Global Change Biology

Global Change Biology (2013) **19**, 1160–1172, doi: 10.1111/gcb.12116

Predicting long-term carbon mineralization and trace gas production from thawing permafrost of Northeast Siberia

CHRISTIAN KNOBLAUCH*, CHRISTIAN BEER†, ALEXANDER SOSNIN‡, DIRK WAGNER§ and EVA-MARIA PFEIFFER*

*University of Hamburg, Institute of Soil Science, KlimaCampus, Allende-Platz 2, 20146, Hamburg, Germany, †Max Planck Institute for Biogeochemistry, Hans-Knöll-Str. 10, 07745, Jena, Germany, ‡Faculty of Geography and Geoecology, University of St. Petersburg, 33, 10th line, 199178, St. Petersburg, Russia, §Helmholtz Centre Potsdam, GFZ German Research Centre for Geosciences, Section 4.5 Geomicrobiology, Telegrafenberg, 14473, Potsdam, Germany

Abstract

The currently observed Arctic warming will increase permafrost degradation followed by mineralization of formerly frozen organic matter to carbon dioxide (CO_2) and methane (CH_4). Despite increasing awareness of permafrost carbon vulnerability, the potential long-term formation of trace gases from thawing permafrost remains unclear. The objective of the current study is to quantify the potential long-term release of trace gases from permafrost organic matter. Therefore, Holocene and Pleistocene permafrost deposits were sampled in the Lena River Delta, Northeast Siberia. The sampled permafrost contained between 0.6% and 12.4% organic carbon. CO_2 and CH_4 production was measured for 1200 days in aerobic and anaerobic incubations at 4 °C. The derived fluxes were used to estimate parameters of a two pool carbon degradation model. Total CO_2 production was similar in Holocene permafrost (1.3 ± 0.8 mg CO_2-C gdw^{-1} aerobically, 0.25 ± 0.13 mg CO_2-C gdw^{-1} anaerobically) as in 34 000–42 000-year-old Pleistocene permafrost (1.6 ± 1.2 mg CO_2-C gdw^{-1} aerobically, 0.26 ± 0.10 mg CO_2-C gdw^{-1} anaerobically). The main predictor for carbon mineralization was the content of organic matter. Anaerobic conditions strongly reduced carbon mineralization since only 25% of aerobically mineralized carbon was released as CO_2 and CH_4 in the absence of oxygen. CH_4 production was low or absent in most of the Pleistocene permafrost and always started after a significant delay. After 1200 days on average 3.1% of initial carbon was mineralized to CO_2 under aerobic conditions while without oxygen 0.55% were released as CO_2 and 0.28% as CH_4. The calibrated carbon degradation model predicted cumulative CO_2 production over a period of 100 years accounting for 15.1% (aerobic) and 1.8% (anaerobic) of initial organic carbon, which is significantly less than recent estimates. The multiyear time series from the incubation experiments helps to more reliably constrain projections of future trace gas fluxes from thawing permafrost landscapes.

Keywords: carbon dioxide, decomposition model, Lena River Delta, methane, organic matter, Siberia, tundra

Received 5 October 2012 and accepted 14 November 2012

Introduction

Permafrost-affected landscapes cover about one quarter of the land surface of the northern hemisphere (Zhang *et al*., 1999). In these landscapes, the permafrost, i.e., earth material which stays perennially frozen, is covered by a thin soil layer (active layer) which thaws during summer and facilitates vegetation growth. According to recent estimates, 352 Pg of organic carbon is stored in the uppermost 1 m of permafrost landscapes and 818 Pg down to a depth of 3 m (Zimov *et al*., 2006a; Tarnocai *et al*., 2009). Comparing these values with the 1500 Pg organic carbon stored in the uppermost 1 m of terrestrial soils (Jobbágy & Jackson, 2000) illustrates the global importance of organic carbon in permafrost.

The effects of current and future climate warming will be stronger in the Arctic than the global average (Trenberth *et al*., 2007). In response to Arctic warming the area of permafrost landscapes will decrease and the thickness of the active layer will increase (Anisimov, 2007; Schaefer *et al*., 2011). The organic carbon that has been preserved frozen in permafrost will then become accessible to microbial degradation resulting in the formation of carbon dioxide (CO_2) and methane (CH_4) (Wagner *et al*., 2007; Lee *et al*., 2012). Hence, permafrost thawing may provoke a positive feedback to climate warming by causing increased greenhouse gas emissions. Recently, a positive feedback of methanogenic communities to warmer periods in the Late Pleistocene and Holocene was shown for the Lena River Delta (Bischoff *et al*., in press).

Correspondence: Christian Knoblauch, tel. +49 (0) 42838 2277, fax +49 (0) 42838 2024, e-mail: christian.knoblauch@uni-hamburg.de

Large organic carbon stocks in tundra ecosystems imply that the Arctic has been a sink of atmospheric CO_2 over long periods of time. Global warming has the potential to change permafrost landscapes from a carbon sink into a carbon source but the response of the Arctic carbon cycle to current changes in permafrost areas is still highly uncertain (McGuire *et al*., 2009). The strong interannual variability of carbon fluxes in Arctic ecosystems (Oechel *et al*., 2000; Groendahl *et al*., 2007; Schuur *et al*., 2009) and the lack of sufficient studies on multiannual greenhouse gas budgets still prevent a clear picture of the current source-sink term of the Arctic tundra. Recent studies indicate an increase in CO_2 release from permafrost-affected landscapes, e.g., due to deeper permafrost thawing (Schuur *et al*., 2009). However, warming of arctic ecosystems may also increase the uptake of atmospheric CO_2 due to a longer growing season (Aurela *et al*., 2004). Beside the consequences of permafrost warming on soil temperature, its effect on soil hydrology will be of imminent importance because increasing soil moisture favors the formation of anaerobic soil conditions and thereby the production of CH_4 (Christensen *et al*., 2004) a greenhouse gas about 25 times more potent than CO_2 on a 100-year time horizon (Forster *et al*., 2007). Since permafrost impedes soil drainage, water saturated soils with anaerobic conditions are widespread and contribute to a substantial source of atmospheric CH_4 (Wille *et al*., 2008).

The sources of organic matter in the permafrost are fossil plant remains that have not been mineralized in the active layer. In contrast, the overlying active layer soils receive fresh organic matter from the current vegetation, which in the tundra are mainly mosses, lichens, grasses, and dwarf shrubs. Hence, the highest carbon concentrations are generally found in surface soils but substantial amounts are also preserved in the widespread Late Pleistocene Ice Complex or Yedoma permafrost deposits of northeastern Siberia, Alaska and northwestern Canada. These 12–80-kyr-old deposits, which are several tens of meters thick, contain on average 1.2–4.8% organic carbon deriving from plant debris and grass roots of the tundra steppe (Zimov *et al*., 2006a; Schirrmeister *et al*., 2011b).

To improve projections on how much and how fast organic carbon from permafrost can be released as trace gases from the northern tundra, it is necessary to better understand the degradability of organic matter in the different permafrost deposits that are projected to thaw in the near future. Data on permafrost organic matter degradability, i.e., how fast and to what extent permafrost carbon can be mineralized to CO_2 and CH_4, are scarce and limited to studies on permafrost in the northern Kolyma region in northeastern Siberia (Dutta *et al*., 2006; Zimov *et al*., 2006a; Lee *et al*., 2012), and continuous and discontinuous permafrost in Alaska (Waldrop *et al*., 2010; Lee *et al*., 2012). Hence, current permafrost–climate feedback models tend to include trace gas production rates in thawing permafrost as driven only from chemical and physical soil properties including soil carbon stocks (Khvorostyanov *et al*., 2008; Koven *et al*., 2011), although recent work has also considered a first-order estimate of aerobic permafrost carbon degradation (Schaefer *et al*., 2011; Schneider von Deimling *et al*., 2012).

The current study aims to improve current estimates of permafrost carbon vulnerability by (i) presenting multiyear measurements of aerobic CO_2 and anaerobic CO_2 and CH_4 production from Holocene and Pleistocene permafrost of the northeast Siberian Lena Delta and (ii) by fitting parameters of a two pool carbon degradation model to these measurements and simulating the long-term CO_2 release from thawing permafrost over a period of 100 years. In addition, we investigated the importance of multiyear incubation measurements for estimating model parameters.

Materials and methods

Sampling sites and sample collection

Samples were collected from Holocene and Late Pleistocene permafrost sediments of the Lena River Delta, Northeast Siberia (73°N, 126°E), which is located in the zone of continuous permafrost. The climate of the southern Lena River Delta is characterized by a low mean annual air temperature (−14.7 °C) and a mean annual precipitation of about 190 mm. Every year, a shallow surface soil layer (active layer) thaws above the permafrost sediments supporting microbial carbon mineralization of unfrozen organic matter for about 4 months per year (Boike *et al*., 2008). However, we did not sample active layer soils but only permafrost sediments below that seasonal thaw layer. The vegetation of the sampling area is dominated by dwarf shrubs, hydrophytes, and mosses (Kutzbach *et al*., 2004). The Lena River Delta can be divided into different geomorphological units. The oldest terrace was formed in the middle to late Pleistocene, consists of fine-grained silty sediments with a high content of segregated ice (Ice Complex) and is covered by Holocene deposits (Wetterich *et al*., 2008). The eastern terrace of the Lena River Delta is of middle Holocene age with several modern floodplains, representing the young, active part of the delta. The surface of the sampling sites is characterized by a microrelief of low centered ice-wedge polygons.

The first study site on the island Kurungnakh (N 72°20, E 126°17) is part of the Pleistocene terrace. Permafrost samples were collected in summer 2002 by drilling a core from the permafrost surface to a depth of 25 m into silty, ice rich deposits at the shore of the Lena River. The unfrozen active layer soil was removed prior to drilling. Additional deep permafrost samples were collected in summer 2008 from the same outcrop in direct vicinity of the original drilling location. These samples were collected at different depths from the frozen upright walls of the exposed outcrop. Before sampling, unfrozen material and about 5 cm of frozen surface material was removed to ensure that only permanently frozen material was sampled. Samples were taken by driving a steel corer (5.6 cm diameter) horizontally into the exposed outcrop. The approximate sampling depth of the outcrop samples was calculated by their ^{14}C-age and the linear fit between organic carbon age and sample depth in the permafrost core. Two different regression lines were applied for samples between 1 and 5 m and between 5 and 24 m (Fig. 1e).

A second set of permafrost samples was collected in summer 2007 on the eastern, Holocene terrace on the island Samoylov (N 72°22, E 126°29). There, a permafrost core was drilled from the permafrost surface into a depth of 4.5 m. Permafrost cores (5.5 cm diameter) were collected both on Kurungnakh and Samoylov with a portable gasoline powered permafrost corer (TKB 15; Kurth Bohrtechnik, Nordhausen, Germany) without the potentially contaminating influence of a drilling fluid. All samples stayed frozen during sampling and were stored frozen at about −8 °C at the Research Station on Samoylov. At the end of the expeditions, samples were transported frozen to Germany and stored frozen until further processing.

Quantification of CO_2 and CH_4 production

Multiyear incubations were conducted over a period of 1200 days in Germany with permafrost sediments from Kurungnakh and Samoylov. To do so, the frozen permafrost cores were subsampled at different depths. All subsamples were thawed (~2 °C) and six aliquots of about 20 g were weighed into 120 ml glass bottles, which were subsequently sealed by rubber stoppers and not opened during the experiment to keep moisture constant. Three aliquots were incubated under aerobic and three under anaerobic conditions in the dark at a constant temperature of 4 °C. For anaerobic incubations, 5 ml of anaerobic distilled water was added and the headspace gas was exchanged by pure nitrogen. Aerobic incubations were carried out with an atmosphere of ambient air. CO_2 and CH_4 concentrations were measured in the aerobic incubations during the initial 200 days of incubation about every week and every other week in the anaerobic incubations. After that period, gas concentrations were analyzed in both aerobic and anaerobic incubations about every other month. The headspace of aerobic incubations was flushed repeatedly with synthetic air (20% O_2, 80% N_2) if the CO_2 concentrations reached values above about 3%.

The amount of CO_2 and CH_4 in the incubation flasks was calculated from the gas concentrations in the headspace,

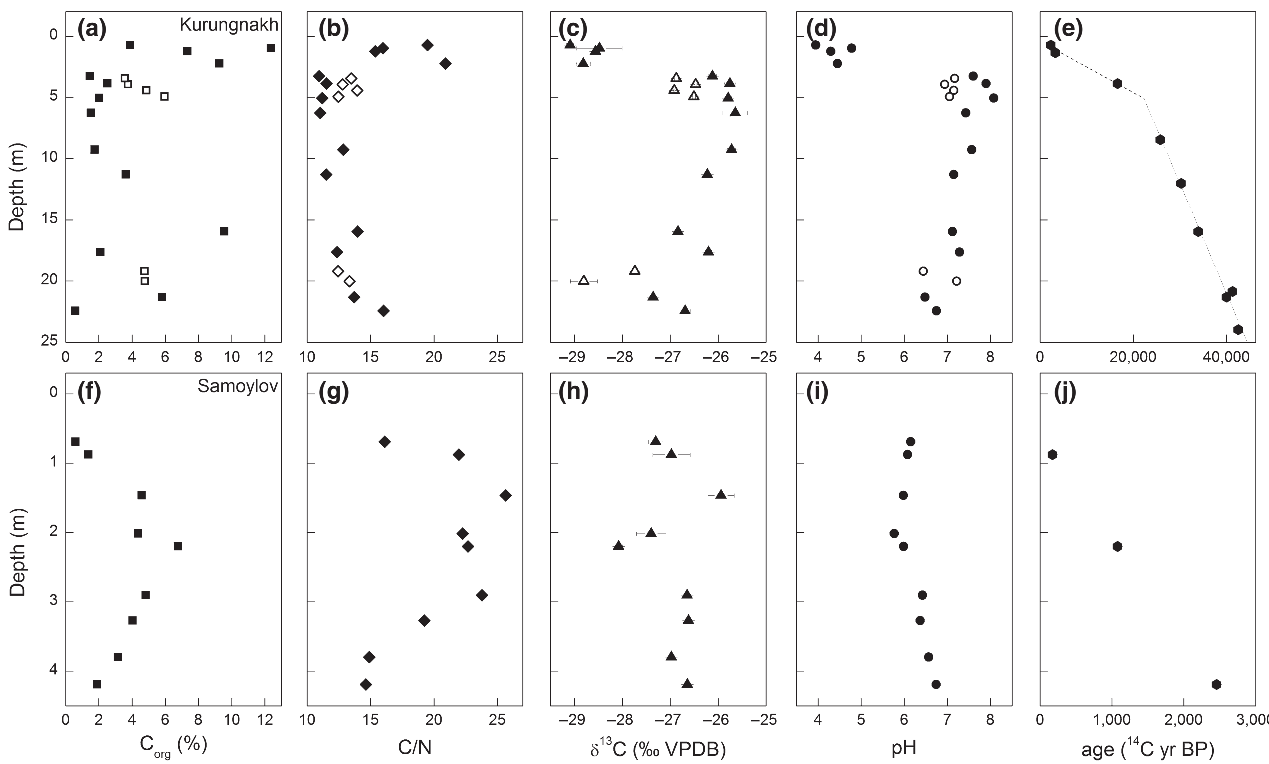

Fig. 1 Vertical profiles of organic carbon (a, f), C/N ratios (b, g), δ^{13}C values of organic carbon (c, h), pH (d, i), and ^{14}C age (e, j) of permafrost deposits from Kurungnakh (a–e) and Samoylov (f–j), Lena River Delta, Northeast Siberia. Closed symbols in panels a–e represent samples taken from a permafrost core, open symbols those from an outcrop in direct vicinity of the coring location (see Materials and Methods). Dashed lines in panel e give the linear regression between sample age and depth in the permafrost core used to calculate the respective depth of the outcrop samples by their ^{14}C-age. Consider different scales for ^{14}C-age in panel (e) and (j).

headspace volume, water content, gas solubility in water, temperature, and pressure using Henry's law. Gas production rates were calculated from a linear fit of CO_2 or CH_4 amount in the bottles using at least four successive measurements and are based on gram dry weight (gdw) of sediment in the incubation bottles. To account for steeply decreasing CO_2 production rates during the incubations, we calculated initial CO_2 production rates from CO_2 production during the first month of incubations and final CO_2 production rates from CO_2 production of the last three (aerobic) to six (anaerobic) months of incubations.

Gas analysis

CH_4 and CO_2 concentrations were determined by gas chromatography (GC 7890; Agilent Technologies, Böblingen, Germany). Gases were separated on a Porapak Q column (1.8 m length, 2 mm ID) and quantified with FID (CH_4) and TCD (CO_2). The inlet, oven and two detector temperatures were 75, 40, 250 °C (FID), and 180 °C (TCD), respectively. Helium served as a carrier gas (27 ml min^{-1}) for the 200 μl of injected sample.

Soil analysis

Total soil carbon and nitrogen were measured with an elemental analyzer (VarioMAX Elementar Analysensysteme GmbH, Hanau, Germany) after the soil had been sieved (<2 mm), milled, and dried at 105 °C. Permafrost pH was measured in a suspension of 10 g of thawed material in 25 ml of distilled water. The ^{14}C-age of selected permafrost samples was measured with an accelerator mass spectrometer at the Leibniz Laboratory in Kiel, Germany and the Poznan Radiocarbon Laboratory, Poland.

The δ^{13}C-values of organic carbon (C_{org}) were measured with an isotope-ratio mass spectrometer (Delta V; Thermo Scientific, Dreieich, Germany) coupled to an elemental analyzer (Flash 2000; Thermo Scientific). Prior to analysis of C_{org}, samples were treated with phosphoric acid (43%, 80 °C for 2 h) to release inorganic carbon. The range of replicate stable carbon isotope measurements was generally less than $\pm 0.2‰$. Values are expressed relative to VPDB (Vienna Pee Dee Belemnite) using the external standards IAEA C6 (-10.8 ‰ vs. VPDB), USGS40 (-26.39 ‰ vs. VPDB), and IVA soil 33802153 (-27.46‰ vs. VPDB).

Decomposition model

The applied carbon decomposition model follows the principles of the Introductory Carbon Balance Model—ICBM (Andrén & Kätterer, 1997). A simple first-order kinetic function represents the change of carbon content in time (dC/dt):

$$\frac{\mathrm{d}c}{\mathrm{d}t} = -k \cdot \mathrm{C}$$

This equation is applied to two carbon pools which differ in the rate constant (k), i.e., how fast the organic matter is decomposed (Meentemeyer, 1978). A fraction h of the degrading material from the fast decomposable pool (labile pool) flows into the slower decomposable pool (stable pool) representing humification (Andrén & Kätterer, 1997). The remaining part ($1-h$) leaves the system as trace gas. The stable pool carbon degradation is assumed to fully contribute to the trace gas flux. The initial condition of total soil organic carbon content is prescribed by the observations. The initial fraction of the labile pool is treated as a parameter. The initial fraction of the stable carbon pool is then calculated as the difference to the total carbon content.

Using a nonlinear least-squares approach with a trust-region-reflective algorithm in MATLAB (MathWorks Inc., Natick, MA, USA), the following model parameters were estimated: decomposition rates, initial labile carbon pool fraction, and the humification coefficient (h). The model was calibrated against the cumulative CO_2 production from each sample and replicate. The turnover time stands for the time when the respective carbon pool is reduced to a fraction of 1/e. A log transformation was applied to estimate the mean turnover time of all samples. Then, the calibrated model was run forward for 100 years for each sample and replicate. In doing so, microbial decomposition processes are assumed to be constantly active during 4 summer months in a year at the temperature of incubation (4 °C) following recent observations at the sampling sites (Boike *et al.*, 2008). All procedures have been repeated with a subset of CO_2 production measurements during the initial 365 days.

Statistics

Statistical tests were conducted using the software SPSS 18 (IBM, New York, NY, USA). The relationship between permafrost characteristics and carbon mineralization was examined using Pearson's correlation. Significances between different normal distributed data sets were analyzed using a Student's *t*-test. In the case of a nonnormal distribution, the data sets were tested using a Mann–Whitney *U*-test.

Results

Permafrost characteristics

The surface permafrost on Kurungnakh, sampled between a depth of 0.7 and 2.2 m, comprised Holocene material with ^{14}C-ages between 2300 and 8700 ^{14}C BP (Fig. 1e). These sediments are underlain by late Pleistocene material with a maximum age of about 42 000 ^{14}C BP at a depth of 22 m (Fig. 1e). The highest organic carbon contents (12.4%, Fig. 1a) were found in the Holocene sediments which were also characterized by a high C/N ratio (~20), low δ^{13}C values (~-29 ‰ VPDB), and a low pH (~4.5) (Fig. 1b–d). The deeper (>3 m) Late Pleistocene sediments can be further divided into two different units. The uppermost material, sampled between 3.3 and 11.3 m developed between 14 000–29 000 BP under a cold and dry climate in the Late Weichselian Stadial

(Sartan). These sediments are underlain by material with a ^{14}C age between 34 000 and 42 000 BP (Fig. 1e) formed in the Late Weichselian Interstadial (Kargin), which was characterized by a relatively warm and wet climate (Wetterich *et al.*, 2008). The Pleistocene sediments differed from the Holocene sediments above in terms of lower C/N ratios (~12), higher $\delta^{13}C$ values (~−26 ‰ VPDB), and higher pH (~7). However, elevated organic carbon concentrations were also found in the Late Weichselian Interstadial sediments at a depth of 16 m (9.6% C) and 21 m (5.8% C).

The permafrost sampled on Samoylov is comprised only Holocene material with a maximum age of 2500 BP (Fig. 1j). The sandy surface sediments were low in organic matter, which increased to a depth of 2.2 m where the content of organic carbon was highest (6.8%, Fig. 1f) and the $\delta^{13}C$ values lowest (−28.1 ‰ VPDB, Fig. 1h). The pH was moderately to slightly acidic and increased only at the bottom of the core to neutral values (Fig. 1i).

Aerobic and anaerobic carbon mineralization rates in permafrost

Mean initial CO_2 production rates in the Holocene surface permafrost of Samoylov (Fig. 2c, d) and Kurungnakh (0.72–2.3 m depth, Fig. 2a, b) did not differ significantly ($P > 0.05$). Maximum rates were measured in the uppermost 2.3 m on Kurungnakh with 9.93 μg CO_2-C gdw^{-1} day^{-1} aerobically and 3.64 μg CO_2-C gdw^{-1} day^{-1} anaerobically. Carbon turnover in the Pleistocene sediments of Kurungnakh below 5 m decreased sharply but rose to a second maximum between 16 and 21 m depth (about 34 000–40 000 BP) with turnover rates similar to those close to the surface (Fig. 2a, b).

CO_2 respiration was highest in all aerobic and anaerobic incubations during the first two months but rapidly decreased toward the end of the experiment (Fig. S1). Under aerobic conditions, final CO_2 production rates (Fig. 2a, c) were 24.1 ± 13.9% of initial rates. Under anaerobic conditions, CO_2 production was below the detection limit in 50% of the samples at the end of the incubation period of 1200 days (Fig. 2b, d). In the remaining anaerobic incubations still showing activity final CO_2 production rates accounted only for 5.6 ± 4.2% of initial rates. The absence of oxygen substantially reduced initial CO_2 production rates in most of the permafrost samples by an average factor of 3.7 ± 2.3. Initial aerobic and anaerobic CO_2 production rates correlated most significantly with the amount of organic carbon and total nitrogen ($R > 0.6$, $P < 0.0001$). Based on bulk carbon content, the initial CO_2 production rates averaged 109.9 ± 73.2 μg CO_2-C g^{-1} C day^{-1} (aerobically) and 33.7 ± 16.7 μg CO_2-C g^{-1} C day^{-1} (anaerobically) (Table S1).

CH_4 production was observed in most of the Holocene and some of the Pleistocene permafrost but initiated only after a significant delay of up to 2 years (Fig. S1). The onset of methanogenesis after a long lag phase was repeatedly associated with rising CO_2 production rates (e.g., Fig. S1-18). Maximum methane production rates in the studied permafrost samples were reached after 200–1200 days (average 963 ± 302 days) and ranged between 0.002 and 1.19 μg CH_4-C gdw^{-1} day^{-1} (Fig. 3).

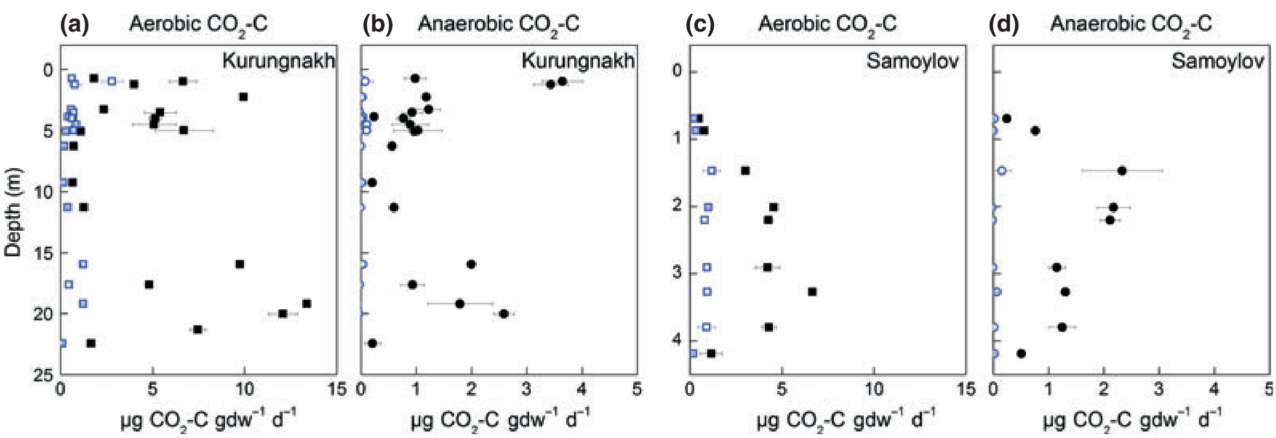

Fig. 2 Initial (closed symbols) and final CO_2 production rates (open symbols) under aerobic (a, c) and anaerobic (b, d) conditions in Holocene and Pleistocene permafrost deposits from Kurungnakh (a, b) and the Holocene permafrost of Samoylov (c, d), Lena River Delta, Northeast Siberia. Initial rates were calculated from CO_2 production during the first month, final from the last 3 (aerobic) to 6 (anaerobic) months of the incubation period of 1200 days and are given per gram dry weight (gdw). Error bars indicate the standard deviation from the average (generally $n = 3$).

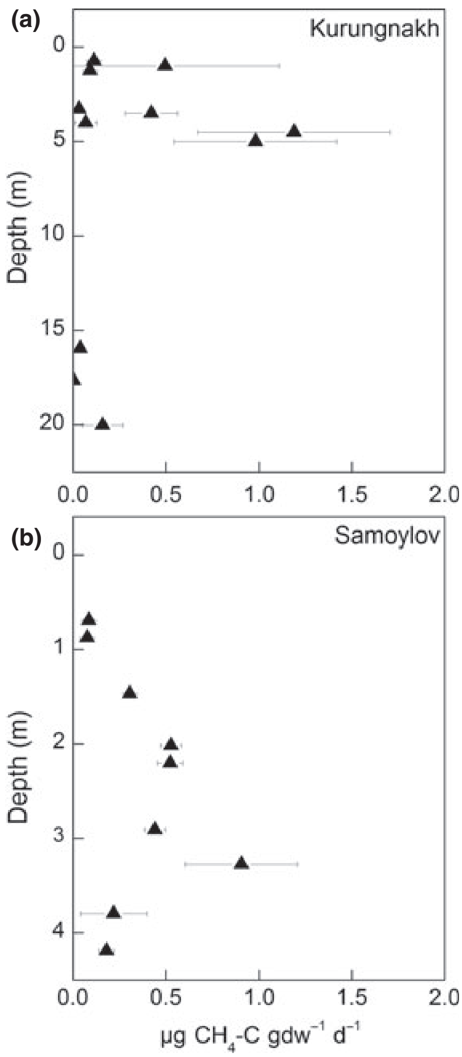

Fig. 3 Maximum CH_4 production rates in permafrost deposits from Kurungnakh (a) and Samoylov (b) calculated per gram dry weight (gdw). Error bars indicate the standard deviation from the average. Maximum rates were detected only after a significant lag time of 200–1200 days (average 963 ± 302 days).

Multiyear carbon mineralization in permafrost

The total amount of carbon mineralized until the end of the incubation period of 1200 days was highly significantly correlated ($R = 0.85$, $P < 0.001$) with initial maximum CO_2 production rates. Permafrost organic matter concentrations were the strongest predictors for aerobic and anaerobic CO_2 production ($R = 0.90$ and 0.75, respectively, $P < 0.001$) followed by the total amount of nitrogen ($R = 0.84$ and 0.58, respectively, $P < 0.001$) and the $\delta^{13}C$ values of organic carbon ($R = -0.60$ and -0.53, respectively, $P < 0.001$). Under aerobic conditions between 0.20 and 3.27 mg C gdw^{-1} (average 1.19 ± 0.82 mg C gdw^{-1}) were mineralized to CO_2 (Fig. 4a, d) but only 0.07–0.51 mg CO_2-C gdw^{-1} (average 0.21 ± 0.12 mg CO_2-C gdw^{-1}) were released in the absence of oxygen (Fig. 4b).

The total amount of carbon mineralized at the end of the incubation period differed in the three investigated permafrost units (Holocene, Late Weichselian Stadial, Late Weichselian Interstadial). CO_2 production in the topmost Holocene permafrost (1.3 ± 0.83 mg CO_2-C gdw^{-1}, aerobic; 0.25 ± 0.13 mg CO_2-C gdw^{-1} anaerobic) was substantially higher than in the underlain deposits (3–11 m) formed in the Late Weichselian Stadial (0.87 ± 0.56 mg CO_2-C gdw^{-1}, aerobic; 0.13 ± 0.06 mg CO_2-C gdw^{-1} anaerobic). But, the older sediments (34 000–42 000 BP) below 15 m that comprise late Weichselian Interstadial permafrost showed again increasing carbon mineralization similar to the topmost Holocene permafrost (1.6 ± 1.2 mg CO_2-C gdw^{-1}, aerobic; 0.26 ± 0.10 mg CO_2-C gdw^{-1} anaerobic) (Fig. 2a, b). However, if total CO_2 production was calculated based on bulk carbon content no differences were found between Holocene and Pleistocene permafrost (Table S1).

In those samples with active methanogenesis, 0.001–0.37 mg CH_4-C gdw^{-1} was produced after 1200 days (average 0.11 ± 0.10 mg CH_4-C gdw^{-1}, Fig. 4c, f). The sum of anaerobic CO_2 and CH_4 production over 1200 days accounted for 25.2 ± 9.2% of the aerobic CO_2 fluxes with an average 70.7 ± 19.7% share of CO_2 among those samples with active methanogenesis.

Until the end of the incubations, between 1.50 and 5.30% (mean 3.11 ± 1.07%) of initial carbon was mineralized to CO_2 under aerobic conditions and 0.27–1.16% (average 0.55 ± 0.23%) under anaerobic conditions. The amount of methane released from those samples with active methanogenesis accounted for 0.005–0.83% (average 0.28 ± 0.23%) of initial carbon.

Modeling carbon turnover from permafrost

The calibrated two pool carbon degradation model agrees well with the observed cumulative CO_2 production both under aerobic and anaerobic conditions. The average deviation between measured cumulative CO_2 production for 1200 days in the individual permafrost samples and the simulated amount (Fig. 5a) was only 1.7 ± 1.6% for aerobic and 3.9 ± 3.4% for anaerobic incubations. However, the outcome of the predicted CO_2 production strongly depended on the length of the incubation time used for fitting the data (Fig. 5a). When using only the data from the first year of the incubations, the average deviation between measured cumulative CO_2 production over 1200 days and the amount predicted by the model increased to 15.5 ± 11.2% and 30.9 ± 21.0% for aerobic and anaerobic incubations,

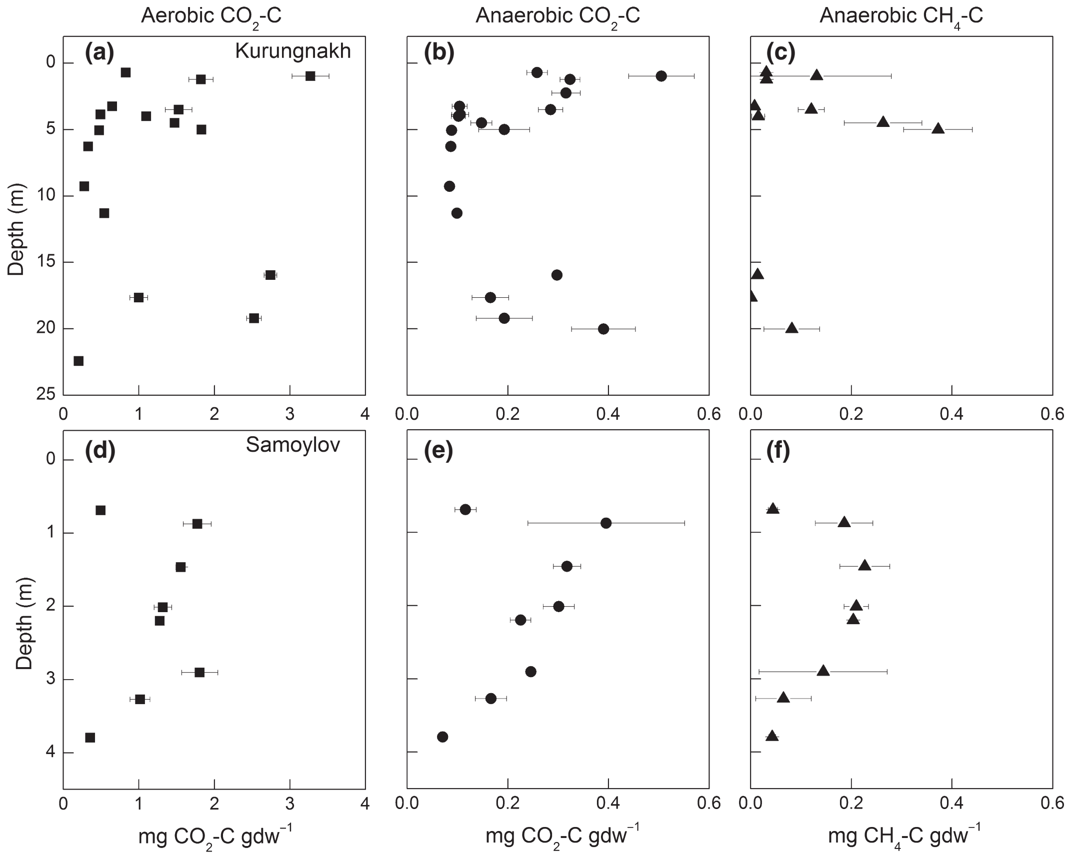

Fig. 4 Total amount of aerobic CO_2 production (a, d), and anaerobic CO_2 (b, e) and CH_4 production (c, f) over the incubation period of 1200 days in permafrost deposits from Kurungnakh (a–c) and Samoylov (d–f), two islands in the Lena River Delta, Northeast Siberia. Data are calculated per gram dry weight (gdw). Error bars indicate the standard deviation from the average (generally n = 3).

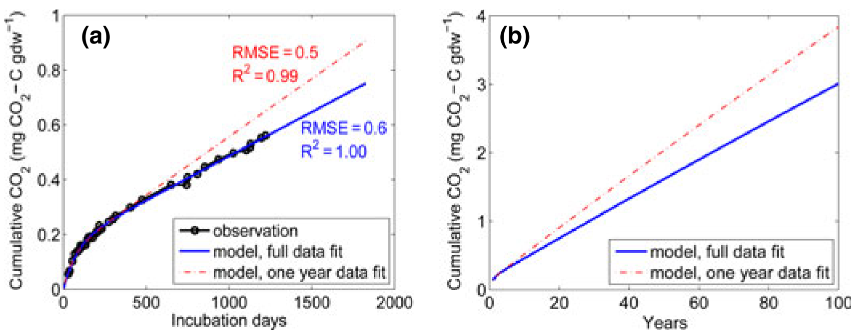

Fig. 5 Typical fit of the two pool carbon degradation model to observed cumulative CO_2 production data (a) and prediction of carbon release over 100 years assuming that organic carbon mineralization takes place only during the thaw period of 4 months per year (b). The aerobic incubation results presented are from a sample collected in 11 m depth (^{14}C age of about 29 000 BP) on Kurungnakh island. Dashed lines give the model fits of the observations from the first year only, the solid line those from the complete data set over 1200 days. CO_2 productions are calculated per gram dry weight (gdw).

respectively. The root mean square error (RMSE) between the measured and the modeled CO_2 production after 1200 days was substantially higher when using only the incubation data for 1 year (RMSE = 151 μg CO_2-C gdw^{-1}) than if using the whole 1200 days data set (RMSE = 14 μg CO_2-C gdw^{-1}). The 100 years projections based on the two data sets (1 year vs. 1200 days) differed by a RMSE of 1817 μg CO_2-C gdw^{-1}.

The projected CO_2 release from the permafrost samples based on the 1200 days incubations were most significantly correlated with the amount of organic carbon ($R = 0.93$, $P < 0.0001$ aerobic, $R = 0.67$, $P < 0.0001$ anaerobic). On average, 5.92 ± 4.35 mg CO_2-C gdw^{-1} are projected to be released in a period of 100 years from the studied permafrost samples under aerobic conditions whereas under anaerobic conditions the model indicated only a production of 0.70 ± 0.51 mg CO_2-C gdw^{-1} (Fig. 6a, b, e, f). These values are equivalent to an average release of $15.10 \pm 4.53\%$ of initial permafrost carbon as CO_2 under aerobic and $1.81 \pm 1.22\%$ under anaerobic conditions (Fig. 6c, d, g, h).

Similar to the total amount of CO_2 produced at the end of the incubation period also the projected release of CO_2 over the 100 years modeling period (Fig. 6) was substantially lower in the permafrost from the Late Weichselian Stadial (4.13 ± 2.46 mg CO_2-C gdw^{-1} aerobically and 0.38 ± 0.23 mg CO_2-C gdw^{-1} anaerobically) than in the Holocene (6.92 ± 4.90 mg CO_2-C gdw^{-1} aerobically and 0.92 ± 0.56 mg CO_2-C gdw^{-1} anaerobically) and the Late Weichselian Interstadial permafrost (7.39 ± 5.82 mg CO_2-C gdw^{-1} aerobically and 0.80 ± 0.56 mg CO_2-C gdw^{-1} anaerobically). However, no significant differences were present if the projected carbon release was calculated based on bulk carbon concentrations (Table S1).

The relative size of the two modeled carbon pools was significantly ($P < 0.001$) different under aerobic and anaerobic conditions. The labile carbon pools were smaller, comprising initially only $2.22 \pm 1.19\%$ and $0.64 \pm 0.28\%$ of total organic carbon under aerobic and anaerobic conditions, respectively (Table 1). These carbon pools were depleted almost completely under both aerobic and anaerobic conditions after 1200 days. Only two samples showed a small contribution of the labile pools (<0.07% of initial C_{org}) at the end of the aerobic incubations. Although the mean contribution of the stable pools also decreased significantly until the end of the incubation period ($P < 0.01$) under aerobic conditions, under anaerobic conditions even no change was detectable ($P > 0.1$). The content of the stable pools was only significantly reduced ($P < 0.001$) under anaerobic conditions (Table 1) when considering the full 100-year projection of organic matter degradation.

The turnover times of the labile pools were about 3 months under aerobic and anaerobic conditions.

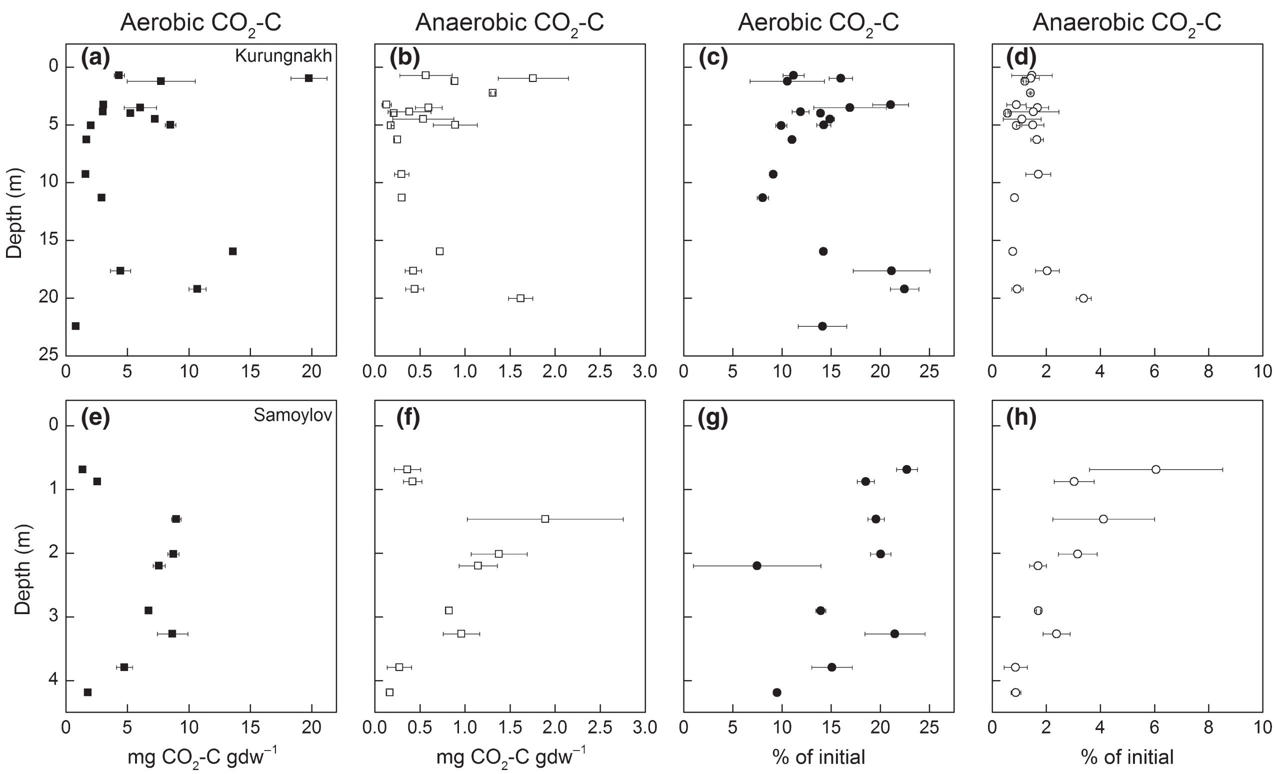

Fig. 6 Predicted amount of CO_2 production for a period of 100 years from permafrost deposits of Kurungnakh (a–d) and Samoylov (e–h) under aerobic (a, c, e, g) and anaerobic (b, d, f, h) conditions by fitting a two pool carbon degradation model to the measured cumulative CO_2 production over a period of 1200 days. Data are given as absolute amounts of CO_2-C production (a, b, e, f) per gram dry weight (gdw) and are also calculated relative to the initial amount or organic carbon in the permafrost (c, d, g, h). Error bars indicate the standard deviation from the average (generally $n = 3$).

Table 1 Turnover times of the two modeled carbon pools, humification coefficient of the labile carbon pool and relative contribution of the two carbon pools under initial conditions, at the end of the incubation period of 1200 days and under projected carbon degradation for 100 years. Numbers are mean values of 26 permafrost samples with one standard deviation

	Aerobic		Anaerobic	
	Mean	SD	Mean	SD
Turnover times of carbon pools (year)				
Labile pool	0.26	1.56	0.21	1.58
Stable pool	170.3	1.43	2652	3.41
Humification coefficient (h) of labile pool	0.55	0.04	0.47	0.07
Initial pool sizes (% of total C_{org})				
Labile pool	2.22	1.19	0.64	0.28
Stable pool	97.78	1.19	99.36	0.28
Pool sizes after 1200 days (% of initial C_{org})				
Labile pool	0.003	0.012	0	0
Stable pool	96.92	1.05	99.46	0.23
Pool sizes after 100 years (% of initial C_{org})				
Labile pool	0	0	0	0
Stable pool	84.91	4.52	98.20	1.22

However, the stable pools had substantially longer turnover times under anaerobic conditions (2652 years) than under aerobic conditions (170 years, Table 1).

Although aerobic and anaerobic CO_2 production could be fitted to the applied ICBM model with high precision, this level of analysis was not possible for methane formation. The main cause was a very long (average 960 $\pm$ 300 days) and not predictable lag time before methanogenesis reached its peak rate.

Discussion

The multiyear measurements of CO_2 and CH_4 production in samples from Northeast Siberian permafrost deposits indicate distinct differences between Holocene and Pleistocene permafrost material. The main predictor for carbon mineralization in the different permafrost samples was the absolute concentration of organic carbon. Although organic matter concentrations and mineralization was similar in Holocene sediments and those formed in the Middle Weichselian interstadial under a climate and vegetation close to modern (Laukhin *et al.*, 2006; Wetterich *et al.*, 2008), organic carbon concentrations and turnover were low in the Late Weichselian Stadial sediments, which developed under a cold and arid climate. However, in addition to the total amount of organic matter, its properties also have to be considered to better constrain estimates of organic matter decomposition from different permafrost deposits of northern Siberia. The higher δ^{13}C-values of organic carbon in the Late Weichselian Stadial deposits, which were correlated with the decreasing carbon mineralization in these sediments, indicate a different source of organic matter and a higher degree of organic matter decomposition than in the overlain Holocene permafrost sediments (Schirrmeister *et al.*, 2011a). In summary, the available data show that mineralization of organic matter in permafrost deposits is not a function of age but instead depends on the absolute amount and quality of organic matter formed under different past climatic conditions.

Relatively high initial turnover rates of permafrost organic matter indicate a substantial fraction of labile carbon in the perennially frozen ground (Dutta *et al.*, 2006; Zimov *et al.*, 2006a; Waldrop *et al.*, 2010; Lee *et al.*, 2012; this study), which becomes available to microbial degradation e.g., by disturbing the intact permafrost structure while preparing the experiment.

The Late Pleistocene permafrost deposits on Kurungnakh belong to the Middle to Late Weichselian Ice Complex deposits or Yedoma, which are widespread in the North Siberian permafrost landscapes (Schirrmeister *et al.*, 2011b). However, the Lena Delta deposits contain more organic carbon but less easily degradable plant remains such as grass roots (Wetterich *et al.*, 2008; Schirrmeister *et al.*, 2011a) than the Ice Complex sediments in the Kolyma lowlands (Zimov *et al.*, 2006b) and in Alaska, whose carbon turnover was studied in previous investigations (Dutta *et al.*, 2006; Zimov *et al.*, 2006a; Lee *et al.*, 2012). Total CO_2 production, calculated on a bulk carbon basis, was substantially lower in the Lena Delta Yedoma deposits after 1200 days (31 mg CO_2-C g^{-1} C aerobically, 5.5 mg CO_2-C g^{-1} C anaerobically) than in Yedoma from the Kolyma region and Alaska after 500 days (110–140 mg CO_2-C g^{-1} C aerobically, 30 mg CO_2-C g^{-1} C anaerobically) (Lee *et al.*, 2012). The higher carbon mineralization in the incubations reported by Lee *et al.* (2012) are likely be affected by the higher incubation temperature they used (15 °C vs. 4 °C in our study) but also indicate substantial differences in carbon degradability between different Yedoma sites and ages.

The two pool carbon degradation model (Andrén & Kätterer, 1997) applied here could be fitted to the obtained laboratory data with high precision since model predictions and measurements of CO_2 production after 1200 days deviated on average only by 1.7% and 3.9% (aerobic and anaerobic incubations, respectively). However, a substantially higher deviation between measurements and model predictions were found if only the results from the first year, and not the whole 1200 days data set were used for model calibration. This finding emphasizes the need for multiyear incubations for reliable projections of CO_2 fluxes from thawing permafrost organic matter.

The calibrated two pool carbon degradation model indicated that the studied permafrost is dominated by slowly degradable organic matter. The average size of the stable carbon pools was 97.8% and 99.4% of C_{org} under aerobic and anaerobic conditions, respectively, which is in the higher range of the stable carbon pool sizes (88.6–99.7% of C_{org}) reported in a survey of European forest soils (Rey & Jarvis, 2006) but much higher than in several north American forest soils (43–64%) (Garten, 2011). The high share of the stable carbon pool in the Lena River Delta permafrost resulted in relatively low projections of CO_2 production for 100 years representing 15% (aerobically) and 1.8% (anaerobically) of initial organic carbon.

Available estimates on long-term carbon release from thawing permafrost, which are based on measurements of carbon mineralization rates, are scarce. Dutta *et al.* (2006) performed a linear extrapolation of aerobic carbon degradation rates in Yedoma permafrost samples incubated for about 1 year. Assuming that 10% of Yedoma permafrost with 46 Pg organic carbon will thaw in the near future, they estimated a release of about 42 Pg carbon over four decades. Using the same number of thawing organic matter in Yedoma permafrost as Dutta *et al.* (2006) the aerobic CO_2 production modeled in this study indicates a release of only about 7 Pg C (15% of initial carbon) from thawing Yedoma permafrost during the next century. These substantially lower estimates do not result from lower carbon degradation rates at the end of the permafrost incubations which were surprisingly quite similar in the Lena River Delta permafrost (0.1–2.8 μg C gdw^{-1} day^{-1}) and the Kolyma Yedoma (0.3–1.6 μg C gdw^{-1} day^{-1}) (Dutta *et al.*, 2006). Rather, these estimates derive from considering different carbon pools in a model representing the nonlinear carbon dynamics. Due to the high contribution of the stable carbon pool with turnover times of centuries, carbon degradation decreases significantly in the time frame considered. Furthermore, our projection of CO_2 production for the next 100 years consider the fact that the active layer soils in permafrost landscapes are completely frozen during most of the year. Freezing substantially reduces, or even ceases, the turnover of organic matter (Mikan *et al.*, 2002), and is the primary driver for the high organic matter accumulation in permafrost.

The projection of about 7 Pg C release from thawing Yedoma permafrost in 100 years is still associated with a huge uncertainty because it is estimated with an oversimplified model, is based on a rough estimate of organic carbon that will become available after continued permafrost warming and does not consider anaerobic carbon mineralization. However, anaerobic conditions, widespread in permafrost landscapes, substantially reduce CO_2 production and the mineralization rate of soil organic matter (Hedges & Oades, 1997; Moore & Dalva, 1997; Lee *et al.*, 2012; this study). This reduction is also shown by the applied model, which estimates significantly smaller fast carbon pools and a 16-fold higher turnover time of the stable carbon pools in the absence of oxygen. Anaerobic conditions in the studied permafrost reduced the projected CO_2 release in 100 years by a factor of 8 (15.1% initial C mineralization aerobically vs. 1.8% anaerobically). A land cover classification of the Lena River Delta identified more than 40% of the land area as a substantial source of CH_4, indicating water saturated, anaerobic conditions at the bottom of the active layer (Schneider *et al.*, 2009). A deepening of the active layer due to permafrost thawing at these landscapes would result in mainly anaerobic degradation of carbon in the former permafrost and hence a substantially lower CO_2 formation than estimated for aerobic conditions.

A general source of uncertainty in the long-term projections of permafrost carbon mineralization in this study is the use of an oversimplified model based solely on carbon mineralization measurements. Microbial processes governing the carbon decomposition are not represented. The degradation of the carbon pools is treated like a radio-active decay and does not consider processes such as the extracellular breakdown of organic matter and further assimilation into microbes. In this study, only respiration measurements were used for constraining decomposition rates. This fact potentially increased the uncertainty of the decomposition rate of slowly decomposable organic matter. Other data sources such as ^{14}C measurements should be used to further constrain the stable pool parameters. However, the estimated turnover time of about 170 years under aerobic conditions gives us confidence in applying the model for a 100-year projection. Our results give a first indication about the vulnerability of soil carbon that has been frozen over millennia. However, the future trajectory of permafrost soil carbon at large scale will be also determined by other processes, such as changes in the hydrological regime, changes in soil structure due to physical and biological soil mixing, and plant–soil interactions changing the microbial community composition (Schmidt *et al.*, 2011). The experimental laboratory data used in this study do not include information about such processes at the ecosystem scale. Long time incubations under natural conditions in the field combined with studies on the active microbial communities can help to reduce these uncertainties.

A further limitation for reliably estimating future trace gas release from thawing permafrost are large uncertainties in the amount of organic carbon that will become available to microbial mineralization when permafrost deposits continue to thaw. The estimated amount of about 1700 Pg C stored in global permafrost deposits (Tarnocai *et al.*, 2009) is not well constrained because it is based on a relatively small data set, in particular concerning the Siberian permafrost landscapes. Recent studies indicate substantially smaller carbon pools in northeast Siberian Yedoma deposits (Schirrmeister *et al.*, 2011a) than previously reported. Hence, further data sets on permafrost carbon pools and quality are needed to reduce the high uncertainties concerning the carbon pools prone to microbial mineralization if permafrost continues to thaw.

Although anaerobic carbon degradation was measured for 1200 days, the quantitative role of methane formation from permafrost samples could not be clearly established. Since methanogenesis started with a very long lag phase and generally did not reach stable production rates until the end of the incubations, we could not model CH_4 production with the applied carbon degradation model. Low initial methane production rates ($<0.01\ \mu$mol gdw^{-1} day^{-1}) have been measured repeatedly in permafrost samples (Bischoff *et al.*, in press; Rivkina *et al.*, 2007; Wagner *et al.*, 2007). Even measurements for more than 1 year indicate the minor importance of methanogenesis in comparison to CO_2 production (Lee *et al.*, 2012). The observed low share of methanogenesis in comparison to CO_2 production might be related to the lower initial abundance of methanogens in permafrost (Waldrop *et al.*, 2010), which increases when permafrost thaws (Mackelprang *et al.*, 2011). The long time of more than one year needed to establish the highest methane production rates, supports the hypothesis of a relatively low abundance of methanogens in permafrost. However, a positive response of methanogenic communities to warmer and wetter periods in the Holocene and Late Pleistocene, as reconstructed from corresponding permafrost deposits of the Lena Delta, supports the assumption of increasing methane production and release when permafrost thaws (Bischoff *et al.*, in press).

The onset of methanogenesis in the long-term incubations was repeatedly accompanied by a concomitant increase in CO_2 production (e.g., Fig. S1-18). This effect was not reported in previous studies and indicates the potential for increasing degradability of permafrost carbon by syntrophic consortia of methanogenic archaea and fermenting microorganisms. Furthermore, the interaction between CO_2 production and methanogenesis, which seems to have substantial significance for total carbon mineralization under anaerobic conditions, is not accounted for in most of the current terrestrial ecosystem models (Beer *et al.*, 2007; Lawrence *et al.*, 2008; Wania *et al.*, 2009; Schaefer *et al.*, 2011). As CH_4 has a stronger climate warming effect than CO_2 (Forster *et al.*, 2007), CH_4 emissions from permafrost landscapes have gained increasing research attention (Wille *et al.*, 2008; Tagesson *et al.*, 2012). However, the amount of CH_4 formed in anaerobic permafrost environments do not reflect the amount emitted to the atmosphere due to substantial oxidation of the CH_4 produced in aerobic surface soils (Knoblauch *et al.*, 2008; Kip *et al.*, 2010). Water saturated tundra soils of the Lena River Delta, characterized by high CH_4 concentrations, may even become sinks for atmospheric CH_4 due to the high CH_4 oxidation rates in the surface soil layer (Liebner *et al.*, 2011). A strong decrease in CH_4 stable isotope signatures in the active layer soils on Samoylov (Preuss *et al.*, 2012) support the interpretation of substantial CH_4 oxidation under *in situ* conditions, which reduces the climate effect of permafrost carbon degradation under anaerobic conditions.

Multiyear measurements of trace gas production from northeastern Siberian permafrost demonstrate a significant amount of labile organic matter in the permafrost that can be readily mineralized after thawing. However, model simulations of aerobic and anaerobic CO_2 production over 100 years predict a substantially lower carbon release from thawing permafrost than currently available first-order estimates. One reason for these lower estimates is the dominance of the slowly degrading carbon pools in the studied permafrost deposits, which are characterized by turnover times of centuries. Another reason for the lower estimates is that the presented model confines microbial carbon degradation to the few months of the year when the soils in permafrost landscapes are not frozen and carbon mineralization takes place. The current study presents the first estimates of long-term CO_2 production form permafrost organic matter under anaerobic conditions and constrains current estimates of aerobic trace gas release from thawing permafrost. However, they still contain substantial uncertainties, particularly in describing the long-term degradation of organic matter through methanogenesis. Future modeling studies are needed to examine soil plant interactions, microbial functions, methanogenesis, and methane oxidation. Furthermore, precise projections of trace gas release from thawing permafrost landscapes need an accurate quantification of the permafrost carbon pools that will become accessible to microbial degradation after permafrost thaw.

Acknowledgments

The authors thank the Russian-German field parties during the expeditions LENA 2002 and LENA 2008, especially Mikhail N. Grigoriev (Permafrost Institute, Yakutsk, Russia), Günter Stoof (Alfred Wegener Institute for Polar and Marine Research, Potsdam, Germany) for their support during sampling on Kurungnakh, Sebastian Zubrzycki for collecting the permafrost core from Samoylov, Birgit Schwinge for laboratory analysis, and Lars Kutzbach, Benjamin Runkle and Lutz Schirrmeister for valuable discussions. Furthermore, we like to thank Ted Schuur, Christina Schädel, and three anonymous reviewers for valuable comments on a previous version of the manuscript. This work was financed in part by a DFG grant (KN 592/5-1) to CK.

References

Andrén O, Kätterer T (1997) ICBM: the introductory carbon balance model for exploration of soil carbon balances. *Ecological Applications*, **7**, 1226–1236.

Anisimov OA (2007) Potential feedback of thawing permafrost to the global climate system through methane emission. *Environmental Research Letters*, **2**, doi: 10.1088/1748-9326/2/4/045016.

Aurela M, Laurila T, Tuovinen J-P (2004) The timing of snow melt controls the annual CO_2 balance in a subarctic fen. *Geophysical Research Letters*, **31**, doi: 10.1029/2004GL020315.

Beer C, Lucht W, Gerten D, Thonicke K, Schmullius C (2007) Effects of soil freezing and thawing on vegetation carbon density in Siberia: a modeling analysis with the Lund-Potsdam-Jena Dynamic Global Vegetation Model (LPJ-DGVM). *Global Biogeochemical Cycles*, **21**, doi: 10.1029/2006GB002760.

Bischoff J, Mangelsdorf K, Gattinger A, Schloter M, Kurchatova AN, Herzschuh U, Wagner D (in press) Response of methanogenic archaea to Late Pleistocene and Holocene climate changes in the Siberian Arctic. *Global Biogeochemical Cycles*, doi: 10.1029/2011GB004238. in press.

Boike J, Wille C, Abnizova A (2008) Climatology and summer energy and water balance of polygonal tundra in the Lena River Delta, Siberia. *Journal of Geophysical Research-Biogeosciences*, **113**, doi: 10.1029/2007JG000540.

Christensen TR, Johansson TR, Akerman HJ *et al.* (2004) Thawing sub-arctic permafrost: effects on vegetation and methane emissions. *Geophysical Research Letters*, **31**, doi: 10.1029/2003GL018680.

Dutta K, Schuur EAG, Neff JC, Zimov SA (2006) Potential carbon release from permafrost soils of Northeastern Siberia. *Global Change Biology*, **12**, 2336–2351.

Forster P, Ramaswamy V, Artaxo P *et al.* (2007) Changes in atmospheric constituents and in radiative forcing. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt Kb, Tignor M, Miller Hl), pp. 129–234. Cambridge University Press, Cambridge, UK.

Garten CT Jr (2011) Comparison of forest soil carbon dynamics at five sites along a latitudinal gradient. *Geoderma*, **167–68**, 30–40.

Groendahl L, Friborg T, Soegaard H (2007) Temperature and snow-melt controls on interannual variability in carbon exchange in the high Arctic. *Theoretical and Applied Climatology*, **88**, 111–125.

Hedges JI, Oades JM (1997) Comparative organic geochemistries of soils and marine sediments. *Organic Geochemistry*, **27**, 319–361.

Jobbágy EG, Jackson RB (2000) The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecological Applications*, **10**, 423–436.

Khvorostyanov DV, Krinner G, Ciais P, Heimann M, Zimov SA (2008) Vulnerability of permafrost carbon to global warming. Part I: model description and role of heat generated by organic matter decomposition. *Tellus Series B-Chemical & Physical Meteorology*, **60**, 250–264.

Kip N, Van Winden JF, Pan Y *et al.* (2010) Global prevalence of methane oxidation by symbiotic bacteria in peat-moss ecosystems. *Nature Geoscience*, **3**, 617–621.

Knoblauch C, Zimmermann U, Blumenberg M, Michaelis W, Pfeiffer E-M (2008) Methane turnover and temperature response of methane-oxidising bacteria in permafrost-affected soils of northeast Siberia. *Soil Biology and Biochemistry*, **40**, 3004–3013.

Koven CD, Ringeval B, Friedlingstein P *et al.* (2011) Permafrost carbon-climate feedbacks accelerate global warming. *Proceedings of the National Academy of Sciences*, **108**, 14769–14774.

Kutzbach L, Wagner D, Pfeiffer E-M (2004) Effect of microrelief and vegetation on methane emission from wet polygonal tundra, Lena Delta, Northern Siberia. *Biogeochemistry*, **69**, 341–362.

Laukhin S, Arslanov K, Shilova G *et al.* (2006) Paleoclimates and chronology of the middle Würm megainterstadial on the West Siberian Plain. *Doklady Earth Sciences*, **411**, 1457–1461.

Lawrence DM, Slater AG, Romanovsky VE, Nicolsky DJ (2008) Sensitivity of a model projection of near-surface permafrost degradation to soil column depth and representation of soil organic matter. *Journal of Geophysical Research*, **113**, doi: 02010.01029/02007JF000883.

Lee H, Schuur EAG, Inglett KS, Lavoie M, Chanton JP (2012) The rate of permafrost carbon release under aerobic and anaerobic conditions and its potential effects on climate. *Global Change Biology*, **18**, 515–527.

Liebner S, Zeyer J, Wagner D, Schubert C, Pfeiffer E-M, Knoblauch C (2011) Methane oxidation associated with submerged brown mosses reduces methane emissions from Siberian polygonal tundra. *Journal of Ecology*, **99**, 914–922.

Mackelprang R, Waldrop MP, Deangelis KM *et al.* (2011) Metagenomic analysis of a permafrost microbial community reveals a rapid response to thaw. *Nature*, **480**, 368–371.

McGuire AD, Anderson LG, Christensen TR *et al.* (2009) Sensitivity of the carbon cycle in the Arctic to climate change. *Ecological Monographs*, **79**, 523–555.

Meentemeyer V (1978) Macroclimate and lignin control of litter decomposition rates. *Ecology*, **59**, 465–472.

Mikan CJ, Schimel JP, Doyle AP (2002) Temperature controls of microbial respiration in arctic tundra soils above and below freezing. *Soil Biology and Biochemistry*, **34**, 1785–1795.

Moore TR, Dalva M (1997) Methane and carbon dioxide exchange potentials of peat soils in aerobic and anaerobic laboratory incubations. *Soil Biology and Biochemistry*, **29**, 1157–1164.

Oechel WC, Vourlitis GL, Hastings SJ, Zulueta RC, Hinzman L, Kane D (2000) Acclimation of ecosystem CO_2 exchange in the Alaskan Arctic in response to decadal climate warming. *Nature*, **406**, 978–981.

Preuss I, Knoblauch C, Gebert J, Pfeiffer E-M (2012) Improved quantification of microbial CH_4 oxidation efficiency in Arctic wetland soils using carbon isotope fractionation. *Biogeosciences Discussion*, **9**, 1–37.

Rey ANA, Jarvis P (2006) Modelling the effect of temperature on carbon mineralization rates across a network of European forest sites (FORCAST). *Global Change Biology*, **12**, 1894–1908.

Rivkina E, Shcherbakova V, Laurinavichius K *et al.* (2007) Biogeochemistry of methane and methanogenic archaea in permafrost. *FEMS Microbiology Ecology*, **61**, 1–15.

Schaefer K, Zhang TJ, Bruhwiler L, Barrett AP (2011) Amount and timing of permafrost carbon release in response to climate warming. *Tellus Series B-Chemical and Physical Meteorology*, **63**, 165–180.

Schirrmeister L, Grosse G, Wetterich S, Overduin PP, Strauss J, Schuur EAG, Hubberten H-W (2011a) Fossil organic matter characteristics in permafrost deposits of the northeast Siberian Arctic. *Journal of Geophysical Research*, **116**, doi: 10.1029/2011jg001647.

Schirrmeister L, Kunitsky V, Grosse G *et al.* (2011b) Sedimentary characteristics and origin of the Late Pleistocene Ice Complex on north-east Siberian Arctic coastal lowlands and islands – a review. *Quaternary International*, **241**, 3–25.

Schmidt MWI, Torn MS, Abiven S *et al.* (2011) Persistence of soil organic matter as an ecosystem property. *Nature*, **478**, 49–56.

Schneider von Deimling T, Meinshausen M, Levermann A, Huber V, Frieler K, Lawrence DM, Brovkin V (2012) Estimating the near-surface permafrost-carbon feedback on global warming. *Biogeosciences*, **9**, 649–665.

Schneider J, Grosse G, Wagner D (2009) Land cover classification of tundra environments in the Arctic Lena Delta based on Landsat 7 ETM+ data and its application for upscaling of methane emissions. *Remote Sensing of Environment*, **113**, 380–391.

Schuur EAG, Vogel JG, Crummer KG, Lee H, Sickman JO, Osterkamp TE (2009) The effect of permafrost thaw on old carbon release and net carbon exchange from tundra. *Nature*, **459**, 556–559.

Tagesson T, Mölder M, Mastepanov M *et al.* (2012) Land-atmosphere exchange of methane from soil thawing to soil freezing in a high-Arctic wet tundra ecosystem. *Global Change Biology*, **18**, 1928–1940.

Tarnocai C, Canadell JG, Schuur EAG, Kuhry P, Mazhitova G, Zimov S (2009) Soil organic carbon pools in the northern circumpolar permafrost region. *Global Biogeochemical Cycles*, **23**, doi: 10.1029/2008gb003327.

Trenberth KE, Jones PD, Ambenje P *et al.* (2007) Observations: surface and atmospheric climate change. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Solomon S, Qin D, Manning M, Chen Z, Marquis M, Kb Averyt, Tignor M, Miller Hl), pp. 235–336. Cambridge University Press, Cambridge, United Kingdom.

Wagner D, Gattinger A, Embacher A, Pfeiffer E-M, Schloter M, Lipski A (2007) Methanogenic activity and biomass in Holocene permafrost deposits of the Lena Delta, Siberian Arctic and its implication for the global methane budget. *Global Change Biology*, **13**, 1089–1099.

Waldrop MP, Wickland KP, White R III, Berhe AA, Harden JW, Romanovsky VE (2010) Molecular investigations into a globally important carbon pool: permafrost-protected carbon in Alaskan soils. *Global Change Biology*, **16**, 2543–2554.

Wania R, Ross I, Prentice IC (2009) Integrating peatlands and permafrost into a dynamic global vegetation model: 1. Evaluation and sensitivity of physical land surface processes. *Global Biogeochemical Cycles*, **23**, doi: 10.1029/2008gb003412.

Wetterich S, Kuzmina S, Andreev AA *et al*. (2008) Palaeoenvironmental dynamics inferred from late Quaternary permafrost deposits on Kurungnakh Island, Lena Delta, Northeast Siberia, Russia. *Quaternary Science Reviews*, **27**, 1523–1540.

Wille C, Kutzbach L, Sachs T, Wagner D, Pfeiffer E-M (2008) Methane emission from Siberian arctic polygonal tundra: Eddy covariance measurements and modeling. *Global Change Biology*, **14**, 1395–1408.

Zhang T, Barry RG, Knowles K, Heginbottom JA, Brown J (1999) Statistics and characteristics of permafrost and ground-ice distribution in the Northern Hemisphere. *Polar Geography*, **23**, 132–154.

Zimov SA, Davydov SP, Zimova GM, Davydova AI, Schuur EAG, Dutta K, Chapin FS III (2006a) Permafrost carbon: stock and decomposability of a globally significant carbon pool. *Geophysical Research Letters*, **33**, doi: 10.1029/2006GL027484.

Zimov SA, Schuur EAG, Chapin FS III (2006b) Climate change: permafrost and the global carbon budget. *Science*, **312**, 1612–1613.

Supporting Information

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

Figure S1. Cumulative amount of CO_2 and CH_4 produced and CO_2 and CH_4 production rates in permafrost samples from the Lena River Delta, Northeast Siberia incubated over a period of 1200 days.

Table S1. Initial CO_2 production rates, cumulative amount of CO_2 produced at the end of the incubation period of 1200 days and projected CO_2 release during 100 years in permafrost samples from Kurungnakh and Samoylov calculated on a bulk carbon basis.