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Glucose addition increases the magnitude and decreases the age of soil respired carbon in a long-term permafrost incubation study

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ABSTRACT

Higher temperatures in northern latitudes will increase permafrost thaw and stimulate above- and belowground plant biomass growth in tundra ecosystems. Higher plant productivity increases the input of easily decomposable carbon (C) to soil, which can stimulate microbial activity and increase soil organic matter decomposition rates. This phenomenon, known as the priming effect, is particularly interesting in permafrost because an increase in C supply to deep, previously frozen soil may accelerate decomposition of C stored for hundreds to thousands of years. The sensitivity of old permafrost C to priming is not well known; most incubation studies last less than one year, and so focus on fast-cycling C pools. Furthermore, the age of respired soil C is rarely measured, even though old C may be vulnerable to labile C inputs. We incubated soil from a moist acidic tundra site in Eight Mile Lake, Alaska for 409 days at 15 °C. Soil from surface (0–25 cm), transition (45–55 cm), and permafrost (65–85 cm) layers were amended with three pulses of uniformly ^{13}C-labeled glucose or cellulose every 152 days. Glucose addition resulted in positive priming in the permafrost layer 7 days after each substrate addition, eliciting a two-fold increase in cumulative soil C loss relative to unamended soils with consistent effects across all three pulses. In the transition and permafrost layers, glucose addition significantly decreased the age of soil-respired CO_2-C with Δ^{14}C values that were 115‰ higher. Previous field studies that measured the age of respired C in permafrost regions have attributed younger Δ^{14}C ecosystem respiration values to higher plant contributions. However, the results from this study suggest that positive priming, due to an increase in fresh C supply to deeply thawed soil layers, can also explain the respiration of younger C observed at the ecosystem scale. We must consider priming effects to fully understand permafrost C dynamics, or we risk underestimating the contribution of soil C to ecosystem respiration.

1. Introduction

Temperatures in northern latitudes are currently increasing by 0.6 °C each decade, a rate that is two times higher than the global average (IPCC, 2013). Higher temperatures can thaw permafrost (Brown and Romanovsky, 2008; Romanovsky et al., 2010, 2013; Harden et al., 2012) and expose previously protected soil organic matter (SOM) to microbial decomposition (Schuur et al., 2015). Though the permafrost region encompasses only 15% of the total global soil area, it stores two times more carbon (C) than the atmosphere: 1330–1580 Pg C (1 Pg = 1 billion metric tons) (Zimov et al., 2006; Tarnocai et al., 2009; Hugelius et al., 2014; Schuur et al., 2015). Microbial mineralization of this stored C can exacerbate the effects of climate change by increasing greenhouse gas concentrations in the atmosphere in the form of carbon dioxide (CO_2) and methane (Schuur et al., 2008).

The mineralization rate of permafrost C is partially controlled by its inherent decomposability (Schädel et al., 2014; Schuur et al., 2015).

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Upon thaw, permafrost C is mobilized (Schuur et al., 2009; Nowinski et al., 2010), and overall soil C losses are high because of the high biolability of organic C in initial stages of decomposition (Dutta et al., 2006; Vonk et al., 2013). However, that initial C is quickly mineralized, and microbes are left with a much larger pool of slowly decomposing C. A previous soil incubation study found that > 85% of the fast decomposing C is depleted after ~3 months of incubation at 15 °C (Bracho et al., 2016), but it amounts to less than 5% of all C in both organic and mineral soil layers (Schädel et al., 2014). Although soil C comprises several different pools with turnover times spanning less than a year to several hundred years (Trumbore, 2000), the majority of the C stored in permafrost is old (Zimov et al., 2006; Schuur et al., 2009). Therefore, we expect that long-term C losses will largely originate from old and slowly decomposing C pools (Schuur et al., 2008; Knoblauch et al., 2013; Schädel et al., 2013, 2014).

Slowly decomposing C that accumulated over hundreds to thousands of years in permafrost (Czimczik and Welker, 2010; Pries et al., 2012) is thought to be relatively energy-poor. A long-term (~1 year) permafrost incubation study revealed that less than 3% of the initial soil bulk C is mineralized in the absence of substrate inputs (Dutta et al., 2006). Without an energy source in the form of fresh organic C, microbial activity decreases (Schimel and Weintraub, 2003); however, this energy limitation can potentially be lifted with an increased input of labile C to soil (De Nobili et al., 2001; Fontaine et al., 2007; Blagodatskaya and Kuzyakov, 2008).

A warmer climate will also increase shrub expansion in tundra ecosystems, which will increase plant productivity and litter input to soil (Chapin et al., 1995; Shaver et al., 2000; Tape et al., 2006; Natali et al., 2012). Priming theory suggests that a greater supply of fast decomposing C from leaf and root litter, root exudates, and dissolved organic C leachate can increase microbial decomposition of native SOM (Bingeman et al., 1953). Studies show that microbes utilize fresh C as an energy source to produce enzymes that assist in the decomposition of organic molecules that are resistant to microbial degradation (Schimel and Weintraub, 2003; Fontaine et al., 2007; Bernal et al., 2016). Some studies have investigated the implication of tundra shrub expansion on SOM decomposition by adding glucose or low molecular weight C to soil, and found no effects of priming (Rousk et al., 2016; Lynch et al., 2018). However, these studies amended surface and O-horizon soils exclusively, which do not reflect the potential priming effects of deep-rooting tundra species (e.g. *R. chamaemorus and E. vaginatum*) whose roots extend to the thaw-front (> 45 cm) (Keuper et al., 2017), and thus may increase C input to deep soils and recently thawed permafrost.

Priming is a particularly interesting phenomenon in permafrost soil because frozen ground is impermeable to dissolved organic C (DOC) infiltration (Walvoord and Kurylyk, 2016). Environmental changes that increase C inputs in deep soil can increase soil C vulnerability to decomposition and loss (Bernal et al., 2016). This means that as permafrost thaws, soil in deep layers may receive fresh C inputs during rain and snow events for the first time in hundreds to thousands of years. A previous study that modeled water movement through soil with underlying permafrost showed that DOC input to deeper layers released more CO_2 (Fan et al., 2013). Fresh C input to soil will also be accompanied by pulses of mineralized N upon permafrost thaw (Rustad et al., 2001; Keuper et al., 2012; Salmon et al., 2018), which could create an ideal environment for higher microbial activity.

A more active microbial community, especially in deep soil layers, can alter soil C dynamics by increasing decomposition of old and slowly decomposing organic C, and accelerate C turnover rates (Fontaine et al., 2007; Paterson et al., 2009). While the stability of old soil C can change in the presence of labile C inputs (Fontaine et al., 2007; Bernal et al., 2016), permafrost priming studies have not measured the age of soil respired C. Furthermore, most incubation studies are conducted in short-term laboratory incubations (< 1 year), and thus only focus on fast-cycling soil C pools (Fan et al., 2013; Wild et al., 2014, 2016). To fully understand permafrost C dynamics and priming effects, we measured the magnitude of soil C loss and the age of respired C.

We hypothesized that amending permafrost soil with multiple pulses of glucose, the most abundant sugar in rhizodeposits (Derrien et al., 2004), or cellulose, the most common polymer in plant litter (Kögel-Knabner, 2002), would: (1) increase soil C decomposition (positive priming), particularly in permafrost where the majority of the C is slow decomposing C (Schädel et al., 2014), (2) sustain higher rates of soil C decomposition over the long-term because microbes will readily use substrates as an energy source following each pulse, and (3) increase the proportion of old C that is respired as a result of soil priming because it comprises the bulk of the soil C pool in permafrost (Schuur et al., 2009).

2. Materials and methods

2.1. Site description

Soil cores were sampled in 2013 from Eight Mile Lake, Alaska (63° 52′ 59″N, 149° 13′ 32″W), where the mean annual temperature is −1.0 °C, and the mean annual precipitation is 378 mm (Schuur et al., 2009). The site is situated on a well-drained, northeast-facing hillslope (700 m) (Natali et al., 2011) in the discontinuous permafrost zone, but is underlain entirely by permafrost (Osterkamp et al., 2009). Though our site is in the subarctic, it exemplifies a region vulnerable to permafrost degradation that is analog to projected conditions in the Arctic as temperatures increase. The site has cryoturbated mineral soil, comprising glacial till and windblown loess, with dominant amounts of quartz and feldspars. The soil type is Gelisol (Soil Survey Staff, 2014) with an organic horizon ~35 cm thick, and C concentrations greater than 20% (Natali et al., 2011; Pries et al., 2012; Plaza et al., 2017b). In 2013, the maximum thaw depth at the peak of the growing season was < 65 cm (Mauritz et al., 2017). The vegetation is moist acidic tundra, dominated by *Eriophorum vaginatum*. Plant species composition includes *Vaccinium uliginosum, Carex bigelowii, Betula nana, Rubus chamaemorus, Empetrum nigrum, Rhododendron subarcticum, V. vitis-idaea, Andromeda polifolia* and *Oxycoccus microcarpus*. Nonvascular plant cover contains feather moss (primarily *Pleurozium schreberi* and *Sphagnum* species), as well as several lichen species (primarily *Cladonia* spp.) (Schuur et al., 2007; Natali et al., 2011; Deane-Coe et al., 2015).

2.2. Soil core collection and processing

Four soil cores were collected in June 2013. The seasonally thawed surface soil was cut using a serrated knife, and the underlying frozen soil was cored using a Tanaka drill with a 7.6 cm diameter hollow bit. Soil was sampled to the depth at which the corer hit rocks (~85 cm). Cores were wrapped in aluminum foil, kept frozen for shipment, and stored until the start of the experiment.

In the lab, the surface vegetation was clipped off, and cores were sectioned to 15 cm at the surface, and 10 cm increments thereafter (0–15 cm, 15–25 cm, etc.) to the end of the core. The organic/mineral horizon demarcation was determined by %C analysis (mineral < 20% C). Rocks were removed, and we accounted for their mass and volume in the bulk soil density calculation. Each depth increment was subsampled for moisture content, and bulk %C, %N, and $\delta^{13}C$ (‰). Bulk C and N concentrations were determined by dry combustion using a Costech Analytical ECS 4010 elemental analyzer (Valencia, CA, USA) (Pries et al., 2012). Stable C isotope data were determined using a Thermo Finnigan Delta V Advantage continuous flow isotope ratio mass spectrometer (ThermoScientific Inc., Waltham, MA, USA). Soil pH was determined using the slurry method with a 1:1 ratio by proportional weight of soil to deionized water. Soil pH was measured using an Orion 2 Star pH Benchtop (ThermoScientific Inc., Waltham, MA, USA).

We measured initial microbial biomass on a subsection of soil that was not incubated. Due to constrains in soil availability, only 3 cores at depths 0–15, 15–25 and 45–55 cm, and only 2 cores at 75–85 cm were

extracted; we did not have enough soil available for extraction at 65–75 cm. Four analytical replicate samples (4–6 g soil) from each individual core and depth increment were homogenized, and soils were extracted with 25 ml 2M KCl. Two of the replicates were amended with 0.25 ml chloroform to lyse microbial cell membranes. Samples were shaken for 1 h, then vacuum filtered through pre-leached Whatman GF/A filters. Extracts were sparged with air for 30 min to volatilize chloroform, and frozen for storage. Dissolved organic C concentrations were measured using a Shimadzu TOC-L analyzer (Kyoto, Japan), and microbial biomass C was calculated as the difference in DOC between extracts performed with and without chloroform (Salmon et al., 2018).

2.3. Incubation

We incubated soil from five different depths, representative of the surface layer (0–15 and 15–25 cm), the organic/mineral transition layer (45–55 cm), and the permafrost layer (65–75 and 75–85 cm), from 4 replicate soil cores. We weighed triplicates (~80 g wet weight) from each depth into 1 L Mason jars and assigned each jar to a treatment: unamended (control), glucose, or cellulose (4 cores x 5 depth x 3 treatments = 60 jars).

We pre-incubated all samples for 4 weeks at 15 °C so that water-logged soils from ice-rich sections (65–75 and 75–85 cm) could air dry to less than 60% water holding capacity (WHC). At the end of the 4 weeks, we amended our samples with uniformly ^{13}C-labeled glucose U-13C6, 24–25 atom% (Cambridge Isotope Laboratories Inc., Andover, MA, USA) or cellulose 97 atom% D from maize (Sigma-Aldrich Co., St. Louis, MO, USA). Soils were amended with 3.5 mg substrate C per gram of initial soil C to account for differences in initial bulk soil %C in each layer. The total concentration added corresponded to 23–84% of the annual net primary productivity (NPP) in our site, scaled to a per gram soil basis (Natali et al., 2012). Labeled substrates were mixed with unlabeled glucose or cellulose (Sigma Life Science, St. Louis, MO, USA) for more diluted δ^{13}C values (Supplemental Table 1). Deionized water was added to the mixtures of finely ground glucose or cellulose so that substrate solutions could be injected in each soil section with a syringe to minimize soil disturbance and maximize distribution. Unamended soils received deionized water only. Moisture was adjusted to ~60% WHC throughout the incubation in all treatments. Soils were aerobically incubated and maintained at 15 °C. A second and third amendment pulse was added at day of incubation (DOI) 153 and 305 (every 152 days). We chose to amend soils every 152 days because Bracho et al. (2016) found that 85–95% of fast-decomposing C is depleted within 100 days of incubation at 15 °C; therefore, we assumed most of the added substrate would be consumed before the next C addition.

2.4. Flux and isotope measurements

Carbon dioxide and δ^{13}C measurements were coupled and measured daily for the first week following each pulse, every 2 days for the second week, and once every ~4 weeks until the next amendment.

Jars were placed in a water bath set to 15 °C, connected to an automated soil incubation system (ASIS) that sequentially measured the CO_2 concentration in each jar by circulating air through an infrared gas analyzer (IRGA) at 0.9 L min^{-1} (Li-820 Licor, Lincoln, Nebraska). Pressure and CO_2 concentrations in each jar were recorded on a data logger (CR1000, Campbell Scientific, Logan UT) every 3 s for 8 min. Carbon dioxide flux, in micrograms of C per gram of initial soil C per day, was calculated as the rate of CO_2-C increase in the headspace of each jar over 3–4 cycles that lasted 8.5 h each. ASIS is a closed-loop system, but individual jar fluxes were corrected for carry over CO_2 based on the CO_2 concentration in the previous jar and the carry over volume, which included the tubbing, IRGA, flow mass controlled, and pump. Details of ASIS are described in Bracho et al. (2016).

After each flux measurement, jar headspace was scrubbed for 5 min with soda lime and incubated at 15 °C for a couple of hours to allow CO_2 to accumulate. We measured $\delta^{13}CO_2$-C on a Picarro G2201-*i* Isotopic CO_2/CH_4 cavity ring-down spectrometer (Picarro Inc., Sunnyvale, California, USA) and recorded the 2 min $\delta^{13}CO_2$-C average for each jar at the end of a 4 min measurement period. We allowed the Picarro cavity to return to ambient $^{13}CO_2$ levels before measuring each jar, and we frequently used a reference CO_2 gas before and after measurements for calibration (Airgas, ASG Los Angeles, CA).

Because of the high number of jars, the incubation was conducted in 2 rounds, staggered in time to manage the high volume of measurements. Each round was treated the same, and treatments were fully interspersed between rounds.

2.5. Priming calculations

In the amended treatments, total CO_2-C flux was a combination of soil-derived C and substrate-derived C, so we applied an isotopic mass balance equation to partition soil-derived C (SOC) from substrate-derived C:

$$C_{SOC} = C_{total} (\delta_{total} - \delta_{substrate}) / (\delta_{SOC} - \delta_{substrate}) \quad (1)$$

Where C_{SOC} is the soil-respired C, C_{total} is total C respired in substrate-amended soils, which includes soil-derived C and substrate-derived C, δ_{total} is the total $\delta^{13}CO_2$-C respired, which includes soil-derived δ^{13}C and substrate-derived δ^{13}C, $\delta_{substrate}$ is the $\delta^{13}CO_2$-C from the added substrate (end-member, Supplemental Table 1), and δ_{SOC} is the soil-respired $\delta^{13}CO_2$-C from unamended samples (end-member). Priming was calculated as the difference in soil-respired C in amended samples and soil-respired C in unamended samples (Mau et al., 2015). A positive value indicated that more soil C was mineralized in amended soils relative to control (i.e. positive priming). A negative value indicated that less soil C was mineralized in amended soils relative to control (i.e. negative priming). All values were reported as micrograms of respired C per gram of initial soil C.

Though we amended soils with cellulose in pulse 1, the dilution of the labeled and unlabeled cellulose made the δ^{13}C signature too similar to that of the soil; therefore, we were unable to use the substrate end-member to calculate priming. For pulses 2 and 3, we used a cellulose substrate with a higher δ^{13}C signature (Supplemental Table 1). We only analyzed and interpreted cellulose data for pulses 2 and 3.

To calculate substrate use, or the amount of substrate that was respired after each pulse, we implemented a mass balance equation to partition substrate-derived C ($C_{substrate}$) from the total C respired (C_{total}):

$$C_{substrate} = C_{total} (\delta_{total} - \delta_{soil}) / (\delta_{substrate} - \delta_{soil}) \quad (2)$$

We calculated the cumulative $C_{substrate}$ respired after each pulse as a percent of the added substrate (3.5 mg $C_{substrate}$ g^{-1} C) by linearly interpolating the respired $C_{substrate}$ values and integrating the entire sampling period of 105 days.

2.6. Radiocarbon

To determine the age of respired soil C, we sampled $\Delta^{14}CO_2$ at DOI 15 and 105 after pulse 1, and DOI 319 (i.e. day 15 after pulse 3). The headspace in each jar was scrubbed free of CO_2 using soda lime to remove any background atmospheric CO_2 contributions. After allowing each headspace to accumulate between 0.5 and 1.0 mg C, based on the most recent flux rates measured, we collected CO_2 in zeolite molecular sieve traps (Alltech 13X; Alltech Associates, Deerfield, IL, USA) for 5 min (Hardie et al., 2005). Each molecular sieve trap was baked at 650 °C to desorb CO_2 (Bauer et al., 1992). Carbon dioxide was cryogenically purified using liquid nitrogen, and reduced to graphite by H_2 reduction with an Fe catalyst on a vacuum line (Vogel et al., 1987). Graphite samples were sent to the UC Irvine W.M. Keck carbon cycle

accelerator mass spectrometry (AMS) laboratory for $\Delta^{14}C$ analysis. Radiocarbon samples are analyzed with the standard oxalic acid II, and the precision of an AMS measurement is ± 2‰, but for many applications this error is smaller than sampling error (Trumbore et al., 2016b).

Radiocarbon values in unamended samples were corrected for mass-dependent fractionation to a $\delta^{13}C$ value of −25‰, which is routinely done to natural abundance samples (Stuiver and Polach, 1977; Trumbore et al., 2016a). For samples amended with enriched ^{13}C substrates, the increase in ^{13}C atoms relative to ^{12}C is not due to mass-dependent isotopic fractionation—that is, ^{14}C is not enriched, only ^{13}C is. Therefore, using $\delta^{13}C = -25‰$ as a fractionation correction would yield an inaccurate $\Delta^{14}C$. Thus, we applied the correction described in Torn and Southon (2001), using the measured $\delta^{13}C_{substrate}$ value as a proxy for the isotopic fractionation correction.

Amended samples had a $\Delta^{14}C$ signature from combined soil and substrate respired C; therefore, we calculated the soil respired $\Delta^{14}C$ fraction (f) using $\delta^{13}C$ signatures of the substrate and SOC with a similar mass-balance equation implemented in the priming calculation:

$$f = (\delta_{total} - \delta_{substrate}) / (\delta_{SOC} - \delta_{substrate}) \quad (3)$$

Where δ_{total} is the total $\delta^{13}CO_2$-C respired, $\delta_{substrate}$ is the $\delta^{13}CO_2$-C from the added substrate (end-member), and δ_{SOC} is the soil-respired $\delta^{13}CO_2$-C from control samples (end-member). We then applied the f of soil respired $\Delta^{14}C$ to the following equation:

$$\Delta^{14}C_{SOC} = \Delta^{14}C_{total} - ((1- f) * \Delta^{14}C_{substrate})/ f \quad (4)$$

This soil respired $\Delta^{14}C$ fraction (f) allows us to calculate the true $\Delta^{14}C$ value of soil respiration ($\Delta^{14}C_{SOC}$) by removing any substrate contribution ($\Delta^{14}C_{substrate}$) from the $\Delta^{14}C$ measured by the AMS ($\Delta^{14}C_{total}$) (Schuur and Trumbore, 2006). The $\Delta^{14}C_{substrate}$ was 10.1‰ and 62.3‰ for glucose and cellulose, respectively.

2.7. Statistical analysis

Statistical analyses of the main effects and interactions on response variables were performed in R (R Development Core Team, 2015) using linear mixed effects models, lme4 package (Bates et al., 2015). To meet normality assumptions, data were log-transformed when necessary. We removed 6 outlier priming (μg CO_2-C g^{-1} soil C) values out of 1347 values (< 1% of the data). Normality and homoscedasticity were visually examined using residual plots.

Samples from each core (n = 4) were measured at 5 different depths (0–15, 15–25, 45–55, 65–75, and 75–85 cm), but the data were analyzed by pooling depth increments into 3 layers: surface (0–15 and 15–25 cm), transition (45–55 cm), and permafrost (65–75 and 75–85 cm) based on statistically similar initial bulk soil %C. Analyzes were performed by including soil layer nested in soil core as a random effect so that depth increments would not be treated as independent replicates. Initial soil properties were tested by incorporating soil layer as a fixed effect. A post-hoc Tukey HSD test was used to determine significant differences between layers.

Priming (μg CO_2-C g^{-1} soil C) was tested in response to soil layer, pulse, day(s) after pulse (DAP), and their interactions. Analyses included a random effect of jar nested in soil layer, nested in core, to account for repeated measurements. We accounted for round (n = 2) as a random effect in our model, but it had no effect on variance, so we dropped the random effect term. We fit separate models for glucose priming and cellulose priming to avoid an unbalanced design because cellulose data was missing in pulse 1. Changes in cumulative soil C loss in the first week after each pulse were calculated as the response ratio: the ratio between samples amended with glucose and corresponding unamended samples.

Soil respired $\Delta^{14}C$ (‰) was tested in response to treatment, layer, and DOI. Analyses also included a random effect of jar nested in layer, nested in core. We did not have to analyze glucose and cellulose independently because we had radiocarbon data for both treatments for the three different sampling periods. However, to meet conditions of homoscedasticity, we analyzed surface layer samples independently from transition and permafrost layers. Surface soils have C stocks that are more homogenous, and have positive $\Delta^{14}C$ values that correspond to modern C that contain elevated 'bomb' $\Delta^{14}C$ values (Turnbull et al., 2016). Transition and permafrost layers are more heterogeneous due to cryoturbation, soil subsidence, and soil formation (Harden et al., 2012), and have negative $\Delta^{14}C$ values as a result of radioactive decay (Turnbull et al., 2016).

We used a backward step-wise model selection to eliminate fixed effects that increased AIC values by 5 or more. Ninety-five percent confidence intervals (CI) for fixed effects were obtained by bootstrapping parameter estimates (1000 iterations). A fixed effect was considered significant if the 95% CI did not include zero (Pinheiro and Bates, 2000).

3. Results

3.1. Soil properties

Soil properties significantly differed between soil layers (Table 1). Bulk density was significantly lower in the surface, but there were no differences between the transition and permafrost layers. Initial bulk soil C and N concentrations significantly decreased with depth; concentrations in the surface were almost 2 times higher than the transition layer, and 4 times higher than the permafrost layer, but there were no significant differences in C:N. Carbon concentrations decreased from about 38% in the surface to 21% in the transition, and to less than 10% in the permafrost layer. Initial bulk $\delta^{13}C$ values were significantly higher in the surface layer, but did not differ between the transition and permafrost layers. Initial microbial biomass was not significantly different between layers, but was marginally higher in the surface (1.22 mg C g^{-1} soil C) than the transition (0.36 mg C g^{-1} soil C) and permafrost layers (0.66 mg C g^{-1} soil C). Soil pH was in the acidic range, and significantly increased with depth.

3.2. Priming effects

The addition of glucose elicited immediate priming responses in both surface and permafrost layers, though these responses differed in sign and magnitude. Priming in the surface layer was mostly negative in the first week after each pulse. We observed significantly negative priming 48 h after each glucose amendment (Surface x 2 DAP: CI −77.36 to −9.09 μg CO_2-C g^{-1} soil C, Fig. 1, Supplemental Table 2) with consistent effects in all pulses.

In the permafrost layer, glucose addition resulted in significant

Table 1
Initial soil properties (mean ± SE) grouped by soil layers. A linear mixed effects model tested the effect of soil layer on bulk density, initial bulk soil organic C and N (%), C:N, initial $\delta^{13}C$ (‰), microbial biomass, and pH. Values not sharing the same letter indicate a significant difference.

Layer	Bulk Density (g/cm3)	Initial C (%)	Initial N (%)	C:N	Initial $\delta^{13}C$ (‰)	Microbial biomass (mg C g^{-1} soil C)	pH
Surface	0.17 ± 0.04[a]	37.96 ± 2.52[a]	1.51 ± 0.11[a]	25.52 ± 2.59[a]	−26.22 ± 0.17[a]	1.22 ± 0.76[a]	3.96 ± 0.09[a]
Transition	0.53 ± 0.15[b]	20.99 ± 3.92[b]	0.86 ± 0.20[b]	25.08 ± 1.88[a]	−27.22 ± 0.19[b]	0.36 ± 0.13[a]	4.77 ± 0.13[b]
Permafrost	0.46 ± 0.03[b]	9.69 ± 3.68[c]	0.37 ± 0.13[c]	24.80 ± 1.50[a]	−27.36 ± 0.23[b]	0.66 ± 0.12[a]	5.12 ± 0.15[c]

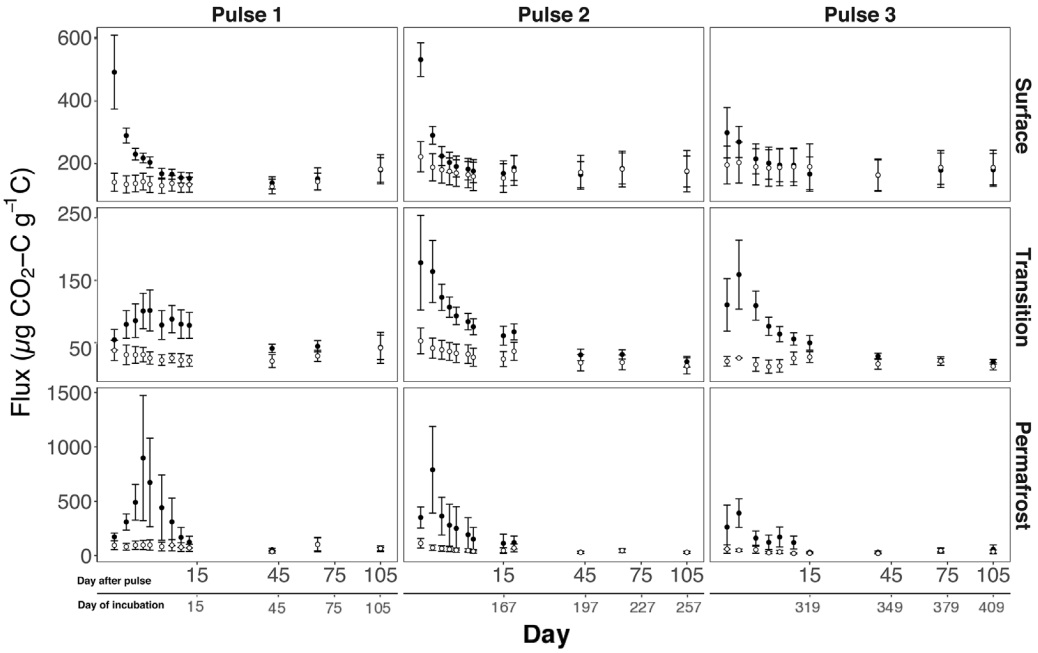

Fig. 1. Priming (μg CO_2-C g^{-1} soil C) in surface, transition, and permafrost layers over time (in days) after glucose pulse (DAP) (primary x-axis). The secondary x-axis indicates day since the start of incubation (DOI). The x-axis was square-root transformed to make it easier to see values in the first 15 DAP. Values above zero indicate higher soil C losses relative to control (positive priming), and values below zero indicate lower soil C losses relative to control (negative priming). Bars are one standard error from the mean, and open circles indicate a significant priming effect. Note that the scale for the y-axis in the permafrost layer is two times higher.

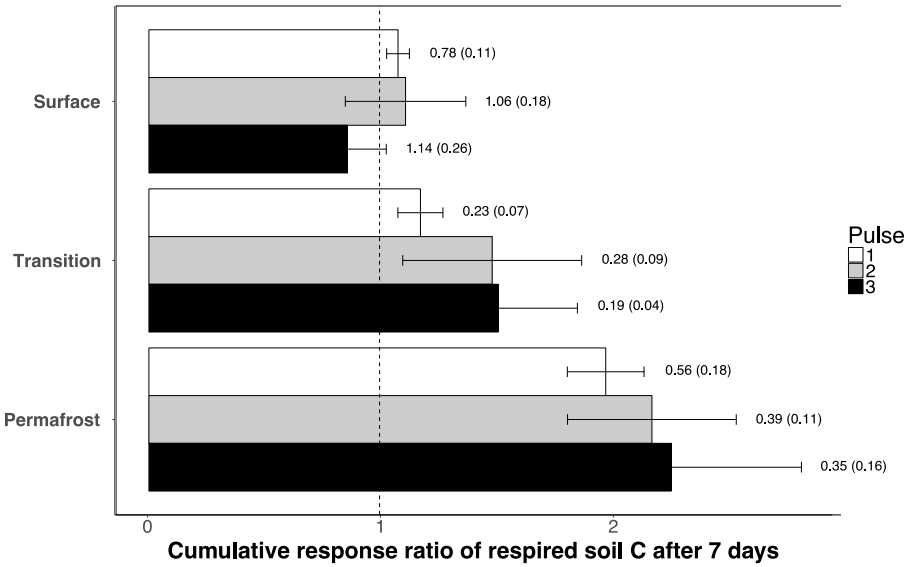

Fig. 2. Cumulative response ratio of respired soil C in glucose treatments relative to respired soil C in unamended samples 7 DAP. Glucose to unamended ratios that are less than 1 indicate negative priming, equal to 1 indicate no priming effect, greater than 1 indicate positive priming. Numbers in the figure are the unamended cumulative soil C losses (mg soil C g^{-1} soil C ± SE) 7 DAP. Bars are one standard error from the mean.

positive priming effects that lasted 7 days after each pulse; this response was similar across all three pulses (Fig. 1, Supplemental Table 2). This strong priming effect in the glucose treatment doubled the cumulative soil C loss relative to the unamended permafrost layer; the cumulative response ratio of soil C loss in glucose treatments relative to control was close to 2 (Fig. 2). There were no significant priming responses in the transition layer, with consistent effects across all three pulses and DAP, although mean values generally showed positive or no priming effects (Fig. 1, Supplemental Table 2).

Cellulose amendments resulted in positive and negative priming responses depending on the soil layer, and in general had a longer, albeit smaller effect on soil C loss than did glucose. In the surface soil, the 3rd cellulose pulse induced significant negative priming that lasted the entire sampling period (Surface x Pulse 3: CI −49.41 to −34.94 μg CO_2-C g^{-1} soil C, Fig. 3, Supplemental Table 2). In the permafrost layer, the 3rd cellulose pulse led to significant positive priming that increased soil C loss (Permafrost x Pulse 3: CI 7.66 to 28.67 μg CO_2-C g^{-1} soil C, Fig. 3, Supplemental Table 2). As with glucose addition, there were no significant priming effects in the transition layer, but mean responses trended towards positive or no priming effects (Fig. 3, Supplemental Table 2).

3.3. Age of respired soil C

In unamended soils, the $\Delta^{14}C$ value of respired C became more negative with depth, indicating that microbes respired older soil C deeper in the soil profile (Fig. 4). Over the course of the incubation, soil respired $\Delta^{14}C$ averaged 42‰ in the surface layer (Intercept: CI 35‰ to 50‰, Table 2), −201‰ in the transition layer (Intercept: CI −296‰ to −110‰, Table 2), and −426‰ in the permafrost layer (Permafrost x DOI 15: CI −516‰ to −334‰, Table 2) (Fig. 4). We observed the highest variability in soil-respired $\Delta^{14}C$ in the permafrost horizon; the respired $\Delta^{14}C$ soil signature in the unamended permafrost layer was significantly more positive on DOI 105 relative to DOI 15 (Permafrost x DOI 105: CI −420‰ to −231‰, Table 2), but by the end of the incubation, the soil-respired $\Delta^{14}C$ was once again similar to DOI 15 (Permafrost x DOI 319: CI −497‰ to −307‰, Table 2).

Glucose treatments significantly increased the $\Delta^{14}C$ value of soil

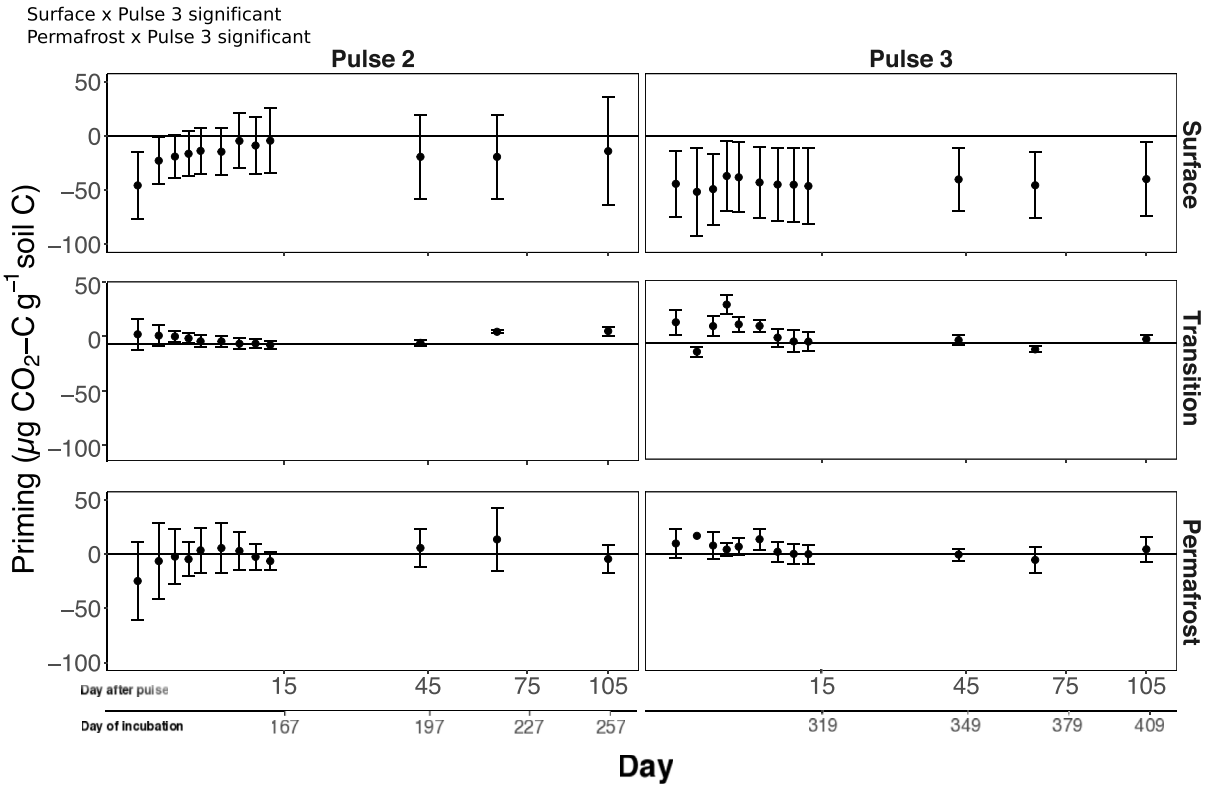

Fig. 3. Priming (μg CO_2-C g^{-1} soil C) in surface, transition, and permafrost layers over time (in days) after cellulose pulse (DAP) (primary x-axis). The secondary x-axis indicates day since the start of incubation (DOI). The x-axis was square-root transformed to make it easier to see values in the first 15 DAP. Labelling was not high enough in Pulse 1 to calculate priming effects (data not shown). Values above zero indicate higher soil C losses relative to control (positive priming), and values below zero indicate lower soil C losses relative to control (negative priming). Bars are one standard error from the mean. Surface and permafrost layers had significantly negative and positive priming, respectively, in Pulse 3.

respired C by 115‰ (Glucose: CI 25‰ to 206‰, Table 2) in the transition and permafrost layers relative to unamended soils in the transition layer (Fig. 4). This means that glucose addition induced mineralization of relatively young soil C in deeper layers. In the surface layer we saw a similar pattern, soil respired $\Delta^{14}C$ values in the glucose treatment were closer to 0‰, which indicates that the respired soil C

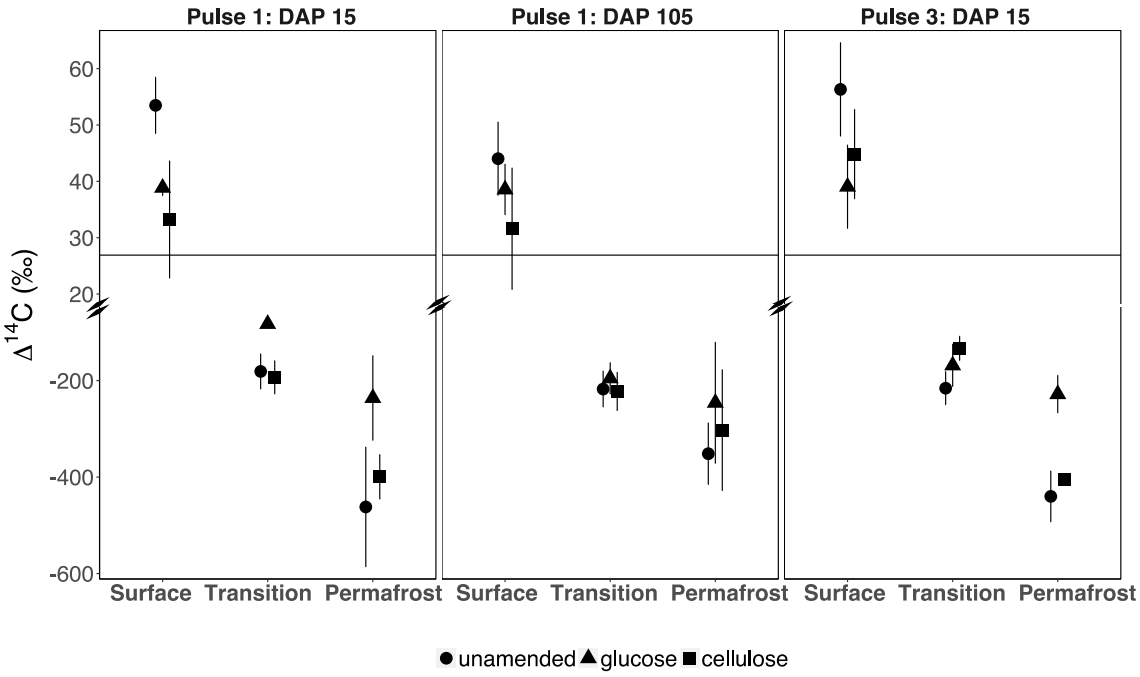

Fig. 4. Mean soil respired $\Delta^{14}C$ (‰) in surface, transition, and permafrost layers by treatment, 15 and 105 days after pulse 1, and 15 days after pulse 3 (DOI 319). Bars are one standard error from the mean. Horizontal line indicates atmospheric $\Delta^{14}C$ concentration in 2013. Note the break in the y-axis.

Table 2
Mixed linear effects model for soil respired $\Delta^{14}C$ at 15 and 105 days after the 1st pulse, and DOI 319 (15 days after the 3rd pulse). The intercept for the surface model represents soil respired $\Delta^{14}C$ (‰) in unamended surface layer, 15 days after pulse 1. The intercept for the deep layers (transition and permafrost) model represents soil respired $\Delta^{14}C$ (‰) in unamended transition layer, 15 days after pulse 1. Coefficients represent effect size on intercept, and significant effects are bolded.

Response variable	Full model	Final Model	Variable	Coefficient	Min CI	Max CI
Soil respired $\Delta^{14}C$ (‰)	Treatment x DOI	Intercept	Intercept (Unamended, Surface, DOI 15)	42.4	34.8	50.1
Soil respired $\Delta^{14}C$ (‰)	Treatment x Layer x DOI	Treatment	Intercept (Unamended, Transition, DOI 15)	−200.9	−295.9	−109.7
		Layer	**Glucose**	**115.4**	**25.1**	**206.3**
		DOI	Cellulose	30.4	−55.5	118.2
		Layer x DOI	DOI 105	−59.5	−121.0	1.4
			DOI 319	−20.1	−76.8	36.8
			Permafrost x DOI 15	**−224.8**	**−314.8**	**−133.3**
			Permafrost x DOI 105	**158.5**	**65.3**	**253.9**
			Permafrost x DOI 319	44.4	−51.7	138.5

was younger relative to unamended soils; however, this difference was not statistically significant. Cellulose did not change the $\Delta^{14}C$ of respired soil C relative to unamended soils.

3.4. Substrate use

Not all the substrate C added was respired by the end of each pulse. The amount of glucose C respired, as a percent of added substrate 105 DAP, was 40–54% in the surface, 37–58% in the transition, and 68–126% in the permafrost layer (Table 3). Out of the total glucose C respired in the permafrost layer 105 DAP, 20–47% was mineralized in the first week, when we observed significant positive priming effects (Table 4). We also observed the highest CO_2 fluxes and $\delta^{13}CO_2$ in the first 7 DAP that often decreased to match unamended concentrations 15 DAP (Supplemental Figures 1 and 2). The cumulative amount of cellulose loss for pulses 2 and 3 ranged from 20–26% in the surface, 16–25% in the transition, and 9–12% in the permafrost layer (Table 3). The cellulose treatment did not elicit a high peak in CO_2 fluxes in the first 7 DAP (Supplemental Figure 3), and $\delta^{13}CO_2$ did not decrease to match unamended values, even after 105 days in pulses 2 and 3 (Supplemental Figure 4).

4. Discussion

Models forecast that 5–15% of the terrestrial permafrost C pool (~130–160 Pg C) is vulnerable to decomposition in this century under current warming trajectories (Schuur et al., 2015). Higher temperatures will also increase shrub expansion in tundra regions (Chapin et al., 1995; Tape et al., 2006), and total belowground plant biomass, root production, and rooting depth (Sullivan et al., 2007; Zamin et al., 2014; Keuper et al., 2017), thus increasing fresh C inputs to soil. Our findings show that adding glucose to permafrost soils can change the magnitude and age of respired soil C.

4.1. Permafrost soil C loss increases with glucose addition

Glucose additions caused a two-fold increase in permafrost soil C loss relative to unamended samples in the first week after each pulse. The additional soil C mineralized in the permafrost layer 7 days after each pulse was 0.71–1.20 mg C g^{-1} soil C, which is 1 to almost 2 times greater than the initial microbial biomass in that layer (0.66 mg C g^{-1} soil C). This suggests that the increase in C loss resulted primarily from an increase in SOM decomposition (real priming effect), rather than an accelerated turnover of the microbial C pool (apparent priming effect) (Blagodatskaya and Kuzyakov, 2008; Blagodatskaya et al., 2011). A previous priming incubation study in Siberian permafrost conducted over 6 days also reported a two-fold increase in SOM decomposition in deep mineral soils amended with glucose (Wild et al., 2014). De Baets et al. (2016) similarly reported significant positive priming effects on a 10-day glucose addition study conducted in mineral soil and permafrost from tussock tundra. Our results corroborate the hypothesis that the addition of an easily decomposable C substrate alleviates energy constraints in deeper soil layers that have higher concentrations of slowly decomposing C.

We hypothesized that amending deeper soil layers with a simple substrate would increase soil C decomposition because slowly decomposing C constitutes most of the C at depth. Our initial soil parameters show that the fraction of slowly-decomposing C increased in the permafrost layer. We observed lower bulk soil $\delta^{13}C$ values at depth, which are common for soils that are waterlogged, and can indicate the accumulation of recalcitrant materials, like lignin (Alewell et al., 2011). The increased fraction of slowly-decomposing C in deeper layers was also reflected in the nuclear magnetic resonance spectra (NMR) analyses performed on subsamples of our soil cores. We found that the proportion of alkyl C relative to *O*-alkyl C increased in the permafrost layer (Plaza et al., 2017a). This pattern in the alkyl/*O*-alkyl ratio represents progressive organic matter degradation, and decreased plant-derived fresh organic matter relative to microbial biomolecules (Baldock and Skjemstad, 2000).

The negative priming effects in the surface layer after each glucose pulse can be attributed to a switch from microbial decomposition of SOM to decomposition of the added, more accessible substrate (Cheng, 1999; Kuzyakov, 2002). These results are consistent with the theory that C availability is not limiting in highly organic and less decomposed soils. Priming studies conducted in boreal, subarctic, and permafrost regions that amended organic surface soils with glucose or low-molecular weight C reported no net priming effects (Hartley et al., 2010; Lindén et al., 2014; Wild et al., 2014; De Baets et al., 2016; Karhu et al.,

Table 3
Cumulative substrate C loss as a percent (% ± SE) of added substrate (3.5 mg substrate C per g soil C) 105 days after each amendment pulse.

	Pulse 1		Pulse 2		Pulse 3	
	Glucose	Cellulose	Glucose	Cellulose	Glucose	Cellulose
Surface	54.4 ± 3.9	NA	39.9 ± 2.4	20.0 ± 2.4	45.9 ± 6.8	25.9 ± 2.0
Transition	58.3 ± 15.0	NA	37.8 ± 7.6	15.6 ± 6.8	36.9 ± 11.7	24.5 ± 5.5
Permafrost	125.9 ± 49.0	NA	67.5 ± 32.2	9.4 ± 2.3	80.2 ± 39.8	11.8 ± 5.8

Table 4
Seven-day cumulative substrate C loss as a percent (% ± SE) of cumulative respired substrate 105 days after each amendment pulse.

	Pulse 1		Pulse 2		Pulse 3	
	Glucose	Cellulose	Glucose	Cellulose	Glucose	Cellulose
Surface	37.9 ± 2.1	NA	40.7 ± 1.8	5.6 ± 0.7	43.4 ± 4.2	6.9 ± 0.5
Transition	13.8 ± 2.4	NA	29.0 ± 5.6	5.6 ± 1.1	24.2 ± 1.9	4.8 ± 0.5
Permafrost	46.6 ± 3.9	NA	47.4 ± 3.7	6.0 ± 1.7	20.0 ± 1.7	5.2 ± 0.9

2016; Rousk et al., 2016; Lynch et al., 2018). Labile C addition to highly organic layers seem to shift microbial substrate utilization to more N-rich compounds, which can reduce total SOM decomposition (Rousk et al., 2016). Considering the entire soil profile, the 7-day cumulative response ratio of respired soil C in the surface layer is very close to 1. The glucose effect on the magnitude of soil C loss in the glucose treatment was negligible, and closely matched rates in unamended surface samples. Meanwhile, positive priming in the permafrost layer doubled the amount of C respired relative to permafrost unamended samples.

The strong negative priming response in surface soils during the 3rd cellulose pulse may reflect the increasing C limitation of microorganisms during long-term incubations (Bracho et al., 2016). Since 74–92% of the added cellulose remained in the soil after each pulse, and the $\delta^{13}CO_2$ was still high 105 DAP, it is possible that microbes relied on the accumulated cellulose as a source of C instead of SOM after almost one year of incubation.

In the permafrost layer; the stimulation of daily CO_2-C production (7.66–28.67 μg CO_2-C g^{-1}soil C) caused by the 3rd cellulose pulse was small compared to the initial microbial biomass in the permafrost layer (660 ± 120 μg microbial C g^{-1}soil C). Thus, we cannot fully attribute this positive priming effect in the cellulose treatment to higher SOM decomposition, but potentially to an increase in microbial turnover (i.e. apparent priming effect) (Jenkinson et al., 1985; Blagodatskaya and Kuzyakov, 2008). If we consider the effect of cellulose addition on the entire soil profile, negative priming effects in the surface were 2–5 times higher than positive priming effects in the permafrost layer.

4.2. Persistent SOM decomposition response to multiple glucose additions

Our results show that over the course of the incubation, each pulse of glucose elicited a priming response. In the permafrost layer, glucose addition consistently doubled soil C loss (Fig. 2). Priming studies that repeatedly amended soils with multiple pulses of substrate C have reported higher soil C losses than single additions at the beginning of an incubation (De Nobili et al., 2001; Hamer and Marschner, 2005).

Glucose was readily used by microbes in the permafrost layer, and 68–126% of the added substrate was completely respired 152 days after each pulse. Out of the substrate respired, 20–47% was respired just in the first week, which is when we observed positive priming effects. Glucose often produces a rapid response in microbial activity (Bernal et al., 2016), and leads to rapid metabolic changes in a wide variety of fast-growing bacteria that utilize it as a substrate (Stotzky and Norman, 1961; Hungate et al., 2015). This fast turnover of glucose in permafrost soil, which can be seen in the rapid decline in CO_2 flux and $\delta^{13}CO_2$ (Supplemental Figures 1 and 2), and the sustained positive priming effects after each pulse, suggest that multiple pulses will continue to stimulate soil C loss, and single-pulse incubation studies might underestimate soil C losses.

4.3. Age of respired soil C decreases with glucose input

Carbon in deep soil layers is mostly old, and its longer mean residence time is due to different biological, physical, and chemical stabilization processes; in permafrost, soil C persistence may also be promoted by low rates of DOC inputs (Schimel et al., 1994; Schuur et al., 2009; Czimczik and Welker, 2010; Walvoord and Kurylyk, 2016). Though a previous study found that soluble C inputs increased the proportion of older CO_2-C fluxes in boreal soils (Lindén et al., 2014), our results indicate that an input of glucose decreased the age of soil respired C in transition and permafrost layers. Glucose amendment induced soil C mineralization that was overall 115‰ higher (younger) relative to soil C respired in unamended and cellulose treatments. Though other permafrost priming studies do not report the radiocarbon age of respired soil C, two priming studies in other ecosystems also reported younger C losses. Blagodatskaya et al. (2011) found that primed SOM decomposition originated mainly from younger C, even though the proportion of young and old C equally contributed to SOM. Sullivan and Hart (2013) conducted a priming experiment at four sites along a substrate age gradient from 0.93 to 3000 ky, and found the greatest cumulative priming in younger sites, while the oldest site experienced either negative or no net priming.

Recent arguments have been raised against the long-standing theory that persistent soil C is found in large humic substances, but rather in a continuum of progressively more decomposed compounds that transition from polymers to monomers as OM is oxidized (Lehmann and Kleber, 2015). Older C fractions are not always composed of complex or recalcitrant compounds (Kleber et al., 2011; Nunan et al., 2015). Observations in a long-term bare-fallow soil that was depleted of plant litter inputs showed that microbial communities became adapted to metabolizing simple and small compounds. Microbes tended to use molecules or derivatives from the Krebs cycle (i.e. α-ketoglutaric acid, citric acid), and were less able to decompose polymers; and although old C molecules can be readily mineralized, the energetic payoff is low (Nunan et al., 2015). The microbial mining hypothesis suggests that SOM decomposition increases when microbes use extracellular enzymes to release nutrients locked in polymers (Craine et al., 2007; Fontaine et al., 2011; Dijkstra et al., 2013). When a fresh C substrate is introduced that increases microbial activity and extracellular enzyme production, microbes can access C and nutrients in more complex polymeric structures. If these complex C structures are younger, then positive priming may increase the proportion of younger C that is respired. Soil C stabilization mechanisms in permafrost are not completely understood, and in general, permafrost C is considered stable primarily due to low temperature constraints on decomposition. Once temperature constraints are lifted, mechanisms like waterlogging, microaggregation, and association with silt and clay particles may also contribute to C stabilization (Six et al., 2002). Future priming studies in permafrost should focus on physical stabilization processes that influence C turnover rates.

A previous study at Eight Mile Lake found that the proportion of old C respired from deeply thawed, experimentally warmed plots, was lower relative to less thawed areas. They attributed this phenomenon to higher plant respiration, which increased the contribution of younger C to ecosystem respiration and diluted the old C signature (Schuur et al., 2009; Hicks Pries et al., 2015). Our results suggest that positive priming in deep soil layers can also contribute to a younger signature of ecosystem respiration. The average $\Delta^{14}C$ in unamended samples was −201‰ (CI: −296 to −110‰) in the transition layer and −426‰ (CI: −516 to −334‰) in the permafrost layer. Priming increased the respired $\Delta^{14}C$ values to −86‰ in the transition layer and −311‰ in the permafrost layer. Though these values still reflect relatively older C,

the change corresponds to $\Delta^{14}CO_2$ values that are usually measured in layers that are 10–30 cm shallower than the depths we incubated. Applying a partitioning model without considering priming effects could cause the model to underestimate deep soil C contribution to ecosystem respiration by attributing them to decomposition of shallower soils that have a greater proportion of younger C.

4.4. Implications for the permafrost-C feedback

Our findings indicate that priming effects can have implications for the magnitude and turnover of soil C in permafrost. Priming doubled permafrost soil C losses in the first week after each pulse, and decreased the overall age of respired soil C. Field ecosystem respiration measurements show that moist acidic tundra sites at Eight Mile Lake are a net annual CO_2-C source to the atmosphere, despite increases in plant biomass (Mauritz et al., 2017). This effect could be exacerbated by increased inputs of easily decomposable C to mineral and permafrost soils. We extrapolated our incubation results to field conditions at Eight Mile Lake by using field soil temperatures to temperature-correct soil C fluxes, and applied a site-specific Q_{10} of 2.6 based on the temperature sensitivity analysis of CO_2 fluxes from soils collected in our site in 2010 (Bracho et al., 2016). Our estimates suggest that priming-induced soil C losses correspond to 4–12% of the cumulative C released during a growing season (235–408 g CO_2-C m^{-2}, reported in Mauritz et al., 2017). Though we must be cautious when relating incubation results to the field, as these estimates are likely high because soils can remain waterlogged after thaw, and our sample size is small, our study suggests that priming may be an important mechanism that exacerbates soil C losses to the atmosphere. Future priming studies should focus on field studies, and measure the radiocarbon age of primed soil C. We must consider priming effects to fully understand permafrost C dynamics, or we may potentially underestimate the contribution of soil C to ecosystem respiration rates.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2018.10.009.

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