ARCTIC MINERAL SOILS LOSE SOC MORE EASILY THAN PEAT SOILS FOLLOWING THAW

A Thesis

by

JILLIAN SANDERS

Submitted to the Graduate and Professional School of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Chair of Committee,	Julie Loisel
Committee Members,	A. Peyton Smith
	David Cairns
Head of Department,	David Cairns

May 2022

Major Subject: Geography

ABSTRACT

It is estimated that the Arctic contains half of the global soil carbon pool, and climate warming will lead to considerable degradation of permafrost. This degradation may lead to the expansion or drainage of Arctic peatlands, which would alter the global carbon budget. Despite numerous Arctic soil incubation experiments and modeling efforts to predict future changes to the global carbon budget, there is still no consensus regarding the responses of Arctic soil carbon to climate warming. To address this uncertainty, we measured carbon dioxide (CO_2) emissions from two soil types (lowland peatland and upland, mineral tundra) using 16 intact, replicate soil cores (8 of each type) that were incubated aerobically at 1 °C and 6.5 °C for 136 days. Soils were sampled from the active layer near Toolik Lake, Alaska, and soil moisture content was maintained near field conditions throughout the incubation process. An additional component of the study measured CO_2 emissions from individual, partitioned soil layers (live biomass vs. organic litter vs. mineral layer) from the same sites as the whole cores. These individual layers were incubated under the same conditions as the whole cores to better understand the sensitivities of different soil types to permafrost thaw and climate warming.

We found that carbon in active layer soils from upland (mineral) sites was more sensitive to decomposition than lowland (peat) soils. Our findings suggest that oxygen availability, soil type, and carbon quality may be more important in controlling soil CO_2 respiration than temperature, as temperature effects were not statistically significant in

the intact incubation experiment or in the partitioned layer experiment. Our findings also highlight potential issues in utilizing homogenized, partitioned soil for incubation studies; in the partitioned layer incubation, average layer C-CO_2 production was 6.1 times greater than intact, whole core C production from the same source material. This finding indicates that Arctic incubation studies utilizing homogenized, partitioned soil may overestimate CO_2 emissions, and that the usage of carbon production values from homogenized soils in earth systems models should be carefully considered or minimized.

DEDICATION

To my family

ACKNOWLEDGEMENTS

I would like to thank my committee chair, Dr. Loisel, for always being available, kind, and thoughtful, and for sharing her love of peatlands with me. I would also like to thank my committee members, Dr. Smith, and Dr. Cairns. Together, my committee chair and members have led me through the course of this research.

Thanks also go to my friends, my fiancé Robbie Swanson, and the Swanson family for supporting me throughout the past few years. I would like to thank my aunt, Dr. Marjorie Bond, for her kind words, help, and statistical knowledge that she shared with me; I do not want to think about how hard statistics would have been without her support. Thanks also go to my colleagues, Hannah Luo and Emily Rabel, who assisted as undergraduate researchers during data collection. To Lauren Didio and Nataleigh Perez, thank you for supporting me and always being available to lend an ear when I needed to talk about science. Thanks also go to the department faculty, and staff for making my time at Texas A&M University a great experience.

Finally, thanks to my mother, Nicole, my sisters, Lauren and Madeline, and my father, Clayton, for their encouragement, patience, and love. I would not be the person I am today if not for their unending support and presence in my life.

CONTRIBUTORS AND FUNDING SOURCES

Contributors

This work was supervised by a thesis committee consisting of Professor Julie Loisel, David Cairns of the Department of Geography and Professor A. Peyton Smith of the Department of Soil and Crop Sciences.

Field sampling in Toolik Lake, Alaska was conducted by Zicheng Yu, Zhengyu Xia, and Ava Scally. Laboratory soil sampling was conducted with the assistance of undergraduate researchers Hannah Luo and Emily Rabel. The site map for Figure 1 was created for this project by Kelly Corzo Rivera. All other work conducted for the thesis was completed by the student independently.

Funding Sources

The work conducted for this thesis was made possible by the National Science Foundation (NSF) under Grant Numbers 1802838 and 1802810. The contents of this work are solely the responsibility of the authors and do not necessarily represent the official views of the NSF.

NOMENCLATURE

C	Carbon
CO_2	Carbon Dioxide
SOC	Soil Organic Carbon
CH_4	Methane
N	Nitrogen
$C\text{-}CO_2$	Carbon in Carbon Dioxide
ESM	Earth Systems Model
GPP	Gross Primary Productivity
Reco	Ecosystem Respiration
ANOVA	Analysis of Variance

TABLE OF CONTENTS

Page

LIST OF FIGURES

Page

LIST OF TABLES

Page

1. INTRODUCTION

1.1. Background

The Arctic region is highly sensitive to changes in global temperature. High-latitude areas are warming at least two times faster than the global average rate, with some areas warming faster than others (IPCC, 2021). This warming will continue to cause changes to ecosystem structure as temperature and precipitation increase throughout the 21st century (Serreze et al., 2000; ACIA, 2005; Pegoraro et al., 2019). Historically, freezing temperatures and high water table depths in the Arctic tundra have limited decomposition rates of organic material, allowing soil organic carbon to accumulate over centuries and millennia (Hobbie et al., 2000). This has allowed the Arctic to be a significant terrestrial carbon sink, accounting for approximately one-half of the earth's total soil carbon pool (Schuur et al., 2015; Hugelius et al., 2020). However, these conditions might be changing, as climate warming has already begun to degrade permafrost, which is expected to lead to the expansion or drainage of some Arctic peatlands (Voigt et al., 2017; Zhang et al., 2017; Taylor et al., 2019), which will impact the global carbon budget and regional hydrological regimes.

One of the reasons C-rich Arctic ecosystems are particularly vulnerable to temperature changes is because of the sensitivity of the northern carbon balance, which depends on the relative effect of temperature on gross primary productivity (GPP) vs. ecosystem respiration (Reco) (La Puma et al., 2007). GPP in the Arctic is limited, and these limitations are often imposed by environmental conditions such as cryoturbated soils, short growing seasons, and low nitrogen availability for Arctic plant communities

(Hobbie et al., 2000; Liu et al., 2018). Coupled with high water table depths and freezing temperatures, the often recalcitrant, poor substrate quality of Arctic plants restricts organic matter decomposition and thus microbial respiration (Shaver et al., 1997). As the Arctic region experiences climate warming through 2100 and beyond, a portion of the sequestered soil carbon could be mobilized by microbial activity, as productivity limitations are ameliorated (Schuur et al., 2015). Although Earth Systems Models (ESMs) do not yet give clear answers to the long-term net carbon balance of soils in general (Crowther et al., 2016), and of Arctic soils in particular (Chadburn et al., 2017), it has been shown that the amount of respired carbon is positively correlated to the extent of warming and the initial size of carbon stocks in the soil (Crowther et al., 2016). In other words, carbon-rich areas that warm rapidly are expected to be large contributors to soil carbon loss to the atmosphere.

Of particular concern is the potential impact of permafrost thaw on Arctic soil dynamics and their associated effect on the global carbon cycle. This is because the total permafrost soil carbon sink amounts to approximately 1035 Pg of carbon, which is almost twice the current atmospheric carbon dioxide (CO_2) burden (Hobbie et al., 2000; Schuur et al., 2015). A significant portion of this soil carbon is found in Arctic peatlands, which contain 120-460 Pg of carbon (Hugelius et al., 2020). As the Arctic warms, there is growing concern that permafrost degradation in peatlands will lead to enhanced microbial respiration that may outpace the immobilization of organic carbon as peat (Turetsky et al., 2020). Numerous studies have estimated the net carbon balance of Arctic soils in the past few decades, including in situ observations (Elberling et al., 2013;

Schuur et al., 2009), warming experiments (Kuhry et al., 2019, Vaughn and Torn, 2019), and modeling efforts (McGuire et al., 2018; Schuur et al., 2015). Despite these studies, there is still no consensus regarding the responses of Arctic soil carbon to climate warming.

As such, a synthesis of incubation studies by Schuur et al. (2015) showed that Arctic climate warming will likely cause a substantial pulse of CO_2 and methane (CH_4) emissions that may be observed over a time period of multiple decades, enhancing the effects of human-caused climate change. Many recent studies agree with this statement (e.g., Plaza et al., 2019; Schuur et al., 2021). That being said, a multitude of empirical and modeling studies argue the opposite: that enhanced vegetation growth due to longer and warmer growing seasons might outpace enhanced microbial respiration, and lead to long-term soil carbon storage in peatlands (Heffernan et al., 2020; Loisel et al., 2021; Alexandrov et al., 2016; Olid et al., 2014; Chaudhary et al., 2020). Lastly, others suggest that increases in net primary productivity and Reco might counterbalance each other, with no net C gain or loss (Vaughn and Torn, 2019; Treat et al., 2021).

1.2. Incubation Experiments

A number of previously published incubation experiments have indicated that CO_2 emissions increase significantly in aerobic, field moisture conditions under warming temperatures (e.g., Bond-Lamberty et al., 2016). As such, a 12-year-long warming experiment from 1996 to 2008 was performed in Zackenberg, Greenland (Elberling et al., 2013), using both field and lab incubations across three sites: a dry acidic heath site with mineral soils, a lowland peat site, and a drained grassland site. In

the lab, the authors incubated the intact soil cores at 5 °C, while field cores were taken at the beginning and end of the 12-year experiment. The authors found that aerobic, drier sites lost substantially more carbon (mineralization) in relation to initial carbon stocks than lowland, more anaerobic sites. Thus, oxygen availability was found to be a key factor in determining the rate of soil carbon decomposition, suggesting that drained sites might experience the most CO_2 losses following permafrost thaw, even though they may not contain the most carbon. This study also highlighted the usefulness of comparing CO_2 emissions from different permafrost soil types.

The aforementioned study by Elberling et al. (2013) is foundational because of their use of intact cores in their incubation experiments. Indeed, laboratory incubations are often performed on homogenized soil layers, which usually involves drying and grinding/blending of soil. This is an issue because homogenizing and disturbing the soil layers impact soil microbial communities and degrade physical protection from soil structures (Vaughn and Torn, 2019; Bastida et al., 2019). In contrast, few studies have designed experiments that may provide conditions that are closer to those experienced in the field, such as Bracho et al. (2016) and Pegoraro et al. (2019). Indeed, while "intact" incubation experiments have been proven an effective method for quantifying greenhouse gas emissions from decomposing permafrost soil (Vaughn and Torn, 2019; Schädel et al., 2020), these incubations also come with a set of challenges, including preserving oxygen availability, reducing carbon toxicity, and maintaining field moisture conditions. For example, the Greenland long-term incubation described above (Elberling et al., 2013) raised important methodological issues pertaining to the maintenance of

aerobic conditions in the lab, which have led to the development of more open-air, automatic soil sampling chambers that more easily maintain aerobic conditions (Bracho et al., 2016; Pegoraro et al., 2019). These systems ensure that conditions inside the soil core do not become toxic by reducing CO_2 buildup.

Drought and wetting events (from non-frozen precipitation) are known to cause significant pulses of CO_2 emissions in soils, and this phenomenon is called the Birch Effect (Birch, 1958). Historically, numerous studies have not reported the flux of CO_2 from soils after rewetting them from dry, considering these pulses as anomalies, and the effect is, therefore, difficult to predict (Smith et al., 2017). To simulate fast-cycling soil carbon on a shorter time scale (less than one year), Kuhry et al. (2020) initiated a 4-day incubation experiment utilizing the Birch Effect wherein cryoturbated soils from sites across Northern Russia were dried and then rewetted. In this study, soils were partitioned by layer type, and respiration rates were compared to those from a longer-term incubation experiment, wherein respiration results were measured on day 343. The authors found that the soil samples in the 4-day experiment had higher respiration rates than the longer-term incubation experiment, which was developed to measure more recalcitrant carbon. This signifies that rewetting and drying events from precipitation may enhance the mineralization of soil carbon following permafrost thaw, however, more studies should be conducted to better understand the impact of rewetting events upon in-situ tundra soils.

Drawing from these recent studies, I measured CO_2 emissions from two soil types (lowland peatland and upland mineral) using intact soil cores that were incubated

at 1 °C and 6.5 °C for 136 days. This time interval captures fast-cycling C losses, which is particularly important for quantifying how the carbon budget may change following thaw. An additional component of the study measured CO_2 emissions from duplicate cores that were partitioned into three individual soil layers that correspond to live biomass, organic litter, and mineral layer. These individual layers were dried and homogenized, and then incubated under the same conditions as the whole cores to better understand the sensitivities of different soil types to climate warming and incubation methods. I am using soil samples from Toolik Lake (Alaska), where changes in tundra vegetation as a result of Arctic warming have already occurred as woody plants have crept further north (Hobbie et al., 2014; Sistla et al., 2013). Using a laboratory incubation experiment with two temperature treatments, I present new CO_2 emission values from both upland (mineral) and lowland (peatland) permafrost soils.

2. METHODS

2.1. Study Area

Toolik Lake, Alaska (Figure 1) is a well-sampled, representative site for tundra studies. The Toolik Lake field station is a part of the Arctic Long-Term Ecological Research (LTER) network and the University of Alaska. The area is in the North Slope Borough of Alaska and sits in the foothills of the Brooks Range. The site experiences an annual average temperature of -8 °C and precipitation amounts are low, averaging about 30 centimeters, with 45% of precipitation falling as snow (Hobbie and Kling, 2014). Full snow cover coverage (100%) occurs in mid-September at the research station, and temperatures remain below freezing on average for 9 months out of the year, rising above the freezing point only in the summer months. Some research has shown that since 1960, the area has warmed by approximately 3.1 °C, or by 0.5 °C each decade (Shulski and Wendler, 2007). However, more recent studies have not found statistically significant trends in surface air temperature from 1989 to 2014 (Hobbie et al., 2017). Despite the discrepancies in air temperature trends, Hobbie et al. (2017) found evidence of ecosystem responses to Arctic warming at Toolik Lake, such as increased plant biomass, weathering of thawed soil, and increased permafrost temperatures at a depth of 20 meters.

The Toolik Lake area is part of the arctic bioclimatic sub-zone E (Walker et al., 2016), where prominent vegetation communities are graminoids such as heath and tussock sedges (*Eriophorum vaginatum*). The soil is characterized as moist, poorly-

drained acidic gelisols with a significant organic layer in the topmost “O” horizon and peat muck at further depths (NRCS, 2006; Hobbie et al., 2017). Radiocarbon dating of peat cores from the area indicates that established peat likely originated between approximately 0 and 300 CE (Common Era), with carbon accumulation rates increasing in recent decades as the peatlands have transitioned to oligotrophic fens (Taylor et al., 2019). A recent discovery of small peat patches dominated by *Sphagnum* moss suggests that incipient peatlands might have been sprouting across the region since the 1980s (Yu et al., 2019; Stansfield et al., 2021).

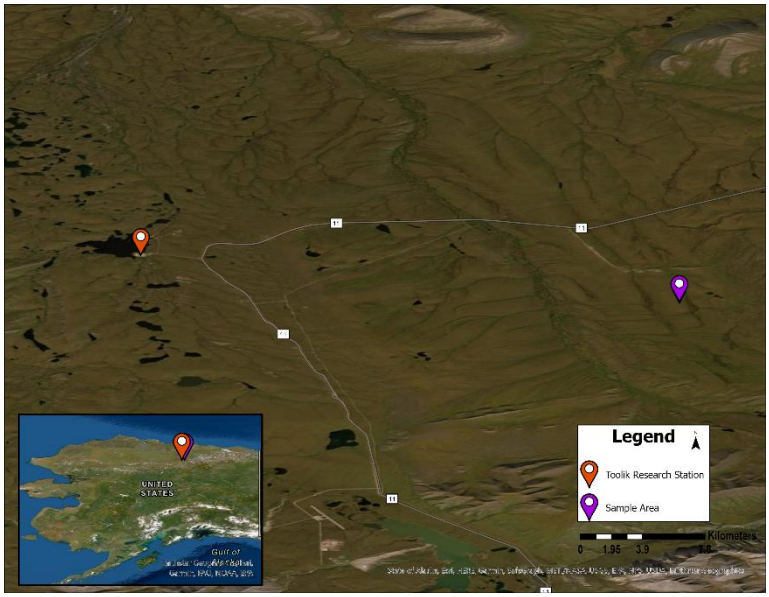


Figure 1. Site map of field sampling near Toolik Lake Field Station. The 16 field cores (8 upland, 8 lowland) were taken from a single ridge in the foothills on the North side of the Brooks Range. This map was created for this project by Kelly Corzo Rivera.

2.2. Field Sampling

A total of 16 intact permafrost cores were collected at 8 "paired sites" in the vicinity of Toolik Lake LTER, AK, in July 2019 (Figure 1). Each paired site is composed of 1 upland core and 1 lowland core, with upland cores representing mineral tundra soil, and lowland cores representing organic wetland/peatland soil (Figure 2). In this study, we refer to "upland vs. lowland" soils to distinguish between these two types of sites. Sampling was conducted along a single ridge located in the foothills of the Brooks Range (68° N, 149° W). A bread knife was used to manually cut the cores from the active layer before extracting the soil by hand. The soil cores were not frozen at the time of collection, as they constitute the active layer (they do not exceed 35 centimeters in length). The cores were cut down to the parent material. The cores were then frozen at the Toolik field station and kept frozen until laboratory analyses.

The surface vegetation of all 8 lowland cores was primarily constituted of undecomposed *Sphagnum* moss as well as creeping Ericaceous plants such as *Vaccinium oxycoccos*. Depth-wise, the peat layers in the lowland soil samples measured between 18 and 34 cm in the field and contained both *Sphagnum* and sedge peat. Mineral layers were present in only 2 of the 8 peat soil samples (later referred to as cores 2 and 9), and these mineral layers measured less than 10 cm in depth in the field. The surface vegetation of all 8 upland soil samples was primarily composed of tussock vegetation (i.e., cottongrass) and true mosses such as *Polytrichum strictum*; these cores had layers of organic litter beneath the live plants. These organic layers in the upland cores measured between 4 and 9 cm in the field. Two of the upland soil samples also contained

layers of orange clay parent material at their base (cores 13 and 16, later split into 13A, 13B, 16A, and 16B).

Figure 2. Example of two soil cores before subsampling. Differences in soil horizons are clearly visible, with peat muck present in core 15 on the bottom of the *Sphagnum*-dominated lowland core (left). Mineral material in core 13 is visible at the bottom of the upland core (right).

2.3. Sample Preparation in the Laboratory

In Fall 2019, 12 of the 16 cores described above were randomly selected for the whole core incubation experiment. Those 12 cores (6 upland, 6 lowland) were thawed, sampled, and placed in clear plastic core liners (3.81 cm diameter). Duplicate cores were prepared for these sites, bringing the total of cores to 12 upland and 12 lowland. Each soil type was then split into two incubators, bringing the total core number to 24 with an N of 6 (6 upland in treatment 1, 6 lowland in treatment 1, 6 upland in treatment 2, 6 lowland in treatment 2). The cores were kept in darkness at 4 °C until the start of the experiment.

Excess core material was further divided into two groups: partitioned layer incubations and analysis for bulk density and soil moisture content. For the partitioned layer incubations, the excess material from the whole cores was separated by substrate type as follows: surface plant, organic litter, and mineral material. These individual layers were then dried in an oven at 30 °C for one week, and then sieved at 2 millimeters. When possible, dry weights of the layers were homogenized to 1.5 g for plant material, 2.5 g for organic material, and 5 g for mineral material. This component of the experiment was prepared in a manner that replicates conventional soil incubation study designs, wherein soil cores are dried and homogenized (e.g., Salomé et al., 2010; Ballhausen et al., 2020; Karhu et al., 2014). Results from the partitioned layer incubations will be compared to CO_2 production from the intact whole cores. Soil set aside for bulk density and moisture content analysis included one mineral and two peat soil cores. These measurements were collected prior to beginning the incubation period,

while the cores were still wet. These measurements were then used to calculate the ideal "field" moisture content of the experimental soil cores.

2.4. Incubation Experimental Design

Whole core incubations officially began on February 2, 2021. We used two Fisher Scientific Thermo Precision incubators, with one set at 6.5 °C and the other at 1 °C, to simulate the temperature sensitivities to two scenarios. Soil cores were split evenly between the 2 incubators: 6 upland + 6 lowland at 1.5 °C, and 6 upland + 6 lowland at 6.5 °C (N=6). Soil cores were left uncapped until 1 hour before sampling, wherein caps were attached to the cores and locked on to prevent gas exchange (Figure 3). To sample CO_2, 30 mL of headspace was drawn from a syringe through a luer lock on the soil core cap. The headspace was then injected into a PP Systems EGM-5 and the value was recorded. The soil cores were sampled 3 times in the first week, then 2 times the following week. In the third week of the incubation, no sampling was conducted due to winter storm Uri, however, the soil lab and the incubators never lost electricity. Sampling was then conducted two times per week for two more weeks, and then once per week for the remainder of the 136-day incubation period.

The partitioned soil layers were incubated aerobically for 100 days under the same temperature treatments as the whole cores (1 °C and 6.5 °C). These soil layers were incubated in 60 mL amber vials at field moisture conditions with the vial caps off to better allow for air exchange within the soil pores and to avoid CO_2 saturation (Bastida et al., 2019). Sampling was similarly conducted with the portable EGM-5 from PP Systems; 5 mL syringes were utilized, and 5 mL of headspace was drawn from each

60 mL amber vial. Consistent quantities of the total container volume were sampled in both experiments. By using a 5 mL headspace for the layer experiment and a 30 mL headspace for the whole core experiment, approximately 8% of the total volume of both containers was sampled. Partitioned soil layers were sampled twice a week for four weeks, then once a week for the remainder of the experiment, with the incubation ending June 14, 2021.

Figure 3. Image of Core 9B. This sample was a lowland peat core incubated in the 6.5C treatment. The sampling gas cap is visible attached at the top. The photo was taken directly after CO_2 sampling with the EGM-5, and the gas cap was removed once measurements were recorded and scrubbed air was injected back into the core.

To our best capacity, core samples were kept at “field moisture conditions”. We used moisture content data to estimate the frequency at which water needed to be added to the whole cores and partitioned layers. We calculated the inferred wet weights of individual soil cores by using the calculated gravimetric water contents from the excess soil material. Deionized water was added to the intact, whole cores until soil weight matched the inferred wet weights. This process was conducted the first day of sampling and then repeated 3 times (on days 23, 45, 77, and 106) to maintain field moisture contents during incubation. Note that, beyond day 100, no more rewetting occurred, to simulate drying conditions. The wet weights of the partitioned layers were calculated using the same procedure, with wetting occurring on the first day of sampling on March 11, 2021. The layers were rewetted 1 additional time on May 25, 2021, when the soil wet weights were approximately 4% different from the original wet weights.

2.4.1. Elemental Analysis

At the end of the incubations, the intact cores and partitioned layers were deconstructed in the lab and prepped for elemental analysis. Whole core material was separated into three layers (plant, organic litter, and mineral) before being weighed and dried at 40 °C for one week. Homogenized layers were also weighed and dried at 40 °C, and after all samples were dry, the soils were weighed again, then homogenized using a standard size 5 (4000 micron) sieve and a mortar and pestle. Subsamples were then placed in 2 mL stainless steel vials and shaken in a retsch ball mill. These subsamples were then placed in foil microbalance capsules and weighed once more before undergoing elemental analysis with a Vario Elementar. Soil organic carbon (SOC)

percentages of the soil samples were calculated using results from the Vario Elementar. For the organic and mineral layers from the intact core (and partitioned layer), at least 2 measurements (duplicates) were obtained and averaged to provide %C, as the particles in those layers were more heterogeneous than the plant layers. For the whole core incubations, the carbon percentage of each soil layer was multiplied by the soil dry weight of that same layer. For instance, in the case of an upland core, the %C of the live plant layer was multiplied by its dry weight; the same was done for the organic litter and the mineral layer. All three values were then summed to yield the total carbon content (in grams) for the whole core. Carbon contents of the partitioned layers were calculated using the same methods; however, the soil layers were not summed since we are interested in the differences in SOC (soil organic carbon) and respiration across soil horizons.

2.5. Data Analysis

Incubation data were compiled using RStudio Version 4.0.3, and we normalized C production by both SOC content and soil dry weight (DW). At the beginning of the whole core incubation experiment, there were issues with negative pressure on sampling days 2 and 3, therefore they were removed from C production analysis. In the event that sampling was conducted on the same whole core twice on one sampling day, respiration rates were averaged. Two whole cores (10A and 10B) missed 4 sampling events (sampling IDs 13, 14, 18 and 19) due to mechanical and human errors. Cumulative C values during these times were interpolated by using the micrograms of $C\text{-}CO_2$ released before and after the missed sampling days.

Goodness-of-fit tests were performed on cumulative specific C production, which was normalized by SOC and by soil DW. Cumulative specific production was log transformed to yield a normal distribution for statistical analysis, which consisted of running 2-way analysis of variances (ANOVAs) and testing model fits to validate the significance levels of the tested variables.

Carbon release between the two incubation experiments (whole cores vs. partitioned layers) was compared to assess any difference that may arise from using these two techniques. A total of 6 upland cores and 6 lowland cores had corresponding "partitioned layers" (from the same sites), allowing us to directly compare soil layer C production data from the whole cores vs. the partitioned layers experiment. Layer specific production (cumulative μg C-CO_2/gdw) was multiplied by the dry weight of corresponding whole core soil horizons, which were calculated during soil deconstruction. For example, for peat core 15A, the organic layer weighed 10.41g and the plant layer weighed 7.17g; the corresponding partitioned organic layer respiration rate was 11068.05 (μg C-CO_2/hour/gdw), and was therefore multiplied by 10.41g. The corresponding partitioned plant layer respiration rate was 13503.94 (μg C-CO_2/hour/gdw) and multiplied by 7.17g. Those two respiration values were then summed and compared to the total respiration (g) for core 15A.

3. RESULTS

3.1. Intact Soil Cores

3.1.1. Soil carbon stocks

Soil carbon stocks. Mean values and standard deviations (SDs) for the intact core soil C stocks are presented by soil type (upland vs. lowland) in Table 1. Greater SOC stocks are reported for the lowland peaty soil cores than for the upland mineral soil cores (Figure 4); a one-way ANOVA confirms the effect of "soil type" on carbon stock for all cores ($F(1) = 6.32$, $p = 0.0197$). For all lowland cores, SOC stocks ranged from 3.17g to 14.72g, with mean values of 8.48g ± 4.17 and 9.82 ± 4.18 for the 1 °C and 6.5 °C treatments, respectively. Mineral core SOC stocks ranged from 2.33g to 9.88g; average SOC totaled 5.46g ± 2.76 in the 1 °C temperature treatment, and 5.39 ± 2.48 in the 6.5 °C temperature treatment. At this stage, it was determined that lowland soil core 2 (duplicates 2A and 2B) was an outlier, as it contained substantially less SOC (3.47% SOC in 2A and 4.25% SOC in 2B vs. a mean of 37.07% SOC for the other peat cores) than the other peaty, lowland cores. Cores 2A and 2B were also the only lowland cores that contained a distinct mineral layer at the base of their profile, making them "non true peat soils" and thus too different from the other samples to allow further statistical analysis. Likewise, mineral soil core 16 (duplicates 16A and 16B) was found to contain substantially more SOC than the other upland soil cores (25.69% SOC in core 16A and 26.07% SOC in core 16B vs. a mean of 4.27% for the other mineral cores), here again making these cores unsuitable replicates for further statistical analysis. In the

homogenized layer incubation experiment, there was another replicate of mineral soil core 16; for consistency, those layers were also removed from further statistical analysis.

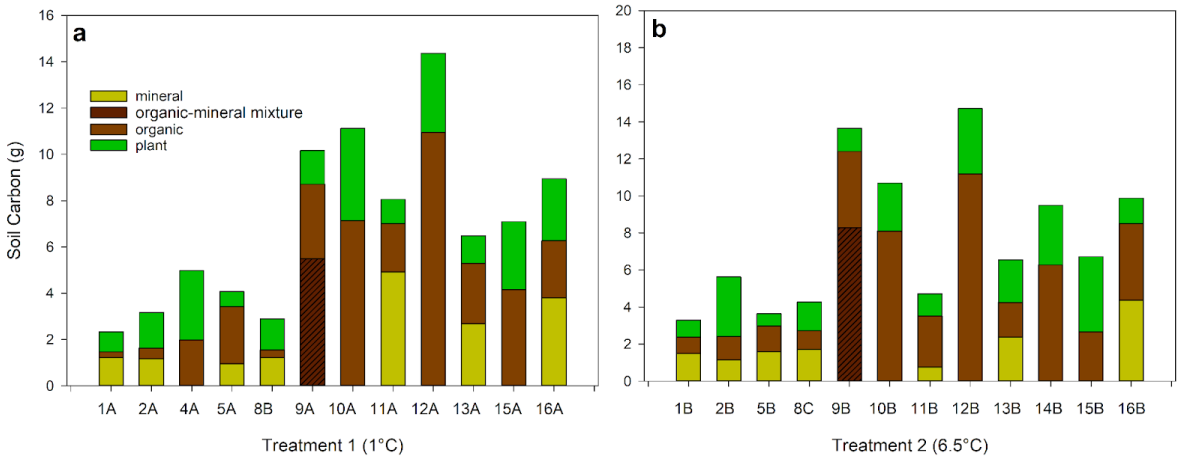


Figure 4. Carbon Stocks in Intact Soil Cores. Soil organic carbon (SOC) was calculated using a Vario Elementar from duplicated, averaged soil samples for the first treatment, 1 °C (a) and the second temperature treatment, 6.5 °C (b). These results showed that peat, lowland cores contained more SOC than upland, mineral cores in both treatments. To demonstrate carbon stock variations in the whole core incubations, all 24 cores were included in this figure.

Table 1. Comparison of Carbon Stocks in the Intact Soil Cores

		SOC (g)	
Temperature (°C)	Soil Type	Mean	Std Dev
1	mineral	5.4623725678	2.7633701407
	peat	8.4806007755	4.1671499157
6.5	mineral	5.3884284617	2.4759431356
	peat	9.8156580217	4.1845114583

3.1.2. Soil C-CO_2 respiration rates (dry weight normalization)

When normalized by soil DW, lowland peat cores lost more C (per gdw) than mineral upland cores (Figure 5). Respiration rates ranged from 0.05 to 6.25 (μg C-CO_2/hour/gdw) (Figure 6), with a mean of 0.64 ± 0.36 (SD) for upland cores under treatment 1, a mean of 0.54 ± 0.56 for upland cores under treatment 2, a mean of 1.44 ± 0.97 SD for lowland cores under treatment 1, and a mean of 1.06 ± 0.68 for lowland cores under treatment 2 (Fig. 7). The ANOVA revealed that soil type (peat vs. mineral) had a statistically significant effect on C production as standardized by soil DW, and explains the difference in means between peat and mineral C release ($F(1)=6.80$, $p=0.019$). Temperature did not have a statistically significant effect on C production rates when normalized by soil DW ($p = 0.33$). The absence of a temperature effect on C production was further validated by the absence of significant r-squared values when fitting soil C production by temperature in a least squares model (not shown).

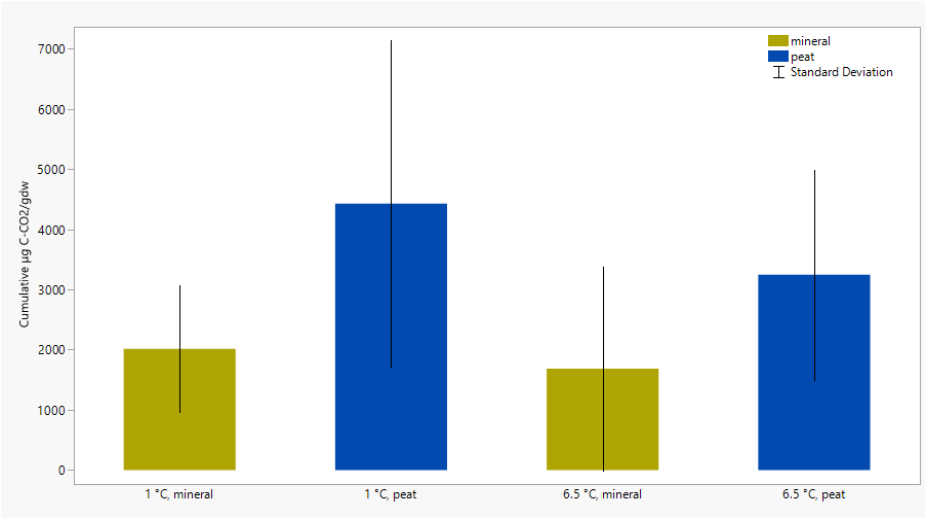


Figure 5. Cumulative C Production from Intact Cores, Dry Weight Normalization. Normalizing C production by soil dry weight results in larger losses of C per GDW by peat (lowland) soils than mineral (upland) soils.

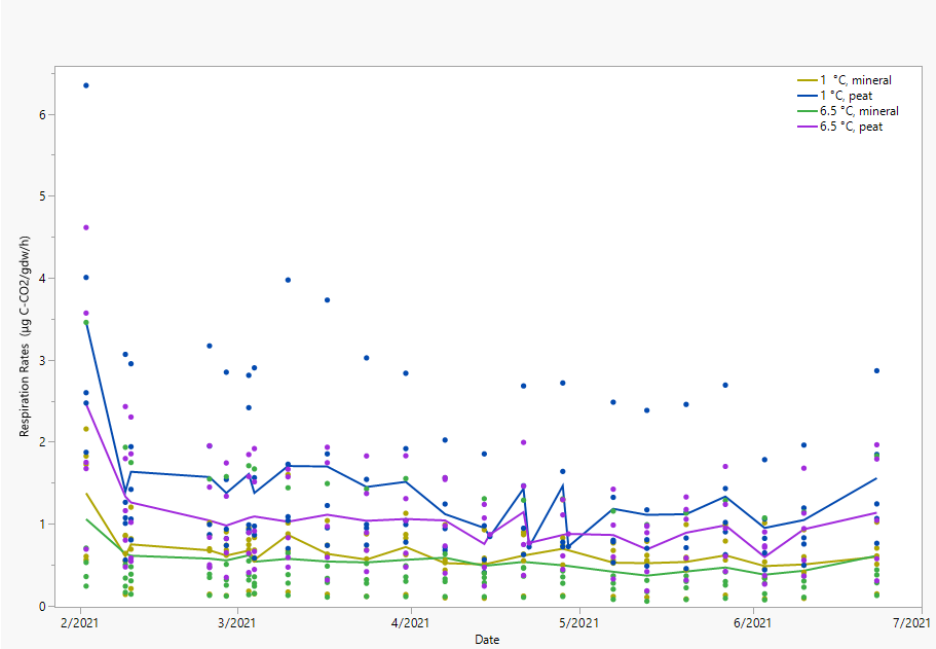


Figure 6. Respiration Rates from Intact Cores, Dry Weight Normalization. When normalized by dry weight, peat cores had higher respiration rates than mineral cores.

3.1.3. Soil C-CO_2 respiration rates (SOC normalization)

Normalizing whole core C production by SOC content resulted in a generally reverse relationship from the normalization by DW. This is expected because upland (mineral) soil cores contained less SOC than lowland (peat) cores. When normalized by SOC, respiration rates ranged from 0.49 to 61.43 (μg C-CO_2/hour/gSOC) (Figure 7), with a mean of 17.60 ± 12.69 for upland cores under treatment 1, a mean of 11.62 ± 5.59 for upland cores under treatment 2, a mean of 3.74 ± 2.38 for lowland cores under treatment 1, and a mean of 2.90 ±1.82 for lowland cores under treatment 2. Here again, soil type (mineral vs. peat) was found to be a statistically significant indicator of C production differences (μg C-CO_2/gSOC), ($F(1)=22.52$, $p= 0.0002$). Similarly to the normalization of C production by soil dry weight, temperature treatments did not have a significant effect on C production differences when normalizing by carbon content ($p = 0.39$). Interestingly, a higher ratio of C was released by mineral cores than by the peat cores in relation to their C stocks (Figure 8).

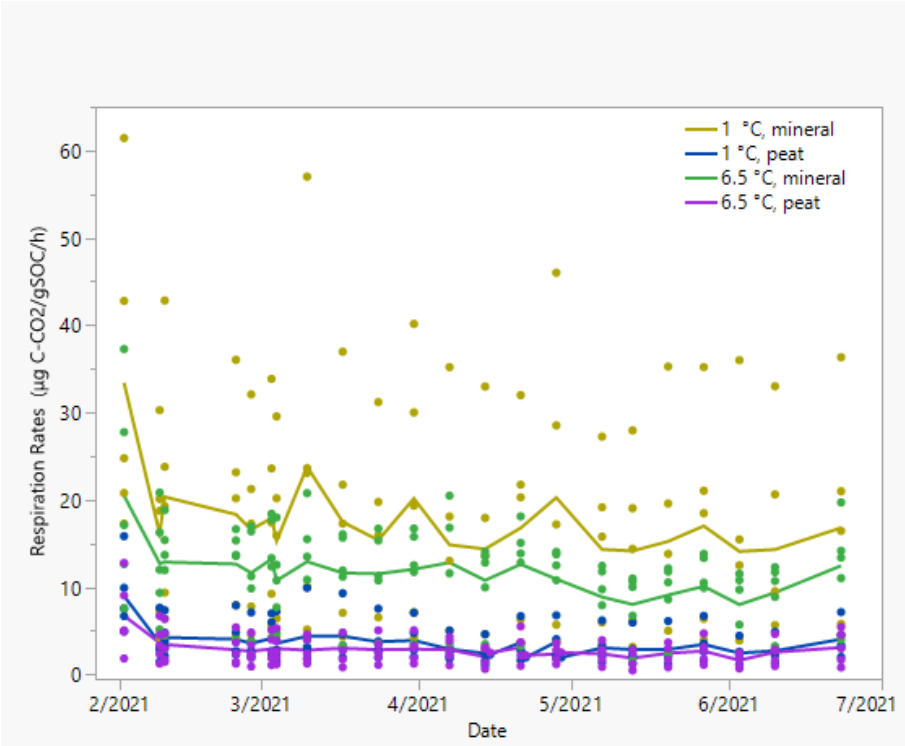


Figure 7. Respiration Rates from Intact Cores, SOC Normalization. Normalizing respiration rates by SOC resulted in higher fluxes per g of C from mineral (upland) cores.

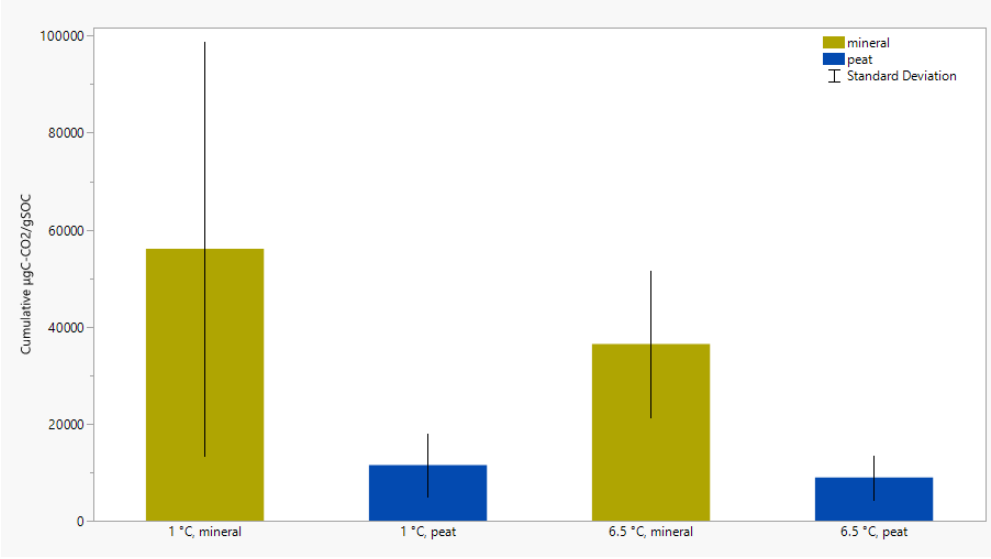


Figure 8. Cumulative C Production from Intact Cores, SOC Normalization. When normalized by g of SOC, cumulative specific production was highest in mineral (upland) cores.

3.2. Partitioned Incubations

3.2.1. Soil carbon stocks

For all soil horizon samples, average C contents were greatest for the organic soil layers, followed by the surface plant layers, and the mineral layers contained the least SOC (Figure 9). Average and SD C contents for each soil type and temperature treatment are listed in Table 2. For the plant layers, C stocks ranged from 0.43g to 0.66g, and average C content totaled 0.58g ± 0.04 in the first (1 °C) temperature treatment and 0.57g ± 0.08 in the second (6.5 °C) temperature treatment. For the organic layers, C stocks ranged from 0.16g to 1.01g, and average carbon contents totaled 0.56 g ± 0.36 and 0.61g ± 0.31 for the first and second temperature treatments, respectively. For the mineral layers, C stocks ranged from 0.07g to 0.89g, and average carbon contents totaled 0.07g ± 0.01 in the first temperature treatment and 0.48g ± 0.38 in the second temperature treatment. Note that for the mineral layers, carbon contents varied more between the temperature treatments due to the observed mixing of mineral and organic soil horizons in core 9 in the 6.5 °C treatment.

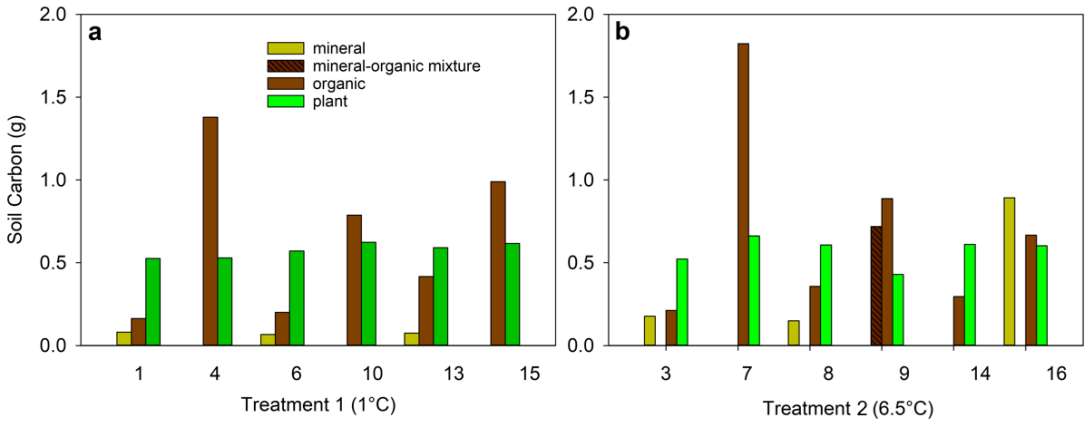


Figure 9. Carbon Stocks in the Partitioned Layer Incubation. Organic soil layers contained the most SOC in both treatment 1 (a) and treatment 2 (b), with lowland source material containing more C than upland source material.

Table 2. Carbon Stocks for Each Soil Type in the Partitioned Layer Incubation Experiment. Mean SOC values and standard deviations are presented by layer type, i.e., "plant", "organic" and "mineral" for both temperature treatments.

		SOC (g)	
Layer Type	Temperature (°C)	Mean	Standard Deviation
mineral	1	0.074465	0.0068408278
	6.5	0.48463125	0.3780458225
organic	1	0.5623260143	0.3614625554
	6.5	0.6059984571	0.3135013818
plant	1	0.5758313	0.0418701748
	6.5	0.5720704333	0.0833802323

3.2.2. Soil C-CO_2 respiration rates (dry weight normalization)

Normalizing soil layer C production by soil DW (μg C-CO_2/gdw) resulted in greater specific production and respiration rates by plant and organic layers than mineral layers (Figure 10). Respiration rates ranged from 1.35 to 29.21 (μg C-CO_2/hour/gdw), with a mean of 8.66 ± 3.20 for all plant layers under treatment 1, and a mean of 9.47 ± 2.70 for all plant layers under treatment 2. For organic layers, average respiration rates were 6.25 ± 4.16 for organic layers under treatment 1, with a mean of 6.73 ± 3.07 for organic layers under treatment 2. For mineral layers, average respiration rates were 3.92 ± 2.36 under treatment 1, with a mean of 2.46 ± 1.26 for mineral layers under treatment 2. The type of soil layer (plant, organic, mineral) was found to have a statistically significant effect on cumulative specific production ($F(2) = 8.48$, $p = 0.0022$), but the effects of field source material (i.e., upland or lowland) were not significant when normalizing by soil DW ($p = 0.38$). Similarly to the whole core incubations, temperature did not have a statistically significant effect on specific production when normalizing by DW ($p = 0.96$).

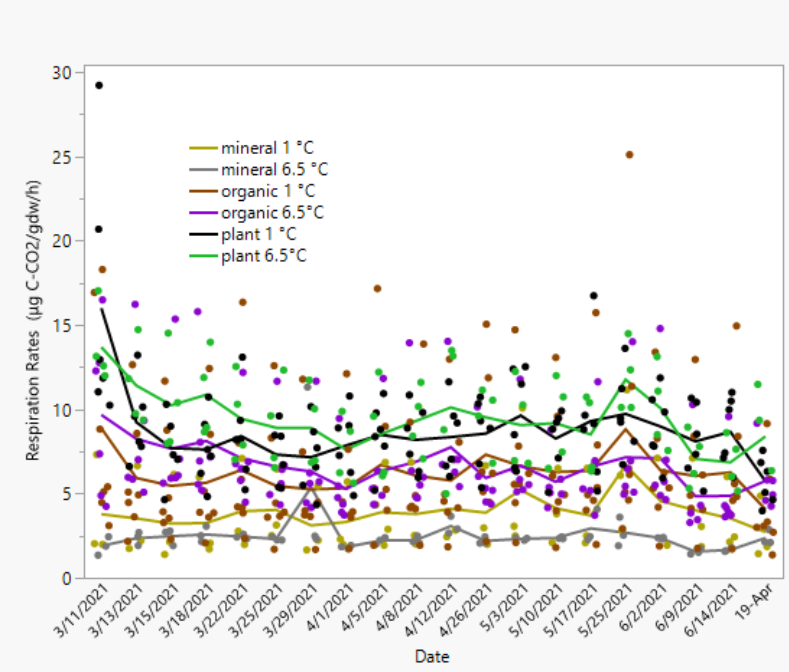


Figure 10. Respiration Rates from Partitioned Layers, Dry Weight Normalization. Similarly to the whole cores, normalizing respiration rates by soil DW results in the highest rates originating from mineral sources.

3.2.3. Soil C-CO_2 respiration rates (SOC normalization)

The homogenized, partitioned soil layer incubations yielded similar trends in respiration rates between soil types when compared to the whole cores. Normalizing soil layer cumulative specific production by SOC content (µg C-CO_2/gSOC) resulted in a greater proportion of C release from mineral soil layers than plant and organic layers (Figure 11). Respiration rates ranged from 3.38 to 379.88 (µg C-CO_2/hour/SOC), with a mean of 21.84 ± 8.61 for all plant layers under treatment 1 (1 °C), and a mean of 24.73 ± 8.15 for all plant layers under treatment 2 (6.5 °C). For organic layers, average respiration rates were 33.73 ± 27.97 for organic layers under treatment 1, with a mean of

30.04 ± 19.03 SD for organic layers under treatment 2. For mineral layers, average respiration rates were 154.90 ± 45.82 under treatment 1, with a mean of 57.60 ± 50.95 for mineral layers under treatment 2. The effect of layer types (in this case, mineral versus plant or organic) was statistically significant ($F(2) = 4.15$, $p= 0.0311$), as well as the effect of field source material, i.e., soil layers that came from upland material lost more C than lowland source materials ($F(1) = 28.85$, $p<.0001$). Temperature did not have a significant effect on C production when normalizing respiration rates by SOC ($p= 0.49$).

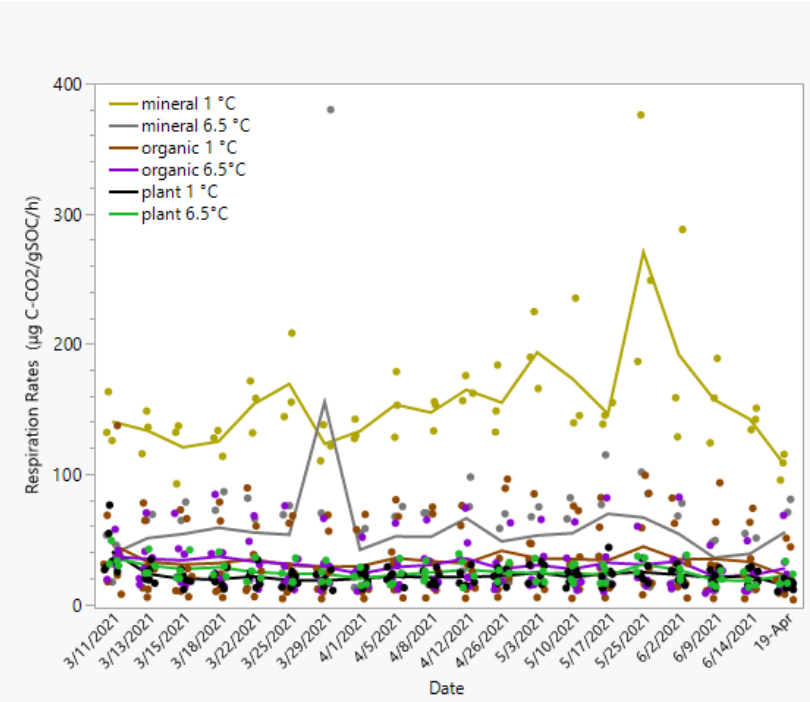


Figure 11. Respiration Rates from Partitioned Layers, SOC Normalization. Normalizing respiration rates by SOC results in higher ratios of C loss from mineral (upland) soil cores.

4. DISCUSSION

4.1. Effects of Soil Type on C Production

Comparisons of upland (mineral) versus lowland (peat) intact soil incubations show that C loss is affected primarily by soil type. Overall, we found that lowland peat soils emitted more C per gram of soil DW compared to upland mineral soils, but the ratio of C loss to initial C stocks was greatest in the mineral soil samples, as shown by the normalization by SOC. Mineral cores lost 4.63% ± 3.20% of SOC on average, compared to 1.02% ± 0.55% lost on average for peat cores. The larger ratio of C lost per gram of SOC by mineral cores indicates that mineral soils may be more sensitive to decomposition than peaty, organic-rich soils.

There are at least two non-competing mechanisms that can explain our finding. First, the lowland cores were wetter than the upland cores. By maintaining field conditions during the incubation, we emulated natural differences in drainage between upland and lowland soils, with wetter and thus lower oxygen availability at the lowland sites. This difference can explain a greater relative C release (expressed as percentage of initial C) from the mineral soils. In their long-term incubation experiment in Greenland, Elberling et al. (2013) came to a similar conclusion. Alternatively, the quality of C from upland and lowland soils also differs. It is well accepted that, although organic-rich soils may contain a greater C pool, a substantial fraction of this carbon is recalcitrant to decay due to lignin-like compounds and phenolics (particularly in the genus *Sphagnum*). A recent incubation study agrees with this idea; the authors linked higher sensitivity of

mineral permafrost soils to decomposition to the fact that mineral soils are less recalcitrant to decay than peat soils (Kuhry et al., 2020).

Carbon-to-nitrogen (C:N) ratios from the horizons of the whole cores indicate highest values for lowland peat cores, with their plant horizons (mean = 53.23 ± 19.99) greater than their counterparts from the upland cores (plant mean = (35.67 ± 6.57 (SD); of course, the mineral layers of the upland cores were characterized by the lowest C:N ratios (mean = 14.21 ± 2.24) (see Appendix Table 1). Organic horizons for both upland and lowland soil cores were similar (upland organic mean = 22.65 ± 4.39, lowland organic mean = 21.83 ± 6.79). Thus, differences in C:N ratio vary the most between surface vegetation at upland and lowland sites and in the mineral (active) layer. Similar results were derived from the partitioned layers experiment (Appendix Table 2). Here we assume that C:N ratio is a suitable proxy for C quality and microbial activity, where high C:N values indicate an "excess" of C (and a limited N supply for decomposers) that slows down decomposition. This indicates a potential linkage between the effects of soil type (and associated C quality) on short-term C production in Alaskan tundra soils.

Schädel et al. (2014) came with a different conclusion when compared to our study and Kuhry et al.'s (2020). Schädel et al. (2014) found that mineral and organic permafrost soils with high C:N ratios were the most vulnerable to C loss; the diverging results may be due to the length of their incubations (multiple years) vs. ours (136 days). Indeed, others (e.g., Enríquez et al., 1993) found that higher carbon concentrations and lignin contents were negatively correlated with decomposition rates. This relationship

may change once the fast-cycling pool is exhausted, and the slow-cycling pool is decomposing.

4.2. No Effects from Temperature Treatments

In both the intact and homogenized layer incubation experiments, and in both the SOC and dry weight normalization, the temperature treatments did not have a significant effect on C production. Goodness-of-fit tests were also performed between C production and temperature, and the lack of significant r-squared values further validated the null hypothesis; in our experiment, temperature effects were not a driving factor in soil respiration. Historically, high latitude soils have shown enhanced sensitivities to temperature increases when compared to lower latitude soils (Karhu et al., 2014; Carey et al., 2016). However, Karhu et al. (2014) homogenized soil cores into a composite prior to incubation, thereby removing physical protections of SOC. The synthesis by Carey et al. (2016) took respiration averages from multiple experimental setups, making it difficult to compare temperature sensitivities at the site-level. In line with our findings, the intact incubation study by Vaughn and Torn (2019) found no differences in temperature sensitivity (C loss) between soil types. This is also the case for another Alaskan soil incubation study that found no significant microbial decomposition response to elevated temperatures (Ballhausen et al., 2020); homogenized soil samples were used. Similarly, an in-situ soil warming experiment (Darrouzet-Nardi et al., 2019) conducted near Toolik Lake found little effects of early snowmelt or warming upon belowground communities. Therefore, it is possible that soil C may be more resistant to temperature warming than previously expected. Again, it is also important to consider

the relative impact of soil wetness vs. temperature. It is possible/expected that temperature sensitivity would be easier to identify and quantify in experimental designs with dry soils, as mostly done. Our findings suggest that oxygen availability and soil type may be more important than soil temperature (at least within the temperature treatments of 1 °C vs. 6.5 °C we used) in controlling soil CO_2 respiration. Those results were found both across our intact cores and the partitioned layers.

4.3. Comparing Intact Soil Incubations to Homogenized Soil

Cumulative specific CO_2 production from the partitioned soil layer incubation was an order of magnitude greater than cumulative C production from the intact, whole core incubation. Likewise, respiration rates were larger in the soil layers than the whole cores. Comparing total C-CO_2 (g) release between corresponding whole cores and soil layers shows that on average, layer C-CO_2 production was 6.1 times greater than intact, whole core C production from the same source material (Figure 12). More specifically, average total partitioned layer C release from upland layers was 8.7 times greater than total C release from upland whole cores (range = 2.74 - 17.23 times). For the peat samples, average total partitioned layer C release from lowland layers was 3.6 times greater than total C release from lowland whole cores (range = 2.40 - 4.72 times). It is plausible that this greater difference across the upland soils (and associated upland partitioned layers) is due to the fact that physical protection is removed during the homogenization process. This finding raises important questions regarding the use of homogenized soil incubations for estimating future CO_2 emissions, as current earth

systems models (ESMs) base their soil parametrization upon Q10 values that are derived from homogenized incubation experiments (e.g., Meyer et al., 2018).

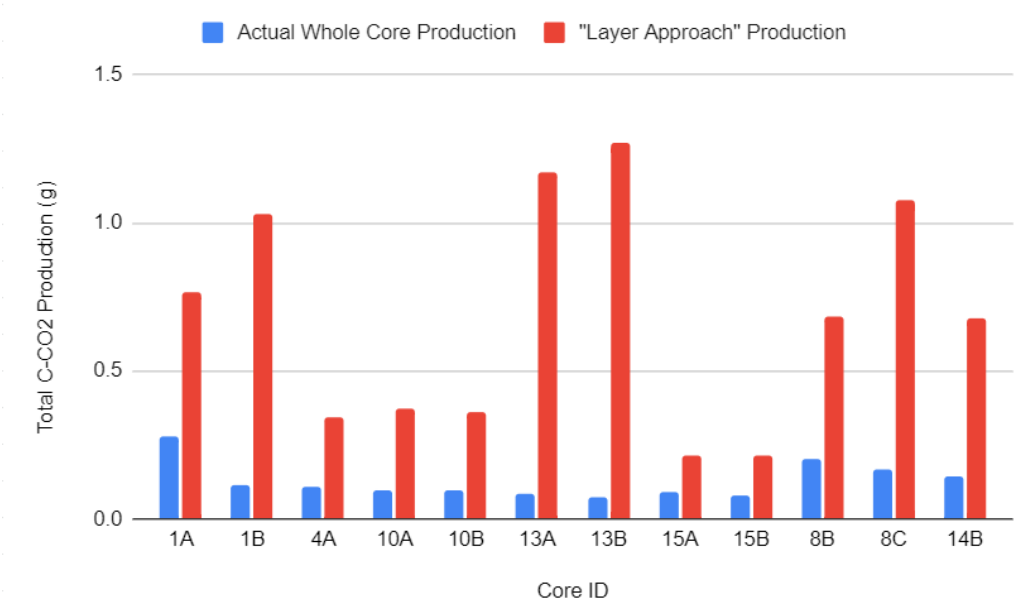


Figure 12. Comparison of C-CO_2 Production Between Intact and Homogenized Soil. The "layer approach" for comparing C production was calculated by multiplying the dry weight of intact soil core horizons times the corresponding respiration rates from matching soil layers in the partitioned soil incubation.

This finding highlights another difficulty that can be encountered when dealing with arctic soils in incubation experiments. In our study, upland soils were found to contain significantly more carbon in their organic layers than in their mineral sediments

(in some instances, SOC contents for organic horizons are more than 20% greater than in mineral horizons). This may not be surprising, but it does bring up potential issues with soil homogenization, particularly in incubation studies that focus on specific depth ranges rather than soil layer types, as these wide variations in carbon contents of soil horizons can cause over- or under-estimations of CO_2 emissions. Thus, in future incubation studies, disturbing and mixing soils across horizons should be minimized, or at the minimum, conducted with careful consideration and explicitly described in the papers.

4.4. Growing Evidence of Peatland Initiation at Toolik Lake, Alaska

In general, the soil cores collected for this study in the foothills of the Brooks Range followed a clear dichotomy; peat (lowland) soils or mineral (upland) soils. However, 2 of our cores fell into another, less clear category, and were therefore removed from the analysis. These cores included cores 2A and 2B, which were sampled from a lowland site (but contained a mineral layer), and cores 16A and 16B, which were collected from an upland site (but were highly organic). These samples were markedly different from the other soil cores in the respective groups in terms of both SOC amounts and in terms of lithology. In the case of cores 2A and 2B, with mineral horizons at their base as well as a peat layer and *Sphagnum* vegetation on top, their stratigraphy might indicate evidence of early peat initiation. Peatlands are relatively young; work by Taylor et al. (2019) showed that peat initiation occurred near Toolik Lake between 0 and 300 CE, and recent work has shown that incipient peatlands dominated by *Sphagnum* may have been spreading since the 1980s near our study sites (Yu et al., 2019; Stansfield et

al., 2021). This indicates that these “uncategorizable” soil cores from our soil incubation may be evidence of recent peat formation and subsequent accumulation of organic carbon. Future work involving radiocarbon dating of these cores is recommended to further investigate potential changes occurring in Alaskan tundra soils.

5. CONCLUSIONS

To investigate the impacts of climate warming upon active layer soils from Toolik Lake, Alaska, we conducted a short-term incubation experiment with two methodologies and soil types. Results from this study indicated that active layer soils from upland (mineral) sites were more sensitive to decomposition than lowland (peat) soils. While CO_2 respiration was greater (per unit of dry soil weight) from the lowland soils, which also contained substantially more SOC than their upland counterparts, relative C loss was greater (when compared to the soil's total C content) in the upland soils. These results might be due to oxygen availability (as the lowland cores were wetter than the upland soils), to the different C quality of the plant types found in each soil type (with lowland plants, and especially *Sphagnum* moss, generally more recalcitrance to decay), or to both factors.

Despite previous expectations that the warmer temperature treatment (6.5 °C) would result in higher C production, temperature effects were not statistically significant in the intact soil incubation or in the homogenized layer incubation. In order to trigger significant changes in C production, larger differences between temperature treatments may be necessary in lab incubations, particularly when field conditions are maintained. Additionally, the lack of effect of temperature on C loss between soil types may indicate that Arctic soil carbon and microbial communities are more resistant to climate warming than previously thought, or that surface wetness is more important in controlling fast C cycling than modest temperature changes. Through the usage of an incubation

experiment with two methodologies, we found that soil homogenization dramatically overestimates C production when compared to the results from the intact cores. In the homogenized soil incubation, mean layer C-CO_2 production was 6.1 times greater than intact, whole core C production from the same source material.

Future work with these datasets will include scaling up the results to similar tundra settings. Applying the differing respiration rates and scaled total C emissions from upland and lowland soils to soil decomposition models will allow for better understanding of future carbon fluxes to the atmosphere. Other future work with this study will include analyzing enzyme markers within the peat and mineral soils, as understanding differences in microbial composition of these tundra soils may elucidate C production differences.

6. REFERENCES

ACIA (2005) *Arctic climate impact assessment*. Edited by J. Berner, C. Symon, L. Arris, O.W. Heal, Arctic Climate Impact Assessment, National Science Foundation (U.S.), and United States. Cambridge ; New York, N.Y: Cambridge University Press.

Alexandrov, G.A., Brovkin, V.A., Kleinen, T. and Yu, Z. (2020) 'The capacity of northern peatlands for long-term carbon sequestration', *Biogeosciences*, 17(1), pp. 47–54. doi:10.5194/bg-17-47-2020.

Ballhausen, M.-B., Hewitt, R. and Rillig, M.C. (2020) 'Mimicking climate warming effects on Alaskan soil microbial communities via gradual temperature increase', *Scientific Reports*, 10(1), p. 8533. doi:10.1038/s41598-020-65329-x.

Bastida, F., García, C., Fierer, N., Eldridge, D.J., Bowker, M.A., Abades, S., Alfaro, F.D., Asefaw Berhe, A., Cutler, N.A., Gallardo, A., García-Velázquez, L., Hart, S.C., Hayes, P.E., Hernández, T., Hseu, Z.-Y., Jehmlich, N., Kirchmair, M., Lambers, H., Neuhauser, S., Peña-Ramírez, V.M., Pérez, C.A., Reed, S.C., Santos, F., Siebe, C., Sullivan, B.W., Trivedi, P., Vera, A., Williams, M.A., Luis Moreno, J. and Delgado-Baquerizo, M. (2019) 'Global ecological predictors of the soil priming effect', *Nature Communications*, 10(1), p. 3481. doi:10.1038/s41467-019-11472-7.

Birch, H.F. (1958) ‘The effect of soil drying on humus decomposition and nitrogen availability’, *Plant and Soil*, 10(1), pp. 9–31. doi:10.1007/BF01343734.

Bond-Lamberty, B., Smith, A.P. and Bailey, V. (2016) ‘Temperature and moisture effects on greenhouse gas emissions from deep active-layer boreal soils’, *Biogeosciences*, 13(24), pp. 6669–6681. doi:10.5194/bg-13-6669-2016.

Bracho, R., Natali, S., Pegoraro, E., Crummer, K.G., Schädel, C., Celis, G., Hale, L., Wu, L., Yin, H., Tiedje, J.M., Konstantinidis, K.T., Luo, Y., Zhou, J. and Schuur, E.A.G. (2016) ‘Temperature sensitivity of organic matter decomposition of permafrost-region soils during laboratory incubations’, *Soil Biology and Biochemistry*, 97, pp. 1–14. doi:10.1016/j.soilbio.2016.02.008.

Carey, J.C., Tang, J., Templer, P.H., Kroeger, K.D., Crowther, T.W., Burton, A.J., Dukes, J.S., Emmett, B., Frey, S.D., Heskel, M.A., Jiang, L., Machmuller, M.B., Mohan, J., Panetta, A.M., Reich, P.B., Reinsch, S., Wang, X., Allison, S.D., Bamminger, C., Bridgham, S., Collins, S.L., Dato, G. de, Eddy, W.C., Enquist, B.J., Estiarte, M., Harte, J., Henderson, A., Johnson, B.R., Larsen, K.S., Luo, Y., Marhan, S., Melillo, J.M., Peñuelas, J., Pfeifer-Meister, L., Poll, C., Rastetter, E., Reinmann, A.B., Reynolds, L.L., Schmidt, I.K., Shaver, G.R., Strong, A.L., Suseela, V. and Tietema, A. (2016) ‘Temperature response of soil respiration largely unaltered with experimental warming’,

Proceedings of the National Academy of Sciences, 113(48), pp. 13797–13802. doi:10.1073/pnas.1605365113.

Chadburn, S.E., Krinner, G., Porada, P., Bartsch, A., Beer, C., Belelli Marchesini, L., Boike, J., Ekici, A., Elberling, B., Friborg, T., Hugelius, G., Johansson, M., Kuhry, P., Kutzbach, L., Langer, M., Lund, M., Parmentier, F.-J.W., Peng, S., Van Huissteden, K., Wang, T., Westermann, S., Zhu, D. and Burke, E.J. (2017) 'Carbon stocks and fluxes in the high latitudes: using site-level data to evaluate Earth system models', *Biogeosciences*, 14(22), pp. 5143–5169. doi:10.5194/bg-14-5143-2017.

Chaudhary, N., Westermann, S., Lamba, S., Shurpali, N., Sannel, A.B.K., Schurgers, G., Miller, P.A. and Smith, B. (2020) 'Modelling past and future peatland carbon dynamics across the pan-Arctic', *Global Change Biology*, 26(7), pp. 4119–4133. doi:10.1111/gcb.15099.

Crowther, T.W., Todd-Brown, K.E.O., Rowe, C.W., Wieder, W.R., Carey, J.C., Machmuller, M.B., Snoek, B.L., Fang, S., Zhou, G., Allison, S.D., Blair, J.M., Bridgham, S.D., Burton, A.J., Carrillo, Y., Reich, P.B., Clark, J.S., Classen, A.T., Dijkstra, F.A., Elberling, B., Emmett, B.A., Estiarte, M., Frey, S.D., Guo, J., Harte, J., Jiang, L., Johnson, B.R., Kröel-Dulay, G., Larsen, K.S., Laudon, H., Lavallee, J.M., Luo, Y., Lupascu, M., Ma, L.N., Marhan, S., Michelsen, A., Mohan, J., Niu, S., Pendall, E., Peñuelas, J., Pfeifer-Meister, L., Poll, C., Reinsch, S., Reynolds, L.L., Schmidt, I.K.,

Sistla, S., Sokol, N.W., Templer, P.H., Treseder, K.K., Welker, J.M. and Bradford, M.A. (2016) 'Quantifying global soil carbon losses in response to warming', *Nature*, 540(7631), pp. 104–108. doi:10.1038/nature20150.

Darrouzet-Nardi, A., Steltzer, H., Sullivan, P.F., Segal, A., Koltz, A.M., Livensperger, C., Schimel, J.P. and Weintraub, M.N. (2019) 'Limited effects of early snowmelt on plants, decomposers, and soil nutrients in Arctic tundra soils', *Ecology and Evolution*, 9(4), pp. 1820–1844. doi:10.1002/ece3.4870.

Elberling, B., Michelsen, A., Schädel, C., Schuur, E.A.G., Christiansen, H.H., Berg, L., Tamstorf, M.P. and Sigsgaard, C. (2013) 'Long-term CO2 production following permafrost thaw', *Nature Climate Change*, 3(10), pp. 890–894. doi:10.1038/nclimate1955.

Enríquez, S., Duarte, C.M. and Sand-Jensen, K. (1993) 'Patterns in decomposition rates among photosynthetic organisms: the importance of detritus C:N:P content', *Oecologia*, 94(4), pp. 457–471. doi:10.1007/BF00566960.

Heffernan, L., Estop-Aragonés, C., Knorr, K.-H., Talbot, J. and Olefeldt, D. (2020) 'Long-term Impacts of Permafrost Thaw on Carbon Storage in Peatlands: Deep Losses Offset by Surficial Accumulation', *Journal of Geophysical Research: Biogeosciences*, 125(3), p. e2019JG005501. doi:10.1029/2019JG005501.

Hobbie, J.E. and Kling, G.W. (eds) (2014) *Alaska's Changing Arctic: Ecological Consequences for Tundra, Streams, and Lakes*. New York: Oxford University Press (The Long-Term Ecological Research Network Series). doi:10.1093/acprof:osobl/9780199860401.001.0001.

Hobbie, J.E., Shaver, G.R., Rastetter, E.B., Cherry, J.E., Goetz, S.J., Guay, K.C., Gould, W.A. and Kling, G.W. (2017) 'Ecosystem responses to climate change at a Low Arctic and a High Arctic long-term research site', *Ambio*, 46(Suppl 1), pp. 160–173. doi:10.1007/s13280-016-0870-x.

Hobbie, S.E., Schimel, J.P., Trumbore, S.E. and Randerson, J.R. (2000) 'Controls over carbon storage and turnover in high-latitude soils: CARBON STORAGE and TURNOVER IN NORTHERN SOILS', *Global Change Biology*, 6(S1), pp. 196–210. doi:10.1046/j.1365-2486.2000.06021.x.

Hugelius, G., Loisel, J., Chadburn, S., Jackson, R.B., Jones, M., MacDonald, G., Marushchak, M., Olefeldt, D., Packalen, M., Siewert, M.B., Treat, C., Turetsky, M., Voigt, C. and Yu, Z. (2020) 'Large stocks of peatland carbon and nitrogen are vulnerable to permafrost thaw', *Proceedings of the National Academy of Sciences*, 117(34), pp. 20438–20446. doi:10.1073/pnas.1916387117.

IPCC. (2021) *Climate Change 2021: The Physical Science Basis.* Cambridge; New York, N.Y: Cambridge University Press. Available at: https://www.ipcc.ch/report/ar6/wg1/

Karhu, K., Auffret, M.D., Dungait, J.A.J., Hopkins, D.W., Prosser, J.I., Singh, B.K., Subke, J.-A., Wookey, P.A., Ågren, G.I., Sebastià, M.-T., Gouriveau, F., Bergkvist, G., Meir, P., Nottingham, A.T., Salinas, N. and Hartley, I.P. (2014) 'Temperature sensitivity of soil respiration rates enhanced by microbial community response', *Nature*, 513(7516), pp. 81–84. doi:10.1038/nature13604.

Kuhry, P., Bárta, J., Blok, D., Elberling, B., Faucherre, S., Hugelius, G., Jørgensen, C.J., Richter, A., Šantrůčková, H. and Weiss, N. (2020) 'Lability classification of soil organic matter in the northern permafrost region', *Biogeosciences*, 17(2), pp. 361–379. doi:10.5194/bg-17-361-2020.

La Puma, I.P., Philippi, T.E. and Oberbauer, S.F. (2007) 'Relating NDVI to ecosystem CO2 exchange patterns in response to season length and soil warming manipulations in arctic Alaska', *Remote Sensing of Environment*, 109(2), pp. 225–236. doi:10.1016/j.rse.2007.01.001.

Liu, X.-Y., Koba, K., Koyama, L.A., Hobbie, S.E., Weiss, M.S., Inagaki, Y., Shaver, G.R., Giblin, A.E., Hobara, S., Nadelhoffer, K.J., Sommerkorn, M., Rastetter, E.B.,

Kling, G.W., Laundre, J.A., Yano, Y., Makabe, A., Yano, M. and Liu, C.-Q. (2018) 'Nitrate is an important nitrogen source for Arctic tundra plants', *Proceedings of the National Academy of Sciences*, 115(13), pp. 3398–3403. doi:10.1073/pnas.1715382115.

Loisel, J., Gallego-Sala, A.V., Amesbury, M.J., Magnan, G., Anshari, G., Beilman, D.W., Benavides, J.C., Blewett, J., Camill, P., Charman, D.J., Chawchai, S., Hedgpeth, A., Kleinen, T., Korhola, A., Large, D., Mansilla, C.A., Müller, J., van Bellen, S., West, J.B., Yu, Z., Bubier, J.L., Garneau, M., Moore, T., Sannel, A.B.K., Page, S., Väliranta, M., Bechtold, M., Brovkin, V., Cole, L.E.S., Chanton, J.P., Christensen, T.R., Davies, M.A., De Vleeschouwer, F., Finkelstein, S.A., Frolking, S., Gałka, M., Gandois, L., Girkin, N., Harris, L.I., Heinemeyer, A., Hoyt, A.M., Jones, M.C., Joos, F., Juutinen, S., Kaiser, K., Lacourse, T., Lamentowicz, M., Larmola, T., Leifeld, J., Lohila, A., Milner, A.M., Minkkinen, K., Moss, P., Naafs, B.D.A., Nichols, J., O'Donnell, J., Payne, R., Philben, M., Piilo, S., Quillet, A., Ratnayake, A.S., Roland, T.P., Sjögersten, S., Sonnentag, O., Swindles, G.T., Swinnen, W., Talbot, J., Treat, C., Valach, A.C. and Wu, J. (2021) 'Expert assessment of future vulnerability of the global peatland carbon sink', *Nature Climate Change*, 11(1), pp. 70–77. doi:10.1038/s41558-020-00944-0.

McGuire, A.D., Lawrence, D.M., Koven, C., Clein, J.S., Burke, E., Chen, G., Jafarov, E., MacDougall, A.H., Marchenko, S., Nicolsky, D., Peng, S., Rinke, A., Ciais, P., Gouttevin, I., Hayes, D.J., Ji, D., Krinner, G., Moore, J.C., Romanovsky, V., Schädel, C., Schaefer, K., Schuur, E.A.G. and Zhuang, Q. (2018) 'Dependence of the evolution of

carbon dynamics in the northern permafrost region on the trajectory of climate change', *Proceedings of the National Academy of Sciences*, 115(15), pp. 3882–3887. doi:10.1073/pnas.1719903115.

Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture (2006) *Toolik, Alaska*. Available at: https://www.nrcs.usda.gov/wps/portal/nrcs/detail//?cid=nrcs142p2_053712 (Accessed: 3 March 2022)

Olid, C., Nilsson, M.B., Eriksson, T. and Klaminder, J. (2014) 'The effects of temperature and nitrogen and sulfur additions on carbon accumulation in a nutrient-poor boreal mire: Decadal effects assessed using ^{210} Pb peat chronologies', *Journal of Geophysical Research: Biogeosciences*, 119(3), pp. 392–403. doi:10.1002/2013JG002365.

Pegoraro, E., Mauritz, M., Bracho, R., Ebert, C., Dijkstra, P., Hungate, B.A., Konstantinidis, K.T., Luo, Y., Schädel, C., Tiedje, J.M., Zhou, J. and Schuur, E.A.G. (2019) 'Glucose addition increases the magnitude and decreases the age of soil respired carbon in a long-term permafrost incubation study', *Soil Biology and Biochemistry*, 129, pp. 201–211. doi:10.1016/j.soilbio.2018.10.009.

Plaza, C., Pegoraro, E., Bracho, R., Celis, G., Crummer, K.G., Hutchings, J.A., Hicks Pries, C.E., Mauritz, M., Natali, S.M., Salmon, V.G., Schädel, C., Webb, E.E. and Schuur, E.A.G. (2019) 'Direct observation of permafrost degradation and rapid soil carbon loss in tundra', *Nature Geoscience*, 12(8), pp. 627–631. doi:10.1038/s41561-019-0387-6.

Salomé, C., Nunan, N., Pouteau, V., Lerch, T.Z. and Chenu, C. (2010) 'Carbon dynamics in topsoil and in subsoil may be controlled by different regulatory mechanisms', *Global Change Biology*, 16(1), pp. 416–426. doi:10.1111/j.1365-2486.2009.01884.x.

Schädel, C., Beem-Miller, J., Aziz Rad, M., Crow, S.E., Hicks Pries, C.E., Ernakovich, J., Hoyt, A.M., Plante, A., Stoner, S., Treat, C.C. and Sierra, C.A. (2020) 'Decomposability of soil organic matter over time: the Soil Incubation Database (SIDb, version 1.0) and guidance for incubation procedures', *Earth System Science Data*, 12(3), pp. 1511–1524. doi:10.5194/essd-12-1511-2020.

Schädel, C., Schuur, E.A.G., Bracho, R., Elberling, B., Knoblauch, C., Lee, H., Luo, Y., Shaver, G.R. and Turetsky, M.R. (2014) 'Circumpolar assessment of permafrost C quality and its vulnerability over time using long-term incubation data', *Global Change Biology*, 20(2), pp. 641–652. doi:10.1111/gcb.12417.

Schuur, E.A.G., Bracho, R., Celis, G., Belshe, E.F., Ebert, C., Ledman, J., Mauritz, M., Pegoraro, E.F., Plaza, C., Rodenhizer, H., Romanovsky, V., Schädel, C., Schirokauer, D., Taylor, M., Vogel, J.G. and Webb, E.E. (2021) 'Tundra Underlain By Thawing Permafrost Persistently Emits Carbon to the Atmosphere Over 15 Years of Measurements', *Journal of Geophysical Research: Biogeosciences*, 126(6). doi:10.1029/2020JG006044.

Schuur, E.A.G., McGuire, A.D., Schädel, C., Grosse, G., Harden, J.W., Hayes, D.J., Hugelius, G., Koven, C.D., Kuhry, P., Lawrence, D.M., Natali, S.M., Olefeldt, D., Romanovsky, V.E., Schaefer, K., Turetsky, M.R., Treat, C.C. and Vonk, J.E. (2015) 'Climate change and the permafrost carbon feedback', *Nature*, 520(7546), pp. 171–179. doi:10.1038/nature14338.

Schuur, E.A.G., Vogel, J.G., Crummer, K.G., Lee, H., Sickman, J.O. and Osterkamp, T.E. (2009) 'The effect of permafrost thaw on old carbon release and net carbon exchange from tundra', *Nature*, 459(7246), pp. 556–559. doi:10.1038/nature08031.

Serreze, M.C., Walsh, J.E., Chapin, F.S., Osterkamp, T., Dyurgerov, M., Romanovsky, V., Oechel, W.C., Morison, J., Zhang, T. and Barry, R.G. (2000) 'Observational Evidence of Recent Change in the Northern High-Latitude Environment', *Climatic Change*, 46(1), pp. 159–207. doi:10.1023/A:1005504031923.

Shaver, G., Smith, Thomas Michael, Smith, T. M., Shugart, H.H., Woodward, F.I. and Shugart, P.H.H. (1997) 'Plant functional types and ecosystem changes in arctic tundras', in *Plant Functional Types: Their Relevance to Ecosystem Properties and Global Change*. Cambridge University Press, pp. 153–173.

Shulski, M. and Wendler, G. (2007) *The Climate of Alaska*. University of Alaska Press.

Sistla, S.A., Moore, J.C., Simpson, R.T., Gough, L., Shaver, G.R. and Schimel, J.P. (2013) 'Long-term warming restructures Arctic tundra without changing net soil carbon storage', *Nature*, 497(7451), pp. 615–618. doi:10.1038/nature12129.

Smith, A.P., Bond-Lamberty, B., Benscoter, B.W., Tfaily, M.M., Hinkle, C.R., Liu, C. and Bailey, V.L. (2017) 'Shifts in pore connectivity from precipitation versus groundwater rewetting increases soil carbon loss after drought', *Nature Communications*, 8(1), p. 1335. doi:10.1038/s41467-017-01320-x.

Stansfield, A., Booth, R., Scally, A., Xia, Z. and Loisel, J. (2021) 'Sphagnum "peat-patch" expansion on the North Slope of Alaska', in. *AGU Fall Meeting 2021*, New Orleans, LA. Available at: https://agu.confex.com/agu/fm21/meetingapp.cgi/Person/714677 (Accessed: 7 February 2022).

Taylor, L.S., Swindles, G.T., Morris, P.J., Gałka, M. and Green, S.M. (2019) 'Evidence for ecosystem state shifts in Alaskan continuous permafrost peatlands in response to recent warming', *Quaternary Science Reviews*, 207, pp. 134–144. doi:10.1016/j.quascirev.2019.02.001.

Treat, C.C., Jones, M.C., Alder, J., Sannel, A.B.K., Camill, P. and Frolking, S. (2021) 'Predicted Vulnerability of Carbon in Permafrost Peatlands With Future Climate Change and Permafrost Thaw in Western Canada', *Journal of Geophysical Research: Biogeosciences*, 126(5). doi:10.1029/2020JG005872.

Turetsky, M.R., Abbott, B.W., Jones, M.C., Anthony, K.W., Olefeldt, D., Schuur, E.A.G., Grosse, G., Kuhry, P., Hugelius, G., Koven, C., Lawrence, D.M., Gibson, C., Sannel, A.B.K. and McGuire, A.D. (2020) 'Carbon release through abrupt permafrost thaw', *Nature Geoscience*, 13(2), pp. 138–143. doi:10.1038/s41561-019-0526-0.

Vaughn, L.J.S. and Torn, M.S. (2019) '14C evidence that millennial and fast-cycling soil carbon are equally sensitive to warming', *Nature Climate Change*, 9(6), pp. 467–471. doi:10.1038/s41558-019-0468-y.

Voigt, C., Marushchak, M.E., Lamprecht, R.E., Jackowicz-Korczyński, M., Lindgren, A., Mastepanov, M., Granlund, L., Christensen, T.R., Tahvanainen, T., Martikainen, P.J. and Biasi, C. (2017) 'Increased nitrous oxide emissions from Arctic peatlands after

permafrost thaw', *Proceedings of the National Academy of Sciences*, 114(24), pp. 6238–6243. doi:10.1073/pnas.1702902114.

Walker, D.A., Daniëls, F.J.A., Alsos, I., Bhatt, U.S., Breen, A.L., Buchhorn, M., Bültmann, H., Druckenmiller, L.A., Edwards, M.E., Ehrich, D., Epstein, H.E., Gould, W.A., Ims, R.A., Meltofte, H., Raynolds, M.K., Sibik, J., Talbot, S.S. and Webber, P.J. (2016) 'Circumpolar Arctic vegetation: a hierarchic review and roadmap toward an internationally consistent approach to survey, archive and classify tundra plot data', *Environmental Research Letters*, 11(5), p. 055005. doi:10.1088/1748-9326/11/5/055005.

Yu, Z., Camill, P., Frolking, S., Loisel, J., Zhuang, Q. and Beilman, D. (2019) 'TundraPEAT—Understanding Peat Expansion in Arctic Tundra in a Warming Climate', in. *21st EGU General Assembly*, p. 1. Available at: https://ui.adsabs.harvard.edu/abs/2019EGUGA..21.2332Y/abstract.

Zhang, Z., Zimmermann, N.E., Stenke, A., Li, X., Hodson, E.L., Zhu, G., Huang, C. and Poulter, B. (2017) 'Emerging role of wetland methane emissions in driving 21st century climate change', *Proceedings of the National Academy of Sciences*, 114(36), pp. 9647–9652. doi:10.1073/pnas.1618765114.

APPENDIX A

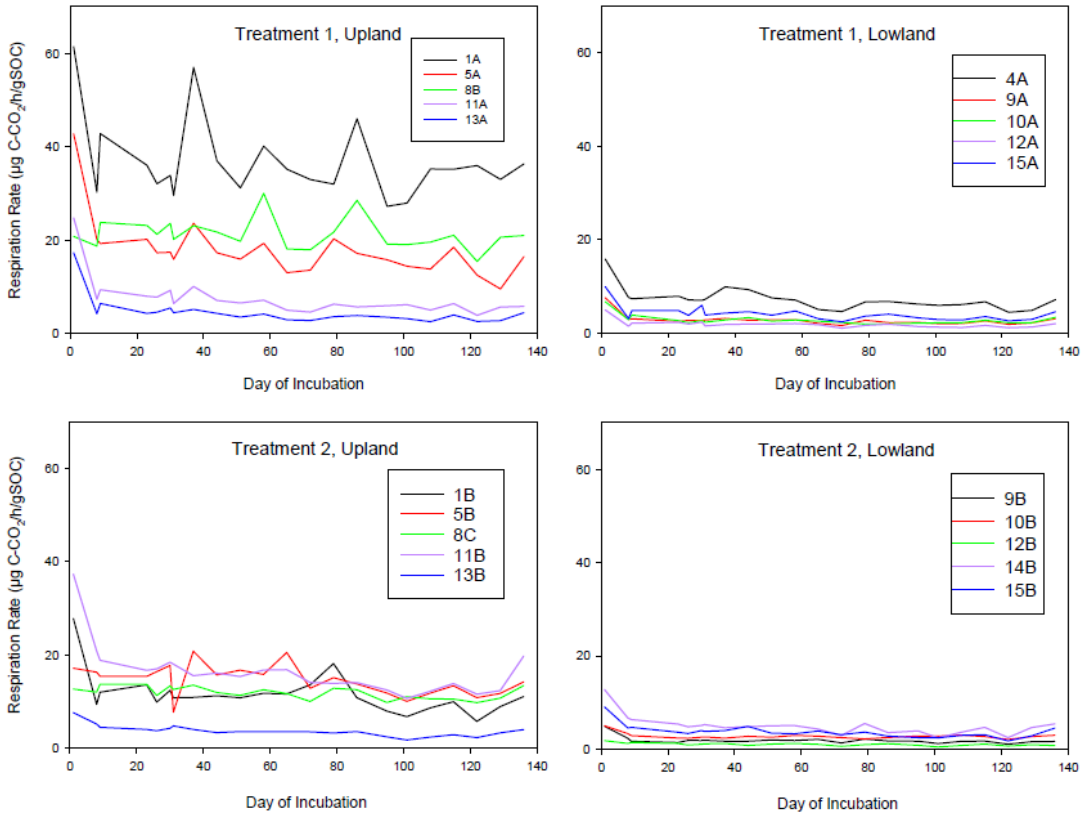
	Type			
	mineral		peat	
	C:N Ratio Average		C:N Ratio Average	
Horizon	Mean	Std Dev	Mean	Std Dev
mineral	14.212768167	2.2388674977	.	.
organic	22.650038333	4.3949171962	21.830601666	6.7896974732
organic/mineral	.	.	16.176658335	0.445630481
plant	35.67153	6.5749976816	53.22973	19.991338057

Appendix Table 1. C:N Ratios from Averaged Duplicate Layer Material from Intact Cores. Empty cells designate a lack of a particular horizon, e.g., lowland soil cores did not contain enough mineral layers to generate a mean or standard deviation.

	Source Soil Type			
	mineral		peat	
	C:N Ratio		C:N Ratio	
Layer Type	Mean	Std Dev	Mean	Std Dev
mineral	15.78722	2.744795687	15.20615	.
organic	21.54899	4.5088142247	31.0151875	20.037426462
plant	34.26292	5.8764578427	44.146566667	13.272257444

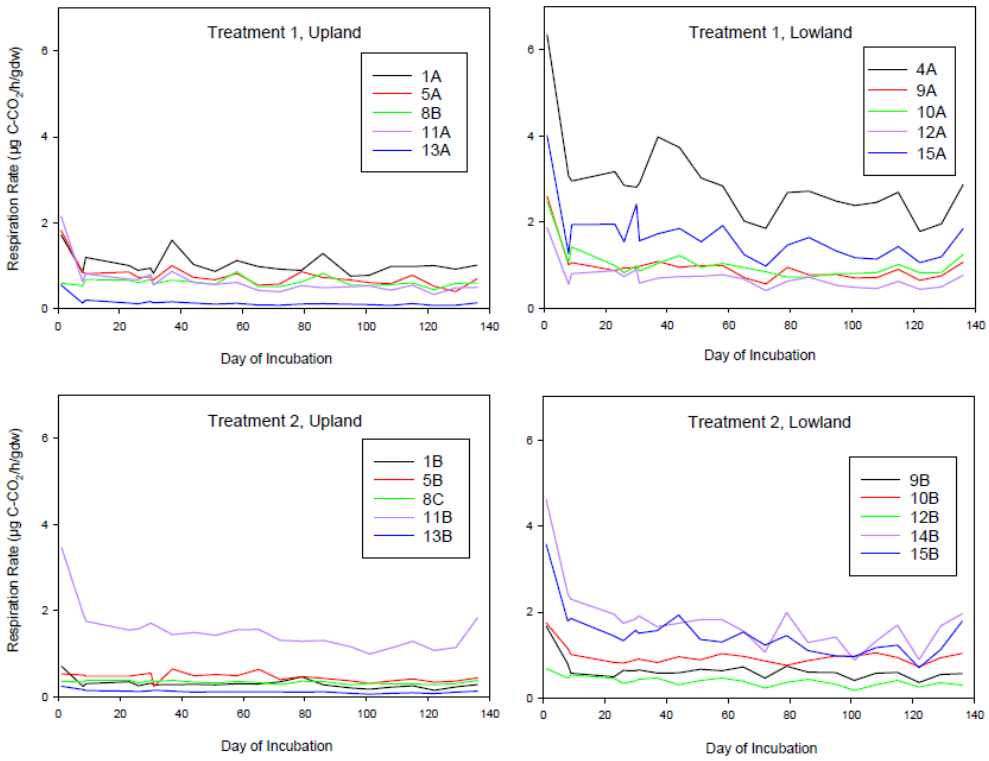
Appendix Table 2. Average C:N Ratios from Partitioned Soil and their Soil Horizons. Material from the partitioned incubation experiment is represented by “plant”, “organic” and “mineral” layer types; note that the peat, lowland soil types did not have enough bottom mineral layers to generate a standard deviation.

APPENDIX B



Appendix Figure 1: Respiration Rates (SOC Normalization) from Intact Cores, Grouped by Temperature and Soil Type.

APPENDIX C



Appendix Figure 2: Respiration Rates (Dry Weight Normalization) from Intact Cores, Grouped by Temperature and Soil Type.