


Drainage enhances modern soil carbon contribution but reduces old soil carbon contribution to ecosystem respiration in tundra ecosystems

Min Jung Kwon^{1,2}  | Susan M. Natali³ | Caitlin E. Hicks Pries^{4,5} |
Edward A. G. Schuur⁶ | Axel Steinhof¹ | K. Grace Crummer⁷ | Nikita Zimov⁸ |
Sergey A. Zimov⁸ | Martin Heimann^{1,9} | Olaf Kolle¹ | Mathias Göckede¹

¹Max Planck Institute for Biogeochemistry, Jena, Germany

²Korea Polar Research Institute, Incheon, South Korea

³Woods Hole Research Center, Falmouth, Massachusetts

⁴Earth Sciences Division, Lawrence Berkeley National Laboratory, Berkeley, California

⁵Department of Biological Sciences, Dartmouth College, Hanover, New Hampshire

⁶Center for Ecosystem Science and Society, and Department of Biological Sciences, Northern Arizona University, Flagstaff, Arizona

⁷Department of Biology, University of Florida, Gainesville, Florida

⁸North-East Science Station, Pacific Institute for Geography, Far-Eastern Branch of Russian Academy of Science, Chersky, Republic of Sakha (Yakutia), Russia

⁹Division of Atmospheric Sciences, Department of Physics, Helsinki University, Helsinki, Finland

Correspondence

Min Jung Kwon, Max Planck Institute for Biogeochemistry, Jena, Germany.
Email: minjung.kwon86@gmail.com

Present Address

K. Grace Crummer, Institute for Sustainable Food Systems, University of Florida, PO Box 110570, Gainesville, Florida 32611

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Abstract

Warming temperatures are likely to accelerate permafrost thaw in the Arctic, potentially leading to the release of old carbon previously stored in deep frozen soil layers. Deeper thaw depths in combination with geomorphological changes due to the loss of ice structures in permafrost, may modify soil water distribution, creating wetter or drier soil conditions. Previous studies revealed higher ecosystem respiration rates under drier conditions, and this study investigated the cause of the increased ecosystem respiration rates using radiocarbon signatures of respired CO₂ from two drying manipulation experiments: one in moist and the other in wet tundra. We demonstrate that higher contributions of CO₂ from shallow soil layers (0–15 cm; modern soil carbon) drive the increased ecosystem respiration rates, while contributions from deeper soil (below 15 cm from surface and down to the permafrost table; old soil carbon) decreased. These changes can be attributed to more aerobic conditions in shallow soil layers, but also the soil temperature increases in shallow layers but decreases in deep layers, due to the altered thermal properties of organic soils. Decreased abundance of aerenchymatous plant species following drainage in wet tundra reduced old carbon release but increased aboveground plant biomass elevated contributions of autotrophic respiration to ecosystem respiration. The results of this study suggest that drier soils following drainage may accelerate decomposition of modern soil carbon in shallow layers but slow down decomposition of old soil carbon in deep layers, which may offset some of the old soil carbon loss from thawing permafrost.

KEYWORDS

carbon source partitioning, drying experiment, ecosystem respiration, permafrost, radiocarbon, soil hydrology

1 | INTRODUCTION

Arctic ecosystems are warming (Huang et al., 2017; Serreze et al., 2000), and this trend is anticipated to continue into the future (Kirtman et al., 2013). Warmer Arctic ecosystems could destabilize the large amount of soil carbon currently stored in permafrost soils (Hugelius et al., 2014), releasing carbon into the atmosphere and accelerating climate change. For accurate predictions of global climate change trajectories, it is essential to estimate the magnitude of the current carbon release as well as understand the causes and underlying mechanisms that govern the responses of permafrost ecosystems to warming.

Soil moisture is likely to undergo drastic changes due to feedback processes with temperature: (1) warmer temperature enhances evapotranspiration, making soil drier, and (2) warming-induced permafrost thaw and ground ice melt, and the subsequent topographical changes modify soil water distribution, making some areas wetter and others drier depending on the original local geomorphology and ground ice distribution (Loranty et al., 2018; Schuur & Mack, 2018). Under current conditions, large areas of Arctic ecosystems are inundated in spite of low precipitation because permafrost below the seasonally thawed soil layers limits drainage. Thawing of ice-rich permafrost due to increasing air and soil temperatures results in ground subsidence and accumulation of melt water, making the soil wetter (Abbott & Jones, 2015; Jorgenson, Shur, & Pullman, 2006; O'Donnell et al., 2012; Osterkamp et al., 2009); but permafrost thaw followed by lateral drainage can cause drier conditions in large parts of permafrost regions (Avis, Weaver, & Meissner, 2011; Lawrence, Koven, Swenson, Riley, & Slater, 2015; Liljedahl et al., 2016). With large spatiotemporal variation in soil hydrology upon permafrost thaw and ice melt, our research focuses on the drying effects on ecosystem respiration (R_{eco}) in one moist and one wet tundra ecosystem. The experiment in moist tundra—which has no standing water for most of the growing season but soils of which are saturated—is to mimic drier conditions due to enhanced evapotranspiration in a warming scenario, while the other experiment in wet tundra—which has water tables close to soil surface (<30 cm) for most of the growing season—is to mimic water drainage following ice-wedge degradation. These two experiments represent a low and a high degree of drying scenarios in warmer Arctic ecosystems.

Drying of tundra ecosystems has been observed to increase the rates of R_{eco} (Kwon et al., 2016; Natali et al., 2015; Oechel, Vourlitis, Hastings, Ault, & Bryant, 1998) because removing excess soil water and increasing oxygen diffusion into soils enhance

the rates of both heterotrophic (Skopp, Jawson, & Doran, 1990) and autotrophic (Chapin, Matson, & Vitousek, 2012) respiration (R_h and R_a). In addition, intensive drying can enhance R_h rates in deep soil layers, leading to the loss of older carbon that had previously been stabilized by cold and wet conditions (Estop-Aragonés et al., 2018). Because of secondary drainage effects, such as modification of vegetation communities and soil thermal regimes following changes in water availability, the net impact of hydrological changes on the permafrost carbon cycle is still uncertain. For example, wetland plant species that possess aerenchyma tissues stimulate decomposition in deep soils by supplying oxygen through roots (Wolf, Drake, Erickson, & Megonigal, 2007), and decrease in their abundance due to drying may reduce decomposition rates in deep soil layers and the transport of old CO_2 to the atmosphere through aerenchyma. To better understand how the rates and sources of R_{eco} respond to drier conditions, we used natural abundance radiocarbon (^{14}C) to partition R_{eco} into autotrophic and two heterotrophic sources (surface and deep soils) from drying manipulation experiments in moist and wet tundra permafrost ecosystems.

2 | MATERIALS AND METHODS

2.1 | Site description

2.1.1 | Healy (moist tundra)

The Drying Permafrost Experimental Heating Research (DryPEHR) site is located in moist tundra at Eight Mile Lake in Healy, Alaska (63.88 N, 149.23 W; Natali et al., 2015). Mean water table depth (WTD; measured as distance from the soil/moss surface to the top of the water table) is ~23 cm and the maximum thaw depth (TD) at the end of the summer season is ~59 cm. Annual mean air temperature (1977–2012) is -1°C , with monthly mean air temperatures ranging from -17°C in January to $+15^\circ\text{C}$ in July, with average growing-season (June to September) precipitation of 232 mm (Western Regional Climate Center, station ID 503585). Organic soil layers of 35–45 cm thickness lie on top of mineral soil layers (Schuur et al., 2009). Dominant plant species include the tussock-forming sedge, *Eriophorum vaginatum*, and shrubs, for example, *Vaccinium uliginosum* (Schuur et al., 2009).

Six blocks of control and drying plots were established in 2011 (Natali et al., 2015). Water was drained using an automated pump system. In addition, a warming treatment (soil warming by adding snow during the winter and then removing it in spring, and air warming by open-top chambers during the growing season) was applied

in combination with drying, resulting in four treatments: control, drained, warmed, and drained + warmed (Table 1). Volumetric water content (VWC) in the top 20 cm of drained plots was decreased by 2%–4% compared to the control plots in August 2012 and 2013 (Supplementary Table S1). Warming treatment increased VWC by 6%–8% due to ground subsidence, lowering the soil surface closer to the water table (Supplementary Table S1; Natali et al., 2015).

2.1.2 | Chersky (wet tundra)

The Chersky study site is located on a floodplain of the Kolyma River near Chersky in northeastern Siberia (68.62 N, 161.35 E). Annual mean air temperature (1906–2013) is -11°C with monthly mean air temperature ranging from -33°C in January to $+13^{\circ}\text{C}$ in July (berkeleyearth.org, station ID 169,921). Average growing-season precipitation for the same period is 115 mm. Organic soil layers of 15–20 cm thickness have accumulated on the top of mineral soil layers (Kwon et al., 2016). The sedge, *Eriophorum angustifolium*, and tussock-forming sedges, *Carex appendiculata* and *C. lugens*, are the dominant plant species (Kwon et al., 2016). Spring floods occur due to snowmelt at the site and in the surrounding river water basin, resulting in an increase of the water level of up to 50 cm above the soil surface in late May or early June. Water level gradually decreases until mid-July as water drains to the nearby rivers.

Experimentally drained areas achieved a water table that was 20 cm deeper than natural conditions in summer 2013 due to a surrounding drainage ditch that was constructed in fall 2004 and which encircled a ~ 200 m diameter area (Merbold et al., 2009). After heavy rains, this difference in water table was temporarily reduced to 6 cm due to delayed drainage (Supplementary Table S1). The drained and control areas are approximately 600 m away from each other and each have 10 plots spaced along transects in ca. 25 m intervals (Table 1).

2.2 | Environmental monitoring

In Healy, VWC was continuously measured at 0–20 cm depth at each plot and recorded half-hourly (CS615 & CS616, Campbell Scientific, Logan, UT, USA). WTD and TD were measured once a week at each plot. Soil temperatures were measured at 5, 10, 20, and 40 cm depths at each plot and recorded half-hourly using constantan-copper thermocouples. For more detailed information, refer to Natali et al. (2015).

TABLE 1 Site setup in Healy and Chersky

| Site | Treatment | Number of plots |
|---------|------------------|-----------------|
| Healy | Control | 6 |
| | Drained | 6 |
| | Drained + Warmed | 6 |
| | Warmed | 6 |
| Chersky | Control | 10 |
| | Drained | 10 |

In Chersky, WTD and TD, as well as soil temperatures at 5, 15, 25, and 35 cm depths were measured and recorded (Th3-s, UMS, Germany) 1 to 3 times a week at each plot. Soil moisture sensors were out of order in 2014, and VWC was estimated using a linear regression model between VWC and WTD from the period when sensors operated ($R^2 = 0.78$, $p < 0.00$). Soil temperatures at 4, 16, and 64 cm depths were measured continuously at four plots, and recorded half-hourly.

In Chersky, *E. angustifolium* cover was measured using the point-intercept method. CO_2 and CH_4 transport rates through *E. angustifolium* were quantified by including a single plant into a cylindrical dark chamber (\varnothing 10 cm \times 50 cm height) and sealing the base with a gas-tight cap that enclosed the plant. The concentrations of $[\text{CO}_2]$ and $[\text{CH}_4]$ were recorded using an Ultra-Portable Greenhouse Gas Analyzer (Los Gatos Research, San Jose, CA, USA; Kwon et al., 2017).

2.3 | Radiocarbon signatures of R_{eco}

In August 2012 and 2013 at Healy, 10 L dark chambers were placed over polyvinyl chloride collars (\varnothing 25.4 cm \times 10 cm height). Headspace CO_2 was scrubbed using soda lime at the approximate rate of R_{eco} in order to maintain a constant CO_2 concentration. The headspace air was scrubbed until a five-chamber volume of air was replaced, then collected with molecular sieves (Alltech 13x, Alltech Associates, Deerfield, IL, USA). CO_2 was desorbed from these molecular sieves by heating them at 625°C (Bauer, Williams, & Druffel, 1992). Extracted CO_2 was purified using liquid nitrogen on a vacuum line and the remaining CO_2 was reduced to graphite by Fe reduction in H_2 . The graphite was sent to the UC Irvine W. M. Keck Carbon Cycle Accelerator Mass Spectrometry Laboratory for radiocarbon analysis. $\Delta^{14}\text{C}$ data were reported after normalization for $\delta^{13}\text{C}$ and correction for the decay between the year 1950 and the measurement time (Equation 1):

$$\Delta^{14}\text{C} (\text{‰}) = \left[F^{14}\text{C} \times e^{\frac{y-1950}{8267}} - 1 \right] \times 1000 \quad (1)$$

where $F^{14}\text{C}$ is the Fraction Modern as given by Reimer, Brown, and Reimer (2004) and y is the year of sampling. R_{eco} (net ecosystem exchange when photosynthetically active radiation is smaller than $5 \mu\text{mol m}^{-2} \text{s}^{-1}$) was continuously measured every 1.5 hr using an automated chamber system (LI-820, LICOR Corp., Lincoln, NE, USA). Data were gap-filled when R_{eco} was not measured and cumulative R_{eco} was estimated by using an exponential relationship between soil temperature and R_{eco} rates (Natali et al., 2015). Continuous R_{eco} rates were measured immediately adjacent of ^{14}C sampling plots (~ 1 m apart) that generally have similar moisture conditions and representative vegetation. Further information on the R_{eco} measurements at Healy can be found in Natali et al. (2015).

In August 2014 at Chersky, a dark chamber (300 L) was placed on the polyvinyl chloride collar, and the concentrations of CO_2 inside the chamber were measured using an Ultra-Portable Greenhouse Gas Analyzer (Los Gatos Research, San Jose, CA, USA). R_{eco} rates were determined and headspace CO_2 was scrubbed using soda lime at a rate

similar to that of R_{eco} to keep the headspace CO_2 concentration constant. This scrubbing replaced a quarter of the headspace CO_2 . Then, headspace gas was circulated through molecular sieves (Alltech 13x, Alltech Associates, Deerfield, IL, USA) to collect 1/8 mmol of CO_2 . CO_2 was desorbed from molecular sieves by heating them at 500°C (Bauer et al., 1992). Extracted CO_2 was purified using the same procedures as described in the previous paragraph for the Healy samples. Radiocarbon analysis was carried out at the ^{14}C analytics laboratory at the Max Planck Institute for Biogeochemistry in Jena, Germany (Steinhof, Altenburg, & Machts, 2017). Continuous R_{eco} was estimated using an exponential relationship between air temperature and measured R_{eco} and continuously measured air temperature, and summed to calculate cumulative R_{eco} (Kwon et al., 2016).

To correct for atmospheric contamination, $\Delta^{14}\text{C}$ values were adjusted for those of atmospheric CO_2 by using of $\delta^{13}\text{C}$ values with a two-pool mixing model (Schoor & Trumbore, 2006). At Healy, $\delta^{13}\text{C}$ values were not measured in the years 2012 and 2013, and the average $\delta^{13}\text{C}$ values of control plots from the previous years (2009–2011) were used instead (Hicks Pries, Schoor, Natali, & Crummer, 2016).

2.4 | Radiocarbon end-member signatures of R_{eco} sources

For $\Delta^{14}\text{C}$ of R_{h} sources in Healy, incubation data from the plots located within the footprint of the experiment used to determine heterotrophic end-members. To measure $\Delta^{14}\text{C}$ of R_{h} sources, soils from 0–25 cm depths were taken from three control plots in July 2009 and in August 2010. It was assumed that carbon stock and composition in control plots in 2009 and 2010 were not significantly different from those in 2012 and 2013. Roots with a diameter of >1 mm were removed, and soil samples separated into three increments (0–5, 5–15, and 15–25 cm) were preincubated at room temperature for 5 days so that respired CO_2 represented decomposition of soil organic carbon rather than root exudates, remaining roots, and mycorrhizae (Högberg et al., 2001). Soils of deeper layers (25–75 cm) were taken in May 2009 and cut into five sections in 10 cm intervals. Roots with a diameter of >1 mm were removed and soils were incubated at room temperature for 10 days to stabilize microorganisms after thaw. R_{h} rates of each depth were measured, jar headspace was scrubbed using soda lime, and soils were incubated under aerobic conditions for 12–72 hr to accumulate 1/8 mmol of CO_2 . Then $\Delta^{14}\text{C}$ was analyzed as described in the previous section.

At Chersky, six soil cores down to the current TDs were taken from each transect in July 2014, and two cores were combined to produce three sets per transect. Each set of cores was divided into 3–4 increments at 7.5 cm intervals. Roots with a diameter of >1 mm were removed, and soils were transferred into beakers and then into 1 L glass jars with distilled water to maintain constant moisture. Soils were preincubated at room temperature for 5 days to minimize the effects of respiration by root exudates, remaining roots, and mycorrhizae (Högberg et al., 2001). The headspace air was scrubbed using soda lime, and then incubated at room temperature under aerobic conditions. R_{h} rates of each depth were measured at the beginning of the incubation, and incubation lasted up to 4 weeks until the

amount of carbon accumulated in the jar reached 1/8 mmol of CO_2 . Then $\Delta^{14}\text{C}$ was analyzed as described in the previous section.

To obtain $\Delta^{14}\text{C}$ of autotrophic end-members ($\Delta^{14}\text{C}_{\text{Ra}}$; aboveground and belowground combined) both for Healy and Chersky, we added 1‰ to the $\Delta^{14}\text{C}$ values of atmospheric CO_2 measured at each site because $\Delta^{14}\text{C}_{\text{Ra}}$ have been shown to be on average 1‰ more enriched compared to those of atmospheric CO_2 (Hicks Pries, Schoor, & Crummer, 2013). Though dominant vegetation species in Chersky are different from those in Healy, both sites are dominated by the same genera of *Carex* and *Eriophorum* species—sedges that respire recent carbon (Hicks Pries et al., 2013), as opposed to woody plants whose roots respire a mixture of young and old carbon (Czimczik, Trumbore, Carbone, & Winston, 2006; Schoor & Trumbore, 2006).

2.5 | Source partitioning

For the partitioning, mean and standard deviation of each source's $\Delta^{14}\text{C}$ were calculated. We divided soil samples into two categories, surface soil (0–15 cm) and deep soil (below 15 cm from the ground surface and down to frozen soil at the time of gas sampling), because respired CO_2 from these depth increments have distinctly different ages. $\Delta^{14}\text{C}$ of surface soils ($\Delta^{14}\text{C}_{\text{surface}}$; modern soil carbon) were enriched due to the “bomb effect” since the 1960s, while $\Delta^{14}\text{C}$ of deep soils ($\Delta^{14}\text{C}_{\text{deep}}$; old soil carbon) were depleted. To calculate $\Delta^{14}\text{C}_{\text{surface}}$ and $\Delta^{14}\text{C}_{\text{deep}}$ from a single core, we averaged $\Delta^{14}\text{C}$ values of each soil depth weighted by its respiration rate that was corrected for average monthly soil temperature using a Q_{10} value of 2.5 (Bracho et al., 2016; Hicks Pries et al., 2013, 2015). Mean and standard deviation were acquired from soil core replicates (Supplementary Table S2). The standard deviations of $\Delta^{14}\text{C}_{\text{Ra}}$ were obtained from plant incubations conducted in Hicks Pries et al. (2013; Supplementary Table S2).

We used Stable Isotope Analysis in R (SIAR, cran.r-project.org/web/packages/siar/index.html) to partition $\Delta^{14}\text{C}$ of R_{eco} to its three sources, that is, surface soil, deep soil, and autotrophs (Parnell, Inger, Bearhop, & Jackson, 2010). The partitioning was performed for each plot (each $\Delta^{14}\text{C}$ of R_{eco} value) separately using noninformative priors. The SIAR method uses the Markov Chain Monte Carlo method to produce probability distributions of each source's contribution. To estimate the contributions of surface soil, deep soil, and autotrophs to R_{eco} , the following two equations were used:

$$\Delta^{14}\text{C}_{\text{Reco}} = f_{\text{surface}} \cdot \Delta^{14}\text{C}_{\text{surface}} + f_{\text{deep}} \cdot \Delta^{14}\text{C}_{\text{deep}} + f_{\text{Ra}} \cdot \Delta^{14}\text{C}_{\text{Ra}} \quad (2)$$

$$1 = f_{\text{surface}} + f_{\text{deep}} + f_{\text{Ra}} \quad (0 < f_{\text{surface}}, f_{\text{deep}}, f_{\text{Ra}} < 1) \quad (3)$$

where $\Delta^{14}\text{C}$ s are $\Delta^{14}\text{C}$ values of R_{eco} and each source, and f is the fractional contribution of each source to R_{eco} . We estimated the mean f -values based on 10,000 possible f -values for source contributions (Supplementary Fig. S1). Using one type of isotope to constrain three unknown f -values may produce uncertain results, but the range of uncertainty strongly depends on the similarity of source isotopic signatures (Phillips & Gregg, 2003). In this study, the three source signatures used in partitioning were distinct at both sites

(Supplementary Table S2), and sensitivity tests revealed robust results (Phillips & Gregg, 2003).

2.6 | Data analysis

An analysis of variance (ANOVA) and a *t* test were performed to investigate whether drying and warming treatment significantly influenced $\Delta^{14}\text{C}_{\text{Reco}}$, as well as contributions of surface soil, deep soil, and autotrophs to R_{eco} at Healy and at Chersky, respectively. For Healy, the ANOVAs had treatments (drying and warming) and years as fixed effects, with blocks as random effects. When significant differences were found, Tukey's post hoc tests followed.

Because the magnitude of the drying treatment effects varied across plots at Healy, we also carried out multiple regression mixed effects model in R. This additional analysis also allowed us to examine the environmental drivers of $\Delta^{14}\text{C}_{\text{Reco}}$ and source contributions. $\Delta^{14}\text{C}_{\text{Reco}}$, the contributions of three sources, and environmental variables were normally distributed after excluding two outlier data points that had $\Delta^{14}\text{C}_{\text{Reco}}$ less than -50% (out of range of mean $\pm 3\text{SD}$). To avoid including variables with large collinearity, a variance inflation factor was checked (cutoff: 5). The predictor

variables included year, treatment, VWC, WTD, TD, and soil temperatures at 5, 10, 20, and 40 cm depths. Among all the variables, significant explanatory variables were selected, including interactions of any two variables, using the leaps package in R (leaps, cran.r-project.org/package=leaps). With these selected variables, the structure of random factors, that is, blocks, was chosen, and then the best fitting set of predictors were selected using a backward selection method (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). The residuals were visually checked to ensure that assumptions of normality and homoscedasticity were met and there were no unexplained patterns in the data. All data analyses were carried out in R version 3.3.2 (R Development Core Team, 2013).

3 | RESULTS

Following drainage at Chersky, the water table decreased by approximately 20 cm in summer of 2013 (*t* test; $t = -4.55$, $p < 0.001$), but this difference was reduced to 6 cm at the time of gas samplings in August 2014 due to several heavy rain days in late July and delayed drainage (*t* test; $t = -1.60$, $p = 0.16$; Supplementary Table S1). The oldest $\Delta^{14}\text{C}_{\text{Reco}}$ (lower abundance of ^{14}C ; depleted $\Delta^{14}\text{C}$) was observed in the

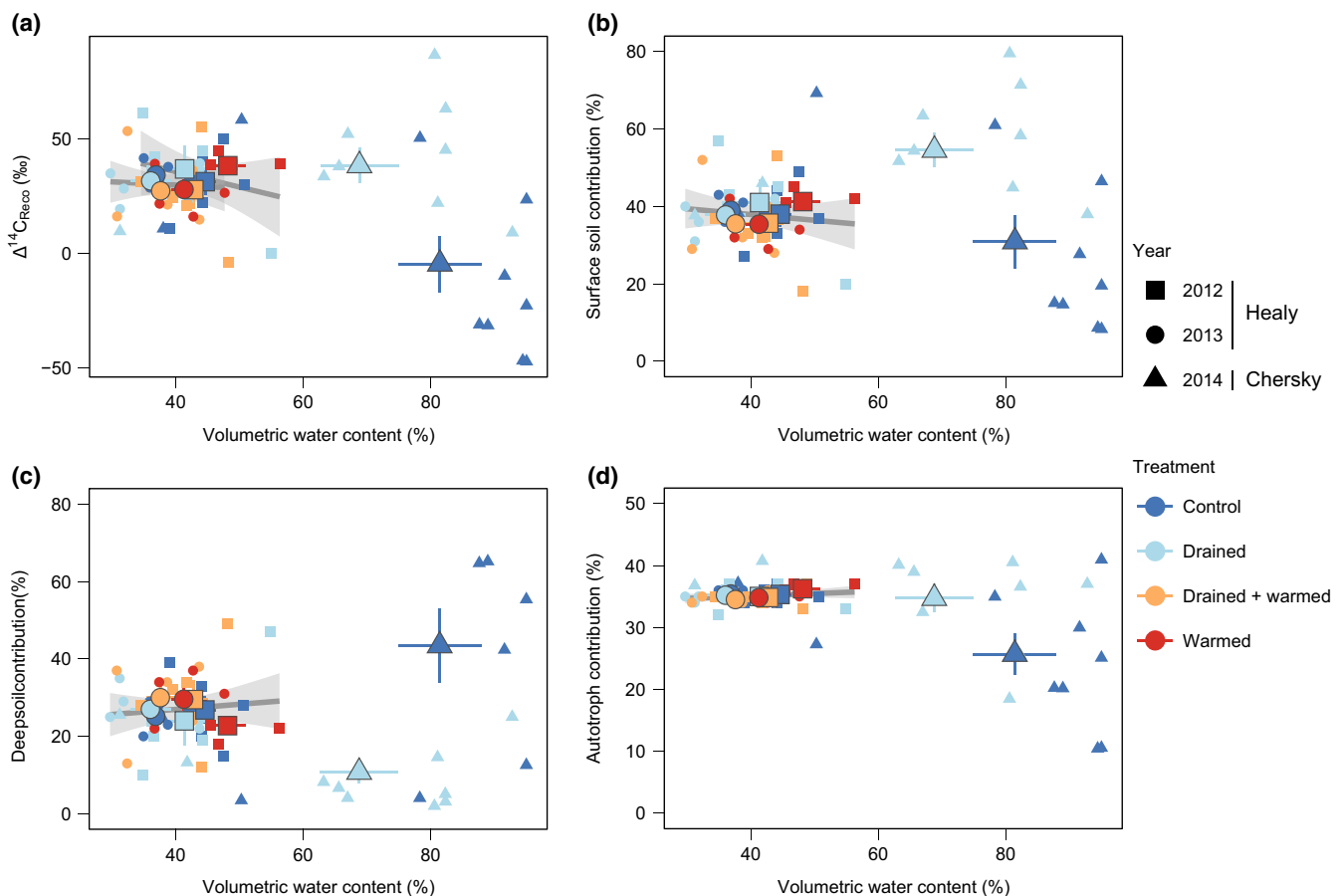


FIGURE 1 $\Delta^{14}\text{C}_{\text{Reco}}$ and contributions of surface soil (0–15 cm; modern soil carbon), deep soil (below 15 cm up to permafrost table; old soil carbon), and autotrophs to R_{eco} . (a) $\Delta^{14}\text{C}_{\text{Reco}}$ (mean \pm SE, large symbols) and individual measurements (small points) of each year and site. Contributions of (b) surface soil, (c) deep soil, and (d) autotrophs to R_{eco} (mean \pm SE). Linear regression lines and confidence intervals for Healy were drawn by year because the absolute $\Delta^{14}\text{C}_{\text{Reco}}$ values were affected by atmospheric $\Delta^{14}\text{C}-\text{CO}_2$, which decreases over time

control plots in Chersky, where soils were wettest (Figure 1). $\Delta^{14}\text{C}_{\text{Reco}}$ in the drained plots became more enriched compared to those in the control plots (t test; $t = -2.97$, $p < 0.01$; Figure 1a) due to increased contributions of surface soil (modern soil carbon) and autotrophs to R_{eco} (t test; surface soil, $t = -2.88$, $p < 0.05$; autotrophs, $t = -2.23$, $p < 0.05$; Figure 1b,d), and decreased contributions of deep soil (old soil carbon; t test; $t = 3.26$, $p < 0.01$; Figure 1c).

There was no significant difference among treatments at Healy in $\Delta^{14}\text{C}_{\text{Reco}}$ (ANOVA; all showed $p > 0.05$) or in the contributions of each source to R_{eco} (ANOVA; all showed $p > 0.05$). However, when soil moisture was treated as a continuous variable, drier soil conditions led to more enriched $\Delta^{14}\text{C}_{\text{Reco}}$ at Healy (Figure 1a, Supplementary Table S3). Similarly, the contribution of each source to R_{eco} was also linked to variations in VWC: VWC was negatively correlated with contributions of surface soil to R_{eco} , while there was a positive trend between VWC and deep soil contributions (Figure 1b–d, Supplementary Table S4).

Soil water content was increased and TDs were deepened as a result of the warming treatment at Healy (Supplementary Table S1), and these changes depleted $\Delta^{14}\text{C}_{\text{Reco}}$, that is, more old carbon was released (Supplementary Table S3 & S4). However, when warming was combined with drying, warming effects were partially suppressed: under the same VWC conditions drying treatment showed larger contributions of surface soil but smaller contributions of deep soil to R_{eco} in comparison to drying and warming treatment (mixed effects model; surface soil, increase in the intercept from 47.1 to 57.8; deep soil, decrease in the intercept from 19.6 to 6.5).

Besides water table, *E. angustifolium* cover at Chersky that showed difference between treatments (t test; $t = 2.13$, $p < 0.05$) significantly correlated with $\Delta^{14}\text{C}_{\text{Reco}}$ (Spearman's correlation; $r_s = -0.76$, $p < 0.001$) and the contributions of deep soil to R_{eco} (Spearman's correlation; $r_s = 0.75$, $p < 0.001$; Figure 2). Water table and *E. angustifolium* cover were correlated as well (Spearman's correlation; $r_s = 0.72$, $p < 0.001$). We did not observe a considerable change in plant biomass of dominant species or normalized difference vegetation index (NDVI) by VWC in Healy (mixed effects models; all showed $p > 0.5$) and no significant modifications in contributions of R_a to R_{eco} due to VWC variations (mixed effects models; $p > 0.5$; Figure 1d; Supplementary Table S4).

In Healy, soils were warmer at the surface (mixed effects model; 5 cm; 2012, $p < 0.001$; 2013, $p < 0.001$; 10 cm; 2012, $p < 0.001$; 2013, $p < 0.001$; 20 cm; 2012, $p = 0.09$; 2013, $p < 0.001$; Figure 3a–b) and colder in deeper layers (mixed effects model; 40 cm; 2012, $p < 0.001$; 2013, $p < 0.01$; Figure 3a–b) as soils were drier. Changes in water table at Chersky also showed similar trends: warmer at shallow soil layers (mixed effects model; 5 cm; $p = 0.08$; Figure 3c) but colder in deeper soil layers (mixed effects model; 15 cm; $p < 0.05$; 25 cm; $p < 0.01$; 35 cm; $p < 0.01$; Figure 3c).

Drier conditions increased R_{eco} rates in August at Healy (Supplementary Table S5; Figure 4a–b). We estimated respiration rates of each source by multiplying R_{eco} rates by the source proportions, and found that drier conditions were associated with

increasing contributions of modern soil carbon and autotrophs while decreasing contributions of deep soil carbon (Supplementary Table S6; Figure 4a–b). Similarly, drainage in the wet tundra ecosystem increased R_{eco} rates by 15% in August although several heavy rain days offset the difference in water table between the control and the drained plots (Figure 4c). The increase in R_{eco} was due to enhanced decomposition of modern soil carbon in shallow layers and autotrophic respiration (t test; surface soil, $t = -4.68$, $p < 0.001$; autotrophs, t test; $t = -3.19$, $p < 0.01$; Figure 4c) in spite of the reduced decomposition rates of deep soil carbon in the dried plots (t test; $t = 3.75$, $p < 0.01$; Figure 4c).

4 | DISCUSSION

4.1 | Effects of drier soil conditions

Drying, resulting in a decrease in soil water content, in moist and wet tundra affected the age of respired CO_2 to the atmosphere. Due to vertical drainage of water within soil layers and the presence of permafrost belowground, the extent of changes in soil water content was larger in surface soil layers than in deep soil layers close to the permafrost table. As a result of more aerobic conditions especially in shallow soil layers, the decomposition rates of these layers increased (Lee, Schuur, Inglett, Lavoie, & Chanton, 2012; Schädel et al., 2016), where modern soil carbon is abundant, and, thus, the age of respired CO_2 became younger. Contributions of R_a to R_{eco} also increased by drier soil conditions because when excess water is removed from moist or wet soils, plant species that tolerate waterlogged conditions but favor unsaturated conditions photosynthesize and respire more actively (Chapin et al., 2012; Saltmarsh, Mauchamp, & Rambal, 2006). The effects of drying on $\Delta^{14}\text{C}_{\text{Reco}}$ and the contributions of each source to R_{eco} at Healy were not as pronounced as at Chersky because of an originally less wet condition than Chersky, a less severe drying treatment, and overlapping ranges of soil moisture conditions among treatments due to heterogeneous micro-topography of the site. Nevertheless, drier soil conditions—variations in VWC—showed

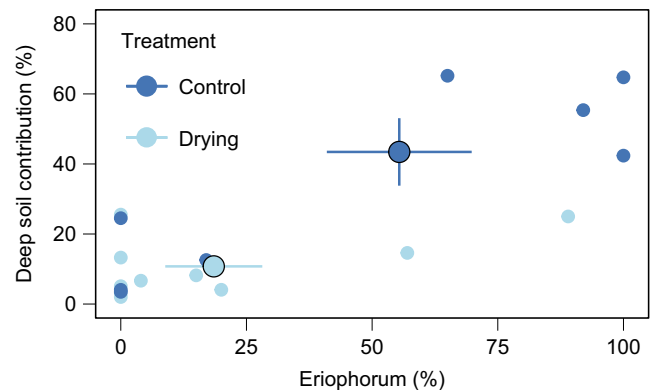


FIGURE 2 Contributions of deep soil (below 15 cm up to permafrost table; old soil carbon) at Chersky in relation to *Eriophorum angustifolium* cover, which is abundant in wet areas (mean \pm SE)

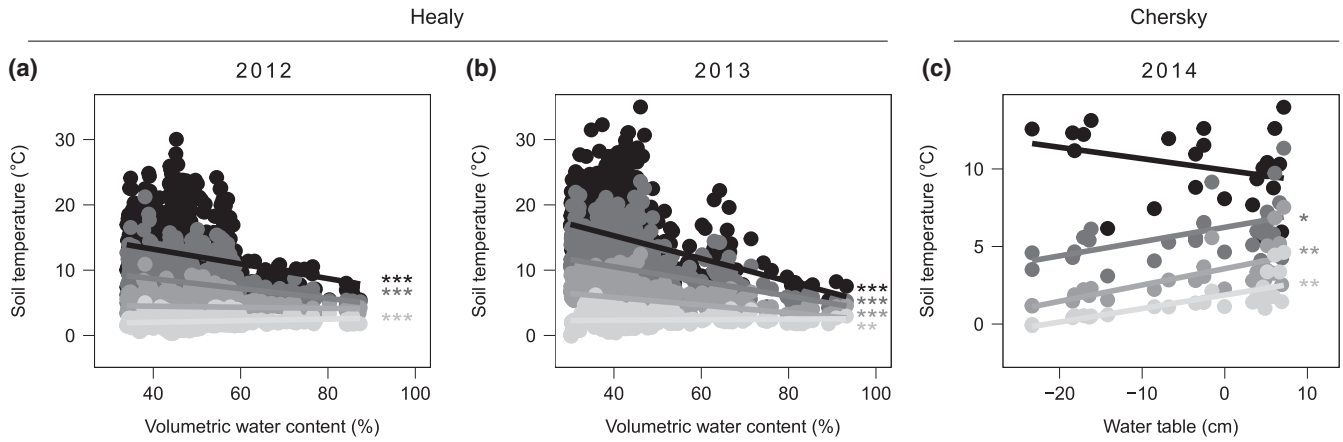


FIGURE 3 Relationships between volumetric water content (%) at 0–20 cm and soil temperature (a, b) at 5, 10, 20 and 40 cm at Healy or (c) water table (cm) and soil temperature at 5, 15, 25, and 35 cm at Chersky, with darker shading representing shallower soil depths. Water table was described relative to the soil surface, with values >0 cm denoting water standing above the soil surface. Statistical significance of mixed effects models is presented with asterisks (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$) next to regression lines. Data are from 12:00–18:00 LT in August each year and averaged on a daily basis

larger contribution of modern soil carbon in shallow soil layers to R_{eco} due to more aerobic conditions, which is well aligned with the results from Chersky.

Warming affected $\Delta^{14}\text{C}_{\text{Reco}}$ and the source contributions, that is, more depleted $\Delta^{14}\text{C}_{\text{Reco}}$ and reduced contributions of modern soil carbon, as reported in previous studies (Hicks Pries et al., 2013; Schuur et al., 2009) through ground subsidence and wetter soil conditions (Jorgenson et al., 2006; O'Donnell et al., 2012; Osterkamp et al., 2009). However, when warming was combined with drying, drying offset warming effects by removing excess soil water in surface soil. The net effects of warming and drying will depend on the intensity of each phenomenon, but the results of this study emphasize that warming and re-distribution of soil water (drying or wetting) due to warming in permafrost regions alter sources of respired CO_2 , and have the potential to counterbalance one another's effects.

4.2 | Effects of soil temperature changes

If drainage only converted deep soil conditions from anaerobic to aerobic, decomposition rates of older soil carbon in these layers would have been enhanced as well because soil carbon in deep soil layers, even in mineral soils or permafrost soils, have been shown to be as easily decomposable as organic soil carbon in shallow layers under aerobic conditions (Knoblauch, Beer, Sosnin, Wagner, & Pfeiffer, 2013; Schädel et al., 2014). However, the proportion of deep soil contribution decreased, while that of surface soil contribution increased following drainage, partly a result of drying effects on soil temperature. Both heat capacity (Abu-Hamdeh, 2003; Lakshmi, Jackson, & Zehrhuhs, 2003) and thermal conductivity (Abu-Hamdeh, 2003) of organic soil decrease with water content. Because of this, shallow soil layers were warmed during the daytime, but the heat

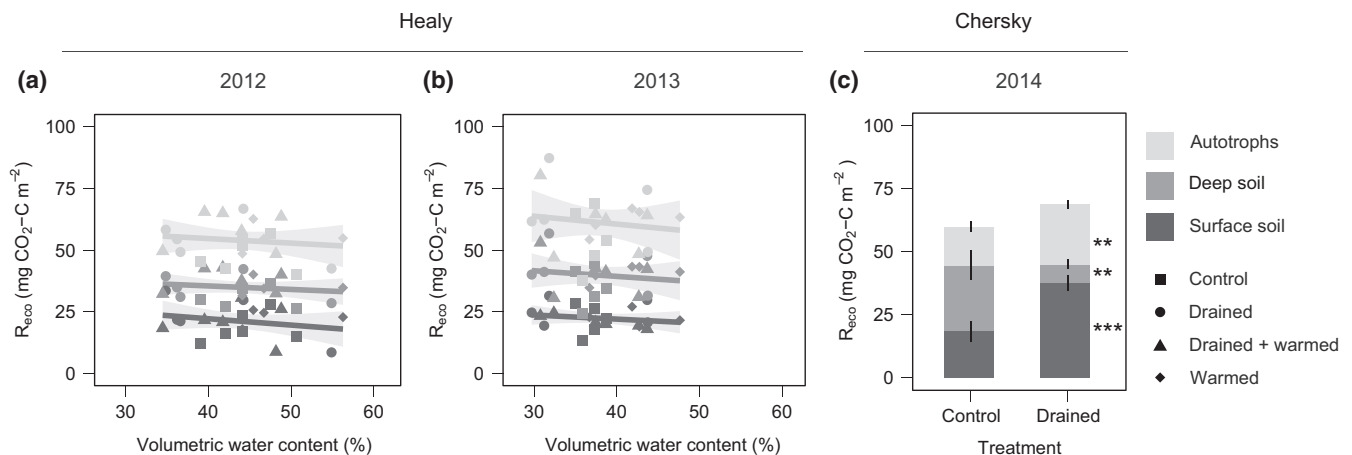


FIGURE 4 R_{eco} with partitioned sources (mean \pm SE). R_{eco} data are from 1 to 20 August each year and multiplied with the contributions of three sources, that is, surface soil, deep soil, and autotrophs. Three sources of Healy are stacked by plot, so R_{eco} values of autotrophs represent the sum of three sources. Statistical significance for Chersky are presented with asterisks (t test; ** $p < 0.01$; *** $p < 0.001$) next to each source, top: autotrophs, middle: deep soil, bottom: surface soil

energy could not be transferred to deeper soil layers due to poor thermal conductivity, keeping the deeper soil layers colder. These findings imply that drying of moist or wet tundra ecosystems and subsequent changes in soil temperatures in the growing season may accelerate decomposition of young soil carbon in shallow soil layers but preserve old soil carbon pools in deep layers and, potentially, in permafrost. Additionally, warmer surface soil temperature may further contribute to raising plant respiration rates (Atkin & Tjoelker, 2003; Dorrepaal et al., 2009; Smith & Dukes, 2013), especially respiration rates of roots, which are exposed to warmer surface soil temperatures (Atkin, Edwards, & Loveys, 2000). For a larger spatial scale, however, the relationship between soil moisture and temperature needs to be interpreted with caution, because it depends on the balance between heat capacity and thermal diffusivity, the degree of soil moisture change in both organic and mineral soil layers, and the thickness of organic layers that serve as an insulator (Lorant et al., 2018; Rouse, Carlson, & Weick, 1992).

4.3 | Effects of plant changes

Continued severe drought may lead to mortality of plant species that are present in moist and wet tundra, changing plant community structure and aboveground biomass (Saltmarsh et al., 2006). *E. vaginatum* and *E. angustifolium*, which are dominant in Healy and Chersky, respectively, are not tolerant to prolonged drought (Phillips, 1954; Wein, 1973). As a result, a decade-long drainage in Chersky decreased *E. angustifolium* abundance but increased shrub abundance and aboveground plant biomass (Kwon et al., 2016), and, thus, increased the contributions of R_a to R_{eco} . This implies that long-term drainage and the subsequent changes in plant communities and biomass alter plant contributions to R_{eco} . Furthermore, changes in plant productivity and composition may alter the rates and contributions of R_h to R_{eco} through root exudates, litter quantity, and litter quality (Chapin et al., 2012). Addition of labile carbon and nitrogen (components of root exudates) usually enhances R_h rates in organic soils where roots are abundant (Lavoie, Mack, & Schuur, 2011; Wild et al., 2016, 2014), and the effects can be more prominent in permafrost soils (Pegoraro et al., 2019). If drying decreases TD, as shown in this study, denser roots in shallow soil layers and more root exudates may enhance modern soil carbon decomposition, while reducing old soil carbon decomposition. However, if warming and drying increases the thawed layer and roots are growing in deeper soil layers, decomposition of old soil carbon may be also accelerated. No significant changes in vegetation composition or biomass were observed at Healy due to less severe drying treatment effects over a relatively short period of time, but consistently drier conditions may modify plant communities and productivity, influencing R_a contributions to R_{eco} . In particular, if mosses and lichens are replaced by vascular plants, which are more productive and have higher aboveground and belowground biomass, contributions of R_a to R_{eco} would be expected to increase.

Given the fact that the abundance of *E. angustifolium* increased with water table, correlations between *E. angustifolium* abundance

and $\Delta^{14}C_{Reco}$, as well as the contributions of deep soil respiration to R_{eco} , may reflect the indirect effects of long-term water table condition on these signals. In addition, the decreased abundance of *E. angustifolium* with a concurrent increase in total aboveground plant biomass following drainage (Kwon et al., 2016) as well as abovementioned drainage effects promoted decomposition of surface soil and autotrophic respiration. Together, this may partially have driven the negative correlation between the abundance of *E. angustifolium* and contribution of deep soil respiration. However, the independent role of *E. angustifolium* in changing $\Delta^{14}C$ patterns should be taken into account. Although the amount of CO_2 measured using a plant chamber included both plant-mediated CO_2 transport and R_a , the amounts of CO_2 and CH_4 transported through *E. angustifolium* were positively correlated with one another (Supplementary Fig. S2), implying that some proportion of R_{eco} at Chersky may be linked to the release of CO_2 from deep soil layers through aerenchyma of *E. angustifolium* (Colmer, 2003). In addition, *E. angustifolium* invests a substantial amount of energy and materials to produce deep roots each year, and its roots respire more than other graminoids that have similar aboveground morphology and metabolism (Billings, Peterson, & Shaver, 1978). These roots may have provided oxygen in deep soil layers and enhanced decomposition rates, and transported soil gas to the atmosphere. Because the abundance of aerenchymatous plants is sensitive to soil water conditions (Andresen, Lara, Tweedie, & Lougheed, 2017; Kwon et al., 2017), a decrease in the abundance of these plants may have partly contributed to a reduced amount of old CO_2 contributing to R_{eco} in dried plots. This result highlights the importance of plant composition in determining old soil carbon losses, which has not been shown previously.

5 | IMPLICATIONS AND FURTHER STUDIES

A combination of different local conditions, such as soil hydrology, adapted vegetation composition, moss or organic soil layer thickness, and distribution of ground ice, and the intensity of warming and drying may yield varying consequences. In this study, a low and a high intensity of drying scenarios following warming were tested in moist and wet tundra. Not only the primary effects of drying (drier soil conditions) but also secondary effects of modified soil temperatures at different soil layers as well as plant biomass and community composition resulted in increased contributions of modern soil carbon and autotrophs, but decreased contributions of old soil carbon to ecosystem respiration. The results of this study emphasize the role of hydrology and a number of related environmental characteristics on the source contributions to ecosystem respiration in the warming Arctic.

The two manipulation experiments in this study mimicked drier conditions due to enhanced evapotranspiration and ice-wedge degradation in the warming scenarios, but did not directly increase evapotranspiration rates or warm topsoil to melt ice wedges. If such changes occurred simultaneously, contributions of autotrophic

respiration and surface soil decomposition to ecosystem respiration would have been higher (Dorrepaal et al., 2009). In addition, if these changes involve permafrost degradation, warmer deep soil temperatures and the release of nutrients, such as nitrogen that is limiting plant productivity (Salmon et al., 2016), would increase contributions of deep soil decomposition as well as autotrophic respiration (Hicks Pries et al., 2016, 2015). Further studies that involve diverse warming and drying scenarios may supplement the results obtained in this study.

Our results are based on observations made in August at both sites, when TDs at the two sites are *ca.* 5–10 cm shallower than the maximum TDs in September, and when plant activities are lower compared to July (NDVI and EVI showing the highest values around July 25 at both sites). Because the highest soil temperatures in shallow and deep soil layers and the highest plant activities occur at different times, the contributions of each source to R_{eco} may vary over the growing season (Hicks Pries et al., 2013). In addition, nongrowing season processes will need to be included to examine the net effects of drainage on year-round R_{eco} rates and the source of their changes. Because nongrowing season R_{eco} contributes substantially to the annual CO_2 balance (Commane et al., 2017; Coyne & Kelley, 1971; Webb et al., 2016; Zimov et al., 1996, 1993), additional studies on how drainage affects R_{eco} rates and sources during the nongrowing season will improve our understanding of the stability of permafrost and active layer carbon pools under climate change.

Previous studies have shown that permafrost degradation following warming increases decomposition rates in deep soil layers (Hicks Pries et al., 2013, 2016; Schuur et al., 2009). The warming treatment at Healy confirmed these mechanisms, but the effects were offset when warming was combined with drying. Permafrost regions in the Arctic are forecast to become warmer (Kirtman et al., 2013; Overland, Wang, Walsh, & Stroeve, 2014), and R_{eco} and old carbon loss rates (Hicks Pries et al., 2016) may increase (Schuur et al., 2015). Our findings show that drying may increase R_{eco} rates while decreasing the decomposition of old soil. In other words, drying in moist and wet tundra may intensify turnover rates of surface soil carbon pools together with enhanced photosynthetic activities (Natali et al., 2015), but reduce decomposition of old carbon stored in permafrost (Hugelius et al., 2014; Schuur et al., 2015). Re-distribution of surface water and interactions between ground thaw and hydrologic changes need to be taken into account to improve predictions of the response of tundra ecosystems to climate change and the susceptibility of carbon pools at different soil depths.

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ORCID

Min Jung Kwon  <https://orcid.org/0000-0002-7330-2320>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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