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## RESEARCH LETTER

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### Special Section:

Understanding carbon-climate feedbacks

### Key Points:

- Combining continuous soil CO<sub>2</sub> flux with  $\Delta^{14}\text{CO}_2$  observations enables a systematic evaluation of carbon cycling in Arctic soils year-round
- Outside the growing season, soil microorganisms rely on older, local soil carbon pools not captured in short-term incubation experiments
- Permafrost warming and thaw is depleting soil carbon pools; fluxes of older carbon are greatest in summer but dominate emissions in winter

### Supporting Information:

Supporting Information may be found in the online version of this article.

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## Closing the Winter Gap—Year-Round Measurements of Soil CO<sub>2</sub> Emission Sources in Arctic Tundra

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**Abstract** Non-growing season CO<sub>2</sub> emissions from Arctic tundra remain a major uncertainty in forecasting climate change consequences of permafrost thaw. We present the first time series of soil and microbial CO<sub>2</sub> emissions from a graminoid tundra based on year-round in situ measurements of the radiocarbon content of soil CO<sub>2</sub> ( $\Delta^{14}\text{CO}_2$ ) and of bulk soil C ( $\Delta^{14}\text{C}$ ), microbial activity, and temperature. Combining these data with land-atmosphere CO<sub>2</sub> exchange allows estimates of the proportion and mean age of microbial CO<sub>2</sub> emissions year-round. We observe a seasonal shift in emission sources from fresh carbon during the growing season (August  $\Delta^{14}\text{CO}_2 = 74 \pm 4.7\text{‰}$ , 37%  $\pm$  3.4% microbial, mean  $\pm$  se) to increasingly older soil carbon in fall and winter (March  $\Delta^{14}\text{CO}_2 = 22 \pm 1.3\text{‰}$ , 47%  $\pm$  8% microbial). Thus, rising soil temperatures and emissions during fall and winter are depleting aged soil carbon pools in the active layer and thawing permafrost and further accelerating climate change.

**Plain Language Summary** The Arctic is warming and large quantities of organic matter in permafrost soils are at risk of becoming decomposed to carbon dioxide (CO<sub>2</sub>) by microbes. Measurements of soil CO<sub>2</sub> emissions do not provide direct estimates of permafrost emissions, however, because CO<sub>2</sub> is produced by microbes and plant roots. Using a new sampler, we collected soil CO<sub>2</sub> in northern Alaska over 3–6 weeks for 2 years and analyzed its radiocarbon content to distinguish CO<sub>2</sub> sources. To calculate CO<sub>2</sub> budgets, we added observations of soil and microbial CO<sub>2</sub> emissions and soil temperature. We find that microbes rely on fresh plant matter in summer but older organic matter from fall to spring; a process not captured by standard laboratory experiments. Thus, warming permafrost soils are not just more rapidly cycling fresh plant litter but losing organic matter that accumulated over decades to millennia.

## 1. Introduction

Climate change is rapidly transforming the Arctic (Post et al., 2019; Steffen, 2006). Permafrost thaw may facilitate microbial decomposition of vast amounts of soil organic carbon (C) ( $472 \pm 27$  Pg C for 0–1 m) (Hugelius et al., 2014) into the greenhouse gases CO<sub>2</sub> and CH<sub>4</sub> (Schuur et al., 2015), accelerating climate and ecosystem changes. Permafrost temperatures in the northern circumpolar continuous permafrost zone have increased by  $0.39 \pm 0.15^\circ\text{C}$  (2007–2016, Biskaborn et al., 2019), concurrent with increases in active layer thickness (*medium confidence*, Meredith et al., 2019). The area underlain by near-surface (within 4 m) permafrost may decrease by 2%–66% (RCP2.6) or 30%–99% (RCP8.5) by 2100, and this loss is projected to release up to 240 Pg C to the atmosphere (Meredith et al., 2019), but the magnitude, timing, and proportions of CH<sub>4</sub> and CO<sub>2</sub> fluxes remain highly uncertain (Schuur et al., 2015; Turetsky et al., 2020).

Non-growing season C emissions are emerging as an important contribution to the annual C balance of Arctic ecosystems (Euskirchen et al., 2012; Fahnestock et al., 1998; Morgner et al., 2010; Oechel et al., 1997; Raz-Yaseef et al., 2017; Watts et al., 2021; Welker et al., 2000, 2004), turning the Arctic into a net C source (Commane et al., 2017; Natali et al., 2019). It remains unclear, however, which soil C pools fuel microbial respiration from fall to spring. Some of this may originate from older C in thawing permafrost, which like fossil fuel combustion, has not participated in the global C cycle for millennia, but may increasingly contribute to land-atmosphere C emissions. Reducing the uncertainty in our understanding of non-growing season emission and the permafrost

C feedback to climate change urgently requires direct, year-round observations of C emissions and sources from permafrost landscapes.

Measurements of the radiocarbon ( $^{14}\text{C}$ ) content of soil-atmosphere C emissions can be used to estimate how rapidly soils may sequester or lose C in response to changes in environmental conditions or net primary productivity (Trumbore, 2006). These data provide an estimate of transit time (the age of C leaving the soil) and can be used to apportion emissions into plant- and microbial contributions and to quantify losses of permafrost C (Estop-Aragónés et al., 2018; Lupascu, Welker, Xu, & Czimeczik, 2014; Schuur et al., 2009).

Soil C emissions are a major component of ecosystem C emissions. A significant proportion of soil C emission originates from the rhizosphere, that is, respiration of plant roots and microorganisms that consume root exudates, which have a similar  $\Delta^{14}\text{CO}_2$  signature to ambient air. Currently (2021), atmospheric  $\Delta^{14}\text{CO}_2$  is about 0‰ following a 70-year decline of  $^{14}\text{C}$  in the atmosphere from a maximum in the 1960s, when testing of thermonuclear weapons resulted in the formation of additional (bomb or modern)  $^{14}\text{C}$  that subsequently mixed into the C cycle and became diluted by  $^{14}\text{C}$ -free fossil fuel  $\text{CO}_2$  emissions (Graven et al., 2020; Levin et al., 2010). Microbial emissions constitute the remainder of the soil C efflux and are either slightly depleted ( $\Delta^{14}\text{C} < 0‰$ , “old”) from decomposition of pre-1950 substrate, or enriched ( $\Delta^{14}\text{C} > 0‰$ , “modern”) from post-1950 substrate. In permafrost soils, microbial emissions of previously frozen C are strongly  $^{14}\text{C}$ -depleted due to radioactive decay ( $\Delta^{14}\text{C} \ll 0‰$ , “ancient”).

Soil C source apportionment studies often combine  $^{14}\text{C}$  analysis of ecosystem (or soil), rhizosphere, and microbial emissions ( $^{14}\text{CO}_2_{\text{eco}}$ ,  $^{14}\text{CO}_2_{\text{rhizo}}$ , and  $^{14}\text{CO}_2_{\text{micro}}$ , respectively) to determine the relative contribution of rhizosphere ( $R_{\text{rhizo}}$ ) and microbial emissions ( $R_{\text{micro}}$ ) to the total ( $R_{\text{eco}}$ ) (Equations 1 and 2). Ecosystem C emissions are collected in the field, rhizosphere C emissions can be measured by incubating roots or approximated from  $^{14}\text{C}$  measurements of atmospheric  $\text{CO}_2$ , and microbial C emissions from laboratory incubation experiments.

$$f_{\text{eco}} = 1 = f_{\text{rhizo}} + f_{\text{micro}} = \frac{R_{\text{rhizo}}}{R_{\text{eco}}} + \frac{R_{\text{micro}}}{R_{\text{eco}}} \quad (1)$$

$$^{14}\text{CO}_2_{\text{eco}} = f_{\text{rhizo}} ^{14}\text{CO}_2_{\text{rhizo}} + f_{\text{micro}} ^{14}\text{CO}_2_{\text{micro}} \quad (2)$$

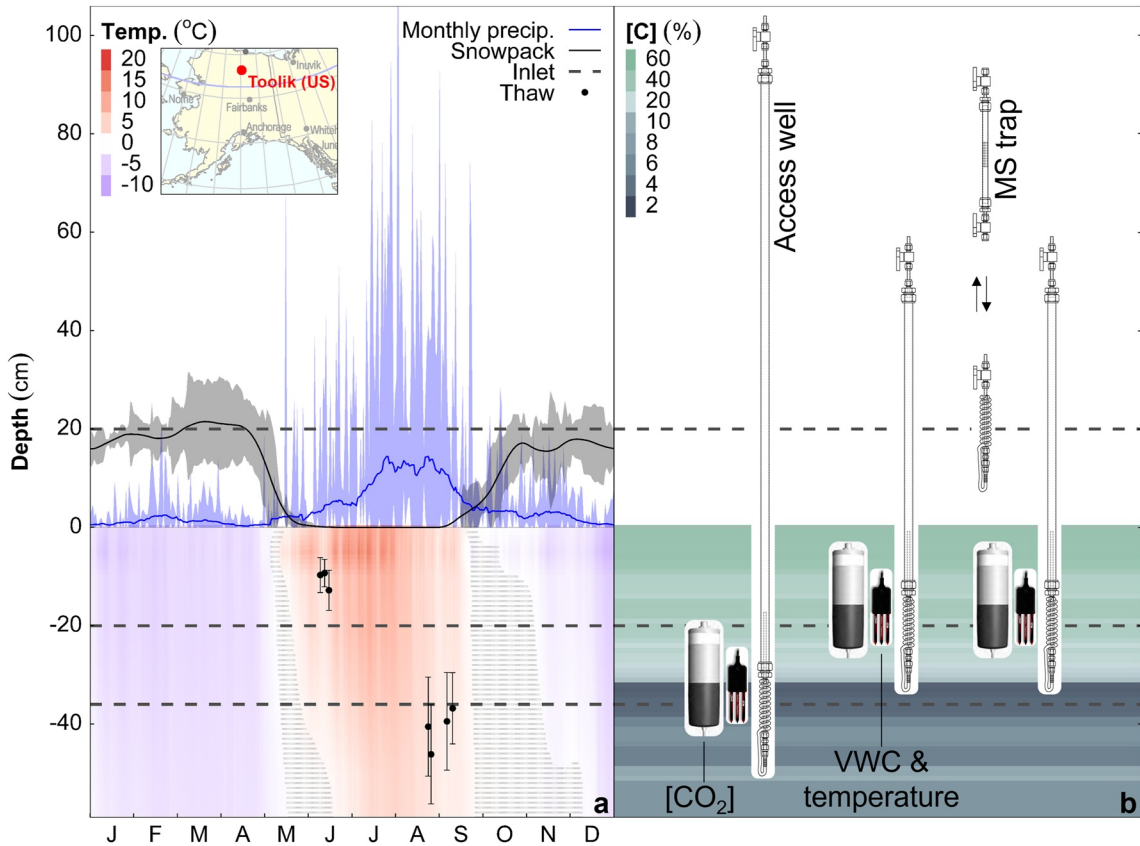
Past studies have advanced our understanding of soil C emissions and their sources from permafrost soils (Hicks Pries et al., 2013, 2016; Lupascu, Welker, Seibt, et al., 2014; Nowinski et al., 2010; Street et al., 2020) but suffer shortcomings. First, to collect sufficient mass for  $^{14}\text{C}$  analysis, common approaches accumulate soil  $\text{CO}_2$  in chambers (Lupascu, Welker, Seibt, et al., 2014) and may remove ambient atmospheric  $\text{CO}_2$  from the headspace (Czimeczik et al., 2006; Hicks Pries et al., 2013; Plaza et al., 2019). Chambers cover the ground for 0.5–48 hr during which the soil  $\text{CO}_2$ -depth gradient is disturbed. This approach only provides a snapshot of emissions and may miss advective fluxes in response to changes in atmospheric pressure or precipitation events (Lupascu, Welker, Seibt, et al., 2014), and due to the high cost of  $^{14}\text{C}$  analysis, most studies collect chamber samples about once a month and few have collected outside the growing season (Lupascu et al., 2018; Winston et al., 1997). Second, the source of microbial C emissions is assessed in incubations (Schädel et al., 2014; Treat et al., 2015) that disrupt the autotroph–heterotroph respiratory continuum (Högberg & Read, 2006). However, we commonly observe a greater range of microbial-respired  $^{14}\text{CO}_2$  in the field than in laboratory incubation studies (Lupascu, Welker, Seibt, et al., 2014).

As permafrost thaws, it is prudent to investigate the vulnerability of its organic matter to decomposition in situ. Here, we use a recently developed a passive  $\text{CO}_2$  sampler (capturing  $\text{CO}_2$  by diffusion, Pedron et al., 2021) to collect soil  $\Delta^{14}\text{CO}_2$  from a graminoid tundra for two years (June 2017–August 2019). These data are then used to apportion soil C emissions into rhizosphere and microbial contributions. The resulting annual  $^{14}\text{CO}_2$ -depth profiles allow us to investigate microbial C sources during the non-growing season. Our approach quantifies the mean age of the land-atmosphere C flux on a monthly to annual scale and provides a basis for a more systematic quantification of permafrost C losses in the rapidly changing Arctic.

## 2. Materials and Methods

### 2.1. Field Site and Sample Collection

We continuously captured soil  $\text{CO}_2$  for  $\Delta^{14}\text{CO}_2$  analysis from a moist acidic tussock tundra near Toolik Field Station, AK, USA (68.625478°N, 149.602199°W, 724 m) with passive samplers consisting of permanently



**Figure 1.** (a) Environmental data during the sampling period (June 2017–September 2019), averaged by day of year and either smoothed (precipitation, snowpack, from Toolik EDC) or modeled from observations (thaw depth). The soil is shaded based on Toolik EDC temperature data, with dots showing zero curtain. (b) Site setup. Permanent access wells attached to exchangeable molecular sieve (MS) traps were suspended above the surface (20 cm,  $n = 1$ ) or buried within the active layer with silicone inlets at  $-20$  (O horizon,  $n = 2$  (tussock/swale)) and  $-36$  cm below the surface (A horizon,  $n = 1$ ) alongside  $[CO_2]$  and VWC + temperature probes within a  $1\text{ m}^2$  area in a moist acidic tundra system near Toolik Field Station, AK, USA ( $68.625478^\circ\text{N}$ ,  $149.602199^\circ\text{W}$ ,  $724\text{ m}$ ). The soil is shaded by C percent of bulk organic matter (averaged from soil cores) and scaled to distinguish organic (green  $> 20\%$ ) from mineral (blue  $< 20\%$ ) soil.

installed access wells (diffusive silicone tubing inlet attached to steel tubing path) connected to exchangeable evacuated cylinders or molecular  $CO_2$  sieve (MS) traps (Pedron et al., 2021). Access wells were buried within the active layer at 20 cm (O horizon,  $n = 1$  each, tussock/swale) and 36 cm (A horizon,  $n = 1$ ) and suspended above the surface (20 cm,  $n = 1$ ), all within a  $1\text{-m}^2$  area (Figure 1b). Samples were collected from June 2017 to August 2019 over periods of 3–6 weeks using canisters (June 2017–September 2017), MS traps (September 2017–September 2018), and alternating canisters and MS traps (September 2018–August 2019). We also collected high-resolution ( $< 2\text{-week}$ ) samples in 0.5 L canisters ( $n = 22$ , 2017 (June, September, November),  $n = 20$ , 2018 (March, August),  $n = 4$ , 2019 (June)).

The data were sequentially corrected for: (a) leakage of ambient air  $CO_2$  into traps or canisters and (b) mixing of ambient air  $CO_2$  into the soil pore space, given the high soil porosity (Hirsch et al., 2004) (Equation 3).

$$^{14}CO_{2\text{cor}} = \frac{^{14}CO_{2\text{spl}} - ^{14}CO_{2\text{air}} * f_{\text{air}}}{1 - f_{\text{air}}} \quad (3)$$

where  $^{14}CO_{2\text{cor}}$  and  $^{14}CO_{2\text{spl}}$  represent the corrected or measured  $\Delta^{14}CO_2$  of a sample, respectively,  $f_{\text{air}}$  the proportion of ambient air  $CO_2$ , and  $^{14}CO_{2\text{air}}$  the  $\Delta^{14}CO_2$  of ambient air.

The proportion of MS trap air- $CO_2$  from leakage was calculated from extraction of a set of traps that were shipped back and forth from the field site and attached, but never opened to access wells ( $n = 8$ ,  $0.16 \pm 0.1\text{ ug C d}^{-1}$ ). The proportion of air- $CO_2$  due to soil-air mixing was calculated from the ratio of air  $[CO_2]$  to soil  $[CO_2]$  at the depth of each inlet, averaged over each sampling period.

We episodically monitored thaw depth with a steel-tipped tile probe in swales, and retrieved continuous environmental data (air and soil temperatures, insolation, precipitation, snow depth) from Toolik's Environmental Data Center (Environmental Data Center Team, 2020) and atmospheric CO<sub>2</sub> concentrations and ecosystem CO<sub>2</sub> fluxes from an eddy covariance (EC) tower at Imnavait Creek (wet sedge tundra, 12 km WSW; Euskirchen et al., 2019). We deployed soil (CO<sub>2</sub>) (Carbocap GMP343, 11 June 2017–25 August 2019, 30-s resolution, Vaisala, Finland) and temperature and volumetric water content (VWC) (Decagon 5 TM, 12 September 2017–26 August 2019, 15-min resolution, METER, USA) probes ( $n = 3$  of each) with the buried access wells (Figure 1b). Data gaps were filled using day-of-year means over the sampling period (~14% of [CO<sub>2</sub>], ~19% of VWC and temperature daily values).

To validate the samplers, we measured ecosystem CO<sub>2</sub> respiration flux ( $R_{\text{eco}}$ ) with traditional dynamic soil chambers installed in June 2017, 10 m away from the access wells. Chamber bases were inserted to 2 cm depth and vegetation was not clipped ( $n = 3$  each, tussock/swale). We collected ambient air CO<sub>2</sub> and chamber  $R_{\text{eco}}$  samples for isotopic analysis in June, September, & November 2017 ( $n = 37$ ), March & August 2018 ( $n = 11$ ), and August 2019 ( $n = 2$ ), and measured  $R_{\text{eco}}$  rate in June and September 2017 ( $n = 39$ ; Lupascu, Welker, Seibt, et al., 2014, 2018).

Growing season chambers were flushed with ambient air before being attached to bases, and isotopes were subsequently corrected for air volume. Chambers sampled in November 2017 ( $n = 3$ ) were left attached to bases at the end of the 2017 growing season, with Bev-A-Line tubing connected to a central point, accessible above snowpack. We flushed their headspace CO<sub>2</sub> with ambient air and sampled after 24 hr of accumulation, thereby minimizing contamination from prior accumulation.

To sample CO<sub>2</sub> for isotope analyses, we left the growing season chambers closed until the CO<sub>2</sub> concentration inside the chamber was at least double that of ambient air (up to 24 hr). After measuring its concentration, the CO<sub>2</sub> was dried (Drierite, W.A. Hammond Drierite Co. Ltd., Xenia, OH, USA) and collected onto u-shaped MS traps ("u-traps," 2 g of powder-free 13X 8 × 12 beads, Grace, USA) by recirculating the headspace air at a rate of 0.5 L min<sup>-1</sup> for 15 min. These MS u-traps used to collect chamber or ambient air CO<sub>2</sub> are distinct from the MS traps previously described in both shape (u-shaped vs. straight) and MS dimension (8 × 12 beads vs. 45–60 mesh) but operate by the same principle of size-selective molecule retention. These data were corrected for mixing of ambient air CO<sub>2</sub> (Equation 3), where the fraction of air-CO<sub>2</sub> was calculated from ratio of air [CO<sub>2</sub>] to chamber-headspace [CO<sub>2</sub>]. Isotope data with a calculated fraction of air >40% ( $n = 23$ , 47% of samples) were likely affected by leakage around the chamber base – a common issue in organic soils and tussock/swale terrain affected by freeze-thaw cycles – and excluded from results.

Growing season  $R_{\text{eco}}$  fluxes were quantified with an infrared gas analyzer and data logger (LI-840, LI-1400, LI-COR Biosciences, Lincoln, NE, USA) at a rate of 0.5 L min<sup>-1</sup>. Emission rates were calculated from the slope of time versus CO<sub>2</sub> concentration curves using linear regression. Winter fluxes were not calculated because accumulating enough headspace CO<sub>2</sub> for <sup>14</sup>C analysis disturbed the soil CO<sub>2</sub> gradient and saturated the headspace, yielding small fluxes with large uncertainties.

We collected soil samples for incubations and bulk soil analyses by cutting rectangular columns of soil from 6 m south of the samplers with either a saw ( $n = 1$  each tussock/swale in thawed soil, September 2017) or electric chainsaw ( $n = 1$  each tussock/swale in frozen soil, March 2018). Cylindrical cores collected by powered corer ( $n = 3$ , 2015) and a modified rotary hole saw ( $n = 2$ , 2019) from a nearby site (moist acidic tussock tundra, <1 km away) were also used after comparison of bulk soil isotopes revealed no significant differences (all 2-sample Student's  $t$ -test  $p > 0.05$  for 10-cm depth bins). Soils were stored frozen in plastic freezer bags.

## 2.2. Laboratory Analyses

At UC Irvine, CO<sub>2</sub> was thermally desorbed from u-traps and MS traps (Pedron et al., 2021) or extracted from canisters (Lupascu, Welker, Seibt, et al., 2014) on a vacuum line and converted to graphite using a sealed-tube zinc reduction method (Xu et al., 2007). Graphite was analyzed for  $\Delta^{14}\text{C}$  with accelerator mass spectrometry (NEC 0.5 MV 1.5SDH-2 AMS) alongside processing standards and blanks with a measurement uncertainty of <3‰ (Beverly et al., 2010).

Soil cores were separated into organic or mineral soil and sectioned into intervals (1.5–14 cm) while frozen. For bulk soil analysis, soil was dried at 60°C to constant mass, weighed, and ground to powder using rotary blade and ball mills for organic and mineral soils, respectively. For  $\Delta^{14}\text{C}$  analysis, samples were combusted in pre-combusted, evacuated quartz tubes with cupric oxide (900°C, 3 hr) and the resulting  $\text{CO}_2$  processed as described above. Bulk soil C was measured alongside processing standards and blanks with EA-IRMS (Fisons NA-1500NC, DeltaPlus XL, Thermo, USA).

Incubations (2–158 g soil) were performed on field-moist samples at 22, 7, and  $-20^\circ\text{C}$  in glass mason jars (0.5–2 L) flushed with  $\text{CO}_2$ -free air and kept in the dark.  $\text{CO}_2$  concentrations were measured periodically with a LI-COR 820, and the respired  $\text{CO}_2$  was extracted and converted to graphite as described above once concentrations reached 30% (17–49 days). Short ( $\sim$ 1-day) incubations were also performed on roots harvested from the September 2017 soil cores on the same day of collection to quantify rhizosphere emissions. These data provided predictive relationships between microbial  $\text{CO}_2$  emissions ( $R_{\text{micro}}$ ), depth, and temperature.

### 3. Data Processing and Soil C Emission Partitioning

Using the data collected during the 2-year study period, we averaged meteorological, soil  $[\text{CO}_2]$ , temperature, VWC, and access well  $\Delta^{14}\text{CO}_2$  data month to month over one year. Access well aggregates were weighted by the period overlapping the beginning and end of each timestep. To account for our 2–6-week sampling periods and data gaps, we chose to represent our data products at calendar month resolution. We found no significant differences in soil  $\Delta^{14}\text{CO}_2$  collected at 20 cm depth under tussock or swale (paired two-tailed  $t$ -test  $p$ -value  $\gg$  0.05).

The steps and assumptions used to determine a surface isotopic flux are detailed in the Supplement (S) and shown conceptually in Figure S5 of Supporting Information S1. We created a monthly  $\Delta^{14}\text{CO}_2_{\text{eco}}$ -depth model using measured predictors along depth (bulk soil  $\Delta^{14}\text{C}$ ) and time (days snow-free, days snow-covered) from the deepest inlet depth ( $-36$  cm) to the organic soil surface (0 cm). Model details are described in S: *Multivariate adaptive regression splines*, and results in Table S2 and Figure S8 in the Supporting Information S1.

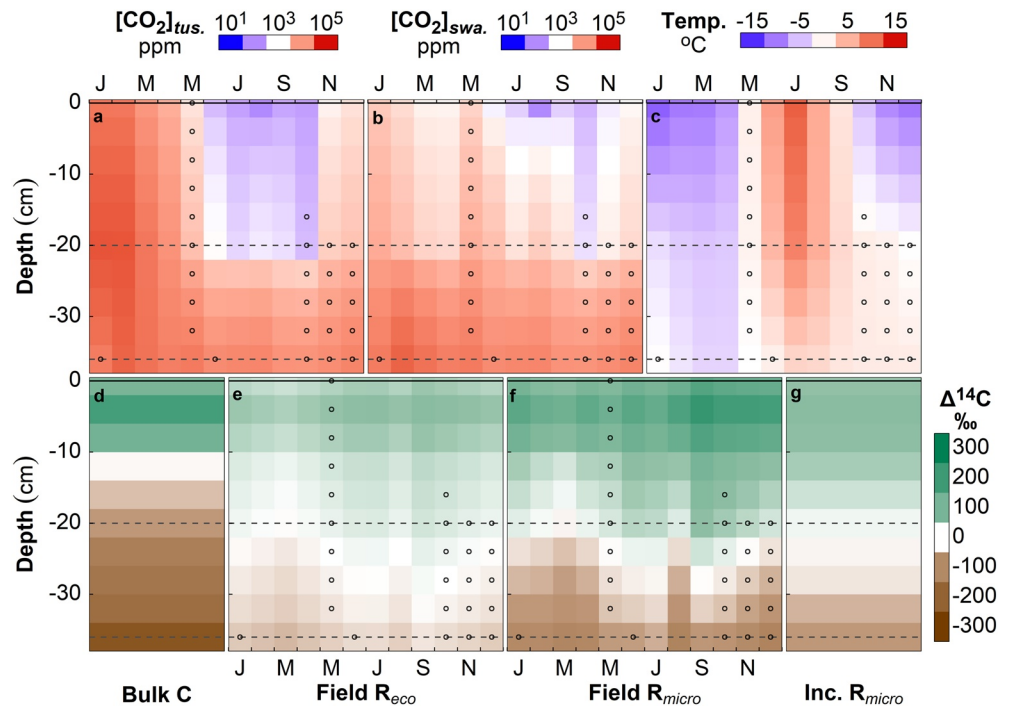
We used our incubation results with the field temperature data to model microbial respiration at each depth.  $R_{\text{micro}}$   $\text{CO}_2$  flux at individual depths were modeled (Table S1, Figures S6a, and S6c in Supporting Information S1) from laboratory soil incubations as an exponentially decaying nonlinear least squares fit ( $R_{\text{NLS}}$  function) of temperature and depth (Equation 4):

$$R_{\text{micro}} = a * \exp(b * \text{Temperature} + c * \text{Depth}) \quad (4)$$

The model was weighted by the inverse square of the incubation flux standard error (error bars in Figure S6a in Supporting Information S1). Model error predictions were calculated from Monte Carlo simulation of confidence intervals ( $R_{\text{predictNLS}} v1.0-4$ ), which allows the construction of more realistic estimates of nonlinear models than a first-order Taylor expansion (simple linearization) approach. This approach may also consider uncertainties in a predictor value, allowing us to propagate the standard error of empirical temperature ( $0.11^\circ\text{C}$  in June at 0 cm to  $0.0009^\circ\text{C}$  in September at  $-20$  cm, Figure S6d in Supporting Information S1) into the model results. This yields  $R_{\text{micro}}$  errors (Figure S6e in Supporting Information S1) which are greatest in the shallow soil during summer (when  $R_{\text{micro}}$  is also maximal), on average  $16\% \pm 4\%$  of  $R_{\text{micro}}$  (mean  $\pm$  sd,  $n = 120$  at monthly resolution).

Summing the column values at each timestep allowed us to estimate the contribution of  $R_{\text{micro}}$  to  $R_{\text{eco}}$  surface emissions for a temporal partitioning of  $f_{\text{micro}}$  versus  $f_{\text{rhizo}}$  (Equation 1). Model details are further described in S: *Non-linear least squares*, and results in Table S1 and Figure S6 in Supporting Information S1. Applying this partitioning to our modeled  $^{14}\text{CO}_2_{\text{eco}}$  at each depth (Equation 2), we calculated  $^{14}\text{CO}_2_{\text{micro}}$ . The column  $^{14}\text{CO}_2$  value (i.e., the surface signature) is the sum of a flux-weighted multi-endmember mixing model at every timestep, where each discrete depth is an endmember. We used Point Barrow air ( $\Delta^{14}\text{C} = 4.2 \pm 3.7$  mean  $\pm$  sd over the sampling period) for  $^{14}\text{CO}_2_{\text{rhizo}}$  (Xiaomei Xu, pers. com.). Considering the fully partitioned column respiration relative to the  $\Delta^{14}\text{C}$  of the available substrate, we finally deduced the fraction and magnitude of  $R_{\text{micro}}$  derived from either permafrost (with bulk soil  $^{14}\text{C}$  at the bottom of the active layer) or recently assimilated soil organic matter (with bulk soil  $^{14}\text{C}$  at the top of the active layer).





**Figure 2.** Upper panels (a–c) show linear interpolations of month of year mean values of environmental data from in situ probes. Surface values for  $[CO_2]$  and temperature were taken from Imnavait Fen EC tower and Toolik EDC, respectively. Bottom panels compare  $\Delta^{14}C$  of (d) bulk soil organic matter, (e) soil  $CO_2$  modeled from (d) and passive sampler observations, (f) microbial  $CO_2$  derived from (e) using temperature-dependent emissions partitioning, and (g) microbial  $CO_2$  from incubations a function of depth (0 cm = top of O horizon) and month of year. *Dashed horizontal lines* show access well inlet depths while *open dots* show zero curtain.

## 4. Results and Discussion

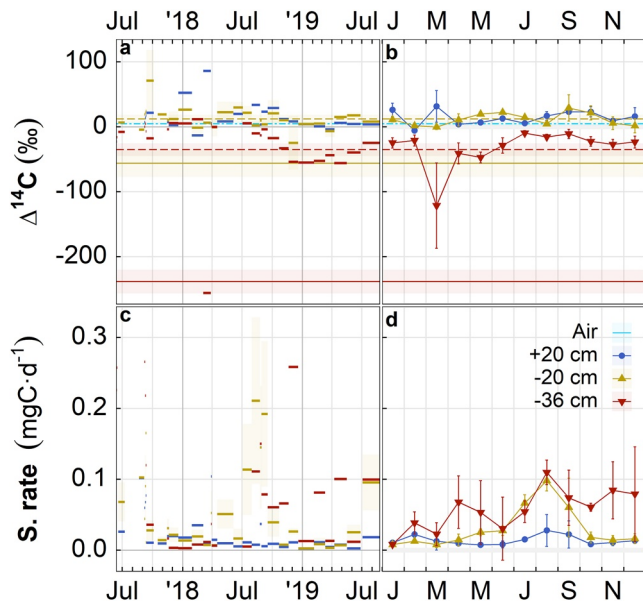
### 4.1. Bulk Soil Properties

The active layer mineral soil is a mottled silt loam (1.0%–19% C, 0.06%–1.1% N) overlain by a 20-cm thick organic layer (21%–46% C, 0.52%–2.8% N) (Figures 1b, S1c, and S1d in Supporting Information S1). As expected for cryoturbated and hummocky terrain, the bulk density increases with depth, yet is highly variable (0.12–2.1 g cm<sup>3</sup> mineral, 0.008–0.38 g cm<sup>3</sup> organic; Figure S1b in Supporting Information S1). Seasonal thaw depth varies from 2 to 73 cm (Figure 1a, 2017–2019), with a maximum in August. Linear models of two local records for August indicate regional active layer deepening (CALM U12 A:  $6.8 \pm 1.4$  cm, 1995–2020; LTER 1989 Moist Acidic Tussock:  $7.1 \pm 3.3$  cm, 1993–2016; prediction changes  $\pm se$ , with both  $p < 0.001$ ), even though no significant trend has been documented for annual air temperatures (Bieniek et al., 2015; Cherry et al., 2014).

The mean age of the bulk organic matter increases with depth from modern ( $\Delta^{14}C \geq 0\text{‰}$ ; organic material deposited/formed after 1950) to approximately 2,000 years BP at about 40 cm depth (Figures 2d and S1e in Supporting Information S1). The bomb-spike is apparent at 5–10 cm depth, indicating organic material formed during the mid-20th century. Consistent with previous work (Lupascu et al., 2018), microbially-respired  $CO_2$  captured by incubation follows a similar trend with depth (Figures 2g and S1e in the Supporting Information S1), but is consistently younger than bulk C (enriched or depleted relative to old ( $\Delta^{14}C < 0\text{‰}$ ) or modern ( $\Delta^{14}C > 0\text{‰}$ ) bulk C, respectively) at the same depths and for the same cores – reflecting preferential microbial consumption of younger organic matter.

### 4.2. Seasonal Patterns in Soil Temperature, Moisture, and $CO_2$

Zero curtain conditions, during which soil temperatures remain near 0°C, were present for 168 days (8 May–26 June, 21 September–17 January from day of year in situ temperature sensor means above 36 cm depth) (Figure 2c).



**Figure 3.** Time series of process-blank corrected (a)  $\Delta^{14}\text{C}$  and (c) sampling rate of soil  $\text{CO}_2$  in graminoid tundra (June 2017–September 2019). Horizontal segments span collection dates for each sample. The horizontal dot-dash line indicates the mean  $\Delta^{14}\text{CO}_2$  in ambient air, dashed lines  $\Delta^{14}\text{CO}_2$  emitted from microbial respiration during laboratory incubations of soils collected within  $\pm 6$  cm of inlets, and solid lines  $\Delta^{14}\text{C}$  of the bulk soil. Shading around lines and segments shows standard error. Panels (b and d) show the same data as (a and c), respectively, averaged by month of year and weighted by sample period within month with standard error bars.

Zero curtain conditions are associated with significant C losses from Arctic ecosystems (Zona et al., 2016) and fall and winter are emerging as critical periods for the annual C budget of the Arctic (Commane et al., 2017; Natali et al., 2019; Oechel et al., 2014). Here we show that the zero curtain remained open through mid-January, confirming previous observations of a 1–2 months longer than expected period of zero curtain conditions and C loss by Arndt et al. (2019).

$\text{CO}_2$  concentrations significantly differed seasonally and with the micro-terrain (Figures 2a and 2b). During the growing season,  $\text{CO}_2$  concentration increased with increasing depth. Concentrations were uniform within the mineral soil, but lower in tussocks than swales, where the soil was denser, moister (Figure S3c in Supporting Information S1), and less exposed to wind. From fall to late winter (January–February),  $\text{CO}_2$  concentrations in the top soil increased, indicating the trapping of  $\text{CO}_2$  under the snowpack as well as a reduction in pore space volume and connectivity. Concentrations were greater in tussocks, where the  $\text{CO}_2$ -depth gradient was reversed. This might indicate lateral flow and accumulation of  $\text{CO}_2$  under tussocks. In spring,  $\text{CO}_2$  concentrations were lower and more uniform, possibly due to the formation of deep cracks, ventilation events, and diminishing biological activity at low temperatures (Figures 2c and S3e in Supporting Information S1).

While the observed  $\text{CO}_2$  concentrations allowed us to validate our  $^{14}\text{CO}_2$  collection rates (Figure 3c), they were not suitable for estimating surface fluxes during periods of snow-cover because gradient methods assume a linear increase of  $\text{CO}_2$  with depth. Thus, we relied on nearby eddy covariance data to estimate surface fluxes (Figure 4).

#### 4.3. Seasonal Patterns in the Age of $R_{\text{eco}}$

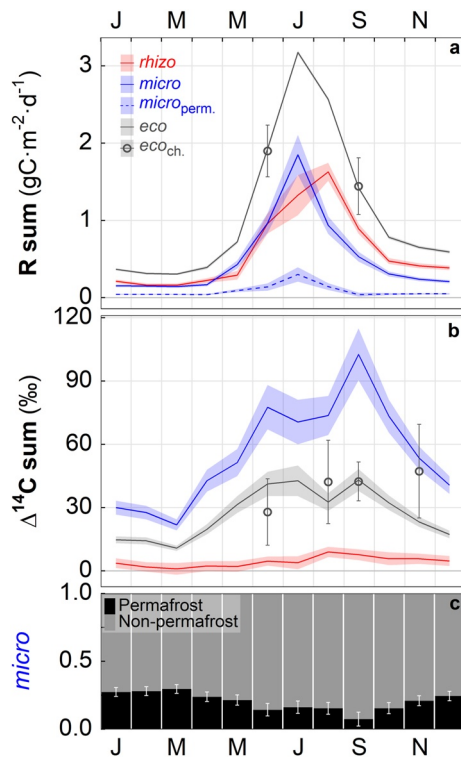
Year-round collection of soil  $\Delta^{14}\text{CO}_2$  revealed a spatial correlation to depth, as well as depth-dependent seasonality (Figures 3a and 3b). These trends are further illustrated using our depth-resolved monthly model of the data (Figures 2e and S8 in Supporting Information S1;  $R^2 = 0.82$ ).  $\text{CO}_2$  captured near the surface is always younger than at depth, with the  $-20$  cm inlet typically capturing bomb-C ( $\Delta^{14}\text{C} > 0$ ) and the  $-36$  cm inlet aged C, which is characteristic of soils developing in stable landscapes (Shi et al., 2020).

The age of soil  $\text{CO}_2$  changes significantly throughout the year (Figure 2e). During the growing-season, the oldest  $\text{CO}_2$  is respired at depth during maximum thaw, temperature (Figure 2c), and  $\text{CO}_2$  production (Figures 2a and 2b), and is significantly younger than bulk soil C. This confirms previous observations (Czimczik & Welker, 2010; Czimczik et al., 2006; Lupascu, Welker, Seibt, et al., 2014) indicating that summer  $\text{CO}_2$  production is fueled to a considerable extent by recent plant assimilates. Moreover soil  $\Delta^{14}\text{CO}_2$  resembles  $\Delta^{14}\text{CO}_2$  produced in incubations of soil segments within  $\pm 6$  cm of each inlet (Figures 2e and 2g). This suggests that short-term incubations capture the typical growing season average of microbial C sources.

From fall and throughout the non-growing season (September–March), soil  $\Delta^{14}\text{CO}_2$  at each depth becomes older (Figure 2e). At 20 cm depth, we recover soil  $\text{CO}_2$  that is  $^{14}\text{C}$ -enriched ( $\Delta^{14}\text{CO}_2 > 0$ ‰) relative to  $\text{CO}_2$  in ambient air at the end of the growing season and becomes  $^{14}\text{C}$ -depleted ( $\Delta^{14}\text{CO}_2 < 0$ ‰) throughout the winter. This pattern is amplified at 36 cm depth. Seasonal trends for  $\text{CO}_2$  captured from the above-surface inlet are similar to those at 20 cm depth.

Our continuous observations uncovered a large seasonal variation in soil  $\Delta^{14}\text{CO}_2$ , with older C pools fueling  $\text{CO}_2$  production during the non-growing season. This shift in  $^{14}\text{CO}_2$ , combined with the increase in soil  $[\text{CO}_2]$  during the zero-curtain period demonstrates that microbial  $\text{CO}_2$  production persists through the fall and into the winter. Thus, our work provides further evidence that non-growing season emissions contribute significantly to the loss of older soil C pools from warming permafrost soils (Commane et al., 2017; Natali et al., 2019).





**Figure 4.** Flux (a) and  $\Delta^{14}\text{C}$  (b) of total surface  $\text{CO}_2$  emissions ( $R_{\text{eco}}$ ) and contributions from the rhizosphere ( $R_{\text{rhizo}}$ ,  $\Delta^{14}\text{C}$  is barrow air) and decomposition of organic matter by heterotrophic microorganisms ( $R_{\text{micro}}$ ). The permafrost-derived portion of  $R_{\text{micro}}$  (c) is also shown as a dashed line in (a). Circles show month of year chamber mean, and all error indicators (bands and bars) show 95% CI.

#### 4.4. Microbial C Sources

Previous studies conducted during the growing season (Czimczik & Welker, 2010; Czimczik et al., 2006; Hicks Pries et al., 2016; Schuur & Trumbore, 2006; Schuur et al., 2009) used incubations to estimate microbial contributions to  $R_{\text{eco}}$  fluxes. Our results (Figures 2f and 2g) show that this approach is a reasonable representation of microbial C sources during the growing season.

However, we find that the range of microbial  $\Delta^{14}\text{CO}_2$  outside the growing season exceeds that observed during our incubation experiments. The age of microbial  $\text{CO}_2$  in the field is frequently older than that of any  $\text{CO}_2$  captured by incubations. In early fall, the presence of older  $\text{CO}_2$  may result from the sampler capturing  $\text{CO}_2$  originating below it and diffusing upwards. As the active layer refreezes, it is more likely that the older  $\text{CO}_2$  originates from the decomposition of locally available, older material. We find that the microbial  $\Delta^{14}\text{CO}_2$  approaches  $\Delta^{14}\text{C}$  of the bulk C (Figure 2d).

Our results demonstrate that short-term incubation experiments do not capture the full range of C sources utilized by soil microorganisms in soils and support the emerging view of a plant-microbe-soil continuum (Högberg & Read, 2006; Sokol et al., 2019) and of dissolved organic matter as a source of microbial C and energy (Roth et al., 2019). Our data suggest that microorganisms rely increasingly on local C sources in fall and winter as they become disconnected from fresh plant exudates and other mobile C sources. Hence, we can expect climate change, via warmer soil temperatures and active layer deepening, to accelerate the loss of older C from permafrost soils during the polar night. This  $\text{CO}_2$  injection of slowly-accumulated soil C pools into the modern atmosphere has the potential to amplify climate warming, leading to more permafrost thaw and more ancient C emissions in the near future.

#### 4.5. Microbial C Contributions to $R_{\text{eco}}$

Ecosystem and microbial respiration in Arctic tundra follow a temperature-dependent seasonal dynamic and are greatest during the growing season, with a maximum in July (Figure 4a). We estimate that microbial contributions ranged from 35% to 60% of  $R_{\text{eco}}$  ( $f_{\text{micro}} = 58\%$ , Figure S7 in Supporting Information S1). The annual column flux-weighted mean  $\Delta^{14}\text{CO}_2$  values of ecosystem and microbial respiration were  $34 \pm 10\text{‰}$  and  $68 \pm 20\text{‰}$  mean  $\pm$  se, respectively (Figure 4b). Column  $\Delta^{14}\text{CO}_2_{\text{eco}}$  was not significantly different from the growing season chamber  $\Delta^{14}\text{CO}_2_{\text{eco}}$  (one sample  $t$ -test  $p$ -value = 0.58, overlapping 95% CI in Figure 4b).

Our continuous observations of soil and ecosystem  $\Delta^{14}\text{CO}_2$  provide unprecedented insight to microbial C sources and enable a more systematic observation of C cycling in Arctic soils by quantifying the loss of ancient permafrost C from thawing permafrost. We find that the oldest (and greatest magnitude of) microbially derived C is produced in mid-summer, but that these emissions are masked by the greater magnitude of respiration in the organic horizons. We show for the first time that non-growing season C emissions are fueled by older C pools, with the greatest relative contribution of permafrost C to microbial (and ecosystem) emissions in fall and winter. Under current conditions, non-growing season microbial emissions accounted for  $18\% \pm 6\%$  (mean  $\pm$  se) of annual soil C emissions,  $22\% \pm 2\%$  of which were derived from permafrost C.

## 5. Conclusions

We combine year-round observations of soil  $\Delta^{14}\text{CO}_2$  in Arctic graminoid tundra with incubation experiments and bulk soil analyses to reveal seasonally dynamic microbial C sources. We show that microbial C emissions during the non-growing season are fueled by older soil C pools and further highlight the polar night as a critical period for climate-vulnerable permafrost C pools.

## Data Availability Statement

Data from the Arctic Observatory Network Imnavait Creek Fen eddy covariance tower (2017–2019) were used to create this manuscript (Euskirchen et al., 2017). Data from Toolik Field Station Environmental Data Center abiotic monitoring were also used (Environmental Data Center Team, 2020). Figures and models were made with R version 4.0.3: <https://cran.r-project.org/bin/windows/base/old/>. The  $R_{\text{micro}}$  model was created with *R nls* function from the base R stats package version 3.6.2. The  $\Delta^{14}\text{C}_{\text{eco}}$  model was created with the R earth package, that builds multivariate regression models (Friedman, 1991). Compiled sensory data and thaw depth observations are available in the Arctic Data Center repositories: <https://doi.org/10.18739/A2Q814S37>; <https://doi.org/10.18739/A2V11VK6H>; and <https://doi.org/10.18739/A2930NV02>.

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