

Potential carbon release from permafrost soils of Northeastern Siberia

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Abstract

Permafrost soils are an important reservoir of carbon (C) in boreal and arctic ecosystems. Rising global temperature is expected to enhance decomposition of organic matter frozen in permafrost, and may cause positive feedback to warming as CO₂ is released to the atmosphere. Significant amounts of organic matter remain frozen in thick mineral soil (loess) deposits in northeastern Siberia, but the quantity and lability of this deep organic C is poorly known. Soils from four tundra and boreal forest locations in northeastern Siberia that have been continuously frozen since the Pleistocene were incubated at controlled temperatures (5, 10 and 15 °C) to determine their potential to release C to the atmosphere when thawed. Across all sites, CO₂ with radiocarbon (¹⁴C) ages ranging between ~21 and 24 ka BP was respired when these permafrost soils were thawed. The amount of C released in the first several months was strongly correlated to C concentration in the bulk soil in the different sites, and this correlation remained the same for fluxes up to 1 year later. Fluxes were initially strongly related to temperature with a mean Q_{10} value of 1.9 ± 0.3 across all sites, and later were unrelated to temperature but still correlated with bulk soil C concentration. Modeled inversions of $\Delta^{14}\text{CO}_2$ values in respiration CO₂ and soil C components revealed mean contribution of 70% and 26% from dissolved organic C to respiration CO₂ in case of two permafrost soils, while organic matter fragments dominated respiration (mean 68%) from a surface mineral soil that served as modern reference sample. Our results suggest that if 10% of the total Siberian permafrost C pool was thawed to a temperature of 5 °C, about 1 Pg C will be initially released from labile C pools, followed by respiration of ~40 Pg C to the atmosphere over a period of four decades.

Keywords: arctic, carbon, decomposition, incubation, isotopes, permafrost, radiocarbon, respiration, Siberia, soil organic matter

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Introduction

Future temperature increases associated with climate change are predicted to be greatest in high latitudes due to rising concentration of atmospheric greenhouse gases and positive feedbacks including albedo change as a result of declining snow and sea ice cover (Cess *et al.*, 1991; Chapman & Walsh, 1993), and from increased shrub and tree cover (Chapin *et al.*, 2005). Current

temperature increases have already been observed in most arctic regions (ACIA, 2004). Proxy climate records show that, from AD 1840 to the mid-20th century, the arctic region globally has warmed to the highest levels in the last four centuries (Overpeck *et al.*, 1997). Regional records show similar patterns for summer temperature in Siberia (Briffa *et al.*, 1995; Hughes *et al.*, 1999), and in Alaska arctic warming accelerated during the 1980s (Osterkamp & Romanovsky, 1999; Serreze *et al.*, 2000). Sustained warming has the potential for other positive feedbacks from terrestrial ecosystems that can amplify warming trends (Cox *et al.*, 2000; Prentice *et al.*, 2001). These feedbacks include effects of changes in soil drainage (Davidson *et al.*, 2000) and enhanced nutrient

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availability (Mack *et al.*, 2004), both of which can affect decomposition rates and may result in net carbon (C) loss from terrestrial ecosystem as an indirect effect of warming.

One of the most likely and important feedbacks from sustained warming in high-latitude ecosystems is the thawing of permafrost soils and the release of soil organic C to the atmosphere by microbial respiration of CO₂ or methane (CH₄; Oechel *et al.*, 1993; Zimov *et al.*, 1993; Goulden *et al.*, 1997; Melillo *et al.*, 2002; Eliasson *et al.*, 2005), or by leaching out as dissolved organic carbon (DOC; Freeman *et al.*, 2004; Frey & Smith, 2005). Soil organic matter is among the largest global reservoirs that exchanges C with the atmosphere at time scales ranging from a few years to several hundreds of years (Schimel, 1995; Trumbore *et al.*, 1996). Boreal and arctic permafrost soils, which remain below -2 °C for at least 2 consecutive years (Davis, 2001), are important reservoirs of a large fraction of the global soil C pool. Cold temperature slows decomposition of soil organic matter and contributes to soils with high organic C content. It is estimated that nearly a third of the world's total soil organic C inventory of top 1 m of soil profile (approximately 455 Pg C) is stored in arctic and boreal regions (Gorham, 1991). This pool of soil C, climatically protected by cold and waterlogged conditions, is thought to be highly susceptible to changes in temperature and permafrost thawing.

While high-latitude ecosystems in general are known to store large amounts of C, there are regional variations in C storage (peatlands, nonpeatlands, lowlands, uplands) that make total soil C storage and response to changes in temperature uncertain (Prentice *et al.*, 2001). Recent work on permafrost soils from Siberia has quantified pools of permafrost C in the deep soil profile (deeper than 1 m) that are substantial (~500 Pg, Zimov *et al.*, 2006) relative to the known pool in the top 1 m. These loess soils found in the ice-rich permafrost region of northeastern Siberia cover an area of about 10⁶ km² (Romanovsky, 1993), and are known as *yedoma* in the Russian literature. These mineral soils have formed syngenetically through loess deposition with average thickness of 25 m (ranging from 10–60 m). The loess deposits contain massive ice wedges, up to 50% by volume, and commonly contain Pleistocene mega-faunal remains (Kuzmin & Orlova, 2004; Vasil'chuk *et al.*, 2005). The organic C concentrations in these soils range from less than 2% to as high as 20% in occasional distinct buried organic layers. Excluding these infrequent organic layers, the mineral soil averages about 2.6% (Schirrmeister *et al.*, 2002; Zimov *et al.*, 2006). In some areas, these yedoma deposits now show signs of thawing (Romanovsky *et al.*, 2001), and may thaw more

in the future (Lawrence & Slater, 2005), thereby releasing stored C to the atmosphere.

Here, we explore the potential C release from deep yedoma soils exposed to elevated temperatures. We present the results of laboratory incubation experiments and isotopic studies on six yedoma soil samples collected from four locations at various depths in northeastern Siberia to demonstrate the dynamics of organic matter decomposition in response to temperature, and to identify the soil organic matter components most susceptible to decomposition upon thawing. Using information about rates and sources to decomposition, we project a potential trajectory of C loss from these permafrost soils when thawed.

Material and methods

Study site

The samples for this study were collected from loess permafrost soils of northeastern Siberia, near the town of Cherskii (68°47'N, 161°20'E), in the northeastern part of the state of Republic of Sakha (Yakutia), Russia (Fig. 1). This region experiences long and cold winters where daily mean temperatures remain below freezing from October to May; the daily mean temperature in January is -36 °C. Summer spans 4 months with daily mean temperatures ranging up to 13 °C during July. Average annual precipitation is 218 mm, with 85 mm occurring as rain, and 133 mm as snow. The thickness of the permafrost active layer (the surface soil layer that thaws during the summer) ranges from ~20 to 180 cm, depending on surface conditions, while below the active layer soils can have up to 70% ice content. The modern vegetation in this region is tundra, shrub tundra and larch forest (*Larix gmelinii*). In the latter two vegetation types, mosses, lichens and dwarf evergreen and deciduous shrubs are common understory components in areas both with and without trees. The soils of this region are classified as mixed loamy Gelisol, derived from loess and moderately weathered colluviums from acidic schist and diorite parent rocks (USDA, 1999). Continuous deposition of aeolian and alluvial sediments over long periods of time has created loess soil deposits 10–90 m thick (mean ~25 m) and prevented the formation of a distinct humus layer at the soil surface as the loess was accumulating. This area was not glaciated during the Pleistocene due to the locally dry climate conditions (Kienast *et al.*, 2005). As the active layer thaws to a similar thickness each summer, roots and other organic matter were gradually incorporated into permafrost at the bottom of the soil profile as the soil surface accumulated new loess.

Field sampling

Yedoma soils were collected frozen from four different locations in northeastern Siberia in 2001 (Fig. 1). The four locations included two tundra sites close to the Arctic Ocean near the mouth of the Kolyma River, at Sukharnaya (69°31'N, 161°52'E) and Medvezhka (69°39'N, 162°31'E). The other two locations were in boreal forest at Duvannyi Yar along the banks of

Kolyma River (68°37'N, 159°02'E), and at Zelenyi Mys (68°48'N, 161°23'E), on the north side of the town of Cherskii. Samples from the first three sites were collected from deep within the soil profile at opportunistic and mostly undisturbed locations (river bank exposure, mine tunnel, lake bank exposure), from depths ~10 m or deeper. At Zelenyi Mys, soil samples were collected from three depths in a continuous profile. The surface sample from Zelenyi Mys consists of the top 10 cm of

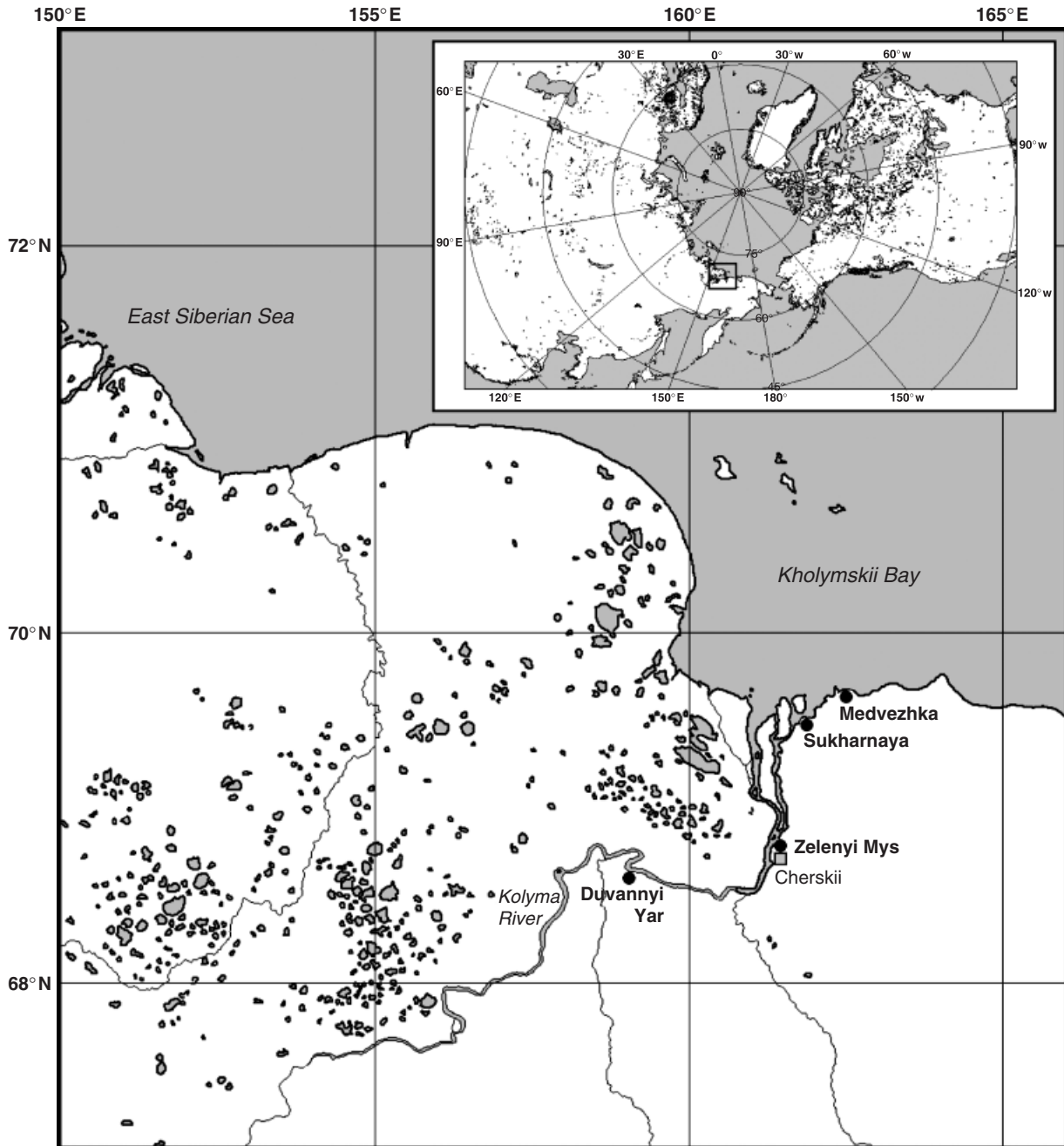


Fig. 1 Site locations of yedoma sampling in Northeastern Siberia near the town of Cherskii. The inset is a large scale polar view with the study area enclosed in the rectangle.

mineral soil within the permafrost active layer that thaws each summer, while other samples from this site were collected below the seasonally thawed active layer, at 2 and 13 m below the soil surface, respectively. The surface sample from Zelenyi Mys can be considered as a modern reference sample that is exposed to decomposition at above-freezing temperatures during the summer and presently receives inputs of modern labile C from actively growing plant roots, DOC, and exudates during the summer, unlike the rest of the permafrost soils. All other samples remain frozen throughout the year and have remained frozen since the time when they were incorporated into the permafrost during the Pleistocene. For sampling at Sukharnaya, Medvezhka and Duvannyi Yar, an axe was used to chop out replicate samples of frozen soil from behind exposed faces that contained intact Pleistocene ice wedges, while a 10 cm diameter drill corer was used for sampling at Zelenyi Mys. The samples were kept frozen continuously after collection and shipped frozen back to the laboratory at the University of Florida, where they were further divided while frozen into 50–100 g subsamples for the various measurements.

Incubation experiment and CO₂ flux measurements

Bulk soil samples from each site were allowed to thaw and then were incubated in the laboratory at 5, 10 and 15 °C with three replicates per site for each temperature treatment. The incubators consisted of airtight glass mason jars fitted with stopcocks for gas sampling. Soils were placed in incubation cups within the glass jars at constant field-capacity moisture, with water on the bottom of the glass jar to maintain humidity. The temperature inside the incubators were precisely maintained at ± 0.4 °C from the set point, and controlled with digital controllers (Omega CN 77343, Omega Engineering Inc., Stamford, CT, USA), with thermocouples placed inside the refrigerator adjacent to the incubation jars. Carbon dioxide concentrations in the jar headspace were measured with a nondispersive infrared (NDIR) gas analyzer (LI-COR 6252, Li-COR Inc., Lincoln, NE, USA), calibrated with certified CO₂-in-air standards with concentrations of 995, 10 000 and 25 000 ppmv. To measure the CO₂ flux, about 10 mL of the jar headspace was removed with a gas-tight syringe and the CO₂ concentration was measured initially, and then measured again at some known time-point (usually 24 h later). Jars were equalized to atmospheric pressure following each sampling by allowing CO₂-free air to enter the jar. Fluxes of CO₂ from the incubation jars were monitored daily for the first 2 weeks and then every other day for a month, followed by monthly measurements. Jars remained capped throughout the

duration of the experiment to maintain high-ambient humidity and were flushed with humidified CO₂-free air whenever the CO₂ concentration in the headspace air exceeded 1.0%. Jars were kept at constant temperature and CO₂ flux was measured over the course of 1 year. To describe the temporal pattern of C release from yedoma, we fitted an exponential curve of the form

$$C_t = C_0(1 - e^{-kt}), \quad (1)$$

where C_t is cumulative C accumulated after time t , C_0 is a constant proportional to initial concentration of C that is available for microbial decomposition, and k is the inverse of the turnover time of decomposition. Curves were fitted separately for two periods of incubation: days 11–50 and days 50–390 representing two different periods in the incubation experiment that may have different rate constants. The initial period (days 1–10) represented increasing flux and was not fitted with an exponential curve. For 1% bulk C content (10 mg g⁻¹), the average value of C_0 for all temperatures was 0.17 mg for days 11–50 and 0.33 mg for days 11–390.

Temperature sensitivity

The temperature sensitivity of decomposition of soil organic matter can be expressed by a Q_{10} function (Kirschbaum, 1995; Dioumaeva *et al.*, 2003; Knorr *et al.*, 2005), which is defined as the ratio of the respiration rate at a temperature $T + 10$ (°C) relative to that at a temperature T (°C). To determine the Q_{10} values, we fit an exponential function to the flux values of the form $f_T = ae^{bT}$, where f_T is the measured cumulative C flux at temperature T (average of three replicates), a and b are constants. The Q_{10} is then given by

$$Q_{10} = f_{T+10}/f_T = e^{b(T+10)-bT} \quad (2)$$

or $Q_{10} = e^{10b}$.

Not surprisingly, the above equation satisfactorily described the relationship for all soils, with R^2 values ranging from 0.81 to more than 0.99, indicating C fluxes were neither limited by C substrate availability nor soil moisture.

Soil fractions

Sub samples of the bulk soil were thawed and separated into an organic matter fragments fraction (mostly fine roots and other coarse fragments), a mineral soil fraction, and a humus fraction by sieving and density separation methods. This separated the bulk soil organic matter into potential labile and refractory components (Trumbore & Zheng, 1996). The fine roots and other macro plant parts were first separated by sieving at 1 mm and flotation in deionized (DI) water; this

comprised the organic matter fragments fraction. The remaining soil was then centrifuged with aqueous sodium polytungstate solution (density 2.1 g cm^{-3}), where the mineral fraction and lighter humus material were separated. The humus fraction, as defined here, floated at density 2.1 g cm^{-3} , whereas the mineral soil fraction sank at density 2.1 g cm^{-3} . All solid components were finally rinsed with DI water and oven dried at 65°C to obtain a dry weight. A separate subsample was thawed in DI water at a ratio of 10:1 g H_2O to grams dry soil. The suspended solids were allowed to settle and the supernatant liquid was centrifuged. The supernatant liquid was filtered at $0.45 \mu\text{m}$, acidified to pH of 2 with nitric acid, and was stored refrigerated for measurements of DOC concentration. After concentration analysis, the remaining liquid was freeze dried to a solid form for ^{13}C and ^{14}C isotope analyses. Thus, we fractionated the bulk yedoma soil C into four separate components: organic matter fragments, humified organics lighter than 2.1 g cm^{-3} , mineral soil C heavier than 2.1 g cm^{-3} , and DOC.

Elemental analyses

The bulk soils and the soil fractions were measured for total C and nitrogen (N) using an elemental analyzer (Costech Instruments, Milan, Italy). Calibration was done with NIST peach leaves standard (SRM 1547, National Institute of Standards and Technology, Gaithersburg, MD, USA). C 44.65%, N 2.93%. Based on repeat measurements of SRM 1547, the 1σ precisions for C and N measurements were $\pm 0.6\%$ and $\pm 2.2\%$, respectively, of the measured values. DOC was analyzed using a Shimadzu DOC analyzer (Shimadzu Corporation, Kyoto, Japan) at University of Colorado, Boulder, CO, USA. The 1σ precision of DOC measurements in the concentration range of $10\text{--}20 \mu\text{g g}^{-1}$ was $\pm 2\%$ of the measured values.

Radiocarbon (^{14}C) measurements

Gaseous samples. Before making isotopic measurements of respiration CO_2 , the headspace of the incubation jars was scrubbed with CO_2 -free air to remove any atmospheric CO_2 . Respired CO_2 then reaccumulated in the jar and the headspace air in the incubation jars was sampled into evacuated 500 mL gas sampling flasks. The CO_2 was then extracted from the flasks 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 stored sealed in Pyrex™ tubes that were prebaked at 550°C .

Solid samples. About 3 mg of the organic soil samples and about 100 mg of the mineral soil samples were

combusted to obtain several milligram of $\text{CO}_2\text{-C}$. These samples were loaded along with 20 mg of CuO wires in 15 cm Vycor™ tubes. Both the CuO wires and the Vycor™ tubes were prebaked in air at 900°C using a muffle furnace. The samples in the Vycor™ tubes were sealed under vacuum along with the CuO wires and combusted in muffle furnace at 900°C for 2 h. The primary standard for ^{14}C analysis was NIST Oxalic acid II (SRM 4990C, National Institute of Standards and Technology), while IAEA-C6 sucrose standard (International Atomic Energy Agency, Vienna, Austria) was analyzed as secondary standard. Anthracite coal cleaned with a standard acid–base–acid treatment was used as a blank. All standards and blanks used for ^{14}C measurements were combusted and purified similarly to the samples.

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

Stable isotope measurements

An aliquot of CO_2 ($\sim 10 \mu\text{mol}$) was transferred during the purification stage to helium flushed 10 mL Exetainer™ vials (Labco Limited, Buckinghamshire, UK) fitted with rubber septum (Tu *et al.*, 2001). $^{13}\text{C}/^{12}\text{C}$ isotope ratios were measured with a Finnigan Delta Plus XL™ continuous flow mass spectrometer coupled with Gas-Bench III™ sampler (Finnigan MAT GmbH, Bremen, Germany). For soil samples, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data were obtained by combustion with the Costech™ CN Analyzer (Costech Instruments, Milan, Italy), which was coupled to the Finnigan Delta XL Plus™ mass spectrometer through a ConfloII™ control unit. Based on repeat

analyses of NIST Peach leaves standard (SRM 1547; $\delta^{13}\text{C}$ –26.06‰, $\delta^{15}\text{N}$ 1.91‰), average 1σ precision was 0.05‰ for $\delta^{13}\text{C}$ and 0.07‰ for $\delta^{15}\text{N}$. Measured mineral $\delta^{15}\text{N}$ values were found to be fractionated due to repeated washing of the sediments, thus, giving high $\delta^{15}\text{N}$ values not possible via mass balance and not biologically likely. Mineral $\delta^{15}\text{N}$ values reported in Table 1 were calculated by difference from the mass balance of the bulk soil and all other soil fractions.

Source partitioning of respiration CO_2

We estimated the relative contribution of the soil C components to the soil respiration CO_2 using the $\Delta^{14}\text{C}$ measurements of the respiration and the organic matter components. Using four different soil components as C sources (DOC, mineral, humus, and organic matter fragments) and one isotope (^{14}C) as tracer, no unique solution for the contribution of each organic type is possible, as the method involves four unknowns. Schuur *et al.* (2003) described a modeling method to determine the possible combinations of sources that can be effectively used for partitioning multiple sources from a mixture. In this study, we have used measured $\Delta^{14}\text{C}$ values of respiration CO_2 and four soil components to partition the potential contributing sources of respiration CO_2 using a computer program IsoSource (Phillips & Gregg, 2003). This program iteratively computes the feasible combinations of the sources which produce the observed composition of the mixture, by allowing the contribution of each source component with small increments of 1% or 2%. The isotopic compositions of the resultant mixture of the sources are compared with the observed values. If the modeled data equal or match the observed values within a small tolerance, the result is stored as a feasible combination. Finally, distributions of all feasible source combinations are presented as histograms.

Results

C, N concentrations and isotopes

The bulk organic C content of the yedoma samples ranged from 0.84% to 2.58% C, a threefold range across all sites (Table 1). The surface sample from Zelenyi Mys had the lowest C concentration with $0.85 \pm 0.11\%$ C, with higher C concentrations at deeper depths (2 and 13 m). In terms of total soil mass, the yedoma samples typically consist of about 98% of mineral soil ($>2.1 \text{ g cm}^{-3}$), more than 1% of humified organic matter ($<2.1 \text{ g cm}^{-3}$), and less than 1% as organic matter fragments (data not shown). These proportions change somewhat when percent of total organic C is consid-

ered, although the mineral soil still comprises the bulk. Mineral fractions ranged from 0.58% to 2.24% C in the frozen samples, varying by a factor of about four among sites (Table 1). In contrast, the humus fraction ranged from 18% to 21% C, while the organic matter fragments ranged from 18% to 28% C. Both of these latter fractions were more consistent among sites as compared with the relative variation in the mineral soil C content. DOC concentrations ranged from 0.06 to $0.87 \text{ mg g dw soil}^{-1}$ (unit in milligram per gram dry weight of soil; Table 1). Again, the surface sample from Zelenyi Mys had lower DOC than the deeper samples at any of the sites. Relative amount of DOC with respect to bulk C for Zelenyi Mys (0.1 m) was also low ($0.68 \pm 0.1\%$), as compared with other sites, where they ranged from $1.03 \pm 0.1\%$ for Duvannyi Yar ($>10 \text{ m}$), to $3.33 \pm 0.3\%$ for Medvezhka ($>10 \text{ m}$). Combining the mass fractions with the percent C of the components shows that about 79% of the organic C in yedoma is associated with the mineral soil, about 15% is present in the humified fraction, 4% exists as organic matter fragments, and the remaining 2% is DOC (Fig. 2). Adding the components together, 21% of the bulk C was contained in organic materials not associated with soil minerals, or dissolved in solution. In many soils, these organic materials are typically the most easily accessible for microbial decomposition while the mineral fraction is typically composed of organic matter more resistant to decay. Here, variation in the organic C contained in the mineral fraction explained much of the variation across sites in bulk C concentration.

The N concentration in bulk yedoma soils ranged from 0.1% to 0.3%, and again most of the N pool was found in the mineral fraction due to the large mass fraction of this component. The mineral fractions had low C/N ratios (5.4–9.2), compared with the humus (13.9–27.0) and roots (5.6–52.0). At Zelenyi Mys (0.1 m), high C/N ratios were observed in the humus and root fractions (27.0 and 52.2, respectively), which could correspond to relatively less decomposed organic matter due to recent inputs to these pools.

The mean $\delta^{13}\text{C}$ of the humus, organic matter fragments, and DOC were statistically indistinguishable at $-25.8 \pm 0.5\%$, $-26.0 \pm 1.1\%$ and $-25.5 \pm 1.0\%$, respectively (average values across six sites), values typical of terrestrial C_3 vegetation (Table 1). The organic C associated with the mineral soil fraction for most sites had higher $\delta^{13}\text{C}$ values ($P < 0.001$) than the humus and organic matter fragments by $1.7 \pm 0.6\%$, possibly indicating preferential loss of ^{13}C depleted labile components or fractionation by microbial respiration. The $\delta^{15}\text{N}$ values of the humus fraction and the organic matter fragments were also similar to typical terrestrial plants, about $2.9 \pm 1.2\%$ and were enriched relative to the

Table 1 Bulk density, elemental concentration and isotopic composition for yedoma soil and component soil fractions (\pm SE)

Sample	Bulk soil										Mineral fraction (>2.1 g cm ⁻³)														
	Density (g cm ⁻³)					C (mg g ⁻¹)					N (%)					C (%)					N (%)				
	C [†] (mg g ⁻¹)	C (%)	$\delta^{13}\text{C}$ (‰)	$\Delta^{14}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\Delta^{14}\text{C}^{**}$ (‰)	C [†] (mg g ⁻¹)	C (%)	$\delta^{13}\text{C}$ (‰)	$\Delta^{14}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\Delta^{14}\text{C}^{**}$ (‰)	C [†] (mg g ⁻¹)	C (%)	$\delta^{13}\text{C}$ (‰)	$\Delta^{14}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\Delta^{14}\text{C}^{**}$ (‰)	C [†] (mg g ⁻¹)	C (%)	$\delta^{13}\text{C}$ (‰)	$\Delta^{14}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\Delta^{14}\text{C}^{**}$ (‰)	
Sukharnaya (>10 m)	1.28	8.4 \pm 0.1	0.84 \pm 0.01	0.09 \pm 0.01	-25.5 \pm 0.1	4.4 \pm 0.1	5.7 \pm 0.2	0.58 \pm 0.02	0.09 \pm 0.01	-25.1 \pm 0.1	4.4 \pm 0.1	—	5.7 \pm 0.2	0.58 \pm 0.02	0.09 \pm 0.01	-25.1 \pm 0.1	4.4 \pm 0.1	—	5.7 \pm 0.2	0.58 \pm 0.02	0.09 \pm 0.01	-25.1 \pm 0.1	4.4 \pm 0.1	—	
Medvezhka (>10 m)	0.74	25.8 \pm 2.3	2.58 \pm 0.23	0.26 \pm 0.02	-26.0 \pm 0.1	3.8 \pm 0.1	22.1 \pm 2.6	2.24 \pm 0.27	0.24 \pm 0.02	-26.0 \pm 0.1	3.8 \pm 0.1	-993 \pm 1	22.1 \pm 2.6	2.24 \pm 0.27	0.24 \pm 0.02	-26.0 \pm 0.1	3.8 \pm 0.1	-993 \pm 1	22.1 \pm 2.6	2.24 \pm 0.27	0.24 \pm 0.02	-26.0 \pm 0.1	3.8 \pm 0.1	-995 \pm 1	
Duvannyi Yar (>10 m)	1.12	11.8 \pm 0.4	1.18 \pm 0.04	0.12 \pm 0.01	-23.0 \pm 0.2	2.6 \pm 0.1	9.3 \pm 0.1	0.94 \pm 0.01	0.11 \pm 0.01	-23.4 \pm 0.3	2.6 \pm 0.2	—	9.3 \pm 0.1	0.94 \pm 0.01	0.11 \pm 0.01	-23.4 \pm 0.3	2.6 \pm 0.2	—	9.3 \pm 0.1	0.94 \pm 0.01	0.11 \pm 0.01	-23.4 \pm 0.3	2.6 \pm 0.2	—	
Zelenyi Mys (0.1 m)	1.11	8.5 \pm 1.1	0.85 \pm 0.11	0.07 \pm 0.01	-25.3 \pm 0.3	4.9 \pm 0.1	4.4 \pm 0.4	0.44 \pm 0.04	0.08 \pm 0.01	-24.6 \pm 0.3	4.9 \pm 0.1	-421 \pm 66	4.4 \pm 0.4	0.44 \pm 0.04	0.08 \pm 0.01	-24.6 \pm 0.3	4.9 \pm 0.1	-421 \pm 66	4.4 \pm 0.4	0.44 \pm 0.04	0.08 \pm 0.01	-24.6 \pm 0.3	4.9 \pm 0.1	-505 \pm 60	
Zelenyi Mys (2 m)	1.00	15.5 \pm 2.3	1.55 \pm 0.23	0.15 \pm 0.03	-22.0 \pm 0.9	4.2 \pm 0.2	13.4 \pm 1.8	1.36 \pm 0.18	0.16 \pm 0.02	-23.4 \pm 0.8	4.3 \pm 0.3	-964 \pm 1	13.4 \pm 1.8	1.36 \pm 0.18	0.16 \pm 0.02	-23.4 \pm 0.8	4.3 \pm 0.3	-964 \pm 1	13.4 \pm 1.8	1.36 \pm 0.18	0.16 \pm 0.02	-23.4 \pm 0.8	4.3 \pm 0.3	-969 \pm 2	
Zelenyi Mys (13 m)	0.62	11.8 \pm 1.5	1.18 \pm 0.15	0.18 \pm 0.02	-24.4 \pm 0.2	2.8 \pm 0.1	8.9 \pm 0.2	0.90 \pm 0.02	0.12 \pm 0.01	-24.4 \pm 0.2	2.8 \pm 0.1	—	8.9 \pm 0.2	0.90 \pm 0.02	0.12 \pm 0.01	-24.4 \pm 0.2	2.8 \pm 0.1	—	8.9 \pm 0.2	0.90 \pm 0.02	0.12 \pm 0.01	-24.4 \pm 0.2	2.8 \pm 0.1	—	

Sample	Humus fraction (<2.1 g cm ⁻³)					Organic fragments				
	C [†] (mg g ⁻¹)	C (%)	$\delta^{13}\text{C}$ (‰)	$\Delta^{14}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	C [†] (mg g ⁻¹)	C (%)	$\delta^{13}\text{C}$ (‰)	$\Delta^{14}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
Sukharnaya (>10 m)	1.6 \pm 0.1	19.6 \pm 0.6	1.2 \pm 0.1	-26.5 \pm 0.1	4.3 \pm 0.1	0.7 \pm 0.3	23.4 \pm 4.5	-26.7 \pm 0.1	—	4.7 \pm 0.0
Medvezhka (>10 m)	2.6 \pm 0.7	18.5 \pm 1.9	1.3 \pm 0.2	-26.4 \pm 0.1	2.9 \pm 0.1	0.5 \pm 0.1	27.7 \pm 5.0	-26.5 \pm 0.3	-991 \pm 2	2.6 \pm 0.0
Duvannyi Yar (>10 m)	2.0 \pm 0.3	20.5 \pm 2.1	1.3 \pm 0.2	-25.6 \pm 0.1	2.1 \pm 0.1	0.3 \pm 0.1	18.0 \pm 0.7	-25.4 \pm 0.3	—	0.7 \pm 0.0
Zelenyi Mys (0.1 m)	1.3 \pm 0.3	28.8 \pm 1.4	1.1 \pm 0.1	-26.0 \pm 0.2	3.7 \pm 0.1	1.0 \pm 0.2	31.9 \pm 2.1	-27.6 \pm 0.5	-552 \pm 70	4.2 \pm 0.0
Zelenyi Mys (2 m)	2.2 \pm 0.3	20.9 \pm 1.1	1.5 \pm 0.1	-25.2 \pm 0.2	3.1 \pm 0.3	0.5 \pm 0.2	24.4 \pm 4.5	-25.1 \pm 0.7	-963 \pm 8	2.8 \pm 0.0
Zelenyi Mys (13 m)	1.9 \pm 0.2	20.8 \pm 0.5	1.5 \pm 0.1	-25.4 \pm 0.1	1.7 \pm 0.1	0.04	19.1	-24.8	—	1.5

Sample	DOC (dissolved organic carbon)		
	C (mg g ⁻¹)	$\delta^{13}\text{C}$ (‰)	$\Delta^{14}\text{C}$ (‰)
Sukharnaya (>10 m)	0.09 \pm 0.02	—	—
Medvezhka (>10 m)	0.87 \pm 0.16	-24.6 \pm 0.3	-938 \pm 29
Duvannyi Yar (>10 m)	0.12 \pm 0.02	—	—
Zelenyi Mys (0.1 m)	0.06 \pm 0.01	-26.5 \pm 0.7	-20 \pm 29
Zelenyi Mys (2 m)	0.30 \pm 0.04	-25.5 \pm 0.5	-851 \pm 3
Zelenyi Mys (13 m)	0.37 \pm 0.05	—	—

*Calculated from mass-balance of mineral, humus and root $\Delta^{14}\text{C}$.

†Calculated from percent carbon multiplied by mass fraction of component. Refers to whole soil while other measurements refer to that component alone.

‡Calculated from mass-balance of bulk, humus and root $\delta^{15}\text{N}$.

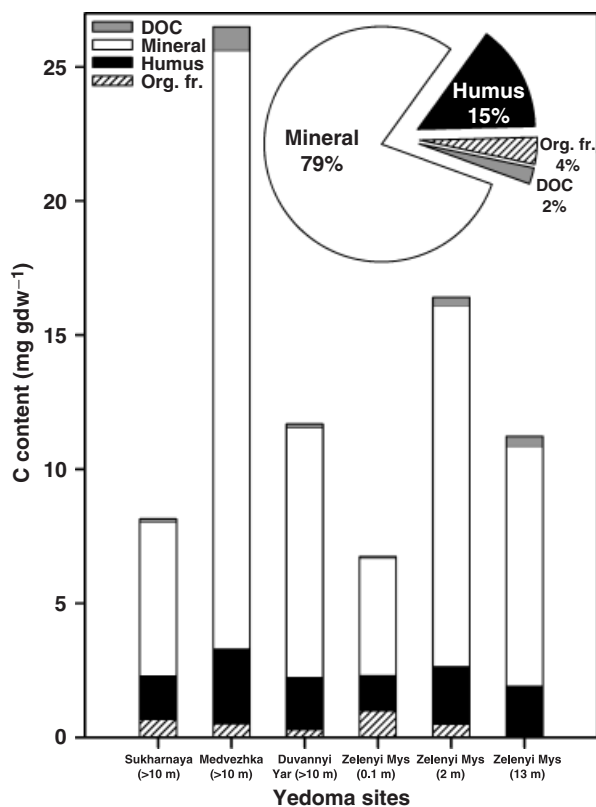


Fig. 2 Contribution of soil fractions in bulk yedoma samples to the total carbon concentration. The *y*-axis is equivalent to percent carbon for the bulk soil sample. The pie-chart (inset) shows the mean proportions of the four components across all six sites.

atmospheric value of 0‰. For all sites except Sukharnaya (>10 m), $\delta^{15}\text{N}$ of mineral organic matter was higher ($P = 0.001$) than the humus fraction and organic matter fragments by $1.2 \pm 0.1\text{‰}$, indicating further enrichment.

We estimated the age of the bulk soil from the ^{14}C content of soil C components at a subset of the sites (Table 1). Estimated bulk $\Delta^{14}\text{C}$ computed from soil C fraction isotope value and relative abundance for Medvezhka (>10 m) and Zelenyi Mys (2 m) are $-993 \pm 1\text{‰}$ and $-964 \pm 1\text{‰}$ (^{14}C -ages $39860 \pm 1150\text{ BP}$ and $26700 \pm 230\text{ BP}$), respectively. The bulk $\Delta^{14}\text{C}$ of Zelenyi Mys (0.1 m) is $-421 \pm 66\text{‰}$ (^{14}C -age $4390 \pm 920\text{ BP}$), reflecting input of modern C from recent vegetation. The $\Delta^{14}\text{C}$ of mineral and humus C were statistically indistinguishable at all sites. At Medvezhka (>10 m) and Zelenyi Mys (2 m), $\Delta^{14}\text{C}$ of organic fragments were also statistically indistinguishable from the mineral and humus C fractions. However, the $\Delta^{14}\text{C}$ of the organic fragments at Zelenyi Mys (0.1 m) was $+110 \pm 21\text{‰}$, significantly younger ($P < 0.001$) as compared to $-505 \pm 60\text{‰}$ and $-552 \pm 70\text{‰}$ for the mineral and humus C fractions, respectively. At all three sites, the $\Delta^{14}\text{C}$ of DOC was significantly higher

($P < 0.04$ for all sites) than that of mineral and humus C fractions, by $55 \pm 29\text{‰}$, $508 \pm 97\text{‰}$ and $114 \pm 9\text{‰}$, respectively.

Incubation CO_2 flux

Most sites showed irregular but generally increasing flux of CO_2 during the first few days of the incubation (Fig. 3). This may indicate acclimation of the yedoma samples to being thawed and the new temperature regime, and the resulting initiation of microbial activity. As the samples were not incubated in sterile conditions, the initial flux period was likely related to the increase in activity of either exogenous or endogenous soil microbes. The fluxes started to increase steadily from the third day, and in all samples, peak CO_2 flux was observed after about 2 weeks of incubation, although the specific peak CO_2 flux and timing of that peak depended on the incubation temperature (Fig. 3). There was more than a fourfold range in the rate of CO_2 flux among sites during the initial period of the incubation. This range in CO_2 flux increased to more than a 10-fold range later in the incubation as the rates at some sites declined to very low levels. For most sites, the CO_2 flux attained a near baseline value of $2\text{--}3\ \mu\text{g C gdw soil}^{-1}\text{ day}^{-1}$ in about 3 months. This result demonstrates the labile nature of some of the organic C stored in yedoma soil, which decomposed in the period of few months once it was thawed and exposed to warmer temperatures. After that, a final baseline of C release ($0.3\text{--}1.6\ \mu\text{g C gdw soil}^{-1}\text{ day}^{-1}$ averaged for three temperatures) was maintained over much longer time periods, beyond 1 year. Thus, cumulative respired CO_2 increased early and then slowed down to a constant rate of increase (Fig 4). The tundra sample from Medvezhka (>10 m) had noticeably higher CO_2 flux (Fig. 4). After 3 weeks, the cumulative amount of C released from Medvezhka (>10 m) was more than three times higher than that from Zelenyi Mys (0.1 m). The reference surface sample from Zelenyi Mys (0.1 m) had lower fluxes than most of the other samples, even though it received current inputs of labile C from actively growing plant roots, DOC, and exudates. The relatively low flux at Zelenyi Mys (0.1 m) compared with other sites demonstrated the lability of soil organic C stored frozen deep in the permafrost.

Differences in flux rates across all sites, including the modern reference, were explained by a highly significant positive relationship between C flux after 30 days and bulk C content (Fig. 5; for all incubation temperatures, $R^2 = 0.93\text{--}0.95$; $P < 0.002$). This result was the same no matter what cumulative C period was used. Correlations between C flux and individual C compo-

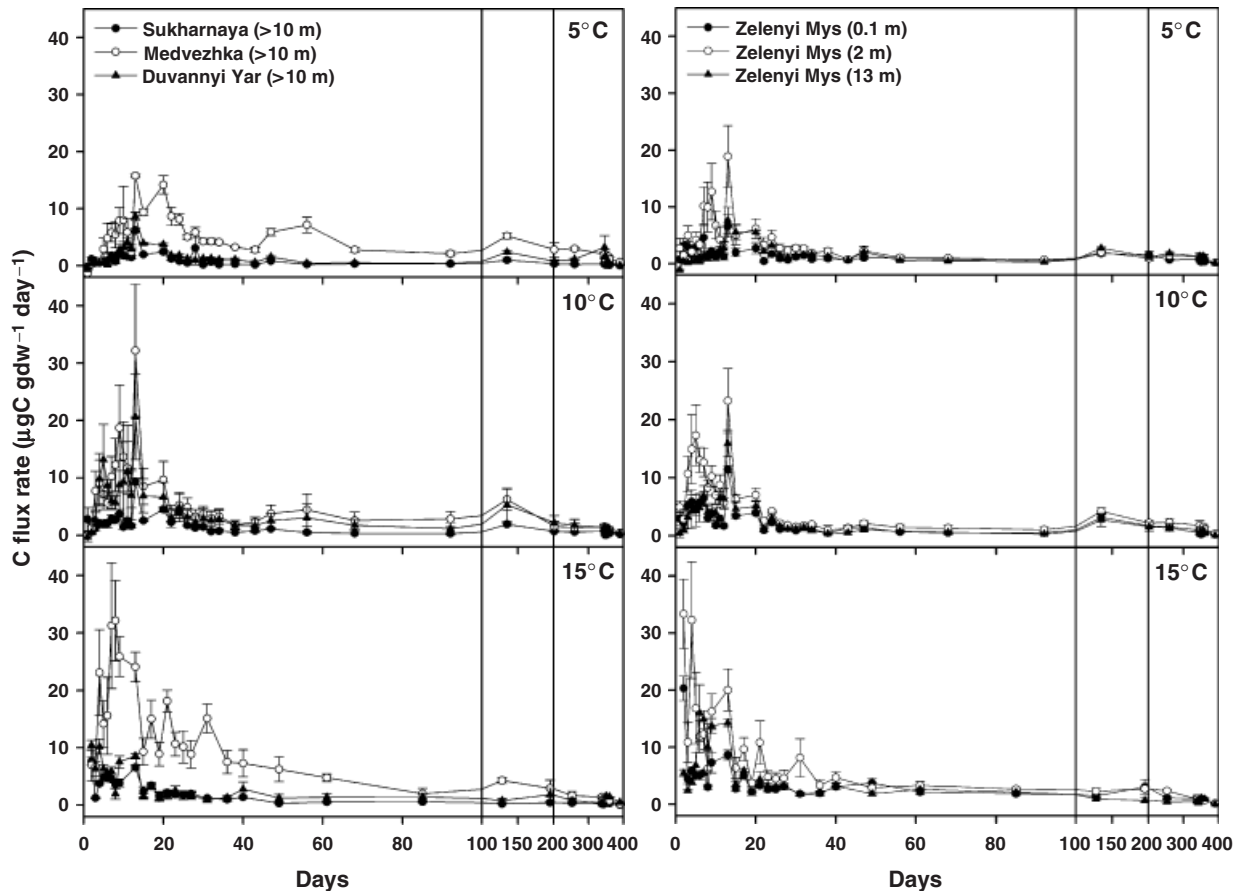


Fig. 3 Carbon flux rates through time over a 1-year incubation experiment at three constant temperatures (mean \pm SE). Black vertical lines delineate changes in the x-axis scale.

nents of mineral soil, humus and DOC were high too (for all incubation temperatures, $R^2 = 0.92\text{--}0.93$, $0.76\text{--}0.82$ and $0.80\text{--}0.87$, respectively; $P < 0.02$). No significant correlation with C flux was observed with organic fragments alone (for all incubation temperatures, $R^2 < 0.02$; $P > 0.79$). Notably, the correlations with bulk C and mineral C were higher than any other components, and the bulk C content was driven by C in the mineral fraction. The increasing slope of the regression line for the 5, 10 and 15 °C incubations clearly demonstrates positive temperature dependence of the flux rates. The regression lines for all temperatures have a similar intercept, corresponding to mean bulk C content of $0.4 \pm 0.1\%$. This may indicate the soil C content that is very resistant to decomposition, perhaps corresponding to a so-called passive C pool. From the slopes of the flux vs. bulk C plots, we determined the mineralization rates of soil organic C, or the percentage of bulk soil C being consumed for respiration. In 1 month, a total of $1.0 \pm 0.1\%$, $1.4 \pm 0.1\%$ and $2.2 \pm 0.3\%$ of the bulk C were released on average from soils incubated at temperatures 5, 10 and 15 °C, respectively. These values

increased to $1.7 \pm 0.1\%$, $2.1 \pm 0.2\%$ and $3.0 \pm 0.4\%$ in 2 months, and $2.1 \pm 0.2\%$, $2.7 \pm 0.4\%$ and $3.1 \pm 0.5\%$ in 3 months. For a yedoma sample with 2.6% bulk C, these 3-month flux rates translate to a loss of $0.55\text{--}0.81 \text{ g C kg soil}^{-1}$. After more than 6 months, when the flux rates attained a steady baseline value for all incubations, the correlation between the flux rates and bulk C was still very high ($R^2 = 0.78\text{--}0.99$; $P < 0.05$). However, this correlation did not include Zelenyi Mys (0.1 m), the modern reference soil, whose average flux rate was almost double that of other sites and did not fall on the trend line. For this baseline period, we calculated a C release rate of $2.65 \pm 0.23\% \text{ yr}^{-1}$ ($0.69 \text{ g C kg soil}^{-1} \text{ yr}^{-1}$ for a yedoma sample with 2.6% bulk C) with no noticeable temperature dependence.

Temperature sensitivity

The Q_{10} values were determined for all sites taking into account the cumulative amount of C released in 30, 60 and 90 days of yedoma incubations, at temperatures of 5, 10 and 15 °C. During the first 30 days of yedoma

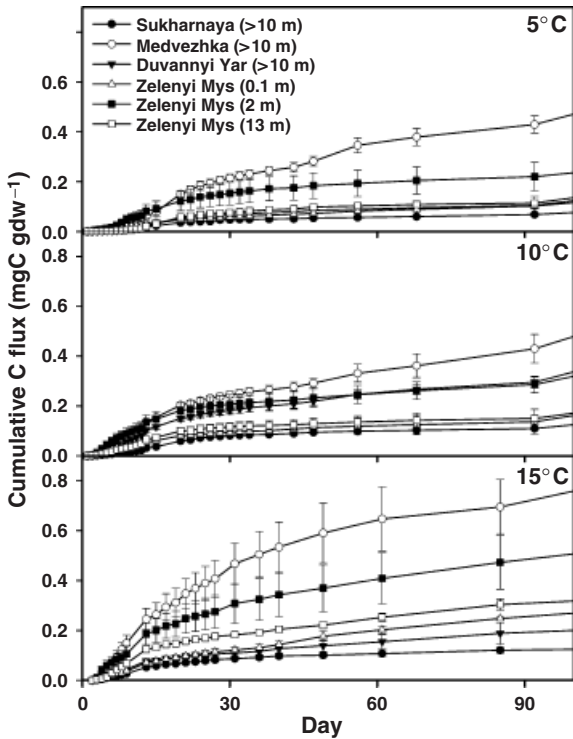


Fig. 4 Cumulative carbon respired from yedoma soil during the first 90 days of incubation (mean ± SE).

incubation, the Q_{10} values range from 1.5 to 2.4 (mean 1.9 ± 0.3 , averaged across all sites). These values practically remain unchanged, ranging from 1.7 to 2.7 after 60 days (mean 2.1 ± 0.4), and 1.7 to 2.9 after 90 days (2.1 ± 0.5). Among the sites, there is no clear difference in the Q_{10} values. Interestingly, no significant difference was observed in the final baseline flux rates after 200 days for different incubation temperatures. This lack of temperature sensitivity could be caused in part by increased depletion of the more labile C in the warmer incubations relative to the cooler incubations.

Isotopes of respired CO₂

Samples of soil-respired CO₂ were collected for all sites incubated at 15 °C for $\delta^{13}\text{C}$ and $\Delta^{14}\text{C}$ measurements after the 98th day of incubation (Table 2). For most sites, the $\delta^{13}\text{C}$ of respiration CO₂ is lower (^{13}C depleted) than the bulk soil $\delta^{13}\text{C}$ by $3.6 \pm 1.8\text{‰}$ ($0.7\text{--}5.9\text{‰}$). For Medvezhka (>10 m) and Zelenyi Mys (2 m), the $\Delta^{14}\text{C}$ of soil-respired CO₂ fell between the $\Delta^{14}\text{C}$ of solid soil C fractions and that of DOC (Fig. 6a–c). For Zelenyi Mys (0.1 m), the $\Delta^{14}\text{CO}_2$ was $22 \pm 15\text{‰}$, significantly higher ($P < 0.001$) than mineral and humus $\Delta^{14}\text{C}$, while in between the value of organic matter fragments ($110 \pm 21\text{‰}$) and DOC ($-20 \pm 29\text{‰}$; Fig. 6b). These

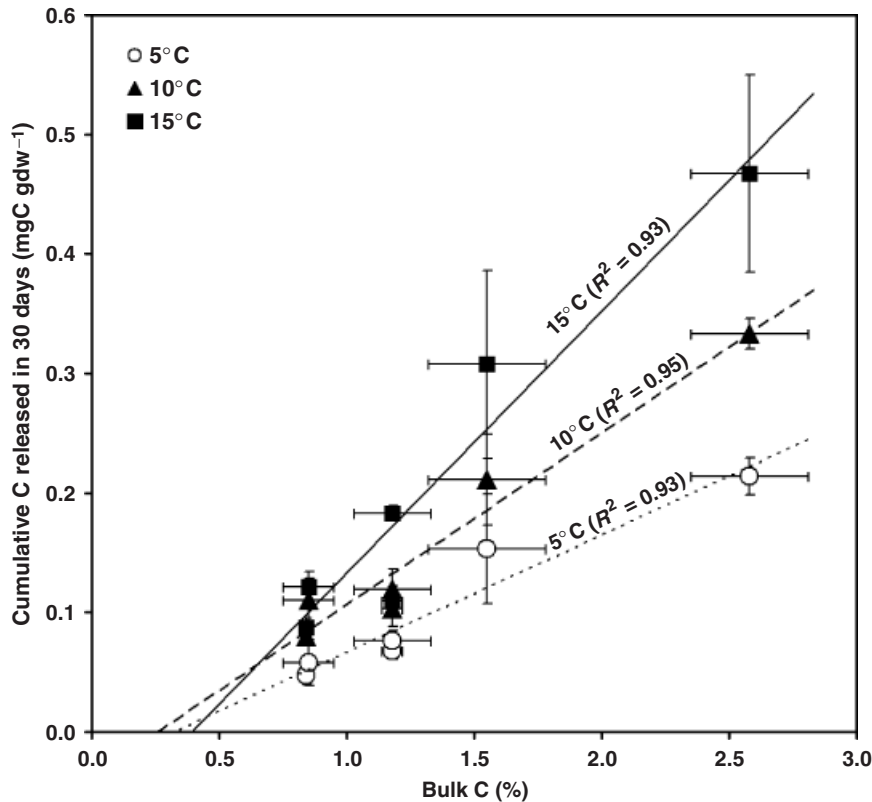


Fig. 5 Correlation between the bulk soil carbon concentration and cumulative respired carbon over the first 30 days of the incubation (mean ± SE).

Table 2 $\delta^{13}\text{C}$ and $\Delta^{14}\text{C}$ of respiration CO_2 from yedoma samples incubated at 15°C (\pm SE)

Sample	$\delta^{13}\text{C}$ (‰)	$\Delta^{14}\text{C}$ (‰)
Sukharnaya (>10 m)	-30.1 ± 0.1	-934 ± 4
Medvezhka (>10 m)	-26.7 ± 0.1	-951 ± 3
Duvannyi Yar (>10 m)	-28.8 ± 0.1	-939 ± 3
Zelenyi Mys (0.1 m)	-29.8 ± 0.1	35 ± 15
Zelenyi Mys (2 m)	-25.3 ± 0.3	-923 ± 10
Zelenyi Mys (13 m)	-27.6 ± 0.5	-948 ± 3

results qualitatively demonstrate the importance of DOC and organic matter fragments to the soil respired CO_2 , even though they constitute only 2% and 4% of the bulk soil C, respectively.

For Medvezhka (>10 m) and Zelenyi Mys (0.1 m) where we analyzed the isotopic composition of soil C fractions, the $\delta^{13}\text{C}$ of the respiration CO_2 falls outside the boundary formed by the individual soil components (Figs 6a, b), although this does not occur in Zelenyi Mys (2 m; Fig. 6c). Thus, the $\delta^{13}\text{C}$ values of respiration CO_2 cannot be explained by the isotopic values and relative utilization of the soil components alone. One must either invoke another unmeasured pool of C, or mass-dependent fractionation that must have occurred during microbial respiration. Because the $\Delta^{14}\text{C}$ values lie within the end-members while the $\delta^{13}\text{C}$ values do not, this points towards mass-dependent fractionation as the more likely explanation. As $\Delta^{14}\text{C}$ values are normalized for ^{13}C fractionation, they are immune to any mass-dependent fractionation effects and directly reflect the $\Delta^{14}\text{C}$ of the relative proportions of organic matter substrate consumed for microbial respiration.

We used the source-partitioning model with $\Delta^{14}\text{C}$ values of the respiration and the soil organic matter components to estimate the possible relative contribution of different source pools to respiration (Figs 7a–c). The relative contribution of each component varied widely among the three sites. At Medvezhka (>10 m), the site with the highest overall fluxes, possible mean contribution to the respiration CO_2 from DOC was 70% (range 59–86%), with about 10% (range 0–41%) of the respiration coming from each of the other three pools. The DOC pool size was largest at Medvezhka (>10 m; Table 1). At Zelenyi Mys (0.1 m), where the DOC pool was the smallest but receives new C input from modern vegetation, had only 24% (0–88%) of its respiration CO_2 from DOC, and 5% (0–18%) from both mineral C and humus. The large majority of CO_2 at this modern reference site was respired from the organic matter fragment pool, which averaged 68% (12–94%) and likely was dominated by recent root inputs. At Zelenyi Mys (2 m), respiration CO_2 appeared to be composed of

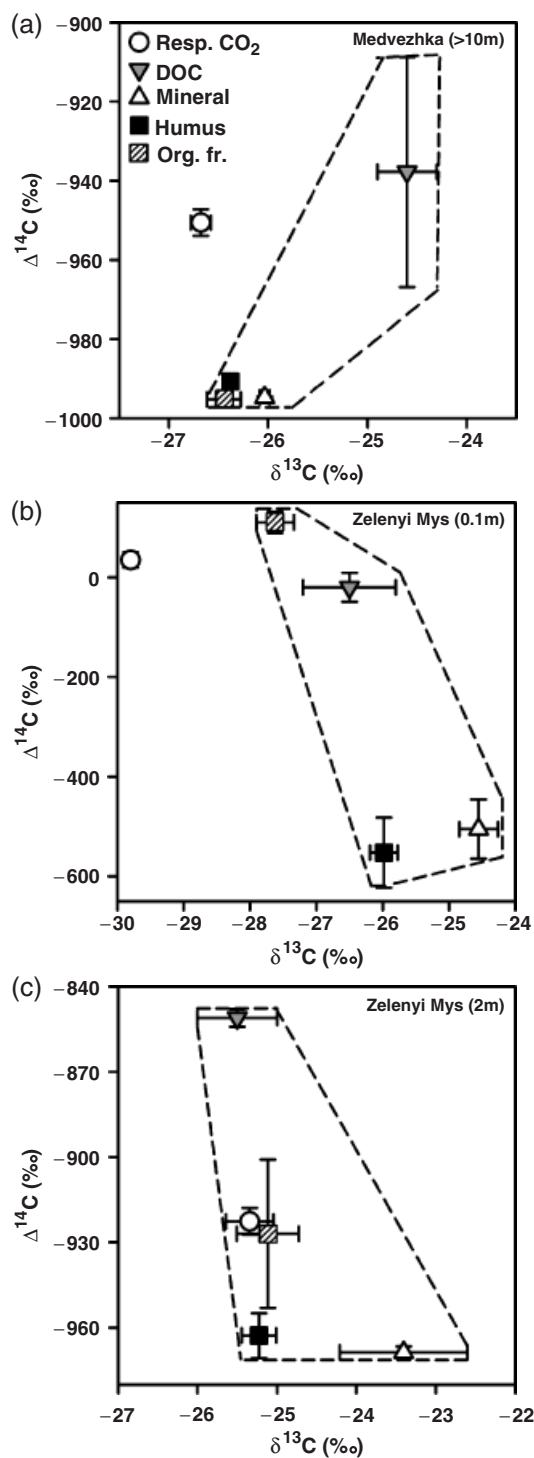


Fig. 6 $\delta^{13}\text{C}$ and $\Delta^{14}\text{C}$ isotopes in soil C components and in respired CO_2 for Medvezhka (>10 m) and Zelenyi Mys (0.1 and 2 m) where the isotopic values of all components were measured (mean \pm SE). The polygon (dashed line) represents the zone within which the isotopic value of respiration CO_2 must lie for a valid mass-balance with four component sources. Note that the respiration CO_2 does produce a valid mass-balance for $\Delta^{14}\text{C}$ (y-axis) but not for $\delta^{13}\text{C}$ (x-axis).

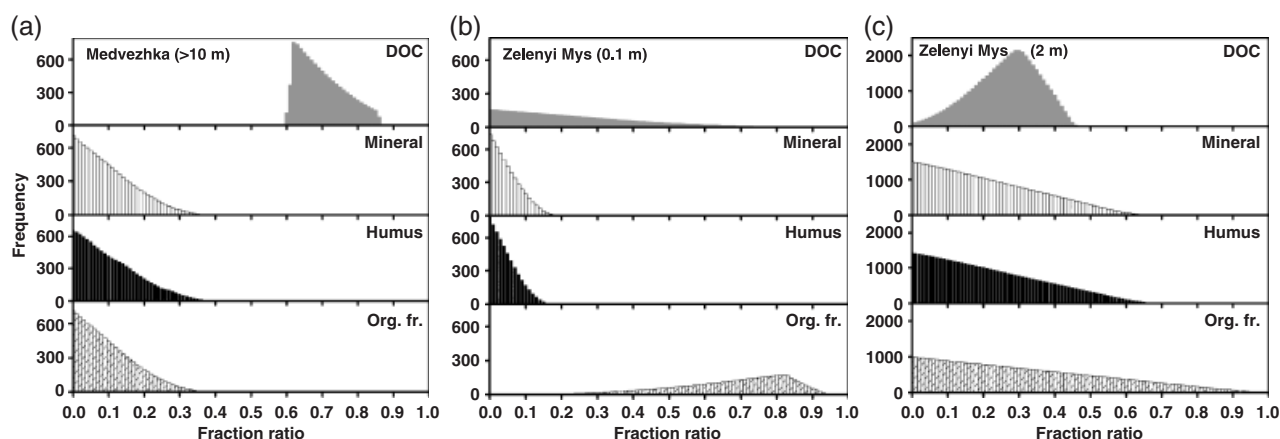


Fig. 7 Source partitioning estimation for Medvezhka (> 10 m) and Zelenyi Mys (0.1 and 2 m) based on $\Delta^{14}\text{C}$ values of respiration and of soil C components. The y -axis denotes the number of possible solutions that matched the observed respiration values; lower numbers and smaller standard deviations on the x -axis demonstrate more constraint on the model predictions.

C respired from each component in roughly equal proportions.

We repeated the partitioning calculations using both the $\Delta^{14}\text{C}$ and $\delta^{13}\text{C}$ data (dual-isotope mode) assuming that there was a constant 2‰ fractionation that occurred to the $\delta^{13}\text{C}$ of respiration (respiration CO_2 lighter by 2‰). This assumed amount was based on a constant fractionation that could have occurred at all three sites where we did the partitioning. Larger fractionation values could not be accommodated at Zelenyi Mys (2 m), whereas a smaller fractionation value could not have been accommodated by the other two sites to make the mass balance equation work. Adding $\delta^{13}\text{C}$ values provided another constraint to the partitioning calculation. As source partitioning in dual isotope mode ($\Delta^{14}\text{C}$ – $\delta^{13}\text{C}$) is constrained by two tracers, the results had narrower ranges and smaller numbers of possible solutions. Interestingly, the partitioning results did not differ substantially from the means estimated using $\Delta^{14}\text{C}$ values alone. At Medvezhka (> 10 m), the mean contribution to respiration CO_2 as determined from dual isotope partitioning were: 86% (80–90%), 6% (0–20%), 4% (0–16%) and 4% (0–15%), from DOC, mineral C, humus and organic fragments, respectively. At Zelenyi Mys (0.1 m), these values were: 4% (0–15%), 2% (0–7%), 5% (0–13%) and 89% (82–94%), respectively. While at Zelenyi Mys (2 m), these values are, 30% (35–46%), 37% (19–68%), 12% (0–43%) and 21% (0–76%), respectively.

Discussion

Amount and age of C released during incubation

The results of the incubation experiments revealed important aspects of C flux from thawing of these deep permafrost mineral soils. After the initiation of incuba-

tion, the flux of CO_2 for all sites rose to a maximum value within about 3 weeks. The amounts of C released was proportional to the bulk soil C content and incubation temperature, and most soils from the permafrost with higher bulk C content released higher amount of C relative to the surface modern reference soil from the active layer at Zelenyi Mys. Over the 2 months following the peak flux, the CO_2 flux gradually decreased to about 5–10% of the peak rate, and continued at that baseline level for the remaining period of incubation. The long-term CO_2 flux for permafrost soil was also strongly related to the bulk soil C content. Mass-balance of component ^{14}C -ages indicated the bulk organic matter to be ~40 ka BP for Medvezhka (> 10 m), ~27 ka BP for Zelenyi Mys (2 m) and ~4 ka BP for the modern reference soil of Zelenyi Mys (0.1 m), although these bulk ages are mixtures of pools with different ages (Table 1). Despite the wider range of bulk organic matter ages, the ^{14}C -age of respiration CO_2 released across all permafrost soil was relatively consistent, ranging from ~21–25 ka BP, whereas bomb-produced ^{14}C dominated respiration in Zelenyi Mys (0.1 m), the only sample that currently received inputs from modern vegetation. Inversion calculations using the isotopic composition of the soil C components and respiration CO_2 indicated the labile C components (e.g. DOC and organic fragments) as the main source of C released, although DOC was much more important in the permafrost soils in comparison with the modern reference where the organic matter fragments dominated.

Temperature sensitivity of decomposition

Our year-long incubation experiment demonstrated the transition of temperature to substrate dependence in

organic-rich mineral soil. During the initial 3 months of incubation, there was a distinct temperature sensitivity for the decomposition rates of permafrost soils with average Q_{10} of 1.9 ± 0.3 at the outset of the experiment. This value is similar to that observed for heterotrophic respiration from laboratory studies with Q_{10} of 2.51 ± 1.37 ($n = 169$) as compiled by Lenton & Huntingford (2003), but low for soils from cold regions (Kirschbaum, 1995).

This temperature dependence was valid only for the organic matter that decomposed during the initial few months of incubation as no temperature dependence was observed after 6 months of incubation ($Q_{10} \sim 1$), although calculating Q_{10} in this manner confounds substrate limitation with temperature effects (Holland *et al.*, 2000). Giardina & Ryan (2000) demonstrated lack of temperature dependence of organic matter decomposition in mineral soils from sites around the world with different temperature regimes, although this conclusion has been both supported (Fang *et al.*, 2005) and refuted (Davidson *et al.*, 2000; Knorr *et al.*, 2005). Apparent temperature independence of decomposition in the advanced stage of incubation do not necessarily indicate weaker or absence of temperature sensitivity of decomposition for the residual organic matter (Davidson & Janssens, 2006). The transition of this temperature dependence can be explained by rapid consumption during the initial phase of incubation of more labile organic matter components with faster turnover rates and smaller C pool size, such as the DOC pool (Kirschbaum, 2004; Knorr *et al.*, 2005). Remaining organic matter may be physically and/or chemically protected by the soil mineral matrix, thus, potentially rendering it insensitive to temperature even as it continues to decompose (Baldock & Skjemstad, 2000). While our experiment did not separate the true effect of temperature alone from changing quantities of C, lack of difference between flux rates at different temperatures suggests that the long-term release of C from these soils will not be strongly dependent on the specific temperature, as long as it is unfrozen. However, the initial pulse of C released in the first 90 days will be more sensitive to temperature.

Sources of CO_2 for heterotrophic respiration

From mass-balance calculations done with $\Delta^{14}C$ values alone, and with dual isotope values ($\Delta^{14}C - \delta^{13}C$), it was evident that DOC was a major contributing substrate for heterotrophic respiration in permafrost samples within the 3–4 months period of incubation, when we measured the isotopes of respiration (Fig. 7). For all sites, the cumulative amount of C released at $15^\circ C$ in 3 months (0.09 – 0.47 mg gdw soil $^{-1}$) closely matched the

size of their initial DOC pool (0.09 – 0.87 mg gdw soil $^{-1}$), with R^2 of 0.87. Organic matter associated with mineral soil and humus contributed to yedoma respiration CO_2 to a varying degree, likely as a consequence of the size of the DOC pool in different samples. As DOC becomes depleted, other pools by difference must increase in importance. For the DOC-poor sample of Zelenyi Mys (0.1 m), recent organic matter fragments contributed most to the respiration CO_2 .

While DOC appeared to support the initial respiration, the strong correlations between the flux rates and bulk C content that was still maintained even in the late phase of the experiment suggested the flux rates were sustained during the final phase of incubation by much larger C pools (Fig. 5 and Table 1). Even though the source partitioning calculation showed DOC to be very important, correlation between DOC and cumulative flux was lower than the correlation with mineral or bulk C, suggesting that all pools contribute to the initial flux in the first 90 days. Indeed, DOC release from mineral surfaces is a combination of the sorption processes of the mineral surface and the solute concentration, thus, the mineral pool may be an important source to the DOC pool (Neff & Hooper, 2002). After the initial release of C soon after thawing, this large mineral C pool will sustain the heterotrophic respiration in these permafrost soils for longer time scales. Thus, at decadal time scales, contribution of mineral and humus C pool will be relatively more important, as can be seen in the source partitioning for Zelenyi Mys (2 m; Fig. 7c). Respiration is expected to continue until the organic C pool is about 0.4% (Fig. 5). This remaining passive soil C pool is likely to have much longer turnover times and corresponds to measurements of European and Alaskan loess soil C content that during the Pleistocene had higher C contents, but have as lost that as the permafrost boundary moved northward at the onset of the Holocene (Zimov *et al.*, 2006).

At Zelenyi Mys (0.1 m), DOC, mineral and humus C pools were small relative to organic fragments that are derived from annual inputs from current vegetation (Fig. 2, Table 1). For Medvezhka (>10 m) and Zelenyi Mys (0.1 and 2 m), younger ^{14}C -ages of DOC compared with ages of mineral and humus C possibly indicate transport of younger and mobile C components across the active layer to the bottom of the soil profiles where it became incorporated into permafrost. The source of this DOC is not entirely from modern vegetation, as indicated by older DOC ^{14}C -ages compared with the organic matter fragments at Zelenyi Mys (0.1 m). Organic matter of various ages contribute to the formation of DOC, which then leaches down the active layer, which can explain the younger DOC

^{14}C -age relative to the other soil C components from the same sample.

Potential of C loss from yedoma

The results from our incubation experiments and elemental analysis of yedoma soils provide clues about the potential of the yedoma C stock to release C in case of thawing. Although each of these soil C components will respond at different time scales, the most important factor that correlated with the amount of C respired was the bulk C content. There were considerable differences in C content among the sites studied here, ranging from $0.85 \pm 0.11\%$ for the thawed modern reference Zelenyi Mys (0.1 m) with generally higher values ($0.84 \pm 0.20\%$ to $2.58 \pm 0.40\%$) for the deeper permafrost soil. In this study, the mean concentration of organic C in yedoma ($1.51 \pm 0.17\%$) was somewhat lower as compared with other more widespread studies. A mean C content of $2.56 \pm 0.38\%$ was been reported for 57 yedoma samples collected along Kolyma River (Zimov *et al.*, 2006). While there were differences in the amount of organic matter fragments and humus trapped in the permafrost (Fig. 2, Table 1), variability in the mineral C fraction actually was the dominant control over variation in C content across sites. Using an average yedoma soil C content of 2.6% ($26 \text{ g C kg soil}^{-1}$), field soil bulk density of 0.7 g cm^{-3} (inclusive of the ice content), mean loess thickness of 25 m, and total aerial extent of 10^6 km^2 , previous estimates are that $\sim 500 \text{ Pg C}$ are presently frozen in yedoma of northeastern Siberia (Zimov *et al.*, 2006). This calculation excludes occasional organic rich peat layers observed in yedoma soil profiles (Schirrmister *et al.*, 2002). It is important to note that the above estimate of total C stock is equal in quantity to an earlier estimate by Gorham (1991) of global high-latitude ecosystems for top 1 m of soil. This approximately doubles the previous estimate of the high-latitude soil organic C pool, and demonstrates the significant size and potential importance of the yedoma C pool relative to other terrestrial C reservoirs.

In the case of warming, the temperature of different yedoma permafrost horizons will rise to different amounts as changing air temperatures propagate into the permafrost. While our research is not intended to simulate the actual rise in soil temperature, we made some estimates of C release based on simple calculations. If we assume only 10% of total yedoma C stock (46 Pg C) thaw when exposed to warming to 5°C , 2% of the bulk C ($\sim 0.9 \text{ Pg C}$ total) will be released in a relatively short period through decomposition of labile C components. Permafrost thawing of this magnitude has been predicted by simulation models of future

permafrost temperatures (Lawrence & Slater, 2005). In our laboratory incubation experiment, even though the long-term C release was apparently temperature independent, it was still sustained at a slow but steady level for the entire period of observation (200 days to 1 year) proportional to bulk soil C content. Our results therefore suggest that, the long-term loss of yedoma C would be sustained at a rate of 2.5% C loss per year or about 1 Pg C yr^{-1} , assuming the thawed yedoma C amounts above. While the initial pulse of C release will be supported by labile C components such as DOC, the long-term C loss will be from slower decomposition of mineral and humus organic matter. Assuming the respiration is sustained until the bulk C concentration of yedoma decreases to 0.4% (from 2.6%), and uniform temperature (of 5°C) throughout the year, this rate would continue for about four decades, until a total of $\sim 40 \text{ Pg C}$ were transferred directly or indirectly to the atmosphere. While seasonal temperature changes would appear to slow this rate of release, once deep permafrost is thawed it is typically buffered from seasonal temperatures at the surface that affect the active layer. While simplistic and not an actual trajectory of release, our results and calculations demonstrate the potential vulnerability and labile nature of the yedoma C stock that has remained frozen since the Pleistocene. Detailed knowledge on yedoma C distribution and nature of the frozen organic matter is crucial to fully evaluate the potential of thawing yedoma to influence the global C cycle.

Conclusions

Laboratory incubations of permafrost soil samples from northeastern Siberia revealed the relatively labile nature of this deep soil organic matter when thawed:

- The flux rates attained maximum value after about 3 weeks of incubation, and increased with incubation temperatures corresponding to mean Q_{10} value of 1.9 ± 0.3 .
- The amount of C released was strongly correlated with bulk C content. After ~ 90 days, $2.1 \pm 0.2\%$, $2.7 \pm 0.4\%$ and $3.1 \pm 0.5\%$ of the bulk C was released as respiration at 5, 10, and 15°C , respectively. Flux of C was correlated highly with mineral soil C, humus and DOC.
- The long-term flux rates for all temperatures (after 200 days and up to 1 year of incubation) stabilized at $1.7 \mu\text{g C g dw soil}^{-1} \text{ day}^{-1}$ with no apparent temperature dependence. During this final phase of incubation, the C release rate was still proportional to bulk C, where $2.65 \pm 0.23\%$ of the organic C pool

was consumed per year across all incubation temperatures.

- Inversion of $\Delta^{14}\text{C}$ and $\delta^{13}\text{C}$ values of soil C components and soil respired CO_2 indicated the major contribution of DOC to the respiration flux from permafrost samples, while the respiration flux from the modern active layer reference soil was dominated by organic matter fragments (such fine roots) decomposition.
- If 10% of the total C stock frozen in deep loess soils in Siberia becomes thawed and exposed to temperatures of 5°C , about 1 Pg of C would be released initially, while about 40 Pg C could be released over four decades. This C release will be from decomposition of organic matter frozen since the Pleistocene, thus, injecting ancient C into the atmosphere.

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References

- ACIA (2004) *Impacts of a Warming Arctic: Arctic Climate Impact Assessment*. Cambridge University Press, Cambridge, UK.
- Baldock JA, Skjemstad JO (2000) Role of the soil matrix and minerals in protecting natural organic materials against biological attack. *Organic Geochemistry*, **31**, 697–710.
- Briffa KR, Jones PD, Schweingruber FH *et al.* (1995) Unusual twentieth-century summer warmth in a 1,000-year temperature record from Siberia. *Nature*, **376**, 156–159.
- Cess RD, Potter GL, Zhang M-H *et al.* (1991) Interpretation of snow-climate feedback as produced by 17 general circulation models. *Science*, **253**, 888–892.
- Chapin FS, Sturm M, Serreze MC *et al.* (2005) Role of land surface changes in Arctic summer warming. *Science*, **310**, 657–660.
- Chapman WL, Walsh JE (1993) Recent variations of sea ice and air temperature in high latitudes. *Bulletin of the American Meteorological Society*, **74**, 33–47.
- Cox PM, Betts RA, Jones CD *et al.* (2000) Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature*, **408**, 184–187.
- Davidson EA, Janssens IA (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature*, **440**, 165–173.
- Davidson EA, Trumbore SE, Amundson R (2000) Soil warming and organic carbon content. *Nature*, **408**, 789–790.
- Davis TN (2001) *Permafrost: A Guide to Frozen Ground in Transition*. University of Alaska Press, Fairbanks, AK, USA.
- Dioumaeva I, Trumbore S, Schuur EAG (2003) Decomposition of peat from upland boreal forest: temperature dependence and sources of respired carbon. *Journal of Geophysical Research*, **108**, 8222, doi: 10.1029/2001JD000848.
- Eliasson PE, McMurtrie RE, Pepper DA (2005) The response of heterotrophic CO_2 flux to soil warming. *Global Change Biology*, **11**, 167–181, doi: 10.1111/j.1365-2486.2004.00878.x.
- Fang C, Smith P, Moncrieff JB (2005) Similar response of labile and resistant soil organic matter pools to changes in temperature. *Nature*, **433**, 57–59.
- Freeman C, Fenner N, Ostle NJ *et al.* (2004) Export of dissolved organic carbon from peatlands under elevated carbon dioxide levels. *Nature*, **430**, 195–198.
- Frey KE, Smith LC (2005) Amplified carbon release from vast West Siberian peatlands by 2100. *Geophysical Research Letters*, **32**, L09401, doi: 10.1029/2004GL022025.
- Giardina CP, Ryan MG (2000) Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. *Nature*, **404**, 858–861.
- Gorham E (1991) Northern peatlands: role in the carbon cycle and probable responses to climatic warming. *Ecological Applications*, **1**, 182–195.
- Goulden ML, Wofsy SC, Harden JW *et al.* (1997) Sensitivity of boreal forest carbon balance to soil thaw. *Science*, **279**, 214–217.
- Holland EA, Neff JC, Townsend AR *et al.* (2000) Uncertainties in the temperature sensitivity of decomposition in tropical and subtropical ecosystems: implications for models. *Global Biogeochemical Cycles*, **14**, 1137–1151.
- Hughes MK, Vaganov EA, Shiyatov SG *et al.* (1999) Twentieth century summer warmth in northern Yakutia in a 600-year context. *The Holocene*, **9**, 629–634.
- Kienast F, Schirmermeister L, Siebert C (2005) Palaeobotanical evidence for warm summers in the East Siberian Arctic during the last cold stage. *Quaternary Research*, **63**, 283–300.
- Kirschbaum MUF (1995) The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. *Soil Biology and Biochemistry*, **27**, 753–760.
- Kirschbaum MUF (2004) Soil respiration under prolonged soil warming: are rate reductions caused by acclimation or substrate loss? *Global Change Biology*, **10**, 1870–1877, doi: 10.1111/j.1365-2486.2004.00852.x.
- Knorr W, Prentice IC, House JI (2005) Long-term sensitivity of soil carbon turnover to warming. *Nature*, **433**, 298–301.
- Kuzmin YV, Orlova LA (2004) Radiocarbon chronology and environment of woolly mammoth (*Mammuthus primigenius* Blum.) in northern Asia: results and perspectives. *Earth-Science Reviews*, **68**, 133–169.
- Lawrence DM, Slater A (2005) A projection of severe near-surface permafrost degradation during the 21st century. *Geophysical Research Letters*, **32**, L24401.
- Lenton TM, Huntingford C (2003) Global terrestrial carbon storage and uncertainties in its temperature sensitivity examined with a simple model. *Global Change Biology*, **9**, 1333–1352.
- Mack MC, Schuur EAG, Bret-Harte MS *et al.* (2004) Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. *Nature*, **431**, 440–443.
- Melillo JM, Steudler PA, Aber JD *et al.* (2002) Soil warming and carbon-cycle feedbacks to the climate system. *Science*, **298**, 2173–2176.
- Neff JC, Hooper DU (2002) Vegetation and climate controls on potential CO_2 , DOC and DON production in northern latitude soils. *Global Change Biology*, **8**, 872–884.

- Oechel WC, Hastings SJ, Vourlitis G *et al.* (1993) Recent change of Arctic tundra ecosystems from a net carbon dioxide sink to a source. *Nature*, **361**, 520–523.
- Osterkamp TE, Romanovsky VE (1999) Evidence for warming and thawing of discontinuous permafrost in Alaska. *Permafrost and Periglacial Processes*, **10**, 17–37.
- Overpeck J, Hughen K, Hardy D *et al.* (1997) Arctic environmental change of the last four centuries. *Science*, **278**, 1251–1256.
- Phillips DL, Gregg JW (2003) Source partitioning using stable isotopes: coping with too many sources. *Oecologia*, **136**, 261–269.
- Prentice IC, Farquhar GD, Fasham MJR *et al.* (2001) The carbon cycle and atmospheric carbon dioxide. In: *Climate Change 2001: The Scientific Basis* (eds. Houghton JT *et al.*), pp. 185–225. Cambridge University Press, Cambridge, UK.
- Romanovsky NN (1993) *Fundamentals of the Cryogenesis of the Lithosphere (in Russian)*. University Press, Moscow, Russia.
- Romanovsky VE, Osterkamp TE, Sazonova TS *et al.* (2001) Permafrost temperature dynamics along the East Siberian transect and an Alaskan transect. *Tohoku Geophysical Journal*, **36**, 224–229.
- Serreze MC, Walsh JE, Chapin FS *et al.* (2000) Observational evidence of recent change in the northern high-latitude environment. *Climatic Change*, **46**, 159–207.
- Schimel DS (1995) Terrestrial ecosystems and the carbon cycle. *Global Change Biology*, **1**, 77–91.
- Schirrmeyer L, Siegert C, Kuznetsova T (2002) Paleoenvironmental and paleoclimatic records from permafrost deposits in the Arctic region of Northern Siberia. *Quaternary International*, **89**, 97–118.
- Schuur EAG, Trumbore SE, Mack MC *et al.* (2003) Isotopic composition of carbon dioxide from a boreal forest fire: inferring carbon loss from measurements and modeling. *Global Biogeochemical Cycles*, **17**, 1001, doi: 10.1029/2001GB001840.
- Scott EM, Bryant C, Carmi I (2003) Pre-testing and homogeneity results for samples used in the Fourth International Radiocarbon Intercomparison (FIRI). *TIRI & FIRI special volume, Radiocarbon*, **45**, 135–150.
- Southon J, Santos G, Druffel-Rodriguez K *et al.* (2004) The keck carbon cycle AMS laboratory, University of California, Irvine: initial operation and a background surprise. *Radiocarbon*, **46**, 41–49.
- Stuiver M, Polach HA (1977) Discussion: reporting of ^{14}C data. *Radiocarbon*, **19**, 355–363.
- Trumbore SE, Chadwick O, Amundson A (1996) Rapid exchange between soil carbon and atmospheric carbon dioxide. *Science*, **272**, 393–396.
- Trumbore SE, Zheng S (1996) Comparison of fractionation methods for soil organic matter ^{14}C analysis. *Radiocarbon*, **38**, 219–229.
- Tu KP, Brooks PD, Dawson TE (2001) Using septum-capped vials with continuous-flow isotope-ratio mass spectrometric analysis of atmospheric CO_2 for Keeling plot applications. *Rapid Communications in Mass-spectrometry*, **15**, 952–956.
- USDA (1999) *Soil Taxonomy: A Basic System of Soil Classification for Making and Interpreting Soil Surveys*. Agriculture Handbook Number 436, 2nd edn. US Department of Agriculture, Natural Resources Conservation Service, Washington, DC, USA.
- Vasil'chuk A, Kim J-C, Vasil'chuk Y (2005) AMS ^{14}C dating of pollen concentrate from Late Pleistocene ice wedges from the Bison and Seyaha sites in Siberia. *Radiocarbon*, **47**, 243–256.
- Vogel JS, Nelson DE, Southon JR (1987) ^{14}C background levels in an accelerator mass spectrometry system. *Radiocarbon*, **29**, 323–333.
- Zimov SA, Schuur EAG, Chapin FS (2006) Permafrost and the global carbon budget. *Science*, **312**, 1612–1613.
- Zimov SA, Zimova GM, Davidov SP *et al.* (1993) Winter biotic activity and production of CO_2 in Siberian soils: a factor in the greenhouse effect. *Journal of Geophysical Research*, **98**, 5017–5023.