter and Heimann 2000, Mastepanov *et al* 2013), there are still large uncertainties about the impact of current and future changes in climate on the CO_2 and CH_4 balance of the Arctic (Kirschke *et al* 2013, Melton *et al* 2013, Olefeldt *et al* 2013).

Most studies reported water table depth to have the strongest influence on Arctic CO_2 and CH_4 emissions as the resultant soil oxygen content controls the occurrence of aerobic respiration and methanotrophy or methanogenesis (Christensen *et al* 2000, Zona *et al* 2009, Parmentier *et al* 2011, Mastepanov *et al* 2013). However, environmental factors in the field tend to co-vary (e.g. in the case of temperature, thaw depth and water table), making any true attribution of primary control difficult from field observations (Zona *et al* 2009). In addition to the controls on production, the role of transport (e.g. ebullition and plant transport) is particularly important for modelling CH_4 emissions (Corbett *et al* 2013, McEwing *et al* 2015, Throckmorton *et al* 2015). Plant transport and ebullition allow CH_4 to bypass the upper soil layers where methanotrophs consume CH_4 (McEwing *et al* 2015, Throckmorton *et al* 2015) and represent the dominant CH_4 transport mechanisms to the atmosphere (Throckmorton *et al* 2015). Previous multifactorial manipulations in the Arctic, which have addressed the impact of hydrological and temperature changes on tundra ecosystems, presented a variety of results (Billings *et al* 1982, Oechel *et al* 1998, Knorr and Blodau 2009, Kane *et al* 2010, Treat *et al* 2014, Knoblauch *et al* 2021). These experiments showed that increased temperature increases soil respiration (Billings *et al* 1982) but either increased (Oechel *et al* 1998) or decreased net carbon storage (Billings *et al* 1982). The decrease in water level stimulated soil CO_2 respiration, decreasing the net soil carbon storage (Billings *et al* 1982, Oechel *et al* 1998) and methanogenesis (Knorr and Blodau 2009). On the other hand, anaerobic soil conditions reduce CO_2 emissions and the global warming potential (GWP) estimated by combining CO_2 and CH_4 emissions (Treat *et al* 2014). In some of these experiments, the interaction between the water and temperature treatments was only significant when the temperature was raised to 20 °C (Treat *et al* 2014).

Elevated temperatures generally lead to higher rates of soil CO_2 respiration (Whalen and Reeburgh 1992, Waelbroeck *et al* 1997, Deslippe *et al* 2012, Dijkstra *et al* 2012); however, the opposite occurs in terms of the effect on CH_4 fluxes, because they increase both CH_4 production and CH_4 consumption (Whalen and Reeburgh 1992, Dijkstra *et al* 2012). Both methanogenesis and methanotrophy are highly temperature limited under Arctic conditions (Moosavi *et al* 1996, Wille *et al* 2008), but methanogenesis is stimulated by temperature to a greater extent than methanotrophy (Dunfield *et al* 1993, Jahn *et al* 2010). Q_{10} represents the factor by which biological processes (including respiration) increase by a 10 °C increase in temperature (e.g. Kirschbaum 1995) and it is widely used to summarise the response of CO_2 and CH_4 fluxes to increased temperature. Methanogenesis has an average Q_{10} of 6, compared to the average Q_{10} for methanotrophy of 2 (Walter and Heimann 2000), suggesting that increased soil temperature should result in higher net CH_4 emissions. Many studies have found that the temperature sensitivity of CO_2 and CH_4 fluxes to warming to be site-specific (Whalen and Reeburgh 1992), dependent on the season (Wilkman *et al* 2018), and sometimes much smaller than expected (Oechel *et al* 1998, Van Huissteden *et al* 2005), adding to the challenges of identifying the response of carbon emission to warming. Soil CO_2 respiration and CH_4 production are also dependent on substrate availability, and high carbon quality and quantity can increase rates of soil CO_2 respiration and CH_4 emission (Joabsson and Christensen 2001, Ström *et al* 2012, Treat *et al* 2014). However, Arctic soils are very rich in carbon (Hugelius *et al* 2014) and soil respiration might be more limited by temperature than by soil carbon input (Allen *et al* 2010, von Fisher *et al* 2010). Finally, soil pH also affects CH_4 production, likely because fermentation products such as organic acids lower pH and inhibit methanogen growth (Svensson 1984, Valentine *et al* 1994, Bergman *et al* 1998). The pH optima of methanogens vary from acidic to neutral (Williams and Crawford 1985, Dunfield *et al* 1993) and a pH below 5.3 inhibits the growth of methanogens (Williams and Crawford 1985).

Overall, many of the uncertainties in the response of tundra ecosystems to climate change stem from the collinearity among key environmental variables, which makes it extremely difficult to tease apart the relative importance of each variable in the field (Walter and Heimann 2000, King *et al* 2002, Zona *et al* 2009, Olefeldt *et al* 2013). Manipulation experiments are a valuable approach for addressing how independent variables, both in isolation and in combination with each other, affect CO_2 and CH_4 emissions by enabling replication and control over confounding or co-varying factors. To unravel the relative importance of future changes

(increases in temperature and a parallel increase in depth of thaw and decrease in water table during the summer), we performed a multifactorial experiment on soil cores from key tundra ecosystems in Alaska. To perform a realistic soil incubation experiment, we housed the cores inside a refrigerated container to recreate soil temperature profiles similar to those observed in the summer in the field in these Arctic ecosystems. The overwhelming majority of previous soil incubations were conducted at a stable temperature of 5 °C–15 °C for the entire soil core (Schädel *et al* 2014). To our knowledge, this is the first experiment performed on intact soil cores from Arctic Alaska reproducing temperature gradients realistic of field conditions in continuous permafrost soils. The goal of this experiment was to identify the response of CO_2 and CH_4 emissions to water table and thaw depth (and soil temperature) in continuous permafrost tundra ecosystems. To test if soil carbon limits CO_2 and CH_4 emissions, as currently assumed, we performed the incubation for a total of 26 weeks. To understand the independent response of the soil carbon emissions to the imposed environmental changes, vegetation was removed. We expected soil CO_2 respiration and CH_4 emissions to maintain a similar basal rate for the entire duration of the experiment, even without vegetation input, because of the large amount of carbon in the soil. We also expected higher CH_4 emissions and lower soil CO_2 respiration with a higher water table in both drier (high centre polygons and rims) and wetter (low centre polygons and troughs) ecosystems, given that anaerobic conditions favour CH_4 production and limit CH_4 oxidation. Finally, we expected that higher temperatures (HIGH T) (and deeper thaw depth (DEEP)) to be associated with both higher soil CO_2 respiration and higher CH_4 emissions, as temperature stimulates the microbial decomposition of organic matter and CH_4 production more than consumption.

2. Materials and methods

2.1. Site description and soil core sampling

The soil cores were sampled at the Barrow Environmental Observatory, 10 km east of the town of Utqiagvik (formerly known as Barrow). This location is within native land set aside for scientific research (figure 1). The vegetation in this area consists of wet sedge tundra (sedge grass/moss wetlands) (Walker *et al* 2005, Davidson *et al* 2016a). This vegetation type accounts for about 30% of the wetlands across the entire circumpolar Arctic (Walker *et al* 2005). The terrestrial ecosystem is underlain by a network of low- and high-centred ice wedge polygons. At the beginning of June 2013, 24 soil cores were extracted using a Snow, Ice and Permafrost Research Establishment (SIPRE) corer, as described in Lipson *et al* (2010). The two dominant ecosystem types of wet sedge polygonized tundra (high-centre polygons and rims classified as 'low water table (DRY)' $N = 13$ and low-centre polygons and troughs classified as 'water table at surface (WET)' $N = 11$) in a stratified random design were included in the analysis (figure 1 and table S1, supplemental material). The sampling was performed at the beginning of the summer, while the soil was still mostly frozen immediately following snow melt, to limit disturbance. The cores were 6.6 cm in diameter and 40 cm deep and included the entire active layer and the upper part of the permafrost (figure 2). The slightly different number of cores from the two ecosystem types ($N = 11$ from the WET vs $N = 13$ from the DRY) was unintended and only noticed after completing the sampling. Immediately after sampling, the cores were wrapped in plastic and stored in an insulated cooler to prevent thawing. They were then immediately transported to our laboratory in Utqiagvik, where they were stored at −20 °C before being shipped to the University of Sheffield, UK. The cores were shipped inside the same insulated container used during the sampling, with dry ice to prevent thawing. This was accomplished by using a fast FedEx international shipping service. Once in Sheffield, the cores were stored in environmentally controlled chambers at the Sir David Read Controlled Environment Facility at −20 °C until the start of the experiment. This temperature corresponds to the minimum soil temperature in the winter/spring at this site (based on field data collected from our meteorological and eddy covariance towers, Zona *et al* 2016).

2.2. Soil core manipulation experimental design

The number of cores was carefully chosen to provide sufficient replicates for each experimental unit: $N = 5$–6 for each of the multifactorial environmental conditions (e.g. HIGH T (and DEEP) and WET, HIGH T (and DEEP) and DRY, etc, figure 3). Soil temperatures were recorded with thermocouples and the water table was measured inside perforated pipes attached to the soil cores (more details below). During the core collection, the cores included substantial litter and other remnants of plant materials (typical of organic peaty soils) from the previous growing season (figure 2(a)). The aboveground plant material was mostly composed of standing dead vascular plants and dormant mosses, with no active vascular plant material (figure 2(a)); the aboveground plant material was removed during week 4 of the experiment to test the impact of environmental treatments on the soil CO_2 and CH_4 emissions in the absence of vegetation inputs. We tested the differences in both CO_2 and CH_4 fluxes right before (week 4) and right after (week 5) vegetation removal across the treatments, revealing no significant difference (see section 2.5). This result is

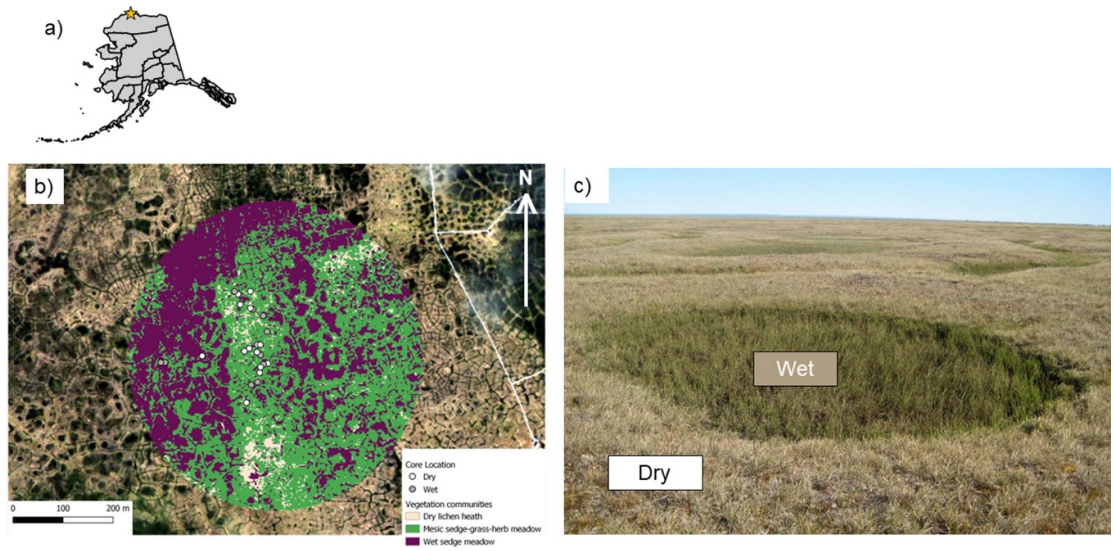

Figure 1. (a) Location of the study site within Alaska. (b) Sampling locations of the 24 soil cores extracted in June 2013 from the Barrow Environmental Observatory, 10 km east of the town of Utqiagvik (formerly known as Barrow). The vegetation map includes the main vegetation types, mapped using a combination of field spectrometry and WorldView2 multispectral imagery (see Davidson *et al* 2016a for more details). The coordinates of the cores are included in table S1. (c) Photograph showing representative WET and DRY ecosystem types at the study site. Adapted from Davidson *et al* (2017). CC BY 4.0.

Figure 2. Experimental set-up of the experiment, including (a) the installation of the thermocouples across the soil profiles, (b) the protection of the cores inside heat shrinks, (c) the installation of the cores inside PVC pipes, (d) the refrigerated enclosure, and (e) the cuvette used for the gas flux measurements.

explained by the fact that core sampling took place right after snow melt, before vegetation development. Therefore, vegetation removal at this time of the season resulted in limited disturbance and only had a minor influence on the fluxes. Decay of root material could have also influenced the CO_2 and CH_4 flux rates, but as these organic soils are rich in carbon and contain substantial roots from previous summers, we expect decaying of fresh roots to have a minor influence on the background fluxes. The influence of fresh roots on CO_2 and CH_4 fluxes was also directly tested at the end of the experiment (when we weighed belowground fine and main root biomass from each of the cores); it was found that root biomass was not correlated with CO_2 and CH_4 fluxes (data not shown).

The air temperature and radiation in the environmentally controlled chamber were selected to represent the average Utqiagvik summer conditions, as defined by data we have been collecting for decades in our meteorological and eddy covariance towers (Zona *et al* 2016). Air temperatures were changed bi-weekly to mirror the natural seasonal progression in temperature during the growing season (see figure S1). The cores were subject to two growing seasons of similar duration, separated by a 3 week freezing period to simulate winter conditions (figure S1). The water table was raised to the surface in all the cores before the 3 week

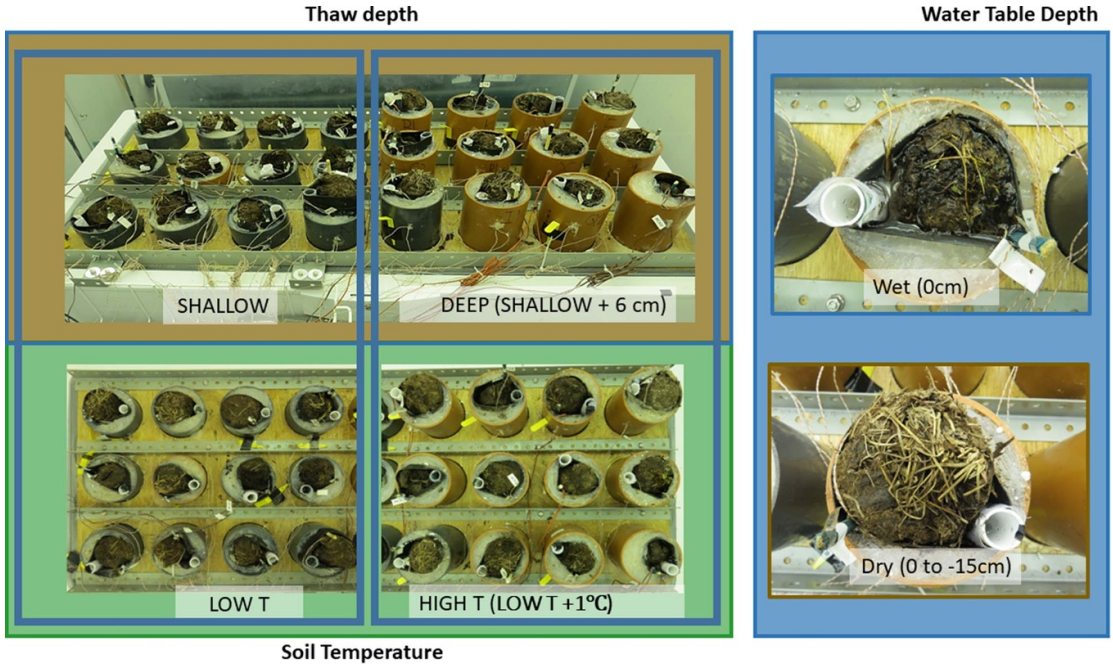

Figure 3. Schematic of the experimental design showing a summary of the treatments (HIGH T was associated with DEEP thaw depth and LOW T was associated with SHALLOW thaw depth) for two water levels (WET cores had a water table at the surface during the entire duration of the experiment, while the water table was dropped to −15 cm below the surface in the DRY cores).

freezing period. The soil cores were inserted into a black heat shrink (RS Components Ltd Corby, Northants, UK), sealed at the bottom and heat shrunk to the core when the soil was still frozen (so as not to disrupt the core itself, figure 2(b)) to create a microcosm that was open to gas and water exchange only at the top (Billings *et al* 1982). The heat shrink was shrunk to the size of the cores with a heat gun in order to limit O_2 diffusion from the sides of the cores (figure 2(b)). For stability, the soil cores were inserted into larger plastic tubes (figure 2(c)). The heat-shrunk cores were inserted in sand, which was sealed at the top with silicon (figures 2 and 3). The bases of the cores were maintained in an insulated and refrigerated enclosure with temperature control (figure 2(d)). The refrigerated enclosure (Williams Electrical, Sheffield, UK) into which the cores were inserted (figure 2(b)) allowed the maintenance of realistic Arctic soil temperature profiles and a frozen permafrost layer (figure S2). The top of the cores was located outside of the temperature-controlled enclosure (figures 2(c), (e) and 3) and subjected to the air temperature in the environmentally controlled chambers, which ranged between about −5–10 °C during the experiment (figures S2 and 4), similar to observed field conditions during the growing season in these Arctic ecosystems. The bottom of the core was maintained below zero (figure S2). In the HIGH T treatment (LOW temperature (LOW T) + 1 °C), the top 16 cm of the cores ($N = 12$) were raised out of the temperature-controlled container, while in the LOW T treatment only the top 9 cm of the cores were outside of the refrigerated enclosure (figures 2 and 3). The temperature differential between the HIGH and LOW T treatments was similar to previous *in situ* manipulation experiments (Oechel *et al* 1998). Due to the tight link between temperature and thaw depth, the cores in the HIGH T treatment also had DEEP (the DEEP was about 6 cm deeper than the shallower thaw depth (SHALLOW), figures 4 and 5). The small temperature difference applied in this experiment is consistent with warming in the Arctic over the last decade, representing actual conditions observed in the field (Christensen 2013). The difference in thaw depth between the temperature treatments was also consistent with the increase in thaw depth reported by the CALM network in Utqiagvik, Alaska, over the last two decades (Biskaborn *et al* 2019).

The water table level in the cores from the 'WET' sites (low-centre polygons and troughs) was maintained at the surface (±1 cm) for the entire duration of the experiment (figures 3 and 4), whereas the level in the cores from the 'DRY' sites (high-centre polygons and rims) was progressively lowered to −15 cm below the surface (figure 4). These water table levels correspond to the average levels found at the sample sites of these ecosystem types (Zona *et al* 2009). The water table was maintained at the surface for 2 weeks in each of the two simulated seasons of the experiment in both ecosystem types, as right after snow melt the entire landscape is flooded (Zona *et al* 2009, 2012). Small plastic pipes (2 cm diameter), with holes at 1 cm intervals, were fastened to each soil core to measure the water table depth throughout the experiment (figures 2(b) and (c)). Each pipe was protected by a fine mesh to prevent soil from entering the pipe and

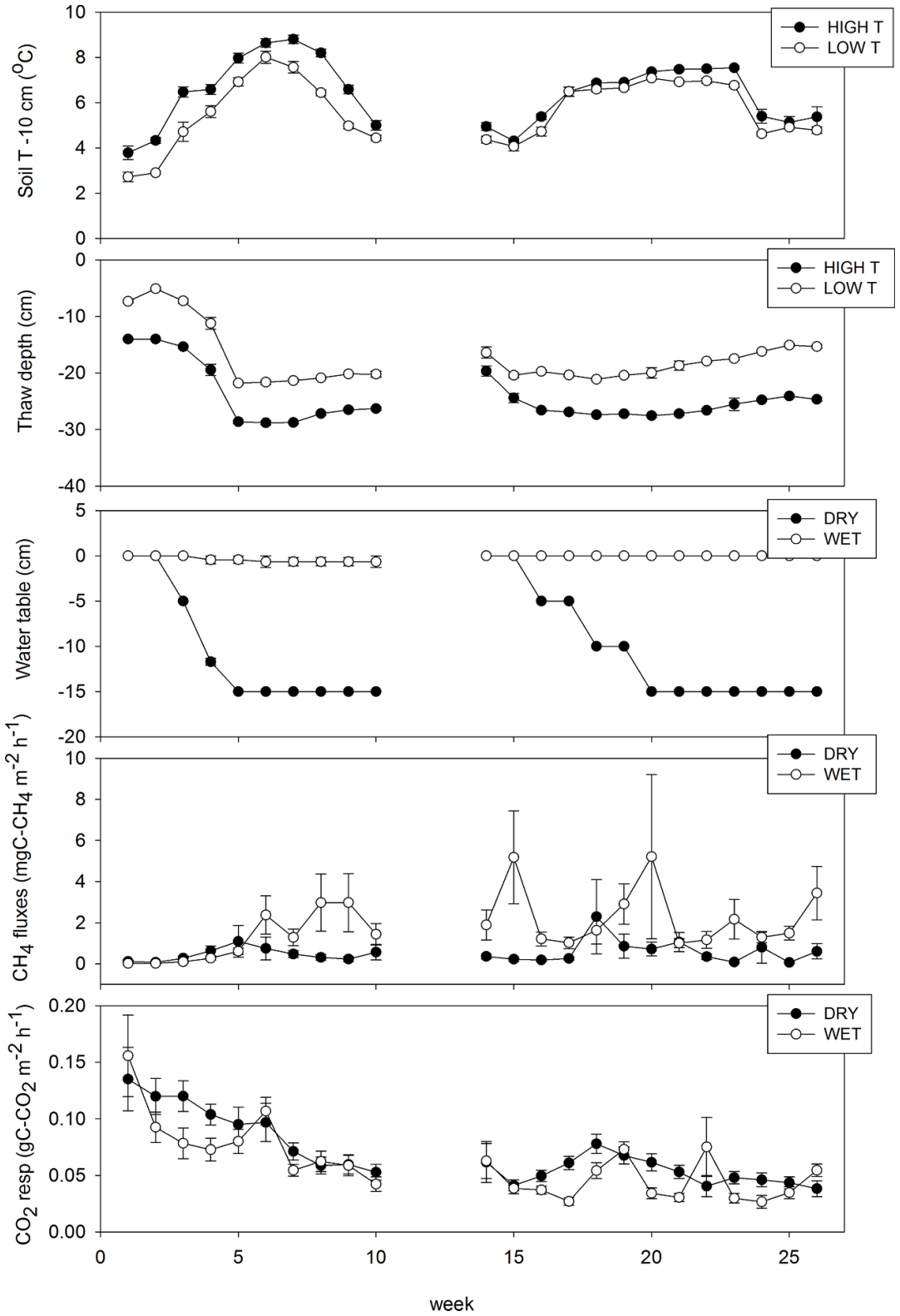

Figure 4. Weekly averages of the soil temperature at −10 cm depth and thaw depth for the HIGH T and LOW T treatments, water table levels for the WET and DRY treatments, soil CO_2 respiration and CH_4 fluxes for the WET and DRY treatments. Error bars are standard error of the mean.

blocking the holes. The water table levels in the WET cores were maintained using distilled water, while evaporation in the environmentally controlled chamber decreased the water table in the DRY cores, with no additional removal of water. The use of distilled water is a common procedure in laboratory experiments on Arctic cores (see Treat *et al* 2015).

Soil temperatures at −30 and −20 cm below the surface of the core profile were measured continuously using Type-T thermocouples (TT-T-20-SLE-1000, Omega Engineering, Inc., Norwalk, CT 06854, USA) in all cores (figure 2). The soil temperatures at 0, −5 and −10 cm were recorded twice a week, at the same time as the measurements of flux, thaw depth and water table depth. Temperatures were recorded every second and averaged every half an hour using a datalogger (CR1000, Campbell Scientific, Logan, Utah, USA) continuously throughout the experiment. A wooden stick was used to measure thaw depth and water table depth, as described in Zona *et al* (2009). The stick used for the thaw depth had a pointed end of 4 mm in diameter that was gently inserted into the cores at a random location each week to limit disturbance to the soil cores.

2.3. Soil CO_2 and CH_4 flux measurements

Soil CO_2 respiration and CH_4 fluxes were measured twice a week using a clear chamber (figure 2(e)) connected to an LGR Ultra-Portable Greenhouse Gas Analyser (UGGA, Model 915–0011, Los Gatos, Research, Palo Alto, CA, USA) in a closed-loop system. Measurements were conducted over two simulated Arctic summer seasons, with 3 weeks of freezing (−5 °C air T and −9 °C average soil T) in between. Temperature was changed following a diurnal cycle to reproduce variations observed in the field and the seasonal increase and decrease observed in the field during the growing season. A custom-built flow-through cuvette (2790 cm^3 volume, 75 cm^2 area) was connected using Teflon tubing attached to a pipe coupler, which was placed on the PVC pipes holding the soil cores, forming a gas-tight seal (figure 2(e)). The cuvette was attached to each soil core for 3 min while the GHG analyser recorded the increase in CO_2 and CH_4 concentration within the system in real time. After completion of each measurement, the cuvette was then lifted from the PVC pipe and left upside down in the chamber for 1 min to allow ambient air levels to re-establish (as confirmed by the real-time gas concentration measurements during this period). This process was repeated for each of the 24 cores twice a week. To ensure consistency, the measurements were carried out at the same time of day and the cores were measured in the same order (the CO_2 and CH_4 fluxes and temperature measurements were performed at the same time). To calculate CO_2 and CH_4 fluxes, we used the rate of change in measured concentration inside the cuvette headspace as obtained by least-squares linear regression (as the concentration increase inside the chamber was linear and showed no significant difference between an exponential fit and a polynomial model in the ANOVA of the two models, data not shown). More details on this method and the equation used in the calculation are included in McEwing *et al* (2015), and in Davidson *et al* (2016b).

The GWP was used to compare the relative importance of C–CO_2 and C–CH_4 emissions. The GWP used for CH_4 was 28.5 Kg CO_2-equiv Kg CH_4^{-1}, (IPCC 2013). The use of the GWP for weighting the climatic impact of instantaneous emissions for different GHGs has been used consistently in the scientific literature (Van der Molen *et al* 2007, Merbold *et al* 2009, Lee *et al* 2012, Treat *et al* 2014, Hashemi *et al* 2021) as a simple metric for estimating the contribution of GHGs to global warming. We are aware that using different timescales and more advanced methodologies affects the relative importance of CO_2 and CH_4 as described in Frolking *et al* (2006), but this modelling is beyond the scope of this paper.

2.4. Total dissolved carbon (TDC), dissolved organic carbon (DOC), total dissolved nitrogen (TDN) and pH in the soil water

Approximately 100 ml of soil water was collected in each core on 29 May 2014 (at the end of the first simulated season of measurements) using 2.5 mm rhizons (Rhizosphere Research Products, Wageningen, Netherlands). Samples were frozen and sent to the Centre for Earth, Planetary, Space & Astronomical Research at the Open University for analysis. TDC was analysed using a Shimadzu TOC-V CSN instrument (Shimadzu Research Laboratory Ltd, Wharfside, Manchester, UK), fitted with a high-sensitivity catalyst, based on a 680 °C combustion catalytic oxidation method with non-dispersive infrared detection. Samples were filtered to 0.45 μm and analysed in total carbon mode, in which TDC is measured (organic and inorganic carbon (IC)). The detection limit of the instrument is <0.1 mg l^{-1} carbon. Various concentrations of potassium hydrogen phthalate certified standards (Sigma-Aldrich) were used for instrument calibration. Quality control checks and blank water samples (Millipore Sigma, Merck KGaA, Darmstadt, Germany, deionized water, resistivity >18 MΩ cm) were analysed during each analytical run to assess drift.

IC was determined using the same instrument (Shimadzu TOC-V CSN). Samples were acidified to $<$pH 3 inline (within the closed injection needle) and the acidified sample was sparged with carrier gas to convert the IC content (carbonates and bicarbonates) to CO_2. The CO_2 was then measured via non-dispersive infrared detection. The instrument was calibrated using standards prepared from pre-dried reagent grade sodium hydrogen carbonate and sodium carbonate. The detection limit of the instrument for IC is <0.3 mg l^{-1}. IC was removed from the sample within the vial by acidifying the sample to $<$pH 3, using 2M hydrochloric acid. DOC concentration was determined by subtracting total TDC and IC. TDN was

analysed with a Shimadzu TOC-V CSN instrument by a catalytic thermal decomposition method (combusted at 720 °C). Nitrogen (N) within the sample is converted to nitrogen monoxide which is then measured using a chemiluminescence detector. The instrument was calibrated using various N standards prepared from special reagent-grade potassium nitrate. The detection limit of the instrument is <0.1 mg l^{-1} N. Quality control checks and blank water samples (Millipore Sigma, deionized water, resistivity >18 MΩ cm) were analysed during each analytical run to assess drift. The fraction of N analysed in the samples was total dissolved N, as samples were filtered through 0.45 μm pore size filters (mg l^{-1} N). The instrument was calibrated using nitrogen standards prepared from special reagent-grade potassium nitrate within the range of 0–10 mg l^{-1}. The detection limit of the instrument is below 0.1 mg l^{-1} N. Quality control checks and blank water samples (Millipore Sigma, deionized water, resistivity >18 MΩ cm) were analysed during each analytical run to assess drift. More details on this instrument and analysis are included in Moore *et al* (2013).

The pH of the soil water in each core was recorded using a Hannah Instruments pH meter (Hanna HI9024D, Smithfield, RI, USA) which was lowered 10 cm into the water-filled pipe connected to each core (used to measure water table). The water was mixed shortly before recording measurements. The pH was measured in weeks 3 and 6 during simulated season one and in weeks 2 and 8 during simulated season two (table S3).

2.5. Statistical analysis

Prior to the analysis described in this section, we tested the distribution of CH_4 fluxes and soil CO_2 respiration using Q–Q plots and a Shapiro test. Given the non-normal distributions, CH_4 fluxes and soil respiration were both log-transformed. In order to test the differences within the ANOVA described in the next paragraph, we selected data from weeks 5–10 in season one and 20–26 in season two, as during these periods the cores were maintained at stable water table, soil temperature and thaw depth levels (figure 4), facilitating the identification of the impact of the treatments. A two-way ANOVA for repeated measures was used to test if soil CO_2 respiration and CH_4 fluxes were significantly different among the treatments (the two water levels: DRY and WET, and the two soil temperature treatments HIGH T and LOW T (and associated thaw depth, DEEP and SHALLOW, figure 3), and the interaction between these factors). The week of measurement (nested into season) and core number were used as random factors to account for the temporal and spatial pseudoreplication (Bates *et al* 2010) using a linear mixed model (nlme package in R). A similar ANOVA analysis with the same random factors was used to test the differences in the soil T at different depths, and the thaw depth, across the four treatment levels (HIGH T (DEEP thaw depth) and DRY, HIGH T (DEEP thaw depth) and WET and LOW T (SHALLOW thaw depth), and DRY and LOW T (SHALLOW thaw depth), etc, see figure 3), to test the actual differences in the environmental conditions across the manipulation scenarios. Linear regression was used to test the significance of the correlation between DOC concentration and median soil CO_2 respiration and CH_4 fluxes during weeks 5–10 in season one and 20–26 in season two of the experiment. We used a similar repeated measures ANOVA (including core number as a random effect) to test the difference in the CO_2 and CH_4 fluxes between week 4 and week 5 (representing before and after vegetation removal, respectively) and used these results to interpret the impact of vegetation removal on the fluxes. The significance of the difference in pH was also evaluated using a two-way ANOVA including temperature and water level treatment using a linear mixed model, including season and core number as random effects. All analyses were carried out in R (version 4.2.1, R Core Team 2022).

3. Results

The different height of the cores above the freezer resulted in a significant difference in the soil temperature at nearly all depths, except at the surface (table 1). The difference in the thaw depth between the two temperature treatments was very significant (table 1) and was relatively larger than the differences in the soil temperatures (figure 5). There was no significant interaction between the soil temperature and water table level (table 1). Soil CO_2 respiration and CH_4 fluxes showed different seasonal trends. Soil CO_2 respiration slowly declined with time from the start of the experiment, most rapidly during the first 7 weeks of the first season of the experiment, while remaining fairly stable during the second season (figure 4). On the other hand, CH_4 fluxes showed more stable emissions during both seasons and no decline over time (figure 4). Soil CO_2 respiration was similar in the DRY and WET plots, while CH_4 emission was significantly higher in the WET plots (figure 6 and table 2). Methane emissions were marked by peak emission events that accounted for the vast majority of total CH_4 emissions, while soil CO_2 respiration presented more stable emission rates, narrower confidence intervals and fewer outliers (figures 4 and 6). Methane emissions from the DRY treatments presented lower emission rates than WET treatments, even when the water table was maintained at the surface (see figure 4, weeks 14–15). The two-way ANOVA of the water table and temperature

Table 1. Statistical results of the repeated measures two-way ANOVA (for soil temperature at the indicated depths and for thaw depth) for the two temperature and thaw depth treatments (HIGH and LOW) and water level treatments (DRY and WET), and their interaction. The week of measurement (nested into season) and core number were used as random factors to account for the temporal and spatial pseudoreplication, using a linear mixed model (nlme package in R). Significant differences ($p < 0.05$) are highlighted in bold.

	Treatment	p-value
Thaw depth	TEMP	**<0.001**
	WATER	0.24
	TEMP*WATER	0.008
Soil T −30 cm	TEMP	**0.0039**
	WATER	0.31
	TEMP*WATER	0.44
Soil T −20 cm	TEMP	0.053
	WATER	0.84
	TEMP*WATER	0.53
Soil T −10 cm	TEMP	**0.0023**
	WATER	0.50
	TEMP*WATER	0.60
Soil T −5 cm	TEMP	**0.015**
	WATER	0.31
	TEMP*WATER	0.71
Soil T 0 cm	TEMP	0.095
	WATER	0.18
	TEMP*WATER	0.21

treatments showed a significant difference in the CH_4 fluxes between the DRY and WET treatments (with higher emissions in the WET treatments), while soil CO_2 respiration was similar across all the treatments (figure 6, table 2). There was no significant interaction between water table levels and temperature treatments neither for soil CO_2 respiration nor for CH_4 fluxes (table 2).

The two-way ANOVA showed no significant difference in DOC among any of the treatments and no significant interaction among them. DOC concentration was not significant in explaining the variability in the median CH_4 fluxes over the entire measuring period, nor was it significant in explaining the variability in the median soil CO_2 respiration. The cores were acidic in all treatments and more acidic in the DRY (pH $= 5.91 \pm 0.30$, median $\pm$ 95% CI) than in the WET treatments (pH $= 6.26 \pm 0.24$, median $\pm$ 95% CI). The pH was significantly higher in the WET cores ($p = 0.011$), but there was no significant interaction between water table levels and temperature treatments. Neither TDC nor TDN were significantly correlated with the median CH_4 fluxes nor with soil CO_2 respiration. The average contribution of the median CH_4 emitted (in terms of CO_2 equivalents) was about 60% of the sum of the total C ($CO_2 + CH_4$) emission in the WET treatments and 20% in the DRY treatments.

4. Discussion

4.1. Environmental controls on soil CO_2 respiration and CH_4 fluxes

The average CH_4 fluxes (0.5 ± 0.1 mgC–CH_4 m^{-2} h^{-1} for the DRY plots to 1.8 ± 0.3 mgC–CH_4 m^{-2} h^{-1} for the WET plots) from this laboratory experiment were similar to those reported from eddy covariance and chambers from the field across the Arctic (Schimel 1995, Zona *et al* 2009, Von Fischer *et al* 2010, Sturtevant and Oechel 2013, McEwing *et al* 2015). This similarity might be surprising, considering that vegetation was not included in our sampling, but is consistent with the dominant role of belowground conditions for CH_4 emission (Zona *et al* 2009). Several peak values in the CH_4 fluxes are consistent with the stochastic nature of these emissions, suggesting the importance of ebullition for CH_4 emission in laboratory studies as in the field (Throckmorton *et al* 2015). Similarly, soil respiration rates (0.069 ± 0.0024 gC–CO_2 m^{-2} h^{-1} for the DRY plots and 0.058 ± 0.0025 gC–CO_2 m^{-2} h^{-1} for the WET plots) were also similar to the ecosystem respiration collected in the proximity of core collection sites (McEwing *et al* 2015, Davidson *et al* 2016b, Wilkman *et al* 2018), suggesting that the soil component also dominates the entire ecosystem respiration in these short-stature tundra environments.

Overall, the hydrological status of the soil exerted dominant control over the fluxes from these tundra soil cores (Oechel *et al* 1998, Christensen *et al* 2000, Parmentier *et al* 2011, Mastepanov *et al* 2013). Very low CH_4

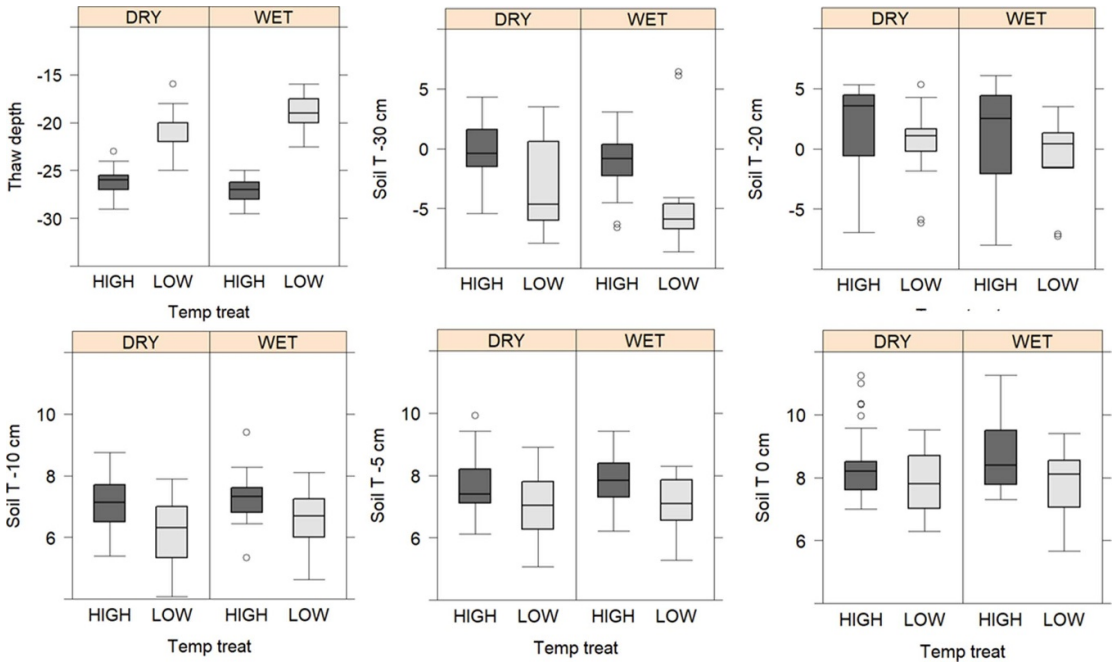

Figure 5. Boxplots of the median thaw depth (cm), and soil temperatures (°C) at the indicated depths during the periods when the cores were maintained at stable water table, soil temperature and thaw depth levels (weeks 5–10 in season one and 20–26 in season two, see figure 4).

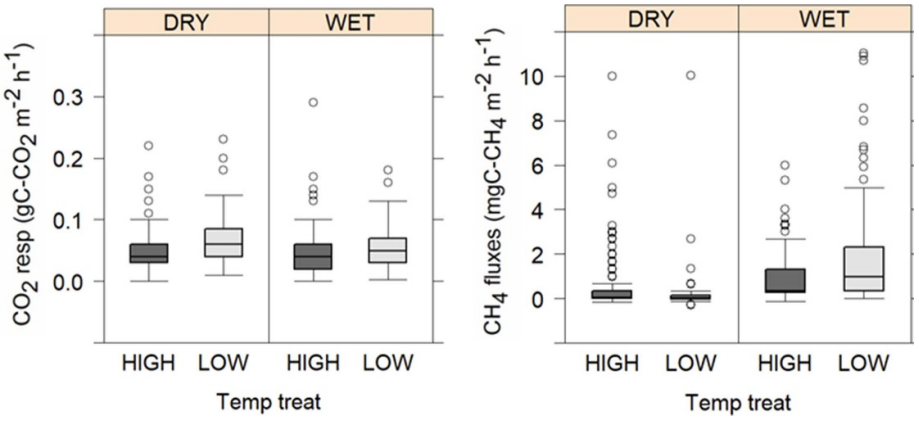

Figure 6. Boxplots of the median soil CO_2 respiration and CH_4 emissions during the periods when the cores were maintained at stable water table, soil temperature and thaw depth levels (week 5–10 in season one and 20–26 in season two, see figure 4).

Table 2. Statistical results of the repeated measures two-way ANOVA (for soil CO_2 respiration and CH_4 fluxes) for the two temperature and thaw depth treatments (HIGH and LOW) and water level treatment (DRY and WET), and their interaction. The week of measurement (nested into season) and core number were used as random factors to account for the temporal and spatial pseudoreplication, using a linear mixed model (nlme package in R). Significant differences ($p < 0.05$) are highlighted in bold.

	Treatment	p-value
Soil CO_2 respiration	TEMP	0.060
	WATER	0.23
	TEMP*WATER	0.26
CH_4 fluxes	TEMP	0.28
	WATER	**0.022**
	TEMP*WATER	0.071

emission was found in soil cores from DRY ecosystems (e.g. polygon rims and centres of the polygons), even with a water table at the surface (figure 4), suggesting that an active methanogenic community is absent in the usually drier ecosystems (Yrjälä *et al* 2011, McCalley *et al* 2014). Methanogenic communities are in fact

generally present in the deeper anoxic soil layers (Lee *et al* 2012, Kim and Liesack 2015) and in soils that are consistently inundated (Treat *et al* 2015). This interpretation is supported by data collected by our team on soil cores in close proximity to the ones used in this experiment, which showed lower relative abundances of methanogens in drier areas (polygon rims vs centres) and shallower layers (Lipson *et al* 2015, 2021). The impact of microtopography (e.g. rim of polygons, low-centre polygons, troughs, etc) is therefore critical to identify the response of carbon fluxes to water table changes in Arctic ecosystems (Moore and Roulet 1993, Lipson *et al* 2010, Brown *et al* 2014). Of course, a methanogenic community can develop over time (Tveit *et al* 2013, Frank-Fahle *et al* 2014, McCalley *et al* 2014), but the timing of this development will vary depending on the ecosystem type and environmental conditions (Høj *et al* 2008, Oldfeldt *et al* 2013, Frank-Fahle *et al* 2014). The similar soil CO_2 emissions in the DRY and WET treatments support the importance of anaerobic CO_2 respiration from these Arctic ecosystems (Updegraff *et al* 2001, Lipson *et al* 2010, Zona *et al* 2012), as substantial anaerobic CO_2 respiration could be sustained by the readily available Fe(III) and humic substances in these Arctic soils acting as alternative electron acceptors (Lipson *et al* 2010).

The difference in soil CO_2 and CH_4 fluxes between the two temperature treatments was statistically not significant, which might be explained by the small difference between temperature treatments (e.g. an average 1 ± 1 °C (st. dev.)) at 5 cm depth, despite the more substantial difference in thaw depth (on average 6 ± 2 cm (st. dev.)). Similar temperature treatments with warming around 0.5 °C (Oechel *et al* 1998) or even between 1.6–4.1 °C (Updegraff *et al* 2001) were also found to not significantly affect CO_2 fluxes (Oechel *et al* 1998) nor CH_4 fluxes (Updegraff *et al* 2001). Temperature manipulation that warmed soil to 7 °C (Binkley *et al* 1994) resulted in a considerable increase in net mineralization. Overall, a more substantial temperature and thaw depth change than what has been observed over the last decade (Christensen 2013) and/or a longer timeframe might be needed to stimulate more pronounced emission of CO_2 and CH_4 from Arctic soils.

The dominant contribution of CH_4 emissions (60%) to the total carbon loss in the WET treatment across both temperature (and thaw depth) levels is in line with the importance of CH_4 emission from these Arctic tundra wetlands (Zona *et al* 2016, Hashemi *et al* 2021). Including CH_4 in the estimate of the total carbon balance has been shown to change the entire balance from a carbon sink into a source in these tundra ecosystems (Hashemi *et al* 2021). The observed increase in permafrost degradation and flooding of several areas across these polygonized tundra systems (Liljedahl *et al* 2016) might further increase these losses. Given the substantial rates of anaerobic soil CO_2 respiration (Lipson *et al* 2010, Zona *et al* 2012, Treat *et al* 2015), a potential increase in flooding of these tundra landscapes (Zona *et al* 2012) can translate into substantial positive feedback on the climate.

4.2. Influence of soil carbon stores and pH

The role of pH on methanogenesis has shown contrasting results, ranging from no correlation between CH_4 production and pH (Bridgham and Richardson 1992), to a negative correlation (Valentine *et al* 1994). In this study, we found significantly higher pH in soils in the WET treatments, which also showed higher CH_4 emissions, consistent with the inhibition of CH_4 production reported for more acidic soils (Svensson 1984, Valentine *et al* 1994, Bergman *et al* 1998). This is consistent with the higher pH in areas with higher water table due to the reduction of solid phase Fe minerals (Lipson *et al* 2010). The lack of correlation between measured fluxes and the soil DOC concentration, and the lack of a decrease in CH_4 emissions during the entire duration of the experiment was probably linked to the large amounts of carbon, including labile carbon, which already exists in these carbon-rich soils (Gilmanov and Oechel 1995, Neff and Hooper 2002, Tarnocai *et al* 2009, Allen *et al* 2010, Von Fischer *et al* 2010). The DOC reported by this experiment was in fact at the highest end of what was reported for these Arctic Alaskan soils (see Lipson *et al* 2012, Davidson *et al* 2016b). Soil CO_2 respiration slightly decreased during the first season of measurements, potentially linked to the decomposition of more easily decomposable carbon (Knoblauch *et al* 2021), but maintained fairly stable values during the second season, probably supported by the decomposition of more recalcitrant carbon (King *et al* 1998). The substantial CH_4 emissions throughout the entire duration of the experiment (without any input from active vegetation) are consistent with previous studies showing that these systems are not carbon limited (Von Fischer *et al* 2007, Zona *et al* 2009, Allen *et al* 2010). These results also highlight the importance of conducting longer-term soil incubation to achieve a more complete understanding of the processes controlling carbon emissions in the Arctic (Schädel *et al* 2014). Future studies should measure DOC in the soil water at multiple times during an incubation experiment to assess potential changes in the source of carbon supporting CO_2 respiration and CH_4 loss over time. Moreover, testing the response of tundra ecosystems with and without vegetation (Voigt *et al* 2019) in a multifactorial manipulation of water level, temperature and atmospheric CO_2 concentration can provide invaluable insights on the response of these systems that mimic field conditions. Finally, investigating the response of CO_2 and CH_4 fluxes in multifactorial experiments simulating the cold period would be critical to reduce uncertainty in the prediction of their response to climate change (Zona *et al* 2016, Natali *et al* 2019).

5. Conclusions

The similar soil CO_2 respiration rates even with a water level at the surface supports the relevance of anaerobic CO_2 respiration from these Arctic tundra ecosystems. The sharp decrease in soil CO_2 respiration rates in the first few weeks of the experiment and the stable CH_4 emissions during the duration of the experiment suggest that soil CO_2 emissions are more related to the input of easily decomposable carbon from vegetation, while CH_4 emissions mainly originate from deeper soil layers (as reported by previous studies, Herndon *et al* 2015) and are supported by the decomposition of more recalcitrant carbon. The non-significant difference between both soil CO_2 and CH_4 emissions between the two temperature treatments suggests that the increase in thaw depth and temperature observed over the last decades might not have been a major contributor to the increased carbon loss from these tundra soils. Increased flooding linked to permafrost degradation or changes in rainfall patterns can, however, result in increased CH_4 emissions and a net increase in the total carbon loss from these ecosystems. Future experiments should compare the response of soil CO_2 and CH_4 emissions to temperature and water table manipulations in the presence and absence of vegetation and include more frequent monitoring of the changes in soil carbon quality and quantity. This could provide more definitive information about the relative importance of vegetation vs older soil carbon for Arctic carbon emissions.

Data availability statement

The data that support the findings of this study are openly available at the following URL/DOI: https://doi.org/10.18739/A2CN6Z15V.

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Conflict of interest

The authors declare that they have no conflict of interest.

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