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Moisture drives surface decomposition in thawing tundra

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[1] Permafrost thaw can affect decomposition rates by changing environmental conditions and litter quality. As permafrost thaws, soils warm and thermokarst (ground subsidence) features form, causing some areas to become wetter while other areas become drier. We used a common substrate to measure how permafrost thaw affects decomposition rates in the surface soil in a natural permafrost thaw gradient and a warming experiment in Healy, Alaska. Permafrost thaw also changes plant community composition. We decomposed 12 plant litters in a common garden to test how changing plant litter inputs would affect decomposition. We combined species' tissue-specific decomposition rates with species and tissue-level estimates of aboveground net primary productivity to calculate community-weighted decomposition constants at both the thaw gradient and warming experiment. Moisture, specifically growing season precipitation and water table depth, was the most significant driver of decomposition. At the gradient, an increase in growing season precipitation from 200 to 300 mm increased mass loss of the common substrate by 100%. At the warming experiment, a decrease in the depth to the water table from 30 to 15 cm increased mass loss by 100%. At the gradient, community-weighted decomposition was 21% faster in extensive than in minimal thaw, but was similar when moss production was included. Overall, the effect of climate change and permafrost thaw on surface soil decomposition are driven more by precipitation and soil environment than by changes to plant communities. Increasing soil moisture is thereby another mechanism by which permafrost thaw can become a positive feedback to climate change.

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1. Introduction

[2] Over 1600 Pg of soil carbon (C) have accumulated in ecosystems underlain by permafrost [*Schuur et al.*, 2008; *Tarnocai et al.*, 2009] because cold, and often freezing, soil temperatures have slowed decomposition rates. Accompanying these cold soil temperatures are extremes in soil moisture that can also limit decomposition. Permafrost acts as a barrier to water drainage, water logging soils and limiting aerobic microbial respiration [*Gebauer et al.*, 1996]. However, many permafrost soils are found in high-latitude tundra ecosystems, where mean annual precipitation is low, similar to deserts and grasslands [*Chapin et al.*, 2002]. Therefore, while deeper soil in the permafrost zone is often waterlogged, the surface soil can dry out quickly, also limiting decomposition.

[3] Permafrost thaw changes the environmental conditions that affect decomposition by increasing soil temperatures and shifting surface hydrology. Many permafrost soils are currently warming, and even thawing, as their temperatures rise above 0°C [*Osterkamp*, 2007; *Romanovsky et al.*, 2010]. This thaw is due to climate change, which has caused air temperatures at high latitudes to increase 2°C over the past 60 years and is expected to cause temperatures to increase 7–8°C over the next century [*IPCC*, 2007]. Thaw can create thermokarst terrain, uneven ground due to soil subsidence following the loss of ground ice [*Osterkamp et al.*, 2009]. What type of thermokarst terrain forms depends on the ecosystem's slope, aspect, and parent material [*Jorgenson and Osterkamp*, 2005]. Thermokarst features change the height of the water table, which is perched on top of the permafrost, making subsided areas wetter while often funneling water from adjacent areas. Thaw-caused soil moisture changes have the potential to affect decomposition more than soil temperature because thaw can lead to extreme soil moisture conditions like submergence or desiccation.

[4] Permafrost thaw can also affect decomposition rates by altering biotic communities. Changes to plant species composition affect the quality of the substrate that supplies decomposition. Permafrost thaw has caused subarctic plant communities to shift from being graminoid and moss

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dominated to being shrub dominated [*Schuur et al*., 2007]. In the arctic, warming is similarly causing a shift to shrub dominance [*Sturm et al*., 2001]. While shrub leaf litter is generally more easily decomposed than graminoid litter, an increase in woody litter from shrubs may slow decomposition rates overall [*Hobbie et al*., 2000; *Hobbie*, 1996]. Warming may also alter substrate quality by increasing nitrogen mineralization [*Rustad et al*., 2001], which can increase decomposition rates by increasing initial litter nitrogen [*Hobbie*, 2005]. Lastly, permafrost thaw can change decomposition rates by altering microbial communities [*Mackelprang et al*., 2011]. It is currently unclear whether permafrost thaw's effect on decomposition will be driven more by environmental or biological changes.

[5] The relative importance of environment and substrate quality in affecting decomposition may be a matter of spatial scale. Over large spatial scales, climate is often considered the most important driver of decomposition, more so than substrate quality or soil organisms [*Lavelle et al*., 1993; *Aertsl*, 2006]. In one meta-analysis of cold biome decomposition, *Cornelissen et al*. [2007] found that temperature and then plant species composition were the most important drivers of litter decomposition. In a similar meta-analysis, *Aerts* [2006] found that warming increased litter decomposition only if there was adequate soil moisture. Smaller-scale studies in cold ecosystems found plant growth form, a determinant of substrate quality, was a more important driver of decomposition rates than climate [*Dorrepaal et al*., 2005; *Baptist et al*., 2010]. In a global meta-analysis of 44 litter decomposition studies, climate was the best predictor of decomposition rates, but within a region, substrate quality was the best predictor [*Aerts*, 1997]. Likely the more variable a driver (e.g., climate or substrate) at a given spatial scale, the more likely it is to control decomposition at that scale.

[6] In this study, we compare the relative effects of permafrost-thaw-induced environmental and substrate changes on decomposition rates in a subarctic tundra. While many studies have investigated litter decomposition in cold ecosystems [e.g., *Hobbie*, 1996; *Hobbie and Gough*, 2004; *Dorrepaal et al*., 2005], to our knowledge, this is the first study to directly investigate how permafrost thaw affects decomposition rates. Understanding how permafrost thaw affects decomposition will allow us to better predict the fate of permafrost soil C. If permafrost thaw increases decomposition rates, these ecosystems may shift from being a C sink, which they have been for thousands of years [*Hicks Pries et al*., 2012] to a C source [e.g., *Schuur et al*., 2009; *Vogel et al*., 2009]. Previous research at this subarctic tundra in Healy, Alaska (AK) addressed whether permafrost thaw increased the respiration of old soil C at depth in the soil profile [*Schuur et al*., 2009; *Hicks Pries et al*., 2013], but this study focuses on controls over decomposition near the soil surface.

[7] We used a common substrate to isolate the influence of environment on decomposition in surface soil across a natural gradient of permafrost thaw [*Schuur et al*., 2009] and an ecosystem warming experiment (Carbon in Permafrost Experimental Heating Research, CiPEHR) [*Natali et al*., 2011]. Seven years of data in the thaw gradient and three years of data in CiPEHR allowed us to investigate causes of interannual variability in decomposition rates and how they interact with permafrost thaw. We hypothesized decomposition rates would be faster where the soils were warmer due to warmer years, permafrost thaw, or experimental heating; however, in areas with deep permafrost thaw, rates may slow because water tables near the soil surface may limit oxygen availability. We also used a common garden to compare the decomposition rates of 12 plant litter types from vascular and nonvascular plants common to this system. We used the data from the common garden to investigate how thaw [*Schuur et al*., 2007] and warming-induced [*Natali et al*., 2012] changes to plant communities affect decomposition rates. We then compared the relative magnitude of environmental and plant community change effects on surface soil decomposition.

2. Materials and Methods

2.1. Study Site

[8] The permafrost thaw gradient and CiPEHR are, respectively, located adjacent to and 2 km east of Eight Mile Lake (EML, 63° 52′ 59″N, 149° 13′ 32″W) in the foothills of the Alaska mountain range in Healy, AK. Their vegetation consists of moist acidic tussock tundra dominated by *Eriophorum vaginatum*. The vegetation also includes the graminoid *Carex bigelowii*, dwarf shrubs *Vacinnium uliginosum*, *V. vitis-idaea*, *Betula nana*, *Rhodendron subarticum*, *Rubus chamaemorus*, *Empetrum nigrum*, and various mosses and lichens. The soils are subgelic Typic Histoturbels and consist of 0.25 to 0.5 m of organic soil atop a mixture of mineral loess deposits and glacial till [*Vogel et al*., 2009]. At the thaw gradient, permafrost temperatures have been monitored via a borehole over the past several decades and are currently around −1°C, making the permafrost susceptible to thaw [*Osterkamp and Romanovsky*, 1999]. The thaw gradient consists of three sites: minimal, moderate, and extensive thaw. The main difference among the sites is the duration of permafrost thaw each has undergone. At the extensive thaw site, permafrost thaw has been documented for the past two decades, but began earlier based on aerial photographs [*Osterkamp et al*., 2009]. As a result, the sites have different degrees of plant community changes [*Schuur et al*., 2007], active layer thickening, and thermokarst formation [*Lee et al*., 2011; *Osterkamp et al*., 2009]. The thaw gradient has had ongoing monitoring of soil temperatures to 40 cm and water table depth at three locations per site, and active layer depth (the maximum depth of unfrozen soil in autumn) and CO_2 fluxes at six locations per site since 2004 [*Schuur et al*., 2009; *Vogel et al*., 2009; *Trucco et al*., 2012].

[9] The CiPEHR experiment began in October 2008 and consists of summer warming (SW) and winter warming (WW) treatments set up in a factorial design resulting in four treatments: control, SW, WW, and annual warming (SW + WW). In the SW treatments, open top chambers (60 by 60 cm) act as small greenhouses passively warming the air by about 1°C during the growing season [*Natali et al*., 2011]. In the WW treatments, snow fences slow prevailing winds, creating deep (>1 m) snowdrifts that insulate soils during the winter [*Natali et al*., 2011]. Excess snow is shoveled off the WW treatments each April so additional water is not added to the soil and snowmelt is not delayed. The WW treatment raises winter soil temperatures by 2–7°C (depending on soil depth), raises growing season soil temperatures up to 1.5°C, and increases the depth of thawed soil during the growing season by 10% [S. Natali et al., Permafrost degradation stimulates carbon loss from experimentally warmed tundra, in revision, 2013]. There are six replicate snow fences. The WW treatment and WW control plots are the north and

south sides of each fence, respectively. SW plots are nested in WW treatment and control plots. CiPEHR has had continuous monitoring of soil temperatures to 40 cm and CO_2 fluxes, weekly monitoring of water table depth during the growing season, and yearly measurements of active layer depth in all treatment plots. For additional information on CiPEHR's experimental design, treatment effects, and data monitoring, see *Natali et al.*, 2011, *Natali et al.*, 2012, and S. Natali et al., in revision, 2013.

2.2. Common Substrate Decomposition

[10] To investigate how environmental changes caused by permafrost thaw and warming affect decomposition, we used a common substrate (cellulose filter paper) incubated in mesh bags. Decomposing cellulose is a widely used method [e.g., *Clymo*, 1965; *Fox and Van Cleve*, 1983; *Wagner and Jones*, 2006] for comparing relative rates of decomposition among environments because it eliminates litter quality variation [*McClellan et al.*, 1990]. While cellulose decomposition is not a good estimator of absolute rates of litter decomposition, trends in cellulose decomposition across environments follow the trends of actual plant litter [*Clymo*, 1965; *Vitousek et al.*, 1994]. At the thaw gradient, 10 bags per site were incubated annually from September 2004 through September 2011. Additionally, a total of 16 bags were incubated in and adjacent to eight thermokarsts south of extensive thaw from September 2008 through September 2009. At CiPEHR, six bags per treatment were incubated annually from September 2008 through September 2011 and during the growing season from late May/early June through mid-September in 2010 and 2011.

[11] Common substrate decomposition bags were constructed from cellulose filter paper (Fisher brand P8 09-802-1B), which was cut into 7.5 by 7.5 cm squares for the thaw gradient and 7.5 × 5 cm rectangles for CiPEHR. Filter papers were individually weighed (Mettler Toledo AX204 balance, 0.1 mg precision) before being put into one of four compartments within each mesh decomposition bag. The mesh bags were made from two pieces of 2 mm mesh fiberglass window screening separated into four compartments and sealed with a heat sealer. The mesh bags measured 21 by 21 cm for the thaw gradient and 21 by 13.5 cm or 10.5 by 13.5 cm for CiPEHR annual and growing season bags, respectively. The CiPEHR decomposition bags were smaller because space was limited in the experimental plots. The compartments were arranged two by two with the longest side of each filter paper piece orientated vertically. The bags were designed to measure decomposition at two depths, from 0 to 10 cm and from 10 to 20 cm. Growing season bags only had the 0–10 cm depth, so they could be placed into the ground earlier in the growing season, once the top 10 cm of soil thawed.

[12] Each decomposition bag was placed into the soil vertically. We first cut a slit into the organic layer using a serrated knife and then used a flat-bladed shovel to insert the decomposition bag into the slit so that the top of the bag was even with the soil surface. Annual decomposition bags were inserted in mid-September each year and left to incubate in the soil for a year. The slits were reused, but new slits were made nearby (<0.3 m) if gaping caused the bags to no longer be in full contact with the soil. Upon removal, the bags were rinsed to remove soil and frozen for transport back to the lab.

[13] At the lab, we dried the decomposition bags at 60°C for 24 h. We used paintbrushes and fine-pointed tweezers to carefully remove soil and roots from the filter papers before measuring their final weight. Since the filter papers quickly absorbed moisture from the air, we measured their initial and final mass at room conditions, which we corrected for moisture absorption. To calculate the correction factor, we weighed a subset of 10 filters before and after drying at 60° C for 24 h and left to come to room temperature in a desiccator; this step was repeated several times during processing. For each filter paper, we calculated a percent mass loss by subtracting the final from the initial weight and dividing by 100. Mass loss of horizontally adjacent filters was averaged to get one number per depth per bag.

2.3. Common Substrate Data Analysis

[14] To investigate site or treatment and sampling date differences in decomposition, we performed analyses of variance (ANOVAs) in JMP (SAS, North Carolina). For the gradient, the main effects were substrate depth, site, and year, while for CiPEHR, the main effects were the winter treatment, the summer treatment nested within the winter treatment, substrate depth, and year. At the gradient, the same locations were used every year, so location nested in site was a random effect. Bag was also a random effect because each bag contained the substrate at 0–10 cm and 10–20 cm. For CiPEHR, the random effects were fence, plot nested within fence, and bag. Differences in community-weighted decomposition constants were tested with ANOVAs using site or treatment as main effects. Mass loss was arcsine square root transformed before analyses. All residuals were checked for normality and homogeneity of variances to ensure the assumptions of ANOVA were met.

[15] The ANOVAs revealed that year was a significant effect in the thaw gradient, so we ran a mixed effect multiple regression in R [*R Development Core Team*, 2012] to explore interannual controls on decomposition. We included average growing season soil temperatures at 10 cm, active layer depth, average water table depth, total growing season precipitation, substrate depth, and site as explanatory variables. Other variables, like temperature at different depths, were left out to limit autocorrelation. Site-level values of water table depth and soil temperature were used in the model. Active layer depth was measured near six of the 10 bags per site; a site-level average was used for the remaining bags (Table S2). More information on soil sensors, rain gauge, and active layer depth monitoring can be found in *Trucco et al.* [2012]. Based on graphical exploration of the data, we included water table by precipitation and active layer depth by precipitation interactions in the model. We used the full model to optimize random effects and variance structures using AIC following *Zuur et al.* [2009]. The model had a first-order autoregressive correlation structure within location to account for the repeated measures and a fixed variance structure with active layer depth. Once random effects were optimized, we performed a series of pair-wise model comparisons using the F test, dropping the least significant explanatory variable each time (highest p value) until only significant explanatory variables remained [*Zuur et al.*, 2009]. The gradient model was fitted with the lme command in the nlme package in R [*Pinheiro et al.*, 2012] using restricted maximum likelihood.

[16] We ran similar mixed effect multiple regressions with the CiPEHR data. CiPEHR had finer scale monitoring of environmental parameters than the gradient so that water table depth, active layer depth, and soil temperature were measured

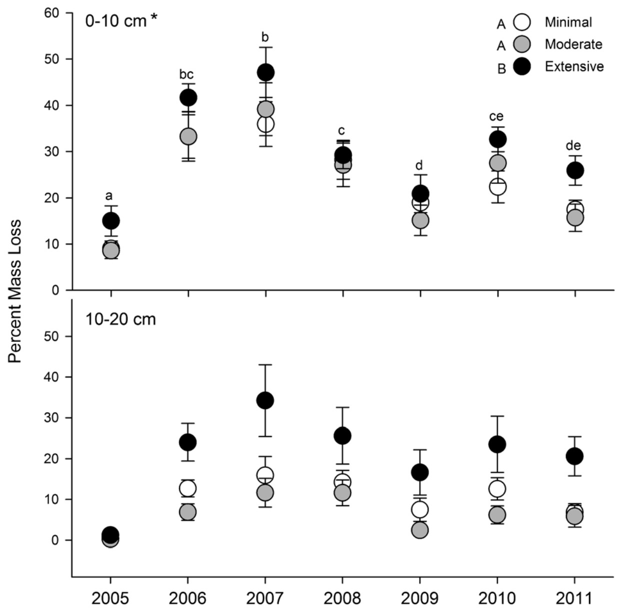

Figure 1. Annual mass loss from the common substrate decomposition bags at the three thaw gradient sites from September 2004 through September 2011 (n = 10 per site per year). The bags were split into two depths—0–10 cm and 10–20 cm—and were incubated from September of one year until September of the following year. The year listed is the year in which the bag was collected. Error bars are the standard error. Capital letters not shared indicate significant differences among sites, lowercase letters not shared indicate significant differences among years, and the asterisk indicates depths were significantly different (α = 0.05).

at each bag's location (Table S3). The CiPEHR regression included average growing season and winter soil temperature at 10 cm, active layer depth, growing season precipitation, water table depth, substrate depth, and treatment as the explanatory variables. Based on graphical exploration, we included an interaction term between substrate depth and water table depth. Plot was included as a random effect, and no variance structure was needed. The same model minus the winter soil temperatures and substrate depth was used for CiPEHR growing season decomposition. We followed the same model comparison procedure as for the gradient to choose the best explanatory variables for CiPEHR annual and growing season decomposition. For all models, explanatory variables were centered and standardized to better interpret interactions and compare effect sizes [*Schielzeth*, 2010].

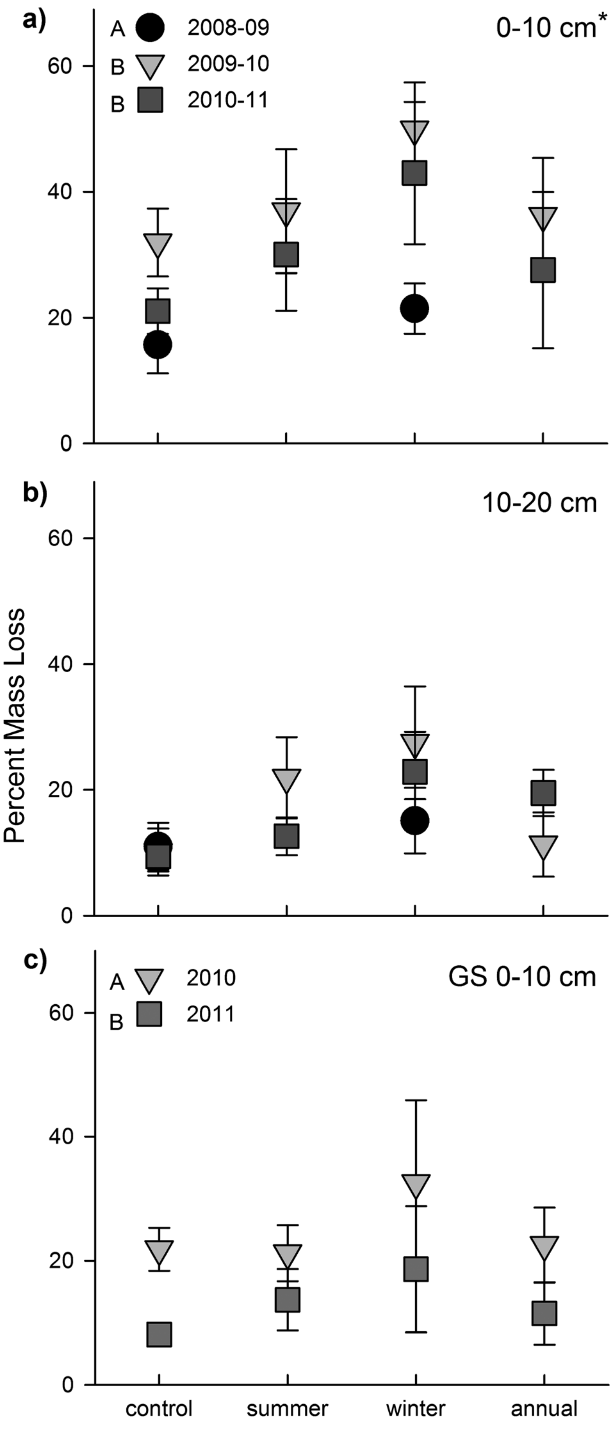

Figure 2. Annual (a and b) and growing season (GS, c) mass loss from the common substrate decomposition bags at CiPEHR (n = 6 per treatment per year). Annual percent mass loss was measured at two depths—0–10 cm and 10–20 cm. Error bars are the standard error. Capital letters not shared indicate significant differences among years, and the asterisk indicates depths were significantly different (α = 0.05). There were no significant differences among treatments.

2.4. Common Garden and Plant Community Decomposition

[17] To investigate how plant community changes caused by permafrost thaw and warming affect decomposition, we first incubated 12 plant litter types for three years in a common garden (i.e., the same site) near the thaw gradient. The litter consisted of leaves from five shrub species (*Betula nana, Vaccinium uliginosum, Rubus chamaemorus, Rhododendron subarticum*, and *Vaccinium vitis-idea*), two moss types (*Dicranum* and *Sphagnum* spp.), one graminoid (*Eriophorum vaginatum*), and 1:1 mixtures of live stem and rhizome tissue from four shrub species (*Betula nana, Vaccinium uliginosum, Rhododendron subarticum*, and *Vaccinium vitis-idea*). Leaves and live woody tissue were collected in September 2007 across 1 km of the thaw gradient, so substrates were a mix of samples from minimal, moderate, and extensive thaw. For deciduous leaf litter, we only collected senesced leaves that were easily

Table 1. Multiple Regression Results for Annual and Growing Season Decomposition of a Common Substrate at the Permafrost Thaw Gradient and Warming Experiment (CiPEHR)[a]

Model	Coefficients	Estimate	SE	t value	p value
Gradient (annual)	Intercept	0.486	0.025	19.3	<0.00001***
	Moderate	−0.015	0.032	−0.46	0.646
	Extensive	0.162	0.033	4.94	<0.00001***
	Depth (10–20)	−0.230	0.022	−10.4	<0.00001***
	Water table	0.0351	0.0090	3.89	0.0001**
	Active layer	−0.0454	0.0012	−3.81	0.0002**
	Precipitation	0.134	0.0096	14.0	<0.00001***
	WT:Precip	0.0348	0.0085	4.08	0.0001**
CiPEHR (annual)	Intercept	0.561	0.029	19.4	<0.00001***
	Depth (10–20)	−0.182	0.028	−6.54	<0.00001***
	Water table	−0.139	0.026	−5.40	<0.00001***
	Depth (10–20):WT	0.0846	0.028	3.02	0.032**
CiPEHR (growing season)	Intercept	−0.017	0.100	−0.17	0.865
	Precipitation	0.0021	0.0004	4.73	0.0001**

[a] Results are from models run using only significant predictors after model selection (see Methods). Variables were standardized to allow effect size comparisons using model estimates.

taken off branches, indicating the petiole had begun to abscise. For evergreen leaf litters, *R. subarticum* and *V.vitis-idea*, we were unable to collect enough senesced leaves, so we also collected live leaves. For mosses, we cut off the green tissue at the top of the moss and used the brown tissue from the next 2 cm. Mosses were also gamma radiated to prevent them from resprouting. For *E. vaginatum*, we collected the current year's standing dead litter and cut off any green tissue remaining on the leaf blades. All litter samples were air dried after collection and stored at room temperature. We tested the effect of using live woody material and evergreen leaves by comparing leaching-caused mass loss of senesced and live litter. Leaching was used as a decomposition proxy because leaching mass loss is significantly correlated with decomposition rate ($R^2 = 0.31$, $p = 0.0027$, $n = 27$; unpublished data, 2011). After 24 h in DI water, there were no significant differences in mass loss between senesced and live litter ($p = 0.63$). We explore consequences of using live litter in the discussion.

[18] To make the litter bags, we carefully homogenized the litter and placed 2 g of substrate into 8 × 12 cm, 0.5 mm mesh bags. The bags were sewn together with polyester thread and labeled with an aluminum tag. The litter bags were deployed in September 2008 into the common garden, which had five blocks. At each block, five lines consisting of the 12 litter types strung together in random order radiated out from a central point. Each litter bag was placed into the moss layer at a slight angle so that the bag was 0 to 1.5 cm below the soil surface. We did this to represent decomposition conditions in the tundra where fresh litter falls in between individual mosses. One line was randomly collected from each block in May 2009, September 2009, May 2010, September 2010, and August 2011. The collected litter bags were frozen for transport to the laboratory. At the laboratory, the litter bags were thawed, rinsed in DI water, and carefully picked through to separate litter from roots and hyphae that had grown into the bags. The litter was then dried for three days at 30°C before being weighed (Mettler-Toledo PG403-S, 0.001 g precision).

[19] Initial litter quality, including %N and C:N, was measured on three subsamples of each substrate. For %C and %N analysis, the litter was ground to a fine powder and then run on an ECS 4010 elemental analyzer (Costech Analytical Technologies, Valencia, CA). Stem and rhizome initial quality was determined separately for each species, but was then averaged by species into a single wood value as the litter bags were a 1:1 mixture of stem and rhizomes.

2.5. Common Garden and Community Decomposition Data Analysis

[20] We calculated community-weighted decomposition constants using decomposition constants from the 12 litter types and ANPP data. To calculate decomposition constants for each litter type, we fit nonlinear regressions of a single-pool exponential decay model in R using nls [*R Development Core Team*, 2012; *Adair et al.*, 2010]. We used the latest plot-level ANPP data available, which was from 2009 for the thaw gradient ($n = 6$ per site) and from 2011 for CiPEHR ($n = 12$ per treatment; Table S1). Aboveground NPP was determined using a method that combines nondestructive point framing with allometric equations; this method has been previously described for both the thaw gradient and CiPEHR [*Schuur et al.*, 2007;

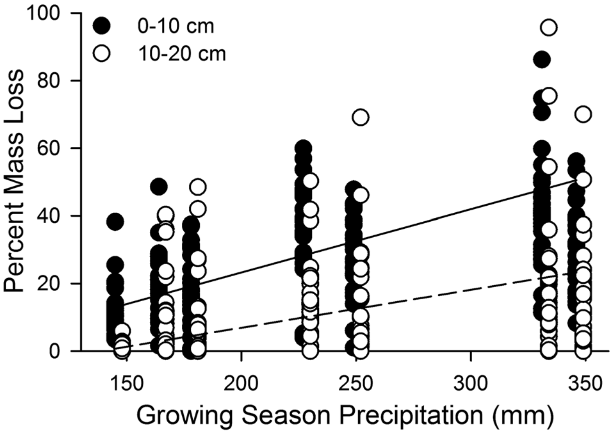

Figure 3. Annual mass loss increased with more growing season precipitation at the thaw gradient. The points are the actual data, and the lines show the average predicted relationship between precipitation and percent mass loss when the other significant predictors (water table depth and active layer depth; see Table 1) are held at their respective means. The solid and dashed lines are the relationships with decomposition at 0–10 cm and 10–20 cm depths, respectively. The precipitation values of the 10–20 cm data were offset by 3 mm to better show all data.

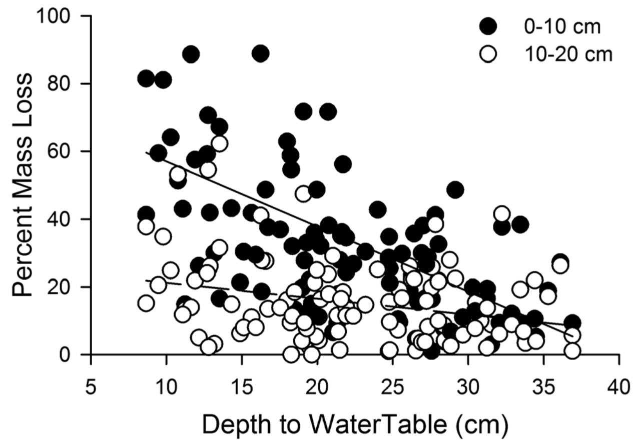

Figure 4. Annual mass loss increased with shallower water tables at CiPEHR. The points are the actual data, and the lines show the average predicted relationship between the average growing season water table and annual mass loss. The solid and dashed lines are the relationships with decomposition at 0–10 cm and 10–20 cm depths, respectively.

Table 2. Initial Quality (n = 3) of 12 Litters in the Common Garden Experiment

Species	C:N	N (%)
Betula nana	37 ± 1	1.36 ± 0.05
Rubus chamaemorus	37 ± 0.8	1.26 ± 0.01
Vaccinium uliginosum	78 ± 2	0.64 ± 0.01
Rhododendron subarcticum	42 ± 0.3	1.27 ± 0.004
Vaccinium vitis-idaea	59 ± 1.3	0.84 ± 0.01
B. nana wood[a]	56 ± 4	0.93 ± 0.07
V. uliginosum wood	76 ± 6	0.67 ± 0.07
R. subarcticum wood	87 ± 6	0.56 ± 0.02
V. vitis-idaea wood	70 ± 2	0.70 ± 0.02
Eriophorum vaginatum	102 ± 6	0.45 ± 0.02
Dicranum spp.	103 ± 4	0.42 ± 0.02
Sphagnum spp.	68 ± 2	0.63 ± 0.02

[a] Wood refers to a 1:1 mixture of stem and rhizome tissue.

Natali et al., 2012]. This method estimated secondary stem growth using growth rates measured in tussock tundra at Toolik, AK [*Shaver et al.*, 2001; *Bret-Harte et al.*, 2002]. To calculate the community-weighted decomposition constant (k_c), we used the following equation:

$$k_c = \sum_1^n \frac{ANPP_s}{ANPP_t} * k_s \tag{1}$$

where $ANPP_t$ is the total ANPP per plot, $ANPP_s$ is the ANPP of a given species and tissue type (leaf or stem), k_s is the decomposition constant of a given species and tissue type, and n is the number of unique species and tissue types. Our common garden did not incubate all species and tissue types found at our sites. For substrates not decomposed here, we used decomposition constants from previous studies and from similar substrates in this study. For *Carex bigelowii* we used a k of 0.155 [*DeMarco*, 2011]. For the evergreen leaves *Empetrum nigrum*, *Andromeda polifolia*, and *Oxycoccus microcarpus*, we used 0.208, an average of our evergreen leaf values following *DeMarco* [2011]. For the stems of *A. polifolia*, *E. nigrum*, *O. microcarpus*, and *R. chamaemorus*, we used 0.096, an average of our woody tissue values. These estimates were used for only 9.5% of total gradient ANPP and 10.2% of total CiPEHR ANPP. We did not correct the community-weighted decomposition constants for site differences because mass loss of our common substrate did not differ among sites at 0–10 cm . Differences in community-weighted decomposition constants were tested with ANOVAs using site or treatment as main effects. Differences in decomposition constants among substrates were compared using an ANOVA with block as a random effect. Decomposition constants were arcsine square root transformed before analyses.

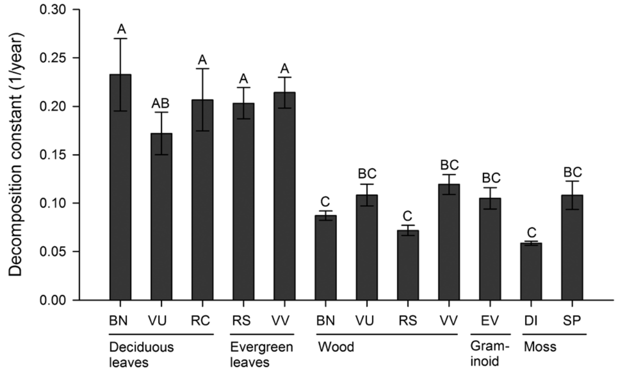

Figure 5. Decomposition constants (k) of 12 litters from the common garden. Error bars are the standard error (n = 5). Capital letters not shared indicate significant differences among litters (α = 0.05). BN = *Betula nana*, VU = *Vaccinium uliginosum*, RC = *Rubus chamaemorus*, RS = *Rhododendron subarcticum*, VV = *Vaccinium vitis-idaea*, EV = *Eriophorum vaginatum*, DI = *Dicranum* spp., and SP = *Sphagnum* spp.

3. Results

3.1. Common Substrate Decomposition

[21] Decomposition of the common substrate differed among sites in the permafrost thaw gradient but not among treatments in the warming experiment. Annual mass loss at the permafrost thaw gradient was greatest in the extensive thaw site ($f_{2,\ 31} = 7.3$, $p = 0.0025$; Figure 1). However, there was a significant site by depth interaction wherein mass loss at extensive thaw only differed from minimal and moderate thaw at 10–20 cm but was similar to minimal and moderate thaw at 0–10 cm ($f_{2,\ 188} = 7.2$, $p = 0.0009$). On average, annual mass loss at 0–10 cm was 26%, and annual mass loss at 10–20 cm was only 12%, a difference that was significant ($f_{1,\ 188} = 210$, $p < 0.0001$; Figure 1). Annual mass loss also showed significant interannual variation over seven years at the thaw gradient ($f_{6,\ 158} = 43.1$, $p < 0.0001$). The CiPEHR annual mass loss data were analyzed in two ways, from fall 2008 through fall 2011 for WW effects and from fall 2009 through fall 2011 for all effects, since the common substrate was not deployed in SW treatments during CiPEHR's first year. There was a weak but nonsignificant trend of WW on annual decomposition at CiPEHR over the three years of the experiment ($f_{1,\ 25} = 2.4$, $p = 0.13$; Figures 2a–b). There was no significant SW effect from fall 2009 through fall 2011 ($f_{2,15} = 1.6$, $p = 0.24$; Figures 2a–b). Growing season mass loss at CiPEHR also did not differ among WW ($f_{1,\ 15} = 0.43$, $p = 0.52$) or SW treatments ($f_{2,\ 15} = 0.54$, $p = 0.59$;

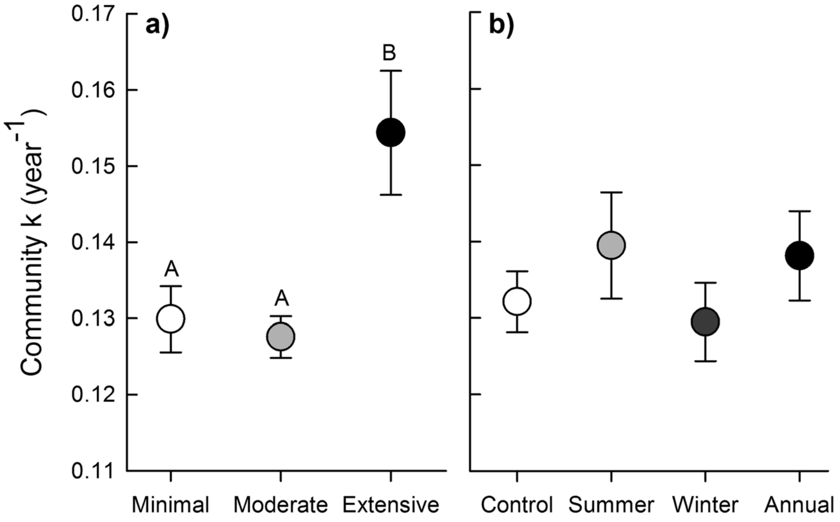

Figure 6. Community-weighted decomposition constants (k) for the sites in the gradient (a, n = 6) and the CiPEHR treatments (b, n = 12). The error bars are the standard error. Capital letters not shared indicate significant differences among sites at the thaw gradient ($\alpha = 0.05$).

Figure 2c). As at the thaw gradient, years significantly differed at CiPEHR: annual mass loss was lowest during 2008–2009 ($f_{2,44} = 6.3$, $p = 0.0038$) and growing season mass loss was greatest in 2010 ($f_{1,20} = 21$, $p = 0.0002$). Again, significantly greater mass loss occurred at 0–10 cm (30%) than at 10–20 cm (16%; $f_{1,68} = 36$, $p < 0.0001$).

[22] In mixed effect multiple regressions, moisture-related variables explained most of the variability in common substrate mass loss at both sites. At the thaw gradient, annual mass loss increased as growing season precipitation increased (Table 1 and Figure 3). While active layer depth and water table also significantly affected mass loss, their effect sizes, as judged by the coefficients of the standardized variables, were only 34% and 26% of precipitation's effect size, respectively (Table 1) [*Schielzeth*, 2010]. Water table significantly interacted with precipitation. Graphic exploration showed that when growing season precipitation was >230 mm, there was a positive relationship between mass loss and depth to the water table, but when precipitation was <230 mm, there was a slight negative relationship. Site and bag depth significantly affected decomposition (as indicated by intercept values from the multiple regression) with extensive thaw having greater decomposition and 10–20 cm having less decomposition than minimal thaw at 0–10 cm (the baseline intercept; Table 1). At CiPEHR, annual mass loss decreased as the depth to the water table increased (Table 1 and Figure 4). Bag depth was a significant fixed effect and interacted significantly with water table (Table 1); the effect of water table was greater at 0–10 cm than at 10–20 cm as indicated by the shallower slope for mass loss at 10–20 cm (Figure 4). Lastly, growing season mass loss at CiPEHR also increased significantly with precipitation (Table 1). Growing season average soil temperature and winter season average soil temperature (tested at CiPEHR only) variables were dropped from all models because they did not significantly affect mass loss independently from active layer depth, which integrates seasonal soil thaw.

3.2. Common Garden and Plant Community Decomposition

[23] Over three years in the common garden, vascular plant leaves decomposed the fastest while mosses and woody material decomposed the slowest ($f_{11,\ 44} = 16.6$, $p < 0.0001$; Figure 5). Out of the vascular plant leaves, *Eriophorum vaginatum* decomposed the slowest and *Betula nana* decomposed the fastest. Decomposition constants were positively related to the litter's initial percent nitrogen ($R^2 = 0.61$, $p = 0.0026$, $n = 12$; Table 2). At the thaw gradient due to different species composition, plant community-weighted decomposition was significantly faster in extensive thaw than at minimal or moderate thaw ($f_2 = 6.97$, $p = 0.0072$; Figure 6a). In contrast, there were no WW ($f_{1,\ 39} = 0.12$, $p = 0.7272$) or SW effects ($f_{2,\ 39} = 1.00$, $p = 0.3757$) on community-weighted decomposition at CiPEHR (Figure 6b).

4. Discussion

4.1. Moisture Controls Decomposition

[24] Moisture was the most important control on decomposition at both the thaw gradient and CiPEHR. In all the regression models, soil moisture-related variables were the most important predictors: precipitation for annual mass loss at the thaw gradient and growing season mass loss at CiPEHR and water table for annual mass loss at CiPEHR. At the thaw gradient, the heterotrophic respiration of old soil C (from 15 to 80 cm in the soil profile) increased with deepening soil thaw, not soil moisture [*Hicks Pries et al.*, 2013]. Our study's contrasting results suggest different mechanisms control decomposition at different depths within the soil profile. While decomposition at depth in permafrost ecosystems is controlled by temperature, decomposition at the surface appears more strongly controlled by moisture. Given that soil below 20 cm is waterlogged at the thaw gradient [*Trucco et al.*, 2012] and CiPEHR [*Natali et al.*, 2012] for much of the growing season, these results imply soil moisture may become a more important driver of deep soil decomposition if

the water table were to recede to a deeper position in the soil profile.

[25] Gradient and CiPEHR study sites differed somewhat in surface decomposition controls. Shallower water tables had a negative effect on decomposition at the gradient and a positive effect on decomposition at CiPEHR. The effect of water table on decomposition at the gradient was dependent on the amount of growing season precipitation. Having the water table close to the surface sped up decomposition in dry years but slowed decomposition in wet years, possibly due to anaerobic conditions. In tundra ecosystems, the water table can be decoupled from growing season precipitation because it depends on the amount of snowmelt and the depth to the permafrost on which the water table is perched. At CiPEHR, the water table's consistent positive effect was likely due to the lack of very wet growing seasons with rainfall > 250 mm during its shorter, three-year record.

[26] Faster decomposition at 0–10 cm than at 10–20 cm in the thaw gradient and at CiPEHR may be the result of the temperature depth gradient, biotic controls, or, again, moisture. Growing season soil temperatures are 2.5°C warmer on average at 10 cm than at 20 cm, but this temperature gradient effect could not be directly included in the models due to autocorrelation among temperatures at different depths. Changes in microbial communities with depth—in an arctic soil, fungi abundance decreased while archaea abundance increased [*Tveit et al.* 2013]—could also explain faster decomposition of cellulose at the surface. However, moisture likely also played a role in the depth differences. The bag depth by water table interaction at CiPEHR, wherein mass loss at 10–20 cm increased more slowly in response to a shallower water table than mass loss at 0–10 cm, could have been caused by inundation of the deeper depth slowing decomposition.

[27] Even though greater precipitation at the thaw gradient and deeper bag depths at CiPEHR dampened decomposition's response to a shallower water table, indicating inundation may slow decomposition, overall, it was surprising that decomposition rates did not reach a threshold of soil moisture that caused them to greatly decrease. In fact, the greatest annual mass loss measured at our sites (but not included in the models) were from within water track thermokarsts downslope from extensive thaw, where the water table was at or near the surface during the growing season. Mass loss in these karsts was 50% at 0–10 cm and 42% at 10–20 cm. Fast decomposition, despite inundation, may have been due to tundra's cold soil water, which holds more oxygen and has less biological oxygen demand than soil water in warmer ecosystems [*Gebauer et al.*, 1996]. Thus, tundra inundation does not quickly result in anaerobic conditions at the soil surface. Furthermore, the water was not stagnant in the water track, and its flow, although very slow, likely enhanced oxygenation.

[28] Soil moisture will be affected by climate change and permafrost thaw in several ways. Climate models predict that latitudes north of 60° could experience 10–20% more precipitation as a result of climate change [*ACIA*, 2005; *IPCC*, 2007] due to increased atmospheric transport of water vapor from low to high latitudes. However, increased evapotranspiration will also dry out the soil surface faster, so whether increased precipitation leads to more soil moisture depends partly on the timing and magnitude of precipitation events. Permafrost thaw alters microtopography and local hydrology in ways both obvious and subtle. When permafrost starts to thaw, there can be an increase in soil moisture near the surface. At CiPEHR, WW has increased the height of the water table (measured from the top of the thaw front), which has led to a 5% increase in surface (0–20 cm) volumetric water content (S. Natali et al., in revision, 2013), as melting ground ice causes surface subsidence. Thermokarst features can increase water availability locally where the ground has subsided but also drain adjacent areas, decreasing surface soil moisture nearby. Permafrost thaw will likely increase soil moisture heterogeneity on a landscape level, increasing surface decomposition in some areas, while reducing surface decomposition in others. For example, decomposition in dry areas adjacent to the aforementioned water track karsts was significantly slower than inside water tracks with only 17% and 3% mass loss at 0–10 and 10–20 cm, respectively ($f_{1,14} = 13.0$, $p = 0.0029$, $n = 8$). Eventually, complete loss of permafrost could substantially lower water tables, greatly reducing soil moisture, and making the surface soil microbes solely dependent upon precipitation. One model predicted that as permafrost degrades over the next century, there will be an initial increase in soil moisture followed by a decline in the areal extent of wet ecosystems in high latitudes [*Avis et al.*, 2011].

4.2. Site Effects

[29] Site was a significant effect at the thaw gradient, but treatment was only a weak, nonsignificant effect at CiPEHR, likely because thaw had been ongoing for only three years in CiPEHR compared to decades at the thaw gradient. Because physical properties of the soil environment such as active layer depth, temperature, and water table were included in the model, faster decomposition at extensive thaw was likely due to a factor we did not measure. Greater nitrogen availability could increase decomposition rates [*McClaugherty et al.*, 1985; *Hobbie and Gough*, 2004], especially because our cellulose substrate was devoid of nitrogen. Soil nitrogen availability can be greater in surface permafrost than in the rooting zone [*Kueper et al.*, 2012]. In extensive thaw, more of this potentially nitrogen-rich soil has been exposed due to its deeper active layer. Extensive thaw's larger plant nitrogen pools [*Schuur et al.* 2007] are evidence for increased nitrogen availability there. Extensive thaw also had greater plant biomass [*Schuur et al.*, 2007], which may prime decomposition through root exudates [*Kuzyakov et al.*, 2007; *de Graaff et al.*, 2010]. Lastly, long-term warming, like extensive thaw has undergone, can alter microbial community structure [*Deslippe et al.* 2012] and increase microbial biomass [*Rinnan et al.* 2013], which also affect decomposition rates.

4.4. Community Decomposition

[30] Community-level decomposition constants are a way to estimate how permafrost thaw and warming-induced changes to plant communities affect ecosystem decomposition rates. In CiPEHR, there were no treatment differences in community-weighted decomposition. Although three years of WW increased graminoid productivity [*Natali et al.*, 2012], it was not enough time to cause substantial changes to the plant community as have occurred at the thaw gradient over decades. At the thaw gradient, decreased graminoid abundance and increased shrubs in extensive thaw [*Schuur et al.*, 2007] led to an overall increase in community-weighted decomposition. A recent natural gradient study also found increasing community-weighted decomposition in

sites with greater shrub abundance [*DeMarco*, 2011]. Both these results are in contrast to *Hobbie* [1996]'s prediction that community decomposition rates would decrease with shrub expansion due to the increased production of recalcitrant woody tissue.

[31] Less graminoid production at extensive thaw increased community decomposition rates because our most abundant graminoid, *E. vaginatum*, had a decomposition constant of only 0.105 per year, which was similar to woody tissue and was much smaller than shrub leaf litter. This constant was 37 to 50% less than previous estimates for *E. vaginatum* from Toolik, AK [*Hobbie and Gough*, 2004; *DeMarco*, 2011]. Our *E. vaginatum* litter likely decomposed slower because it had about half the nitrogen and double the C:N ratios as *E. vaginatum* litter from those studies. Collection methods of senescent tissue were similar, so differences in litter quality were likely caused by site. Our woody tissue had slightly faster decomposition constants (ranged from 0.07 to 0.011) than found in Toolik by *Demarco* [2011] (ranged from 0.05 to 0.08), both of which were faster than the 0.025 constant measured by *Hobbie and Gough* [2004]. The increase in woody decomposition rates at our site may be due to warmer mean annual temperatures or our use of live stems and rhizomes. If our wood decomposed too fast due to being collected live, the community decomposition constants may be overestimated. Using average wood k values from the previous studies (0.07 and 0.025) caused our community decomposition constants at extensive thaw to decrease by 8 to 14% and at minimal thaw to decrease 4 to 7%. Despite our use of live litter, decomposition of our evergreen leaf litter did not systematically differ from previous studies [*Hobbie and Gough* 2004; *DeMarco*, 2011].

[32] Previous community decomposition estimates for tundra ecosystems did not include moss productivity [*Hobbie and Gough* 2004; *DeMarco*, 2011], which could greatly affect estimates because mosses decompose more slowly than other plant functional groups [*Lang et al.*, 2009]. The CiPEHR estimate would not be affected by this omission as moss productivity was similar across treatments [*Natali et al.*, 2012]. Moss production at the thaw gradient, measured in 2004, was 147, 55, and 25 g biomass m^{-2} y^{-1} at extensive, moderate, and minimal thaw, respectively [*Schuur et al.*, 2007]. If we include those ANPP numbers in the calculation of a site-averaged community decomposition constant (using an average moss constant from Figure 5), decomposition constants become similar among sites, ranging from 0.122 at minimal thaw to 0.129 at extensive thaw. Plant community effects on decomposition at our site are therefore small, but will be dependent on future changes to moss productivity.

4.5. Relative Effects of Environment and Substrate Changes

[33] The relative effects of moisture on decomposition are greater than the effect of changing plant community composition. A 57% decrease in graminoid productivity and a concurrent 47% increase in shrub productivity caused by permafrost thaw [*Schuur et al.*, 2007] only increased the decomposition constant by 21%, and including moss productivity negates that increase. In contrast, a similar 50% increase in precipitation from 200 to 300 mm per growing season increased mass loss in the top 10 cm of soil by almost 100%, and a 50% decrease in depth to the water table from 30 to 15 cm increased mass loss in the top 10 cm of soil by over 100%. Therefore, surface decomposition is being driven more by precipitation variability and changes to the soil environment than by changing plant communities.

[34] Looking forward, a predicted 20% increase in arctic precipitation [*ACIA*, 2005; *IPCC*, 2007] would increase growing season precipitation at our site from the mean of 224 mm to 270 mm, resulting in a 40% increase in surface decomposition. Future effects of plant community may rely on moisture too because moss productivity is negatively related to water table depth and the ratio of shrub foliar to woody biomass is positively related to water table depth [*Bubier et al.* 2006]. Although, the overall decomposition effect of less moss and more wood litter, or more moss and less wood litter, is likely similar. The future effect of moisture is therefore likely to be stronger than the future effect of plant community change. However, plant communities can affect soil moisture: the water-retaining properties of moss can mitigate the effect of drought, promoting the decomposition of vascular leaf litter [*Jackson et al.* 2011; *Jackson et al.* 2013].

4.6. Relationship Between Decomposition and Carbon Flux

[35] The contribution of heterotrophic respiration to surface soil CO_2 efflux is an important component of ecosystem respiration and net ecosystem exchange. Annual substrate mass loss in the top 10 cm of soil was positively related to growing season ecosystem respiration at CiPEHR where flux and decomposition measurements were paired (regression with plot as a random effect, $R^2 = 0.10$, $p = 0.004$). Increased moisture availability has been shown to increase tundra ecosystem respiration [*Zona et al.* 2012; *Dagg and Lafleur*, 2011], a response that may be driven, in part, by surface soil decomposition. A meta-analysis of tundra warming experiments found that ecosystem respiration responses to warming were smaller where conditions were moist or wet indicating increased soil moisture may buffer ecosystem C losses against warming temperatures [*Oberbauer et al.*, 2007]. However, our study indicates increased soil moisture corresponds to greater decomposition rates and ecosystem respiration and therefore promotes C loss.

[36] As climate change causes permafrost to thaw and precipitation to increase across tundra ecosystems, decomposition rates and ecosystem respiration will change as a result of shifting soil moisture availability. This research suggests that increased moisture will lead to increased decomposition losses and that moisture has a stronger effect on surface soil decomposition than soil temperature. Most current research on the permafrost thaw climate change feedback focuses on temperature effects because ultimately temperature controls whether the soil is frozen or not, but once thawed, soil temperature may become a less important driver relative to soil moisture.

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