Effects of arctic shrub expansion on biophysical vs. biogeochemical drivers of litter decomposition

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Abstract. Climate warming in arctic tundra may shift dominant vegetation from graminoids to deciduous shrubs, whose functional traits could, in turn, alter biotic and abiotic controls over biogeochemical cycling of carbon (C) and nitrogen (N). We investigated whether shrub-induced changes in microclimate have stronger effects on litter decomposition and nutrient release than changes in litter quality and quantity. In arctic tundra near Toolik Lake, Alaska, USA, we incubated a common substrate in a snow-addition experiment to test whether snow accumulation around arctic deciduous shrubs altered the environment enough to increase litter decomposition rates. We compared the influence of litter quality on the rate of litter and N loss by decomposing litter from four different plant functional types in a common site. We used aboveground net primary production values and estimated decay constant ($k$) values from our decomposition experiments to calculate community-weighted mass loss for each site. Snow addition had no effect on decomposition of the common substrate, and the site with the highest abundance of shrubs had the lowest decomposition rates. Species varied in their decomposition rates, with species from the same functional type not always following similar patterns. Community-weighted mass loss was 1.5 times greater in the high shrub site, and only slightly decreased when adjusted for soil environment, suggesting that litter quality and quantity are the primary drivers of community decomposition. Our findings suggest that on a short time scale, the changes in soil environment associated with snow trapping by shrubs are unlikely to influence litter nutrient turnover enough to drive positive snow–shrub feedbacks. The mechanisms driving shrub expansion are more likely to do with shrub–litter feedbacks, where the higher growth rates and N uptake by shrubs allows them to produce more leaves, resulting in a larger litter N pool and faster internal cycling of nutrients.

Key words: Arctic; climate change; deciduous shrubs; decomposition; litter quality; snow manipulation.

INTRODUCTION

Temperatures in the Arctic region are warming at twice the rate of the rest of the globe (Hassol 2004, Serreze and Francis 2006, Kaufman et al. 2009, Screen and Simmonds 2010), altering the structure and function of ecosystems (Chapin et al. 1995, Chapin and Shaver 1996, Shaver et al. 2000, Mack et al. 2004) by causing a shift in species composition from one previously dominated by graminoids to an increase in the abundance and expansion of shrubs (Jia and Epstein 2003, Stowe et al. 2004, Tape et al. 2006, Jia et al. 2009, Forbes et al. 2010, Elmendorf et al. 2012). Increasing shrub dominance will increase plant productivity and biomass, resulting in more uptake of atmospheric CO$_2$ (Cahoon et al. 2012) and the storage of more C aboveground in woody tissue or belowground in rhizomes (Shaver and Chapin 1991), roots, and ectomycorrhizal fungi (Clemmensen et al. 2006). In addition, more woody stems associated with shrubs could mean more C stored in coarse woody debris and stems, which decompose slowly (Hobbie 1996). Taken together, these effects of shrub expansion have been identified as a negative carbon cycling feedback to climate warming. Biophysical feedbacks to regional climate, however, may be in the opposite direction. Shrublands have a lower albedo than tundra, which can lead to an increase in absorbed solar radiation during the snow-free period, resulting in a positive feedback to regional warming (Chapin et al. 2005). In addition, deciduous shrubs in fertilized tundra cycled C and N faster than in unfertilized tundra, resulting in a net loss of deep soil C (Mack et al. 2004). Soils in naturally occurring shrub tundra similarly store less C than those in graminoid tundra (Ping et al. 1997). Thus, net positive feedbacks to warming are possible if increased shrub cover alters ecosystem structure and function so that soil C stocks decrease. Since the Arctic stores 20–30% of the total amount of terrestrial soil-bound C (McGuire et al. 2009) and woody vegetation is predicted to increase by as
much as 52% by 2050 (Pearson et al. 2013), it is important to better understand the mechanisms behind these potential feedbacks to climate change.

The mechanisms that drive shrub expansion are not well understood. It has been hypothesized that shrubs may enhance their dominance and growth through increased nutrient availability associated with shrub-induced changes in the abiotic environment. The snow–shrub hypothesis suggests that taller and more abundant shrubs accumulated greater snow depth due to greater retention of snowfall (e.g., less snow lost to wind events) and trapping of wind-distributed snow than tundra areas with fewer shrubs (Sturm et al. 2001, 2005, Pomeroy et al. 2006). This deeper snow cover insulates the soil, maintaining warmer temperatures through the winter. By altering the abiotic environment through trapping snow and maintaining warmer soil temperatures, shrubs can influence the biogeochemical processes that drive nutrient cycling. Decomposition of litter is the major pathway by which nutrients are recycled and made available for plant uptake in these nutrient-limited systems. Changes in the environment can influence rates of litter decomposition. However, it has not been directly tested whether the amount of snow trapped by deciduous shrubs alters the environment enough to stimulate litter decomposition and increase litter nutrient release.

Previous studies have shown that snow acts as an insulator that can increase soil temperature (Brooks et al. 1996, 1998, Grogan and Jonasson 2003, Schimel et al. 2004, Wahren et al. 2005) and the availability of water to soil microorganisms (Romanovsky and Osterkamp 2000, Mikan et al. 2002), potentially regulating the rate at which microbes and fungi can break down litter over the winter. Indeed, litter decomposition has been found to occur in the winter and under snow (Stark 1972, Hobbie and Chapin 1996, McLaren and Turkington 2010, Saccone et al. 2013), and to be higher in areas that have deeper snow cover (Baptist et al. 2010, Saccone et al. 2013). If faster turnover of litter N results in an increase in plant-available N, then snow accumulation by shrubs could indirectly influence N availability by maintaining warmer soil temperatures in fall and winter, and allowing a longer window for microbial breakdown of litter substrates, increased N release, and higher rates of N supply to plants, resulting in a positive plant–soil feedback that promotes further shrub expansion.

Shrubs may also have effects on decomposition and N release that are independent and opposite of their effects on winter soil temperatures. For example, in moist acidic tundra, the deciduous shrub Betula nana allocates 79% of its total annual aboveground biomass to new and old stems (Shaver et al. 2001) that decompose three times slower than leaves and one to eight times slower than leaves and stems from graminoids and evergreen shrubs (Hobbie 1996). A compositional shift to more deciduous shrub dominance may thus alter nutrient turnover through biotic controls by a shift toward larger inputs of slowly decomposing litter (Hobbie 1992, Buckeridge et al. 2010). By slowing nutrient turnover and decreasing plant-available N, this litter could drive a negative plant–soil feedback that would slow shrub expansion.

These two competing mechanisms lead to the question of whether changes in microclimate or changes in litter quality and quantity have stronger effects on litter decomposition and nutrient release. This question has been studied in mesic (Hector et al. 2000, Knops et al. 2001, Scherer-Lorenzen 2008) and dry (McLaren and Turkington 2010) grasslands and temperate forests (Hobbie et al. 2006, Vivanco and Austin 2008), but has not been as well studied in Arctic tundra systems, particularly in the context of shrub expansion. Will positive or negative plant–soil feedbacks prevail as shrubs expand in the Arctic? Although there is much evidence to suggest that shrubs can influence their environment to alter key biogeochemical processes that control plant nutrient supply, there have been no published studies to date that have directly tested the effect of added snow (at the depth that would be trapped by shrubs) or increased shrub cover on litter decomposition. In addition, within the Alaskan Arctic, most decomposition studies have largely occurred in graminoid-dominated moist acidic or nonacidic tundra. We know relatively little about how the environment of shrub tundra may influence litter decomposition.

The goal of our study was to understand the relative importance of mechanisms through which arctic deciduous shrubs affect litter decomposition and N dynamics. Our objectives were threefold: (1) to test whether snow addition, at a rate realistic for increasing shrub abundance, altered the environment for decomposition enough to stimulate rates of litter mass and N loss, (2) to compare how litter C quality and the relative availability of C to N influenced the rate of litter mass and N loss, and (3) to better understand how the changes in plant species composition associated with the shift from graminoid- to shrub-dominated tundra influence community decomposition. We hypothesized that across three sites that represented a gradient in shrub abundance and height, (1) the addition of snow would slow temperature decline in the winter and lead to faster decomposition and net N release from litter, (2) decomposition and net N release would covary positively with lignin : N ratios, and (3) community-weighted mass loss would be lowest in the shrub-dominated sites, because of the greater abundance of woody litter.

To test our hypotheses, we measured litter quality, quantity, decomposition, and net N release across three plant communities that represented natural variation in shrub abundance across the landscape (DeMarco et al. 2011). In each community, we manipulated snow depth using snow fences. To test for the effects of site and snow on decomposition and net N release, we decomposed a common substrate in all sites and treatments. We decomposed litters from multiple plant functional
groups in a common environment, hereafter referred to as a common garden, to control for differences in microclimate and directly test the effect of litter quality on decomposition. Finally, we combined these studies with aboveground net primary production estimates to calculate community-weighted mass loss rates.

**Methods**

**Study area**

All sites are located near Toolik Field Station at the Arctic Long Term Ecological Research (LTER) site (68°38' N, 149°38' W, elevation 760 m) in the foothills region on the North Slope of the Brooks Range, Alaska, USA. This area is a younger landscape glaciated during the late Pleistocene. It includes large areas of the Itkillik I (deglaciated ~ 60,000 yr) and Itkillik II (deglaciated ~ 10,000 yr) glacial drifts (Hamilton 1986). The entire foothills region of the Brooks Range is treeless and underlain by continuous permafrost, 250–300 m thick (Osterkamp and Payne 1981). Mean annual air temperature is around −10°C, with average summer temperatures from 7–12°C. Annual precipitation is 318 mm, with 43% falling as snow (data available online).\(^5\) Average snow depth is 50 cm, although snow distribution can be variable due to redistribution by wind. Snowmelt occurs in early May.

In the fall of 2005, three sites were selected for the snow manipulation experiment that varied primarily in deciduous shrub abundance, hereafter referred to as low, medium, and high shrub sites. These sites are described in detail in DeMarco et al. (2011). In short, sites were chosen to have similar state factors (climate, parent material, time since deglaciation) but varied in the abundance of deciduous shrubs (Jenny 1994). The same species of deciduous shrubs (Betula nana and Salix pulchra) are found at all three sites (except S. richardsonii, which is found only at the medium shrub site). However, percent cover of deciduous shrubs increases from 15% to 94%, and their canopy height increases from 4 cm to 50 cm across sites. All sites are within 1 km of each other, and have similar parent material, time since last glaciation (Itkillik I, 60,000 yrs), and regional climate, although microclimates vary across sites due to differences in slope and aspect. Elevation changes from about 764 m at the low shrub site to 741 m at the medium and high shrub sites.

Our low shrub site was located in moist acidic tussock tundra, where the vegetation consists of approximately equal biomass of graminoids (Eriophorum vaginatum and Carex bigelowii), dwarf deciduous shrubs (B. nana, Vaccinium uliginosum, and S. pulchra), evergreen shrubs (Ledum palustre ssp. decumbens and V. vitis-idea), and mosses (Hylocomium splendens, Aulacomnium turgidum, Dicranum spp., and Sphagnum spp.; Shaver and Chapin 1991). Our medium shrub site was located in riparian tundra where the deciduous shrubs are of intermediate size. The vegetation consists of graminoids (primarily C. bigelowii), deciduous shrubs (B. nana, V. uliginosum, S. pulchra, and S. richardsonii), and mosses (H. splendens and Dicranum spp.). Our high shrub site was located in riparian tundra dominated by tall deciduous shrubs and has predominantly deciduous shrubs (B. nana, S. pulchra, and some Potentilla fruticosa), with some evergreen or wintergreen shrubs (V. vitis-idea and Linnaea borealis), forbs (Polygonum bistorta, Petasites frigidus, Stellaria longipes, Valeriana capitata, and Artemisia alaskana), graminoids (Poa arctica, C. bigelowii, and Calamagrostis canadensis), and mosses (Sphagnum spp. and H. splendens).

**Snow manipulation**

To determine the influence of increased snow depth on litter decomposition, snow fences that represented maximum regional shrub height (1.5 m high) were set up in the fall of 2005 at all three sites to manipulate snow depth (DeMarco et al. 2011). Two treatments, control (ambient snow) and drift (manipulated snow), were set up at each site. For all sites, subplots on the drift side of the fences were located in the zone of maximum snow accumulation, which was relatively uniform. Within each treatment, 18 2 × 10 m plots, with 1-m buffer strips between, were established. For this study, six plots per treatment (n = 6) were randomly assigned to measure litter decomposition. Remaining plots were used for other experiments not described here.

Soil temperature at 5 cm within the organic layer was measured continuously (1–3 h intervals) from July 2006–May 2009 in each study plot (n = 3–4 plots within each treatment and site) using I-button temperature data loggers (IButtonLink, East Troy, Wisconsin, USA). Mean daily soil temperatures were calculated for all plots within each treatment and site for each year. Mean growing season and winter soil temperatures were calculated from the mean daily temperatures from each plot within each treatment and site. I-buttons were not always installed or removed on the same day; therefore we only analyzed data from days in which we had data for all sites and treatments. The growing season included measurements taken from 1 July to 1 August of that year and included years 2006, 2007, and 2008. Winter growing season includes measurements taken from 1 September through 1 May of the following year and includes winters from 2006–2007, 2007–2008, and 2008–2009.

The snow fences produced snow packs in treatment plots that were, on average, 87, 96, and 104 cm deeper than ambient snow depth for the low, medium, and high shrub sites, respectively. Snow addition increased average winter soil temperatures by 3°C and summer soil temperatures by 2°C in the high shrub site; the medium and low shrub sites showed similar trends, although the differences between treatments were smaller in magnitude (DeMarco et al. 2011).

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\(^5\) http://ecosystems.mbl.edu/ARC
Common substrate experiment

To directly test the effect of microclimate and snow addition on litter decomposition rates, we incubated the senesced leaves from a common substrate, *B. neoalaskana* (Sarg.), in the ambient and snow-manipulated plots across all three sites. Senesced leaves were collected from trees growing near Fairbanks, Alaska, USA. Leaves were still attached to the trees, but the petiole had already started to abscise. This common substrate was used because the large leaf size and relative abundance allowed us to collect enough material for our study. Leaves were air dried, well mixed, and then subsampled for litter bags. One gram of leaves was sewn into 2-mm mesh bags, 8 × 8 cm in size. Litter bags were incubated beneath the live moss and litter layer starting in early June of 2006. The moss and litter in this system are well mixed, so bags were inserted in this layer. Four identical bags were strung together for four separate annual harvests. Bags were placed in six treatment plots in each site, with three sub-replicates within each plot. Bags were removed in July of 2007, 2008, and 2009, and were kept frozen until they could be processed.

At time of processing, bags were thawed and then gently rinsed with deionized (DI) water to remove soil and loose litter attached to the outside of the bag. All original leaf litter was removed, dried at 45°C for a minimum of 48 h, and weighed. To determine the percentage of C and N of the litter, samples were ground to a fine powder on a Wiley mill, with a no. 40 mesh screen, and then analyzed using an ECS 4010 elemental analyzer (Costech Analytical, Valencia, California, USA). Percentage of initial mass remaining was calculated by dividing the incubated mass by the initial mass and multiplying by 100. Percent of initial C (ICR) and initial N remaining (INR) was calculated by the following equations:

\[
\text{ICR} = \left( \frac{L_{\text{mass}} \times L_{\text{Carbon}}}{L_{\text{mass}} \times L_{\text{Carbon}}} \right) \times 100,
\]

\[
\text{INR} = \left( \frac{L_{\text{mass}} \times L_{\text{Nitrogen}}}{L_{\text{mass}} \times L_{\text{Nitrogen}}} \right) \times 100.
\]

Common garden experiment

To compare differences in litter decomposition rates among species, we incubated senesced leaf litter from 10 vascular plant and three moss species, and stem litter from four shrub species collected across eight sites located in the Arctic Foothills region on the North Slope of the Brooks Range (Table 1). Three of the sites were the control plots at the low, medium, and high shrub sites. Four sites were located in alder-dominated (*Alnus viridis* spp. *fruticosa*) tall deciduous shrub tundra; two near the Sagavanirktok River and two along the Dalton Highway, ~32 km north of Toolik Field Station. Alders are one of the deciduous shrubs that have been documented as expanding in many arctic regions. One site was in the control plots in a previously set up experiment in moist acidic tundra (referred to as species removal; Breit-Harte et al. 2008). All litter was collected and processed using the same methods as described in the common substrate experiment, except that only 1.6-mm mesh bags, 4 × 8 cm in area, were used, and leaf samples were replicated six times, while stem litter was replicated three times. For the litter collected at the species removal site, litter bags were installed in July of 2003 and removed in July of 2004, 2005, 2007, and 2008. Litter collected from the other sites was installed in the field as litter bags in early June of 2006 and replicate bags were removed in July of 2007, 2008, and 2009 and processed as described previously.

Calculations

The exponential decay constant, *k*, was determined by assuming a single exponential decay model (Olson 1963): \( M_t = M_0 e^{-kt} \), where \( M_t \) is litter mass at time *t*, and \( M_0 \) is initial mass. The slope of the regression of proportion of initial mass remaining against time was used to determine the decay constant for each substrate at each site.

Initial litter quality

A subsample of each leaf and stem collection was analyzed for percentage of C, percentage of N, and C quality to determine the quality of the litter substrates prior to decomposition. Percentage of C and N was determined from samples that had been ground to a fine powder on a Wiley mill, with a no. 40 mesh screen, and then analyzed using an ECS 4010 elemental analyzer. C quality measurements were carried out on an ANKOM fiber analyzer (Ankom Technology, Macedon, New York, USA) and included determination of (1) soluble cell contents (carbohydrates, lipids, pectin, starch, and soluble protein), (2) hemicelluloses plus bound proteins, (3) cellulose, and (4) lignin plus other recalcitrants (Ryan et al. 1990).

Community-weighted mass loss

To separate out the effect of changes in species composition vs. changes in the microenvironment associated with shrub expansion on community level decomposition, we used measured aboveground net primary productivity (ANPP) and *k* values to calculate a community-level mass loss for each of the three shrub sites (Appendix A: Table A1). We followed the procedure outlined in Hobbie and Gough (2004). We harvested biomass in July of 2007 from the control treatments of the three snow fence sites (DeMarco et al. 2011). Total ANPP (g m⁻² yr⁻¹) per plot (\( n = 8 \) replicates per site) was calculated by summing new apical biomass (g/m²) for that year, i.e., of each tissue type from each species found within that plot. Our ANPP calculations were only for vascular plants and thus do not include mosses, lichens, or belowground parts such as rhizomes or roots. We estimated the
contribution of secondary stems to ANPP by multiplying the ANPP of species likely to produce woody tissue by a proportion determined by Bret-Harte et al. (2002). These were 0.158, 0.181, and 0.079 for B. nana, S. pulchra, and L. palustris spp. decumbens, respectively. We followed the methods outlined in Hobbie and Gough (2004) and assumed that C. tetragona and V. uligonosum resembled L. palustris in their proportional secondary growth, and S. reticulata, S. glauca, and S. richardsonii all resembled S. pulchra in their proportional secondary growth. We also assumed Andromeda polifolia, Arctostaphylos alpina, Dryas integrifolia, Empetrum nigrum, Rubus chamaemorus, V. vitis-idaea, and Linnaea borealis had negligible secondary growth. We assumed inflorescences would have similar k values as foliar litter from the same species and thus used foliar k values for inflorescences. This method assumes all new production that year ends up as litter. For deciduous shrub leaves, this is a valid assumption, as they lose all of their leaves at the end of the growing season. Evergreen shrubs and graminoids can retain leaves through the winter, and thus we may be overestimating litter production for these species.

The mass loss for each plant species and their parts (inflorescences, leaves, and stems) was calculated by multiplying the species’ ANPP by that species’ decay constant, k, from the common garden experiment to produce an ANPP-weighted mass loss for each species. ANPP-weighted mass loss values were summed across all species in a plot to produce community-weighted mass loss values (see Appendix A: Table A5 for full list of ANPP and k values used for each species present).

To determine how differences in site environments contributed to community mass loss, we adjusted the community-weighted k values for site-specific differences in decomposition rates. We divided site mean k values for the common substrate, B. neoalaskana, by the mean k value for B. neoalaskana that was decomposed in the common garden (k = 0.256). The proportional difference between the k value from the common garden and the shrub sites was multiplied by the species-specific k values to correct for differences in decomposition found across the shrub sites. The adjusted species-specific k values were summed to obtain a decay k constant for the entire community. This method assumes that all species and tissues respond the same way as B. neoalaskana when decomposed in different environments, and does not take into account any site by species interactions. Evidence of site by species interactions are rare, because most decomposition studies do not conduct full factorial incubations where all species are incubated in all environments. In moist acidic and moist nonacidic tundra, B. nana stem decomposition followed the opposite pattern between the two sites compared to the other species decomposed (Hobbie and Gough 2004).

Species decomposed in our common garden contributed 93% of ANPP. For the species that contributed the remaining 7% of ANPP, we used k values from other published studies within the region or substituted k values for species with similar growth forms. For all forbs we used the decay constant for P. bistorta reported by Hobbie and Gough (2004), which was decomposed in moist acidic tundra not far from our common garden site. For Calamagrostis spp., Poa arctica, and Juncus spp., we used an average of the k values for Carex spp. and E. vaginatum (k = 0.18) from our common garden. For Empetrum spp., L. borealis, and Cassiope spp. leaves, we used an average of k values from Ledum spp. and V. vitis-idaea from our common garden. For stems of these three species, we used an average of k values from B. nana and S. pulchra stems (k = 0.08).

**Statistical analysis**

To test our hypotheses about the effects of site and snow depth on decomposition of the common substrate, we used two-way ANOVA (JMP 7.0, SAS Institute, Cary, North Carolina, USA). Relationships between k and initial litter quality indices for 10 vascular plant species decomposed in the common garden were tested using single regression analysis with k as the dependent variable and the litter quality indices of interest as the independent variable. The effect of changes in litter quality/quantity on community mass loss and the effect of changes in environment on community mass loss were tested using two separate one-way ANOVAs with site as the main effect. Tukey’s HSD test was used as a post hoc test when ANOVAs were significant at P < 0.05. Data were tested for normality (Shapiro-Wilks), and ln-transformed when necessary to achieve homogeneity of variance. When homogeneity of variance could not be achieved, data was analyzed using a Kruskal-Wallis nonparametric test.

**Results**

**Effect of added snow on soil temperature**

Snow addition significantly increased winter soil temperatures by an average of 1–4°C across all three

<table>
<thead>
<tr>
<th>Group</th>
<th>Species</th>
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<tbody>
<tr>
<td>Graminoids</td>
<td>Carex bigelovii, Eriophorum vaginatum</td>
</tr>
<tr>
<td>Deciduous shrubs</td>
<td>Alnus crispa viridis spp. fruiticosa, Betula nana, Betula neoalaskana</td>
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<tr>
<td></td>
<td>(Sarg.), Rubus chamaemorus, Salix pulchra, Vaccinium uliginosum</td>
</tr>
<tr>
<td>Evergreen shrubs</td>
<td>Ledum decumbens, Vaccinium vitis-idaea</td>
</tr>
<tr>
<td>Mosses</td>
<td>Aulacomnium turgidum, Hylocomium splendens, Sphagnum spp.</td>
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</table>
There were significant differences in soil temperature across sites with snow addition and across years, but there were no significant interactions among the main effects. Soil temperatures were highly variable across years. In general, the low shrub site had both lower summer and winter soil temperatures compared to the medium and high shrub sites.

Common substrate experiment

After three years, snow addition did not significantly alter mass remaining of the common substrate (two-way ANOVA; treatment; $F_{1,36} = 1.4, P = 0.24$ [Fig. 2]) but there was a significant difference across sites (site; $F_{2,36} = 13.6, P < 0.001$) and a significant interaction between site and treatment (site × treatment; $F_{2,36} = 3.5, P = 0.04$). When the effects of treatment were tested for each site independently, treatment was not significant at the low shrub site (one-way ANOVA; treatment; $F_{1,11} = 1.9, P = 0.20$) and was only marginally significant at the medium (treatment; $F_{1,11} = 3.4, P = 0.10$) and high shrub sites (treatment; $F_{1,12} = 3.6, P = 0.09$). There was a trend for greater mass loss in the ambient treatment at the low shrub site, but greater mass loss occurred in the snow-addition treatment at the medium and high shrub sites (Appendix B: Table B1). Decomposition rates ($k$), N remaining, or C remaining were also not significantly different under snow addition, although there was a trend for higher $k$ rates and less N and C remaining in the snow-addition treatment (Figs. 2 and 3). However, initial N remaining showed a significant site by treatment effect. When the main effect of treatment was tested for each site separately, only the low shrub site showed a significant effect of treatment on N remaining after three years (treatment; $F_{1,11} = 122.2, P = 0.03$). In contrast to the effect of snow addition, decomposition rates and N and C remaining varied significantly across sites (Fig. 3). The litter decay rate, $k$, was highest at the low shrub site, losing 10% and 6% more mass and 8% and 6% more C than in the medium and high shrub sites, respectively. Initial N remaining followed a different pattern, with mineralization of litter N occurring at the low shrub site only, but immobili-
ization occurring at both the medium and high shrub sites. The proportion of initial C:N remaining decreased with an increase in shrub abundance (Fig. 3).

Common garden experiment

After three years of incubation, neither site of origin nor species had an effect on the percentage of initial mass remaining or decay rate of leaf and stem litter from *B. nana* and *S. pulchra*, despite significant differences in their initial litter quality (Appendix C: Tables C1 and C2).

Initial leaf litter quality significantly differed across species for all indices measured, although species within the same growth form were not always similar in their initial litter quality (Table 3). Deciduous shrubs had up to two times more N in their leaves than evergreen shrubs, graminoids, and mosses (species: $\chi^2 = 38.3$, df = 7, $P < 0.0001$). Evergreen shrubs had the highest percentage of C in their leaves, followed by deciduous shrubs (except *R. chamaemorus*), graminoids, mosses, and the graminoid *E. vaginatum* (species: $\chi^2 = 40.0$, df = 7, $P < 0.0001$). Evergreen shrubs, mosses, and the graminoid *E. vaginatum* had high C:N ratios in their leaves, while the deciduous shrubs *R. chamaemorus* and *V. uliginosum* had the lowest C:N ratios (species: $F_{2,32} = 72.2$, $P < 0.0001$). The evergreen shrubs and the deciduous shrub *B. nana* had lignin : N ratios that were two to four times higher than the deciduous shrubs, *R. chamaemorus* and *V. uliginosum*, and the graminoids (species: $F_{9,53} = 72.2$, df = 6, $P < 0.0001$). Graminoids had 1.5–4 times more hemicellulose in their leaves, compared to evergreen and deciduous shrub leaves (species: $F_{6,32} = 90.1$, $P < 0.0001$). Graminoids also had the highest percentage of cellulose in their leaves, two to four times more than in evergreen and deciduous shrubs. *B. nana* had the least percentage of cellulose in its leaves compared to all six of the other species (species: $F_{6,32} = 157.3$, $P < 0.0001$). *B. nana* also had the highest percentage of lignin, followed by evergreen shrubs and the deciduous shrubs, *R. chamaemorus* and *V. uliginosum*. Graminoids had the least amount of lignin in their leaves (species: $\chi^2 = 27.4$, df = 6, $P < 0.0001$).

After five years of decay, *R. chamaemorus* leaf litter lost 1.5–6 times more mass than leaf litter from the other six species of vascular plants and three species of mosses collected at the same moist acidic tundra site and decomposed in the same common garden (Fig. 4; IMR species: $\chi^2 = 36.5$, df = 7, $P < 0.0001$). Species within the same functional group did not always follow the same pattern in their rates of decomposition (Fig. 4). Leaf litter from the deciduous shrubs *B. nana* and *V. uliginosum* had decay constants that were similar to that of the evergreen shrub *L. decumbens*, and the graminoid *E. vaginatum* had a higher decay constant than those of the evergreen shrub *V. vitis-idaea* and the graminoid *C. bigelowii*. Mosses had the lowest decay constants compared to the other seven vascular plant species decomposed in our experiment.

In a comparison with all 10 vascular species decomposed in our common garden, leaf litter decay rates were
Decay constants, initial C and N remaining, and the proportion of initial C:N remaining for the common substrate (means ± SE), *B. neoalaskana*, decomposed across three sites (low, medium, and high) and two snow fence treatments (ambient and snow addition) and calculated for the entire 3-yr decomposition time period. Results of two-way ANOVAs are displayed for each variable with site and treatment as the main effects and site by treatment (*S × T*) interaction. In each panel, data points that share a lowercase letter are not significantly different at the *P*, 0.05 level.

**Table 3.** Initial litter quality for senesced leaves of seven species of vascular plants collected from plots in a moist acidic tundra community and incubated in a common site.

<table>
<thead>
<tr>
<th>Species</th>
<th>N (%)</th>
<th>C (%)</th>
<th>C:N</th>
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<tr>
<td>Graminoids</td>
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<tr>
<td><em>Carex bigelowii</em></td>
<td>1.34 ± 0.04</td>
<td>42.39 ± 0.20</td>
<td>31.91c ± 1.14</td>
</tr>
<tr>
<td><em>Eriophorum vaginatum</em></td>
<td>0.87 ± 0.04</td>
<td>42.15 ± 0.13</td>
<td>8.90a ± 2.11</td>
</tr>
<tr>
<td>Deciduous shrub</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Betula nana</em></td>
<td>1.67 ± 0.06</td>
<td>44.59 ± 0.15</td>
<td>26.94c ± 0.93</td>
</tr>
<tr>
<td><em>Rubus chamaemorus</em></td>
<td>1.90 ± 0.04</td>
<td>40.53 ± 0.57</td>
<td>21.32d ± 0.38</td>
</tr>
<tr>
<td><em>Vaccinium uliginosum</em></td>
<td>1.74 ± 0.05</td>
<td>43.63 ± 0.10</td>
<td>25.15d ± 0.79</td>
</tr>
<tr>
<td>Evergreen shrub</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Ledum decumbens</em></td>
<td>1.03 ± 0.03</td>
<td>47.83 ± 0.30</td>
<td>46.64b ± 1.25</td>
</tr>
<tr>
<td><em>Vaccinium vitis-idaea</em></td>
<td>0.81 ± 0.03</td>
<td>45.15 ± 0.16</td>
<td>56.05a ± 2.31</td>
</tr>
<tr>
<td>Mosses</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Aulacomnium turgidum</em></td>
<td>0.81 ± 0.07</td>
<td>37.36 ± 3.32</td>
<td>46.10b ± 1.01</td>
</tr>
<tr>
<td><em>Hylocomium splendens</em></td>
<td>0.87 ± 0.16</td>
<td>40.71 ± 0.23</td>
<td>46.61b ± 0.70</td>
</tr>
<tr>
<td><em>Sphagnum spp.</em></td>
<td>0.88 ± 0.02</td>
<td>38.96 ± 0.17</td>
<td>44.40b ± 0.71</td>
</tr>
</tbody>
</table>

**Notes:** Data are presented as means ± SE. Different letters within the same foliar trait indicate that values are significantly different at the *P* < 0.05 level from post-hoc tests after running one-way ANOVAs comparing each variable across species (*n* = 6 individual replicates). Cell soluble refers to soluble cell contents (carbohydrates, lipids, pectin, starch, and soluble protein).
only weakly related to some of the litter quality indices measured. The percentages of C and cell soluble contents were positively correlated with decay rates (C; $r^2 = 0.23$, $n = 21$, $P = 0.03$, cell soluble contents; $r^2 = 0.23$, $n = 21$, $P = 0.03$, cellulose; $r^2 = 0.23$, $n = 21$, $P = 0.04$ [Appendix D: Fig. D1]). For stem litter, the percentage of cellulose was the only litter quality index that correlated positively with decay rates, explaining 55% of the variation in stem decay rate (Appendix D: Fig. D2; $r^2 = 0.55$, $n = 9$, $P = 0.01$).

Table 3. Extended.

<table>
<thead>
<tr>
<th>Cell soluble (%)</th>
<th>Hemicellulose (%)</th>
<th>Cellulose (%)</th>
<th>Lignin (%)</th>
<th>Lignin : N</th>
</tr>
</thead>
<tbody>
<tr>
<td>41.87$^b$ ± 2.61</td>
<td>28.39$^b$ ± 1.25</td>
<td>24.47$^b$ ± 0.90</td>
<td>4.81 ± 0.93</td>
<td>3.60 ± 0.64</td>
</tr>
<tr>
<td>35.79$^b$ ± 2.38</td>
<td>30.82$^b$ ± 0.66</td>
<td>27.16$^b$ ± 0.46</td>
<td>4.30 ± 0.37</td>
<td>4.91 ± 0.43</td>
</tr>
<tr>
<td>62.76$^a$ ± 0.75</td>
<td>10.15$^c,d$ ± 0.47</td>
<td>7.39$^c$ ± 0.47</td>
<td>19.44 ± 0.31</td>
<td>11.72 ± 0.29</td>
</tr>
<tr>
<td>64.98$^a$ ± 1.54</td>
<td>17.87$^b$ ± 1.12</td>
<td>9.82$^{d,e}$ ± 0.58</td>
<td>6.78 ± 0.57</td>
<td>3.54 ± 0.22</td>
</tr>
<tr>
<td>69.71$^a$ ± 0.11</td>
<td>9.49$^{d,e}$ ± 0.23</td>
<td>10.52$^{d,e}$ ± 0.09</td>
<td>8.35 ± 0.36</td>
<td>4.83 ± 0.33</td>
</tr>
<tr>
<td>63.29$^a$ ± 0.99</td>
<td>8.14$^d$ ± 0.41</td>
<td>12.14$^{c,d}$ ± 0.30</td>
<td>16.08 ± 0.36</td>
<td>15.66 ± 0.38</td>
</tr>
<tr>
<td>60.93$^a$ ± 0.75</td>
<td>13.29$^c$ ± 0.85</td>
<td>13.22$^c$ ± 0.27</td>
<td>11.19 ± 1.45</td>
<td>14.09 ± 2.26</td>
</tr>
</tbody>
</table>
Community-weighted mass loss

Community-weighted mass loss that took into account differences in litter quality and quantity across sites was greatest in the high shrub site compared to the medium and low shrub sites (site: \(F_{2,30} = 3.5, P = 0.05\)). This was primarily driven by the higher overall ANPP found at the high shrub sites compared to the medium and low shrub sites (site: \(F_{2,30} = 7.0, P < 0.01\)), because the proportion that ANPP contributed to community mass loss (mass loss/ANPP) was similar across sites (low = 0.16, medium = 0.15, and high = 0.15). Community-weighted mass loss that took into account both differences in litter quality and quantity and the environment was greater in the low and high shrub sites than the medium shrub site (site: \(F_{2,30} = 4.4, P = 0.03\); Fig. 5) suggesting that different mechanisms may be driving these differences at each of the sites.

DISCUSSION

Microenvironment controls over litter decomposition

Surprisingly, we were unable to detect any effect of added snow on decomposition of the common litter substrate after three years of incubation, despite a 2°C increase in soil temperature during the growing season and a 4°C increase during the winter. Walker et al. (1999) also found no effect of deeper snow on litter decomposition after two years of decomposing *Betula nana* leaf litter under ambient and up to 3 m of added snow in tussock tundra near Toolik Lake. In contrast, in an alpine tundra community, Baptist et al. (2010) found a trend for greater litter mass loss in late snowmelt sites, presumably due to warmer soil temperatures in the spring prior to snowmelt. Using the same species of litter as our common litter experiment, Hobbie and Chapin (1996) found differences in litter mass loss between arctic tundra microsites whose summer soil temperatures differed by 4°C, with greater mass loss occurring in the warmer microsites. In addition, litter mass loss in lab incubations that included warming treatments of either 2°C or 6°C above the ambient growing season temperatures showed an increase in mass loss with increased temperature (Hobbie 1996, Jonasson et al. 2004). Two out of the three studies had temperature differences that were twice as high as ours, which may explain why they found significant differences in litter mass loss with change in temperature, while our study did not. At these sites, temperature may not be the main control over decomposition. Site-specific differences in soil moisture, nutrient availability, litter quality and quantity, and the decomposer community may play a larger role in decomposition in these arctic and alpine communities.

When comparing decomposition of our common substrate across our three sites, the common litter decomposed faster in the low shrub site compared to the medium and high shrub sites, even though ambient soil temperatures at the medium and high shrubs sites were actually warmer than at the low shrub site both during the growing season and over the winter. Soil temperature differences across these sites are of the same magnitude as the differences in soil temperature we saw when we added snow. Since we did not see strong differences in decomposition when we added snow and elevated soil temperatures, this suggests that other factors such as moisture, soil nutrients, or the decomposer communities may be more important than small (<4°C) changes in temperature for driving decomposition at our sites. Soil moisture was not measured over the 3-yr incubation period, but measurements in June of 2006 showed no difference in soil moisture across sites (DeMarco et al. 2011) and could not explain the differences we found in litter decomposition across the sites.

Previous research from these sites has shown that percentage of N of the top 10 cm of soil at the medium and high shrub sites is twice as high as the percentage of
N at the low shrub site at the same soil depth (DeMarco et al. 2011) and is highly positively correlated with litter initial N remaining (%) and initial C:N remaining (%), but negatively correlated with decay constants (Fig. 6). This suggests that soil nutrients may play an important role in controlling litter decomposition and nutrient release at our sites. Over our 3-yr incubation period, litter decomposed at the low shrub site mineralized litter N, while litter decomposed at the medium and high shrub sites immobilized N. Thus, sites with greater soil N have lower rates of decomposition and higher retention of N on litter. In our study, sites that had greater bulk soil N also had higher rates of net N mineralization, suggesting greater N availability (DeMarco et al. 2011). Greater soil N availability has been found to stimulate (Hobbie 1996, Aerts et al. 2006), repress (Prescott 1995, Magill and Aber 1998, Aerts et al. 2006), or have no effect (McClaugherty et al. 1985, Prescott 1995, Hobbie 1996, Aerts et al. 2003, 2006) on litter decomposition rates, and can lead to N immobilization in some systems (Gallardo and Merino 1992, Magill and Aber 1998, Hobbie 2005, Aerts et al. 2006) but see McClaugherty et al. (1985). These varying responses of litter decomposition to external N may have been attributed to interactions between the initial quality of the litter and the availability of nitrogen in the soil.

In a meta-analysis of 24 litter decomposition studies in which external N was experimentally manipulated, Knorr et al. (2005) found that external N availability and litter quality interact to influence decay rates, with N additions stimulating decomposition of high-quality litters (<10% lignin content), while inhibiting decay of low-quality (>20% lignin content) litters. The “microbial N mining” hypothesis suggests that this pattern occurs because some microbes use labile C to decompose recalcitrant organic matter in order to acquire N (Fontaine and Barot 2005, Moorhead and Sinsabaugh 2006). Therefore, we would expect microbial N mining to increase decomposition of low-quality litter when it is incubated in soils with low soil N. Our highest decomposition rates were seen at the low shrub site where soil N (DeMarco et al. 2011) is low and soil microbial activity is N-limited (Lavoie et al. 2011, Sistla et al. 2012), suggesting that decomposition at this site was driven by microbes mining N. In contrast, in a high soil N environment, nitrogen is readily available to microbes, therefore it is not necessary for them to mineralize litter to acquire N, which results in suppression of litter decomposition. Indeed there is evidence that this can occur in laboratory incubations using leaf litter from a range of plant functional types and multiple soil types collected in southern Africa (Craine et al. 2007) and in field studies using leaf litter from the same

![Fig. 6. Soil N (means ± SE) for each site vs. decay constant (k), initial C remaining, initial N remaining, and the proportion of initial C to N remaining of the common substrate, B. neoalaskana, decomposed at each site over a 3-yr period.](image-url)
species but with varying litter quality and soil nutrient availability (Talbot and Treseder 2012). The B. neoalaskana litter we used for our study was of low quality with both a high C:N ratio (72 ± 0.60; mean ± SE) and percentage of lignin (19 ± 2) and was decomposed across sites that varied in soil N availability (DeMarco et al. 2011). Therefore the microbial N mining hypothesis may help explain why we saw a linear pattern of decreased rates of decomposition and an increase in N immobilization with increasing soil N at our sites.

The N immobilization we found at our high shrub site may also be explained by interactions with soil nutrient availability and the high lignin content of our litter. High nutrient content in soils can suppress the production of fungal ligninase (Carreiro et al. 2000, Sinsabaugh et al. 2002), which is induced by low N availability (Keyser et al. 1978), resulting in low rates of decomposition. Fungal communities between tussock tundra and shrub tundra soils sampled near Toolik Lake differ at the phyla and subphyla levels; however, we do not know whether the species responsible for breaking down lignin or the production of ligninase differs between these two plant communities (Wallenstein et al. 2007). These tussock tundra soils are dominated by slow-growing microbes that have high affinities for C substrates of low quality and quantity. In contrast, shrub tundra soils are dominated by microbes that have high growth rates with high nutritional requirements for C substrates of higher quality and quantity (Fierer et al. 2007, Wallenstein et al. 2007). It is possible that microbes at the low shrub site are better at decomposing litter that is of low quality than the microbes at the high shrub site, and that microbes at the high shrub site immobilize more N because they have a higher nutrient demand when mineralizing C. Low-quality litters can also contain high tannin contents, which can bind to N and become incorporated in the lignin fraction, decreasing decomposition and increasing immobilization of N (Gallardo and Merino 1992, Aerts et al. 2003). Although we did not measure tannins in our litter, others have found that Betula spp. leaves can have more polyphenols than Salix spp. and Populus spp. leaves (Palo 1984). In addition, litter of B. papyrifera grown under elevated CO₂ increased tannin content by as much as 81%. When decomposed in a common garden, this high tannin content litter had lower rates of decomposition and higher N immobilization compared to litter from ambient CO₂ conditions, which had lower tannin levels (Parsons et al. 2004).

Results from our common substrate experiment suggest that, at least on a short time scale, any effect shrubs have on soil microclimate via their ability to trap snow will have little influence over nutrient turnover through the decomposition of aboveground litter. How shrubs influence decomposition of belowground litter (roots and rhizomes) remains uncertain. In contrast, changes in soil nutrient availability and/or changes in soil microbial community associated with an increase in deciduous shrub abundance will likely decrease the rate at which litter decomposes, assuming that the native litter responds similarly to the common substrate we used in our experiment. The litter of B. neoalaskana had a higher C:N ratio than the deciduous shrub litter native to these sites but similar lignin content; thus, we assume that when native litter is decomposed at the high shrub site it would respond in the same way as our common substrate.

Litter quality controls over litter decomposition

Members of a plant functional group (i.e., deciduous, evergreen, graminoid, etc.) are often similar in their litter chemistry and decomposition rates (Hobbie 1996, Hector et al. 2000, Hobbie and Gough 2004). Comparisons of litter decomposition among species and functional groups in this experiment suggest that decomposition rates of arctic plants cannot be generalized using functional group designations, because species within the same functional group did not always follow the same pattern of decomposition. For example, the evergreen shrub, Ledum decumbens, and the graminoid, Eriophorum vaginatum, had decomposition rates that were similar to those of the deciduous shrubs, B. nana and Vaccinium uliginosum. Their decomposition rates were higher than other species within their functional groups; Ledum decumbens had higher rates than the evergreen shrub Vaccinium vitis-idaea, and Eriophorum vaginatum had higher rates than the graminoid Carex bigelowii. This is in contrast with other decomposition studies within this region (Hobbie 1996, Hobbie and Gough 2004), perhaps because our study included more species of deciduous and evergreen shrubs than were used in previous studies. Decomposition rates varied significantly among species. Of the 10 vascular plant species we decomposed, Rubus chamaemorus had the highest quality litter and the fastest rate of decomposition, losing about 70% of its mass over a 3-yr period. Aerts et al. (2006) also found that R. chamaemorus decomposed more quickly than three other subarctic bog species. In contrast, mosses had the lowest decomposition rates, only losing about 30% of their mass over the same period. Differences among the rest of the species were relatively small. A change in species composition in the Arctic could lead to alterations in community decomposition rates and nutrient turnover if the change includes an increase in the relative abundance of R. chamaemorus and a decrease in mosses as seen in fertilized tussock tundra in Alaska where R. chamaemorus dominates the understory and moss cover is reduced (Chapin et al. 1995).

Litter quality and quantity vs. microclimate controls over litter decomposition

Based on our results, changes in litter quality and quantity via shrub expansion will increase total community-weighted mass loss. This appears to be primarily
driven by changes in litter quantity, rather than litter quality and microenvironment. For example, the low and medium shrub sites had similar ANPP rates and similar mass loss rates, even when differences in litter quality among the sites were taken into account. This suggests that either the quality of litter among the two sites is not different enough to cause differences in community mass loss, or that litter quality is not the main driver of decomposition at these two sites. Of the three sites, the high shrub site had the highest ANPP and the highest mass loss, suggesting that the high quantity of litter produced at the high shrub site is driving the large mass loss from this site. The magnitude of difference in mass loss among the sites, however, is slightly minimized if changes in the soil microenvironment are taken into account, with a trend for an increase in mass loss at the low shrub site and a decrease in mass loss with increasing shrub abundance. This suggests that community-weighted mass loss is more sensitive to shrub-induced changes in the amount of litter inputs than to shrub-induced changes in the soil microenvironment.

Carbon loss of our litter closely followed that of mass loss (Fig. 2). Initial percentage of C of our litter was between 40% and 45%. Therefore, we can assume that community C loss would follow a similar pattern as mass loss, with the absolute values of C loss being about half those of mass loss. Based on these assumptions and our data, shrub expansion will lead to about a 55% increase in C loss from litter. However, we do not know the exact fate of the C lost from the litter, which can be released back to the atmosphere as carbon dioxide, leached into the soil as dissolved organic C, or be incorporated as soil organic matter and microbial biomass. Previous research at these sites show that soil C pools in the top 10 cm at the medium and high shrub sites have 40–60% more C stored in them compared to the soil C pool at the low shrub site (DeMarco et al. 2011). This suggests that a larger portion of the C lost from litter is most likely remaining in the soil at the medium and high shrub sites compared to the low shrub site.

We assumed that litter from all species within shrub communities will respond to the environment in the same ways as the common litter we incubated. However, it is possible that differences in litter quality may interact with site environment at the high nutrient site, resulting in a different pattern than what we saw with our common litter. Litter quality and site interactions are not always reported, as many decomposition studies do not conduct a full factorial experiment where all litter types are incubated in all environments. However, Hobbie and Gough (2004) did show that B. nana stem decomposition followed the opposite pattern when incubated in moist acidic and moist nonacidic tundra compared to the other species decomposed at the same sites.

**Conclusions**

Our study suggests that on a short time scale, the changes in soil temperature and moisture associated with additional snow trapping by shrubs are unlikely to influence litter nutrient turnover enough to drive the positive snow–shrub feedbacks proposed by Sturm et al. (2001). The mechanisms driving shrub expansion are more likely to do with shrub–litter feedbacks, where the higher growth rates and N uptake by shrubs allows them to produce more leaves, resulting in a larger litter N pool and faster internal cycling of nutrients (DeMarco et al. 2011). Retention of N in litter during the early stages of decomposition in shrub sites may be beneficial for soil organic matter decomposition and could help explain why we see more soil N and greater N mineralization at the medium and high shrub sites.

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**Literature Cited**


**Supplemental Material**

**Appendix A**

Aboveground net primary productivity for each species within each shrub community and their corresponding $k$ values (*Ecological Archives* E095-164-A1).

**Appendix B**

Initial mass, carbon, and nitrogen remaining, and decay constants for the common substrate, *Betula neoalaskana* (*Ecological Archives* E095-164-A2).

**Appendix C**

Initial litter quality of leaves and stems of *Betula nana* and *Salix pulchra* collected across the shrub gradient sites (*Ecological Archives* E095-164-A3).

**Appendix D**

Regression analysis of initial litter quality and litter decay constants (*Ecological Archives* E095-164-A4).