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Initial Stages of Tundra Shrub Litter Decomposition May Be Accelerated by Deeper Winter Snow But Slowed Down by Spring Warming

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ABSTRACT

The Arctic climate is projected to change during the coming century, with expected higher air temperatures and increased winter snowfall. These climatic changes might alter litter decomposition rates, which in turn could affect carbon (C) and nitrogen (N) cycling rates in tundra ecosystems. However, little is known of seasonal climate change effects on plant litter decomposition rates and N dynamics, hampering predictions of future arctic vegetation composition and the tundra C balance. We tested the effects of snow addition (snow fences), warming (open top chambers), and shrub removal (clipping), using a full-factorial experiment, on mass loss and N dynamics of two shrub tissue types with contrasting quality: deciduous shrub leaf litter (*Salix glauca*) and evergreen shrub shoots (*Cassiope tetragona*). We performed a 10.5-month decomposition experiment in a low-arctic shrub tundra heath in West-Greenland. Field incubations started in late fall, with harvests made after 249, 273, and 319 days of field incubation during early spring, summer and fall of the next year, respectively. We observed a positive effect of deeper snow on winter mass loss which is considered a result of observed higher soil winter temperatures and corresponding increased winter microbial litter decomposition in deep-snow plots. In contrast, warming reduced litter mass loss during spring, possibly because the dry spring conditions might have dried out the litter layer and thereby limited microbial litter decomposition. Shrub removal had a small positive effect on litter mass loss for *C. tetragona* during summer, but not for *S. glauca*. Nitrogen dynamics in decomposing leaves and shoots were not affected by the treatments but did show differences in temporal patterns between tissue types: there was a net immobilization of N by *C. tetragona* shoots after the winter incubation, while *S. glauca* leaf N-pools were unaltered over time. Our results support the widely hypothesized positive linkage between winter snow depth and litter decomposition rates in tundra ecosystems, but our results do not reveal changes in N dynamics during initial decomposition stages. Our study also shows contrasting impacts of spring warming and snow

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addition on shrub decomposition rates that might have important consequences for plant community composition and vegetation-climate feedbacks in rapidly changing tundra ecosystems.

INTRODUCTION

Although decomposition of plant litter plays a major role in the global carbon (C) cycle, Earth system model predictions are currently hampered by limited knowledge on the potential contrasting winter and summer climate change impacts on decomposition rates through their effects on microbial decomposer communities and plant-soil nitrogen (N) dynamics (Bonan and others 2013; Wieder and others 2013). Climatic changes in the Arctic could influence plant decomposition rates, which in turn might affect tundra C and N cycling (Hobbie 1996) and tundra ecosystem C storage (Mack and others 2004; Lupascu and others 2014). Changes in plant decomposition rates might alter the N availability in nutrient-poor tundra ecosystems that in turn might modify plant species composition through plant–plant and plant–microbe competition for N (Sistla and others 2014). As a result, changes in plant decomposition rates might alter the tundra C balance by modifying the quality and quantity of soil organic matter inputs (Cornelissen and others 2007). If arctic warming would lead to higher plant decomposition rates (Aerts 2006) and associated N-release (Hobbie 1996), plant functional types such as deciduous shrubs with high N uptake capacity and high potential growth rates might increase in dominance (Elmendorf and others 2012a).

As a result of the expected rising air temperatures (IPCC 2013) and changes in winter precipitation regimes (Bintanja and Selten 2014) in the tundra biome during the coming century, tundra shrub growth is expected to proliferate, with shrubs increasing in stature and cover (Myers-Smith and others 2011; Elmendorf and others 2012b). By trapping snow with their branches during the winter-time, shrubs can locally increase the snow depth and thus raise winter soil temperatures, thereby potentially increase winter soil mineralization rates (Schimel and others 2004) and plant N availability (Vankoughnett and Grogan 2014). When shrubs are able to acquire higher amounts of N under deep-snow conditions, as recently demonstrated in High-Arctic tundra (Blok and others 2015; Semenchuk and others 2015), a positive feedback can set up between shrub height growth and winter snow depth. This positive feedback has been termed the "snow-shrub hypothesis" (Sturm and others 2001). Despite observations of enhanced plant decomposition rates with deeper snow along natural snow depth gradients (Saccone and others 2013; Carbognani and others 2014) and increased winter soil respiration rates under deeper snow (Natali and others 2014), there is of yet no direct experimental evidence that deeper snow accelerates litter decomposition rates in arctic tundra ecosystems (DeMarco and others 2014).

Shrubs might alter the microclimate during summer in contrasting ways: on one hand, shrubs might reduce the surface albedo and create atmospheric heating (Chapin and others 2005; Sturm and others 2005a), but on the other hand, they might also lead to summer soil cooling by shrub shading (Blok and others 2010; Myers-Smith and Hik 2013). These shrub-induced changes in summer air and soil temperatures might, however, also indirectly affect decomposition rates through changes in soil moisture, as microbial decomposer communities are water dependent (Robinson and others 1995; Hicks Pries and others 2013). Shrub-controlled changes in winter soil temperatures might have carry-over effects on summer decomposition and soil respiration rates (DeMarco and others 2011), which might offset growing season carbon gains by increased plant productivity (Natali and others 2012, 2014) and thus create a positive feedback to tundra shrub expansion by increasing N availability to shrubs (Sturm and others 2005b). It is therefore important to simultaneously study winter and summer climate change impacts on tundra shrub decomposition rates to increase the understanding of tundra vegetation-climate feedbacks (Wookey and others 2009).

When shrubs grow taller they could potentially increase soil microbial activity by changing soil thermal conditions during winter and summer, but they could also produce greater amounts of litter and thereby create a positive feedback to N-release and shrub expansion (Sturm and others 2005b; Buckeridge and others 2010). An expansion of shrubs might also modify tundra decomposition rates by causing a shift in community-weighted plant functional traits (Cornelissen and Makoto 2013), for example, by increasing leaf lignin content, which might reduce decomposition rates

(Cornelissen and others 2007) and ecosystem C and N cycling (Freschet and others 2012). However, the sensitivity of litter decomposition to warming has been shown to be inversely related to litter quality, with high-quality litter exhibiting a smaller decomposition response to temperature than low-quality litter because of microbial enzyme kinetics (Fierer and others 2005). Predictions on the net effect of climatic changes on tundra litter decomposition rates thus require knowledge on species-specific decomposition responses to changes in microclimate (Sundqvist and others 2011).

To summarize, changes in both winter and summer climate might feedback to shrub growth in tundra ecosystems through changes in decomposition rates and litter nitrogen release (Wookey and others 2009). However, winter and summer climate change effects on decomposition rates have not been well studied, especially in combination. Here, we studied the interactive effects of snow addition (snow fences), warming (open top chambers), and shrub removal (clipping), using a full-factorial experiment, on mass loss rates and nitrogen dynamics in two contrasting arctic plant tissue types: deciduous shrub *Salix glauca* leaf litter and evergreen shrub *Cassiope tetragona* green shoots. We assessed how treatment effects on decomposition rates differed among the winter, spring, and summer season during a 10.5-month incubation period in the field. Field incubations started in late fall, with harvests made after 249, 273, and 319 days of incubation during early spring, summer, and fall of the next year. We hypothesized (i) deeper snow will result in greater plant tissue mass loss and N-release during winter by soil warming but reduced mass loss in spring because of longer snow cover; (ii) warming will increase decomposition rates and N-release during spring, but decrease decomposition rates in summer because of microbial moisture limitation; (iii) shrub removal will decrease decomposition rates by lowering surface temperature through an increase in surface albedo; (iv) snow addition will have a larger relative effect on decomposition rates than warming (open top chamber) because of the long winter period; and finally, (v) we hypothesized treatments will have a greater effect on decomposition of low-quality *S. glauca* leaf litter than on high-quality green *C. tetragona* shoots.

MATERIALS AND METHODS

Site Description and Experimental Setup

The study was performed at a mesic tundra site in the Blæsedalen valley (69°16′N, 53°27′W) on the South-tip of Disko Island, West-Greenland (Fig. S1). The area has a typical low-arctic climate with a mean annual (1992–2012) air temperature of −3.0°C, warmest monthly mean air temperature during July (7.9°C), and coldest monthly mean air temperature during March (−14.0°C), measured at Arctic Station, approximately 3 km from the research site (Hansen and others 2006). The vegetation at the experimental site (max vegetation height c. 10 cm) is dominated by *Betula nana*, *Vaccinium vitis-idaea*, *Empetrum nigrum*, *Salix glauca*, *Cassiope tetragona*, and lichens (Table 1). Tall *Salix glauca* shrubs are present in close vicinity of the experimental site, but are confined to snowdrift areas at the foot of hill slopes and terrain with high topographic relief and have similar winter snow depths as in our snow manipulation plots. Soils consist of basaltic rock fragments, covered by a thin (5–10 cm) organic horizon with mean carbon to nitrogen ratios (C:N) of 22.5 (unpublished data A. Michelsen). The research site lies within the discontinuous permafrost zone. We cannot ascertain the exact active layer depth in our experimental plots by probing because of the large rocks in the soil, but two soil profiles showed that soils thawed to approximately 1.5 m during late-July 2012.

During July 2012, we established an experiment to manipulate winter snow depth, temperature, and shrub cover (Fig. S1). Six replicate blocks, each with a 14.7-m-long and 1.5-m-tall snow fence, were established to create snowdrifts on the leeward (south) side of the fences during winter (snow addition). On each side of the fences, four plots measuring 2 × 2 m were laid out. Plots were located between 3 and 8 m from the fence on the leeward snow-accumulation side of the fence in the area of maximum snow build-up and between 6 and 11 m from the fence on the windward side with ambient snow conditions. Half of the plots were covered year-round (starting 17/18 July 2012) by 35-cm-tall and 3-mm-thick polycarbonate hexagon open top chambers (OTCs) to increase air temperature, measuring 150 cm diameter at the base and 85 cm diameter at the top (warming). In half of the plots, shrubs were clipped at the surface during late-summer 2012 (shrub removal). Vascular and non-vascular plant cover, biomass data of removed shrub biomass, and shrub leaf-to-aboveground stem biomass ratios are presented in Table 1. The three main treatments snow addition (S), warming (W), and shrub removal (R) were combined in a full-factorial design across 6 blocks (n = 6 plots per treatment combination), yielding 48 plots in total. Soil temperatures (5-cm depth) and surface air temperatures (1–2 cm above the soil

Table 1. Plant Cover (n = 48 plots), Removed Biomass (From Plots with Shrub Removal Treatment, n = 24 plots), and Leaf:Branch Mass Ratios (From Plots with Shrub Removal Treatment, n = 24 plots)

Functional group/species	Cover (%)	Biomass removed (g dry weight m^{-2})	Leaf/branch mass (ratio)
Deciduous shrub	55.0 (3.7)	92.6 (9.6)	
Betula nana	24.8 (3.0)	73.0 (9.5)	0.6 (0.2)
Salix glauca	4.7 (0.8)	8.1 (1.2)	0.9 (0.1)
Vaccinium uliginosum	25.5 (1.7)	11.6 (1.6)	0.7 (0.0)
Evergreen shrub	27.4 (2.2)	66.8 (6.4)	
Cassiope tetragona	7.3 (0.9)	40.3 (5.3)	2.2 (0.1)
Empetrum nigrum	16.3 (1.9)	26.4 (3.3)	1.2 (0.1)
Graminoid	1.0 (0.2)		
Forb	3.9 (0.6)		
Moss	11.2 (1.2)		
Lichen	25.4 (1.9)		
Litter	19.0 (1.0)		

Values are means (n = 48 plots for plant cover data; n = 24 plots for biomass and leaf/branch ratio data) ± SE (between brackets). No differences in plant cover were measured between treatments at the start of the experiment; therefore, only overall means are shown. Cover was measured during summer 2012 (before shrub removal treatment commenced) and expressed as number of hits recorded in a 70*70 cm square frame with 100 grid points. A hit was recorded when a pin, vertically lowered from the top of the canopy to the ground, touched a species. A single species could be recorded multiple times per grid point. Further, shrub biomass data from shrub removal plots are presented (removed during July 2012), together with associated leaf-to-branch ratios per shrub species removed.

surface) were measured continuously in all plots of three and two blocks, respectively (n = 2–3 plots treatment combination^{-1}), using TinyTag PB-5001 thermistor probes (Gemini Data Loggers, UK) and logged every hour. Soil moisture was measured continuously (integrated over 0- to 5-cm depth) in all plots of three blocks (n = 2–3 plots treatment combination^{-1}) using Decagon EC-5 water content sensors (Decagon Devices, WA, USA) and logged every 10 min. Snow depth measurements were carried out at 1-m intervals in all snow fences during late March 2013 in transects perpendicular to the fences, extending 10 m on each side. Winter snow depth and snowmelt timing was determined from daily photographs taken by automated cameras that captured three complete blocks.

^{15}N-Labeling, Plant Collection, and Litterbag Construction

Within 20 m of the experimental snowfence blocks, fourteen 1 m^2 "spray plots" were established, with half of these spray plots dominated by evergreen shrub _Cassiope tetragona_ and half of the spray plots dominated by deciduous shrub _Salix glauca_. Spray plots were sprayed six times with a 5 mM solution of 98+ at.% ^{15}N-urea (Cambridge Isotope Laboratories, Inc., USA) during a two-week period in mid-July 2012 using a pressurized plant sprayer to create leaf and shoot material enriched in the heavy N isotope ^{15}N. Before spraying commenced, all _S. glauca_ leaf litter deposited during previous years was removed to prevent mixing

with ^{15}N-enriched litter and to assess ^{15}N natural abundances. For determination of _C. tetragona_ shoot-^{15}N natural abundances, green shoot tips from the shrub removal plots within the six experimental blocks were used. Each spray plot received 0.5 L of the ^{15}N-urea solution per spray round in the form of a fine mist, equal to a total of 0.2 g ^{15}N m^{-2} for the six spray rounds combined. After spraying, plots were covered with a clear transparent foil for 24 h to achieve maximum ^{15}N-uptake by shoots and leaves, a method applied successfully before by Zeller and others (1998). Freshly senesced _S. glauca_ leaf litter and _C. tetragona_ green shoots were collected from the spray plots during leaf senescence in mid-September 2012. Collected litter and shoots were oven-dried for 24 h at 40°C to constant weight. After drying, green shoot tips of _C. tetragona_ were separated from older shoot parts as ^{15}N-urea uptake through leaves presumably occurred mostly in the most recent green shoot increments. We used _C. tetragona_ green shoot tips with low C:N ratios and _S. glauca_ leaf litter material with high C:N ratios. Green _C. tetragona_ shoots most likely decompose faster than old growth gray _C. tetragona_ shoot increments and as such cannot be regarded as true litter. The green _C. tetragona_ shoot parts we used thus likely overestimated initial decomposition rates of _C. tetragona_ litter. However, our aim was to determine climate change impacts on mass loss and N dynamics during early decomposition stages using two very contrasting plant tissue types. We did not attempt to compare evergreen versus deciduous shrub litter

responses to warming or generalize responses across all tundra plant functional types. Samples of ±0.35 g dry *S. glauca* leaf litter and ±0.5 g *C. tetragona* green shoot tips were weighed to a precision of 0.1 mg. Samples were sealed into 30 cm^2 mesh bags (hereafter referred to as *litterbags*) using non-corroding staples. The mesh material had 0.68 mm openings and an open surface area of 67%, allowing water and micro-arthropod passage, while preventing leaf and shoot fragments from falling out of the litterbags (Bokhorst and Wardle 2013).

Litterbag Incubation Experiment

Three litterbags of each type were placed in all 48 plots of the experiment on October 9, 2012, 1 day after the first post-growing season winter snowfall event. Litterbags were laid out horizontally on the ground and pinned tight to the surface of the plots using non-corroding steel nails. Of each litterbag type, 10 samples were kept for determination of initial litter chemistry and ^{15}N-concentrations. The first set of litterbags (one litterbag per shrub tissue type per plot) was collected immediately after snowdrifts were completely melted on the leeward side of the fences on June 14, 2013 (winter incubation). The second set of litterbags was collected by the end of spring, July 8, 2013 (winter + spring incubation). The final, third set of litterbags was collected by the end of summer, August 23, 2013 (winter + spring + summer incubation).

Mass Loss, Litter Chemistry, and Isotopic Composition

Harvested litterbags were air-dried for several days immediately after sampling before shipment to the lab, where leaf and shoot mass was determined after oven drying at 40°C for 96 h. Mass loss was determined as the fraction of initial mass lost after field incubation. Mass loss rates were calculated by dividing mass loss fractions by the incubation time in days to assess differences in decomposition rates across seasons. After mass loss determination, samples were ground to a fine powder. Approximately 3–4 mg ground *S. glauca* or *C. tetragona* material was packed into tin capsules to determine N isotopic ratios (^{15}N:^{14}N), N concentrations (%N), and C concentrations (%C) on an Isoprime isotope ratio mass spectrometer (Isoprime Ltd., Cheadle Hulme, UK) coupled to a CN elemental analyzer (Eurovector, Milan, Italy). The standard deviation of isotope measurements of the standards was ±0.2 ppm (‰) for δ^{15}N. Total pools of ^{15}N in *S. glauca* leaves and *C. tetragona* shoots were calculated from ^{15}N-enriched atom percentages (atom% ^{15}N$_{sample}$ = 100*$R_{standard}$*((δ^{15}N$_{sample}$/1000 + 1)/(1 + $R_{standard}$ *(δ^{15}N$_{sample}$/1000 + 1)). ^{15}N-enrichment atom% relative to *S. glauca* litter and *C. tetragona* shoot ^{15}N$_{natural\ abundance}$ (atom%^{15}N$_{excess}$) were calculated by deducting atm%^{15}N$_{natural\ abundance}$ values from atm%^{15}N$_{sample}$. Total pools of ^{15}N$_{excess}$ in *S. glauca* leaf litter and *C. tetragona* shoots incubated in plots were calculated by multiplying litter and shoot dry mass with atom%^{15}N$_{excess}$ values.

Statistical Analyses

Effects of snow addition, warming (OTC), and shrub removal on surface air temperature, soil temperature, soil moisture, litter mass loss, N-pools, ^{15}N-pools, %C, %N, and C:N ratios in remaining leaf litter and shoot mass were analyzed separately per incubation period (winter, spring, summer) using the PROC MIXED procedure in SAS Enterprise Guide 6.1. Analyses of treatment effects on litter parameters were performed separately per litter type (*S. glauca* leaves, *C. tetragona* shoots). Cumulative treatments effects (winter + spring, winter + spring + summer) were also analyzed for each litter parameter. We performed mixed-model analyses to assess seasonal treatment effects on all litter parameters, whereby we took into account the previous-season winter and winter + spring variances as fixed factor for analysis of treatment effects during spring and summer, respectively. Bonferroni corrections were applied by down-adjusting the significance threshold level threefold, taking into account the three repeated litterbag samplings over time. Thus, *P*-values below 0.017 were considered statistically significant. Data were natural log-transformed where needed to achieve normal distributions. Snow addition, warming (OTC), shrub removal, and their interactions, were selected in the models as fixed factors. Block was selected as random factor in the mixed models. We reduced the models step-wise by subsequently eliminating the three-way and the two-way interactions when these interactions were non-significant. Fixed effects were determined by the Restricted Maximum Likelihood (REML) method and degrees of freedom were estimated by the Kenward–Roger method. Remaining total N-pools and ^{15}N-pools in leaves and shoots were calculated as percentage of initial pre-incubation leaf and shoot N and ^{15}N-pools, respectively. We used paired t-tests to assess whether leaf and shoot N-pools and ^{15}N-pools changed significantly over time compared to initial leaf and shoot N- and ^{15}N-pools.

RESULTS

No significant interaction effects among main treatments were observed for any of the measured variables. Therefore, only main treatment effects are presented here.

Snow Depth, Soil and Surface Air Temperature, and Soil Moisture

Winter snow depth reached up to approximately maximum 140 cm in deep-snow plots on the leeward side of the fences and reached a maximum of approximately 40 cm in windward-located ambient snow plots, covering the OTCs completely during a great part of the winter. A spring warming event resulted in almost snow-free conditions (3 ± 2 cm) in ambient snow plots on March 26, 2013, whereas a thick snow layer remained until June 14, 2013 in snow addition plots (86 ± 5 cm).

The snow addition treatment significantly increased surface air temperatures by approximately 1.7°C during the winter period ($F_{1,9} = 12.6$, $P < 0.01$), but not during spring and summer (Fig. 1A; Table 2). Winter soil temperatures were significantly higher in snow addition plots by 1.6°C compared to ambient snow plots ($F_{1,18} = 61.6$, $P < 0.001$), but 1.6°C lower than ambient snow plots during spring ($F_{1,18} = 9.2$, $P < 0.01$; Fig. 1B; Table 2). Snow addition did not significantly affect soil temperatures during summer. Soil moisture was not significantly affected by the snow addition treatment during any period (Fig. 1C; Table 2).

The OTCs had a small significant warming effect (0.6°C) on winter soil temperature compared to ambient plots ($F_{1,18} = 7.9$, $P < 0.05$), but not on winter surface air temperature. During spring ($F_{1,8} = 14.0$, $P < 0.01$) and summer ($F_{1,8} = 64.4$, $P < 0.001$), the OTCs significantly increased surface air temperature by, respectively, 2.2 and 2.7°C compared to plots without OTCs, but soil temperatures were not significantly different during spring and summer (Fig. 1A, B; Table 2). The OTCs did not significantly affect soil moisture during any season (Fig. 1C; Table 2), neither did they affect the timing of complete snowmelt.

Shrub removal did not significantly affect surface air temperature or soil temperature, nor did it affect soil moisture during any measurement period (Table 2).

Litter Mass Loss and Nitrogen Pools

Winter litter mass loss was significantly higher by 47% for *S. glauca* leaves ($F_{1,39} = 25.8$, $P < 0.001$)
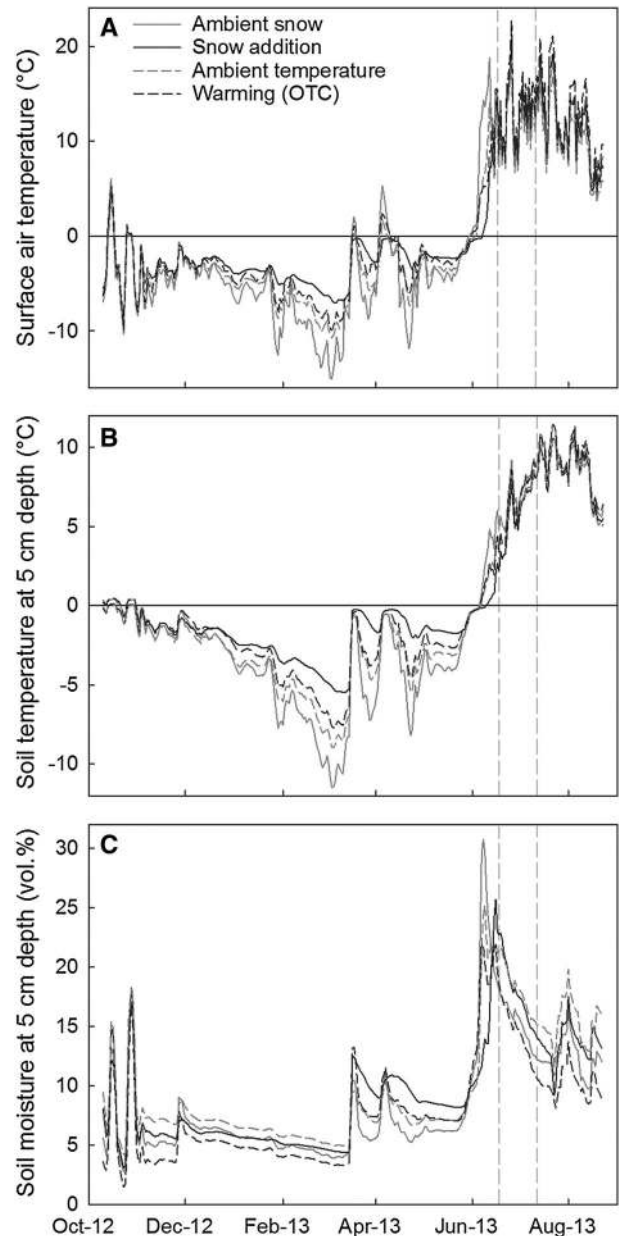

Figure 1. A Surface air temperature, **B** soil temperature at 5-cm depth, and **C** soil moisture integrated over 0- to 5-cm depth during the decomposition experiment, presented separately for main treatments snow addition and warming (OTC), as well as their non-manipulated controls. Values are daily means ($n = 7–12$ plots treatment^{-1}), with gray and black continuous lines showing values in ambient snow and snow addition plots, respectively. The *gray* and *black dashed lines* show values in ambient temperature and warmed (OTC) plots, respectively. *F*- and *P*-values of treatment effects are presented in Table 2. The vertical *dashed gray lines* indicate the start of the spring and summer period. Only snow addition and warming treatments showed persistent significant effects and are therefore presented.

Table 2. Treatment Effects on Surface Air/Soil Temperature and Soil Moisture during the Winter, Spring, and Summer Incubation Periods

	Snow addition	Warming (OTC)	Shrub removal
Surface air temperature			
Winter	12.6**	3.1	0.0
Spring	0.3	14.0**	3.1
Summer	0.2	64.4***	2.8
Soil temperature (5-cm depth)			
Winter	61.6***	7.9*	3.6
Spring	9.2**	0.1	5.0
Summer	2.7	3.4	1.5
Soil moisture (0–5 cm depth)			
Winter	0.0	0.1	4.1
Spring	1.0	0.8	4.2
Summer	0.0	4.0	1.7

Measurements were made during winter (10 October 2012 to 14 June 2013), spring (15 June to 8 July 2013) and summer (9 July to 23 August 2013) incubation periods. Temperature was measured at the soil surface and at 5-cm depth using soil thermistor loggers (n = 2–3 plots treatment^{-1}). Soil moisture was measured over 0- to 5-cm depth using soil moisture loggers (n = 2–3 plots treatment^{-1}). Shown are F-values of main treatment effects snow addition, warming (OTC), and shrub removal, with asterisks indicating the significance level (*P < 0.05; **P < 0.01; ***P < 0.001). No interaction effects between main treatments were observed for any of the measured variables; therefore, only main treatments were included as explanatory variables in the statistical mixed models.

and higher by 33% for *C. tetragona* shoots ($F_{1,39} = 9.8$, $P < 0.01$) in snow addition plots compared to litter mass loss measured in ambient snow plots (Fig. 2A; Table 3). The positive effect of deeper snow on mass loss remained significant throughout spring and summer for both *S. glauca* leaves and *C. tetragona* shoots when looking at cumulative mass losses (Fig. 2A), but not when analyzed separately for the spring and summer incubation periods and winter and winter + spring litter mass loss variances were taken into account (Table 3). A major proportion of the cumulative mass loss during the approximately 11-month incubation period took place during winter, with 87% of total *C. tetragona* mass loss and 72% of total *S. glauca* mass loss occurring during the snow-covered period (Fig. 2A). Total N-pools and ^{15}N-pools were not significantly affected by the snow addition treatment in either *S. glauca* leaves or *C. tetragona* shoots (Fig. 2B, C). Total N-pools of *C. tetragona* shoots did change significantly over time, with net N-immobilization occurring after winter [t(47) = −4.41, $P < 0.001$] and winter + spring incubation [t(47) = −3.95, $P < 0.001$], followed by net N-release to pre-incubation values after winter + spring + summer incubation [t(47) = 0.73, $P > 0.01$, Fig. 2B]. No changes in *S. glauca* total N-pools were observed over time during the incubation experiment (Fig. 2B). Urea-^{15}N spraying led to heavily enriched pre-incubation litter δ^{15}N-values, on average $2174 \pm 134\textperthousand$ for *C. tetragona* shoots and $6057 \pm 368\textperthousand$ for *S. glauca* leaf litter. Temporal patterns in ^{15}N-pools differed between species, with

S. glauca leaves showing a significant loss during the winter incubation period [t(47) = −3.70, $P < 0.001$], whereas for *C. tetragona* shoots a ^{15}N-pool loss was only apparent after the entire 11-month incubation period [t(47) = −4.09, $P < 0.001$, Fig. 2C].

Warming (OTC) had a significant negative effect on *S. glauca* leaf ($F_{1,38} = 7.1$, $P < 0.05$) and *C. tetragona* shoot ($F_{1,43} = 7.6$, $P < 0.01$) mass loss during spring, but did not significantly affect mass loss during summer (Table 3). The strongest significant warming effect was observed on cumulative *S. glauca* mass losses over the full winter–summer incubation period ($F_{1,44} = 8.3$, $P < 0.01$), showing 15% lower mass loss in warmed plots by late August compared to ambient temperature plots (Fig. 2D). For *C. tetragona* shoots, cumulative mass losses were not significantly reduced in plots with OTCs compared to ambient temperature plots (Fig. 2D). Warming (OTC) did not significantly affect total N- (Fig. 2E) or ^{15}N-pools (Fig. 2F) during any incubation period (Table 3).

Shrub removal had a small positive effect on *C. tetragona* mass loss during the summer incubation period, but not on *S. glauca* leaf litter decomposition (Table 3). No significant effects of shrub removal on *S. glauca* leaf or *C. tetragona* shoot N-pools were observed (Fig. S2C, D, Table 3), neither were ^{15}N-pools not significantly affected by the shrub removal treatment for either *S. glauca* leaves or *C. tetragona* shoots during any incubation period (Table 3).

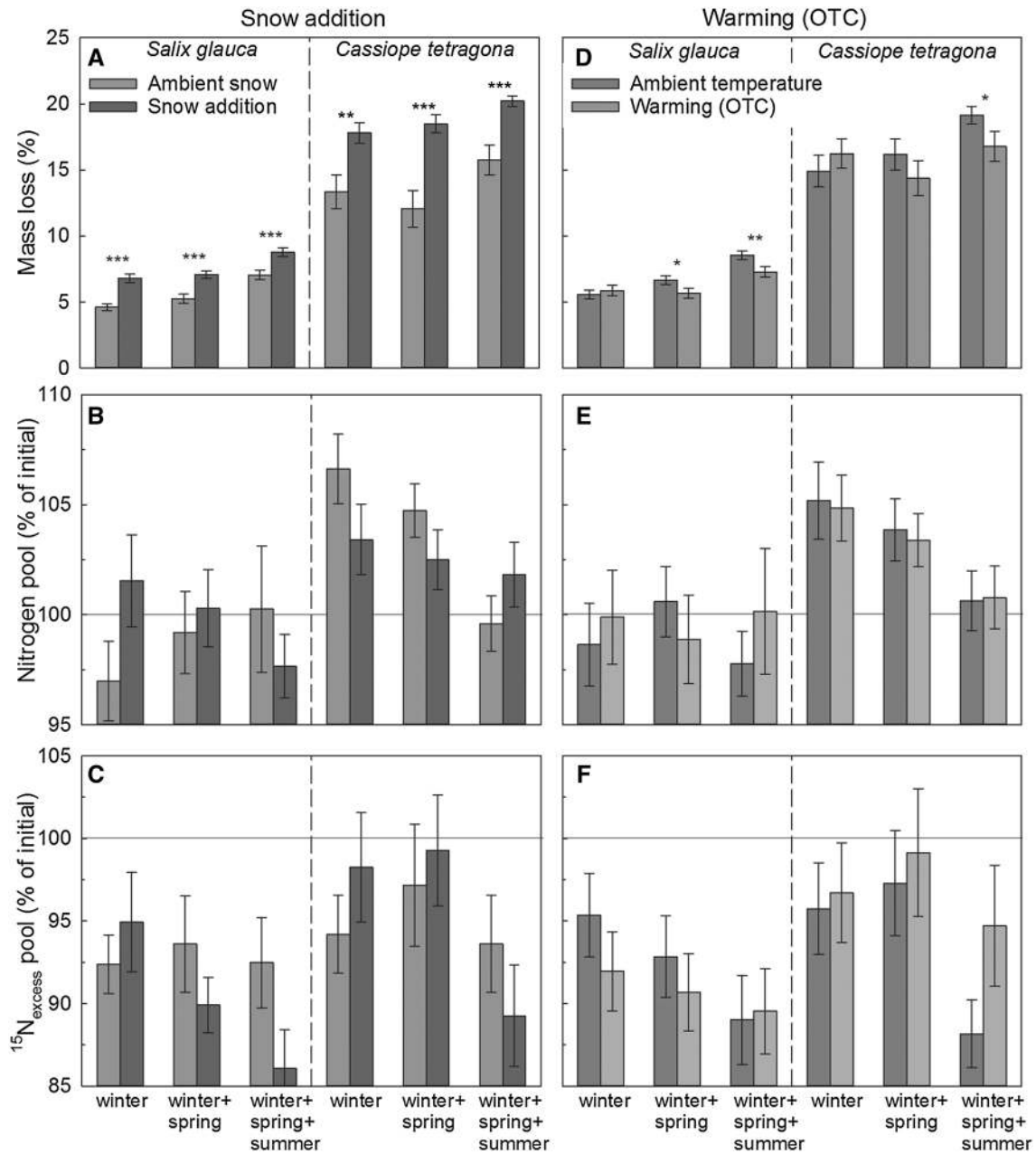Mean mass loss rates were relatively constant throughout the entire incubation period, but de-

Figure 2. Mass loss (**A**, **D**), percentage total remaining nitrogen (N) pool (**B**, **E**), and percentage total remaining ^{15}N pool (**C**, **F**) of *Salix glauca* leaf litter and *Cassiope tetragona* shoots in plots with snow addition (left column) and warming (OTC) (right column) after incubation during winter, winter-spring, and winter-spring-summer. Values are means ($n = 24$ litterbags treatment[-1] incubation period[-1]). Symbols above bars indicate significance levels of treatment: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. F-values and statistics on all main treatment effects are presented in Table 3. Only snow addition and warming showed significant treatment effects and are therefore presented. Full data of mass loss, total N-pools, ^{15}N-pools, %C, %N, and C:N ratios per treatment combination and statistical results on all main treatment effects are presented in Figure S2 and Table S3. Note the vertical axis is stunted for panel **B**, **C**, **E**, and **F**. Gray horizontal lines represent initial pre-incubation N-pool and ^{15}N-pool values ($n = 10$ litterbags litter type[-1]).

clined in snow addition plots after the winter incubation period for *C. tetragona* shoots, but not for *S. glauca* leaves. *Cassiope tetragona* shoot mass loss

rates showed a similar decline in warmed plots (OTC) after the winter incubation period, but not for *S. glauca* leaves (Fig. 3).

Table 3. Treatment Effects on Leaf/Shoot Mass Loss, Nitrogen Pools, and ^{15}N-nitrogen Pools during the Winter, Spring, and Summer Incubation Periods

	Mass loss (%)	N-pool (%initial)	^{15}N-pool (%initial)
Winter incubation period			
Salix glauca			
Snow addition	25.8***	2.7	0.5
Warming (OTC)	0.2	0.2	0.9
Shrub removal	2.6	0.1	0.1
Cassiope tetragona			
Snow addition	9.8**	2.0	1.0
Warming (OTC)	0.5	0.0	0.1
Shrub removal	0.0	1.6	2.3
Spring incubation period			
Salix glauca			
Snow addition	7.6**	0.0	1.4
Warming (OTC)	7.1*	0.5	0.4
Shrub removal	0.9	0.7	4.9*
Cassiope tetragona			
Snow addition	6.0*	1.9	0.2
Warming (OTC)	7.6**	0.1	0.1
Shrub removal	0.0	0.1	0.9
Summer incubation period			
Salix glauca			
Snow addition	4.0	0.8	2.3
Warming (OTC)	4.0	0.7	0.1
Shrub removal	0.0	1.9	1.1
Cassiope tetragona			
Snow addition	1.3	1.3	0.9
Warming (OTC)	3.5	0.0	2.9
Shrub removal	7.2*	0.9	0.1

*Shown are F-values of main treatment effects snow addition, warming (OTC), and shrub removal on percentage mass loss, percentage remaining total N-pool, and percentage remaining total $^{15}N_{excess}$ pool in Salix glauca leaf litter and Cassiope tetragona shoots during the winter, spring, and summer incubation periods, with asterisks indicating level of significance (*P < 0.05; **P < 0.01; ***P < 0.001). No interaction effects between main treatments were observed for any of the measured variables; therefore, only main treatment effects are presented.*

DISCUSSION

Snow Depth Effects on Litter Decomposition

Our study shows significant positive effects of experimental snow addition on shrub decomposition rates, partly supporting the snow–shrub hypothesis that the positive interaction between shrub growth and winter snow depth can drive tundra shrub expansion by enhancing winter plant decomposition rates and increasing litter N-release and shrub N uptake (Sturm and others 2005b; Hallinger and others 2010). However, this hypothesis was based on correlations between snow depth and shrub height along natural gradients and was not experimentally validated as a positive feedback mechanism to explain the observed increase in shrub cover across the tundra biome (Tape and others 2006; Myers-Smith and

others 2011). Our results provide a mechanistic explanation for the observed positive shrub growth response to deeper winter snow that has been observed earlier in a snow manipulation experiment in High-Arctic Svalbard (Blok and others 2015). Our results are in line with litter incubation studies performed along transects of natural snow depth gradients in alpine tundra grasslands (Baptist and others 2010; Saccone and others 2013; Carbognani and others 2014), which all show consistent positive effects of late versus early snowmelt on decomposition rates. Comparable experimental studies on the effects of elevated snow depth on plant litter decomposition rates performed in arctic tundra ecosystems are rare, but so far have not shown any significant effects of deepened snow on decomposition rates. Recently, DeMarco and others (2014) showed significant effects of shrub cover on decomposition rates of a common substrate in a
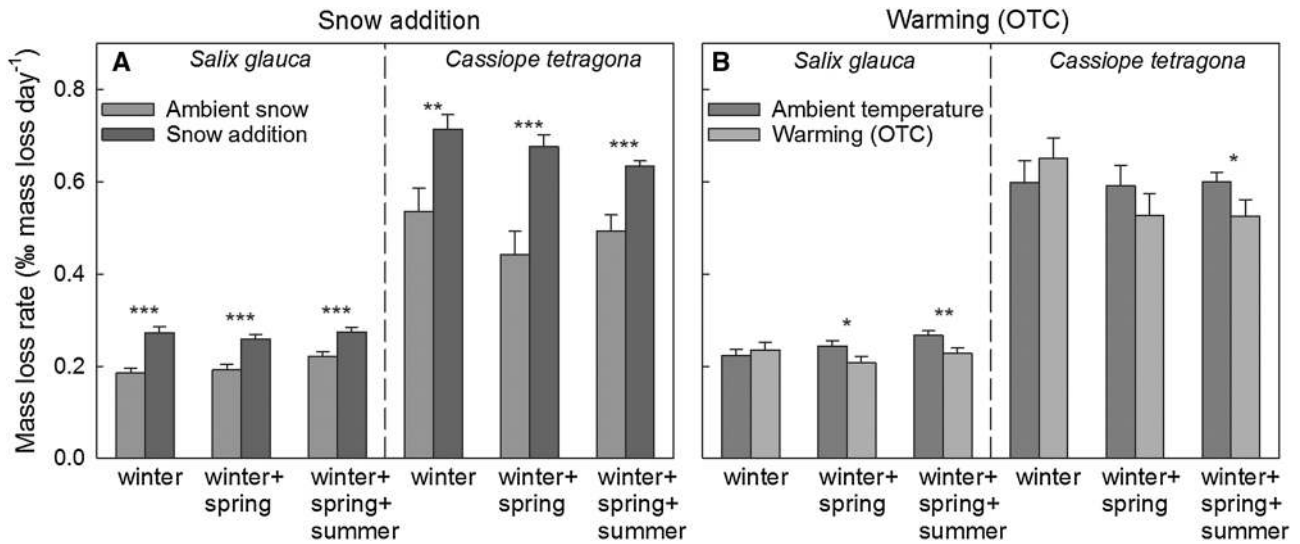
Figure 3. Average daily mass loss rates of *Salix glauca* leaf litter and *Cassiope tetragona* shoots in plots with snow addition (**A**) and warming (**B**) after incubation during winter, winter-spring, and winter-spring-summer. Values are means ($n = 24$ litterbags treatment^{-1} incubation period^{-1}). Symbols above bars indicate significance levels of treatment: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$. Only snow addition and warming (OTC) showed significant treatment effects and are therefore presented.

tundra ecosystem, but not of experimentally increased snow depth. Aerts and others (2012) measured mass loss of graminoid (*Calamagrostis lapponica*), deciduous shrub (*Betula nana*) and perennial herb (*Rubus chamaemorus*) leaf litter after 2 and 4 years incubation in plots with elevated and ambient snow depths, but did not observe significant snow depth effects on mass loss for any litter type. Likewise, Walker and others (1999) did not show significant effects of snow depth on *Betula nana* mass loss in a tundra ecosystem even with a large snow depth increase (2–3 m). Although all three of these experimental studies do not reveal significant effects of winter snow depth on mass loss, they do indicate non-significant greater mass loss in snow addition plots compared to ambient snow plots. The high replication number in our three-way factorial experiment might have compensated for the random variation that is inherent in decomposition studies and thereby allowed detection of significant treatment effects. Although the absolute differences in first-year mass loss were small between snow-manipulated and ambient snow plots in our study, relative mass loss differences between treatments were substantial and comparable to differences in mass loss observed between markedly contrasting plant functional types such as graminoids and evergreen shrubs (Cornelissen and others 2007).

Our results do not support the hypothesis that increased litter decomposition rates, driven by deeper snow, initiate a positive feedback to taller shrub growth through higher winter litter N-mineralization (Sturm and others 2001). We cannot, however, exclude the possibility that deeper winter snow increases litter N-mineralization during later stages of decomposition. Although in our experiment litter mass loss increased with deeper winter snow, we did not observe a significant effect of snow addition on litter N dynamics during the entire incubation period. This result is in line with results from a 3-year litter incubation experiment in Alaska that used snow fences to manipulate snow depth (DeMarco and others 2014) but is in contrast to another Alaskan litter decomposition study showing a significant net N-release during the first winter of litter decomposition (Hobbie and Chapin 1996). In our study, N-pools of *C. tetragona* shoots revealed a different temporal pattern than N-pools of *S. glauca* leaves and showed initial N-immobilization during winter, followed by net N-release during spring and summer towards pre-incubation N-pool values. This pattern might be explained by a rapid microbial colonization of *C. tetragona* green shoots, with low C:N ratios, by fast-growing microbial communities during the earliest stages of decomposition in the winter-time, followed by a rapid succession in spring and summer towards slower-growing microbial communities in sequential litter decay stages coinciding with lower *C. tetragona* shoot C:N ratios (Voriskova and Baldrian 2013). We observed loss of leaf and shoot

¹⁵N-pools, but stable or increasing total N pools during first-year decomposition, suggesting colonization of microbes might have compensated for leaching of sugars and amino acids from leaves and shoots.

A major part of the first-year mass loss occurred during winter, which is consistent with a seasonal litter decomposition study in an Alaskan tundra site by Hobbie and Chapin (1996). Leaching of soluble organic substances during the first stages of decomposition during winter might have been responsible for the observed high winter mass loss rates, and could decline during later decomposition stages of cellulose and lignin degradation (Berg and McClaugherty 2003). An experiment that mimicked extreme winter warming events and mid-winter snowmelt, conducted in Northern Sweden, did not reveal significant effects on decomposition rates despite the large changes in temperature involved during the warming events (Bokhorst and others 2010). The authors concluded that little or no decomposition occurs during the winter season and all litter mass loss is by leaching during fall, although a more recent study suggests that the effects of snow depth on decomposition are species dependent (Bokhorst and others 2013b). In our study, we cannot exclude the possibility that leaching caused most of the observed winter mass loss. Soil moisture conditions during winter were the same between snow addition and ambient snow plots and thus were not likely causing the observed differences in mass loss, suggesting that higher winter temperatures in the litter layer drove higher rates of microbial decomposition of litter during the snow-covered winter incubation period. Previous experimental work demonstrated that microbial activity can continue during winter at temperatures well below zero, resulting in higher soil N-mineralization rates with deeper snow (Schimel and others 2004). This result supports the hypothesis that microbial degradation might have contributed to the observed increase in winter mass loss in snow addition plots. Indeed, bacterial growth has been found to continue down to $-7°C$ in the relatively mild climate zone of sub-arctic Sweden (Rinnan and others 2009), well below daily average winter surface air temperatures measured in our snow addition plots. Fungal activity has been found to persist at even lower temperatures (Pietikåinen and others 2005), further supporting the hypothesis that plant litter decomposition might continue during winter-time under a deep-snow layer.

Snowmelt occurred unusually early at our research site during 2013, the year when litterbags were harvested. This early melt resulted in pronounced differences in snow melt timing between ambient and snow addition plots of up to two months. Nevertheless, extreme differences in snowmelt timing also occurred naturally at our site, depending on local topography, shrub height, and exposure. The vegetation in our experiment will not likely grow to a height to achieve the degree of snow accumulation through shrub snow-capture as achieved by our snow fences. However, tall shrubs (up to 1.5 m tall) do occur in our research area and accumulate similar depths of snow, but are restricted to patches in the landscape with high relief. We observed that these tall shrub patches with thick snow cover melted out around the same time as our snow-manipulated plots.

Spring and Summer Warming Effects on Litter Decomposition

In contrast to our second hypothesis, the warming treatment (OTC) reduced decomposition during spring (but not during summer), which we consider might be due to the indirect negative effect of warming on litter moisture content, leading to microbial water limitation in the top surface litter layer. We hypothesize that the litter layer might have dried out more quickly in the OTCs than in the ambient temperature control plots (Robinson and others 1997; Schimel and others 1999; Sjögersten and Wookey 2004; Bokhorst and others 2013a). Hicks Pries and others (2013) recently showed moisture limitation was the most significant driver of decomposition rates in arctic tundra. Together with our results, this result suggests that predicted warmer and drier arctic growing conditions in the coming decades might decrease litter decomposition rates in tundra ecosystems during the snow-free growing season, possibly reducing C and N cycling rates and thus providing a negative feedback to shrub expansion by decreasing N availability to shrubs. This hypothesis might partly explain the spatial heterogeneity in the growth response of shrubs to temperature in arctic tundra, observed to be strongest in moist tundra but declining towards drier tundra, which might be linked to differences in N-limitation for shrub growth across tundra moisture gradients (Myers-Smith and others 2015). We did not observe a significant effect of warming (OTC) on mass loss during the summer period, possibly because this period had more precipitation events and pulses of moisture supply to the litter layer than during the dry spring period (Fig. 1C).

Shrub Removal Effects on Litter Decomposition

We did not find evidence supporting our third hypothesis, as we observed no consistent effect of shrub removal on decomposition rates, with only *C. tetragona* shoot decomposition showing a small significant positive response during the summer incubation period. This result is in agreement with a study on shrub canopy height effects on decomposition rates performed in a Canadian arctic tundra site that found no differences in litter decomposition rates in plots with or without a shrub canopy (Myers-Smith and Hik 2013). At our site, the effect of shrub removal might have been limited because of the low-statured vegetation, whereas greater effects of shrub removal on albedo-driven changes in surface temperature could be expected in tall shrub tundra (Bonfils and others 2012). Similarly, the effect of shrub shading on decomposition of leaves and shoots incubated at the top of the soil/lichen surface might have been limited because of the short stature of shrubs at our site.

Winter versus Summer Warming Effects on Litter Decomposition

Our results provided support for our fourth hypothesis, as we observed greater (positive) effects of our snow addition treatment compared to the (negative) effects of our summer warming treatment on litter mass loss, despite the average higher surface air temperature increase achieved by the OTCs during spring and summer compared to the winter surface soil warming achieved by the snow addition treatment. Instead, this difference in treatment effect among the winter and spring/summer incubation periods might be attributed to the relative longer period of time that plots were exposed to the snow addition compared to the warming (OTC) treatment. Our results suggest that under a climate change scenario whereby both winter snow precipitation and summer temperature would increase, the earlier effect on litter decomposition rates might dominate. However, the litter decomposition response to winter snow addition is likely related to the amount of snow addition, as well as dependent on drought conditions during the snow-free season. Moisture conditions of the surface litter layer, where we incubated the litters, are highly responsive to spring and summer weather conditions. As such, the OTCs might have had a positive effect on litter mass loss if growing season conditions were cool and wet instead of the dry and warm growing season conditions during the course of our experiment, assuming that the negative effect of the OTCs on litter mass loss was related to microbial water limitation. We did not observe any interaction effect among the winter snow addition and spring/summer warming treatments, suggesting that the earlier treatment did not have carry-over effects that influenced the effects of warming on litter decomposition during the growing season.

Species-Specific Litter Decomposition Responses

Our fifth hypothesis, stating that the decomposition response to treatments is greater for low-quality tissue, was confirmed by greater effects of both snow addition and warming on litter mass loss of *S. glauca* leaves compared to green *C. tetragona* shoots. This result suggests that decomposition of recalcitrant plant matter might be more affected by climatic changes than fast-decomposing material. However, the short incubation period in our study allows only an assessment of climate change impacts on early decomposition stages. Longer term climate effects on litter decomposition rates might differ from short-term effects through their impact on N-release and plant-soil feedbacks because net litter N-mineralization has been found to require several years in cold tundra ecosystems (Aerts and others 2012).

CONCLUSIONS

Our results show that while deeper snow speeds up shrub decomposition during initial decomposition stages during winter, deeper snow does not promote net litter N-release. However, this result does not preclude the possibility that positive feedbacks between snow, litter decomposition rates, and shrub growth might occur during later stages of decomposition stages when litter N-mineralization does occur. In contrast to the observed positive effects of deeper snow, spring warming reduced decomposition rates, possibly because of microbial moisture limitation. In summary, our study shows contrasting impacts of deeper winter snow and spring warming on shrub decomposition rates, highlighting the importance of taking into account both winter and growing season climate change impacts on shrub decomposition rates in tundra ecosystems. These climate-driven changes in decomposition rates might have important consequences for plant community composition and vegetation-climate feedbacks in rapidly changing tundra ecosystems. Future research is needed to

integrate summer and winter climate change effects on tundra litter decomposition rates. Novel experimental studies are required to assess if climate change-driven changes in litter decomposition rates may be linked to changes in shrub nitrogen acquisition, thus providing a mechanistic explanation for the widespread expansion of shrubs observed in tundra ecosystems during the last decades.

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DATA ACCESSIBILITY

Data used in this study will be deposited in the Dryad ecological data archive after acceptance of the manuscript (www.datadryad.org).

OPEN ACCESS

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