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The rate of permafrost carbon release under aerobic and anaerobic conditions and its potential effects on climate

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Abstract

Recent observations suggest that permafrost thaw may create two completely different soil environments: aerobic in relatively well-drained uplands and anaerobic in poorly drained wetlands. The soil oxygen availability will dictate the rate of permafrost carbon release as carbon dioxide (CO_2) and as methane (CH_4), and the overall effects of these emitted greenhouse gases on climate. The objective of this study was to quantify CO_2 and CH_4 release over a 500-day period from permafrost soil under aerobic and anaerobic conditions in the laboratory and to compare the potential effects of these emissions on future climate by estimating their relative climate forcing. We used permafrost soils collected from Alaska and Siberia with varying organic matter characteristics and simultaneously incubated them under aerobic and anaerobic conditions to determine rates of CO_2 and CH_4 production. Over 500 days of soil incubation at 15 °C, we observed that carbon released under aerobic conditions was 3.9–10.0 times greater than anaerobic conditions. When scaled by greenhouse warming potential to account for differences between CO_2 and CH_4, relative climate forcing ranged between 1.5 and 7.1. Carbon release in organic soils was nearly 20 times greater than mineral soils on a per gram soil basis, but when compared on a per gram carbon basis, deep permafrost mineral soils showed carbon release rates similar to organic soils for some soil types. This suggests that permafrost carbon may be very labile, but that there are significant differences across soil types depending on the processes that controlled initial permafrost carbon accumulation within a particular landscape. Overall, our study showed that, independent of soil type, permafrost carbon in a relatively aerobic upland ecosystems may have a greater effect on climate when compared with a similar amount of permafrost carbon thawing in an anaerobic environment, despite the release of CH_4 that occurs in anaerobic conditions.

Keywords: active layer, Alaska, carbon isotopes, methane, radiocarbon, relative climate forcing, substrate quality, yedoma

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Introduction

In the past century, high latitude ecosystems have undergone drastic changes due to global scale warming (Serreze *et al*., 2000; ACIA, 2005). Increased air and soil temperatures have contributed to increased temperatures of deep permafrost (ground that is frozen more than two consecutive years) (Osterkamp & Romanovsky, 1999; Hinzman *et al*., 2005). Permafrost is distributed across 14% of the global land surface within boreal forest, tundra and arctic desert (Tarnocai *et al*., 2009). A recent estimate projected that permafrost soil stores over 1600 Pg of carbon (C), which represents approximately 50% of global terrestrial C as soil organic matter and is approximately double the C present in the atmospheric pool (Schuur *et al*., 2008; Tarnocai *et al*., 2009). The frozen conditions of permafrost have prevented active decomposition of plant litter inputs and soil organic matter, which has been accumulating since the end of the last glacial period (Harden *et al*., 1992) and beyond in some locations (Schirrmeister *et al*., 2002; Zimov *et al*., 2006). Therefore, increased permafrost temperatures as a result of climate change may expose a large pool of stable C stored in permafrost to microbial decomposition.

In ice-rich permafrost areas, permafrost thaw is often followed by land surface subsidence called thermokarst due to melting of the ice wedges and lenses that formerly sustained the ground structure (Davis, 2001; Jorgenson *et al*., 2006). As a result of thaw effects on surface hydrology, soil organic matter emerging from permafrost can be exposed to either aerobic or anaerobic conditions. In areas of relatively well-drained soils

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such as slopes or uplands, thermokarst creates patchy microtopographic depressions (Schuur *et al.*, 2008). Well-drained soils in the thermokarst zone may create optimum soil moisture conditions for microbial decomposition of soil organic matter (Zimov *et al.*, 2006). In contrast, expansion of thaw lakes in lowlands, as seen in areas of continuous permafrost (Smith *et al.*, 2005; Jorgenson *et al.*, 2006; Jorgenson & Shur, 2007) often leads to waterlogging and anoxia (oxygen limitation) resulting in slower decomposition of soil organic matter. Lastly, shrinking thermokarst ponds and lakes has been observed in the discontinuous permafrost zone (Yoshikawa & Hinzman, 2003; Smith *et al.*, 2005; Riordan *et al.*, 2006; Marsh *et al.*, 2009), which may lead to faster decomposition of soil organic matter as aerobic conditions become more prevalent in some landscapes.

In addition to differences in C release rate, the decomposition of permafrost C under different environmental conditions affects the type of greenhouse gas that is released. Northern wetlands within the permafrost zone are reported as a long-term sink of atmospheric CO_2, but a source of CH_4 as C is used as an alternate electron acceptor when oxygen is limited (Smith *et al.*, 2007; Conrad, 2009). Drained lakes may shift from being a sink for CO_2 and source of CH_4, to being a source of CO_2, whereas CH_4 release decreases due to oxidation of CH_4 by surface methanotrophs or the cessation of CH_4 production. Under anaerobic conditions, a wide range of CO_2 to CH_4 ratios have been observed. However, in general, C release as CO_2 is greater than as CH_4 (Segers, 1998). Although the magnitude of CH_4 production is smaller than CO_2, CH_4 has a greater global warming potential ($GWPCH_4 = 25$) than CO_2 ($GWPCO_2 = 1$) over a 100-year time period (IPCC, 2007). This suggests that although total C release can be attenuated under anaerobic conditions, emission of a more potent greenhouse gas such as CH_4 may contribute more to climate change when compared with CO_2 emissions alone from aerobic conditions. Therefore, the full magnitude of the climate effect from permafrost C release depends in large part on the soil environment experienced by thawing permafrost C, which will control the rate and form of C release.

The objective of this study was to quantify CO_2 and CH_4 release over a 500-day period from permafrost soil under aerobic and anaerobic conditions and to compare the potential effects of these emissions on future climate change by estimating their relative climate forcing in these two different soil environments. In addition, we investigated soil quality factors that could affect variability in the rate of permafrost C release and its effect on climate. We conducted laboratory incubations using permafrost soils collected from Alaska and Siberia that spanned a wide range of site and soil characteristics across the permafrost zone. We hypothesized that total C release would be greater under aerobic conditions, but the potential climate forcing from the C release may be greater under anaerobic conditions because microbes are more active under aerobic conditions, whereas CH_4 has greater effects on climate. Furthermore, we hypothesized that the potential effects on climate from aerobic and anaerobic production of greenhouse gases would be positively correlated to soil pH and various soil substrate qualities such as soil C, nitrogen (N), and C to N ratio, in particular, because soil pH may dictate the availability of electron transport needed for methanogenesis and these substrates may be limiting factors to microbial activity.

Materials and methods

Soil sampling and preparation

Twelve different types of frozen soils were collected from seven geographical locations in Alaska and Siberia (Fig. 1; Itkillik I, Itkillik II, Sagavanirktok, ToolikKarst, EML, Fox, and Siberia). All of the soil samples were collected in the continuous and discontinuous permafrost zone; however, they varied in soil C and N content, type of aboveground vegetation, parent material, parent material age, and pH. Three soil cores were collected at each sampling location as replicates. Soil cores were collected from four different locations on the North Slope of the Brooks Range in Alaska near Toolik Lake Biological Station (68.63N, −149.72E). The moist acidic tussock tundra sites were located on the Itkillik I glacial drift (hereafter, Itkillik I), the non-acidic tundra sites were on the Itkillik II glacial drift (hereafter, Itkillik II) (Hobbie *et al.*, 2002). The Sagavanirktok glacial drift (hereafter, Sagavanirktok) is much older in parent material age and is considered acidic tundra (Walker & Everett, 1991). The fourth set of soil samples was collected from a recently formed thermokarst gully near Toolik Lake (ToolikKarst); this site is also located on the Sagavanirktok glacial drift (Bowden *et al.*, 2008).

Additional soil cores were collected from a moist acidic tundra site at Eight Mile Lake (EML) research site located in the Interior Alaska, on the foothills of the Alaska Range just outside of Denali National Park (63.88N, −149.25E). The EML gradient sites were established on a natural gradient containing three different intensities of permafrost thaw and thermokarst development (Minimal Thaw, Moderate Thaw, and Extensive Thaw; hereafter EML-mMin, EML-mMod, and EML-mExt for mineral soils and EML-oMin, EML-oMod, and EML-oExt for organic soils) (Schuur *et al.*, 2007, 2009; Osterkamp *et al.*, 2009; Vogel *et al.*, 2009). These three locations are the closest to one another geographically, with all sites within 1 km.

Soil cores were collected from near the town of Fox, Alaska (64.95N, −149.72E) along the Steese Highway, where deep soils were visible in vertical exposures due to land use (hereafter, Fox). Soil cores were also collected from Zelenyi Mys (68.80N, 161.38E) along the Kolyma River in Siberia (hereafter, Siberia). Both these sites consist of loess silt deposition with

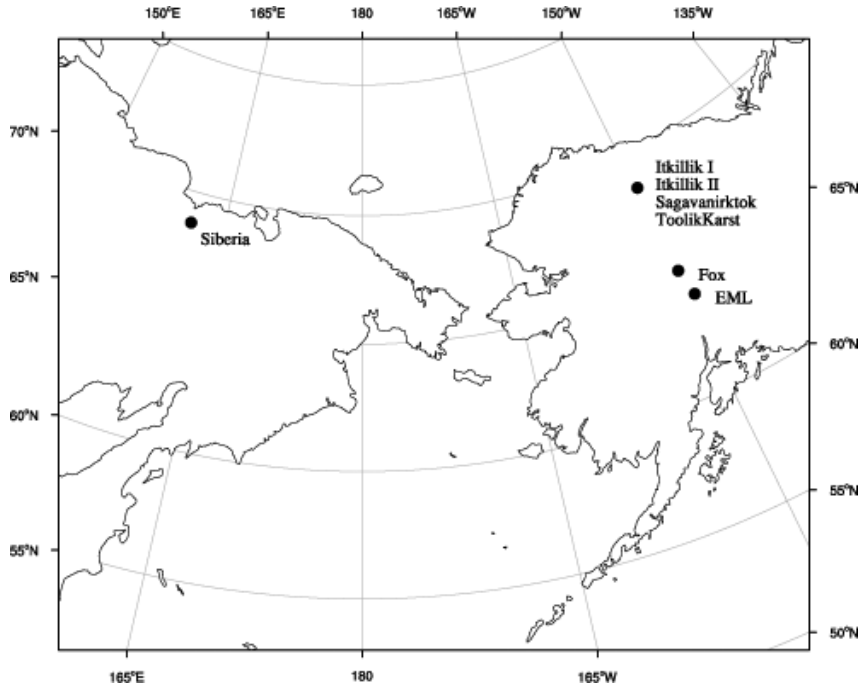

Fig. 1 A map of soil sampling locations with site names indicated next to the closed circles.

the local term in Siberia for this soil type being Yedoma (Zimov *et al.*, 2006). The soil samples were collected within 1 m from the ground surface, mostly within the surface permafrost, except Fox and Siberia, which were collected from a depth of approximately 10 m from the ground surface within permafrost layer.

For all the soils, only the deepest mineral soil layers of each soil core were used, with the exception of the surface organic soils from the three EML gradient sites, which were used as reference surface organic soils. All soil samples were kept frozen at −80 °C after collection and shipped frozen to the University of Florida for further analysis. The soils were thawed and separated into organic and mineral layers at the laboratory prior to the incubation set up.

Soil analyses

Soil C and N content were analysed using an elemental analyzer (Costech ECS 4010, Valencia, CA, USA). Calibration was done with NIST standard peach leaves (SRM 1547, National Institute of Standards and Technology, Gaithersburg, MD, USA): C 44.65%, N 2.93%. Based on repeated measurements of SRM 1547, the 1σ precisions for C and N measurements were ±0.6% and ±2.2%, respectively, of the measured values. Soil pH was measured using oven dried (60 °C) soil samples. The soils were diluted 1 : 5 using deionized water and stabilized. We measured the pH of stabilized soil solution using Orion pH metre (Thermo Orion model 250; Orion Instruments, Beverly, MA, USA). We corrected the measured soil pH to deioinized water pH of 7.0, because the deionized water used for this measurement was pH 5.1, which resulted in lower soil pH than expected.

Laboratory incubation experiment and the rate of CO_2/ CH_4 production

We prepared 1-L canning jars with airtight lids and attached Luer-lock™ stopcocks on the lid for gas sampling. Approximately 50–100 g of soil with field moisture content were placed in each jar and kept at 15 °C for aerobic soil incubations. Aerobic jars were flushed periodically when the headspace CO_2 concentrations reached over 10 000 ppm with humidified CO_2-free air to minimize build up of CO_2. The incubation temperature was chosen at 15 °C with the intention of comparing our results with the previous soil incubation study that used the same subset of Siberian soils (Dutta *et al.*, 2006).

The aerobic soils were kept at field moisture conditions, most of which were near field capacity (free draining) moisture levels due to high ice content. For anaerobic soil incubations, we added 150 mL of deionized water to each jar to completely submerge the soil and flushed them with helium gas (He) to remove any dissolved oxygen in the soil, water, and head space of the jar. For calculations of CO_2 and CH_4 production rates, we corrected CO_2 and CH_4 concentrations using solubility constant of these gases in water (1.959 g L^{-1} for CO_2 and 0.019 g L^{-1} for CH_4 at 15 °C). We used anaerobic indicator strips (BBL GasPak™; BD, Franklin Lakes, NJ, USA) to confirm that the environment in the jar was completely anaerobic. We observed slightly lower pressure in the anaerobic incubation jars that are resulted from gas sampling over time (from small difference created between sampling headspace gas and injecting back equivalent volume of He gas), which confirms that there was no mixing between the headspace gas and outside air. The jars remained closed

throughout the experiment to maintain anaerobic conditions for anaerobic jars and to maintain humidity for aerobic jars. Soils were incubated under these conditions for over 500 days.

We sampled 10 mL from the headspace in the jars using an air-tight syringe and measured CO_2 with an infrared gas analyzer (LI-COR 6252; Li-COR Biosciences, Lincoln, NE, USA) attached to an injection valve and loop (Valco 6-port injection valve, 5 mL injection loop; Valco Instrumental Company Inc., Houston, TX, USA) calibrated with certified CO_2-in-air standards with concentrations of 608, 1000, and 10 000 ppmv. We used a gas chromatograph (Shimadzu GC-FID, Column 1/8″ SS 45/60 Carboxen 1000; Shimadzu Scientific Instruments, Columbia, MD, USA) to measure CH_4 from anaerobic incubations using 1% CH_4 as a standard. For aerobic incubations, we collected gas samples daily for 2 weeks, then every other day for 1 month, weekly for the next month, biweekly for the subsequent 2 months and then monthly thereafter. For anaerobic incubations, we collected gas samples weekly for 2 months, biweekly for 2 months, and monthly thereafter. We injected the same amount of He gas back into the anaerobic jars when the gas samples were drawn out for measurement to equilibrate negative pressure created in the jars from sampling. The same procedure was used for aerobic jars, but humidified CO_2-free air was used instead of He gas. Replacing the sampled amount of headspace gas by CO_2-free air or He gas resulted in dilution of the CO_2 and CH_4 concentrations in the jars. We accounted for this dilution factor when calculating CO_2 and CH_4 concentrations and rates of gas production.

Soil enzyme assay

We measured potential β-glucosidase activity to assess microbial activity involved in the extracellular breakdown of soil organic matter. We analysed β-glucosidase both at the outset, and during the aerobic and anaerobic incubations. One subsample of soil (approximately 3 g of soil with field moisture content) was taken at the initial step of the soil incubation and analysed for soil enzyme activity. The other sub-samples were incubated separately under the same conditions as described previously in separate 25 mL glass vials under aerobic and anaerobic conditions. The aerobic vials were maintained at field moisture conditions and the anaerobic vials were filled with 5 mL of water, submerging the soil sample, and were purged with He gas in the beginning of the incubation.

After 125 days of incubation, we analysed the incubated soils to observe changes in potential β-glucosidase activity under aerobic and anaerobic conditions. The enzyme assay was conducted using the fluorescent model substrate 4-methylumbelliferone and glucopyranoside in acetate buffer at pH 5.0. The soil samples were placed in 10 mL of acetate buffer and homogenized using brief agitation with Tissue Tearor Model 398 (Biospec Products, Bartlesville, OK, USA). A 1/10 dilution of soil slurry was transferred to a microtiter plate, and enzyme substrate solution was added to bring the final concentration to 200 μM. Samples were incubated for 2 h in the dark at room temperature. We terminated the assay by adding 10 μL of 0.1 M NaOH, and the fluorescence results were read on a Bio-Tek Model FL600 fluorometric plate reader (Bio-Tek Instruments Inc., Winooski, VT, USA) at 450 nm emission and 330 nm excitation wavelength (Prenger & Reddy, 2004). The enzyme activity was determined as fluorescence units using a standard curves made with methylumbelliferone (MUF). Quencing curves were prepared to correct for the quenching ability of the soil using one of each of the soil samples for the same standard curves (Freeman *et al*., 1995). The results were reported as mmol MUF per g of dry soils weight per hour.

Stable isotope measurements

We quantified stable isotopes of C and N in the soils used in the incubation to compare isotopic composition of soils and the gas emitted from these soils. The $^{13}C/^{12}C$ and the $^{15}N/^{14}N$ isotope ratios were measured with a Finnigan Delta Plus XL continuous flow mass spectrometer (Finnigan MAT GmbH, Bremen, Germany) coupled to a Costech CN Analyzer (Costech Instruments, Milan, Italy). Results were expressed as delta (δ) values and ‰ deviations from standard reference materials. We used NIST certified sucrose standard and peach as working standards (SRM 1547: $\delta^{13}C = -26.06‰$, $\delta^{15}N/^{14}N = 1.91‰$). Average 1σ precision for the isotopes was 0.05‰ for $\delta^{13}C$ and 0.07‰ for $\delta^{15}N$ calculated from repeated measurements of SRM 1547.

The headspace gas of the aerobic jars was trapped for $\delta^{13}C$-CO_2 analysis after approximately 1 year of soil incubation. Air was pumped from the headspace at 1 L min^{-1} for 10 min through a molecular sieve (13X) to trap the entire volume of CO_2 to prevent fractionation of ^{13}C. Before sampling for isotopic analysis, the headspace of the jars was scrubbed with CO_2-free air to remove any atmospheric CO_2. Respired CO_2 then reaccumulated in the jars for several days to accumulate 1 mg of respired CO_2-C. In the laboratory, the molecular sieve traps were heated to 625 °C to desorb CO_2, then purified and analysed for ^{13}C (Bauer *et al*., 1992). The $\delta^{13}C$-CO_2 was analysed via direct injection into an isotope ratio mass spectrometer attached to a Gas Bench gas chromatograph (GC-IRMS; Finnigan Delta S, Bremen, Germany).

The headspace of the anaerobic incubation gas samples was collected after approximately 1-year of soil incubation using a 22-gauge needle attached to 25 mL plastic syringe. Two full syringes were injected sequentially into an evacuated 25 mL serum vial fitted with a butyl rubber septum, which was then transferred under positive pressure to the laboratory for $\delta^{13}C$-CO_2 and $\delta^{13}C$-CH_4 analyses. A portion of each sample was analysed via direct injection into the GC-IRMS (Finnigan Delta S) to determine $\delta^{13}C$-CO_2, $\delta^{13}C$-CH_4 and CH_4 concentration (Chanton *et al*., 2006). Laboratory standards were calibrated against NIST standards; precision for $\delta^{13}C$ measurements was ±0.2‰ on the basis of repeated measurements of a working standard. From these data, apparent fractionation factors for $^{13}C/^{12}C$ were determined for each location and site. The apparent fractionation factors for $CO_2 \rightarrow CH_4$ (α) were calculated after (Hines *et al*., 2008). Variability in α reflect differences in the relative importance of methanogenic pathways, where larger α values are typical of CO_2 reduction and smaller

values are representative of the increased importance of acetate decarboxylation (Whiticar, 1999; Conrad *et al.*, 2002; Chanton *et al.*, 2006).

Radiocarbon measurements

We collected CO_2 from the headspace of aerobic jars as an indicator of approximate age of CO_2 derived from the incubation after approximately 1 year of soil incubation. The samples were collected using the same method used for $^{13}CO_2$ analysis described in the previous section. In the laboratory, the molecular sieve traps were heated to 625 °C to desorb CO_2, and cryogenically purified in a vacuum line by slowly passing the air through a water-trap (at −70 °C) and a liquid nitrogen (LN_2) trap. Purified CO_2 samples were sealed in Pyrex tubes that were prebaked at 550 °C.

A portion of the sample CO_2 was converted to graphite by reacting with H_2 in presence of Fe catalyst (Vogel *et al.*, 1987). The graphite samples were pressed into targets and sent to the W. M. Keck Carbon Cycle Accelerator Mass Spectrometry facility at University of California, Irvine (Southon *et al.*, 2004) for ^{14}C analysis. All ^{14}C results were expressed as $\Delta^{14}C$ after correcting for any mass-dependent fractionation of ^{13}C (Stuiver & Polach, 1977). The negative $\Delta^{14}C$ values of the samples indicate old C whose ^{14}C content significantly decreased from its original amount by radioactive decay, whereas positive values of $\Delta^{14}C$ indicate presence of excess nuclear bomb ^{14}C produced after the late 1950s (Trumbore, 2000). Typical 1σ precisions of $\Delta^{14}C$ measurements for modern samples were better than ±3‰. The average background $\Delta^{14}C$ measured on coal blanks was −998.0 ± 0.5‰. Samples from Fourth International Radiocarbon Intercomparison exercise (Scott, 2003) were analysed to check the accuracy of the ^{14}C results, which agreed with their reported consensus values within 1σ limits of error.

Data analyses

Carbon mineralization from the soil incubation experiment was calculated by multiplying the number of days by mean CO_2 and CH_4 production rates for those days. Cumulative C mineralization was calculated from the sum of C mineralization over 500 days of soil incubation. The cumulative C release under anaerobic conditions was also expressed in CO_2 equivalents calculated by adding cumulative C release as CO_2 with cumulative C release as CH_4 multiplied by 25 (GWP of CH_4). This accounts for the stronger warming potential of CH_4 relative to CO_2. Relative climate forcing (Schuur *et al.*, 2008) was estimated for a single soil type using the ratio between cumulative C released as CO_2 production under aerobic conditions divided by C release under anaerobic conditions as CO_2 and CH_4 production, expressed in CO_2 equivalents by multiplying the CH_4 by a GWP of 25 [Eqn (1)].

$$\text{Relative climate forcing} = \frac{\text{Cumulative production of aerobic } CO_2}{\text{Cumulative production of anaerobic } CO_2 + (25 \times \text{cumulative production of anaerobic } CH_4)} \quad (1)$$

Pearson's correlation was used to examine the relationship among soil characteristics and relative climate forcing from cumulative gas production. Paired *t*-tests were used to compare initial β-glucosidase activity with activity after 125 days of incubation. Statistical analyses were conducted using JMP 7.0.2 (SAS Institute Inc., Cary, NC, USA) and R 2.11.1 (R Development Core Team).

Results

Soil substrate quality

The permafrost soils used in this study by design showed a wide range of mean soil%C; the lowest soil% C was found in deep Yedoma soils from Fox, Alaska and Siberia (1.1%), whereas the highest was found in surface organic horizons from the EML gradient sites in interior Alaska (Table 1). The %C and N were mass based calculation and highest %C in the permafrost mineral soil was 16.5 ± 0.3%, which is typical of cryoturbated organic matter mixed within the mineral soil at depth. The %N in soils ranged from 0.1% to 1.0%, which resulted in a range of C to N ratios from 5.4 to

Table 1 Substrate quality of soil samples used in the incubation study. Values in parentheses are standard errors

Sites	Soil type	Location (N, E)	Depth (cm)	%C	%N	C : N	pH
Itkillik I	Mineral	(68.6, −149.7)	42–66	6.1 (0.2)	0.3 (0.0)	19.3 (0.4)	6.0 (0.1)
Itkillik II	Mineral	(68.6, −149.7)	40–55.5	9.3 (4.0)	0.6 (0.3)	14.3 (0.8)	6.7 (0.2)
Sagavanirktok	Mineral	(68.6, −149.7)	42.5–66	5.0 (0.8)	0.2 (0.0)	19.8 (2.5)	6.2 (0.0)
EML-mMin	Mineral	(63.9, −149.3)	56–76	13.3 (11.1)	0.6 (0.5)	23.8 (3.7)	6.5 (0.2)
EML-mMod	Mineral	(63.9, −149.3)	62–90	9.4 (5.8)	0.3 (0.2)	26.2 (4.1)	6.6 (0.1)
EML-mExt	Mineral	(63.9, −149.3)	70–83	16.5 (0.3)	0.7 (0.0)	21.9 (0.9)	5.9 (0.7)
ToolikKarst	Mineral	(68.6, −149.7)	Below 1 m	2.7 (0.6)	0.2 (0.0)	14.3 (0.0)	7.2 (0.0)
Fox	Mineral	(65.0, −149.7)	Within 10 m	1.1 (0.6)	0.1 (0.0)	6.8 (2.3)	9.1 (0.2)
Siberia	Mineral	(68.8, 161.4)	Within 10 m	1.1 (0.1)	0.1 (0.0)	8.9 (0.0)	8.4 (0.4)
EML-oMin	Organic	(63.9, −149.3)	5–15	40.6 (1.5)	1.0 (0.1)	40.7 (6.4)	5.3 (0.1)
EML-oMod	Organic	(63.9, −149.3)	5–15	41.4 (0.8)	1.0 (0.2)	45.5 (9.9)	5.2 (0.0)
EML-oExt	Organic	(63.9, −149.3)	5–15	40.1 (3.3)	0.9 (0.0)	45.8 (3.4)	5.5 (0.1)

45.8 (Table 1). Soil pH ranged from 5.2 to 9.1, where surface organic soils were slightly more acidic than deeper mineral soils in the same sampling locations. The deep mineral soils with low %C showed higher soil pH levels than shallow mineral soils ranging from pH 7.2 to 9.1. Soil pH presented in our study was slightly higher than those reported for typical soil pH of the North Slope (Gough *et al.*, 2000), likely because the reported values were pH of surface organic soil. Whereas, our soils were mineral layer soils collected within the surface 1 m below the organic layer.

Carbon mineralization under aerobic and anaerobic conditions

Overall, the magnitude of CO_2 production rates per gram of dry soil were an order of magnitude greater under aerobic conditions than anaerobic conditions and in organic soils than in mineral soils (Fig. 2). Organic soils showed sharp peaks or sharp decline in the rate of CO_2 production in the beginning, whereas mineral soils showed a gradual increase over the first 3–5 days of the incubation and thereafter gradually declined. Under aerobic conditions, CO_2 production rates reached a quasi steady-state baseline level by 30 days of incubation, whereas under anaerobic conditions CO_2 production rates did not reach a baseline level until 150 days of incubation. On the other hand, the CH_4 production rates from some soil samples, such as Itkillik I and II and organic layers from the EML gradient sites did not reach steady-state until 300 days of incubation. The CH_4 production rates were extremely low in mineral soils especially in the soils with low %C content.

Cumulative C release under aerobic and anaerobic conditions

In this study, we expressed cumulative C release in two different forms; first, cumulative C release *per gram of dry soil* that shows quantitative release of C (expressed as mg C gdw^{-1} soil) and second, cumulative C release

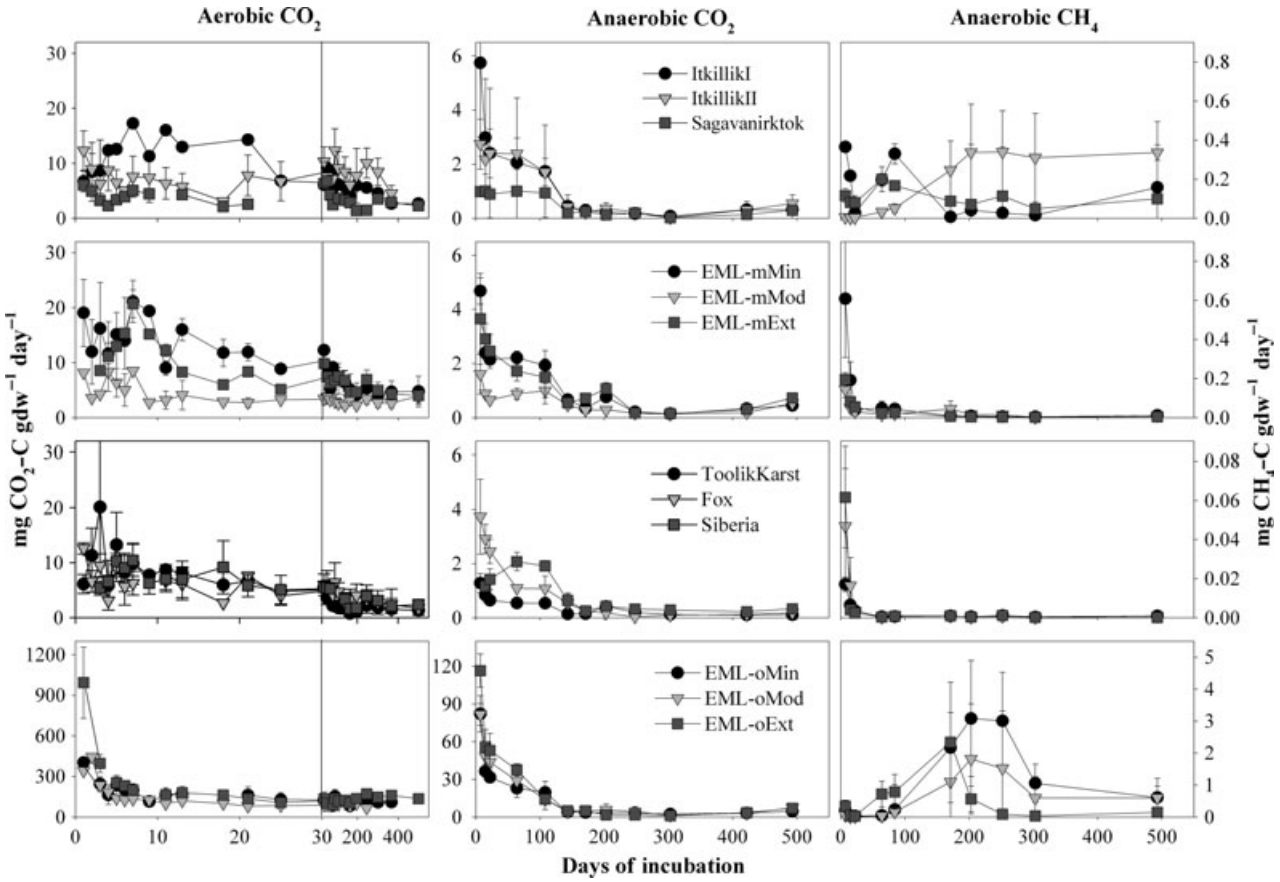

Fig. 2 The rate of CO_2 and CH_4 production over 500 days of permafrost incubation at 15 °C under aerobic and anaerobic conditions. Error bars indicate standard errors (n = 3). Note that the x-axes for aerobic CO_2 are split between 0 and30 days and 30–600 days, and the scale of y-axes are different for each panel.

per gram of soil C that shows the qualitative nature of the stored C (expressed as mg C g^{-1} C) independent of C quantity.

On a per gram soil basis, cumulative C release was 4–10 times greater under aerobic conditions than anaerobic conditions over 500 days of incubation at 15 °C (Table 2). In addition, the magnitude of C release was over 20 times greater in organic soils than in mineral soils (Table 2). Although, the magnitude of C release was greater under aerobic conditions, C release under aerobic and anaerobic conditions was highly correlated (Data S1 and S2). Cumulative C released under aerobic conditions over 500 days of incubation ranged from 1.07 to 3.42 mg C gdw^{-1} soil in mineral soils and from 39.60 to 71.89 mg C gdw^{-1} soil in organic soils (Fig. 3 and Table 2). Under anaerobic conditions, total C release was from 0.16 to 0.54 mg C gdw^{-1} soil (up to 0.12 mg C gdw^{-1} soil as CH_4) in mineral soils and from 5.85 to 7.04 mg C gdw^{-1} soil (0.18 to 0.59 mg C gdw^{-1} soil as CH_4) in organic soils (Fig. 3a, b and Table 2). Total C release was generally greater in organic soils than mineral soils from the North Slope, whereas Alaska soils (Itkillik I, Sagavanirktok, and ToolikKarst) showed the highest CH_4 contribution to total C release (up to 27% of total anaerobic C release as CH_4; Table 2). In most other mineral soils under anaerobic conditions, cumulative C released as CH_4 was as low as 0.2% of total C release.

The patterns of cumulative C release across sites altered when fluxes were expressed per gram of soil C as this metric eliminates differences in C concentration (amount) leaving only differences in C quality (Table 2 and Fig. 3c, d). The range of fluxes under aerobic conditions was 15.70–182.08 mg C g^{-1} C both in mineral and organic soils over 500 days of permafrost soil incubation. Cumulative C released per gram of soil C in Siberia and Fox soil samples were statistically not different than the three organic soils and were generally higher than the other mineral soils. The range of cumulative C released per gram of soil C under anaerobic conditions was 2.72–35.19 mg C g^{-1} C (0.02–1.44 mg C g^{-1} C as CH_4) in mineral and organic soils over 500 days of permafrost soil incubation, with the Siberia and Fox soils having the highest C release of all samples by this metric, even greater than the organic soils.

The CO_2 and CH_4 released under anaerobic conditions, expressed together in CO_2 equivalents, ranged from 0.17 to 20.51 CO_2 equivalent per gram of dry soil and 3.63 to 50.40 CO_2 equivalent per gram of soil C, which resulted in relative climate forcing ranging from 1.4 to 7.1 across all soil types (Table 2). Mean relative climate forcing values are all over 1, which represents that the net warming effect of the aerobic incubations was greater than the anaerobic incubations. Soils with

Table 2 Cumulative C release per gram of dry soil and per gram of soil C for over 500 days of incubation at 15 °C under aerobic and anaerobic conditions. Relative climate forcing (RCF) was calculated by dividing total C release under aerobic conditions by anaerobic CO_2 equivalent (CO_2 production + 25 × CH_4 production). The values represent means and values in parentheses are standard errors (n = 3; Itkillik I only had one). The CH_4 % contribution is the % amount of CH_4 production in total anaerobic C release. The aerobic to anaerobic ratio represent the ratio between total C release under aerobic and anaerobic conditions

	Aerobic (mg C gdw^{-1} soil)	Anaerobic (mg C gdw^{-1} soil)		Aerobic (mg C g^{-1} C)	Anaerobic (mg C g^{-1} C)		CH_4	Aerobic to anaerobic	
Sites	CO_2-C	CO_2-C	CH_4-C	CO_2-C	CO_2-C	CH_4-C	contribution (%)	ratio	RCF
Itkillik I	2.63 (–)	0.46 (–)	0.0428 (–)	44.25 (–)	7.67 (–)	0.72 (–)	8.6	5.3	1.7
Itkillik II	3.42 (0.93)	0.42 (0.06)	0.1162 (0.0589)	39.46 (12.67)	4.81 (0.75)	1.12 (0.30)	26.7	6.3	1.5
Sagavanirktok	1.78 (0.31)	0.21 (0.01)	0.0443 (0.0101)	36.49 (10.36)	4.17 (0.37)	0.91 (0.31)	21.5	7.1	1.4
EML-mMin	2.88 (0.69)	0.50 (0.02)	0.0132 (0.0061)	37.64 (19.36)	8.64 (5.78)	0.09 (0.04)	2.7	5.6	3.5
EML-mMod	1.43 (0.45)	0.23 (0.05)	0.0078 (0.0026)	15.70 (3.93)	2.67 (0.52)	0.09 (0.03)	3.2	6.0	3.3
EML-mExt	2.87 (0.70)	0.44 (0.02)	0.0063 (0.0001)	17.39 (4.03)	2.68 (0.18)	0.04 (0.00)	1.4	6.4	4.9
ToolikKarst	1.33 (0.87)	0.16 (0.03)	0.0006 (0.0003)	45.16 (25.35)	5.82 (0.34)	0.02 (0.01)	0.4	8.3	7.1
Fox	1.07 (0.17)	0.27 (0.03)	0.0008 (0.0006)	111.76 (29.16)	29.96 (9.10)	0.06 (0.02)	0.3	3.9	3.6
Siberia	1.66 (0.33)	0.41 (0.05)	0.0007 (0.0003)	144.46 (27.25)	35.12 (3.15)	0.07 (0.02)	0.2	4.1	3.9
EML-oMin	39.60 (9.48)	5.85 (0.95)	0.5862 (0.2946)	96.79 (21.45)	14.32 (2.08)	1.44 (0.74)	11.6	6.2	2.4
EML-oMod	45.00 (17.06)	6.14 (1.05)	0.5353 (0.3476)	114.27 (46.54)	15.43 (3.00)	1.31 (0.86)	9.3	6.7	4.3
EML-oExt	71.89 (8.92)	7.04 (0.93)	0.1749 (0.0917)	182.08 (31.61)	17.44 (1.72)	0.43 (0.22)	2.3	10.0	7.1

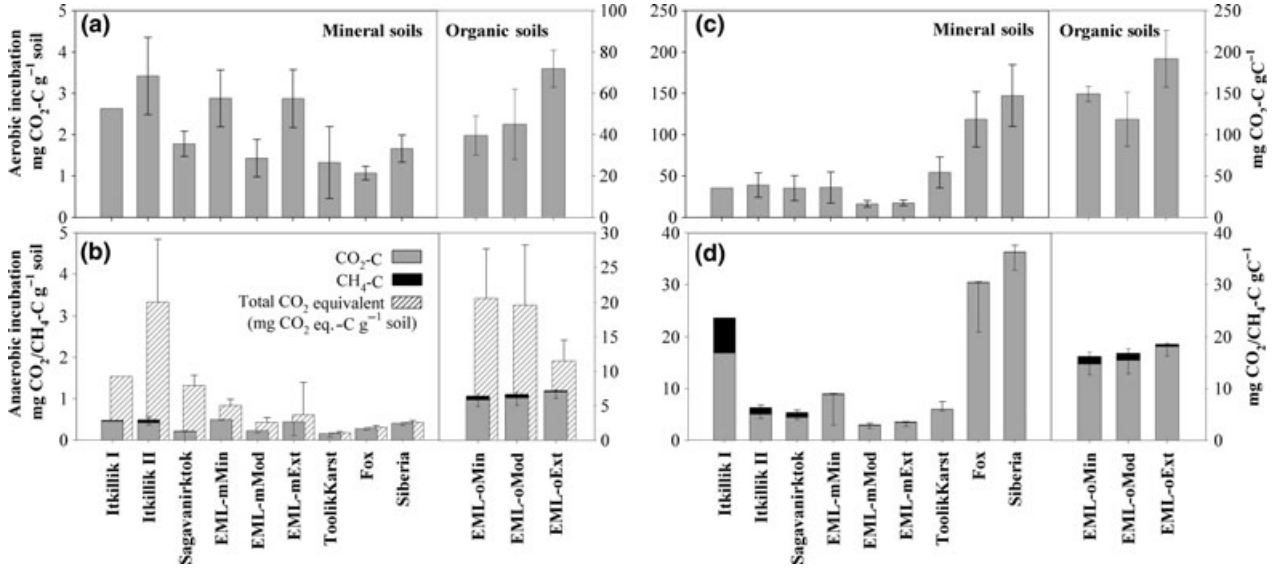

Fig. 3 Cumulative C *per gram of dry soil* release via CO_2 under aerobic conditions (a) and by CO_2 and CH_4 under anaerobic conditions and CO_2 equivalent effect on climate from C release under anaerobic conditions (b) over 500 days of incubation at 15 °C. Error bars indicate standard errors. Note the difference in *y*-axis between organic and mineral soils. Cumulative C release *per gram of soil C* by CO_2 under aerobic conditions (c), and by CO_2 and CH_4 under anaerobic conditions (d) over 500 days of incubation at 15 °C. Downwards standard error bars in panel (b) and (d) are for CO_2-C production, whereas upwards error bars are for CH_4-C production.

the lowest relative climate forcing were mineral soils from the North Slope of Alaska as a result of high CH_4 production relative to CO_2 under anaerobic conditions. In these soils, CH_4 release was exponentially correlated to relative climate forcing, whereas CO_2 release under aerobic and anaerobic conditions were not correlated to relative climate forcing (Data S1 and S2). Soils with the highest relative climate forcing were the ToolikKarst soil and organic layers from EML gradient sites due to extremely low production of both CO_2 and CH_4 in ToolikKarst soil and high CO_2 and low CH_4 production in EML gradient sites under anaerobic conditions.

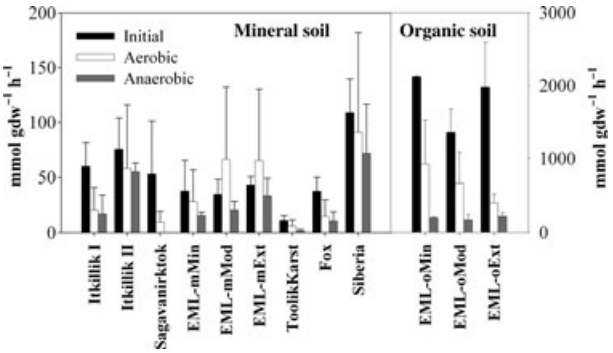

Fig. 4 Initial soil β-glucosidase activity per gram of dry soil and after 125 days of incubation at 15 °C under aerobic and anaerobic conditions. Error bars indicate standard error.

Soil β-glucosidase activity

Soil β-glucosidase activity decreased in aerobic and anaerobic incubations over 125 days, corresponding with the observed decrease in respiration through time. Initial soil β-glucosidase activity ranged from 0.035 to 2.12 mmol g^{-1} h^{-1} (Fig. 4), and was over 30 times greater in organic soils than in mineral soils. After incubation, however, the ratio between the rate of β-glucosidase activity for both under organic soils and mineral soils decreased to 15 and 8 under aerobic conditions and anaerobic conditions respectively. The range of soil β-glucosidase activity in mineral soils was 0.035–0.11 mmol g^{-1} h^{-1}, and spanned 1.36–2.12 mmol g^{-1} h^{-1} in organic soils. After 125 days of incubation under aerobic and anaerobic conditions, mean soil β-glucosidase activity was significantly lower than initial activity in both aerobic ($P = 0.013$) and anaerobic conditions ($P = 0.002$). In all cases, soil β-glucosidase activity was lower in the soils incubated under anaerobic conditions ($P = 0.029$) than that under aerobic conditions, but this did not show any clear patterns between mineral and organic soils.

Correlation between C release and soil characteristics

Cumulative C released per gram of dry soil over 500 days of incubation, expressed in CO_2 equivalents for both the anaerobic and aerobic incubations, was

positively correlated to %C, %N and C to N ratios of soil and negatively correlated to soil pH ($P < 0.001$ for all regressions; Data S3), confirming the quantitative aspects of soil C and N in controlling permafrost C release. The variability in relative climate forcing was not statistically correlated to any of the substrate quality measured in our study (regression not shown). Correlations of cumulative C released per gram of soil C and soil%C, %N and pH (Fig. 5) were not as apparent than that shown with C released per gram of dry soil (Data S3); there seem to be U-shape correlation between C release and %C in soil and soil pH suggesting that soil quality has some important defining parameters not captured by bulk soil characteristic measurements.

Isotopic signatures of soil and gases produced during the incubation

The $\delta^{13}C$ signatures in bulk soils were statistically not different in mineral and organic soils, but ranged from -24% to $-30‰$ across sites reflecting the imprint of the C_3 plant photosynthetic pathway combined with decomposition processes (Table 3). The $\delta^{15}N$ signatures showed difference in mineral and organic soils and were correlated to the approximate depth of the soils ($P = 0.002$, $r = 0.787$). The mineral soils were more enriched in $\delta^{15}N$ (0.42–2.86‰) than the organic soils (−0.68–0.04‰), and soil $\delta^{15}N$ was negatively correlated to soil%N ($P = 0.023$, Table 1). The $\delta^{13}C$ and $\delta^{15}N$ bi-plot showed clear cluster of soil types (Data S4) and were multicorrelated to the depth of soils ($P < 0.001$, $r = 0.810$).

Most of the $\delta^{13}C$-CO_2 from aerobic respiration was significantly enriched relative to the $\delta^{13}C$ signatures of bulk soil material (Table 3). Among the samples, $\delta^{13}C$-CO_2 from aerobic respiration ranged from -27.56 to $-20.39‰$. On the other hand, $\delta^{13}C$-CO_2 and $\delta^{13}C$-CH_4 from anaerobic respiration showed differences within the samples reflecting the importance of CH_4 production overall in addition to CH_4 production pathway in our incubation study. The range of $\delta^{13}C$-CO_2 in anaerobic incubation was from -23.45 to $-11.01‰$, and the range of $\delta^{13}C$-CH_4 in anaerobic incubation was from -78.62 to $-44.57‰$. Enriched $\delta^{13}C$-CO_2 over the level of atmosphere in some samples was not a result of mixing with atmospheric CO_2, but presumably due to CH_4 production. The apparent fractionation factors (α) indicated that there was a shift in CH_4 production pathway from organic ($\alpha > 1.050$, CO_2 reduction) to mineral ($\alpha < 1.050$, acetate decarboxylation) soils collected from the three EML sites. All mineral soils showed $1.030 < \alpha < 1.050$, which indicates that the dominant CH_4 production pathway was acetate decarboxylation (Fig. 6).

The $\Delta^{14}CO_2$ values of respired CO_2 in the aerobic incubations ranged from -390 to $-207‰$ in mineral soils (Table 3), which represent a radiocarbon age of 1800–3910 years before present, although this is likely to be derived from soil C representing a mixture of ages. This radiocarbon age was positively correlated to the approximate depth of soil samples used in this incubation study ($P = 0.103$, $r = 0.725$). Respired CO_2 in the organic surface soil layer that we sampled for radiocarbon showed a positive value, reflecting the influence

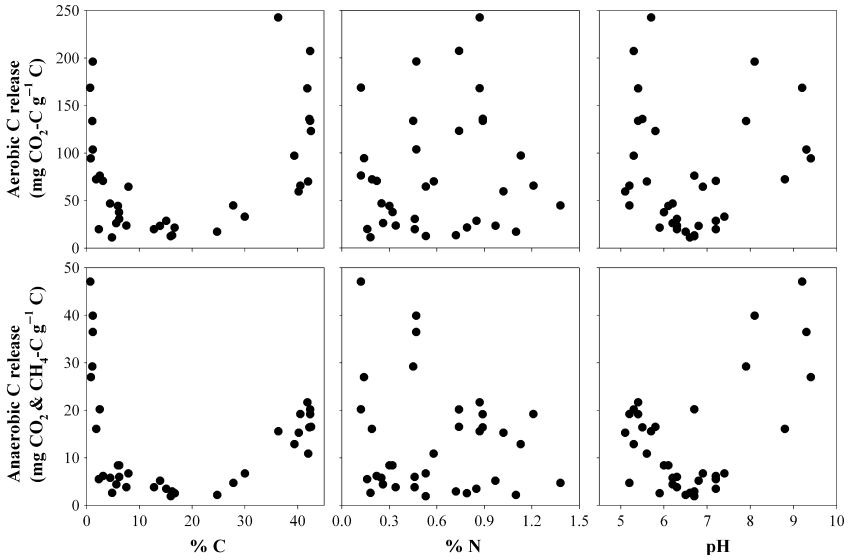

Fig. 5 The correlation among soil %C, %N and pH and cumulative C release per gram of soil C in permafrost soils after 500 days of incubation at 15 °C under aerobic and anaerobic conditions.

Table 3 Stable isotopic signatures of C and N in permafrost soils used in the incubation. Stable isotopic signatures of C from respired CO_2 and CH_4 and radioactive carbon signatures of respired CO_2 from aerobic incubations. The values are mean of three samples, and values in parenthesis are standard errors. The respired CO_2 and CH_4 for $\delta^{13}C$ and $\Delta^{14}C$ analyses were trapped at day 365 from the beginning of soil incubation

	Soil		Aerobic	Anaerobic		
Sites	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}CO_2$ (‰)	$\delta^{13}CO_2$ (‰)	$\delta^{13}CH_4$ (‰)	$\Delta^{14}C$
Itkillik I	−26.28 (0.03)	1.90 (0.07)	−22.80 (2.41)	−11.01 (2.13)	−44.57 (5.03)	−390
Itkillik II	−26.27 (1.03)	0.79 (0.11)	−22.73 (1.15)	−15.81 (1.90)	−54.80 (4.91)	−235
Sagavanirktok	−29.52 (2.42)	0.42 (0.37)	−25.82 (0.67)	−16.71 (1.39)	−47.75 (3.40)	−207
EML-mMin	−26.71 (0.16)	0.76 (0.09)	−24.17 (0.61)	−16.03 (0.61)	−48.31 (3.70)	−381
EML-mMod	−27.59 (0.49)	0.62 (0.14)	−26.18 (0.21)	−23.41 (0.50)	−58.29 (1.48)	−300
EML-mExt	−26.96 (0.12)	0.84 (0.06)	−26.27 (0.17)	−23.12 (0.20)	−56.16 (−)	−368
ToolikKarst	−25.40 (0.19)	1.13 (0.45)	–	−7.52 (0.81)	−60.42 (9.65)	–
Fox	−25.87 (0.55)	2.19 (1.04)	−22.82 (−)	−22.26 (0.39)	−55.07 (−)	–
Siberia	−24.36 (0.33)	2.86 (0.04)	−24.48 (1.90)	−23.45 (0.43)	−51.42 (−)	–
EML-oMin	−25.60 (0.70)	0.04 (0.64)	−24.61 (0.91)	−17.59 (1.98)	−71.81 (10.91)	–
EML-oMod	−26.40 (0.21)	0.02 (0.31)	−24.78 (1.01)	−13.97 (4.56)	−78.62 (5.46)	242
EML-oExt	−26.81 (0.68)	−0.68 (0.26)	−26.69 (0.44)	−20.52 (1.40)	−65.14 (4.32)	–

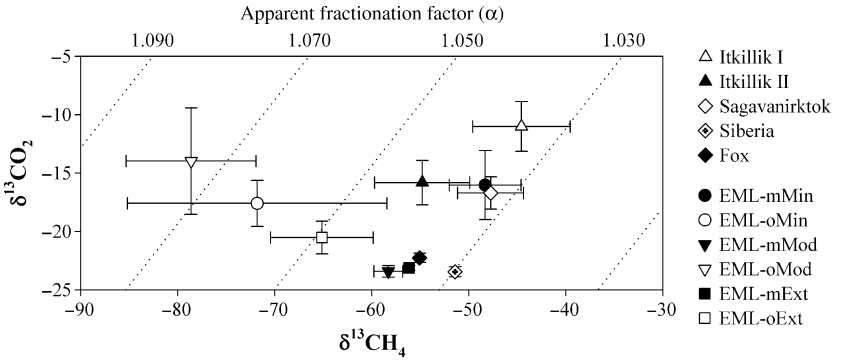

Fig. 6 The relationship between $\delta^{13}C$-CH_4 and $\delta^{13}C$-CO_2 in respiration under anaerobic conditions. The dotted line represent apparent fractionation factor (α); the dominant pathway of CH_4 production $\alpha > 1.050$ is considered CO_2 reduction and $1.030 < \alpha < 1.050$ is considered acetate decarboxylation. Open symbols represent organic layers collected at 5–15 cm depth relative to the moss/soil surface.

of modern atomic weapons testing. It is important to note that the CO_2 trapped for ^{14}C analysis was conducted after 1 year of permafrost soil incubation and the most labile soil C had already been released, but does indicate that old C is available for microbial decomposition at that time in the incubation.

Discussion

Our measurements of permafrost C release under aerobic and anaerobic conditions over 500 days showed that the rate of total C release (quantity of C) was approximately six times greater under aerobic conditions than anaerobic conditions regardless of soil type (Table 2). Supporting this, β-glucosidase activity was twice greater under aerobic conditions compared with anaerobic conditions (Fig. 4). In general, higher soil enzyme activity indicates faster breakdown of C bonds, and suppressed enzyme activity results in lower rate of C release. Lower enzyme activity in an anaerobic incubation compared with aerobic incubation in our study corresponds with lower rate of C release under anaerobic conditions. Variability in relative climate forcing compared with total C release was due to variability in CH_4 production with its high GWP. The disparity between total C release and relative climate forcing implies that the effects on climate from anaerobic C release were greater than simple quantitative C loss.

The patterns of aerobic and anaerobic C release were highly correlated (Data S1), suggesting that substrate quality of the soil samples influenced both aerobic and anaerobic decomposition similarly. Relative climate forcing was most correlated to variability in CH_4 production (Data S1 and S2), indicating that the form of C

release is as important as the quantity of C release in understanding the potential effects on climate from total C release. However, even with high GWP of CH_4, the potential effects on climate from permafrost C release were greater under aerobic conditions because of the offsetting factor of lower overall C release quantity under anaerobic conditions. Therefore, our results suggest that it is crucial to understand the balance between CO_2 and CH_4 release to better predict effects on present and future climate change under dynamic permafrost landscape and soil conditions that influence the rate and quality of greenhouse gas release.

On a per gram of soil basis, the magnitude of C release was over 20 times greater in organic soils than mineral soils (Fig. 3a, b). Typically, organic matter mineralizes at a much faster rate in organic soils than in mineral soils not only due to larger quantity of labile C available in organic soils but also due to more diverse microbial community present in organic soils than mineral soils (Schimel & Chapin, 2006). Dominant microbial community was shown to be different in active layer and deep permafrost soil, but this may reflect a lower diversity of organic substrates in the deeper soil (Waldrop *et al*., 2010). On a per grams C basis, however, C release in organic and mineral soils were statistically not different under aerobic and anaerobic conditions (Fig. 3c, d). Faster C release per gram C shown in some of the soils with lowest C content (i.e. Fox and Siberia) supports previous studies that suggest deep permafrost C may be very labile especially in Yedoma soils, where surface accumulation of mineral soil trapped relatively fresh organic matter in syngenetic permafrost (Dutta *et al*., 2006; Zimov *et al*., 2006; Waldrop *et al*., 2010).

The role of soil C and N in organic matter decomposition is well understood; organic matter decomposes faster when larger quantity of C and N are labile and the quality of N (represented as C to N ratio) is higher (Aerts, 1997). Therefore, the rate of C release per gram of dry soil should be linearly correlated to %C (Data S3), but correcting the rate of C release per gram of soil C removes the bias of C quantity embedded in soil C. The U-shape correlation between cumulative C release per gram of soil C and soil%C (Fig. 5) shown in our study suggest that deep permafrost soils are very labile to microorganisms to utilize even though there is less C available and they may have distinct characteristics compared with other mineral soils within the surface 1 m. This may result from the differences in original permafrost C preservation between loess and alluvial deposited Yedoma soils (Zimov *et al*., 2006) and surface permafrost soils accumulated as a result cryoturbation.

Although the correlation between the rate of permafrost C release per gram of soil and soil%C, %N and pH was apparent (Data S3), the correlation between C release per gram C and the same soil characteristics seemed less clear (Fig. 5). The role of soil pH seems more complex: soil pH and the rate of C release or the rate of organic matter decomposition has shown a positive relationship (Chapin *et al*., 2002; Fierer & Jackson, 2006), negative relationship (Bridgham *et al*., 1998), U-shape relationship (Ste-Marie & Pare, 1999) and no-relationship (Cotrufo *et al*., 1994). Several studies have shown that soil pH affects the rate of CH_4 production (Goodwin & Zeikus, 1987), but less is known about the controls on the rate of organic matter decomposition under anaerobic conditions and the balance between CO_2 and CH_4 production. In addition, soil pH alters soil microbial community (Lauber *et al*., 2009). In our study, majority of the lower pH soils belonged to organic soil layer, and we were not able to clearly understand the effects of soil pH either on the rate of C release, nor the quality of C release from suite of permafrost soils we incubated.

In contrast to our expectations, soil substrate quality as measured did not explain the variability in CH_4 production (Data S3), nor did it explain relative climate forcing (graph not shown). We investigated variability in the pathway of CH_4 production, to better understand its production characteristics. The two major pathways of methanongenesis are acetate decarboxylation and CO_2 reduction. The ratio between δ^{13}C-CH_4 and δ^{13}C-CO_2 (Fig. 6) suggest that CO_2 reduction was relatively dominant in organic soils, and acetate decarboxylation was dominant in mineral soils. Globally, the dominant pathway of CH_4 production is generally by acetate decarboxylation (Lovley & Klug, 1986; Conrad, 2009). However, CO_2 reduction is known to be the major pathway of CH_4 production in northern peatland environments (Hornibrook *et al*., 1997; Horn *et al*., 2003), with the exception of upper layers of nutrient rich fens (Kelley *et al*., 1992; Chasar *et al*., 2000) and Siberian mires (Kotsyurbenko *et al*., 2004), where acetate decarboxylation is the dominant mechanism. Unfortunately, illumination of the dominant pathway of CH_4 production still did not explain the variability in relative climate forcing from our study. It is important to note that our observations of δ^{13}C-CO_2 and δ^{13}C-CH_4 were taken at exactly 1 year after the starting of the incubation. As the jars have not been opened for the duration of 1 year incubation for the anaerobic conditions, our results from mixture of full year C release may be different from the observations taken during the early stages of soil incubation or field measurements that emphasizes C release from the labile pool. We speculate that the rate of CH_4 production may be influenced by availability of electron acceptors than the common substrate qualities or

dominant mechanism of CH_4 production such as Fe (III) (Dubinsky *et al*., 2010).

The CO_2 and CH_4 production estimated from our study represented the potential C release and climate effects from permafrost soils under aerobic and anaerobic conditions. However, our laboratory observations do not project a complete and realistic balance between uptake and release of different greenhouse gases in permafrost zone on a landscape scale. A proportion of CH_4 may be consumed by methanotrophs in the soil surface and become oxidized even before it mixes with atmosphere (Raghoebarsing *et al*., 2005; Kip *et al*., 2010). Spotty CH_4 production including CH_4 ebullition form thermokarst lakes (Walter *et al*., 2006) can only be observed on a large scale, but they can be a significant source of greenhouse gas production, although our incubations should have measured total CH_4 release due to complete flushing while sampling (Walter *et al*., 2007). Lastly, it is important to indicate that there may be soil CH_4 uptake under aerobic conditions (Nesbit & Breitenbeck, 1992; Le Mer & Roger, 2001) that would reduce warming effects on climate.

We addressed the overall question of whether thawing permafrost C is likely to have a greater influence on climate if it decomposes in an aerobic environment or an anaerobic environment. In summary, our study showed that permafrost C released in relatively aerobic upland systems is likely to result in greater effects on climate compared with permafrost C released in an anaerobic wetland environment, despite the release of CH_4 that occurs from anaerobic conditions. Although numerous studies have shown permafrost C release, we show additional effects of greenhouse gas emissions on further climate change under aerobic and anaerobic conditions that may be created as a result of permafrost thaw and thermokarst development. Furthermore, our results will help parameterize and validate ecosystem and climate models of C release from permafrost thaw and soil inundation, which creates a positive feedback to further climate change via greenhouse gas emissions.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. Correlation matrix for C release over 500 days of permafrost incubation at 15 °C under aerobic and anaerobic conditions per gram of dry soil. Each panel indicate total CO_2-C release under aerobic conditions (aeroCO_2), total CO_2-C release under anaerobic conditions (anaeroCO_2), total CH_4-C release under anaerobic conditions (anaeroCH_4), total C release under anaerobic conditions (anaerototal), and relative climate forcing (RCF). The correlation coefficients are indicated in the table.

Data S2. Correlation matrix for C release over 500 days of permafrost incubation at 15 °C under aerobic and anaerobic conditions per gram of soil C. Each panel indicate total CO_2-C release under aerobic conditions (aeroCO_2), total CO_2-C release under anaerobic conditions (anaeroCO_2), total CH_4-C release under anaerobic conditions (anaeroCH_4), total C release under anaerobic conditions (anaerototal), and relative climate forcing (RCF). The correlation coefficients are indicated in the table.

Data S3. The relationship between %C, %N, C to N ratio, and soil pH in soils and CO_2 equivalent climate forcing from C mineralized per soil dry weight after 538 days of incubation at 15 °C under aerobic and anaerobic conditions. The correlations shown here were all statistically significant ($P < 0.001$).

Data S4. The patterns of soil $\delta^{13}C$ and $\delta^{15}N$ used in the incubation study (A) and their distribution with approximate depth of soil profile (B).

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