Polar Biol (2016) 39:1283–1295
DOI 10.1007/s00300-015-1853-2

ORIGINAL PAPER

Soil carbon storage, respiration potential, and organic matter quality across an age and climate gradient in southwestern Greenland

Julia I. Bradley-Cook[1] · **Ross A. Virginia**[2]

Received: 27 December 2014 / Revised: 29 November 2015 / Accepted: 30 November 2015 / Published online: 12 December 2015

Abstract Geological factors influence biological cycling of organic carbon in soils but are not well represented in our understanding of Arctic carbon dynamics. Landscape age, for instance, directly affects quantity and quality of soil carbon, which are two strong controls of the temperature sensitivity of soil organic matter. We investigated soil carbon storage, respiration potential, and organic matter quality for microbial decomposition across a climate and landscape age gradient in southwest Greenland that deglaciated during the Holocene. We measured soil respiration during a 370-day laboratory incubations of active layer soils collected from four study areas across this gradient (ages 1.8×10^2, 6.8×10^3, and 1.0×10^4, coinciding with a climate gradient from drier inland to wetter coastal terrain) and used a soil respiration model comparison approach to assess the substrate quality of stored organic matter for microbial decomposers. Soils store more than three times greater organic carbon at the 10,000-year-old, maritime climate study areas than the 180-year-old, continental climate study areas. Respiration rates were highest in the surface soils of the coastal areas. Model comparisons reveal important heterogeneity in the quality of organic matter for microbial decomposition between areas: coastal soils were best modeled by both one- and two-pooled models, and inland soils were best represented by one-pooled respiration models. Together, the measures of carbon quality (C:N, CO_2 production, and model parameters estimating initial CO_2 production rates from different organic matter pools) show that shallow soils at the southern coastal area, Kobbefjord, had the highest respiration rates from the recalcitrant carbon pool. This study reveals differences in carbon storage and turnover associated with landscape age and climate factors in western Greenland. When applied to thermodynamic theory, which predicts that temperature sensitivity increases with carbon recalcitrance, our findings suggest that carbon stored in coastal soils may be more sensitive to climate warming than inland soils.

Keywords Climate change · Soil organic carbon · Decomposition · Organic matter quality · Landscape age · Arctic

Introduction

Soil organic carbon (SOC) storage represents a long-term balance between the net inputs and losses of biological carbon belowground. It is widely accepted that soil-forming factors constrain soil development and determine the size and stability of this pool (Jenny 1941), yet geological controls on biological carbon cycling are not well represented in our understanding of carbon dynamics.

Arctic ecosystems play a particularly important role in the global carbon cycle. Arctic terrestrial ecosystems cover approximately 25 % of the earth's vegetated land surface (McGuire et al. 2009), and arctic permafrost soils contain an estimated 1300 Pg of carbon (Hugelius et al. 2014) due to low soil temperatures and slow decomposition rates. Soils represent the largest pool of carbon in the region and comprise nearly half of global belowground organic carbon (McGuire et al. 2009). The soils of southwestern Greenland are classified as arctic brown soils, with humus-poor class

✉ Julia I. Bradley-Cook
Julia.I.Bradley-Cook.GR@Dartmouth.edu

[1] Ecology and Evolutionary Biology Program, Department of Biological Science, Dartmouth College, Hanover, NH, USA

[2] Environmental Studies Program, Dartmouth College, Hanover, NH, USA

at inland and northern areas, like Kangerlussuaq and Sisimiut, and humus-rich class at coastal southern areas, around Nuuk (Jones et al. 2009). Estimates of soil carbon stocks in the region vary substantially. Estimates downscaled from circum-Arctic soil carbon models fall in the range from 15 to 40 kg m^{-2} (Jones et al. 2009), while coastal soils in Disko, Greenland, range from 2.6 to 28.2 kg m^{-2} depending on the land cover type (Jensen et al. 2006).

Research on soil organic carbon (SOC) controls in the Arctic has focused on climate and environmental conditions (Hobbie et al. 2000; Van Wijk et al. 2003; Sjogersten and Wookey 2005; Shaver et al. 2006), plant–soil interactions (Chapin and Shaver 1989; Shaver et al. 2001; Weintraub and Schimel 2005; Ehrenfeld et al. 2005), soil fauna (Nielsen and Wall 2013), micro-topography (Sullivan et al. 2008; Zona et al. 2011), relief (Giblin et al. 1991; Nadelhoffer et al. 1991; Stieglitz et al. 2003), and deposition history (Knoblauch et al. 2013). Landscape age, on the other hand, is a geological variable that is not well represented, but is of interest because organic carbon accumulates and undergoes biological and physical processing over time. Pioneering work by Crocker and Major (1955) in Glacier Bay, Alaska describes organic carbon accumulation during primary succession following glacier retreat. Landscape age can also modify the quality of soil carbon, i.e., the decomposability of stored carbon, which is a strong determinant of biological carbon loss (Bosatta and Agren 1999). Whittinghill and Hobbie (2011) observed differential metabolism across an 11,000–4.8 million year chronosequence as a result of increased carbon stabilization from calcium cation bridging in younger soils (Whittinghill and Hobbie 2012). A gap remains in our understanding of how landscape age controls soil carbon quality in regions deglaciated during the Holocene. This study compares soils across southwestern Greenland, which has deglaciated within the past 11,000 years. During development following deglaciation, soils may experience internal biological and physiochemical processing that control soil carbon quality.

In this study, we investigated how time since deglaciation and climatic factors affect the accumulation and quality of SOC for microbial decomposition in southwestern Greenland. Specifically, we addressed the following questions: (1) how do soil carbon storage and respiration potential vary with landscape age across southwest Greenland? (2) does soil organic matter quality vary with landscape age? and (3) how do carbon storage and quality vary by depth within the active layer? We hypothesize that landscape age will be a primary control on soil carbon storage and respiration potential, such that the quantity of carbon and respiration potential linearly increase with time since deglaciation. We considered two alternative hypotheses about how soil organic matter quality, as represented by the respiration rate of carbon, will change as a result of soil development over the landscape age: (1) recalcitrance pool respiration rates will be higher in older landscapes as a result of internal microbial processing of organic matter that produces recalcitrant byproduct compounds, (2) recalcitrant pool respiration rates will be lower in older landscapes, as observed in Alaska by Whittinghill and Hobbie (2011), due to reduced chemical protection. Lastly, we hypothesize that deep soils would have higher carbon content and lower organic matter quality at the older coastal areas as a result of soil development and microbial processing.

To answer these research questions, we collected soils from four study areas along a gradient in southwestern Greenland that span a range of current climatic conditions and a landscape age of 180 to approximately 10,000 years. We conducted long-term laboratory incubations to compare soil respiration and determine how much of the stored carbon is biologically available under controlled environmental conditions. Soil carbon quality affects organic matter quality and is represented through a variety of indices, including density fractionation and stoichiometric ratios (Bosatta and Agren 1999). We used stoichiometric ratios as measures of soil organic matter quality and mechanistic models of soil respiration decay in long-term laboratory incubations to partition the respiration rates of carbon pools and determine soil organic matter quality. Our study provides a cross-site perspective of SOC that can inform interpretation of observational and experimental studies that examine variation in soil carbon associated with characteristic land cover types and sensitivity of carbon dynamics to abiotic conditions.

Methods

Site description and field data collection

We chose four study areas in the low Arctic shrub tundra ecosystem of southwestern Greenland to capture a 10,000-year landscape age gradient from the margin of the Greenland ice sheet to the coast (Fig. 1a; Table 1). At each study area, we conducted a ground-based survey to identify potential sites that control for vegetation, relief, and aspect based on the following criteria: dwarf shrub vegetation cover (*Salix glauca* and *Vaccinium uliginosum*) and shallow slopes (less than 15°) with a north-facing orientation (20° west of north to 10° east of north). We focused on these criteria because vegetation type influences carbon inputs and soil environment, shallow slopes allow for soil drainage, and north-facing slopes experience less direct insolation. Shrub cover was absent at the youngest study area, so we located transects on glacial till with sparse herbaceous vegetation (Table 2). We identified at least five eligible sites per study area, which were separated by up to

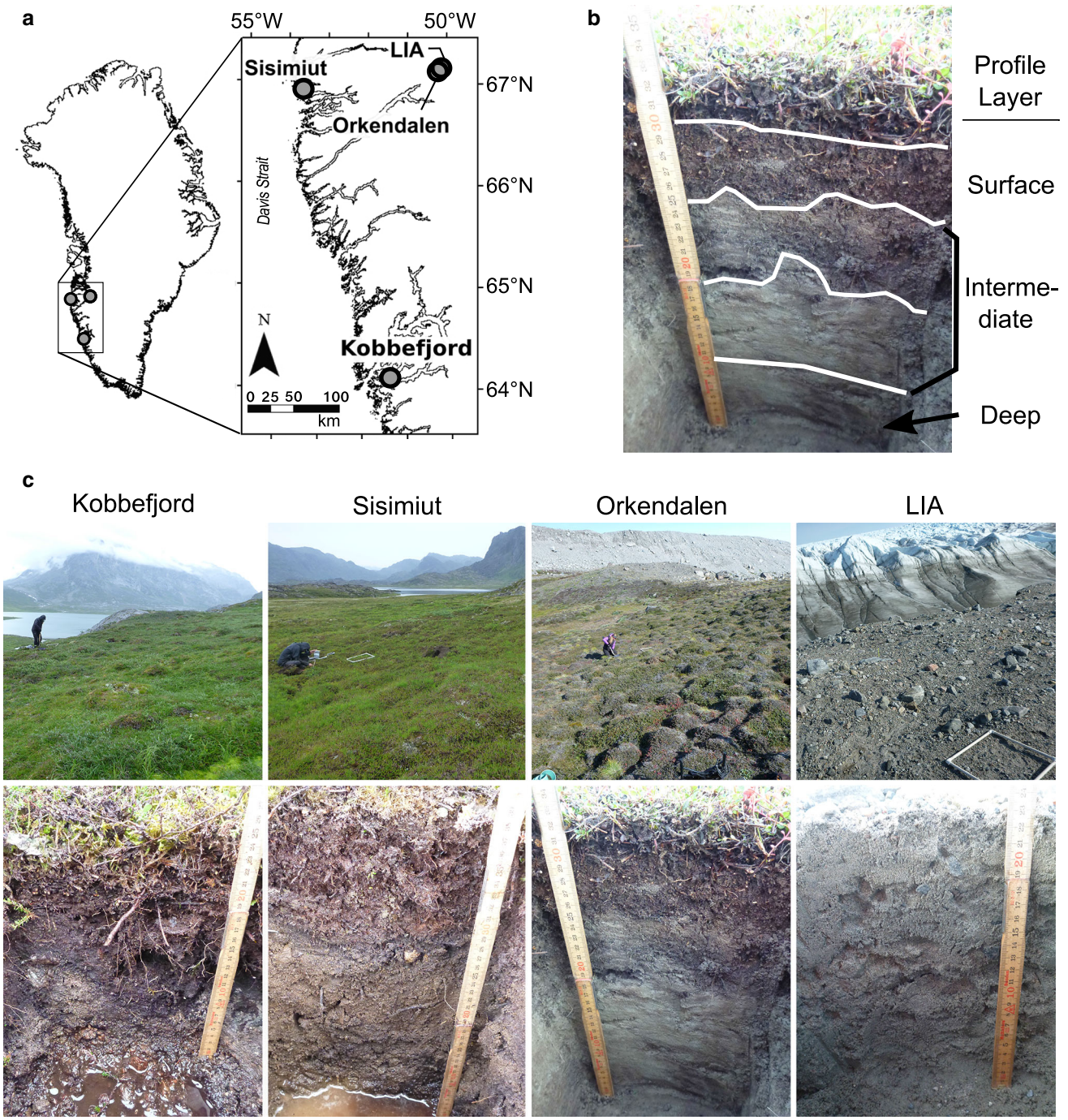

Fig. 1 **a** Map of southwestern Greenland with the study areas indicated by *gray circles*. **b** A representative soil profile with *white lines* delineating visually classified horizons and corresponding soil layers. **c** Representative photographs of transect sites (*top*) and soil profile (*bottom*) for each study area. Soil profiles show development of organic horizon from the youngest to oldest study areas (*right* to *left*)

2 km at Kobbefjord (KOB), 4.6 km at Sisimiut (SIS), 0.8 km at Orkendalen (ORK), and 0.2 km at Little Ice Age moraine (LIA). We randomly selected three sites among the set of eligible sites in each study area. To capture soil heterogeneity (including micro-topography, such as hummocks) at each site, we haphazardly placed a 10-m transect perpendicular to the slope and dug three pits evenly spaced along each transect, for a total of 9 pits in each study area, and a total of 36 pits in the whole study. Prior to digging each soil pit, we surveyed vegetation within a 25-cm^2 quadrant at the sampling location. We identified all species present in the canopy and sub-canopy, visually estimated

Table 1 Age and climate characteristics of the study areas

Study area	Landscape age (years)	Geographic position	Annual temp (Mean, °C)[§]	Growing season temp (Mean, Jun–Aug, °C)[§]	Annual precip (Mean, mm)[¶]
Little Ice Age moraine (LIA)	180	Inland	−5.7	9.2	252
Orkendalen (ORK)	6800*	Inland	−5.7	9.2	252
Sisimiut (SIS)	10,000[#]	Coast	−3.9	5.3	623
Kobbefjord (KOB)	10,000[#]	Coast	−1.4	5.5	1005

Annual temperature and precipitation are means of long-term data from meteorological stations located in neighboring towns (LIA & Orkendalen (Kangerlussuaq): 1973–1999, Sisimiut & Nuuk: 1961–1990)

* Levy et al. (2012)

[#] Roberts et al. (2009)

[§] Danish Meteorological Institute

[¶] Mernild et al. (2015)

Table 2 Description of transects within each study area

Transect	Area	Coordinates	Elevation (m)	Shrub cover (%)/total veg (%)	Bulk density, 0–10 cm (g/cm^3)	SOC stock (kg/m^2)
LIA-1	Little Ice Age	N67° 09.705′ W50° 06.823′	464	0/9	1.44	0.25
LIA-2	Little Ice Age	N67° 09.707′ W50° 06.886′	476	0/0	1.44	0.09
LIA-3	Little Ice Age	N67° 09.711′ W50° 07.024′	473	0/0	1.44	0.11
ORK-1	Orkendalen	N67° 09.386′ W50° 06.286′	415	69/80	0.71	3.62
ORK-2	Orkendalen	N67° 09.652′ W50° 06.933′	457	67/69	0.71	7.67
ORK-3	Orkendalen	N67° 09.683′ W50° 06.929′	46	60/73	0.71	3.07
SIS-1	Sisimiut	N66° 55.956′ W53° 37.017′	63	94/96	0.27	10.87
SIS-2	Sisimiut	N66° 56.199′ W53° 35.708′	49	91/98	0.27	9.44
SIS-3	Sisimiut	N66° 57.509′ W53° 41.243′	132	88/98	0.27	17.49
NU-1	Nuuk	N64° 07.654′ W51° 22.607′	40	97/98	0.15	7.63
NU-2	Nuuk	N64° 07.630′ W51° 22.912′	59	96/99	0.15	6.80
NU-3	Nuuk	N64° 08.217′ W51° 24.448′	42	89/89	0.15	8.82

percent cover of each species, and measured the maximum and average height of the canopy, an indirect measure of biomass in dwarf shrubs (Elzein et al. 2011).

Within each soil pit, we collected samples based on visual classification of the soil profile. We classified the soil samples into three profile layers: "surface," "intermediate," or "deep." "Surface" soils were dark brown, organic, low bulk density samples within 10 cm of the surface. The deepest mineral samples collected were labeled as "deep." All samples taken between the surface and deep soils were labeled as "intermediate." The only non-vegetated study area, LIA, had no visible organic horizon or profile development, so we collected only two increments: the top 5 cm and the underlying 10 cm (Fig. 1b). Because we sampled visually detectable horizons, the number of samples varied between areas (number of samples at each study area: KOB = 30, SIS = 30, ORK = 36, LIA = 18). Prior to collecting soil samples, we measured soil temperature at each sample depth with a digital temperature probe and volumetric water content using a handheld Theta Probe Model ML2x (Delta T Devices). We collected samples using a spoon that was cleaned with a kimwipe in between samples to minimize cross-contamination. To measure bulk density, we cut cubic samples from one of the three pits in each transect with a serrated knife. We measured the dimensions of each bulk density sample with a ruler, dried them at 105 °C, and calculated average bulk density for each study area. We calculated the mean temperatures at each area for the deep and surface soils and used a one-way ANOVA to test for differences between areas. Soil pits were dug and sampled between August 1–21, 2012.

We took in situ soil respiration measurements with a Li-Cor 8100 infrared gas analyzer (IRGA; Lincoln, NE, USA) on August 15, 2012. We set up 3 transects in the proximity of the LIA and ORK soil pits, each containing 2 or 3 20-cm collars (a total of 7 collars per site). Collars sat for at least 20 min following installation into the soil to minimize the

effect of physical disturbance on CO_2 exchange. For each measurement, we discarded the first 20 s of data to allow air pressure and CO_2 concentration to stabilize in the chamber. After this 20-s interval, we measured CO_2 flux over a 2-min observation. Additionally, we recorded soil temperature at 3 cm depth. The close proximity of the inland sites made it possible to conduct comparative in situ flux measurements at ORK and LIA, but we were unable to take measurements at coastal sites because of logistical constraints. Results of linear mixed effects model (R version 3.0.2) were used to evaluate study area as a predictor of soil respiration rate, with transect included as a random effect.

Laboratory analysis and incubations

We froze field samples at −4 °C and shipped them back to the Biogeochemistry Laboratory (Dartmouth College, Hanover, NH) where we stored them at −20 °C before thawed for processing and analysis. We sieved samples to separate the 2 mm size fraction, which we kept for further analysis. For organic samples with partially decomposed plant material, we removed roots larger than 5 mm in diameter and homogenized the samples by hand mixing. To determine organic carbon and nitrogen concentrations, we dried, ground using a sapphire mortar and pestle, and acidified the soils with HCl to eliminate inorganic carbon before we analyzed them on a Carlo Erba NA 1500 elemental analyzer (Carlo Erba Instruments, Milan, Italy).

We conducted 370-day incubations to measure soil respiration potential and characterize the quality of soil organic matter for microbial decomposition for each soil sample. We thawed soils at 4 °C for 8 days before we placed 25 g of soils in half-pint ball jars and incubated them at 5 °C and 100 % water-holding capacity in Percival Scientific incubators. The temperature treatment was selected to mimic realistic growing season temperatures. Soils across the west Greenland gradient experience a range of water content, soils at the coast experience near-saturated conditions for prolonged periods, and all soils experience high moisture contents during the early season due to winter snow melt (Anderson et al. 2009). The soils were incubated for 2 days before the beginning of the first measurement. We measured CO_2 production on days: 4, 7, 14, 28, 42, 68, 77, 121, 232, 324, and 370. At 48 h prior to each sampling point, we sealed jars and flushed the headspace with CO_2-free gas and returned the jars to incubate. We extracted 10 mL gas sample from the jar headspace with a syringe and injected the sample into a Li-Cor 8100 IRGA to measure CO_2 concentration in the headspace gas.

To derive the CO_2 production, we quantified the headspace volume for each sample by measuring the headspace CO_2 concentration before and after injecting a known amount of CO_2 into a CO_2-free, sealed jar. We calculated the difference and used a dilution function to calculate the volume (Curiel Yuste et al. 2007). We multiplied CO_2 concentration by headspace volume to determine total CO_2–C respired during the sampling interval.

Carbon storage and soil respiration potential

We compared SOC for surface and deep soils at each study area by averaging the mean carbon concentrations of each transect for each layer in each study area ($n = 3$ for each layer and area combination) and conducting a two-way ANOVA with study area and profile depth as predictor variables of the mean SOC of each transect. For each soil pit, we measured SOC storage by multiplying carbon concentration by the bulk density derived from representative samples and by the depth interval of each sample within the top 20 cm. We applied the same bulk density profile to the three pits within each transect. We tested for study area differences in SOC by one-way ANOVA and conducted a Tukey's HSD post hoc multiple comparisons test ($\alpha = 0.05$) to evaluate differences in SOC storage among study areas.

To compare total soil respiration potential of all samples, we compared cumulative CO_2 production. We calculated cumulative CO_2 production by multiplying the mean CO_2 respiration rates of neighboring sample dates by the time interval between the sample dates and summing the time-corrected CO_2 production for the full incubation period. We conducted a full two-way ANOVA to test for differences in the effect of study area, depth, and the study area–depth interaction on cumulative CO_2 production.

To compare soil respiration rates for each pit, we aggregated cumulative CO_2 production for samples within the 0–20 cm depth interval of each pit.

$$\text{CO}_2\ \text{Production} = \text{Cumulative}\ \text{CO}_2 \times \text{Bulk Density} \times \text{depth interval}$$

where production is μg CO_2–C cm^{-2}, cumulative CO_2 is μg CO_2–C g $soil^{-1}$, bulk density is g soil cm^{-3}, and depth interval is cm. We omitted samples deeper than 20 cm from these calculations in order to maintain a uniform depth across sites. Some samples straddled the 20 cm depth threshold, in which case we adjusted the depth interval to generate standard 20 cm profile for all soil profiles. We used linear mixed effect models to test soil profile as a predictor of CO_2 production. CO_2 data were log-transformed to fit assumption of normality. We identified significant differences between soil profiles using a Tukey's HSD test.

Soil carbon quality across landscape age and climate gradients

We determined microbial quality of soil organic matter using stoichiometric and modeling approaches. First, we

determined the carbon-to-nitrogen (C:N) ratio for surface and deep samples. We tested for differences in C:N between soil profiles and layers using a two-way ANOVA.

Second, we used quantitative models based on biological mechanisms to compare soil respiration over the incubation period. Our objective was to compare the temporal pattern of change in the rate of microbial CO_2 production from the incubated soils and to use the derived model parameters to gain inference about study area differences in carbon mineralization potential and decay dynamics of soil organic matter decomposition. We fit three candidate models to respiration data of each sample (113 total samples) using nonlinear least squares parameter estimation. The candidate models were a one-pooled linear, one-pooled exponential decay, and two-pooled exponential decay model,

1. One-pooled linear: $R = m \times x + b$
2. One-pooled exponential: $R = a \times e^{kt}$
3. Two-pooled exponential: $R = \left(a_1 \times e^{k_1 t}\right) + \left(a_2 \times e^{k_2 t}\right)$

R is CO_2 respiration (μg C–CO_2 g soil^{-1} day^{-1}), m is the linear slope (μg C–CO_2 g soil^{-1}), x is time (days), b is the intercept (μg C–CO_2 g soil^{-1} day^{-1}), a is the scaling coefficient (μg C–CO_2 g soil^{-1} day^{-1}) that represents the initial respiration rate of the entire soil C pool (a), the "fast"-decomposing (a_1), or the "slow"-decomposing (a_2) carbon pool, k is the decay rate of the single pool (day^{-1}) of the single pool (k), the "fast"-decomposing (k_1), or recalcitrant pool (k_2); t is time in days. The two-pooled model predicts that the "fast"-decomposition (also known as the labile pool) decays more rapidly than the "slow"-decomposing (recalcitrant) pool ($k_1 > k_2$) and can be observed by elevated CO_2 production rates during the initial phase of the incubation. Therefore, we interpret CO_2 production at the end of the incubation to be from a recalcitrant pool. It is possible to use microbial respiration data to model the size and decay rates of soil carbon pools (see Riggs et al. 2015), but our analysis focuses on differences in soil respiration rates and the decay of these rates during the incubation period. We used Akaike's information criterion to identify the best (lowest AICc) and other plausible models (ΔAICc < 2) for each sample.

All analyses were conducted in R version 3.0.2 statistical programming language (R Development Core). Nonlinear least squares parameter estimation and AICc were conducted with the AICcmodavg version 1.35 package in R.

Results

Site and environmental conditions

Mean surface soil temperature was lower at ORK (inland, 6.8 k y.o. area) than at LIA (inland, 180 y.o. area), KOB (coastal, 10 k y.o. area), and SIS (coastal, 10 k y.o. area; soil temperatures: 7.3, 10.1, 9.8, 11.0 °C, respectively; $F_{3,31} = 11.74$, $P < 0.01$). Deep soil mean temperatures were lower at SIS (4.4 °C) and ORK (4.6 °C) than at KOB (8.6 °C) and LIA (8.3 °C), which are the most southern area and the unvegetated inland area, respectively ($F_{3,\ 29} = 19.11$, $P < 0.01$). Soil moisture in surface samples was highest at KOB and lowest at LIA, with no difference between SIS and ORK (mean volumetric water content: KOB = 31.0 %, SIS = 21.6 %, ORK = 21.1 %, LIA = 10.3 %; $F_{3,31} = 18.74$, $P < 0.01$). The depth of surface soils varied across vegetated study areas as a result of organic horizon thickness (average depth, cm: KOB = 8.3, SIS = 7.1, ORK = 4.9, LIA = no organic horizon). Mean soil pit depth was 26.4, 32.3, 34.4, and 15 in KOB, SIS, ORK and LIA, respectively.

Shrubs dominated the sites selected for sampling in all but the youngest study area (LIA), but the coverage was highest at the coast (in the oldest study areas, KOB and SIS). Shrub canopy cover ranged from 88 to 97 % at KOB and SIS, which was higher than ORK, which had 60–69 % coverage (Table 2). *Betula nana* was present at all vegetated sites and was particularly abundant at ORK, where it comprised 59 % of the total shrub canopy. *Empetrum hermaphroditum* was dominant in the shrub canopy at the oldest study areas, KOB and SIS (KOB = 43 %, SIS = 73 % cover), but was absent from the ORK sites. *S. glauca* was observed in small percentages at all vegetated study areas (KOB = 5 %, SIS = 5 %, ORK = 1 %). *V. uliginosum* was present at all sites, but was most common at KOB (30 %) and ORK (18 %) compared to SIS (2 %). *Rhododendron groenlandicum* was present at KOB and ORK (11 and 0.5 %, respectively). Herbaceous species were also present in the sub-canopy: *Equisetum arvense* and *Salix arctica* (SIS), *Bistorta vivipara* (SIS and ORK), *Pyrola grandiflora*, and *Cerastium alpinum* (ORK). Mean shrub canopy height was higher at coastal areas than inland (KOB = 7.5 cm, SIS = 6.9 cm, ORK = 4.0 cm; $F_{2,24} = 5.56$, $P < 0.01$).

Carbon storage and respiration potential

Soil organic carbon (SOC) varied by study area and depth (Fig. 2a). The two-way ANOVA revealed a significant effect of study area ($F_{3,16} = 54.8$, $P < 0.01$), layer ($F_{1,16} = 163.6$, $P < 0.01$), and the interaction between study area and layer ($F_{3,16} = 39.3$, $P < 0.01$) on soil carbon concentration. Within each profile layer, our findings supported our hypothesis that SOC concentration increases with landscape age, with the highest values at oldest coastal study areas (mean ± 1 SE (%): KOB = 47.03 ± 0.01, SIS = 40.07 ± 3.45, ORK = 8.50 ± 2.23, LIA = 0.05 ± 0.01). SOC concentration of deep soils was also highest at the coastal study areas,

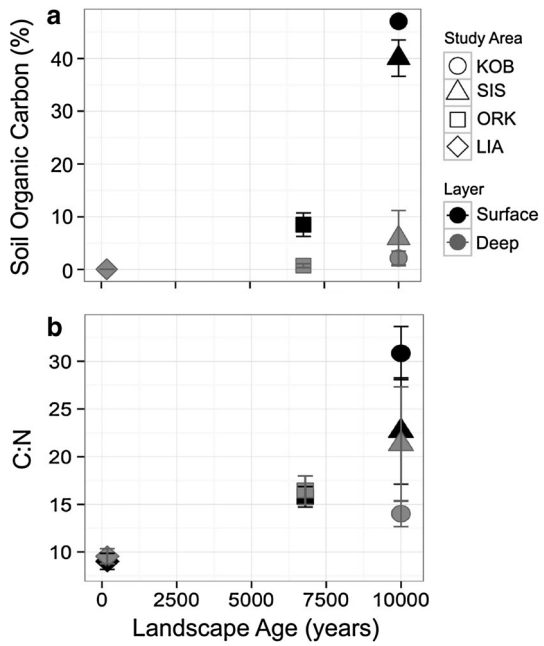

Fig. 2 **a** SOC increases nonlinearly with time since deglaciation (landscape age), particularly for surface soils. **b** C:N increases with landscape age. *Symbol* indicates study area means (±1 SE) for surface and deep soils (in *black* and *gray*, respectively)

although the magnitude of increase across the transect was not as great as in surface soils (mean carbon concentration ± 1 SE (%): KOB = 2.17 ± 1.30, SIS = 5.9 ± 5.22, ORK = 0.73 ± 0.38, LIA = 0.05 ± 0.02). SOC concentrations of surface soils were 5 times greater at 10,000–year-old study areas than the 6800-year-old study area and 3 times greater than in deep soils (Fig. 2a). The carbon accumulation in the surface soils at the coastal study areas showed distinct profile development as compared with the weak profile development in the inland younger study areas (Fig. 3). SOC was 6–22 times greater in surface soils than in mineral soils in vegetated study areas (all areas excluding LIA) (Fig. 2a).

Estimated organic carbon storage for reconstructed 20 cm soil profiles varied by study area ($F_{3,8} = 12.7$; $P < 0.01$), with highest stocks in coastal soils compared with inland soils (mean ± 1 SE, kg cm^{-2}: KOB = 7.75 ± 0.59, SIS = 12.60 ± 2.48, ORK = 4.79 ± 1.45, and LIA = 0.15 ± 0.05) (Table 2). SIS carbon stock was higher than that of both LIA and ORK, while KOB stocks were elevated relative to LIA (Tukey HSD; $P < 0.03$). Our hypothesis was partially supported by the trend that carbon storage increases with landscape age, but did not explain the finding that carbon storage at SIS was higher than KOB, which have the same landscape age.

Soil respiration potential, as measured by cumulative production of CO_2, varied by study area ($F_{3,102} = 14.370$, $P < 0.01$) and profile class ($F_{2,102} = 30.637$, $P < 0.001$), with a significant interaction effect ($F_{5,102} = 6.260$, $P < 0.01$) (Fig. 4). KOB surface soils had the highest mean cumulative CO_2 production (352.617 ± 62.393 ug CO_2–C g soil^{-1}) and LIA soils had the lowest (3.727 ± 0.134 µg CO_2–C g soil^{-1}), which supported our hypothesis that soil respiration potential would be highest at the older study areas. Mean cumulative CO_2 production in KOB surface soils was 1.4, 3.4, and 94.6 times higher than SIS, ORK, and LIA soils, respectively. Deep soils from the coastal study areas had 3.3 times higher mean CO_2 production rate than deep ORK soils and 4.4 times higher than LIA soils. Soils in the intermediate depth class produced more CO_2 at KOB and SIS than ORK and LIA.

The integrated respiration potential for soils within the top 20 cm was best described by the linear mixed effects model that included study area as a fixed effect (ΔAICc = 9.876). Surprisingly, we found no evidence of differences among the vegetated study areas across the gradient, but cumulative respiration at vegetated study areas was between 3.5 and 5.0 higher than LIA (Tukey HSD, $P < 0.01$; back-transformed mean CO_2 production, kg C–CO_2 m^{-2}: KOB = 4.52, SIS = 5.15, ORK = 3.68, LIA = 1.04; Fig. 5). After correcting for variations in bulk density between study areas, the respiration potential for soil profiles is comparable.

In-situ observations of CO_2 flux support the laboratory soil respiration patterns observed between inland study areas (ORK and LIA). Soil respiration rates varied by study area, with the average rates at ORK study areas nearly five times greater than the rates determined at the LIA study areas (mean CO_2 flux ± 1 SE, µmol CO_2 m^{-2} s^{-1}: ORK = 2.27 ± 0.57, LIA = 0.56 ± 0.28). While temperature can increase microbial decomposition and observed flux rates, the higher flux rates at the ORK study area were not positively associated with temperature differences between the two study areas: ORK soils were 3.5 °C cooler than the minimally vegetated LIA soils (mean soil temp ± 1 SE, °C: LIA = 11.96 ± 0.24, ORK = 8.48 ± 0.10).

Soil organic matter quality

Two-way ANOVA showed that C:N varied by study area ($F_{3,16} = 7.5$, $P = 0.002$), with a study area–layer interaction ($F_{3,16} = 3.5$, $P = 0.04$) but did not vary with profile layer ($F_{1,16} = 3.5$, $P = 0.08$). C:N increased by threefold in surface soils from the LIA to KOB (Fig. 2b), which supports the alternative hypothesis that carbon quality decreases with landscape age. At ORK, the C:N ratio of the surface and deep soils did not differ. While profile layer was not a statistically significant predictor of C:N, the data point to strong carbon quality differentiation by soil layer at KOB, with a reduced C:N in deep soils. Deep soils at the

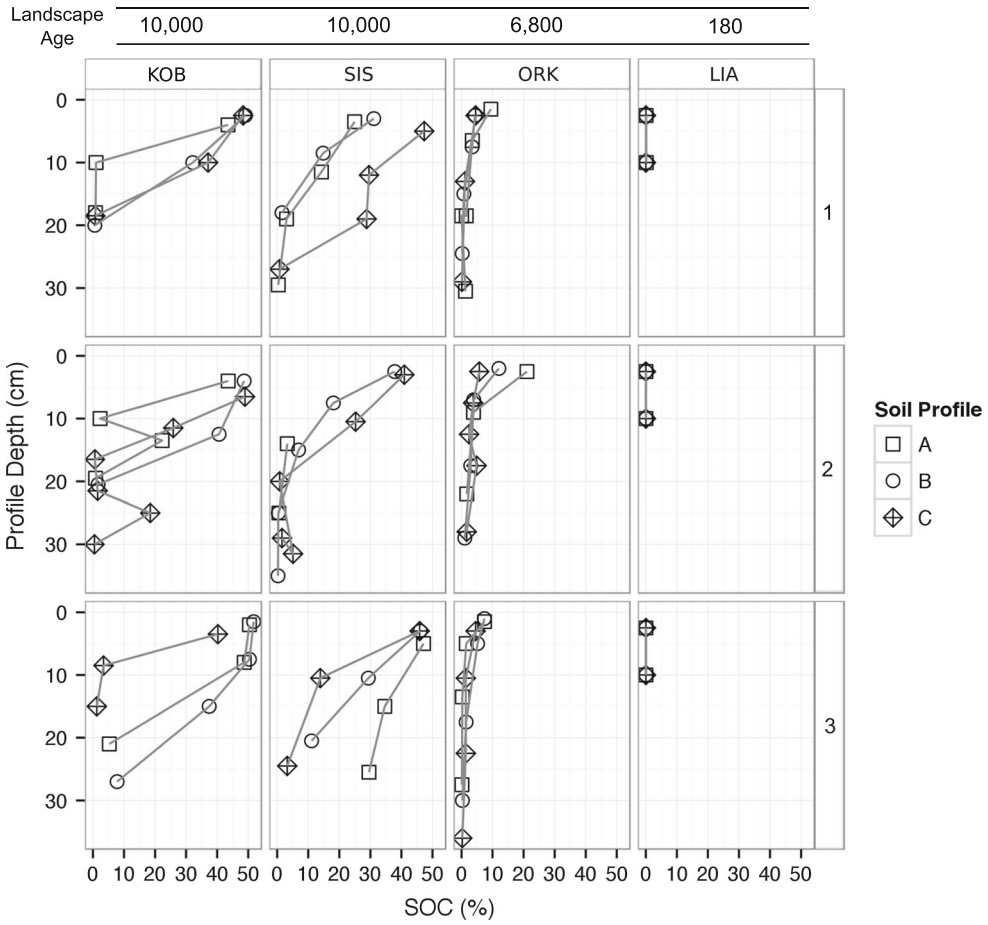

Fig. 3 Soil organic carbon concentration profiles from the four study areas (*columns*), with three transects within each area (*rows*). Each transect contained three pits (*shapes*) to represent local heterogeneity

coastal study areas had comparable C:N relative to the deep soils at ORK. C:N was lowest at the youngest study area, LIA, where the low carbon concentration was coupled by a high ratio of nitrogen.

In the model comparison for incubation respiration rates, linear and one-pool models were the only plausible models for most soils (ΔAICc < 2 for 97 of 114 samples, Fig. 6), with the highest intercepts at the coastal areas, and most rapid decline in surface soils. In the inland areas (LIA and ORK), the linear model had the best fit and the one-pool exponential model fit equally as well. Linear decline of respiration of LIA soils occurred at a rate of -0.011 ± 0.015 and -0.010 ± 0.014 μg CO_2–C per day for surface and deep soils, respectively. ORK soils with linear fit demonstrated higher respiration rates and rate of declines for surface soils than deep soils (surface: $m = -0.410 \pm 0.129$ μg C–CO_2 g soil^{-1}, $b = 363.2 \pm 22.1$ μg C–CO_2 g soil^{-1} day^{-1}; deep: $m = -0.010 \pm 0.015$ μg C–CO_2 g soil^{-1}, $b = 13.3 \pm 2.6$ μg C–CO_2 g soil^{-1} day^{-1}). Of the coastal samples with linear model as a plausible fit, the most rapid decline and highest intercept were observed at KOB (surface: $m = -0.589 \pm 0.340$ μg C–CO_2 g soil^{-1}, $b = 1120.7 \pm 58.4$ μg C–CO_2 g soil^{-1} day^{-1}; deep: $m = -0.072 \pm 0.030$ μg C–CO_2 g soil^{-1}, $b = 37.3 \pm 5.2$ μg C–CO_2 g soil^{-1} day^{-1}), and SIS was also high relative to the inland areas (surface: $m = -0.299 \pm 0.178$ μg C–CO_2 g soil^{-1}, $b = 592.6 \pm 30.5$ μg C–CO_2 g soil^{-1} day^{-1}; deep: $m = -0.045 \pm 0.032$ μg C–CO_2 g soil^{-1}, $b = 41.2 \pm 5.5$ μg C–CO_2 g soil^{-1} day^{-1}).

KOB had multiple samples that fit the two-pool decay model, allowing for a comparison of the quality of soil organic matter in surface and deep soils. The average estimate of labile pool parameters showed that this "fast"-decomposition pool had a higher initial CO_2 production rate that declined more quickly in surface soils than deep soils (mean ± 1SE, surface: $a_1 = 1395 \pm 729$ μg C–CO_2 g soil^{-1} day^{-1}, $k_1 = 7.394 \pm 0.974$ day^{-1}; deep: $a_1 = 118 \pm 80$ μg C–CO_2 g soil^{-1} day^{-1}, $k_1 = 6.328 \pm 0.214$ day^{-1}). The respiration rate of the surface soil recalcitrant pool declined at a similar rate to that of the deep soils, with a trending toward a higher initial respiration rate (surface: $a_2 = 3521 \pm 2180$ μg C–CO_2 g soil^{-1} day^{-1}, $k_2 = 1.854 \pm 0.509$ day^{-1}; deep: $a_2 = 731 \pm 464$ μg C–CO_2 g soil^{-1} day^{-1}, $k_2 = 1.312 \pm 0.475$ day^{-1}), but there was substantial variation in the small set of samples with a two-pool model fit (Fig. 7). These two-pool model results allow us to test our

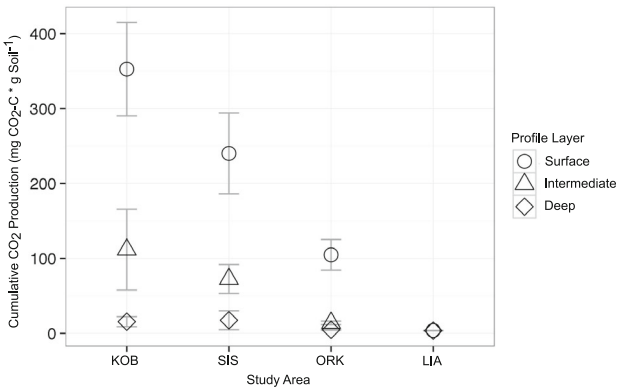

Fig. 4 Cumulative CO_2 production varies by study area and profile layer. *Symbols* are mean values (±1 SE) for each profile layer

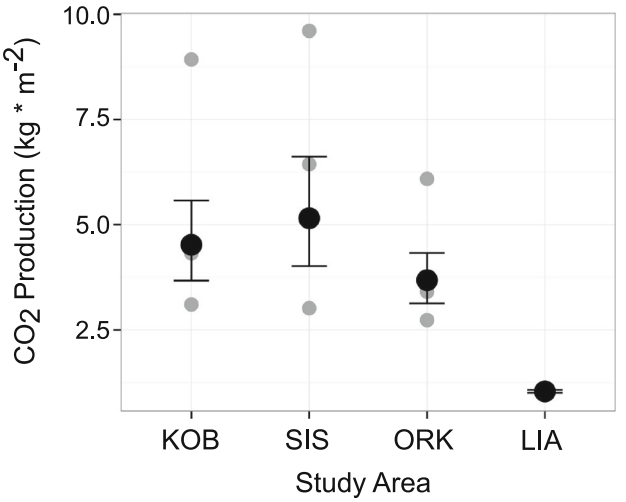

Fig. 5 Cumulative CO_2 production for soils within the top 20 cm varies by study area. LIA CO_2 production is significantly lower than other study areas, but there is no difference between vegetated study areas. *Black circles* are study area means (±1 SE); *gray symbols* are site (transect) averages within each study area

hypothesis about changes in quality by soil layer and revealed that surface soils have more carbon available for microbial decomposition and show a tendency of decreased recalcitrance in deep soils. For the northern coastal area, SIS, linear and one-pool models were both plausible in the majority of samples (28 of 30), but two surface samples were well represented by the two-pool model (Fig. 6). Of these two samples, one contained the two-pool decay as the only plausible model and it had a high CO_2 production rate from the labile carbon pool with a rapid decay rate of the CO_2 production rate and a lower CO_2 production rate from the recalcitrant pool with a slower decay rate than the average of the KOB samples that display a two-pool model fit ($a_1 = 1119.5 \pm 47.9$ µg C–CO_2 g soil^{-1} day^{-1}, $k_1 = 7.246 \pm 0.352$ day^{-1}, $a_2 = 2645.4 \pm 2770.9$ µg C–CO_2 g soil^{-1} day^{-1}, $k_2 = 0.839 \pm 0.590$ day^{-1}). The other SIS sample had a recalcitrant pool with a large variance that overlapped with zero ($a_2 = 20{,}604 \pm 28{,}305$ µg C–CO_2 g soil^{-1} day^{-1}, $k_2 = 0.671 \pm 0.670$ day^{-1}). This comparison of two-pool parameters between coastal areas suggests that KOB surface soils have a higher CO_2 production rate from the recalcitrant pool, which points to the importance of controls on soil carbon quality other than landscape age. Many of the two-pool models did not converge (21 of 30 SIS samples). At KOB, the two-pool model was best for 11 of 30 samples, and the one-pool exponential model was best for one sample, but the linear and one-pool models were plausible for many of the samples (18 of 30; Fig. 6). The two-pool model did not converge for 11 of 30 KOB samples.

Soil respiration rates were highest in the surface samples from KOB and SIS (Fig. 8a). We observed no differences in respiration rates of surface coastal soils within the first 2 weeks of sampling, but starting at day 28, KOB maintained consistently higher CO_2 production rates than all other study areas. Surface CO_2 production at inland areas was lower than the surface coastal areas. CO_2 production rates in the ORK soils were approximately 30 % lower than coastal areas and had a detectible decline over the duration of the incubation. LIA CO_2 production was negligible relative to the other study areas, with values that did not exceed 30 µg C–CO_2 g soil^{-1} day^{-1}, which was 0.3 times the lowest production rate of ORK soils and approximately 0.04 times that of the coastal areas.

In deep soils, the most prominent differences were observed at the first sample point (day 4), where KOB had the highest CO_2 production rate (Fig. 8b). Aside from KOB, no study areas demonstrate elevated CO_2 production during the initial phase of incubation. After day 4, we observed no differences between the two coastal areas, which had only marginally higher CO_2 production than the ORK deep soils. LIA soils have negligible CO_2 production per dry soil mass as compared to older areas with established vegetation cover (Fig. 8a).

Discussion

Soil carbon storage and potential controls

Landscape age is known to control soil carbon accumulation in a range of dynamic Arctic systems, including coastal sites undergoing isostatic rebound (Jensen et al. 2006) and drained thaw lake basins (Bockheim et al. 2004). We observe a nonlinear increase in SOC storage across the 10,000-year age gradient in southwestern Greenland. This nonlinearity provides evidence for multiple controls on carbon accumulation, including biological, climate effects and their interactions. Shrub canopy height, a proxy for aboveground biomass, was higher at coastal sites than at

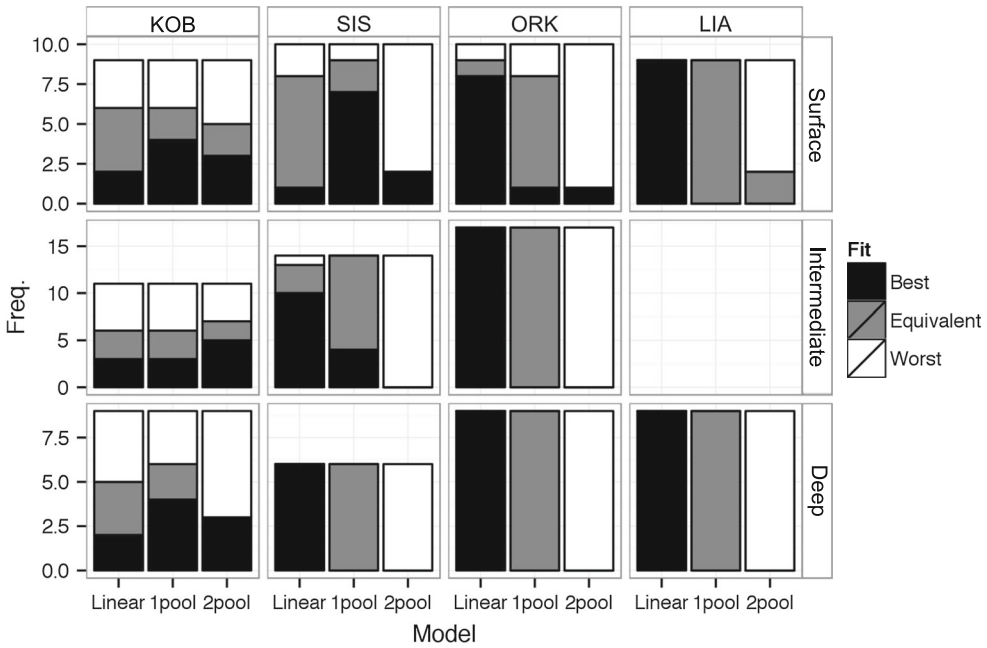

Fig. 6 Summary of ΔAICc results comparing linear, one-pooled and two-pooled models for surface, intermediate and deep soils across study areas. The panels present the model fit results by area (*column*) and soil layer (*row*); frequency is the count of samples in the subset. *Shading* indicates the relative fit of each model for the set of samples in each panel (*black* ΔAICc = 0, *gray* ΔAICc < 2; *white* ΔAICc > 2). Young and deep soils (LIA, ORK intermediate and mineral, SIS mineral) were best described by linear and one-pooled models, whereas older surface soils (KOB, SIS surface and intermediate, and ORK surface) had more variable behaviors among samples

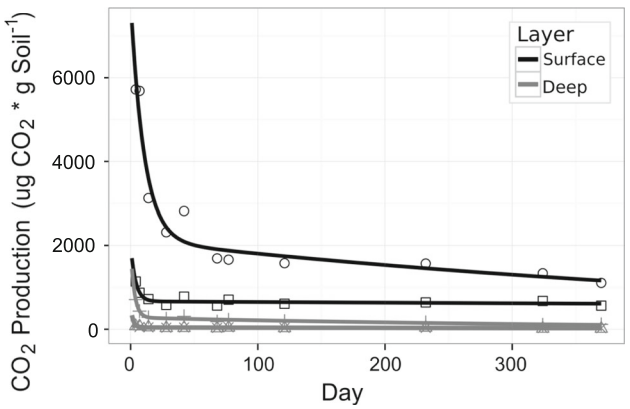

Fig. 7 CO_2 production from surface and deep soil samples at KOB that were best described by the two-pooled respiration model. *Black symbols* indicate shallow soil measurements ($n = 2$) and *gray symbols* indicate deep soil ($n = 3$). *Lines* show decay over the course of the incubation period for shallow (*black*) and deep (*gray*) soils

ORK. Greater primary production likely results in an increase in soil carbon inputs through litter fall and root turnover and exudation. The stability of additional soil carbon inputs could also be tied to seasonal variation associated with the climate regimes represented across the gradient. During the growing season, the lower air temperature and higher annual precipitation on the coast may suppress decomposition rates and reduce soil carbon losses compared

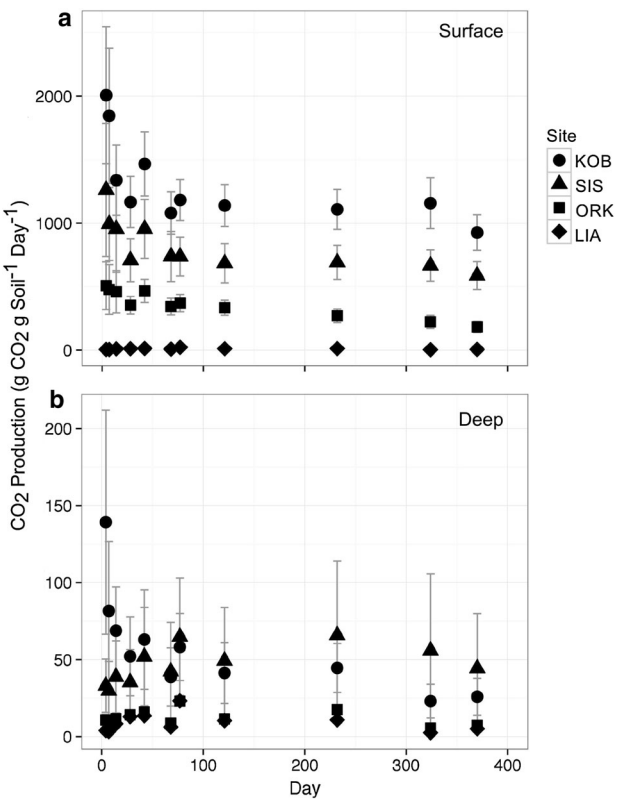

Fig. 8 Mean CO_2 production rates for **a** surface and **b** deep soils over a 370-day incubation. Data points are study area averages (±1 SE), with symbol shape indicating study area

with warmer and drier interior soils. Alternatively, during the winter season, warmer temperatures and greater snow coverage increase winter soil temperatures on the coast and may lead to greater carbon losses relative to the interior.

Our estimates of SOC in these shrub sites are at the lower end of the estimates of SOC for Greenland tundra and comparable ecosystems in other locations. Available regionally downscaled estimates range from 15 to 40 kg cm^{-2} (Jones et al. 2009). These estimates do not account for landscape-level variation in SOC and represent a soil profile depth of 100 cm. In addition, they are derived from a sparse collection of point measurements (Jensen et al. 2006). We observed an average carbon stock of 10.2 kg cm^{-2} at coastal study areas, which corresponds with SOC recorded in well-drained *S. glauca* and *B. nana* land cover type in Disko, Greenland (8.4 ± 2.4 kg cm^{-2} recorded for 60 cm profile; Jensen et al. 2006). At the landscape level, organic carbon storage is known to vary with vegetation cover. While shrub vegetation is a common land cover type in Greenland, it is not associated with the most carbon-rich soils in the southwest Greenland tundra ecosystem: Graminoid-dominated fen contains largest carbon pools in Disko (28.2 ± 22.1 kg cm^{-2}, Jensen et al. 2006) and soil carbon concentration is higher under *S. glauca* and *Kobresia myosuroides* than *B. nana* in Kangerlussuaq area (Ozols and Broll 2003).

SOC is an ecosystem property that reflects a number of biotic and abiotic factors and interactions (Schmidt et al. 2011), including some that we were unable to represent in our analysis. Climate and carbon accumulation recorded in lake sediments provide evidence of changes in productivity in western Greenland during the Holocene (Bennike 2000), yet it is uncertain how that climate history of the study area affects SOC quality. Additionally, microbial community composition can determine temperature response and is known to vary at the landscape scale and by soil depth (Karhu et al. 2014).

Availability of organic matter quality for microbial decomposition

Landscape age has been shown to be related to organic matter quality over the 10^4- to 10^6-year timescale in the Alaskan Arctic (Whittinghill and Hobbie 2012) as well as in permafrost sediments dated to 2000 and 42,000 ybp (Knoblauch et al. 2013). Our study demonstrates that soil respiration potential varies across a more recent Holocene landscape age gradient (10^2–10^4 years) in southwestern Greenland. Surface soils on the coast have highest carbon mineralization rates; elevated rates during the initial measurements suggest that labile carbon in these soils is more available for decomposition. KOB soils have the highest CO_2 production rates for the duration of the incubation, including after 300 days, which suggests that the quality of the organic matter was higher overall at KOB. The two-pool model results also suggest that quality of organic matter in the slower-cycling pool was higher at KOB than SIS for surface soils. Since KOB and SIS were deglaciated in the same time period, the lower recalcitrance of the slower-cycling KOB is not a result of landscape age, but points to other controls on soil carbon processes. Climate is a possible control, where the warmer temperatures at KOB could increase microbial processing and higher precipitation could increase losses of labile DOC through lateral movement.

The soil respiration decay model comparison results show that there is substantial variation in model fit across surface samples, which suggests that spatial variation in near-surface soil processes, such as litter and root inputs and decay, can alter soil carbon quality. In contrast, deep soils have a reduced soil respiration potential and consistent model behavior across study areas. KOB was the only area for which the deep soils exhibited elevated respiration rates during the initial incubation period, pointing to the presence of a higher quality or more labile carbon at depth. Possible sources of labile carbon in deep soils include leaching of soluble and particulate carbon from surface soils through the soil profile, root exudation and turnover in mineral soils, and lateral inputs from groundwater flow.

The soil respiration decay model fitting informs our predictions of how these pools of carbon will respond to warming. Kinetic theory predicts that temperature sensitivity decomposition increases as SOC becomes more recalcitrant, and mineralization of labile pools shows the lowest response to temperature change (Bosatta and Agren 1999). Our results show that across the age transect the coastal surface soils have higher respiration rates from the recalcitrant carbon pool, and according to the theoretical model of temperature sensitivity, this pool is predicted to be the most temperature sensitive. These results imply that microbial decomposition of coastal soils has the greatest potential for increased CO_2 flux to the atmosphere per unit of climate warming. However, experimental and observational studies demonstrate that the temperature–sensitivity relationship as a function of carbon quality is variable and may be method dependent (Conant et al. 2011).

Our comparison of soil respiration models over the incubation period revealed that neither the one-pool nor two-pool models can be applied to the full collection of samples. The failure of any one model to fully represent the CO_2 incubation dynamics indicates that there is important heterogeneity in organic matter quality and quantity across study areas and by profile depth. Instead of a single model to characterize all of the soils, we can capture the range of soil respiration behaviors by dividing the set of samples into two categories: young and mineral soils, and surface

soils from the coast, particularly those found in KOB. The young and mineral soils were best characterized by one-pool models. The older surface soils were best modeled by two-pool models, indicating the presence of two separate carbon pools with differing biological availability for mineralization. For the samples that were best represented by the two-pool model, the one-pool exponential decay model tends to underestimate the total amount of CO_2 respired during the incubation period. In a comparison of total carbon respired over the incubation derived by the integration of the one- and two-pool model parameters, we found that the two-pool model yields higher estimated CO_2 flux, with a median of 8.4 % higher than the total soil respiration estimated by the one-pool model during the incubation period (first quartile = 2.1 %, third quartile = 47.7 %). Thus, if we were to use the one-pool model, which best represents the majority of soils, to predict soil respiration for all soils, we would underestimate soil respiration for the most carbon-rich soils. Our results reveal important heterogeneity in the partitioning of the soil carbon pool into labile and recalcitrant fractions across southwestern Greenland. As a consequence, any attempt to uniformly apply one of the models would result in a loss of information about the microbial availability of carbon and potential sensitivity to abiotic changes.

Conclusions

Using field sampling and long-term laboratory incubations, we measured the soil carbon storage and microbial availability of carbon across a Holocene landscape age and climate gradient in southwest Greenland. The quantity of soil carbon storage and the soil respiration potential was highest at coastal sites, which are older and have a maritime climate. SOC concentration increased nonlinearly across the gradient, which indicates that factors other than landscape age, for example climate or positive feedbacks associated with plant–soil interaction, likely modify the rate of carbon accumulation. Stoichiometric carbon quality (C:N) was lowest in KOB surface soils and highest at LIA. CO_2 production was highest at KOB surface soils throughout the incubation period, including in the final measurements, which points to the presence of a large recalcitrant carbon pool in these southern coastal surface soils. A comparison of the KOB soils that demonstrated a two-pool decay during laboratory incubations showed that surface soils tend to have higher-quality recalcitrant organic matter pools than deep soils at this southern coastal study area. The behavior of soil respiration varied among the samples, such that no single respiration decay model could capture the dynamics of the full set of samples. For most soils, the linear and one-pool decay models were the best model and the two-pool model did not converge. However, for the 12 samples best described by the two-pool model, the one-pool model underestimates total respiration from these soils. In a comparison of integrated 20-cm soil profiles, soil carbon storage was highest at the coastal study areas, and soil respiration potential is similar in vegetated areas across the transect. This study informs our understanding of regional variation in quantity and quality of soil carbon to decomposition in southwestern Greenland and demonstrates the importance of incorporating landscape age and climate variables in landscape-scale carbon models. Changes over geological timescales are important for soil development and can influence carbon inputs and microbial activity in Arctic soils, which control carbon accumulation and sensitivity to climate warming.

Acknowledgments We thank Courtney Hammond-Wagner and Phoebe Racine for assistance in the field and laboratory. Angela Spickard and Paul Zietz at Dartmouth provided laboratory support. We are grateful to Josephine Nymand, Louise Holm Christensen, and Stine Hojlund Pedersen for guidance and hospitality at Nuuk Basic Field Station in Kobbefjord; CH2M Hill Polar Services for logistical support in Kangerlussuaq; Lauren Culler for providing comments on the manuscript. This research was supported by a grant from The Explorers Club Exploration Fund to Julia Bradley-Cook and a National Science Foundation IGERT Grant (Award No.: 0801490) to Ross Virginia. Additional support was provided by the Institute of Arctic Studies, Dickey Center for International Understanding, Dartmouth.

References

Anderson NJ, D'Andrea W, Fritz SC (2009) Holocene carbon burial by lakes in SW Greenland. Glob Change Biol 15:2590–2598. doi:10.1111/j.1365-2486.2009.01942.x

Bennike O (2000) Palaeoecological studies of Holocene lake sediments from west Greenland. Palaeogeogr Palaeoclimatol Palaeoecol 155:285–304. doi:10.101/S0031-0184(99)00121-2

Bockheim JG, Hinkel KM, Eisner WR, Dai XY (2004) Carbon pools and accumulation rates in an age-series of soils in drained thaw-lake basins, Arctic Alaska. Soil Sci Soc Am J 68:697–704. doi:10.2136/sssaj2004.6970

Bosatta E, Agren GI (1999) Soil organic matter quality interpreted thermodynamically. Soil Biol Biochem 31:1889–1891. doi:10.1016/S0038-0717(99)00105-4

Chapin FS, Shaver GR (1989) Differences in growth and nutrient use among arctic plant growth forms. Funct Ecol 3:73–80. doi:10.2307/2389677

Conant RT, Ryan MG, Agren GI, Birge HE, Davidson EA, Eliasson PE, Evans SE, Frey SD, Giardina CP, Hopkins FM, Hyvonen R, Kirschbaum MUF, Lavalle JM, Leifeld J, Parton WJ, Steinweg JM, Wallenstein MD, Martin Wetterstedt JA, Bradford MA (2011) Temperature and soil organic matter decomposition rates—synthesis of current knowledge and a way forward. Glob Change Biol 17:3392–3404. doi:10.1111/j.1365-2486.2011.02496.x

Crocker RL, Major J (1955) Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. J Ecol 43:427–448

Curiel Yuste J, Baldocchi DD, Gershenson A, Goldstein A, Misson L, Wong S (2007) Microbial soil respiration and its dependency on carbon inputs, soil temperature and moisture. Glob Change Biol 13:1–18. doi:10.1111/j.1365-2486.2007.01415.x

Danish Meteorological Institute. Climatic Normals for Greenland. http://www.dmi.dk/groenland/arkiver/klimanormaler/. Accessed 23 Sept 2014

Ehrenfeld JG, Ravit B, Elgersma K (2005) Feedback in the plant-soil system. Annu Rev Environ Resour 30:75–115. doi:10.1146/annurev.energy.30.050504.144212

Elzein T, Blarquez O, Gauthier O, Carcaillet C (2011) Allometric equations for biomass assessment of subalpine dwarf shrubs. Alp Bot 121:129–134

Giblin AE, Nadelhoffer KJ, Shaver GR, Laundre JA, McKerrow AJ (1991) Biogeochemical diversity along a riverside toposequence in arctic Alaska. Ecol Monogr 61:415–435. doi:10.2307/2937049

Hobbie SE, Schimel JP, Trumbore SE, Randerson JR (2000) Controls over carbon storage and turnover in high-latitude soils. Glob Change Biol 6:196–210. doi:10.1046/j.1365-2486.2000.06021.x

Hugelius G, Strauss J, Zubrzycki S, Harden JW, Schuur EAG, Ping CL, Schirrmeister L, Grosse G, Michaelson GJ, Koven CD, O'Donnell JA, Elberling B, Mishra U, Camill P, Yu Z, Palmtag J, Kuhry P (2014) Estimated stocks of circumpolar permafrost carbon with quantified uncertainty ranges and identified data gaps. Biogeosciences 11:6573–6593. doi:10.5194/bg-11-6573-2014

Jenny H (1941) Factors of soil formation: a system of quantitative pedology. Dover Publications, New York

Jensen L, Schmidt L, Hollesen J, Elberling B (2006) Accumulation of soil organic carbon linked to Holocene sea level changes in West Greenland. Arct Antarct Alp Res 38(3):378–383. doi:10.1657/1523-0430(2006)38[378:AOSOCL]2.0.CO;2

Jones A, Stolbovoy V, Tarnocai C, Broll G, Spaargaren O, Montanarella O (2009) Soil atlas of the Northern Circumpolar Region. Office for Official Publications of the European Communities, Luxembourg

Karhu K, Auffret MD, Dungait AJ, Hopkins DW, Prosser JI, Singh BK, Subke JA, Wookey PA, Agren GI, Sebastia MT, Gouriveau F, Bergkvist G, Meir P, Nottingham AT, Salinas N, Hartley IP (2014) Temperature sensitivity of soil respiration rates enhanced by microbial community response. Nature 513:81–84. doi:10.1038/nature13604

Knoblauch C, Beer C, Sosnin A, Wagner D, Pfeiffer EM (2013) Predicting long-term carbon mineralization and trace gas production from thawing permafrost of Northeast Siberia. Glob Change Biol 19:1160–1172. doi:10.1111/gcb.12116

Levy LB, Kelly MA, Howley JA, Virginia RA (2012) Age of the Orkendalen moraines, Kangerlussuaq, Greenland: constraints on the extent of the southwestern margin of the Greenland Ice Sheet during the Holocene. Quat Sci Rev 52:1–5. doi:10.1016/j.quascirev.2012.07.021

McGuire AD, Anderson LG, Christensen TR, Dallimore S, Guo L, Hayes DJ, Heimann M, Lorenson TD, Macdonald RW, Roulet N (2009) Sensitivity of the carbon cycle in the Arctic to climate change. Ecol Monogr 79(4):523–555. doi:10.1890/08-2025.1

Mernild SH, Hanna E, McConnell JR, Sigl M, Beckerman AP, Yde JC, Cappelen J, Malmros JK, Steffen K (2015) Greenland precipitation trends in a long-term instrumental climate context (1890–2012): evaluation of coastal and ice core records. Int J Climatol 35:303–320. doi:10.1002/joc.3986

Nadelhoffer KJ, Giblin AE, Shaver GR, Laundre JA (1991) Effects of temperature and substrate quality on element mineralization in six Arctic soils. Ecology 72:242–253. doi:10.2307/1938918

Nielsen UN, Wall DH (2013) The future of soil invertebrate communities in polar regions: different climate change responses in the Arctic and Antarctic? Ecol Lett 16:409–419. doi:10.1111/ele.12058

Ozols U, Broll G (2003) Soil ecological processes in vegetation patches of well drained permafrost affected sites (Kangerlussuaq—West Greenland). Polarforschung 73:5–14. http://hdl.handle.net/10013/epic.29907

Riggs CE, Hobbie SE, Bach EM, Hofmockel KS, Kazanski CE (2015) Nitrogen addition changes grassland soil organic matter decomposition. Biogeochemistry 125:203–219. doi:10.1007/s10533-015-0123-2

Roberts DH, Long AJ, Schnabel C, Davies BJ, Xu S, Simpson MJR, Huybrechts P (2009) Ice sheet extent and early deglaciation history of the southwestern sector of the Greenland Ice Sheet. Quat Sci Rev 28:2760–2773. doi:10.1016/j.quascirev.2009.07.002

Schmidt MWI, Torn MS, Abiven S, Dittmar T, Guggenberger G, Janssens IA, Kleber Markus, Kogel-knabner I, Lehmann J, Manning DAC, Nannipieri P, Rasse DP, Weiner S, Trumbore SE (2011) Persistence of soil organic matter as an ecosystem property. Nature 478:49–56. doi:10.1038/nature10386

Shaver GR, Bret-Harte SM, Jones MH, Johnstoone J, Gough L, Laundre J, Chapin FS (2001) Species composition interacts with fertilizer to control long-term change in tundra productivity. Ecology 82:3163–3181. doi:10.1890/0012-9658(2001)082[3163:SCIWFT]2.0.CO;2

Shaver GR, Giblin AE, Nadelhoffer KJ, Thieler KK, Downs MR, Laundre JA, Rastetter EB (2006) Carbon turnover in Alaska tundra soils: effects of organic matter quality, temperature, moisture and fertilizer. J Ecol 94:740–753. doi:10.1111/j.1365-2745.2006.01139.x

Sjogersten S, Wookey PA (2005) The role of soil organic matter quality and physical environment for nitrogen mineralization at the forest-tundra ecotone in Fennoscandia. Arct Antarct Alp Res 37:118–126. doi:10.1657/1523-0430(2005)037[0118:TROSOM]2.0.CO;2

Stieglitz M, Shaman J, McNamara J, Engel V, Shanley J, Kling GW (2003) An approach to understanding hydrologic conductivity on the hillslope and the implications for nutrient transport. Glob Biogeochem Cycles. doi:10.1029/2003GB002041

Sullivan PF, Arens SJT, Chimner RA, Welker JM (2008) Temperature and microtopography interact to control carbon cycling in a high arctic fen. Ecosystems 11:61–76. doi:10.1007/s10021-007-9107-y

Van Wijk MG, Clemmensen KE, Shaver GR, Williams M, Callaghan TV, Chapin FS, Cornelissen JHC, Gough L, Hobbie SE, Jonasson S, Lee JA, Michelsen A, Press MC, Richardson SJ, Rueth H (2003) Long-term ecosystem level experiments at Toolik Lake, Alaska, and at Abisko, Northern Sweden: generalizations and differences in ecosystem and plant type responses to global change. Glob Change Biol 10:105–123. doi:10.1111/j.1365-2486.2003.00719.x

Weintraub MN, Schimel JP (2005) Nitrogen cycling and the spread of shrubs control changes in the carbon balance of arctic tundra ecosystems. Bioscience 55:408–415. doi:10.1641/0006-3568(2005)055[0408:NCATSO]2.0.CO;2

Whittinghill KA, Hobbie SE (2011) Effects of Landscape Age on Soil Organic Matter Processing in Northern Alaska. Soil Sci Soc Am J 75:907–917. doi:10.2136/sssaj2010.0318

Whittinghill KA, Hobbie SE (2012) Effects of pH and calcium on soil organic matter dynamics in Alaska tundra. Biogeochemistry 111:569–581. doi:10.1007/s10533-011-9688-6

Zona D, Lipson DA, Zulueta RC, Oberbauer SF, Oechel WC (2011) Microtopographic controls on ecosystem functioning in the Arctic coastal plain. J Geophys Res 116:1–12. doi:10.1029/2009JG00124