Variable respiration rates from incubated permafrost soil extracts in the Kolyma River lowlands region of Northeast Siberia

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Thawing permafrost soils supply dissolved organic carbon (DOC) to aquatic systems; however, the magnitude, variability, and fate of this DOC is not well constrained. The objective of this study was to examine respiration potentials from soil DOC derived from seasonally-thawed and near-surface (<1.5 m) permafrost soils collected from five different locations in the Kolyma River Basin, NE Russia. We measured soil bulk organic carbon (OC) content, water-soluble macronutrients (DOC, NH_4, PO_4), and the heterotrophic respiration potentials of the extract DOC in five-day laboratory incubations. DOC concentrations in our soil extracts ranged from 2.8-27.9 mg L^{-1} (mean 13.5 ± 2.5 mg L^{-1}, n = 14). Mean carbon respiration was 0.13±0.08 mg C (-0.03-0.47 mg C, n=16) and 8.86-31.35% total DOC (8.7-31.4%, n=14). While DOC concentration in the extracts was a function of bulk soil OC concentration, we did not find a relationship between respiration rates and soil OC or DOC concentrations. Respiration was highest in top active layer soils (10-15 cm depth) but varied widely among sites. Respiration potentials were lowest at the bottom of the seasonally-thawed active layer (30-50 cm depth), and C respiration of icy, organic-rich Pleistocene-aged permafrost (yedoma) extracts varied across geographic locations (0.04-0.47 mg C respired, 8.7-31.4% total DOC). Despite the small sample size, our study indicates that near-surface soils and permafrost in the Kolyma River Basin are spatially variable in terms of both soil OC content and soil extract respiration rates and that OC contents do not predict C respiration rates. While a larger sample size would be useful to confirm these results at broader geographic scales, these initial results suggest that soil OC heterogeneity should be taken into account in efforts to determine the fate of soil OC released from permafrost-dominated terrestrial ecosystems to aquatic ecosystems following permafrost thaw.

Keywords: arctic, carbon, permafrost, respiration, Russia, yedoma

Introduction

Perennially frozen ground (permafrost) contains a vulnerable carbon (C) pool susceptible to warming and thaw (Zimov et al. 2006a; Schuur et al. 2008; Schuur et al. 2015). Permafrost covers 22% of the Northern Hemisphere (Brown et al. 1998) and contains an estimated 1140-1580 Pg of organic carbon (OC)— approximately half of the world's below ground OC (Hugelius et al. 2014; Schuur et al. 2015). Temperatures in the Arctic have increased an average of 0.6˚C per decade over the last 30 years, which is twice as fast as the global average (IPCC 2013). This climate warming triggers the release of permafrost OC via permafrost thaw and erosion, exporting large amounts of terrestrial C to aquatic environments (Striegl et al. 2005; Frey and McClelland 2009; Vonk et al. 2013; Cory et al. 2014; Larouche et al. 2015) and making previously frozen OC from a range of soil depths available for microbial decomposition (Goulden et al. 1998; Dutta et al. 2006; Schuur et al. 2008; Tarnocai et al. 2009; Vonk et al. 2013; Mann et al. 2014). Thaw depths of the seasonally-thawed active layer rapidly respond to warming air temperatures (Hinkel and Nelson 2003; Frauenfeld et al. 2004) and active layer thicknesses are projected to increase as a result of climate warming, releasing factions of previously frozen OC from near-surface permafrost (Zhang et al. 2005; Frey and McClelland 2009).

Deepening active layers are projected to increase the degree of interaction between soils and water (Neff et al. 2006; Battin et al. 2008; Davydov et al. 2008; Frey and McClelland 2009), allowing water-soluble factions of recently-thawed OC to dissolve into soil water. The permafrost underlying the active layer prevents the subsurface flow from percolating deeper (Wickland et al. 2007), facilitating soil water export which, in turn, may lead to an increase in the export of permafrost OC to inland waters (Vonk et al. 2013; Spencer et al. 2015). Dissolved fractions of terrestrial OC can fuel microbial respiration and the production of greenhouse gasses (Ågren et al. 2008; Battin 2008; Wang et al. 2014). When terrestrial dissolved organic carbon (DOC) enters aquatic systems, a portion is further mineralized to CO_2, which can escape to the atmosphere or be assimilated by plants and algae living in the water (Tao and Lin 2000; Vonk et al. 2013). Other potential fates of terrestrially-derived DOC in aquatic systems are export via transportation, sequestration via flocculation and sedimentation, or bioassimiliation by microbes and organisms through aquatic food webs (Cole et al. 2007; McGuire et al. 2010).

Up to 40% (210-456 Pg C; Strauss et al. 2013; Walter Anthony et al. 2014) of permafrost soil OC is stored in ice-rich loess-dominated soils referred to as *yedoma*. Formed in unglaciated regions of Siberia, Alaska, and NW Canada during the late Pleistocene (Soloviev 1959; Zimov et al. 2006a; Kanevskiy et al. 2011), yedoma soils are thick (<50 m) silt-dominated deposits rich (2-30%) in OC for mineral soils (Schirrmeister et al. 2011a). Yedoma is extensive in NE Siberia, where it underlies an area of over 1,000,000 km^2 and averages 25 m in thickness (Romanovskii 1993; Zimov et al. 2006a). Evidence shows yedoma deposits are currently thawing (Romanovsky et al. 2010), but the potential for greenhouse gas production by microbial decomposition of organic matter in thawed yedoma soils has been studied with limited geographic and spatial scope (Zimov et al. 1997; Zimov et al. 1993; Dutta et al. 2006; Walter et al. 2007a; Lee et al. 2012; Mann et al. 2012; Knoblauch et al. 2013; Vonk et al. 2013).

Ancient (20,000-35,800 yr bp) DOC from yedoma soils has found to be more biolabile than Arctic stream, river, and permafrost DOC from non-yedoma systems (Vonk et al. 2013; Mann et al. 2014; Drake et al. 2015; Spencer et al. 2015). However, it has been suggested that the OC content of yedoma soils is not evenly distributed across geographic space and stratigraphic layers (Dutta et al. 2006; Zimov et al. 2006a and 2006b; Schirrmeister et al. 2011a).

Respiration rates of ancient (21,700 yr bp) DOC from a single yedoma outcrop in the Kolyma River Basin, NE Siberia were found to be 1.3-1.6 times higher than those of modern DOC collected from different sites in the same yedoma-dominated watershed (Mann et al. 2014). This suggests that location and particular permafrost soil forming processes could affect the magnitude of potential C release from thawing permafrost. In order to estimate the potential magnitude of gas production from thawing yedoma, the soil OC content of which is geographically variable, it is important to gain a better understanding the potential respiration rates of water-soluble soil OC collected from a wide distribution of sites.

Water-soluble OC derived from soil extracts is representative of the most mobile and labile fractions of soil OC (Ohno et al. 2009; He et al. 2011) which can be readily utilized by microbes (Matzner and Borken 2008; Wang et al. 2014). Therefore, in permafrost-dominated regions, examining C respiration rates from soil extracts collected from a variety of environments with varying amounts of disturbance and available OC provides a useful perspective as to how climate change may alter C cycling dynamics in these systems. The objective of this study was to quantify the variability of water-soluble soil OC respiration potentials from 16 active layer and thawed shallow (<1.5 m) permafrost soils from five different landscapes in the Kolyma River Basin, NE Siberia, Russia using laboratory incubations of soil extracts mixed with river water as a proxy for water-soluble permafrost OC biolability in inland waters. This study was performed as part of the National Science Foundation's POLARIS Project (www.thepolarisproject.org), a summer research program for undergraduate students. Despite a small sample size and limited geographic scope, we hypothesized that the C respiration potentials of incubated extracts would be directly related to soil OC content and that the OC contents and C respiration potentials would be spatially variable on scales of both stratigraphic layers and geographic locations.

Materials and methods

Study site and sample collection. The Kolyma River Basin is the largest arctic river basin entirely underlain by continuous permafrost, spanning ~650,000 km^2 across NE Siberia (Vtyurin 1975; Griffin et al. 2011; Holmes et al. 2011). The Kolyma River Basin is largely underlain by yedoma permafrost and the DOC in its rivers shifts from modern (Δ^{14}C > 100‰) C in the spring to older (Δ^{14}C < 0‰) C in the fall, suggesting the origin of the DOC transitions from shallow to deeper soils as the active layer seasonally deepens (Neff et al. 2006). We collected soil samples at five sites in the Kolyma River Basin in July 2010 (Table 1; Figure 1). The sites were selected to be representative of various yedoma-dominated landscapes in the mixed forest region of the Kolyma River watershed. Duvyanni Yar is a ~30-40 m tall yedoma outcrop exposed by the Kolyma River through thermokarst and thermoerosion. Shuchi Lake and Tube Dispenser Lake are first generation thermokarst (thaw) lakes formed in thick yedoma permafrost (>40 m) within 5 km of the town of Cherskii. The Rodinka soil pit (160 m above sea level) was dug in the Finish Creek valley on the SW flank of Rodinka mountain, where the yedoma horizon is relatively thin (~15 m), near faded thermokarst and solifluction features. The Bulldozer site refers to a lower elevation slope beneath Rodinka mountain, 60 m above sea level. The Bulldozer site is a field of residual thermokarst mounds (baydzherakhs) where the surface four meters of the soil profile have thawed following bulldozer excavation and removal of the surface organic horizon and active layer (60-80 cm) in 2003. The surface at our study soil profiles at Duvyanni Yar and Shuchi Lake had not been disturbed previously. In contrast, bulldozer and natural thermokarst activity had removed much of the overlying peat prior to our sampling at the Tube Dispenser

Lake, Rodinka, and Bulldozer study sites. We report surface vegetation species at each site in the Supplementary Information (Table S1). With the exception of the Duvyanni Yar site, none of the sample sites exhibited signs of cryoturbation (Figure S1 in Supplementary Information).

We delineated soil profiles at each sample location from either cross-sectional permafrost exposures or soil pits (Table 1). We determined the thickness of the active layer at these sites by probing to the depth of permafrost at the time of sampling (July), which was prior to the maximum thickness of seasonally thawed active layer (September). Samples to examine soil characteristics (gravimetric soil moisture, bulk density, and organic matter content) were collected in ~10 cm intervals at each soil profile. Samples for soil extract chemistry and respiration experiments were collected from four depths along soil profiles representative of different potential regions for soil-water interactions. The top (10-15 cm) and bottom (30-50 cm) of the seasonally thawed active layer, determined using July thaw depths, represent regions of near-surface soils which presently experience seasonal freeze-thaw cycles that process and degrade OC. The transient layer (70-100 cm), consisting of permafrost soils thawed approximately 7,000-5,000 y.a. during the Holocene thermal optimum that subsequently re-froze under colder climate conditions (Sher et al. 1979; Schirrmeister et al. 2011b), represents near-surface soils which do not thaw seasonally today but may seasonally thaw in a future warmer climate. Yedoma permafrost, sampled at depths greater than 100 cm below the ground surface and representing older Pleistocene-aged permafrost that has not thawed during the Holocene based on the presence of massive ice wedges adjacent to our sampling. These samples represent near-surface permafrost soils where the OC has not been previously degraded by freeze-thaw cycles during the Holocene. The depth of the boundary between the transient layer and yedoma permafrost was determined by assuming the tops of visible ice wedges represented the maximum historic active layer thaw depth at that site. In total we collected 16 (4 top active layer, 4 bottom active layer, 4 transient layer, and 4 yedoma; Table 2) samples for soil extract chemistry and respiration experiments. Each of these samples was divided into two subsamples and stored (holding time ≤10 days) in the dark at 15 ºC prior to analysis.

Soil characteristics. We analysed all of the soil characteristics samples (n = 44) and one of each soil extract chemistry and respiration experiment subsample pair (n = 16) for gravimetric soil moisture, bulk density, and organic matter content. Gravimetric water content was determined as the difference in mass between the soil at field moisture and the oven-dried (105 °C for 48 hours) soil over the mass of the oven-dried soil. Bulk density was measured as the dry soil mass divided by the soil subsample volume. We determined soil organic matter content by calculating the mass difference between the oven-dried and ashed (400 ºC for 4 hours) soil. In our calculations we assumed soil OC content was fifty percent of soil organic matter mass (Pribyl 2010). Grain size distribution was determined using standard hydrometer methods (Interstate Standard 2008), with results presented in the Supplementary Information (Table S2).

Soil extract chemistry. Soil extracts were prepared from the second of each respiration experiment soil subsample pair (n = 16) by vigorously mixing a 100 g subsample of soil at field moisture with 1 L deionized water for 30 minutes. The extract was filtered through a precombusted (450 ºC for 4 hours) glass microfiber filter (0.7 µm, Whatman GF/F) to remove particulate organic matter and analyzed for ammonium (NH_4-N; detection limit 5 µg L^{-1}) using a fluorometric method (Taylor et al. 2007) and soluble reactive phosphorous (PO_4-P; detection limit 10 µg L^{-1}) using the molybdenum-blue method (Rigler 1966). Dissolved organic carbon (DOC) content was quantified using a Shimadzu TOC-V using established protocols (Mann et al.

2012). We calculated the fraction of water soluble OC as the ratio between the mass of DOC extracted and the mass of total OC in the bulk soil utilized to make the extract.

Respiration experiments. We conducted heterotrophic respiration experiments on permafrost soil extracts mixed with water from the Panteleikha River as a proxy for water-soluble OC bioavailability in inland waters. The Panteleikha River drains an area of 1,500 km^2 and is a tributary to the Kolyma River. Panteleikha River water was obtained from ~1 m depth on July 27, 2010. We analysed a subsample of river water for DOC, NH_4-N, and PO_4-P using the methods described in the previous section. Respiration potentials were measured by incubating 60 mL of the prepared soil extract with 240 mL of unfiltered Panteleikha River water within standard 300 mL biological oxygen demand (BOD) bottles (Wheaton). Duplicate experimental incubation vials were prepared for each of the 16 soil extract samples. Two BOD bottles containing 300 mL unfiltered Panteleikha River water were prepared as an experimental control. All incubation vials were tightly sealed and maintained in the dark at 20 °C, the approximate temperature of the Panteleikha River's near-surface water in July.

We calculated biological oxygen (O_2) demand using standard methods as the loss of dissolved O_2 over a five-day period (APHA 1992). We determined dissolved O_2 concentrations in the bottles using a benchtop BOD O_2 probe (YSI 556; accuracy $\pm$ 0.2 mg L^{-1}); none of the bottles reached anoxia within the five-day period. Oxygen consumption was converted to C respiration by assuming that all dissolved O_2 loss was due to aerobic respiration and each unit loss in O_2 corresponded to a unit production of carbon dioxide (CO_2). The calculated CO_2 production over the incubation period was multiplied by the ratio of carbon's atomic mass to oxygen's atomic mass (0.375) to determine the mass of C respired in each incubation vial.

We report the C respiration of each sample in terms of: total C respired (mg), net C respired from the soil extract (mg), the mass of C respired per gram soil OC (mg C g OC^{-1}), and the fraction of total DOC respired (%). Total C respiration from the BOD bottle is reported as cumulative C respired from both the river water and the soil extracts during the five-day BOD incubation period. Net C respiration from the soil extract is reported as the total C respiration from the BOD bottle minus the mean C respiration measured in the river water controls. The mass of C respired per gram soil OC was calculated by dividing the net C respiration from the soil extract by the mass of OC in the soil used to prepare the extract. We calculated the fraction of DOC respired by dividing the total C respiration by the measured amount of total DOC within the BOD bottle. All respiration data are presented as mean ± standard error (SE) together with a reported sample size, where n represents the number of soil extract samples. An n value of 1 represents the mean of duplicate laboratory incubation vials containing extract from a single field soil sample.

Statistics. All statistical analyses were conducted using MATLAB (R2013a Student Version) software. Soil OC contents and all soil extract data (NH_4-N, PO_4-P, DOC, net C respiration, C respiration g soil OC^{-1}, % DOC respired) were tested for normal distribution using the Jarque-Bera test. The data for DOC, net C respiration, and % DOC respired were found to be consistent with a normal distribution at the $\alpha = 0.05$ level. Data for soil OC, soil extract NH_4-N and PO_4-P concentrations, and C respiration g soil OC^{-1} were not consistent with a normal distribution at the $\alpha = 0.05$ level; these variables were log-transformed to improve normality. Since half of our data parameters were found to be inconsistent with a normal distribution, we determined the statistical significance of differences in soil OC and extract parameters between soil layers and sampling sites using the nonparametric Mann-Whitney U-test. We determined all correlations using Spearman's rank correlation coefficients. Both the differences and correlations were considered statistically significant when $p \leq 0.05$ ($\alpha = 0.05$ confidence level). Finally, we conducted forward stepwise multiple linear regressions to examine how well our tested soil [log(OC)] and extract [DOC, log(NH_4-N), log(PO_4-P)] parameters predicted the measured C respiration [net C respiration, log(C respiration g soil OC^{-1}), and % DOC respired]. Terms were added to the stepwise regression models using the standard SSE criterion.

Results

Soil characteristics. Soil dry bulk density ranged from 0.21-1.13 g cm^{-3} (median 0.70 g cm^{-3}, mean 0.67 ± 0.23 g cm^{-3}, n = 44) and gravimetric water content ranged from 7.2-70.7% moisture (median 24.0%, mean 28.1 ± 16.7%, n = 45; Figure S2). Soil bulk OC content ranged from 1-20.5% by mass (median 1.7%, mean 2.7 ± 3.3% OC, n = 46). Soils from Duvyanni Yar (1.7-20.3% OC, median 2.9%, mean 4.9 ± 5.5%, n = 11) and Shuchi Lake Ridge (1.2-12.9% OC, median 1.2%, mean 2.7 ± 4.1%, n = 8), the two sites which had not experienced prior disturbance, had higher levels of bulk soil OC (p = 0.021 and 0.001, respectively) compared to other sampling sites. There were no additional statistically significant differences in soil characteristics between sampling sites or soil stratigraphic layers.

River water and soil extract chemistry. River water from the Panteleikha River had initial nutrient concentrations of 50.0 ± 5 µg L^{-1} NH_4-N, 310.0 ± 10 µg L^{-1} PO_4-P, and 4.83 mg L^{-1} DOC (Table 2). Ammonium (NH_4-N) concentrations extracted from the soil samples ranged from 24.8-4,573 µg L^{-1} NH_4-N (median 250 µg L^{-1}, mean 747 ± 437 µg L^{-1}, n = 11). Extracted soluble reactive phosphorous (PO_4-P) concentrations ranged from 7.3-90.4 µg L^{-1} PO_4-P (median 28.6 µg L^{-1}, mean 31.7 ± 6.4 µg L^{-1}, n = 12). Dissolved organic carbon (DOC) concentrations in the soil extract varied by an order of magnitude, ranging from 2.8 to 27.9 mg L^{-1} (median 9.1 mg

L^{-1}, mean 13.5 ± 2.5 mg L^{-1}, n = 14). Soils with higher OC contents extracted more DOC (r = 0.58, p = 0.029). Fractions of water soluble OC in our extracts ranged from 0.15-1.78% (median 0.57%, mean 0.71 ± 0.14% OC, n = 14). There were no statistically significant differences in soil extract chemistry between sampling sites or soil stratigraphic layers. Full river water and soil extract chemistry results are shown in Table 2.

Carbon respiration. Total C respiration during the five-day incubation period ranged from 0.17-0.67 mg C (median 0.28 mg, mean 0.33 ± 0.08 mg, n = 16; Table 3). The fraction of total DOC (river water DOC plus soil extract DOC) respired during the incubation period ranged from 8.9-31.4% (median 17.8%, mean 18.2 ± 1.7%, n = 14). Soil extract respiration ranged from -0.03 to 0.47 mg C (median 0.08 mg, mean 0.13 ± 0.08 mg, n = 16) and -0.42 to 5.21 mg C g soil OC^{-1} (median 0.62 mg C g soil OC^{-1}, mean 1.32 ± 1.77 mg C g soil OC^{-1}, n = 16). Extract samples from the Shuchi Lake Ridge bottom active layer, Duvyanni Yar bottom active layer, and Tube Dispenser Lake transitional layer respired less C than the river water control. Overall, the bottom active layer had lower C respiration potentials (total C respired and C respired from soil extract) than the other stratigraphic layers (p = 0.012 for both; Figure 2). There were no statistically significant differences in C respiration between sampling sites (Figure S3). Full C respiration results are shown in Table 3.

Correlation analyses did not show any statistically significant relationships between C respiration, soil OC contents, and extract DOC, NH_4-N, or PO_4-P concentrations. Forward stepwise multiple linear regression analyses revealed that the mass of soil extract C respired (mg) and the fraction of total DOC respired (%) could be estimated by the log-transformed NH_4-N concentrations in the soil extracts (p = 0.046 and 0.043, respectively; Table 4). Carbon respiration in terms of C respired per g soil OC was not predicted by any measured parameters in the final linear model. Complete data for the linear regression models are presented in Table 4.

Discussion

Our results indicate that soils in the Kolyma River Basin, NE Siberia are spatially variable in terms of soil OC content. Soils from Duvyanni Yar and Shuchi Lake Ridge had significantly ($p < 0.05$) higher OC contents compared to the other sampled sites. We hypothesize this is due to lack of prior disturbance removing much of the surface vegetation, allowing modern plants and roots to provide greater fresh OC input at these two sites. The observed variance in yedoma (Pleistocene permafrost) OC content across sites (1.5–3.0% OC) suggests that soil OC is unevenly distributed across the yedoma-permafrost dominated landscape. This outcome would be expected given that, even within a single site, soil OC content can vary by an order of magnitude throughout the vertical profile of tens of meters due to paleoenvironmental differences during the Pleistocene and Holocene (Tarnocai et al. 2009; Schirrmeister 2011a).

Samples collected from the bottom active layer had lower mean C respiration rates than the other stratigraphic layers in our study ($p = 0.012$). Soils in the bottom active layer currently experience seasonal freeze-thaw cycles, which degrades soil OC and promotes increased water-soluble OC release (Wang et al. 2014). Although soils in the top active layer also experience annual freezing and thawing, the top active layer receives inputs of fresh, labile OC from modern plants which are densely rooted in this layer, while soils in the bottom active layer presumably receive lower inputs of fresh organic matter from modern plants. In addition, deeper active layer depths in late summer cause increased water residence times in the bottom active layer compared to the top active layer, which increases soil-water interaction and can potentially facilitate OC dissolution and export (Neff et al. 2006; Wickland et al. 2007; Frey and McClelland 2009).

However, it is important to note that in natural systems this process is highly watershed-dependent and, depending on local environmental and permafrost conditions, increased soil-water interaction can also lead to the sorption of DOC to mineral soils (McDowell and Wood 1984; Neff and Asner 2001; Frey and McClelland 2009).

The C respiration rates of shallow yedoma (Pleistocene silt-dominated permafrost) in our study were highly variable by site. The yedoma soil extract from Duvyanni Yar respired 3.4 times more C than the averaged yedoma extracts from the Tube Dispenser Lake, Rodinka, and Bulldozer sites, although its soil OC content was on average only 1.3 times higher. This suggests that the yedoma OC was more bioavailiable at the Duvyanni Yar site and yedoma organic matter quality is not homogenous across the Kolyma River Basin, which concurs with the findings of Mann et al. (2014) concerning the spatial variability of DOC biolability in the same watershed. We did not observe statistically significant differences in C respiration potentials when comparing the transient layer and the yedoma. We had hypothesized that extracts from the transient layer would respire less C than extracts from the Pleistocene permafrost due to the most labile fractions of its OC pool being previously degraded by freeze-thaw cycles and microbial respiration during the Holocene thermal optimum (Sher et al. 1979; Schirrmeister et al. 2011b; Vonk et al. 2013; Wang et al. 2014). While the lack of a statistically significant difference in C respiration rates may be due to our small sample size, it is also possible that near-surface yedoma with the potential to thaw from deepening active layer thicknesses may not have significantly higher proportions of bioavailiable OC when compared to the overlying shallow transient layer permafrost.

We observed lower respiration rates in 25% of vials containing soil extracts compared to the control vials containing only river water (Table 3), suggesting that the soil extracts in these samples may contain inhibitory organic compounds that reduce DOC decomposition in aquatic systems. For instance, phenolic compounds have been found to inhibit both bacterial abundance and microbial metabolism, even in the presence of high OC and nutrients (Fenner and Freeman 2011; Mann et al. 2014). While we did not measure OC composition or quality in our study, these results suggest soil OC composition must also be taken into account when estimating potential C respiration potentials from recently-thawed permafrost.

Previous studies have shown that permafrost disturbance, including thermokarst activity, can export large amounts of labile DOC to inland waters (Vonk et al. 2013; Abbott et al. 2014). However, in our study there were no statistically significant differences in C respiration between previously undisturbed profiles (Duvyanni Yar and Shuchi Lake Ridge) and sites where the surface had been previously disturbed (Bulldozer Site, Tube Dispenser Lake, Rodinka). This is consistent with findings from Larouche et al. (2015), which showed that labile DOC fractions in Alaskan inland waters were not significantly altered by disturbance. Previously undisturbed sites in our study had higher OC contents in their profiles, and higher OC contents in bulk soil samples positively correlated with higher DOC levels in our soil extracts ($r = 0.58$, $p = 0.029$). Although the fractions of water-soluble OC in our soil samples were low (0.15-1.78%), the proportions of soil OC extracted in our study were consistent with general proportions of water-extractable soil organic matter in total soil organic matter (2-5%; Ellerbrock et al. 1999; He et al. 2011). While higher soil OC contents correlated with higher DOC concentrations in our soil extracts, higher extract DOC concentrations did not lead to higher C respiration potentials and soil extract C respiration potentials did not correlate with soil OC contents in our study. Our finding that higher extract DOC concentrations did not necessarily yield higher C respiration potentials contradicts previous studies in which higher DOC concentrations in inland waters led to increased release of CO_2 (Algesten et al. 2005; Battin et al. 2008; Lapierre et al. 2013).

One possible explanation is that C respiration in our study is limited by an alternative factor other than DOC concentrations. For instance, macronutrient availability, organic matter composition, and microbial communities within our incubations may have influenced extract C respiration rates observed in this study. Prior studied have found that landscape-scale variation in soil C bioavailability can be linked to soil C to N ratios, with higher values leading to more C respiration (Schuur et al. 2015). In aquatic systems, nutrient concentrations and ratios in the environment could limit C respiration when they deviate from the Redfield ratio (16 N : 1 P) or microbial N:P biomass ratios (7 N: 1 P; Cleveland and Liptzin 2007). Previous studies in arctic aquatic ecosystems found bacterial production is usually limited by phosphorous (Granéli et al. 2004; Hobbie and Laybourn-Parry 2008), but we did not find a statistically significant positive relationship between extract C respiration potentials and PO_4-P concentrations in our study. Our multiple linear regression analyses indicated positive correlation between C respiration and ammonium (NH_4-N) concentrations in the soil extracts, suggesting potential N limitation in our system. However, since ammonium is only a fraction of the total N pool, we are unable to determine if there is significant correlation between C respiration and C to N ratios in our study.

Approximately 8.9-31.2% of the total DOC in our incubation vials was respired during our 5-day incubation period. This is consistent with several prior laboratory incubations which found that only 4-60% of DOC from soils is available for microbial respiration (Kalbitz et al. 2003; Holmes et al. 2008; Vonk et al. 2013; Larouche et al. 2015; Spencer et al. 2015). While we acknowledge the limitations of using laboratory incubations to extrapolate what proportion of water-soluble soil OC will be respired upon entering inland waters, we note that our incubation period (t = 5 days) is consistent with mean residence times it takes water to move from permafrost thaw sites to the Kolyma River main stem (3-7 days; Vonk et al. 2013). In the Kolyma River Basin and other inland water sites, the proportion of soil OC available for microbial respiration, and by extension the soil's net C respiration potential, increases as initial processing and breakdown by ultraviolet light makes OC compounds more bioavailable for heterotrophic respiration and the production of CO_2 (Cory et al. 2013). Other studies suggest up to 22% of DOC can be sequestered by reactive iron and thus made unavailable for C respiration (Salvadó et al. 2015). Therefore, further research is necessary to understand the full C respiration potential of water-soluble OC from the Kolyma River yedoma region's thawing permafrost as it is processed *in situ*.*Conclusions*. Examining soil OC quantity and quality can lead to a better understanding of how much soil C can be immediately processed following permafrost thaw and water-soluble OC release to inland waters. Our study indicates that, while soil OC content is spatially variable in the Kolyma River Basin, it is not necessarily an indicator of C respiration potentials upon permafrost thaw and export to inland waters. Sites which had not experienced prior disturbance had higher soil OC contents, but there were no statistically significant differences in C respiration potentials between disturbed v. undisturbed sites in our study. This suggests alternative OC quality parameters, including exposure to freeze-thaw cycling, the extent of seasonal interactions with water, and the presence of inhibitory organic compounds, may also play a role in water-soluble C respiration potentials. It is also important to consider factors which may alter *in situ* C respiration from thawing permafrost, such as DOC sorption to mineral soils and the additional physical procession DOC experiences after being released to inland waters, when estimating the true magnitude of C release from thawing permafrost soils.

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Tables

Table 1. Location, sampling dates, profile delineation method, total depth of profile, depth to the permafrost table, and prior observable disturbance at the time of sampling for the soil profiles in this study. See Table S1 in the Supplementary Information for surface vegetation cover at each site.

Site	Lat.	Long.	Date sampled	Profile delineation method	Profile depth (cm)	Depth to permafrost table (cm)	Prior surface disturbance
Shuchi Lake Ridge	68.748ºN	161.384 ºE	8 July 2010	Soil pit	93	55	None
Duvyanni Yar	68.630ºN	159.154 ºE	20 July 2010	Thermokarst exposure	370	35	None
Bulldozer Site	68.698ºN	161.539 ºE	9 July 2010	Thermokarst exposure	80	- [a]	Removal of surface 60-80 cm by bulldozer activity in 2003
Tube Dispenser Lake	68.897ºN	161.407 ºE	12 July 2010	Soil pit	190	70	Thermokarst activity
Rodinka	68.724ºN	161.588 ºE	14 July 2010	Thermokarst exposure	190	103	Thermokarst activity and thermal erosion

[a] Did not reach permafrost table in this profile

Table 2. Soil sample depths, bulk density, field moisture content, organic carbon (OC) content, water extractable OC fractions, and measured dissolved organic carbon (DOC), ammonium (NH_4-N), and orthophosphate (PO_4-P) concentrations for all soil extracts and Panteleikha River water from different sampling sites and stratigraphic layers in the Kolyma River Basin. Each line in the table represents one soil sample collected and processed as described in the Materials and methods.

Sample			**Soil Properties**				**Soil Extract Chemistry**		
Site	Stratigraphic layer[a]	Depth (cm)	Dry bulk density (g cm^{-3})	Field moisture (%)	OC content (%)	Fraction water extractable OC (%)	DOC (mg L^{-1})	NH_4-N (μg L^{-1})	PO_4-P (μg L^{-1})
Shuchi Lake Ridge	TAL	15	0.78	35	13.0	0.33	27.85	- [b]	- [b]
	BAL	50	0.60	18	1.5	0.45	5.55	24.83	33.79
	TL	90	0.45	19	1.5	0.23	2.82	2608	36.67
Duvyanni Yar	TAL	15	0.97	65	20.5	0.27	19.15	118.0	7.29
	BAL	35	0.49	22	2.5	0.15	3.01	255.1	59.30
	TL	70	0.22	48	4.0	1.06	22.11	360.0	23.47
	PP	150	0.56	36	2.5	1.02	16.37	4573	10.26
Bulldozer Site	PP	80	0.82	10	1.5	0.68	9.13	74.11	47.49
Tube Dispenser Lake	TAL	10	0.74	24	1.0	1.19	9.03	87.30	BDL[c]
	BAL	30	0.74	24	1.0	- [b]	- [b]	- [b]	- [b]
	TL	70	0.74	47	1.5	- [b]	- [b]	- [b]	28.61
	PP	110	0.35	36	1.5	0.84	8.10	249.8	90.37
Rodinka	TAL	15	0.75	12	2.5	0.23	5.08	- [b]	- [b]
	BAL	40	0.67	20	2.5	0.36	7.28	81.95	22.88
	TL	100	0.70	38	2.5	1.78	27.66	- [b]	28.61
	PP	120	1.04	38	3.0	1.40	25.95	533.4	22.57
Panteleikha River	River Water	~100	N/A	N/A	N/A	N/A	4.83	50.00	310.0

[a] TAL = Top Active Layer; BAL = Bottom Active Layer; TL = Transient Layer; PP = Pleistocene Permafrost

[b] Parameter was not measured.

Table 3. Mass of initial dissolved organic carbon (DOC) in the BOD bottles, the initial DOC partitioning between soil extract DOC and river water DOC, the amount of carbon (C) respired during the five day incubation ± standard error between duplicate bottles, C respired from the soil extracts (net C respiration – river water control), C respired per g soil OC (C respired from soil extract / mass soil OC used to make the extract), the fraction of total DOC (river DOC + extract DOC) respired, and the effect of the soil extract on C respiration. The effect of the soil extract on C respiration was determined as positive (+) or negative (-) based on if C respiration from the soil extracts was higher or lower than the river water control, respectively.

Sample		**DOC**			**C Respiration**				
Site	Stratigraphic layer [a]	DOC contribution from soil extract (mg C)	DOC contribution from river water (mg C)	Net initial DOC in BOD bottle (mg C)	Total C respired in BOD bottle (mg C)	C respired from soil extract (mg C)	C respired per g soil OC (mg C g OC^{-1})	Fraction of total DOC respired (%)	Effect of soil extract on C respiration [c]
Panteleikha River	River Water	N/A	1.45	1.45	0.20 ±0.01	N/A	N/A	13.82	N/A
Shuchi Lake Ridge	TAL	1.67	1.16	2.83	0.50 ±0.05	0.30	0.59	17.48	+
	BAL	0.33	1.16	1.49	0.17 ±0.02	-0.03	-0.41	11.34	-
	TL	0.17	1.16	1.33	0.35 ±0.03	0.15	2.06	26.02	+
Duvyanni Yar	TAL	1.15	1.16	2.31	0.44 ±0.02	0.24	0.56	19.17	+
	BAL	0.18	1.16	1.34	0.19 ±0.00	-0.01	-0.09	14.05	-
	TL	1.33	1.16	2.49	0.45 ±0.03	0.25	2.00	18.12	+
	PP	0.98	1.16	2.14	0.67 ±0.27	0.47	4.90	31.35	+
Bulldozer Site	PP	0.55	1.16	1.71	0.24 ±0.01	0.04	0.50	14.33	+
Tube Dispenser Lake	TAL	0.54	1.16	1.70	0.36 ±0.01	0.16	3.51	20.99	+
	BAL	- [b]	1.16	- [b]	0.24 ±0.01	0.04	0.88	- [b]	+
	TL	- [b]	1.16	- [b]	0.18 ±0.01	-0.02	-0.42	- [b]	-
	PP	0.49	1.16	1.65	0.50 ±0.02	0.30	5.21	30.28	+
Rodinka	TAL	0.30	1.16	1.46	0.30 ±0.09	0.10	0.76	20.62	+
	BAL	0.44	1.16	1.60	0.20 ±0.01	0.00	0.00	12.82	--

	TL	1.66	1.16	2.82	0.26 ±0.13	0.06	0.66	9.28	+
	PP	1.56	1.16	2.72	0.24 ±0.02	0.04	0.36	8.86	+

[a] TAL = Top Active Layer; BAL = Bottom Active Layer; TL = Transient Layer; PP = Pleistocene Permafrost

[b] Parameter was not measured.

[c] + indicates increased respiration; - indicates supressed respiration; -- indicates no change

Table 4. Results from forward stepwise multiple linear regression analyses examining C respiration as the response variable in terms of soil extract C respired (mg), C respired per gram soil OC (mg C g OC^{-1}), and the fraction total DOC respired (%). Soil OC contents and soil extract DOC and log(PO_4-P) concentrations did not predict C respiration in any model. Soil extract log(NH_4-N) concentrations predicted C respiration in terms of soil extract C respired (mg) and the fraction total DOC respired (%). Carbon respiration per gram soil OC had no significant predictor variables in the final regression model.

Parameter		**C Respiration**		
		Soil extract C respired (mg C)	C respired per g soil OC (mg C g OC^{-1})	Fraction total DOC respired (%)
β_0 [Intercept]	Value	-0.760	1.149	0.502
	SE	0.545	0.085	7.811
	p-value	0.201	0.113	0.950
β_1 [log(NH_4-N)]	Value	0.221	-[a]	3.225
	p-value	0.046	-[a]	0.043
	SE	0.094	-[a]	1.341
Regression Model	df	8	9	8
	RMSE	0.45	0.27	6.46
	R^2	0.411	-[b]	0.420
	p	0.046	-[b]	0.043

[a] Parameter was not in final regression model

[b] No parameters were significant ($p \leq 0.05$) in final regression model

Figure Captions

Figure 1. Map showing the five soil sample sites in the Kolyma River Basin, Northeast Siberia, Russia (a) and photographs showing locations of the sample sites, marked using white triangles (b-f). Surface vegetation data for each site are presented in Table S1 in the Supplementary Information. The Bulldozer site (b), located in the Rodinka mountain piedmont, is in a field of residual thermokarst mounds (baydzherakhs) with the Kolyma and Panteleikha Rivers floodplain visible in the distance. The Tube Dispenser Lake profile (c) was collected near exposures of melting ice wedges on the southern slope of the Tube Dispenser Lake, a thermokarst lake. The Rodinka site (d), located on the lower slope of Rodinka mountain, was collected near faded thermokarst and solifluction forms in the Finish Creek valley. The flourishing violet, yellow, and white flowers indicate the site is in the first succession stadium following completion of active thermokarst and thermal erosion. The Shuchi Lake Ridge site (e) is located within a “drunken forest,” formed due to yedoma ice complex degradation and sediment sliding into the southern wall of the thermokarst Shuchi Lake. Finally, the Duvyanni Yar site (f) was collected from the Duvyanni Yar thermokarst and thermoerosional exposure, cut by the Kolyma River, of the Late Pleistocene ice complex. Photographs (b-f) by V.V. Spektor.

Figure 2. Carbon respiration separated by site (left) and by stratigraphic layer (right). The top graphs show the mass of C respired from the soil extracts (mg C); the middle graphs show the mass of C respired per g soil OC (mg C g OC^{-1}); the bottom graphs show the fraction of total DOC respired during the 5-day incubation period (%).