The impacts of shrub abundance on microclimate and decomposition in the Canadian Low Arctic

by

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Abstract

Increasing deciduous shrub abundance in the Arctic could alter the biotic and abiotic controls on carbon (C) cycling in these ecosystems. *Betula glandulosa (*Michx.) leaf litter was decomposed at three sites of differing shrub abundance in the Canadian Low Arctic for one year. Summer and winter microclimate along with soil nutrients were monitored and lab incubations simulated autumn temperatures and leaching conditions. At the high shrub site, warmer winter soil temperatures contrasted with cooler summer temperatures likely due to deeper snow and greater thickness of moss and organic soil layers compared to the other sites. However, surface mass loss was significantly higher at the shrubbier site only after a full year suggesting that microclimate was not the only influencing factor. At all sites, large mass losses (21-26%) occurred between August and May with no significant differences among sites. The laboratory study suggested that much of the mass loss occurred shortly after litterfall in autumn.

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1. Introduction

Marine, terrestrial and atmospheric studies have demonstrated that the climate of the Arctic has warmed significantly in the last 30 years (Serreze et al., 2000) and is projected to warm in the future (Hinzman et al., 2005; Woolings et al., 2014; Christensen et al., 2013). A growing body of observational and experimental evidence suggests that this warming may lead to changes in plant communities across the Arctic including a shift to greater shrub species abundance (Fraser et al., 2014; Myers-Smith et al., 2011; Sturm et al., 2001; Tape et al., 2006). This is partly attributed to the ability of certain shrubs like *Betula nana* (L.) to maintain a large population of long shoots, which elongate rapidly when resource availability is increased (Bret-Harte et al., 2001; 2002; Wookey et al., 2009). This gives them a competitive advantage over other tundra plants; consequently, in favorable growing conditions such as warmer temperatures and increased nutrient availability, deciduous shrubs like *Betula nana* proliferate (Wookey et al., 2009).

An increase in deciduous shrub biomass, cover and abundance has been observed across high-latitude ecosystems in northern Alaska (alder) (Sturm et al., 2001; Tape et al. 2006), the Western Canadian Arctic (alder and willow) (Fraser et al., 2014; Mackay & Burn, 2011; Myer-Smith, 2011) and the Canadian High Arctic *(Cassiope tetragona)* (Weijers et al., 2017). Changes in vegetation community structure have the potential to modify ecosystem reflectance and surface-atmosphere exchanges of energy and biogeochemical cycles through the soil-plant-atmosphere continuum. For example, greater shrub abundance may change snow melt rate and timing (Marsh et al., 2010), reduce summer soil thaw rates (Blok et al., 2010), increase winter soil temperatures through snow

trapping (Sturm et al., 2001; 2005) and have negative effects on tundra species richness through the loss of shade-intolerant species (Pajunen et al., 2011; Price & Morgan, 2008). Greater shrub abundance may also affect carbon (C) storage, the C cycle (Cahoon et al., 2012) and the surface energy balance of tundra ecosystems (Chapin et al., 2005). Year-round temperature sensitive processes could be modified by the expansion of shrubs such as decomposition and nitrogen (N) cycling in winter (Nobrega & Grogan, 2007), summer (Buckeridge & Grogan, 2010) and fall/spring shoulder seasons (Bokhorst et al., 2010). Increasing deciduous shrub abundance may directly alter biomass quality and abundance (De Deyn et al., 2008), but also alter abiotic characteristics of the environment, which can influence biogeochemical processes that drive nutrient cycling and soil C storage. For example, past research has demonstrated that shrubs increase plant productivity and biomass in previously graminoid dominated tundra ecosystems, thereby enhancing uptake of atmospheric CO_2 and storage of more C in plant tissues (Bret-Harte, 2002; Shaver & Chapin, 1991), which could work as a negative C cycle feedback to climate warming. Yet long term fertilization studies of deciduous shrubs have demonstrated enhanced C and N cycling compared to unfertilized tundra, resulting in a net loss of deep soil C (Mack et al., 2004), which could result in a positive C cycle feedback to climate warming. Since northern circumpolar regions store 1035±150 Pg of terrestrial soil-bound C (Hugelius et al., 2014), which is over two times the amount stored in the atmosphere (Le Quere et al., 2016), it is crucial that research focus on the mechanisms that drive these potential feedbacks to warming.

Many studies note the importance of snow-shrub interactions on winter biological processes like enhanced microbial activity under shrub canopies (Sturm et al., 2001; 2005). This has led to the snow-shrub hypothesis that suggests that shrub canopies can trap snow and insulate soils in the winter, potentially increasing winter decomposition and soil nutrient availability, which create conditions that promote further shrub growth (Sturm et al., 2001; Buckeridge et al., 2010; Weintraub & Schimel, 2005).

In the spring, shrubs that extend above the snow intercept incoming shortwave radiation, lowering the albedo, and may accelerate local snow melt (Sturm, 2005). Earlier snow melt could extend the length of the growing season and alter timing of phenological development (Sedlacek et al., 2015). This could accelerate the biogeochemical processes that drive nutrient cycling and shrub expansion (DeMarco et al., 2014; Callaghan et al., 2011; Forbes, 2015). Yet with taller canopies and greater leaf area, shrubs may counteract the positive winter effects on soil temperatures by shading the surface, resulting in cooler soils and less soil thaw (Blok et al., 2010), which may slow decomposition processes. The intertwined relations between vegetation structure, microclimate, snow cover and biogeochemical cycling complicate understanding the implications of shrub expansion. In a global meta-analysis of 44 litter decomposition studies, climate was the best predictor of decomposition rates, but within a region, substrate quality was the best predictor (Aerts, 1997). Decomposition of plant litter is an important way by which nutrients are made available for plant uptake in nutrient limited Arctic ecosystems (Kampichler & Bruckner, 2009). Most decomposition studies in the Arctic have focused on graminoid

dominated tundra (Hobbie & Chapin, 1996; Hobbie & Gough, 2004; Güsewell, S. & Verhoeven, 2006), and few studies have quantified the influence of shrub canopies on ecosystem functions such as decomposition (DeMarco et al., 2014; Myers-Smith et al., 2011) or N cycling (Buckeridge et al., 2010; Myers-Smith et al., 2015). DeMarco et al. (2014) demonstrated significant effects of shrub abundance on community weighted mass loss, but determined that changes in soil temperature and moisture associated with snow trapping by shrubs did not influence litter nutrient turnover to drive positive snow-shrub feedbacks. Instead, they found that higher growth rates and N uptake by shrubs allowed for greater leaf biomass production, resulting in a larger litter N pool and faster internal cycling of nutrients and therefore greater mass loss under shrubs. The goal of this study is to quantify both microclimate and leaf litter decomposition rates among three sites of differing shrub abundance to gain insight on how shrub expansion might influence C storage and nutrient cycling processes. To achieve this aim, litter mass loss rates of a common litter were quantified at three low Arctic sites that vary in *Betula glandulosa* (Michx.) shrub abundance and height at the Daring Lake Tundra Ecosystem Research Station in the Canadian Southern Arctic Ecozone in the Northwest Territories.

The specific objectives of the study were:

1) Determine whether summer, fall and winter, annual decomposition rates of *Betula glandulosa* (dwarf birch) leaf litter differ among the three sites and among two soil profile positions (surface and buried 10 cm deep);
2) Quantify summer and winter microclimate differences among these sites and their potential effects on decomposition rates; and

3) Characterize the timing of litter mass loss and nutrient release (C and nitrogen) with field and laboratory analysis.

The results of this study were used to test the following hypotheses:

(1) The snow-shrub hypothesis postulates that shrubs trap snow and insulate soils over the winter leading to warmer winter temperatures (Sturm et al., 2001), while greater shrub abundance shades the soil surface and increases transpiration rates during the summer (Pearson et al., 2013), leading to cooler summer soil temperatures and lower summer soil moisture. Thus, in this study, it is hypothesized that there will be variation in summer and winter microclimate characteristics across the three sites, with lower summer soil temperatures, lower summer soil moisture, and higher winter soil temperature at plots with highest shrub abundance.

(2a) Vegetation feedbacks associated with more deciduous shrubs and larger inputs of higher quality (high N) litter likely promote greater nutrient cycling by microbes (Bukeridge et al., 2010). Thus it is expected that decomposition rates of *Betula glandulosa* will be greatest at the site with greater shrub abundance

(2b) Previous research has found that buried litter (at 10 cm) loses more mass than surface litter, possibly due to buried litter's better contact with the soil environment (e.g. Hobbie & Chapin, 1996; Beare et al., 1992). Thus, it is expected that decomposition rates will be greatest below the surface (10 cm) compared to on the ground surface.

(3a) Past research has demonstrated significant litter mass loss over the winter period (e.g. Abougendia & Whitman, 1979; Hobbie & Chapin, 1996; DeMarco et al., 2014), thus it is expected that there will be significant mass loss over the cold season (August-May)

(3b) Warmer relative temperatures under a deepened snow pack has been hypothesized to allow for continued microbial breakdown during winter (Hobbie & Chapin, 1996); however, recent work has suggested that leaching and active microbial breakdown in autumn is responsible for observed large winter mass loss in many studies (Bokhorst et al., 2010; 2013). It is hypothesized that much of this loss occurs in the first few weeks after litterfall (in simulated autumn conditions).

(3c) Warmer temperatures generally increase microbial activity (Davidson & Janssens, 2006), and other studies have found that decomposition of fresh organic litter by leaching results in high initial DOC values as much of the easily degradable organic compounds are removed (Qualls & Haines, 1992; Magill & Aber, 2000). Thus it is expected that the lab leaching experiment will show concentrations of dissolved organic carbon (DOC, organic C compounds less than 0.45 μm diameter) leached from birch litter will be greatest in the first few weeks after lab incubations begin (Magill & Aber, 2000), and higher incubation temperatures will be associated with greater rates of litter decomposition and release of DOC (Neff & Hooper, 2002).

(4) Mineralization of nutrients from plant litter and soil organic matter is restricted by low nutrient concentrations in the litter and the soil environment (Robinson, 2002; Hobbie, 1996; Hobbie & Chapin, 1996). This implies that greater nutrient availability at the site with greater shrub abundance could promote greater nutrient mineralization from

the litter. Thus, it was hypothesized that there will be enhanced N release from the litter at the site with greater shrub abundance.

To test these hypotheses, a field litter decomposition experiment was established to assess litter decomposition rates and nutrient dynamics of the dominant deciduous shrub species, *B. glandulosa* over a one-year period. Furthermore, soil microclimate, litter quality and snow/permafrost thaw depth were measured to help understand the spatial and/or temporal variation of litter decomposition among the three sites. Additionally, we compared these dynamics between surface and buried (10 cm below ground) litter. In general, laboratory incubations have demonstrated an increase in decomposition rates with temperature and, the effect of moisture on decomposition rates increases with temperature (Nadelhoffer et al., 1991), so we were interested in whether these findings held true for below ground decomposition. Lab incubations were also established to quantify litter decomposition rates and leaching at a finer temporal resolution than what was possible in the field study. The overarching research objective in this thesis was to investigate the potential response of nutrient cycling to Arctic shrub expansion and associated climate warming.

This thesis is divided into five main sections. Chapter 2 reviews existing literature of the experiment and laboratory experiment considerations. Chapter 3 describes the research design for the lab and field studies. Chapter 4 presents the results of the experiments, while Chapter 5 discusses the results within a broader context. The final conclusion chapter synthesizes the main findings in this study.

2. Background

2.1. Evidence & mechanisms for shrub expansion

The Arctic has experienced regional surface warming over the past three decades of about 1˚C per decade (Christensen et al., 2013). General circulation models consistently predict that regional warming will be most intense at high latitudes (Christensen et al., 2013; Houghton et al., 2001). Warmer temperatures can modify biogeochemical processes that affect ecosystem structure and function. The Arctic typically experiences short growing seasons, low rates of plant productivity and nutrient cycling due to low temperatures and the presence of permafrost (Chapin et al., 1988). However, with increasing growing season temperatures (Chapin et al., 2005), plant productivity may increase (Jia et al., 2003), and one of the expected responses is long-term change in tundra vegetation communities (Myer-Smith et al., 2015).

Temperature is a key control for reproduction and can provide conditions favourable for deciduous shrub encroachment. Low temperatures and limited soil moisture and nutrient availability constrain the development of Arctic shrubs (Jonsdottir, 2011). Most shrubs grow slowly and must take advantage of the short growing season, and the energy and nutrient demands of sexual reproduction are often prohibitive under these limitations (Bliss, 1971; Billings, 1987). Consequently, most Arctic shrub species reproduce vegetatively as this strategy allows plants to instead invest energy in foraging for resources in cold and barren environments, as well as recycle and share nutrients

within a clonal colony (Bliss, 1971). Sexual reproduction is important however, as it produces offspring with higher genetic variability, which can increase an individual's chances for survival in changing environmental conditions (Angers-Blondin et al., 2017). Warmer temperatures promote seed viability and germination in northern plants (Meunier et al., 2007; Angers-Blondin & Boudreau, 2017), which is important for stimulating colonization of new sites (Eriksson, 1996). Increasing genetic diversity within clonal populations may improve shrubs' capacity to adapt to a changing environment (Angers-Blondin & Boudreau, 2017), allowing for further shrub encroachment.

There are three mechanisms for increasing shrub cover: infilling of existing shrub patches, increase in growth potential (height), and colonization of areas beyond a species' previous range limit (Myers et al., 2015). For example, expansion of *Salix* and *Betula* shrub species into existing shrub patches has been observed in Alaska (Sturm et al., 2001; Tape et al., 2006) and the Canadian High Arctic (Hill & Henry, 2011) over the last 30 years. Increased canopy height of shrub cover has also been observed for *Salix* species in the Western Arctic (Lantz et al., 2010) and *Betula* species in the Eastern Canadian Arctic (Tremblay, 2012) over the last 50 years. Population infilling can be associated with both clonal growth and by the successful establishment of new seeds; however, the colonization of new sites relies on the successful establishment from seeds (Angers-Blondin et al., 2017). The advancement of alder shrub line has been noted in Alaska over the last 50 years (Dial et al., 2007) and of *Salix* spp. in mountain valleys in the Western Canadian Arctic over the last 30 years (Myers-Smith et al., 2011) and these are likely evidence of successful reproduction. Angers-Blondin & Boudreau (2017) note that

under current and future climate change, sexual reproduction will likely become more prevalent, and that dwarf shrubs may use the dual strategy of filling in gaps by establishing from seed and then spreading vegetatively to exploit resources.

Certain shrub species such as *Betula nana* take advantage of warmer temperatures and enhanced resource availability by recruiting apical meristems to elongate short shoots and increase long shoot production so as to increase access to soil nutrients (Bret-Harte et al., 2001; 2002; Wookey et al., 2009). When resources are abundant, this developmental plasticity gives them a competitive advantage over other tundra plants. *Salix* and *Ledum* (Aiton) *spp*. do not have such an ability to adapt meristem activity and may be limited in their ability to respond to enhanced resource availability (Bret-Harte et al., 2001). However, there is a tradeoff between the attributes that give plants like *Betula nana* the ability to acquire resources and grow quickly and characteristics such as secondary metabolites and long-lived leaves that permit retention of resources in unproductive habitat (Lambers & Poorter, 1992; Grime et al., 1997). Under control conditions, *Betula spp*. have smaller ramets and smaller relative growth rates in length than *Salix spp*., likely due to *Betula*'s investments into non-photosynthetic structures that confer their growth plasticity. Consequently, in favourable growing conditions such as increased air temperature and nutrient availability, deciduous shrubs like *Betula nana* proliferate, while other shrub species like *Salix* may succeed when resources are less abundant (Wookey et al. 2009).

Several short-term experimental studies have provided evidence that warmer temperatures result in shrub growth in the low Arctic (Chapin et al. 1995; Walker et al. 2006). For example, Chapin et al. (1995) found that under experimental warming conditions, there was an increase in canopy cover and height compared to control plots. However, other studies have found that warmer air temperatures result in lower soil temperatures possibly due to insulation of soil by plant cover which buffers the soil against air temperatures (Coulson et al., 1993; Wookey et al., 1993). Additionally, warmer temperatures may enhance evaporation and reduce litter moisture, which can limit microbial litter decomposition (Hicks Pries et al., 2013) and reduce C and N cycling rates, which would discourage shrub expansion (Blok et al., 2016). Robinson et al. (1995) found that sites with low soil nutrient availability have a limited response to warming, suggesting that soil quality is important for determining where shrubs may establish. A study in the High Arctic did not see a strong response to warming, indicating a possible connection between the capacity of plants to respond to changing environmental conditions and growing season temperature and length (Svoboda & Henry, 1987). The lower diversity in the High Arctic may restrict community level responses, as there are fewer responsive species and phenotypes (Svoboda & Henry, 1987). Nevertheless, many researchers attribute recent shrub expansion at high latitudes to global warming (Tape et al., 2006; Jia et al., 2009; Walker et al., 2006; Chapin et al., 2005). In the last few decades, increases in shrub abundance have been documented in Arctic and subarctic tundra ecosystems in northern Alaska (Sturm et al. 2001; Tape et al. 2006), the Northwest Territories (Lantz et al., 2010; Mackay & Burn, 2011), Northern Quebec and Siberia (Forbes et al., 2010). In the Canadian Arctic, regions

dominated by dwarf shrub species have demonstrated the largest increase in absolute peak NDVI between 1982 and 2006 (Jia et al., 2009). High resolution repeat aerial photography demonstrates an increase in woody shrub cover in Tuktoyaktuk Coastal Plain ecoregion of the Western Canadian Arctic between 1985 and 2011(Fraser et al., 2014). Increases in shrub abundance have also been associated with a shift in plant community composition and a decrease in species diversity (DeMarco et al., 2014; Walker et al., 20016; Chapin et al., 1995; Gough & Hobbie, 2003).

Higher temperatures may indirectly promote shrub growth through stimulation of soil organic matter decomposition and mineralization of organic N, which results in more plant available N (Nadelhoffer et al., 1991; Hobbie & Chapin, 1996; Chapin & Shaver, 1996). Warmer conditions increase enzyme activity, which enables faster biochemical reactions and subsequent mineralization of nutrients (Davidson & Janssens, 2006). Fertilization experiments demonstrate that Arctic species are nutrient limited (Shaver & Chapin, 1980; Mack et al., 2004), with reports of dramatic increases in plant productivity following N or phosphorous (P) additions (Bret-Harte et al., 2001). N and P availability can limit productivity in tussock moist acidic tundra (Shaver & Chapin, 1980; Chapin et al., 1995), tussock moist non-acidic tundra (Gough & Hobbie, 2003), heath tundra (Gough et al., 2002) and dwarf shrub communities (Baddeley et al., 1994). Furthermore, in a meta-analysis of 24 litter decomposition studies, N additions were found to stimulate decomposition of high quality litters (<10% lignin content) and inhibit decay of low-quality (>20 % lignin content) litters (Knorr et al., 2005). The quality of the litter

influences mineralization rates by microbial communities, which play a major role in controlling soil N cycling (Aerts et al., 2006; Wallenstein et al., 2007). The C:N is a ratio of the mass of C to N in a substance and can indicate the decomposability of the material (Di Palo & Fornara, 2015; Moreno et al., 2017). For example, graminoid and moss vegetation have a higher C:N ratio relative to other litters (e.g. deciduous shrub litter), contributing to a large, but low-quality C supply to tussock soils (Wallenstein et al., 2007). Conversely, organic material with a higher proportion of N stimulates mineralization by microbes (Abbasi et al., 2015).

Greater abundance of deciduous plants can alter litter quality but also result in greater litter input, which may act as both a positive and negative feedback to shrub growth. For example, Buckeridge et al. (2010) note that the tall birch hummock ecosystem produced 2.5 times more litter mass than birch hummock ecosystem. Shrub biomass has a large woody component that increases the total C:N ratio in the litter which may create a more recalcitrant litter that decomposes slower (Mack et al., 2004; Hobbie, 1996). The deciduous shrub *Betula nana* has been found to allocate 79% of its total biomass to new and old stems (Shaver et al., 2001), which decompose one to eight times slower than leaves and stems from graminoids and evergreen shrubs found in Alaskan Arctic tundra (Hobbie, 1996). A shift to more recalcitrant woody litter that decomposes slowly could lead to a decrease in plant-available N (Hobbie, 1992), which could act as a negative plant-soil feedback. However, although shrub litter has a large woody component, the leaf litter generally has lower C:N compared to graminoids and mosses (DeMarco et al.,

2014) and has been found to contribute to a small, but highly labile pool of bioavailable C that is N rich (Wallenstein et al., 2007; Weintraub & Schimel, 2005). Circumpolar decomposition studies have noted that litter C:N is a good inverse predictor of decomposition rates and that deciduous shrub litter actually loses mass more rapidly than graminoid or evergreen shrub litter (Aerts & Chapin, 2000; Aerts et al., 2006; Cornwell et al., 2008; Quested et al., 2003). Buckeridge et al. (2010) note that larger inputs of high quality *B. glandulosa* leaf litter promoted soil N cycling and enhanced shrub growth within canopy forming birch tundra. Thus, shrub dominated tundra may have high inputs of low C:N leaf litter, but the rates of litter decomposition may be tempered by the contribution of mosses, stems and other woody litter. Further investigation is required to determine how litter-nutrient feedbacks influence shrub expansion.

The shift in community composition from tussock tundra to shrub tundra changes the chemical composition of substrates that are supplied to the soil and likely microbial communities and abundance. Wallenstein et al. (2007) examined fungal and bacterial community structure in tussock and shrub organic and mineral soil and determined that shrub soils were dominated by Proteobacteria while tussock and intertussock soils were dominated by Acidobacteria. Acidobacteria are characterized by slow growing 'K-selected' bacteria, which are adapted to compete and survive when resources are limited (Fierer et al., 2007), whereas Proteobacteria tend to grow in soils with high C mineralization rates and exhibit '*r*-selected' attributes, which are adapted to periods of rapid growth when resources are abundant (Fontaine et al., 2003). The *r*-selected

bacteria likely access the highly labile pool of bioavailable C in shrub soils and then die or become dormant when the fresh organic matter is used up (Weintraub & Schimel, 2005). K-strategists likely become relatively abundant in the later stages of the organic matter decomposition process when energy rich compounds have been metabolized by the *r*-strategies and only polymerized compounds remain (Fontaine et al., 2003). These results suggest that soil microbial communities are likely altered by increasing shrub abundance through changes in quantity of fresh organic material inputs (Robinson et al., 1995; Hick & Pries, 2013).

Evidently, the quality and quantity of shrub litter inputs can have different effects on soil nutrient cycling and shrub growth feedbacks. However, other local scale variations in litter inputs can influence soil nutrient composition and cycling. For example, mosses mediate soil properties and processes, with moss-derived organic soils characterized by a low bulk density, cooler soil temperatures in the summer, higher litter C:N, and slower rates of soil decomposition (Bueno et al., 2016; Gornall et al., 2011; Buckeridge et al., 2010). Shrub species will have also have varying C:N ratios – *Betula nana* has been reported to have a higher C:N ratio than *Betula glandulosa* (DeMarco et al., 2014; Buckeridge et al., 2010) that may contribute to different vegetation dynamics at a local scale. Therefore, local scale investigations of vegetation community composition and soil properties are important to determine the relevant microclimate and litter quality/quantity influences on decomposition and nutrient release.

2.2. Shrub influence on carbon cycling

Shrub expansion may influence the C budget of Arctic landscapes through a number of mechanisms that impact the uptake of atmospheric C, storage of C in biomass aboveground (Shaver & Chapin, 1991), and the release of new and old C stored belowground (Mack et al., 2004). Carbon enters the soil through litter inputs, and once in contact with the surface, leaf litter will lose mass through leaching, fragmentation and chemical breakdown by decomposers (Hobbie & Chapin, 1996). This leads to the release of CO_2, DOC, and mineral nutrients and creates a pool of recalcitrant organic materials (Magill & Aber, 2000; Davidson & Janssens, 2006). Warming may accelerate tundra soil organic matter decomposition and result in ecosystem C losses to the atmosphere (Kirschbaum, 2000), but it could also increase nutrient mineralization and result in enhanced plant biomass production, promoting net C storage (Davidson et al., 2000). Satellite records of areas in Alaska dominated by Arctic tundra have demonstrated an increasing trend in greenness, which has been attributed to an increase in shrub biomass (Jia et al., 2003; 2009; Forbes, 2010). Communities dominated by deciduous shrubs including willows (*Salix spp*.), birch (*Betula spp*.) or alder (*Alnus* L. *spp*.) have the highest plant productivity when compared to other tundra plant communities (Shaver & Chapin, 1991). Additionally, shrub biomass has a large woody recalcitrant component, that decomposes more slowly than graminoid dominated litter in some cases (Hobbie, 1996). Thus, conversion to shrub tundra might promote both plant and soil C storage by slowing soil decomposition and increase aboveground ecosystem C accumulation (Shaver et al., 2001; Bret-Harte et al., 2002).

Belowground, soil organic carbon (SOC) stocks are highly variable in Arctic soils and may be vulnerable to future changes in climate and nutrient conditions. Low temperatures and high soil moisture restrict aerobic decomposition of organic matter (Hobbie, et al., 2000), contributing to slow mineralization rates and enhanced soil C storage (Davidson & Janssens, 2006). Tundra SOC can be highly variable among land cover class and soil horizon. Drier environments tend to have lower SOC (Hugelius et al., 2010; Campeau et al., 2014), and areas with more soil moisture support more vegetation leading to greater organic inputs to the soil (Grogan, 2012). The upper 1 m of soil tends to store more SOC than deeper depths, and in general the highest mean SOC storages are in the organic soils (Hugelius et al., 2014). Organic soils and permafrost affected soils store more SOC below 1 m depth, with thick sediment regions having greater C stored than thin sediment regions (Hugelius et al., 2014).

Total ecosystem C storage depends on the balance between plant production and decomposition, and some work has suggested that SOC stocks are substantially lower in deciduous shrub tundra (*Betula nana*) than in adjacent lower productivity in tundra heath systems (Wilmking et al., 2006;). Wilmking et al. (2006) studied a region in Northwest Alaska with recent treeline advance, collecting soil cores at a treed site, shrub site and tussock tundra which were all underlain by permafrost. Despite higher productivity at the shrub tundra site (and thus enhanced aboveground C storage) compared to tussock tundra, these C gains were offset by belowground C losses to decomposition.
They found that tundra sites had up to 22.2 kg C m^{-2} compared to shrub tundra sites with 9.7 kg C m^{-2}, and observed a thinning of organic layer in the shrub tundra sites.

The researchers hypothesized that the transition from tussock to shrub tundra lead to a decrease in permafrost depth, increased drainage and subsequent decomposition or mineralization of large portions of organic matter. Long term research on SOC stocks by Mack et al. (2004) of moist acidic tundra plots in Alaska found that fertilization increased nutrient availability and plant productivity, shifting the species composition from slow growing species to more productive shrubs over the course of the 20 year experiment. Although C stored aboveground increased (due to accumulation of woody shrub biomass and litter), this was offset by a greater loss of soil C in deep organic (>5 cm depth) and upper mineral soil layers, and resulted in a net loss of nearly 2000 g C m^{-2} over the 20-year period. Furthermore, Nadelhoffer et al. (1990) collected soil cores in the foothills region of Alaska and found that naturally occurring shrub tundra characteristic of warmer sites has less soil C storage than tussock tundra despite a greater N availability at the shrub site. These results suggest that decomposition may be sensitive to changes in nutrient availability, and nutrient addition could stimulate aboveground C storage in shrubs, but that this aboveground storage could be offset by enhanced belowground soil decomposition and C loss.

Winter processes may also play a role in release of SOC under shrub tundra. Shrubs trap snow, which can insulate soils and reduce cooling rates, thereby allowing microbial activity to continue throughout winter (Sturm et al., 2005; Schimel et al., 2004). Warmer temperatures underneath the snowpack could maintain more active microbial communities (Schimel et al.,2004), which might result in higher winter respiration rates (Sullivan, 2010) that could promote loss of SOC.

Leaching is another way by which C is lost from the litter. Early stage litter decomposition (within a year of litter fall) tends to be faster than later stages because it is dominated by soluble C loss (ie. DOC), through leaching or microbial breakdown (Gartner & Cardon, 2004; McLaren et al., 2017). Terrestrial DOC is a complex mixture of low and high molecular weight compounds that are derived from vegetation, litter, soil leachates, plant root exudates, microbial enzymes and biomass (Thurman, 1985; Guggenberger & Zech, 1994; Wickland et al., 2007). The fate of DOC is of special importance to C cycling in both terrestrial and aquatic environments. It can act as a microbial substrate (Marschner & Kalbitz, 2003), a vector for the movement of dissolved nutrients between ecosystems (Cleveland et al., 2004), and an electron donor in redox reactions (Dahm et al., 1998). Thus, DOC plays a role in supplying and removing C from the terrestrial and aquatic ecosystems via soil and plant litter leaching (Pinsonneault et al., 2016). Organic compounds exist along a continuum of biodegradability ranging from a high quality labile fraction to a comparatively larger, lower quality recalcitrant fraction resistant to biodegradation (Magill & Aber, 2000; Qualls & Haines, 1992). The biodegradability of organic compounds depends on the source and composition of DOC (Pinnoseault et al., 2016). For example, high carbohydrate concentrations in DOC (i.e. leaf litter) tend to enhance biodegradation rates, as carbohydrates in DOC serve as the main substrate for microorganisms and tend to be readily consumed (Kalbitz et al., 2003). Conversely, higher proportions of polyphenols in litter can slow decomposition rates. Polyphenols such as tannins are a group of plant secondary metabolites that contribute to plant colours and plant defenses against herbivory and decay. They can

alter N availability by forming complexes with cytoplasmic proteins in litter, which results in reduced N availability to decomposers, thereby slowing decomposition rates (Hattenschwiler & Vitousek, 2000). High molecular weight tannins can bind more proteins than low molecular weight tannins and are generally more resistant to decay (Zhang et al., 2009; Naumann et al., 2013). Different vegetation species can affect DOC's biodegradability (Pinnoseault et al., 2016). For example, DOC from birch stands (*Betula pubescns*) have been found to be more degradable and produce more DOC than spruce species (Kiikkilä et al., 2006; 2011). Qualls & Haines (1992) measured the biodegradability of different forest solutions and found that degradation rate of leach leachate was greater than degradation rate of solutions streams and from lower in the soil profile. Thus leaf litter is likely an important source of easily metabolized DOC for microbial metabolism (Magill & Aber, 2000). DOC bioavailability decreases with time because microbial communities selectively consume the more labile substances first (Middleburg, 1989). These results suggest that DOC from deciduous shrub leaf litter may be an important source of easily metabolized DOC for microbes.

DOC is an important compound for terrestrial C cycling, but is also an important output from ecosystems and to downstream C cycling. DOC decomposition may be influenced by extrinsic factors like temperature, microbial composition, nutrient availability (Koehler et al., 2012) and intrinsic molecular properties such as size, aromaticity and reactivity (Kalbitz et al., 2013). Aromatic C content is a general characteristic of the pool of molecules that comprise DOC and is an indicator of DOC reactivity in a number of environmental processes (Mladenov et al., 2006; Weishaar et al., 2003). For

example, DOC derived from vegetation and soil organic material has been found to have higher reactivity compared to DOC derived from submerged vascular plants in aquatic systems (Catalán, 2013). The higher reactivity may reflect a more labile DOC character in vegetation/soil derived DOC, which implies that it may be an important input for bacterial communities in the receiving water body (Catalán, 2013). Warmer temperatures could stimulate DOC production by enhancing microbial activity and increase decomposition rates (Christ & David, 1996). Further work distinguishing the controls on DOC release from litter will improve understanding of how C cycling may be influenced by a changing climate.

2.3. Shrub influence on abiotic environment

Shrub encroachment is a key change in Arctic vegetation structure that can alter the abiotic environment and influence biogeochemical processes that drive nutrient cycling. The snow-shrub hypothesis suggests that tall shrubs tend to capture more snow, reduce compaction (and conductivity) of the snow pack (Domine et al., 2016) and insulate the ground, limiting cooling relative to tundra with less and/or denser snowpacks (Sturm et al., 2001). Experimental manipulations using shrub removal (Myers-Smith et al., 2011) and snow fences (Myers-Smith et al., 2011; Buckeridge et al. 2010) have demonstrated that deeper snow depth leads to warmer winter surface soil temperatures (Grogan & Jonasson, 2003; Schimel et al., 2004; Sturm et al., 2005) and can increase litter decomposition rates (Baptist et al., 2010) and N cycling (Nobrega & Grogan, 2007; Buckeridge et al., 2010). Microbial activity may occur through winter even when temperatures are below 0˚C (Hobbie & Chapin, 1996; Coxon & Parkinson, 1987).

In sub-zero temperatures, water-soil particle interactions and surface tension can allow for unfrozen water to exist at temperatures as low as -40˚C (Anderson & Morgenstern, 1973; Hinzman et al., 1991). However, the high matric potentials results in very thin liquid water film (Anderson & Morgenstern, 1973) that likely restricts significant microbial functioning.

Freeze-thaw cycles, which are more prevalent during warmer winters (Foster et al., 2016) and below shallower snow packs (Bokhorst et al., 2013; Wipf et al., 2015) promote organic material mass loss by fragmenting litter and causing the release of soluble compounds that are either respired as CO_2 or leached during spring run-off. Experimentally induced freeze-thaw cycles in deep snow packs have also been shown to enhance nutrient release and litter decomposition compared to shallow snow locations (Wipf et al., 2015). In most studies, it is not conclusive whether biological activity (i.e. polymer breakdown via enzymes) or physical processes like fragmentation or leaching were responsible for winter mass loss (Aber et al., 1990; Hobbie & Chapin, 1996). However, a study by Stark (1972), demonstrated a direct link between biological activity and mass loss in the winter, finding that about 80% of the first year's mass loss of Jeffrey pine (*Pinus jeffreyi)* litter occurred during winter months by black fungal hyphae and other animal and bacteria living under the snow at 0 to -1˚C.

Observations of winter mass loss have been challenged by results from recent field and laboratory studies. Lab and field decomposition studies by Bokhorst et al. (2010; 2013) provide evidence suggesting that winter decomposition is almost non-existent and that

observations of mass loss across the cold season is actually the result of leaching in "shoulder seasons" before the ground freezes (eg. autumn and spring) prior to the onset of "true winter". It is important to resolve this uncertainty surrounding the timing of litter mass loss because of its link to the contribution to the annual ecosystem C budget of Arctic ecosystems. Additionally, if autumnal leaching is a major factor in litter decomposition, then it brings into question the relative importance of mechanisms such as the snow-shrub hypothesis for influencing litter decomposition rates.

A major uncertainty in the hypothesized snow-shrub feedback loop is whether summer effects counteract positive winter effects on soil temperature and decomposition (Sturm et al., 2001). During the spring, shrubs that extend above the snow intercept incoming shortwave radiation, lowering the albedo and may initially accelerate local snow melt; however, shading by shrub branches extending above the snow can lengthen the duration of melt (Sturm, 2005; Marsh et al., 2010). Earlier snow melt could prolong the growing season, alter timing of phonological development, increase exposure to frost and change moisture availability among other effects (Sedlacek et al., 2015). Furthermore, with taller canopies and greater leaf area, shrubs may temper the positive winter effects on soil temperatures by shading the surface (Myers-Smith et al., 2011; Pomeroy et al, 2006). Light penetration through canopies decreases exponentially with increasing leaf area following Beer-Lambert Law (Monsi & Saeki, 2005). Denser shrub cover that leads to both shading and thicker organic soil layers with reduced thermal diffusivity, will result in soils which warm less with a shallower active layer (Blok et al., 2011). This may serve to limit soil microbial activity and slow rates of decomposition

(Blok et al., 2011). Compared to mineral soils, organic material acts as an insulator, with low thermal conductivity and relatively high heat capacity when wet (Hinkel et al., 2001). The presence of a thick moss-organic layer mitigates the transfer of energy down into the soil during the spring and summer, typically leading to cooler temperatures in the summer compared to mineral soils (Bonan & Dhugart, 1989). Blok et al. (2010) found that soils experience greater thaw depth and warmer summer soil temperatures when *Betula nana* canopies were experimentally removed. Lantz et al. (2013) found higher ground temperatures in summer and early winter at an open shrub cover site compared to a dense shrub tundra site, which suggests that soil shading and the resultant effect on soil temperatures is dependent on the density of shrubs that form the canopy (Lantz et al., 2013; Sturm et al., 2005). It is not known what the density threshold is that results in large changes for abiotic parameters such as soil temperature, but it appears that high densities of shrubs can offset some of the positive feedback between shrub cover and warming.

Additionally, some studies report a decrease in plant species diversity under shrub canopies due to the loss of shade-intolerant species (Price & Morgan, 2008; Pajunen et al., 2011). Therefore, shade-tolerant moss species such as *Sphagnum* could expand with shrub species (Paradis et al., 2016), replacing formerly lichen dominated environments (Tremblay et al., 2012). Mosses have a high degree of phenotypic plasticity in response to a wide range of temperatures, with the ability to switch between metabolic activity and rest (Turetsky et al., 2012). They have a cooling effect on soils in the summer due to their low thermal conductivity, and when combined with shade provided by shrub

canopies, could favour the persistence of permafrost (Zimov et al., 2006; Paradis et al., 2016).

2.4. Field and lab considerations

These uncertain interactions between shrubs, microclimate, and nutrient cycling are important to both vegetation change and C cycling questions. Thus, it is important to determine the extent to which climate, litter quality and quantity interact to drive decomposition. In terrestrial ecosystems, decomposition of plant litter is commonly assessed using the litter bag method, which consists of enclosing plant tissue of a known mass and chemical composition in a mesh container (Heal, 1997). The litterbag technique has been used since the 1960s and enables the study of decomposition dynamics (mass loss, nutrient loss) in situ under field conditions (Kampichler & Bruckner, 2009). The technique is simple and inexpensive to set up, thus is widely employed, and using it in this study will allow for better comparisons between other studies using similar methods. However, there are some important shortcomings to using this technique, which inform the type of results one gets in an experiment. Kampichler & Bruckner (2009) note that low numbers of replicate bags cast doubt on some studies' results, as the estimation of the parameters of the decay function are less reliable when there are fewer data points to fit the function. Furthermore, the mesh bag will alter the microclimate of the dead material, by restricting movement and evaporation (Bokhorst & Wardle, 2013). Additionally, mesh size may influence the amount of mass that can be lost from the litterbag. A coarser mesh size dramatically enhances decomposition when compared to finer mesh size, potentially due to greater exposure to leaching events. Finer mesh sizes may impede microbial

colonization of litter. Researchers tend to be inconsistent in the choice of mesh size, bag size and amount of litter chosen, which can add uncertainty in comparing results of these studies. For example, DeMarco et al. (2014) enclosed 1 g of *Betula nana* litter in 8 × 8 cm bags with a mesh size of 2 mm, Myers-Smith et al. (2011) and Hobbie & Chapin (1996) used a mesh size of 1 mm with 10 × 10 cm bags to enclose 0.5 g *Betula* litter and 5 g of moss litter respectively, and Bokhorst et al. (2013) enclosed 1 g of Scots pine in a 6 × 6 cm bags with a mesh size of 1 mm. Moisture and microbial litter colonization rates could be different due to mesh design and litter type, as could the causes of litter fragmentation and decomposition – with soil animals having larger influence on decomposition of litter in coarse mesh and microbial activity a greater influence on fine mesh sizes. Furthermore, loss of litter through fragmentation by soil fauna can depend heavily on the structure and toughness of the leaves (Bokhorst & Wardle, 2013). Thus, careful consideration of the parameters used for other litter decomposition studies is important when attempting to compare results.

Alternative methods to investigate litter decomposition include litter cages, mesocosm studies, and the intact core method (Dornbush et al., 2002). Litter cages enclose litter in small mesh frames that help to avoid leaf compression that litterbags sometimes cause and simulate natural deposition of leaf litter on the substrate. They are typically used to investigate the role of macrofauna in surface decomposition. Consequently, mesh sizes tend to be larger (e.g. Tanaka et al. (2006) uses mesh sizes of 25 mm × 25 mm), so as to allow access by macrofauna, but can lead to higher incidence of litter loss through the mesh. A mesocosm study simulates the environmental conditions of the study site in an

experimental enclosure and incorporates several levels of biological complexity. For example, Schlief & Mutz (2009) investigated the impact of microbial mediated litter decomposition under different stream flow regimes, and set up the mesocosm would be filled with a representative density of litter, macroinvertebrate and detritus for that system. This method allows examination of interaction between several variables under controlled conditions; however as it is a model of real world conditions, it simplifies or excludes some of the other interactions that influence litter decomposition (Stewart et al., 2013). It can also be time consuming to set up and monitor. Finally, the intact core method is often used to investigate decomposition of belowground plant constituents such as roots, as it preserves the connections between roots, soil and rhizophere microbial communities (Sun et al., 2013). This method is often used instead of the litterbag technique, as root litter decomposition is frequently misrepresented due to enhanced loss of fine litter (Kampichler & Bruckner, 2009).

Both field and lab decomposition methods are used in this study. Field decomposition experiments are valued as a set of observations taking place in the natural environment. However, many aspects of litter decomposition are difficult to study and control for in the field. For example, winter mass loss is difficult to assess due to lack of access to the field site, thus a parallel laboratory experiment under simulated conditions will help answer questions such as how decomposition processes might operate during the autumn and winter. A laboratory decomposition experiment allows for the investigation of decomposition at a finer temporal scale than what is possible in the field and allows for precise control of temperature and moisture variables. Though a laboratory experiment

has a high level of internal validity, its contrived conditions do not transfer easily to the natural environment and thus the experiment can suffer from a low external validity (Slaymaker, 1991). To enhance comparison of the lab study to the field study, careful review of the methodology other similar lab/field decomposition studies (e.g. Bokhorst et al., 2010; Magill & Aber, 2000) was done so as to design a comparable experiment. The key consideration for the experimental design was to emulate methods of other studies with similar objectives. For example, DeMarco et al. (2014) had a similar interest in determining how shrub abundance influence litter decomposition rates; thus, the type of litter chosen, the amount of litter used and the duration of this study aligns closely with the DeMarco et al (2014) study in order to allow for better comparisons. Similarly, the lab studies sought to reproduce some of the findings in Bokhorst et al. (2010), so the experimental designs are similar.

3. Methods

3.1. Site Description

The three field study sites are located close to the Tundra Ecosystem Research Station (TERS) which is on the northern shore of Daring Lake, central Northwest Territories, Canada (64˚C 52' N, 111˚ 35' W). TERS is approximately 70 km above the tree line and 300 km northeast of Yellowknife and is within the Southern Arctic (Ecosystem Classification Group 2012; Figure 1). Weather records from the Daring Lake weather station between 1996 and 2014 indicate average daily air and soil (5 cm depth) temperature of -29.1˚C and -20.4˚C, respectively in January and 13.5˚C and 11.5 ˚C, respectively in July. Average minimum and maximum air temperatures in January vary widely from -38.0˚C to -17.3˚C, respectively and from 6.6˚C to 19.5˚C, respectively in July. Annual average temperature is -7.9˚C. The snow-free season lasts approximately 120 days (ranging from early June to late September), with an average summer (June through August) rainfall of 141 mm. The tundra landscape in this region includes exposed bedrock outcrops and many lakes, where the latter cover approximately 30% of the surface (Lafleur & Humphreys, 2008). The study region is underlain by continuous permafrost with seasonal thaw to a maximum depth of 0.3-1.2 m depending on the soil type and vegetation cover. Soils in this region typically have a thin surface organic horizon in drier areas (less than 0.1m) and a thicker organic horizon in wetter areas (up to 0.7m), overlying coarse mineral soil (Humphreys & Lafleur, 2011).

In July 2015, study plots were established near three long-term eddy-flux tower sites. The three sites exhibited distinct natural variations in shrub abundance, hereafter termed

low shrub, medium shrub and high shrub sites (Figure 2). All three sites are within 3 km of each other (Figure 1) located on relatively flat terrain.

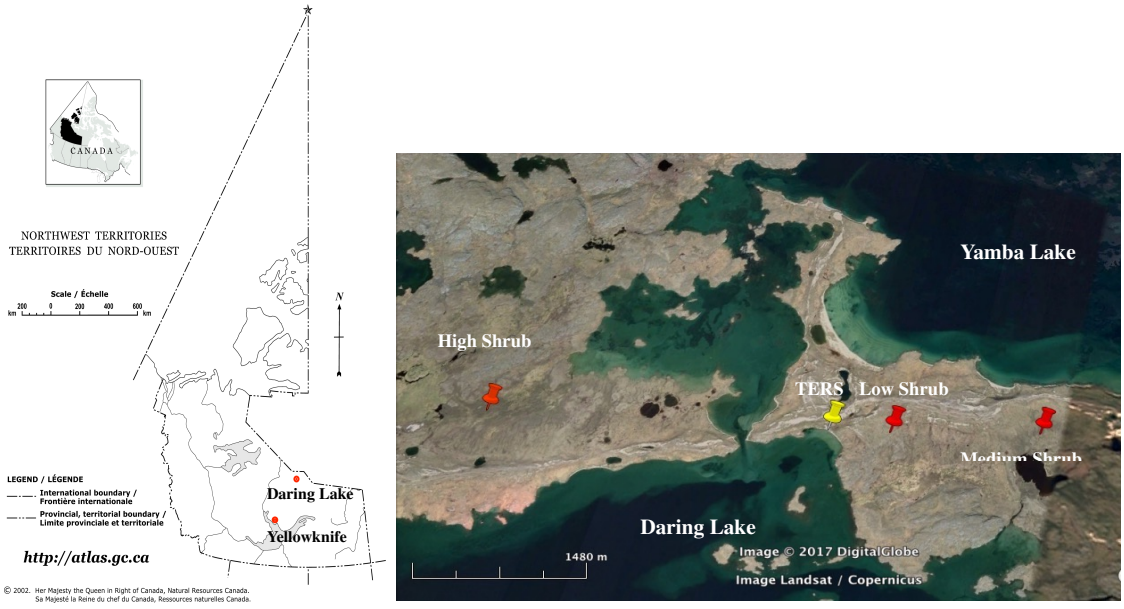

Figure 1. Location of Daring Lake, NT and sampling sites. Litter was collected near the high shrub site. TERS = Tundra Ecological Research Station.

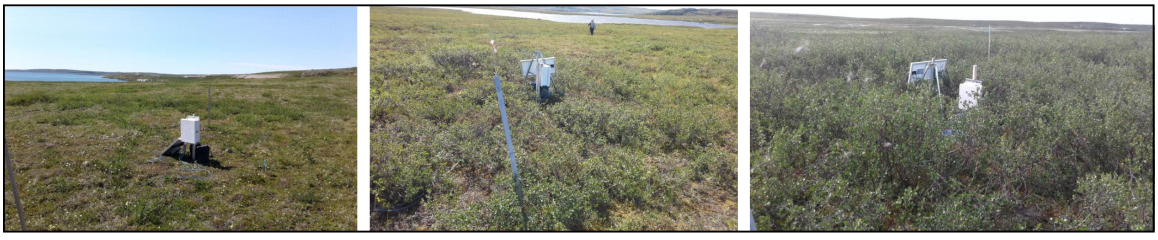

Figure 2. Images illustrating the differences in vegetation characteristics and *B. glandulosa* shrub abundance at the low, medium and high shrub sites, from left to right. The top of the datalogger enclosure used to record soil temperatures at each site, was roughly 1 m above the ground.

The study plots at the low shrub site were located in Circumpolar Arctic Vegetation Map (CAVM) designated S1 tundra (including erect dwarf shrub tundra & G4, tussock-sedge, dwarf-shrub, moss tundra), a local upland area with well-drained sandy loam soil on the slope extending down from the esker to the north (Figure 1). Total LAI (calculated using the point intercept method) at peak biomass was 2.66 with *B. glandulosa* contributing 10.2% to the total. The average height (± 1 standard error (SE) of *B. glandulosa* was 28.5 ± 0.2 cm within the study plots. Ground cover is dominated by lichen species (78.9 ± 5.0%) and to a lesser extent, mosses (16.5 ± 4.9%).

The medium shrub site (CAVM designation S1) is located approximately 1 km north-east of the low shrub site and is on terrain very gently sloping down from the esker north of the site. The vegetation community structure is similar to that of the low shrub site, and both sites are located on silt loam soil. Total green LAI at peak biomass was 4.00 with *B. glandulosa* contributing 35.2% to the total. The average height (± 1 SE) of *B. glandulosa* was 45.9 ± 0.2 cm within the study plots. Ground cover is dominated by moss species (91.7± 2.0%) with a smaller portion of lichen species (6.7± 1.9%) compared to the low shrub site.

The high shrub site (CAVM designation S2) is located approximately 2.5 km south-west of the low shrub site at the toe of the slope down from the esker lying south of the site (Figure 1). Total LAI at peak biomass was 4.63 with deciduous shrubs *B. glandulosa* and some *Salix* spp. individuals contributing 43.0 and 6.4% to total LAI, respectively. The average height (± 1 SE) of *B. glandulosa* and *Salix* spp. was 133.1 ± 0.3 cm within the

study plots. Ground cover here is entirely dominated by moss species (96.5± 1.1%) with no lichen cover.

3.2. Litter bag study design

Each site was divided into a grid (size of grid dependent on the boundaries of the shrub condition of interest). Within the grid, five replicate 8 m × 3 m plots were randomly chosen at least 30 m apart and ensuring the plots visually represented the typical *B. glandulosa* abundance of each site.

In July 2015 approximately 600 g of green *B. glandulosa* leaves were collected approximately 350 m west of the high shrub site. *B. glandulosa* leaf litter was chosen due to the interest in studying shrub effects on decomposition and because of its relative abundance compared to other shrub species allowed us to collect enough material for the study. Leaves were air dried to a constant mass, mixed and subsampled for the litter bags. Approximately 1 g of litter was inserted into seam-sealed 1 mm fibre-glass mesh bags, 8 × 8 cm in size. This would allow passage of most microfauna but not macrofauna into the litter. In August 2015, a total of 600 litter bags were set out on the surface and 10 cm below the surface at the 5 replicate plots at the three sites. Within the plots, the litter bags were placed along 5 transects, spaced approximately 0.5 m apart from each other. Each transect contained 4 surface and 4 buried litterbags, spaced approximately 1 m apart. Surface bags were nailed to the ground through their tag, and then a buried bag was attached to it with fishing line. This bag was buried next to the surface bag by inserting a small shovel into the soil (cutting moss and woody material as necessary), then wedging up the soil to slip the litterbag underneath. A subsample of litter bags (4

surface bags and 4 buried bags along a transect at each replicate plot, for n=20 surface and n-20 buried bags per site per collection), were collected in early spring (May 2016) and summer (August 2016) to determine mass and nutrient loss. Note only a partial collection of buried bags in May 2016 was possible. Buried bags were collected at 1 plot at the high shrub site (n=4), 3 at the medium shrub site (n=12) and 4 at the low shrub site (n=16). After each collection, bags were immediately frozen until they could be processed at Carleton University. Remaining litter bags will be collected in the same manner every August until 2019 for later analyses.

Retrieved litter bags were thawed in the lab and tissue samples and cleaned (brushed to remove soil, sand and foreign foliar tissues). They were then oven-dried (65˚C) to a constant mass, weighed and ground with a mortar and pestle such that they could pass though a 0.5 μm mesh sieve. An additional subsample was ground for %C and %N determination with a LECO TruSpec C/N analyzer at Queen's University, Kingston. Initial leaf chemistry was determined from subsamples of *B. glandulosa* taken from each site (n=5 leaves at medium and low shrub site and n=10 at high shrub site).

3.3. Decomposition calculations

3.3.1. Initial litter weight

As the initial leaves were air dried rather than oven dried, a moisture correction was applied to the initial weight of the litter. To calculate the correction factor between air-dried and oven-dried samples, a subsample of the air dried litter was oven dried at 65˚C to a constant weight, and the moisture correction factor was determined as a fraction of the oven dried weight to the air dried weight. This factor was applied to all initial litter weights.

3.3.2. Soil correction

The contents of the litter bags, especially those of buried bags, typically contain a mixture of the decomposing original material and some soil from the surrounding area (Nadelhoffer & Blair, 1992). Some of the soils had high organic matter content and contributed to the apparent organic matter mass of the litter. Despite cleaning the litter (ie. gently brushing the leaves), it was apparent that the buried litter still had soil contamination, and it was determined that the dry weight needed to be corrected for soil infiltration before determining mass loss or calculating decomposition rate constants. The methods in Harmon et al. (1999) were followed to perform soil corrections. A subsample of the ground litter from a buried and surface sample from each subplot was ashed (4h at 450˚C) and the mass remaining expressed based on percent ash-free dry mass (AFDM) of the initial and final litter samples. Then, to correct for soil contamination the following soil correction equation established by Blair (1988) was used:

$$F_{litter}=(M_{AF\text{-}sample} - M_{AF\text{-}soil}) / (M_{AF\text{-}litter} - M_{AF\text{-}soil}) \quad (1)$$

where
F_{litter} is the proportion of litter bag sample mass that is actually litter;
$M_{AF\text{-}sample}$ is the % AFDM of the entire litter bag sample;
$M_{AF\text{-}soil}$ is the % AFDM of the surface soil at the site;
$M_{AF\text{-}litter}$ is the % AFDM of the initial litter;

The weight of the litter bag sample was multiplied by the correction factor (F_{litter}) to obtain the weight of the remaining litter.

The accumulation of soil in the litter bag also affects apparent N and C concentrations in the litter. Therefore, the nutrient concentrations of buried litter bag samples contaminated with soil (as indicated by reductions in % AFDM) were corrected using the following equation (Blair, 1988):

$$N_{litter}=[N_{sample}-(F_{soil} \square N_{soil})] / F_{litter} \quad (2)$$

where
N_{litter} is the nutrient concentration in the residual litter;
N_{sample} is the nutrient concentration of the entire litter bag sample;
N_{soil} is the nutrient concentration of the soil;
F_{litter} is the proportion of the litter bag sample that is litter (from the above soil correction equation);
F_{soil} is the proportion of the litter bag sample that is actually soil (1- F_{litter})

With the soil correction applied to the buried bags, the % of initial N was then calculated as:

$$\% \text{ of Initial N} = (\text{Final litter N\%} / \text{Initial litter N\%}) \times 100\% \quad (3)$$

3.3.3. Decomposition rate constant

There are several models that can be used to describe mass loss with time and derive the decomposition rate constant, k. The simplest is the single negative exponential model of the form $X_t/X_0=e^{-kt}$ where X_t/X_0 is the ratio of litter mass remaining at time t to initial litter mass, t is time elapsed, and e is the base of the natural logarithm (Berg & McClaugherty, 2008). This model produces a single decomposition rate constant:

$$k = -\log(X_t/X_o) /t \ . \qquad (4)$$

k values in this study were calculated for 3 time periods: annual, fall/overwinter (using the May collection data), and growing season. In the latter case, this model likely overestimates the k value since the mass loss over time is not likely to be exponential in that time frame. The single negative exponential model assumes a constant rate of decay (Berg & McClaugherty, 2008). The first year of mass loss is typically faster compared to later years for many species of litter (e.g. McLaren et al., 2017), as many soluble organic compounds are leached or decomposed relatively easily. As litter decay continues, the relative proportion of recalcitrant compounds in the litter such as lignin increases, so decomposition may slow down relative to the first year. Thus, most leaf litter does not decay at a constant rate as assumed by the single exponential model, but can be divided into early rapid phase and later slower phase. As decomposition of this litter continues, it may eventually be appropriate to use the double exponential model to account for the changing substrate quality (Lousier & Parkinson, 1976).

$$M_t = Ae^{-k1t} + Be^{-k2t} \quad (5)$$

where t is the time, and k1 and k2 are rate constants for quickly and slowly decomposing fractions of the litter respectively. The amount of each fraction is given by A and B, respectively.

3.4. Vegetation, soil and environmental variable measurements

An overview of vegetation and soil characteristics and microclimate variables measured at each site is described in Table 1. Soil temperature was measured continuously at 2 and 10 cm depths at one plot in each of the three sites. Eight replicate thermocouples at both depths were instrumented at each subplot as of July 2, July 4, and July 6 2015 for the medium, low and high shrub sites, respectively. Signals were recorded on a CR 21X datalogger (Campbell Scientific Inc., Logan, UT, USA), stored on storage modules and downloaded to the computer later. Soil temperature measurements were taken every 10 minutes and stored as average, maximum and minimum values for each 24 hour period. Measurements began in July 2015. Gaps in the data record due to power problems occurred between October 2015 – May 2016, December 2015 – May 2016 and February - May 2016 at the high, low, and medium shrub sites, respectively.

Between July 2015- August 2015 and July 2016-August2016, average soil volumetric moisture content was measured by a Hydrosense II probe (0-20 cm VWC) by inserting the probe (Campbell Scientific Inc., Logan, UT, USA) vertically to a depth of 20 cm from the soil surface. Each sample measures the period (μs), which is the dielectric permittivity of the soil between sensor rods and a computed value of % soil volumetric water content based on the default logarithmic instrument calibration. Eight

measurements were taken at each plot. At these same locations, thaw depth was determined by pushing a metal probe to the depth of resistance.

Leaf Area Index (LAI) was manually measured with a LAI 2200 Plant Canopy Analyzer (LI-COR Inc, Lincoln, NE) every 7-10 days between July 2015-August 2015 and July 2016 – August 2016 to characterize the vegetation during the mid growing season and early fall. A view restrictor with a 270˚ opening was used to remove the user from the view. Additionally, the point intersect method (Bonham, 1989) was used to assess vegetation characteristics near the estimated time of peak biomass (last week of July). Green plant part abundance and height was surveyed using 240 point-intercepts in each 8 □10 m plot. Six 10 m transects, set up 1 m apart from each other were used to assess vegetation characteristics. Forty points (defined by dropping a ~2 mm diameter, 50 cm long pin) spaced 0.25 m apart were surveyed along each of the transects. For each pin drop, the number of pin contacts with green leaves was recorded along with the species or in the case of graminoids, only the plant functional type/category was noted. If no vascular vegetation was contacted but the pin contacted moss/lichen/soil, this was noted separately. For each transect, vascular plant LAI was calculated. LAI was calculated as the number of green vascular plant "hits" divided by the number of pin drops (240) and multiplied by 100%. Additionally, moss and lichen cover was determined by the number of pin drops that hit moss and lichen, divided by 240 and multiplied by 100%.

Snow depth was determined at each site from two sampling periods in early May 2016

and 2017 before substantial snow melt occurred. Snow density (mass/volume) was measured with a metal corer at each site in a single pit near a randomly chosen plot. The depth of each snow layer with distinct characteristics was measured and cored.

Nutrient availability was determined at each site in spring 2016 and summer 2016 using anion and cation exchange resin probes (Plant Root Simulator™ probes, Western Ag Innovation Inc., Saskatoon, Saskatchewan, Canada). Four cation and four anion probes were installed at 0-10 cm depth at each replicate plot for each site. They were installed between May 18-21 2016 and retrieved between July 2-4, 2016. Another set was installed and removed between July 2-4 2016 and August 9-11, 2016, respectively. When removed, probes were cleaned with deionized water, placed in clear plastic bags and shipped on ice to Western Ag Innovations lab for analysis. PRS probes act as an ion sink to adsorb any ionic species (soil nutrients) that are supplied from the soil over time, mimicking absorption by plant roots. In this study, they are used to investigate how the bio-availability of nutrients such as nitrates and phosphates differ between sites as well as the timing of nutrient release from these sites in the spring and summer period. Anion probes monitor nitrate, phosphate, sulfate, iron, and manganese, and cation probes monitor potassium, calcium, ammonium and magnesium.

Table 1. Schedule for measuring vegetation, soil, and microclimate variables at each site during the Summer 2015 and 2016 field seasons. Measurement method details are described in the text.

Variable	Measure-ment frequency	Number of samples/ plot	Summer 2015	Spring 2016	Summer 2016	Measurement method
LAI_{2200}	weekly	8	x		x	LI-COR LAI-2200 Plant Canopy Analyzer
Green LAI	once mid-summer	1			x	Point intercept method
Volumetric soil water content	weekly	8	x		x	Campbell Scientific HydroSense II probe
Thaw depth	weekly	8	x		x	Metal probe
10 cm soil temperature	weekly	8	x		x	Digital thermometer
2 cm soil temperature*	10 min	8	x	x	x	thermocouples connected to datalogger
10 cm soil temperature*	10 min	8	x	x	x	thermocouples connected to datalogger
Nutrient availability#	cumulative 6 week measure-ment	4		x	x	Plant Root Simulator Probe (Western AG)
Snow depth	once early May	8		x		Metal probe

* Continuously recorded soil temperature was measured in only one plot/site, with n=8 thermocouples per plot per depth. 10 min readings were stored on the datalogger as daily average, maximum and minimum values.
# 4 replicates were combined to give only 1 analysis/plot.

In July 2016, biomass and soil characteristics were assessed at three soil pits roughly 1 m away from 3 of the 5 plots at each site. Before harvesting biomass and digging soil pits, 25 pin drops were made at the intersection of grid lines 10 cm apart within a 50 × 50 cm grid for a total of 25 pin drops using the same method described above to compute % vascular cover, % moss cover, and vascular plant LAI. Canopy height for each site was determined by averaging the height of the 10 tallest shrubs in each subplot, and then taking the mean value across subplots.

After measuring LAI, plants were cut to ground level, separated by species or plant functional type and dried in paper bags. This was to determine the relative contribution of different vascular plant species to the total aboveground biomass. Only living aboveground vascular plants were harvested, and thus the biomass calculations do not include standing litter, mosses, lichens or belowground constituents like rhizomes or roots. Leaf biomass was measured by sorting harvested material by species, removing leaf material from branches, drying leaves at 35 ˚C to a constant weight and recording the weights.

Soil samples were collected using cores with a diameter of 4.8 cm and depth of 2.5 cm and were taken from the surface at 5 cm intervals until the frozen layer was reached. These soil samples were air dried and then dried at 65 ˚C to constant weight for the calculation of bulk density. Subsamples were used for particle size distribution analysis using the pipette method of sedimentation analysis (Deshpande & Telang, 1950) and % C

and % N determination with a LECO TruSpec C/N analyzer. Soil Organic Carbon and Soil Organic Nitrogen for the depths of 0-20 cm and 0-40 cm was determined by summing the Soil Organic Carbon content for each layer.

3.5. Laboratory decomposition and leaching experiments

Since access to the field site was not possible in fall or winter, in order to investigate decomposition rates related to autumn conditions (i.e. the period before the ground is frozen), a laboratory mass loss study was conducted. The lab study investigated mass loss rates of litter under two temperature treatments: 20 ˚C and 5 ˚C to simulate summer and autumn field temperatures. The procedure follows that of Bokhorst et al. (2010). Samples of *B. glandulosa* leaf litter were collected in July 2016 near the high shrub site and air dried to a constant mass. Litter subsamples were weighed to 0.5 ± 0.01 g, then placed in a clean widemouthed mason jar with a 7.8 cm diameter. Samples were incubated at either 20 of 5 ˚C (room temperature) temperature (n = 17 per treatment). Samples were rewetted with a site-specific soil water extract to re-inoculate the litter with its microbial community. Inoculant was made by combining 1 L of Deionized (DI) water with 150 g of organic soil from the top 20 cm of the high shrub site, shaking vigorously and then allowing to settle for 48 hours before applying 25 ml of inoculant to each jar. One jar from each temperature treatment was immediately processed after wetting by oven-drying at 35˚C for approximately 24 hours, reweighing and grinding for loss on ignition and %C and %N analysis as described for the litter bag study. A set of two samples from each temperature treatment were collected two days after the microbial inoculant was applied, followed by weekly sampling 5 times for a total 30 day incubation period. The final 2 jars at each temperature were transferred to a -5˚C climate chamber and collected

after a 115 day incubation period and processed as described above.

To establish the rate and quality of DOC released from the litter, a leaching study was established that loosely follows the protocols of Magill & Aber (2000). Fresh *B. glandulosa* leaf litter was collected near the high shrub site and air dried as described earlier. Litter was incubated for 15 weeks in polypropylene cups with flat, perforated bottoms. Cups were lined with pre-weighed acid-washed glass wool (soaked in 10% HCL for 24 h then rinsed with deionized water), oven dried at 65˚C for 24 h and then weighed. Each cup was filled with 0.3 ± 0.1 g of air-dried litter, covered with plastic wrap and secured with an elastic band. This weight/area of 80 g m^{-2} was equivalent to summer litter production based on July 2016 biomass measurements and scaled to the area of the cup. Cups were separated into three temperature treatments: 20˚C, 5˚C and 2˚C, with n=4 cups per treatment, for a total of n=12 cups. An additional cup per treatment was filled only with preweighed glass wool to serve as a blank (n=3).

Over the 15 week study, cups were leached with 30 ± 1 ml of DI water every week for 7 weeks and then every two weeks until the end at week 15. Following the initial leaching, 25 ml of microbial inoculant were added to each cup to re-inoculate the litter with the local soil microbial community. The total water applied was equivalent to the expected summer precipitation in the region (125 mm over a 112 day incubation).

Leachate samples were filtered through filters (Whatman sterile cellulose nitrate membrane filters with a 0.45 μm pore size) into scintillation vials. Spectral ultraviolet absorbance (SUVA) was used to assess the aromatic character of the DOC. As increasing DOC concentration increases absorbance in the UV range, UV light is normalized to the concentration of DOC (American Waterworks Association, 2011). Therefore, SUVA is determined to be the absorbance per unit of DOC (mg L^{-1}):

$$\text{SUVA (L mg}^{-1}\text{ C m}^{-1}) = [\text{UV}_{254}\text{ (cm}^{-1}) \text{ x } 100\text{ (cm/m)}]/\text{ DOC (mg L}^{-1}) \quad (6)$$

Leachate samples were analyzed on the Agilent Cary 60 UV-Vis spectrophotometer and a quartz cell with a 2 cm path length was used, along with a blank with DI water. The SUVA method is a surrogate indicator of how aromatic a DOC molecule is and the average absorptivity of a DOC molecule. Spectra obtained from a complex mixture of molecules like DOC are generally considered to represent the average of individual compounds that comprise the mixture (Weishaar et al., 2003). Additionally, molecular weight is inversely correlated with the E_2/E_3 quotient (or ratio of absorbance at 250 nm to that at 365 nm) (Peuravuori & Phihlaja, 1997; Lou & Xie, 2006), thus serving as a proxy to give an estimate of the molecular weight change induced by photo-degradation. a_{254} was also reported as an uncalibrated measure of the absolute aromaticity. Next, each sample was acidified to a pH of 3-4 to arrest microbial activity and then sent for DOC analysis using a TOC-5050 Total Organic Carbon analyzer at McGill University, Montreal, Quebec. After the last leaching, the remaining litter was dried and reweighed to calculate total mass loss.

3.6. Statistical analyses

Data was first assessed with a Shapiro Wilks test for normality. In cases where the data did not pass the Shapiro Wilks test, the data was plotted to visually assess the distribution. Part of the reason for violation of normality may be due to the fact that a few measurements had low sample sizes (ie. only 5 plots per site). ANOVA is not very sensitive to moderate deviations in normality (McDonald, 2009; Harwell et al., 1992; Lix et al., 1996). Therefore, where data did not pass the Shapiro Wilks test but the study design was balanced (equal sample sizes per group) and the standard error variation within the group was small (less than 1), the decision was made to proceed with ANOVA without transforming the data (e.g. bulk density). In cases where data distributions deviated substantially from normal and obvious outliers were apparent, these outliers were removed and ANOVA was run (litter nutrient analyses). Litterbag mass loss data was non normal according to the results from the shapiro-wilks test; however, when the raw data was plotted as a histogram it did not look non-normal. Still, buried litterbags had unequal sample sizes, so residuals within each plot were inspected. The median residual was -0.04, but the largest was 3.55, so I wanted to test that one group wasn't driving all of the variability. From visual inspections of plots of the buried litter bag residuals against fitted values for each of the plots, it was determined that the variability within the plots was similar, though variability of the one plot at the high shrub site was slightly larger than the rest. Harwell et al. (1992) note that small sample sizes with large variance may produce an inflated alpha error rate. However, non parametric alternatives to the

anova such as the Kruskal-Wallis test are also sensitive to heterogeneity of variance, so there was no evident advantage to using this non parametric test for buried bags, despite data being non normal. Thus, given the fairly even distribution of the raw data plotted as a histogram, as well as the lack of patterning of residuals against the fitted values, along indications previous research that ANOVA is robust to small deviations in normality (Glass et al., 1972), it was decided that the the linear mixed model would be the best model to test for mass loss and nutrient differences among sites with the mass loss data.

The statistical analyses were carried out using R (version 3.3.2, R Core Team, 2016). Differences in initial litter %C and %N, soil characteristics such as bulk density, as well as lab litter mass loss were determined using a one factor analysis of variance ('stats' package, R, R Core Team, 2016). As with many multi site decomposition studies, the observation of decomposition rates and microclimate variable values was pseudoreplicated (Hurbert et al., 1984). For example, we could not replicate our measurements at another "high shrub" site as there was none within the Daring Lake area that were feasible to access. One way to compensate for this was to have high within site replication of litterbag and microclimate variable sampling at each site. This would help capture the controlling factors within a site and also ensure that the influence of among site variation in factors on decomposition rates were not over inflated relative to within site variation (Bradford et al, 2016). Mixed effect models, which estimate both fixed and random effects can be useful when dealing with this problem, as they include random effects which help account for variation in the response variable that is not related to the

effect of the variable of interest. Thus linear mixed models ('nlme' package, Pinheiro et al., 2016) were used to test for differences among the three sites in microclimate variables including: maximum thaw depth and maximum snow depth, total LAI, soil temperature and VWC. The F statistics, degrees of freedom and p values are reported in Appendix A. 2. As each plot was measured 8 times in the same location every week during the sampling period, plot and measurement location were treated as a random effect in these models, with measurement location nested within plot. Linear mixed models were also used to test for differences in litter mass loss, %C, %N, and C:N of the litter and bulk nutrient differences across sites and harvest dates. Plot was treated as the random effect. A mixed effects model was also used in the laboratory leaching study to determine differences in DOC, SUVA and total N between temperature treatment groups over time. As the 12 treatment cups were leached weekly, cup was treated as the random effect. In the laboratory mass loss study, a single factor ANOVA ('stats' package, R Core Team, 2016) was used to assess differences between the two temperature treatments and over time. In all cases, when a significant treatment effect was found ($P<0.05$), Tukey's HSD post hoc tests were used to examine the differences in the response variable among groups (using lsmeans, R statistical package or stats, R statistical package depending on whether linear mixed model was employed). A 95% confidence interval is also reported in Appendix A for the means using the lsmeans (Lenth et al., 2016) and multcomp (Hothorn et al., 2008) packages in R.

4. Results

4.1. Vegetation

Vegetation characteristics differed in a number of ways between the study sites (Table 2). The *B. glandulosa* of the high shrub site had over 10 and 3 times the aboveground biomass and was 5 and 3 times taller compared to the low and medium shrub sites, respectively. At peak growing season, total green LAI (measured with the point intercept method) and total plant biomass LAI (measured with the LAI2200) was least at the low shrub site and greatest at the high shrub site although only significantly greater than the medium shrub site in 2016 (Table 2). The proportion of green LAI attributed to *B. glandulosa* was 35% and 43% at both the medium and high shrub sites, respectively compared to 10% at the low shrub site. Understory ground cover differed greatly with little moss and over 80% lichen cover at the low shrub site in contrast to little or no lichen and over 90% moss cover at the medium and high shrub sites (Table 2).

Among the three sites, *B. glandulosa* leaf biomass was inversely related to other vascular plant leaf biomass. Greatest *B. glandulosa* was at the high shrub site and greatest leaf biomass from plants other than *B. glandulosa* was at the low shrub site (Table 2). As a result, there were no significant differences in total leaf biomass. Thus, significantly greater total aboveground plant biomass at the high shrub site was due to greater mass of stems and other plant parts at this site.

Table 2. Vegetation characteristics at the three study sites. Values are means (±1 SE) of the plots at each site. Unique superscript letters indicate significant differences within a row, determined from a TukeyHSD post hoc test where significance ($P<0.05$) was obtained from ANOVA. Statistical test results are given in A.2.

Characteristics	**N per site**	**Low**	**Medium**	**High**
2016 Vegetation Cover and LAI measured with the point intercept method[1]				
Canopy height (cm)	50	28.5 (1.14)^{a}	45.9 (1.64)^{b}	133.1 (2.75)^{c}
Total 'green' LAI (m^2 m^{-2})	5	2.7 (0.2)^{a}	4.0 (0.2)^{b}	4.6 (0.5)^{b}
% LAI *B. glandulosa*	5	10.2 (0.6)^{a}	35.2 (4.7)^{b}	43.0 (3.8)^{b}
% moss cover	5	16.5 (4.9)^{a}	91.7 (2.0)^{b}	96.5 (1.1)^{b}
% lichen cover	5	78.9 (5.0)^{a}	6.7 (1.9)^{b}	0.0 (0.0)^{b}
2015 and 2016 LAI_{2200} measured with the Plant Canopy Analyzer (LAI2200)				
LAI_{2200} (m^2 m^{-2})				
2015[2]	40	0.2 (0.04)^{a}	1.5 (0.07)^{b}	1.5 (0.05)^{b}
2016[3]		0.2 (0.02)^{a}	1.3 (0.05)^{b}	1.5 (0.04)^{b}
Peak Growing Season LAI_{2200} (m^2 m^{-2})				
2015 (DOY 202)	40	0.1 (0.02)^{a}	1.2 (0.08)^{b}	1.5 (0.08)^{c}
2016 (DOY 210)		0.1 (0.03)^{a}	1.3 (0.11)^{b}	1.7 (0.09)^{b}
Aboveground Vascular Plant Biomass				
B. glandulosa plants (g m^{-2})	3	62.0 (28.6)^{a}	213.8 (90.0)^{ab}	776.2 (220.6)^{b}
Other vascular plants (g m^{-2})	3	287.5 (22.4)^{ab}	164.9 (57.5)^{a}	370.7 (32.5)^{b}
Total vascular plants (g m^{-2})	3	349.5 (50.9)^{a}	378.6 (45.9)^{a}	1146.9 (241.6)^{b}
B. glandulsa leaves (g m^{-2})	3	12.1 (4.5)^{a}	32.0 (11.2)^{a}	73.3 (15.9)^{b}
Other plant leaves (g m^{-2})	3	169.0 (9.9)^{a}	81.0 (37.9)^{ab}	67.2 (3.5)^{b}
Total leaves (g m^{-2})	3	181.1 (14.4)^{a}	113.1 (27.4)^{a}	140.5 (12.9)^{a}
Initial Leaf Chemistry (Sampled July 2015)				
Initial leaf % C	5-10	47.9 (0.4)	47.0 (0.2)	47.3 (0.4)
Initial leaf % N	5-10	2.2 (0.05)^{ab}	1.9 (0.05)^{a}	2.4 (0.13)^{b}
Initial C:N	5-10	22.0 (0.6)	25.0 (0.6)	20.5 (1.3)

[1]Surveyed during peak of growing season between Day 202 and Day 208
[2]Surveyed twice between Day 202 and 208
[3]Surveyed 6 times between Day 184 and 220

C:N and %C leaf chemistry was similar for *B. glandulosa* samples from across sites while %N and C:N was only significantly greater at the high site *vs* the medium shrub site. Only the high shrub leaf litter was used for the decomposition experiment, and so the %N and C:N of the litter is expressed relative to the high shrubs initial values.

4.2. Microclimate

There were also differences in microclimate conditions among sites (Table 3). Larger temperature differences were observed between the low and high shrub sites in the winter than in the summer (Figure 3). Both 2 and 10 cm soil temperatures generally peaked in early August 2016 reaching weekly average daily maximums of 13.4˚C, 12.3˚C and 10.4˚C at 2 cm at the low, medium and high shrub sites, respectively (Figure 3, Appendix A.1). There were significant differences in manually measured 10 cm soil temperature during the growing season with both the medium and high shrub sites 3-4˚C cooler than low shrub site and with no significant difference between the high and medium shrub sites (Table 3). Minimum temperatures occurred in late February 2017 reaching weekly average daily minima of -16.1, -12.2, and -8.1˚C at 2 cm at the low, medium and high shrub sites, respectively (see A.1).

Thaw depth increased over the growing season at all sites and maximum thaw depth at the high shrub site was significantly shallower compared to the low and medium shrub sites in 2016 (Table 3). Volumetric water content varied over the growing season, and in both years the high shrub site was 5 and 10% wetter compared to medium and low shrub sites, respectively. Additionally, the taller shrubs at the high shrub site were associated with deeper snow and lower surface snow density in spring 2017 (Table 3).

Table 3. Summer 2015 and 2016 soil characteristics of three sites with differing shrub abundance. Values are means (±1 SE) unless otherwise stated. DOY is day of year last thaw measurement made or of snow depth before melt started. Unique superscript letters indicate significant differences within a row, determined from a TukeyHSD post hoc test where significance ($P<0.05$) was obtained from ANOVAs. Statistical test results are given in A.2

Soil properties during study	**Low**	**Medium**	**High**
Maximum thaw depth (cm)			
2015 (DOY 205)	66.3(1.4)^{a}	43.5 (1.4)^{b}	30.0(1.3)^{b}
2016 (DOY 220)	91.3 (5.9)^{a}	65.6 (3.8)^{b}	48.1 (2.9)^{c}
Volumetric water content (0-20cm) (%)			
2015[1]	23.8 (2.1)^{a}	30.3 (1.0)^{ab}	37.9 (1.4)^{b}
2016[2]	23.0 (1.51)^{a}	29.1(1.05)^{ab}	34.2 (1.51)^{b}
Manual Summer Temperature (10cm) (˚C)			
2015[1]	6.1 (0.2)^{a}	2.5 (0.2)^{b}	2.1 (0.2)^{b}
2016[2]	7.7 (0.3)^{a}	4.3 (0.2)^{b}	4.3 (0.3)^{b}
Peak Manual Summer Soil Temperature 2015 (Day 202)	5.8 (0.2)^{a}	1.8 (0.2)^{b}	2.0 (0.2)^{b}
Peak Manual Summer Soil Temperature 2016 (DOY 185)	10.2 (0.2)^{a}	6.1 (0.3)^{b}	4.8 (0.3)^{c}
2016 Snow Depth (cm) (DOY 125)	8.9 (5.7)^{a}	16.8 (6.4)^{ab}	34.8 (5.5)^{b}
2017 Snow Depth (cm) (DOY 125)	31.5 (4.7)^{a}	49.7 (2.9)^{b}	70.8 (2.6)^{c}
2017 Snow Density (DOY 125)			
Snow density (g cm^{-3})	0.266	0.276	0.295
total depth of measurement (cm)	19	41	61
Snow density surface layer (g cm^{-3})	0.47	0.325	0.308
Layer Depth (cm)	4.5	13	14

[1]Surveyed twice between Day 202 and 208
[2]Surveyed 6 times between Day 184 and 220

Figure 3. Weekly average soil temperature at one plot at each site at 2 cm and 10 cm depth. There are eight replicate thermocouples per depth in the plot, which record temperature every 10 minutes that is then averaged by day.

4.3. Soil properties

The soils differed among the three sites primarily in the depth of surface organic matter with an average %C greater than 25% down to approximately 20 cm at the high shrub site compared to only 5 cm at the low and medium shrub sites (Table 4). By visual inspection, the depth of surface organic layer (LFH horizon) ranged from 15-22.5 cm at the high shrub site, 5-17.5 cm at the medium shrub site and 0-12.5 cm at the low shrub site (Table 5). Consequently, the 0-20 cm soil bulk density was less at the high shrub site and %N was greater (Table 4). Soil C:N differed, but not significantly among sites (Table 4; A.4.1).

Total N and C integrated over the top 20 cm of the soil profile was significantly greater by about 3 times at the high shrub site with about 17 kg C m^{-2} and just under 1 kg N m^{-2} compared to the medium and low shrub sites.

At 10 cm depth, the supply of total N ions (ammonium and nitrate) was greatest at the medium shrub site in the spring and at the high shrub site during the summer (Table 6). The supply of total N ions was dominated by ammonium. The supply rate of phosphorous was highest at the low shrub site for both sampling periods. However, site differences were not significant for any of the nutrient supply rates except for Sulfate (A.4)

Table 4. Summer 2016 soil characteristics. For % C, % N, and C:N ratio, values are means (±1 SE) of n=3 plots, except where indicated with a †, which indicates that only two plots were analyzed (ie. soils at these depths were frozen and could not be collected at one of the plots). Unique superscript letters indicate significant differences within a row, determined from a TukeyHSD post hoc test where significance ($P<0.05$) was obtained from ANOVAs. See A.4 for statistical tables.

Characteristic	**Low**	**Medium**	**High**
% Nitrogen			
0-2.5cm	1.00 (0.18)^{a}	1.97(0.10)^{b}	2.01 (0.03)^{b}
5-7.5cm	0.16 (0.08)^{a}	0.20 (0.07)^{a}	1.91 (0.08)^{b}
10-12.5 cm	0.08 (0.02)^{a}	0.10 (0.02)^{a}	1.82 (0.40)^{b}
15-17.5 cm	0.06 (0.01)^{a}	0.13 (0.02)^{a}	1.68 (0.50)^{b}
20 – 22.5cm	0.05 (0.01)	0.22 (0.08)	0.20 (0.07)†
25-27.5 cm	0.05 (0.01)^{a}	0.09 (0.01)^{b}	0.06 (0.01)^{a†}
30-32.5 cm	0.06 (0.00)^{a}	0.09 (0.02)^{b†}	0.04 (0.01)^{a†}
40-42.5cm	0.03 (0.01)	0.07 (0.00)†	0.02 (0.01)†
% C			
0-2.5cm	30.4 (5.6)^{a}	45.2 (0.5)^{ab}	49.1 (0.6)^{b}
5-7.5cm	3.9 (2.1)^{a}	3.8 (1.6)^{a}	36.5 (1.1)^{b}
10-12.5 cm	1.7 (0.5)^{a}	1.3 (0.2)^{a}	30.2 (4.8)^{b}
15-17.5 cm	1.1 (0.03)^{a}	2.0 (0.3)^{a}	27.1 (7.5)^{b}
20 – 22.5cm	0.9 (0.06)	4.9 (2.1)	4.3 (1.5)
25-27.5 cm	0.9 (0.09)^{a}	1.6 (0.2)^{b}	1.0 (0.2)^{ab†}
30-32.5 cm	1.0 (0.15)	1.4 (0.3)†	0.9 (0.1)†
40-42.5cm	0.7 (0.07)	0.9 (0.01)†	0.7 (0.1)†
C:N			
0-2.5cm	27.9 (1.5)^{a}	23.2 (1.2)^{b}	24.5 (0.3)^{ab}
5-7.5cm	22.3 (4.1)	15.4 (2.0)	19.2 (0.7)
10-12.5 cm	20.2 (2.4)^{a}	12.7 (0.9)^{b}	18.4 (1.7)^{ab}
15-17.5 cm	21.4 (3.2)	16.2 (0.5)	19.5 (2.5)
20 – 22.5cm	20.5 (3.0)	18.7 (1.7)	21.0 (0.2)†
25-27.5 cm	18.9 (2.9)	16.3 (0.6)	17.7 (0.7)†
30-32.5 cm	18.4 (2.6)	14.8 (0.8)†	23.8 (1.1)†
40-42.5cm	28.0 (6.4)	14.3 (0.2)†	56.4 (20.5)†
Bulk Density (g/cm^3)			

0-2.5cm	0.30 (0.07)[a]	0.18 (0.03)[ab]	0.11 (0.01)[b]
5-7.5cm	0.87 (0.25)	0.45 (0.19)	0.15 (0.02)
10-12.5 cm	1.05 (0.21)[a]	1.04 (0.12)[a]	0.30 (0.08)[b]
15-17.5 cm	1.35 (0.12)[a]	1.01 (0.10)[ab]	0.78 (0.14)[b]
20 – 22.5cm	1.46 (0.08)	1.21 (0.11)	1.02 (0.22)[†]
25-27.5 cm	1.44 (0.05)	1.29 (0.11)	1.33 (0.05)[†]
30-32.5 cm	1.36 (0.11)	1.27 (0.18)[†]	1.34 (0.04)[†]
40-42.5 cm	1.44 (0.13)	1.44 (0.04)[†]	1.43 (0.10)[†]

Table 5. Range of depth of LFH horizon and total soil organic carbon (SOC) and nitrogen (N) integrated through the soil profile to a depth of 20 and 40 cm (±1 SE) using results listed in Table 4. Unique Superscript letters indicate significant differences within a row, determined with a TukeyHSD post hoc test where significance ($p<0.05$) was obtained from ANOVAs. See A.4 for statistical tables.

Characteristic	**Low**	**Medium**	**High**
Depth of LFH horizon (cm)			
Discernible Organics	0-12.5	5-17.5	15-22.5
Sphagnum Moss	0-2.5	5-12.5	10-17.5
Total Soil Organic Carbon and Soil Organic Nitrogen (kg m^{-2})			
SOC (0-20 cm)	5.55 (2.48)[a]	5.37 (0.81)[a]	17.04 (2.74)[b]
SOC (0-40 cm)	8.04 (2.26)[a]	10.30 (1.32)[a]	46.24 (27.08)[a]
Soil N (0-20 cm)	0.19 (0.05)[a]	0.29 (0.03)[a]	0.94 (0.23)[b]
Soil N (0-40 cm)	0.33 (0.08)[a]	0.58 (0.04)[a]	2.89 (1.95)[a]

Table 6. Nutrient supply rates (µg 10 cm-2 6 weeks-1) for spring (May-June) and summer (July-August) buried period. PRS probes inserted into top 10 cm of soil at the three sites. Values are means (±1 SE). Unique Superscript letters indicate significant differences within a row, determined with a TukeyHSD post hoc test when ANOVA tests were significant ($p<0.05$). Values in bold highlight significant differences between burial periods for the same site, determined with a TukeyHSD post hoc test where significance ($p<0.05$) was obtained from ANOVA (see A.4)

NUTRIENT (µg 10 cm^{-2} 6 $weeks^{-1}$)	**BURIAL PERIOD**	**Low**	**Medium**	**High**
PO_4	SPRING	5.0 (1.0)^{a}	2.0 (0.4)^{b}	3.5 (0.4)^{ab}
	SUMMER	6.5 (2.2)	6.0 (1.3)	5.0 (2.0)
NH_4	SPRING	6.0 (0.9)	23.4 (17.3)	9.6 (1.7)
	SUMMER	11.8 (3.89)	11.6 (5.12)	23.2 (6.06)
Total N	SPRING	7.6 (0.7)	24.4 (17.0)	11.8 (1.8)
	SUMMER	13.2 (3.8)	12.8 (5.1)	27.2 (6.1)
S	SPRING	**4.0 (0.3)**^{ab}	6.5 (1.5)^{a}	**3.0 (0.5)**^{b}
	SUMMER	**11.0 (1.1)**	9.6 (1.3)	**11.6 (1.6)**
Mn	SPRING	7 (2.8)	12.9 (4.0)	17.4 (6.0)
	SUMMER	15.7(8.1)	2.1 (0.8)	4.8 (1.8)
Fe	SPRING	70.0 (40.1)	105.4 (50.0)	21.6 (15.4)
	SUMMER	11.0 (1.1)	9.6 (1.3)	11.6 (1.6)
Ca	SPRING	177.6 (37.1)	376.6 (152.4)	136.4 (53.9)
	SUMMER	304.0 (64.5)^{a}	137.2 (25.3)^{b}	187.4 (29.9)^{ab}
Mg	SPRING	115.4 (21.7)	211.0 (77.1)	93.0 (26.0)
	SUMMER	174.0 (34.5)	84.8 (20.7)	124.4 (25.7)
K	SPRING	149.8 (27.0)	158.8 (18.4)	171.6 (33.5)
	SUMMER	145.4 (30.2)	89.6 (17.9)	77.6 (15.3)

4.4. Litter mass loss

There were significant differences in litter mass loss between bag depth, incubation period, and sites (Table 7; Table 8). The initial mass losses over the fall and winter periods were larger than losses through the summer at all sites and at both litter bag burial depths (Figure 4).

In general, buried bags lost more mass than surface bags across all three sites and time periods, with significant differences observed at the medium and low shrub sites (Table 7). The litter bags at the high shrub site lost more mass at the surface relative to the other two sites. In contrast, there were no significant differences in mass loss for buried bags among sites (see A.3.9).

Based on the mass loss data and an exponential model, average annual decay rates for surface bags were 0.35 $year^{-1}$ with a range of 0.25 – 0.43 $year^{-1}$ (6.83×10^{-4} - 11.87×10^{-4} day^{-1}) (Figure 5). Burial enhanced the decay rate with an average annual k value of 0.42 $year^{-1}$ and a range of 0.35 – 0.46 $year^{-1}$ (9.58×10^{-4} – 12.67×10^{-4} day^{-1}) for buried bags with no significant differences among sites. Overall, mean decay rates based on the exponential model for the three growing season months (between May 2016 and August 2016) were not significantly different than decay rates over fall and winter (between August 2015 and May 2016) (Figure 5, Appendix A.3.1). However, the exponential model would not be the most appropriate model for the summer period as the period with most rapid decomposition likely occurred in the fall immediately after placement.

Table 7. Mean (±1 SE) % mass loss and % nutrient concentrations in the litter bag leaf litter between Aug 2015 and May or Aug 2016. Superscript represents significant differences among sites, determined with a TukeyHSD test where ANOVA were significant ($p<0.05$). Asterisk represents significant differences between buried and surface bags within the same collection period at a given site, determined through a TukeyHSD test where ANOVA were significant ($p<0.05$) (see A.3 for statistical tables)

Variable	**Collection**	**Low**	**Medium**	**High**
Litter Bag Mass Loss (%)				
Surface Bag	May August	23.1 (0.3) 28.9 (0.7)^{a*}	21.8(1.3)* 27.7(0.8)^{a*}	25.3 (0.7) 32.5 (1.0)^{b}
Buried Bag	May August	26.9 (1.8) 35.0 (1.7)*	28.7 (1.4)* 35.0 (0.7)*	26.9 (10.0) 32.2 (1.0)
Litter C %				
Surface	May August	49.1(0.13) 49.8 (0.10)	49.6 (0.2) 49.5 (0.1)*	49.5 (0.2)* 50.1 (0.1)*
Buried	May August	49.9 (0.42)^{a} 50.1 (0.74)^{ab}	49.9 (0.4)^{a} 51.4 (0.3)^{a*}	44.0 (2.6)^{b*} 49.0 (0.2)^{b*}
Litter N %				
Surface N	May August	3.3 (0.02)^{a*} 3.5 (0.02)^{a}	3.7 (0.04)^{b} 3.8 (0.04)^{b}	3.6 (0.04)^{b*} 3.8 (0.04)^{b}
Buried N	May August	3.1 (0.04)^{a*} 3.4 (0.04)^{a}	3.7 (0.04)^{b} 3.9 (0.03)^{b}	2.8 (0.30)^{a*} 3.8 (0.05)^{b}
C:N proportion				
Surface	May August	14.9 (0.1)^{a*} 14.4 (0.1)^{a*}	13.5 (0.1)^{b} 13.2 (0.1)^{b}	13.7 (0.1)^{b*} 13.3 (0.1)^{b}
Buried	May August	16.2 (0.2)^{a*} 15.3 (0.1)^{a*}	13.5 (0.1)^{b} 13.2 (0.1)^{b}	15.7 (0.6)^{ab*} 12.9 (0.2)^{b}

Table 8. Results of linear mixed models for litter mass loss. Site (Low, Medium, and High shrub sites), Collection Date (May 2016 and August 2016) and Bag Type (Surface and Buried) were treated as fixed effects, and Plot within a Site was treated as the random effect. Where ANOVA were significant (P<0.05), TukeyHSD test was performed (see A.3.9).

	Fixed Effects			
		DF	*F*-value	*P*-value
Overall	Site	2,12	1.33	0.30
	Collection Date	2,215	96.18	**<0.001**
	Bag Type	1,215	32.38	**<0.001**
	Site x Collection Date	2,215	0.92	0.40
	Site x Bag Type	2,215	7.29	**0.001**
	Collection Date x Bag Type	1,215	0.17	0.68
	Site x Collection Date x Bag Type	2,215	0.50	0.61
Surface Bags	Site	2,12	7.08	**0.01**
	Collection Date	1,101	93.3	**<0.001**
	Site x Collection Date	2,101	0.49	0.61
Buried Bags	Site	2,12	0.46	0.644
	Collection Date	1,102	21.73	**<0.001**
	Site x Collection Date	2,102	0.26	0.77
May Collection	Site	2,12	0.26	0.78
	Bag Type	1,74	12.0	**0.0009**
	Site x Bag Type	2,74	1.046	0.36
August Collection	Site	2,12	0.048	0.95
	Bag Type	1,129	22.04	**<0.001**
	Site x Bag Type	2,129	7.14	**0.001**

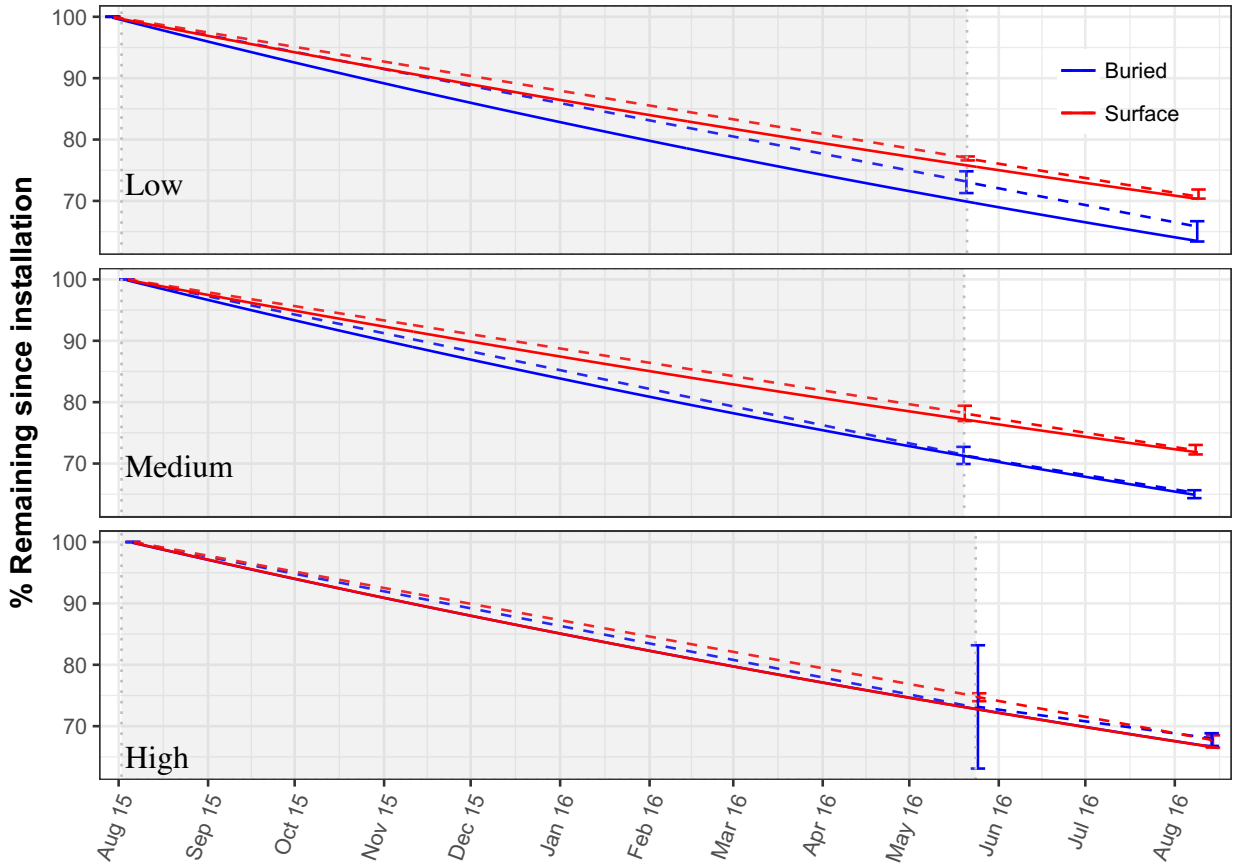

Figure 4. Percent mass loss of *B. glandulosa* leaf litter over a year at the three sites, with collections in May and August. Values are means, bars are standard error (± 1 SE). Significant differences between sites are indicated in Table 7. Solid lines represent the exponential decay model with annual k values computed from the August 2016 litter bag collection.

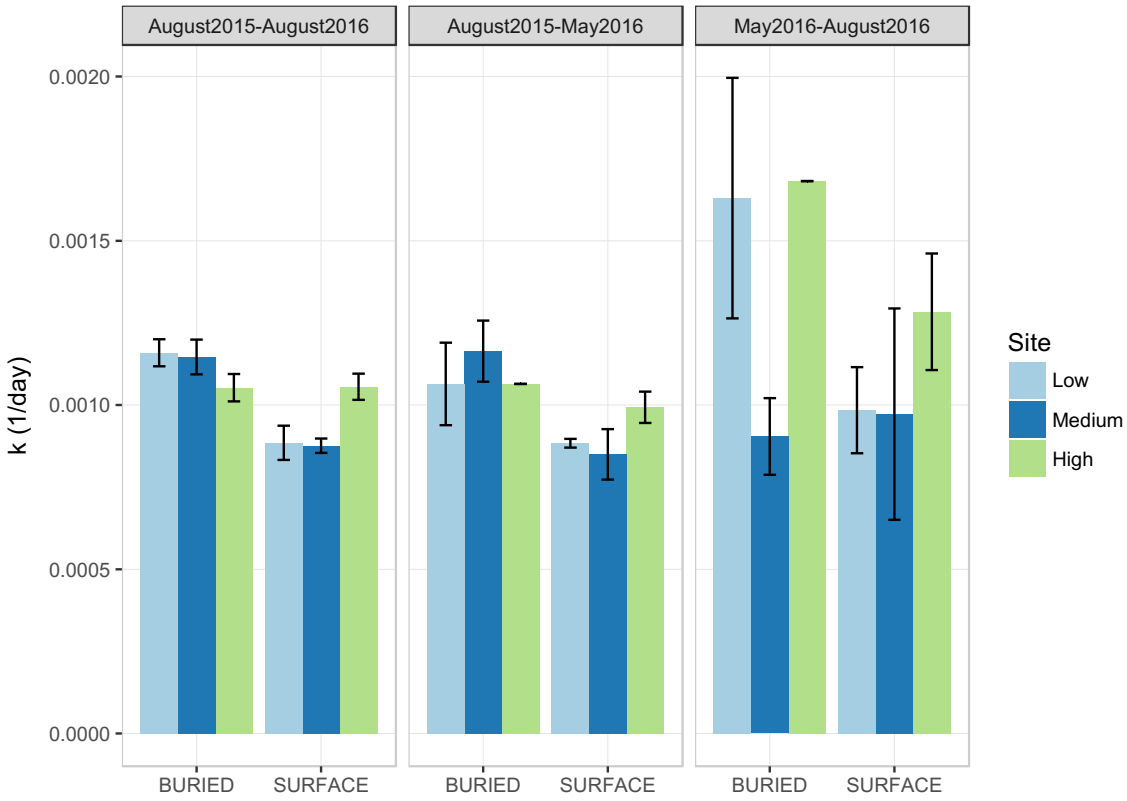

Figure 5. Decay constants for *Betula glandulosa* leaves at the three sites for three in-situ incubation periods. Values are means (±1 SE) of n=5 plots, except when retrieval in May was not possible, in which case values are means (±1 SE) of the number of plots retrieved at each site. See Methods for further explanation.

4.5. Litter C:N analyses

Initial litter %N was 2.38%, initial %C was 47.3% and initial C:N was 19.9. In general, all sites' litter N concentrations increased over time indicating immobilization of N. Generally, more N was immobilized at the medium and high shrub sites than at the low shrub site (Figure 6). Litter C:N decreased over time and most strongly for the medium and high shrub sites relative to the low shrub sites (Figure 7).

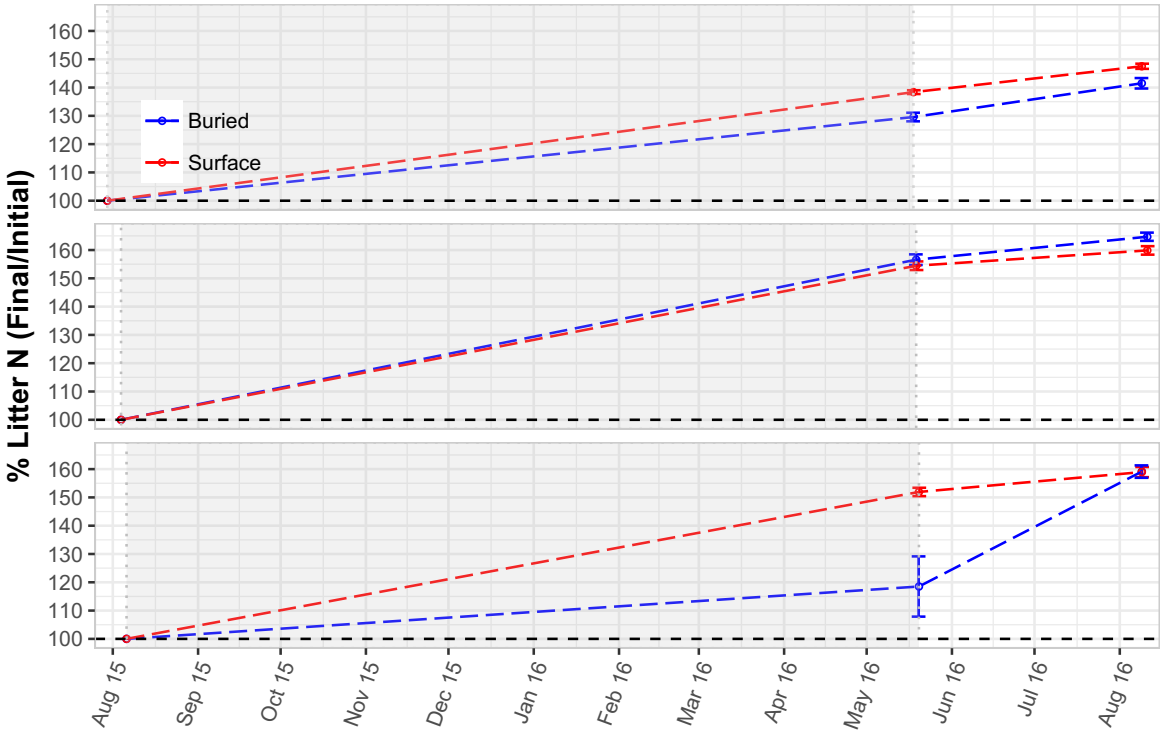

Figure 6. Calculated as the ratio of Final to Initial Litter N remaining. Percentages higher than 100% indicate a net immobilization. Values are means and bars are standard error (± 1 SE). Significant differences between sites and burial types indicated in Table 7.

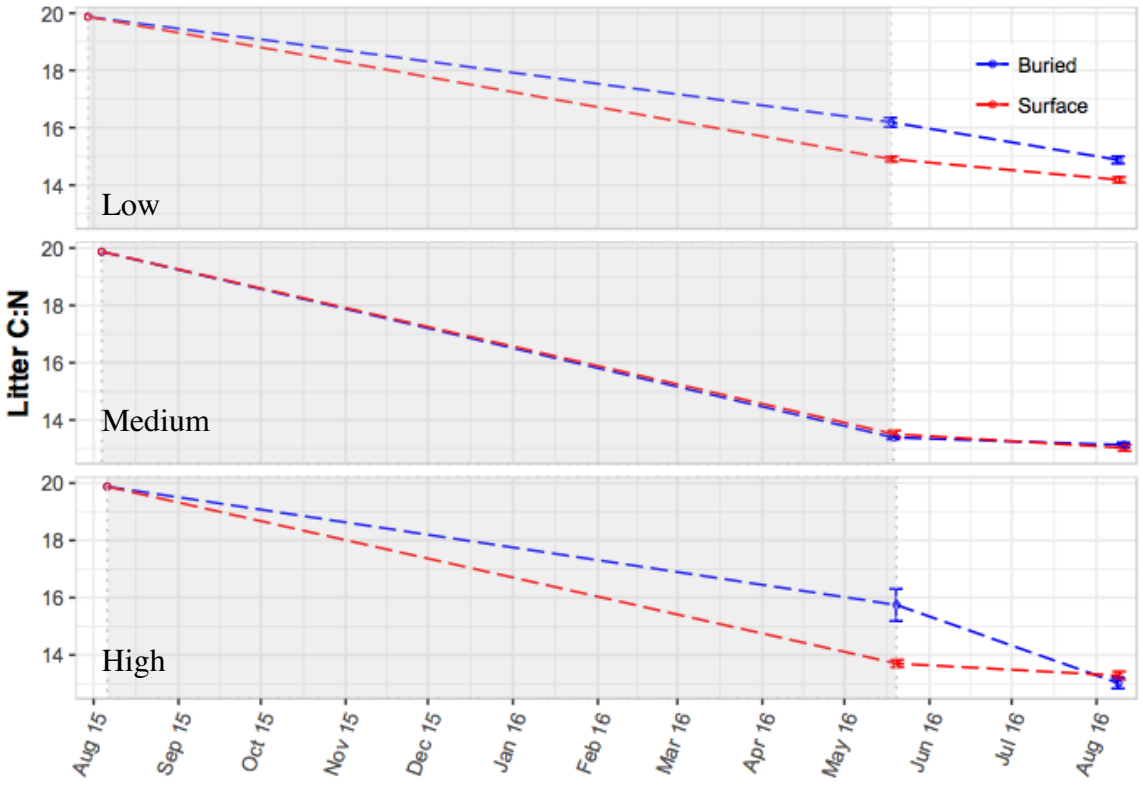

Figure 7. Average proportion of litter C:N over time. Values are means and bars are standard error (± 1 SE). Significant differences indicated in Table 7.

4.6. Litter incubation

In the laboratory incubation, litter experienced approximately 22% mass loss over the 110 day study (Figure 8). Litter lost significant mass over time (Appendix A.5.4). Temperature did not strongly influence mass loss differences, except on day 14 ($F_{1,2}$=19.6, P=0.047) and day 21 ($F_{1,2}$=63.1, P=0.015), in which significantly more mass loss occurred in the 20˚C treatment. Once frozen at -5 ˚C, there was no further significant loss in mass (Figure 8).

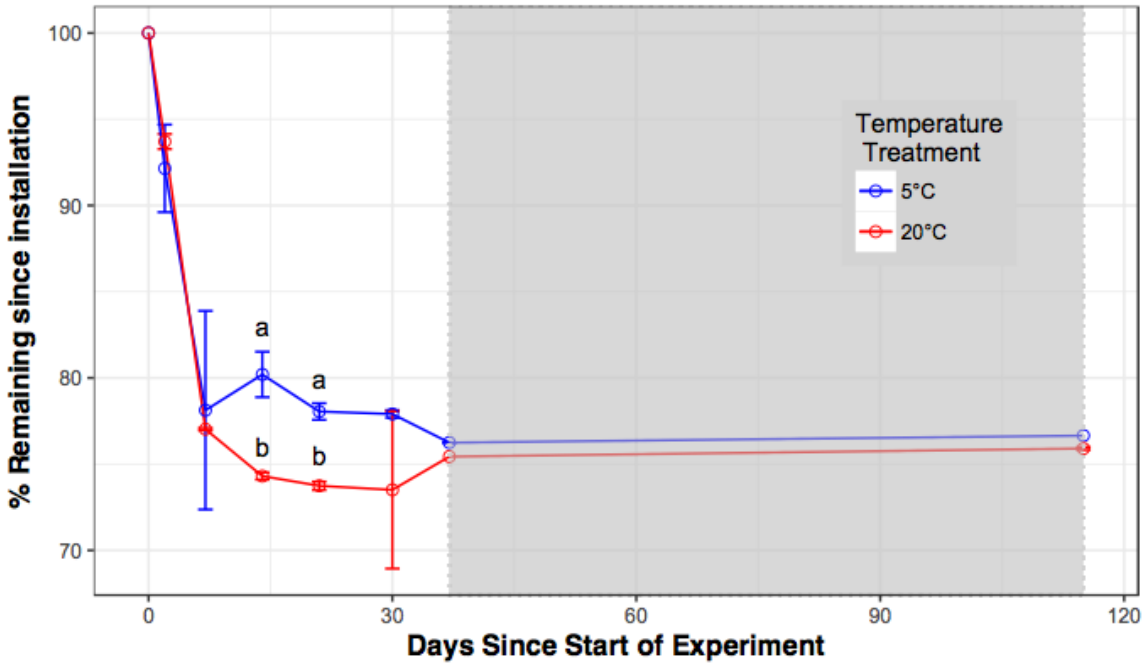

Figure 8. *Betula glandulosa* litter mass remaining after 30 days incubation at 5˚C and 20˚C. Data points represent mean of sets of litter samples (n=2 per treatment) collected immediately after incubation in soil water extracts (day 2), followed by weekly sampling. Different letters represent significant differences between temperature treatments for that collection date. Grey fill represents period in which remaining samples were moved to a -5˚C freezer for the remainder of the experiment (until day 115).

4.7. Litter incubation and leaching

In the 4 month laboratory leaching study, DOC and total N concentrations peaked after the first week, then dropped rapidly during the first month of weekly leaching treatments (Figure 9). DOC:TN also peaked in the first week and dropped over time. $SUVA_{254}$ rose over the course of the first month suggesting the production of more aromatic DOC compounds (Figure 10). The absolute concentration of aromatics (and a_{254}) peaked within the first two weeks of the experiment and then slowly declined, but there

was no significant differences among temperature treatments (Appendix A.5.1, A.5.2). The ratio of a250 and a365 is inversely related to molecular weight and indicated a trend towards decreasing molecular weight over time (Olefeldt, 2013). At the end of the study, leaf mass loss as determined by dry weight of the leaf litter remaining, ranged between 32-43% of initial mass, and was significantly different between treatments. Mass loss was greater for the 20˚C treatment compared to mass loss in the 5˚C and 2˚C treatments (Appendix A.5.1., A.5.3). There was no significant difference in mass loss for the 5˚C and 2˚C treatments.

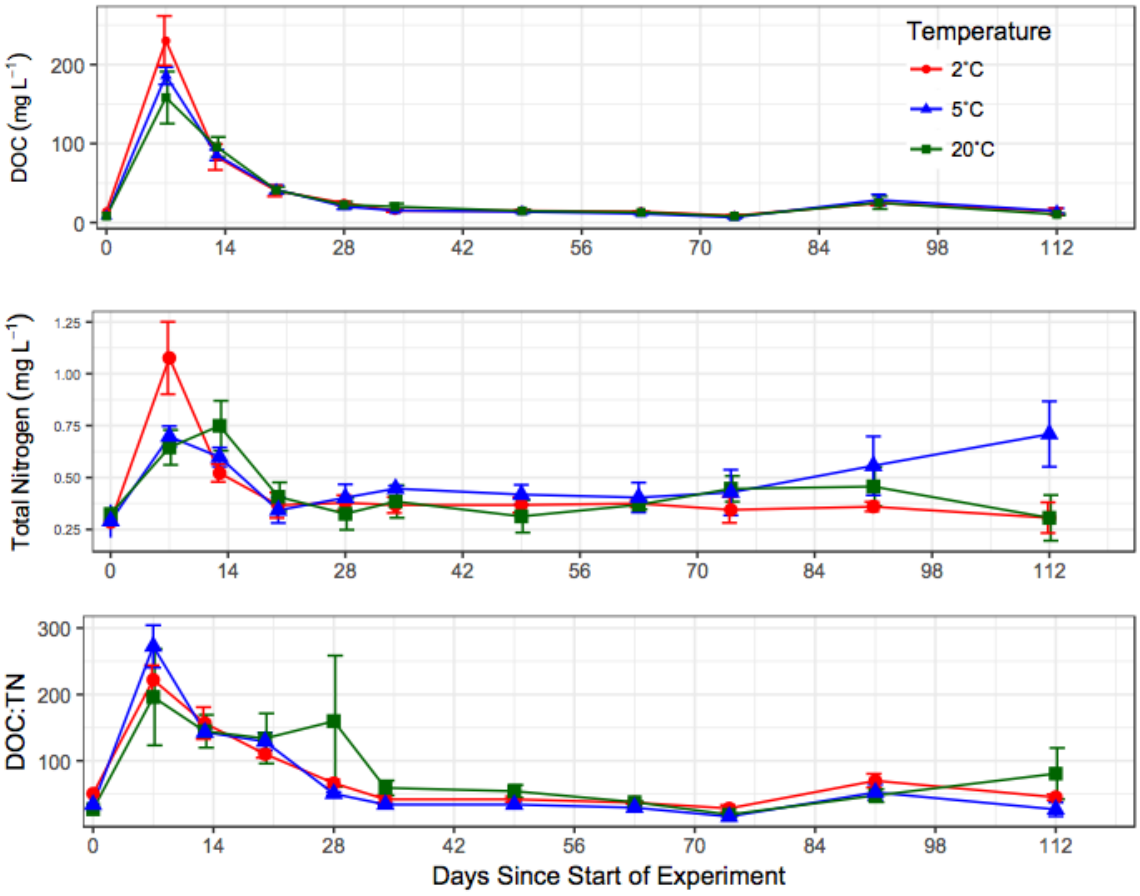

Figure 9. DOC, total Nitrogen and DOC:total Nitrogen concentration detected in the leachate values over the course of the 4 month leaching experiment of *B. glandulosa* leaves. Values are averages of 3 replicates per temperature treatment. Bars are ± 1 SE.

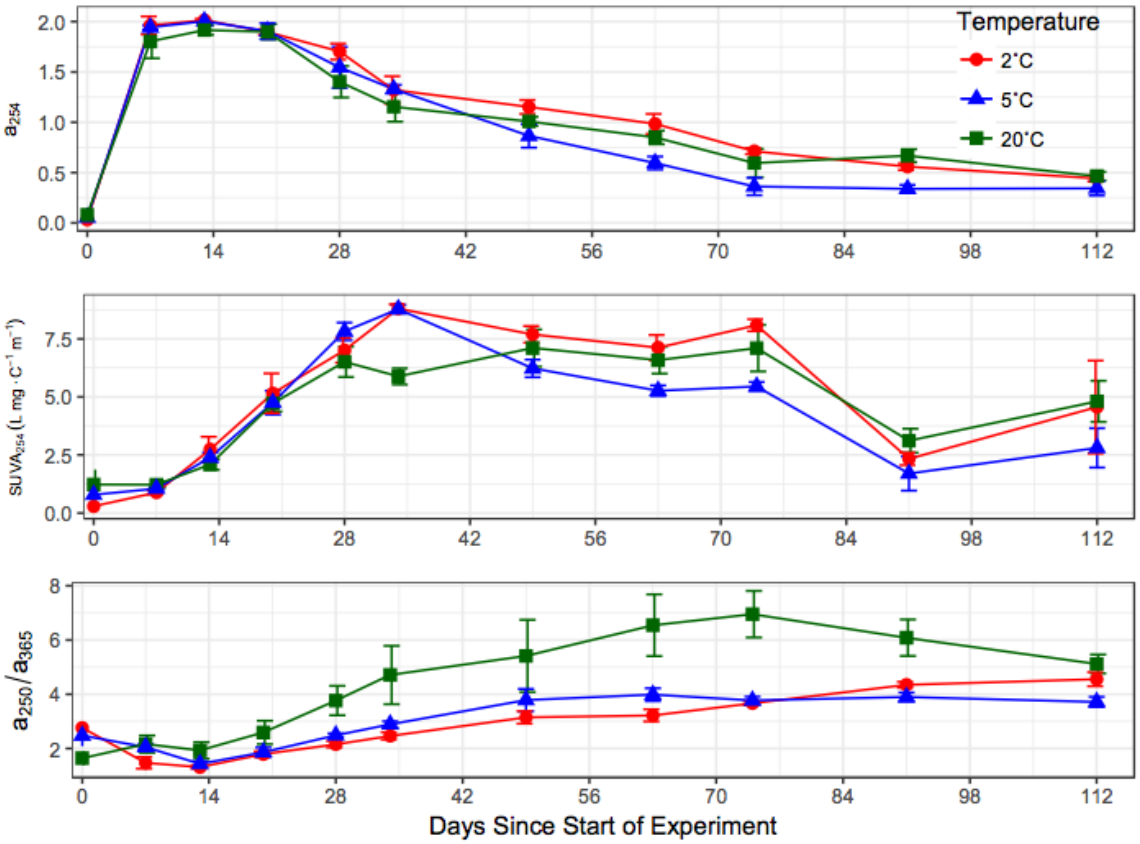

Figure 10. Absorptance characteristics, a_{254}, a_{250}/a_{365} and $SUVA_{254}$, detected in leachate over the course of 4 month leaching experiment of *B. glandulosa* leaves. Values are averages of 3 replicates per temperature treatment. Bars are ± 1 SE.

5. Discussion

5.1. Microclimate controls on decomposition

The findings of this study lend some support to Sturm et al.'s (2001) snow-shrub hypothesis, which suggests that the presence of shrubs creates a deeper snowpack and warmer soil conditions that promotes nutrient mineralization and further shrub growth. Microclimate variables such as temperature and moisture can influence decomposition rates, and varied among the three sites. The high shrub site soils were relatively wet and cool in summer but remained much warmer in winter likely as a result of insulation by the deeper and less dense snow pack, as discussed by Sturm et al. (2001) and found in other studies (Pomeroy et al., 2006; Grogan & Jonasson, 2003; Schimel et al., 2004; Sturm et al., 2005).

A major uncertainty in the hypothesized snow-shrub positive feedback loop is whether summer microclimatic effects counter positive winter effects on decomposition (Sturm et al., 2001). Greater shrub cover has been postulated to shade the soil and keep soil temperatures cool (Myers-Smith et al., 2011; DeMarco et al., 2014). There was less thaw at the continuously monitored plots at the high shrub site compared to the medium and low shrub sites. As expected, LAI was significantly greater at the high *vs* low shrub site lending support to the conclusion that soil shading may contribute to temperature differences between the high and low shrub site. However, LAI was similar between the high and medium shrub sites except during peak LAI in summer 2016 . The similarity in growing season LAI was expected as more evergreen species at the medium shrub site resulted in greater early and late season LAI and offset larger peak season LAI at the

high shrub site. As a result, these findings suggest that factors other than soil shading by shrubs likely played a role in explaining cooler summer soil temperatures at the high shrub site compared to the medium shrub site.

Manipulation experiments have shown the importance of moss ground cover and organic surface soil layers on reducing heat flux into the soil (Block et al., 2011; Bueno et al., 2016; Gornall et al., 2007). Moss layers and underlying organic soils (peat) are highly porous with low thermal conductivities compared to mineral soils. Gornall et al. (2007) found that a thicker moss layer results in both lower soil temperatures during the growing season and reduced temperature fluctuation compared to shallow moss layers. Furthermore, they found that a deeper moss layer delayed the onset of soil thaw for several weeks after snow melt. Additionally, mosses have low evapotranspiration rates, which promotes the retention of water in this layer and can lead to development of waterlogged soils (Zimov et al., 1995). The high shrub site had a thicker moss and organic soil layer/LFH layer than the other two sites and greater volumetric water content. The combined effect may have resulted in higher heat capacity and lower thermal diffusivity of the soils, which would limit soil warming and thaw. In contrast, the low shrub site's significantly warmer 10 cm manual and continuously measured soil temperatures in summer were likely a combined effect of less shading and moist mineral soils with a thin organic layer and little moss cover which maximized heat diffusivity.

After a full year, the surface bags at the high shrub site had significantly greater mass loss and higher decay rates than at the medium and low shrub sites. However, there were no significant differences among sites for the surface bags collected in May nor for the buried bags for any period. Thus, it is difficult to directly link microclimate to these trends as the warmer winter period did not appear to increase overwinter mass loss at the high shrub site and the cooler summer soil temperatures did not appear to inhibit mass loss. There are only a few studies that directly compare the effect of microclimate on litter decomposition. Hobbie & Chapin (1996) found differences in litter mass loss between sites whose summer soil temperatures differed by 4˚C, with greater mass loss occurring in warmer microsites. However, DeMarco et al. (2014) decomposed *B. nana* litter at three sites with varying levels of shrub coverage over a three-year period, and found higher decomposition rates in their lower shrub density plots, despite being slightly wetter and cooler in summer than the medium and higher shrub density plots. Several microenvironment conditions in that study differed from this one: there was a greater thaw depth at the high shrub site compared to their low and medium sites, a thicker organic layer and lower bulk density at the low shrub site compared to the medium and high shrub sites. This combination of factors which offset cooling and warming effects may have led to the small differences in temperature and moisture between their high and low shrub sites (temperature differences were <1˚C) compared to those seen in our study. In addition, local topography can influence moisture conditions and nutrient mobilization which may have contributed to differences between the characteristics noted by DeMarco et al. (2014) and this study's high and low shrub sites. Lower slope position and depressions typically have higher levels of N and organic matter than higher slope

positions or ridgetops (Schimel et al., 1985), which was true for both DeMarco et al. (2014) and this study. At Daring Lake, the high shrub site was located at the base of very gently sloping terrain while the low shrub site was located mid-slope on more wind exposed and well-drained terrain.

DeMarco et al. (2014) concluded that other factors such as soil nutrients, litter quality or the decomposer communities may be more important than small differences in temperature for driving decomposition. Robinson et al. (1997) also found that soil/litter quality rather than soil temperature drives soil N mineralization and decomposition processes in Arctic ecosystems. Christiansen et al. (2016) note that although warmer temperatures generally enhance surface decomposition processes, this is only as long as the associated increase in evapotranspiration does not lead to moisture limitation of microbial activity.

5.2. Litter quality/quantity controls on decomposition, soil C and soil N

Greater near-surface soil organic C at the high shrub site is also challenging to reconcile with greater litter bag mass loss at the surface at that site and no significant mass loss differences in buried bags among sites. However, from visual inspection of the soils, it is likely that more of the organic matter at that site is *Sphagnum*-derived rather than deciduous shrub-derived when compared to the organic matter at the medium and low shrub sites. *Sphagnum* moss is known for its low decomposability compared to vascular plants (Hobbie, 1996; Lang et al., 2009; Turetsky et al., 2012). This has been attributed to its low N concentration and relatively recalcitrant lignin-like compounds

(Lang et al., 2009; Turetsky et al., 2010). In addition, the cooling effect of mosses as discussed above and by Blok et al. (2011) can slow decomposition and enhance storage of soil C (Hobbie et al., 2000). The local topography at the high shrub site had more convergent elements than the other sites being located at the toe slope of the esker running east-west at Daring Lake. This may have contributed to wetter conditions in this area. At Daring Lake, there is a clear positive relationship between soil moisture and near-surface soil organic C stocks (Campeau et al., 2014). In the tundra, where rainfall is not overly abundant, areas with more soil moisture may support more vegetation (i.e. greater above ground biomass) leading to greater organic inputs to the soil (Grogan, 2012). Wetter soils alleviate the moisture limitation of microbes and promote soil biological activity to decompose organic matter (Blok et al., 2016). Wetter soil can also create anoxic conditions that promote soil C storage. Thus wetter soils at the high shrub site and the relatively greater input of *Sphagnum* moss to the soil likely contributed to significantly more SOC compared to medium and low shrub sites.

Soil characteristics varied among sites with soils having more N and lower C:N at the high shrub relative to the low shrub site. Available soil N (ammonium and nitrate) in the summer was greater in the high shrub site compared to the other two sites, although these differences were not significant. Although total leaf biomass was not significantly different among sites, the high shrub site contributed significantly greater amounts of *Betula* leaf litter to the soil than the other two sites. Previous research near these sites has shown that soil N pools and cycling rates were ~ 3 times larger in tundra with greater shrub abundance and height than in neighbouring dwarf birch hummock

tundra (Buckeridge et al., 2010). The relatively high N concentrations in the litter may promote faster surface and soil decomposition rates (Buckeridge et al. 2010). Buckeridge et al. (2010) suggests this may be due to higher levels of DOC available to microorganisms and lower litter C:N, which promotes mineralization by soil microbes (Fierer et al., 2007; Aerts et al., 1997). Ge et al. (2016) found that %N was greater by 0.2% in *B. glandulosa* leaves at the high shrub *vs* medium and low shrub sites. Litter %N of other species was not determined for this study, but other studies have found that *B. nana* litter has a higher relative %N compared to neighbouring vascular plant species such as *Ledum decumbens* and *Vaccinium vitis-idaea* (L.) (e.g. DeMarco et al., 2014). Thus it is possible that high inputs of deciduous shrub litter with higher %N contributed to the larger overall pool of soil N in the high shrub site relative to the other sites.

Although it was expected that the soil C:N would be lowest at the high shrub site due to the relatively greater input of N from deciduous shrub litter, there were no significant differences between high and medium shrub sites while the low shrub site had the highest soil C:N. Lower C:N may reflect highly decomposed soil organic material, high turnover rates, and/or less recalcitrant substances (Gundersten et al., 1998; Ollinger et al., 2002; Björk et al., 2008). Previous studies have found that deciduous shrub litter was more recalcitrant compared to herbaceous litter (De Deyn et al., 2008), and that soil decomposition rates decreased with increasing shrubs due to more recalcitrant substrate supply (Hobbie, 1996; Cornelissen et al., 2007). However, *B. glandulosa*, is generally a less recalcitrant litter than other birch litter (*B. nana*) or evergreen shrubs

(Buckeridge et al., 2010). Thus, at the low shrub site, the higher C:N in the remaining litterbag litter confirms that less decomposition has occurred (since all litter samples started with the same C:N). The higher C:N of the low shrub site soil may be due to less decomposition but could also be due to litter inputs with higher C:N as leaf biomass was comparable among sites but there was far less high quality *B. glandulosa* litter inputs. The relatively higher C:N of the high shrub compared to the medium shrub site may be due to the relatively greater inputs of recalcitrant *Sphagnum* moss to soil organic material. The medium shrub site had a thinner *Sphagnum* moss layer so may have been more strongly influenced by inputs of high quality *Betula* litter.

This study calculated the ratio of final %N to initial %N, but did not adjust for litter weights, so may overestimate the amount of Nitrogen accumulated over time. Still, it was evident that over the course of the experiment there was a net accumulation of N at all three sites. Previous work has found that greater soil N availability stimulated litter decomposition rates (Hobbie, 1996, Aerts et al., 2006) and lead to N immobilization in some systems (Gallardo & Merino 1992, Magill & Aber, 1998, Hobbie 2005, Aerts et al., 2006). Conversely, other studies have shown greater N availability to repress (Aerts et al., 2006) or have no effect (Hobbie, 1996) on litter decomposition rates. In a study with a similar experimental set up, DeMarco et al. (2014) found that bulk soil N at the medium and high shrub sites were twice as high compared with bulk soil N at the low shrub site. They found that sites with greater soil N had lower rates of litter decomposition and higher retention of N on the leaves. They suggest that microbes at sites with fewer shrubs may be suited for decomposing litter that is of

low quality than microbes at the sites greater shrub abundance. Potentially the high shrub site may immobilize more N because they have a higher nutrient demand when mineralizing C substrates of higher quality and quantity (DeMarco et al., 2014; Fierer et al., 2007; Wallenstein et al., 2007). Wallenstein et al. (2007) compared fungal and bacterial community composition between shrub tundra and tussock tundra, and found that vegetation was the primary driver of microbial community composition in Arctic tundra soils. They determined that graminoid litter in tussock tundra supported large populations of K-selected bacteria, but shrub soils were dominated by *r*-strategist bacteria. K-selected strategists are adapted to compete and survive when resources are limited (low nutrient availability) and exhibit slow growth rates, whereas *r*-selected strategists have high nutritional requirements and grow rapidly when resources are abundant (Fierer et al., 2007). Fontaine et al. (2003) notes that *r*-strategist bacteria grow quickly on fresh plant litter containing simple and soluble substrates, taking up much of the available substrates before the slower K-strategist communities increase in population. So, the relatively high input of fresh, high quality shrub litter to shrub soils may stimulate *r*-strategist decomposers versus K-strategist decomposers, and thus indirectly stimulate more decomposition of the surface litter bags at the high shrub site. As discussed later, soil microenvironment conditions in buried bags likely influenced the mass loss rates more so than differences in microbial community makeup.

It is possible that the presence of litter from particular plant functional types influences the preferences and behaviour of decomposers that could drive different rates of C and N loss at these sites (Handa et al., 2014). An increase in deciduous shrubs can result in a

decrease in plant species diversity and functional group representation (Chapin et al., 1995; Gough & Hobbie, 2003; DeMarco et al., 2014). Shrubs can produce a dense canopy that allows only shade tolerant species to survive below. The relatively greater presence of *Sphagnum* at the high shrub site could be related to its capacity to tolerate shading by shrubs. Handa et al. (2014) note that reduction in plant diversity can in turn reduce the functional diversity of decomposer communities and slow cycling of litter C and N (i.e. increased C and N loss with increased functional diversity). However, in my study, plant species richness was similar among sites. From the point intercept measurements, 7 vascular plant species were identified at the high shrub site, 8 at the medium shrub and 10 at the low shrub site. Thus, the influence of relative species diversity on microbial abundance and type was likely small.

The phenolic content of the litter may also have implications for rates of N mineralization/immobilization. Phenolics can act as C substrates for microbes (Schimel et al., 1996; Steltzer & Bowman, 2005; Dorrepal et al., 2007), which increases N retention on the leaf; however, higher concentrations of plant phenolics and lignin can slow decomposition (Hobbie, 1996; Taylor et al., 1989). Plant phenolic types can also vary among species (Graglia et al., 2001). Others have found that *Betula* spp. leaves have more polyphenols than *Salix* spp. and *Populus* spp. leaves (Palo, 1984; Graglia et al., 2001; Ruuhola et al., 2013). In particular, low molecular weight phenolics such as tetramers, flavonoids and lignans are more easily biodegraded than high molecular weight tannins (Kraus et al., 2002), and act as substrate for microbial growth substrate on the

leaf, thereby leading to increased N immobilization (Hätenschwiler et al., 2005). Aerts et al. (2006) found %N content to increase on *B. nana* litter and suggested that the litters phenolics were likely comprised of low molecular weight phenolics such as flavonoids which do not inhibit decomposition. Thus it is possible that the *B. glandulosa* litter bags in this study contained a large proportion of low molecular weight polyphenols which contributed to microbial N immobilization on the litter.

5.3. Surface *vs* buried litter impacts on decomposition

The interactions between microclimate and soil quality likely had different effects on buried and surface litter. Mean annual decay rates for each site in this study ranged from 0.33 – 0.39 year^{-1} for surface bags and 0.40 – 0.44 year^{1} for buried bags. DeMarco et al. (2014) found *B. neolaskana* (Sarg.) to decay at the surface with rates of 0.21 – 0.31 year^{-1} for a period of three years in Arctic tundra in Alaska. Zhang et al. (2008) synthesized data on surface litter bag decomposition rates using 293 k values from 70 studies at sites across the globe, and noted a general decrease in *k* values with increasing latitude. Globally, the median and mean decay rates were 0.30 and 0.58 year^{-1}, respectively while *k* values tended to be lower on average, 0.15-0.20 year^{-1}, in tundra for litter types that included graminoids, moss, roots, woody and broadleaved litter. Silver & Miya (2001) conducted a large synthesis study of first year decay rates for buried bags containing root litter. They found average decay rates ranging from 0.18 year^{-1} for large (>5 mm root diameter) to 0.83 year^{-1} for small (< 2 mm) root diameters.

Overall, the decay rates observed in this study are slightly greater than rates observed in other tundra studies but did support previous findings that buried bags would lose more mass than surface bags (e.g. Hobbie & Chapin, 1996). Greater mass loss is expected as the buried bags have better contact with the soil relative to surface bags, providing access to soil moisture (Hobbie & Chapin, 1996) and more opportunities for microbial and faunal interactions (Beare et al., 1992). Beare et al. (1992) determined that the abundance and biomass of microbial and faunal groups were greater on buried litter than surface litter and that buried litter decay rates (1.4-1.7% day^{-1}) were 2.5 times faster than rates for surface litter (0.5-0.7% day^{-1}). In my study, buried bag decay rates in the low and medium shrub plots were between 1.2-1.3 times faster over winter and 1.3 times faster over the year. The difference may be due to Beare et al. (1992)'s study being much shorter (56 days), capturing initial decomposition differences, whereas our study was unable to capture early mass loss rates.

In my study, the lack of difference between buried and surface litter bag decomposition at the high shrub site may have been due to the different microclimate and soil characteristics at that site that may have offset burial impacts. At the high shrub site, 10 cm soil temperatures were significantly cooler than at the low shrub site which may have slowed decomposition at depth. Also, the soil organic matter content was higher and bulk density was lower at this depth compared to either the low or medium shrub sites. Low bulk density and high porosity may have reduced the physical contact with the organic soils and limited matric water flow. Strong et al. (2004) noted that large air filled pores 60-300 μm had a negative influence on organic matter decomposition due to thin water films which restricted microbial movement (Wong & Griffin, 1976). This also could have

resulted in slower diffusion of nutrients to the decomposition site. Thus larger pore spaces in soils at the high shrub site may have inhibited microbial and water flow to the buried bags, and combined with cooler temperatures, could have resulted in less decomposition.

In the field decomposition study, another factor that can influence differences in decomposition rates between surface and buried bags is the presence of standing or flowing water during spring snowmelt. During the snow melt period, water tables are at or near the surface as melt water infiltrates organic soils but is limited by impermeable mineral or ice rich layers such that saturation and water flow is concentrated near the surface (Carey, 2003). Thus near-surface runoff due to snow melt would likely most affect surface rather than buried bags, which at most sites did not thaw until a week or two after snow melt (anecdotally observed). The high shrub site soils thawed the slowest and most of the bags could not be retrieved during the May field trip despite similar snow melt dates at the sites. As noted earlier, this delayed thaw may be attributed to the deeper moss mats at the high shrub site that slowed heat transfer through the soil (Gornall et al., 2007). Thus, overland and near-surface flow likely would have lasted longer at the high shrub site. This standing water becomes enriched with DOC as near surface soils accumulate stores of soluble C and nutrients since the last flushing event (from previous rain or snowmelt) (Carey, 2003). The nutrients associated with soil water are used by soil microbes and plants, or are retained by the soil (McArthur & Marzolf, 1987). Standing water DOC is an important nutrient source (Magill & Aber, 2000), and as noted by

Buckeridge et al. (2010), high levels of DOC can stimulate N cycling by soil microorganisms. Chapin et al. (1999) found higher rates of microbial activity in water track soils (zones of preferential flow) relative to surrounding soils. Thus, surface litterbags at the high shrub site may have experienced a longer incubation in standing water, which could have promoted decomposition and contributed to the significantly greater mass loss at this site relative to the other two sites after a full year.

5.4. Seasonal differences in decomposition

The mass loss lab study simulated decomposition at 5˚C and 20˚C and then at -5 ˚C and found approximately 22% mass loss total. This compared fairly well to the fall and overwinter mass loss rates in the field (between 21%-28% for all sites and burial types). Both experiments agreed well with other studies that have demonstrated mass loss of approximately 20% between autumn and spring (Bleak 1970; Abouguendia & Whitman, 1979; Moore, 1983; Hobbie & Chapin 1996; Bokhorst et al., 2013; DeMarco et al., 2014). The mass loss study suggests that the majority (90%>) of mass loss occurs during the first week after litter fall regardless of ambient temperature and that no loss actually occurs during winter itself when temperatures are below 0˚C. At Daring Lake, senescence of *B. glandulosa* occurs in late August/early September when air temperatures are on average 7˚C. Air temperature remains below zero typically by October and snowfall remains on the ground by October (based on 1994-2015 meteorological record at Daring Lake). Although it was impossible to access the field site to confirm these early fall mass loss rates, environmental conditions were similar to the 5˚C incubation and could have supported these mass loss rates. Notably, this study did not include a soil substrate for litter to decompose on, and no additional moisture was added to litter after microbial

inoculant was applied. Thus decomposition rates could have been impacted by microbial moisture limitations, or supply of soil microbes to the litter, potentially leading to an underestimate of mass loss rates in the lab.

The lab study results also support other studies' contentions that past observations of winter litter mass loss are not the result of active winter decomposition but instead represent leaching of organic compounds released in autumn (Bokhorst et al. 2010; 2013). This is further supported by the leaching study, in which, regardless of temperature treatment, 66% of the total DOC leached over the entire experiment was released from the litter pack within 2 weeks of the start of the study. This is also in agreement with study of *Betula nana* leaching (e.g. Magill & Aber, 2000).

The SUVA method was used as a surrogate indicator of how aromatic a DOC molecule is. Surface water $SUVA_{254}$ values tend to be low (1-6 L mg-C^{-1} m^{-1}; Hansen et al., 2016) compared to Arctic soil interstitial water, which have been reported to be 8.0-10 L mg-C^{-1} m^{-1} for interstial soil water in Northwest Alaska (Jaffé, et al., 2008; Guo et al., 2015). Typically, less aromatic molecules are associated with high quality fractions such as low litter C:N and hydrophilic fractions (Weishaar et al., 2003), and more aromatic molecules are associated with low quality fractions such as compounds with high C:N, hydrophobic compounds and lignin, which decompose more slowly (Olefeldt et al. 2013). In our leaching study, $SUVA_{254}$ rose over the first month of leaching from 0-8 mg^{-1} C L^{-1} and

stabilized at around 7.5 mg^{-1} C L^{-1} for much of the study, suggesting that % aromaticity was high for much of the experiment. Aromaticity peaked by the end of the first month, and remained steady until about 2.5 months into the experiment, upon which it diminished slightly to around 3.0 mg^{-1} C L^{-1}. The pattern of DOC and TN concentrations along with the increasing aromaticity indicates that much of the readily leachable compounds are removed shortly after the simulated litter fall, and may contribute to overall losses observed in the litter decomposition experiment.

In my study, the reported range of a_{250}/a_{365} was between 3 and 7.5, which represented a range of weight-averaged molecular DOC weight between ~10 and 1kDa (Peuravuori & Pihlaja, 1997; Lou & Xie, 2006). Magill & Aber (2000) note that contrary to the expectation that low molecular weight compounds are labile, many of these small compounds are tannins or phenols, which are in fact most resistant to decay, whereas cellulose, despite it being a large polymer, is comprised of glucose that can be decomposed by a wide range of microorganisms, and may be easily accessed and consumed. This may help to explain findings that high molecular weight DOC is generally more bioavailable than low molecular weight (Steinberg, 2013), and thus tends to be leached first, as observed in our study.

Lower C:N over time may indicate the presence of dissolved organics that are more highly decomposed (Melillo et al., 1982; Currie et al., 1996). McGill & Cole (1981) hypothesized that soil decomposers generally don't selectively hydrolyze N containing compounds in response to N limitation, but instead that N mineralization depends on C

mineralization. Qualls & Haines (1992) determined that DOC from freshly fallen autumn leaves were highly biodegradable compared to DOC in stream water and soils in a forested watershed, and attributed this to its high hydrophilic neutral fraction. This fraction includes a group of organic hydrophilic compounds that are highly mobile because they are water soluble, and the researchers found that about half of this fraction consisted of carbohydrates. Thus it is possible in this study that the presence of an easily decomposable carbohydrate fraction in *B. glandulosa* litter left a more N rich refractory component (Qualls & Haines, 1992) which lead to the decrease in C:N over time. Currie et al. (1996) also found that seasonality influences DOC:DON flux, with fresh litter leaching dominating initially after litterfall, resulting in high DOC:DON ratios, while in the summer, the solubilization of decomposition products and secondary compounds would dominate leading to lower DOC:DON ratios (Currie et al., 1996). Evidently, DOC aromaticity and molecular size can influence bioavailability, or the fraction of the DOC pool that is available for rapid microbial degradation (Weishaar et al., 2003). This leaching study provides evidence that much of the labile DOC and DON was leached within the first few weeks after the start of the experiment, with the trend for high molecular weight near the start of the experiment possibly indicating leaching of large glucose polymers, which could also explain why C:N decreased over time. As concluded by other studies (Magill & Aber, 2000; Qualls & Haines, 1992), this evidence suggests the less recalcitrant materials were leached earliest in the incubation.

6. Conclusion

This study suggests that on a short 1 year time scale, differences in soil temperature and moisture associated with differences in shrub abundance are unlikely a major factor driving litter decomposition processes or are offset by other important factors related to soil nutrients that may be influenced by topographic position and soil substrate. The mechanism that is driving decomposition is more likely to do with shrub-litter feedbacks, where enhanced shrub growth and N uptake allow them to produce more leaves, which results in greater inputs of N to the soil that in turn promotes faster nutrient cycling. This study suggests that the snow shrub feedbacks may be responsible for warmer winter soil temperatures, but that lab simulations of autumn conditions suggest that much of the winter mass loss observed occurred in the first few weeks after litterfall (when temperatures were still above 0˚C) due to leaching of organic compounds. The following hypotheses were tested in this study:

(1) It was hypothesized that there would be variation in summer and winter microclimate characteristics across the three sites with lower summer soil temperature and lower summer soil moisture and higher winter soil temperature at plots with the highest shrub abundance. There were significant differences among sites in terms of thaw depth (least at high shrub), snow depth (most at high shrub), 2 cm soil temperature in summer (highest at low shrub), in winter (lowest at low shrub), and 10 cm soil temperature in summer (lowest at high shrub). At the plot where temperatures were measured

continuously, VWC were significantly *greater* (not lower as hypothesized) at the high shrub site compared to low and medium shrub, and LAI was significantly greater in the high shrub site compared to the low shrub, but not different from the medium shrub site. In line with the snow shrub hypothesis (Sturm et al., 2001; 2005), the high shrub site had greater relative snow depths, which may have contributed to the warmer relative winter temperatures observed at the high shrub sites compared to the other two sites. Soil shading by deciduous leaf biomass may help explain the relatively cool summer temperatures in the high shrub site compared to the low shrub site, but not for the medium shrub site. The greater relative thickness of moss at the high shrub site compared to the other two sites may have acted as an insulator to the ground, slowing the transfer of summer heat to the soil (Gornall et al., 2007), and helping to retain moisture (Zimov, 1995) that kept soils cool. The combined effect of low thermal conductivity and greater volumetric water content could have limited soil warming and thaw, contributing to both the shallower active layer depth and cooler soils at the high shrub site in the summer.

(2a) There was a small but significant difference among sites in surface litter decomposition rates in August; however in general decomposition rates were similar across sites, which was contrary to expectations. These results suggest that the interaction of soil nutrient availability and microenvironment difference mitigate the influence of any one factor on decomposition rates including soil nutrient availability, microclimate, and microbial community composition and abundance. The greater rates of decomposition in surface litter bags after a whole year at the high shrub site may have been a result of longer incubations within DOC-rich surface meltwater and greater populations of r-

selected microbial communities as a result of relatively greater amounts of high quality fresh deciduous litter compared to the other two sites.

(2b) Buried bags did lose more mass than surface bags at the low and medium shrub site, but mass loss rates were not different at the high shrub site. As others have suggested, direct contact with the soil may have promoted greater soil microbial access to the litter (Hobbie & Chapin, 1996; Beare et al., 1992), which could have enhanced decay. The lack of difference at the high shrub site could be due to relatively cool 10 cm soils and/or lower bulk density and higher pore spaces within the soil, which might have restricted water and bacterial movement (Wong & Griffin, 1976).

(3a) As expected, there was significant mass loss differences between litterbag collections in May 2016 and August 2016. (3b) The results from mass loss incubation and leaching incubations which simulated autumn temperatures suggested that much of this loss occurred in the first few weeks after leaching begins, and no mass loss occurred in subzero conditions, supporting previous experiment findings by Bokhorst et al. (2010; 2013). Mass loss rates in the lab incubation (~22%) were similar to those seen in the field (21-28% for all bag types in May), suggesting that the lab study was a good proxy for the field experiment. (3c) As hypothesized, the leaching incubation demonstrated rapid initial loss of DOC and DON from fresh litter within 2-3 weeks of litter fall. The larger, easily soluble compounds were degraded first, followed by smaller low molecular weight compounds (e.g. tannins) that degrade more slowly (e.g. Magill & Aber, 2000). Aromaticity increased over the first month and stabilized at around 7.5 mg^{-1} C L^{-1}, which

added further evidence that much of the readily available organic compounds were leached within the first few weeks of simulated litterfall. Thus, for the field study, which set litterbags out in August and collected them in May, it is likely that active microbial breakdown and litter leaching occurred during the shoulder seasons, rather than "true winter" when soils are mostly frozen.

(4) Contrary to the expectation that there would be enhanced N release from the litter under greater levels of birch shrub coverage, litter immobilized N at all three sites and to the greatest extent at the medium and high shrub sites. Aerts et al. (2006) observed similar results and noted that *Betula* species have high phenolics concentrations, which could act as substrates for microbial growth (Schimel et al., 1998; Steltzer & Bowman, 2005) and increase litter N retention while not impeding decomposition (Aerts et al., 2006). Greater soil N has also been found to stimulate litter decomposition rates (Aerts et al., 2006; Hobbie, 1996), and can lead to N immobilization (Gallardo & Merino, 2006). The greater amount of N accumulation on the high shrub site litter bags may have been due to the greater relative amounts of soil N cycling in that system compared to the low shrub site. The microbes at this site might have immobilized more N because they have a higher nutrient demand as they are normally mineralizing C substrates of higher quality and quantity (DeMarco et al., 2014; Fierer et al., 2007; Wallenstein et al., 2007).

The goal of this study was to understand the potential for shrub abundance at Daring Lake to influence microclimate and decomposition processes. Climate warming and long-term vegetation change in the Arctic is expected to continue to alter ecosystem structure

and function, resulting in ecosystems dominated by deciduous shrubs that allocate more biomass, C and N to woody stems in some regions. Results from this study suggest that shrubs may be associated with enhanced snow depth, less soil thaw depth, lower summer temperature, higher soil moisture, and greater near surface (0-20 cm) soil N and C, which could be indicative of future conditions of some Arctic ecosystems. However, with only small differences in mass loss among sites, the interaction of soil nutrient availability and microclimate difference likely mitigated the influence of any one factor associated with shrub abundance. Further work distinguishing the relative importance of litter quality and quantity, nutrient cycling, and microclimate on microbial litter decomposition is needed to reconcile results from this study and others with contrasting findings.

This study focused on the first year of mass loss in a low Arctic ecosystem. Early decomposition rates tend to be related to climate and concentrations of water soluble nutrients and structural carbohydrates in the litter, while later decomposition rates are more influenced by lignin concentrations in the litter (Gartner & Cardon, 2004). This research is part of an ongoing project to investigate how shrub abundance influences decomposition processes over a 5-year period. Collections of *Betula* litter started in 2016 and will continue annually in August until 2019. The goal of the longer term study is to investigate how later stage decay rates are altered under different levels of shrub abundance, as well as when and in what quantity C is lost from the litter. A better understanding of interactions between vegetation change and C and nutrient cycling will be critical to the prediction of Arctic feedbacks on climate change into the future.

Appendices

APPENDIX A

A.1. Soil and vegetation characteristics at the one plot from each site with continuously monitored temperature

Table A.1.1. Vegetation Characteristics of Plot A for each of the three sites. Thermocouples were installed at this plot to continuously monitor temperature. Superscript letters which differ within a row indicate a significant difference.

Characteristics	**Low**	**Medium**	**High**
2016 Vegetation Cover and LAI[1]			
Canopy height (cm)	22.9 (0.21)^{a}	44.7 (0.24)^{b}	95.7 (0.26)^{c}
Groundcover vegetation LAI (m^2 m^{-2})	2.9	3.7	3.4
% LAI *B. glandulosa*	9.9	36.2	42.5
% moss cover	15.0	88.3	95.8
% lichen cover	79.6	7.9	0.0
LAI_{2200} (m^2 m^{-2})			
2015[2]	0.3 (0.1)^{a}	1.6 (0.16)^{b}	1.3 (0.1)^{b}
2016[3]	0.1 (0.02)^{a}	1.2 (0.16)^{b}	1.8 (0.14)^{b}
Peak Growing Season LAI_{2200} (m^2 m^{-2})			
2015 (DOY 202)	0.1 (0.04)^{a}	1.1 (0.18)^{b}	1.3 (0.08)^{b}
2016 (DOY 210)	0.03 (0.02)^{a}	1.2 (0.16)^{b}	1.8 (0.14)^{c}
Max Thaw Depth (cm)			
2015 (DOY 208)	66.3 (2.1)^{a}	43.5 (2.0)^{b}	30.1 (2.1)^{b}
2016 (DOY 217)	90.5 (1.3)^{a}	65.9 (3.8)^{b}	35.4 (1.2)^{c}
Volumetric water content (0-20cm) (%)			
2015[2]	29.2 (1.6)^{a}	27.9 (1.1)^{a}	42.9 (1.1)^{b}
2016[3]	25.6 (2.1)^{a}	26.5 (1.6)^{a}	40.1 (1.6)^{b}
Snow Depth (cm)			
2017 (DOY 125)	17.2 (1.8)^{a}	46.7 (2.6)^{b}	72.1 (0.9)^{c}
Average daily maximum 2 cm soil temperature (Week 26, 2016) (˚C)	13.4 (0.5)^{a}	12.3 (0.6)^{b}	10.4 (0.5)^{c}
Average daily minimum 2 cm soil temperature (Week 10, 2017) (˚C)	-17.4 (0.1)^{a}	-14.8 (0.2)^{b}	-9.0 (0.1)^{c}
Average daily maximum 10 cm soil temperature (Week 33, 2016) (˚C)	9.6 (0.4)^{a}	6.1 (0.2)^{b}	3.9 (0.3)^{c}
Average daily minimum 10 cm soil temperature (Week 10, 2017) (˚C)	-16.1(0.3)	-12.2 (0.2)	-8.1 (0.7)
Average annual 2 cm soil temperature	-2.40	-2.08	-0.79
Average annual 10 cm soil temperature	-2.79	-2.59	-1.76
Average Depth of LFH horizon (cm)	3.2 (0.4)	4.7 (0.7)	>10

[1]Surveyed during peak growing se1ason between DOY 202 and DOY 208
[2]Surveyed three times between DOY 185 and 208
[3]Surveyed six times between DOY 184 and 220

Table A.1.2. Results of linear mixed model tests for Table A.1.1. Site and Week were treated as fixed effects and Thermocouple ID was treated as the random effect.

Characteristics		DF	F	P
Canopy Height	Site	2,27	131.9	**<0.0001**
LAI 2015	Site	2,21	41.65	**<0.0001**
	Week	1,21	17.38	**0.0004**
	Site x Week	2,21	7.11	**0.0044**
LAI 2016	Site	2,21	45.11	**0.0001**
	Week	1,117	0.38	0.54
	Site x Week	2,117	3.21	**0.044**
Peak LAI 2015	Site	2,21	146.58	**<0.0001**
Peak LAI 2016	Site	2,21	54.55	**<0.0001**
Snow 2017	Site	2,12	34.89	**<0.0001**
Snow 2017	Site	2,19	227.45	**<0.0001**
Thaw Depth 2015	Site	2,21	64.55	**<0.0001**
	Week	1,21	1.31	0.2655
	Site x Week	2,21	0.12	0.8857
Thaw Depth 2016	Site	2,21	85.2	**<0.0001**
	Week	1,116	276.3	**<0.0001**
	Site x Week	2,116	20.13	**<0.0001**
VWC 2015	Site	2,21	31.83	**<0.0001**
	Week	1,21	22.73	**0.0001**
	Site x Week	2,21	8.94	**0.0015**
VWC 2016	Site	2,12	26.4	**<0.0001**
	Week	1,117	8.14	**0.0051**
	Site x Week	2,117	6.73	**0.0017**
Temperature (continuously monitored	Site	2,21	226.223	**<0.0001**
	Day	1,141	1.755	0.187

between 2016 and 2017)	Site x Day	2,141	5.133	**0.007**

Table A.1.3 Tukey HSD Pairwise comparisons for significant ANOVA in Table A.1.2 Differences in Group number indicate significant difference between rows. The lsmeans and multcomp package in R were used to determine differences.

		Mean	Standard Error	DF	95% C.I.	Group
Canopy Height	Low	22.9	3.25	29	[16.25, 29.55]	1
	Medium	44.7	3.25	27	[38.02, 51.37]	2
	High	95.7	3.25	27	[89.03, 102.37]	3
LAI 2200 (m^2 m^{-2}) 2015	Low	0.25	0.11070	21	[0.02, 0.48]	1
	Medium	1.29	0.11070	21	[1.06, 1.52]	2
	High	1.61	0.11070	21	[1.39, 1.85]	2
LAI 2200 (m^2 m^{-2}) 2016	Low	0.17	0.12819	14	[-0.10, 0.45]	1
	Medium	0.12	0.12819	12	[0.97, 1.53]	2
	High	1.62	0.12819	12	[1.34, 1.90]	2
Max Thaw Depth 2015	Low	67.47	3.40	23	[60.44, 74.50]	1
	Medium	44.40	3.40	21	[37.33, 51.46]	2
	High	21.02	3.40	21	[13.95, 28.07]	3
Max Thaw Depth 2016	Low	90.56	2.41	23	[85.75, 95.55]	1
	Medium	65.87	2.41	21	[60.86, 70.89]	2
	High	35.36	2.41	21	[30.35, 40.37]	3
Peak LAI 2015	Low	0.08	0.12	23	[-0.17, 0.33]	1
	Medium	1.13	0.12	21	[0.88, 1.38]	2
	High	1.30	0.12	21	[1.05, 1.55]	2
Peak LAI 2016	Low	0.03	0.12	23	[-0.22, 0.28]	1
	Medium	1.21	0.12	21	[0.95, 1.45]	2
	High	1.79	0.12	21	[1.54, 2.04]	3

Volumetric Water Content 2015	Low Medium High	29.16 27.16 42.91	1.47 1.47 1.47	21 21 21	[26.09, 32.22] [24.83, 30.97] [39.84, 45.97]	1 1 2
2016	Low Medium High	25.54 26.49 40.08	1.59 1.59 1.59	23 21 21	[22.25, 28.83] [23.20, 29.78] [36.79, 43.37]	1 1 2
Snow Depth 2017	Low Medium High	17.21 46.66 71.50	1.86 1.86 1.74	21 19 19	[13.35, 21.08] [42.77, 50.55] [67.86, 75.14]	1 2 3
Average daily maximum 2cm soil temperature (Week 26, 2016)	Low Medium High	13.40 12.31 10.42	0.41 0.41 0.41	23 21 21	[12.20, 14.54] [9.51, 13.93] [7.59, 13.23]	1 2 3
Average daily minimum 2cm soil temperature (Week 10, 2017)	Low Medium High	-17.4 -14.8 -9.0	0.79 0.79 0.79	23 21 21	[-17.69, -17.13] [-15.49, -14.14] [-9.66, -8.31]	1 2 3
Average daily maximum 10cm soil temperatures (Week 33, 2016)	Low Medium High	9.56 6.10 3.89	0.19 0.19 0.19	23 21 21	[9.17, 9.95] [5.71, 5.50] [3.49, 4.29]	1 2 3
Average daily mnimum (10cm) soil temperature (Week 10, 2017)	Low Medium High	-16.1 -12.2 -8.1	0.73 0.73 0.73	23 21 21	[-16.58, -15.68] [-13.31, -11.13] [-9.23, 7.05]	1 2 3

A.2. Statistics tables for vegetation and microclimate characteristics

Table A.2.1. Results of linear mixed models across all three sites, with 5 plots per site. Site and Week sampled (if relevant) were treated as the fixed effect and plot id (flagged area where repeat sampling took place, n=8 per plot) was treated as the random effect.

		DF	F	P
LAI 2015	Site	2,12	76.01	**<0.0001**
	Week	1,115	34.98	**<0.0001**
	Site x Week	2,115	11.41	**<0.0001**
LAI 2016	Site	2,12	94.96	**<0.0001**
	Week	1,560	0.13	0.724
	Site x Week	2,560	14.07	**<0.0001**
VWC 2015	Site	2,12	11.28	**0.0017**
	Week	1,139	21.51	**<0.0001**
	Site x Week	2,139	4.93	**0.0085**
VWC 2016	Site	2,12	8.34	**0.0054**
	Week	1,560	80.47	**<0.0001**
	Site x Week	2,560	6.69	**0.0013**
Thaw Depth 2015	Site	2,12	30.74	**<0.0001**
	Week	1,115	8.35	**0.005**
	Site x Week	2,115	0.43	0.65
Thaw Depth 2016	Site	2,12	19.44	**<0.0001**
	Week	1,561	746.71	**<0.0001**
	Site x Week	2,561	27.51	**<0.0001**
Manual Temperature (2015)	Site	2,12	72.55	**<0.0001**
	Week	1,115	60.86	**<0.0001**
	Site x Week	2,115	21.54	**<0.0001**
Manual Temperature (2016)	Site	2,12	54.52	**<0.0001**
	Week	1,560	192.73	**<0.0001**
	Site x Week	2,560	0.66	0.515

Canopy Height	Site	2,12	68.3	**<0.0001**
Moss	Site	2,12	210.3	**<0.0001**
Lichen Cover	Site	2,12	200.89	**<0.0001**
Green LAI	Site	2,12	9.339	**0.0036**
Peak LAI 2015	Site	2,12	131.8	**<0.0001**
Peak LAI 2016	Site	2,12	68.48	**<0.0001**
Maximum Thaw Depth (2015)	Site	2,12	22.74	**<0.0001**
Maximum Thaw (2016)	Site	2,12	23.96	**<0.0001**
Peak Manual Soil Temperature (2015)	Site	2,12	83.73	**<0.0001**
Peak Manual Soil Temperature (2016)	Site	2,12	80.59	**<0.0001**

Table A.2.2 Tukey HSD Pairwise comparisons for significant ANOVA (from linear mixed model) in Table A.2.1 Differences in Group number indicate significant difference between rows. The lsmeans and multcomp package in R were used to determine differences.

	Site	lsmeans	Standard Error	DF	CI (95%)	Group
Canopy Height	Low Medium High	28.46 45.88 113.48	5.43 5.43 5.43	14 12 12	[16.80, 40.11] [34.04, 57.72] [101.64, 125.3]	1 2 3
Green LAI	Low Medium High	2.66 4.01 4.63	0.33 0.33 0.33	14 12 12	[1.96, 3.36] [3.29, 4.72] [3.91, 5.34]	1 2 3
% Moss cover	Low Medium High	16.50 91.67 96.42	3.10 3.10 3.10	14 12 12	[9.87, 23.13] [84.93, 98.40] [89.68, 103.15]	1 2 2
% Lichen cover	Low Medium High	7.89 6.67 0	3.10 3.10 3.10	14 12 12	[72.29, 85.54] [-0.06, 85.54] [-6.72, 6.72]	1 2 3
% LAI B. glandulosa	Low Medium High	10.16 35.19 42.97	3.53 3.53 3.53	14 12 12	[2.60, 17.72] [27.51, 42.87] 32.38, 50.65]	1 2 3
LAI 2015 LAI 2016	Low Medium High Low Medium High	0.22 1.51 1.56 0.21 1.26 1.48	0.08 0.08 0.08 0.06 0.06 0.07	14 12 12 14 12 12	[0.03, 0.04] [1.32, 1.70] [1.37, 1.75] [0.06, 0.36] [1.11, 1.41] [1.33, 1.64]	1 2 2 1 2 3
LAI 2015 peak LAI 2016 peak	Low Medium High Low Medium High	0.09 1.23 1.53 0.14 1.32 1.65	0.07 0.07 0.07 0.10 0.10 0.10	14 12 12 14 12 12	[-0.05, 0.23] [1.09, 1.37] [1.38, 1.67] [-0.06, 0.34] [1.10, 1.52] [1.44, 1.85]	1 2 3 1 2 2

contd…

	Site	Mean	Standard Error	DF	CI (95%)	Group
Maximum Thaw Depth (2015)	Low Medium High	66.31 43.46 30.09	3.84 3.84 3.84	14 12 12	[58.07, 74.54] [35.10, 51.83] [21.72, 38.47]	1 2 2
Maximum Thaw Depth (2016)	Low Medium High	91.32 65.60 48.10	4.44 4.44 4.44	14 12 12	[81.78, 100.84] [55.92, 75.27] [38.42, 57.77]	1 2 3
VWC 2015	Low Medium High	22.9 30.06 37.99	2.24 2.24 2.25	14 12 12	[18.13, 27.75] [25.18, 34.95] [33.08, 42.89]	1 2 3
VWC 2016	Low Medium High	22.92 28.99 34.77	2.01 2.01 2.02	14 12 12	[[18.60, 27.25] [24.60, 33.37] [30.37, 39.17]	1 2 3
Manual Temperature 2015	Low Medium High	6.08 2.49 2.02	0.26 0.26 0.26	14 12 12	[5.53, 6.47] [1.92, 3.06] [1.44, 2.59]	1 2 3
Manual Temperature 2016	Low Medium High	7.68 4.37 4.26	0.26 0.26 0.26	14 12 12	[7.10, 8.25] [3.68, 4.84] [3.78, 4.96]	1 2 2
Peak Manual Temperature (DOY 202)	Low Medium High	1.81 2.00 5.83	0.25 0.25 0.25	14 12 12	[5.30, 6.36] [1.27, 2.35] [1.45, 2.54]	1 2 2
Peak Manual Temperature (DOY 185)	Low Medium High	10.23 6.04 4.78	0.32 0.32 0.32	14 12 12	[9.56, 10.91] [5.36, 6.73] [4.08, 5.49]	1 2 3
Snow Depth 2016 (DOY 125)	Low Medium High	8.94 16.84 34.77	5.87 5.87 5.87	14 12 12	[-3.67, 21.54] [4.03, 29.65] [21.95, 47.57]	1 12 2
Snow Depth 2017 (DOY 125)	Low Medium High	31.54 49.66 70.82	3.49 3.49 3.49	14 12 12	[24.05, 39.03] [42.05, 57.27] [63.21, 78.41]	1 2 3

Table A.2.3 Tukey HSD (stats package, R statistical package), pairwise comparisons for significant ANOVAs for biomass, and initial %C, %N and CN of the litter. P value below 0.05 indicates a significant difference between pairs.

Pairwise		CI	P value
B. glandulosa plants	Low – Medium Low – High Medium - High	[-449.35, 752.87] [113.08, 1315.311] [-38.68, 1163.55]	0.73 **0.03** 0.06
Other Vascular	Low – Medium Low – High Medium - High	[-297.3, 52.05] [-91.41, 257.89] [31.19, 380.50]	0.16 0.37 **0.03**
Total Vascular plants	Low – Medium Low – High Medium - High	[-599.93, 658.25] [168.34, 1426.53] [139.18, 1397.37]	0.99 **0.02** **0.02**
B. glandulosa (leaf only)	Low – Medium Low – High Medium - High	[-29.94, 69.86] [11.36, 111.16] [-8.60, 91.20]	0.48 **0.02** 0.10
Other Vascular (leaf only)	Low – Medium Low – High Medium - High	[-186.52, 10.55] [-200.36, -3.29] [-112.37, 84.68]	0.07 **0.04** 0.90
Total leaves	Low – Medium Low – High Medium - High	[-151.94, 15.89] [-124.48, 43.35] [-56.45, 111.37]	0.10 0.36 0.60
% C	Low – Medium Low – High Medium - High	[-2.77, 0.89] [-2.23, 0.95] [-1.29, 1.89]	0.41 0.57 0.88
% N	Low – Medium Low – High Medium - High	[-0.79, 0.21] [-0.24, 0.48] [0.06, 0.93]	0.31 0.48 **0.02**
C:N	Low – Medium Low – High Medium - High	[-2.08, 7.99] [-5.88, 2.84] [-8.84, -0.12]	0.31 0.64 **0.04**

A.3. Linear mixed model results for litter decay and nutrient differences

Table A.3.1. Results from mixed linear models for decay rate (k value) differences that treated plot as the random effect.

		DF	**F**	**P**
Overall Differences	Site	2,44	1.524	0.229
	Period	2,44	2.793	0.0721
	Bag Type	1,44	9.734	**0.0032**
	Site x Period	4,44	1.1348	0.3526
	Site x Bag Type	2,44	1.3954	0.2585
	Period x Bag Type	2,44	0.2675	0.7665
	Site x Period x Bag Type	4,44	1.3319	0.2731
Fall/overwinter: Aug 2015-May 2016	Site	2,12	0.1432	0.868
	Bag Type	1,5	9.301	**0.028**
	Site x Bag Type	2,5	0.7973	0.501
Growing season: May 2016–August 2016	Site	2,12	0.999	0.397
	Bag Type	1,5	2.172	0.201
	Site x Bag Type	2,5	1.012	0.4272
Annual: Aug 2015 – Aug 2016	Site	2,10	0.468	0.6396
	Bag Type	1,10	31.06	**0.0002**
	Site x Bag Type	2,10	8.091	**0.0081**

Table A.3.2 TukeyHSD pairwise comparison where ANOVA from Table A.3.1 were significant. The lsmeans and multcomp package in R were used for comparison. Significant differences between groups if group number is difference between a row.

Period	site	Bag Type	lsmean	SE	df	lower CL	upper CL	group
August 2015 - May 2016	medium	SURFACE	0.0008	0.0001	14	0.0006	0.0011	1
August 2015 - August 2016	medium	SURFACE	0.0009	0.0001	14	0.0006	0.0012	12
August 2015 - May 2016	low	SURFACE	0.0009	0.0001	14	0.0006	0.0012	12
August 2015 - August 2016	low	SURFACE	0.0009	0.0001	14	0.0006	0.0012	12
May-Aug 2016	medium	BURIED	0.0009	0.0002	14	0.0005	0.0013	12
May-Aug 2016	medium	SURFACE	0.0010	0.0001	14	0.0007	0.0013	12
May-Aug 2016	low	SURFACE	0.0010	0.0001	14	0.0007	0.0013	12
August 2015 - May 2016	high	SURFACE	0.0010	0.0001	14	0.0007	0.0013	12
August 2015 - August 2016	high	BURIED	0.0011	0.0001	14	0.0008	0.0013	12
August 2015 - August 2016	high	SURFACE	0.0011	0.0001	14	0.0008	0.0013	12
August 2015 - May 2016	high	BURIED	0.0011	0.0003	14	0.0004	0.0017	12
August 2015 - May 2016	low	BURIED	0.0011	0.0002	14	0.0007	0.0014	12
August 2015 - August 2016	medium	BURIED	0.0011	0.0001	14	0.0009	0.0014	12
August 2015 - August 2016	low	BURIED	0.0012	0.0001	14	0.0009	0.0015	12
August 2015 - May 2016	medium	BURIED	0.0012	0.0002	14	0.0008	0.0015	12

May-Aug 2016	high	SURFACE	0.0013	0.0001	14	0.0010	0.0016	12
May-Aug 2016	low	BURIED	0.0016	0.0002	14	0.0013	0.0020	2
May-Aug 2016	high	BURIED	0.0017	0.0003	14	0.0010	0.0023	12

Table A.3.3. Results of linear mixed model for %N difference between sites and harvest dates. Plot was treated as the random effect.

	%Nitrogen			
		DF	F	P
Overall	Site	2,12	45.95	**<0.0001**
	Collection Date	1,196	75.6	**<0.0001**
	Bag Type	1,196	8.63	**0.004**
	Site x Collection Date	2,196	1.82	0.165
	Site x Bag Type	2,196	11.86	**<0.0001**
	Collection Date x Bag Type	1,196	11.36	**0.001**
	Site x Collection Date x Bag Type	2,196	11.26	**<0.0001**
Surface Bags	Site	2,12	47.84	**<0.0001**
	Collection Date	1,95	43.76	**<0.0001**
	Site x Collection Date	2,95	0.96	0.376
Buried Bags	Site	2,12	32.56	**<0.0001**
	Collection Date	1,89	34.60	**<0.0001**
	Site x Collection Date	2,89	9.69	**<0.0001**
May Collection	Site	2,12	69.14	**<0.0001**
	Bag Type	1,67	34.56	**<0.0001**
	Site x Bag Type	2,67	27.96	**<0.0001**
August Collection	Site	2,12	20.59	**0.0001**
	Bag Type	1,117	0.06	0.80
	Site x Bag Type	2,117	3.91	**0.02**

Table A.3.4 TukeyHSD pairwise comparison where ANOVA from Table A.3.1 were significant. The lsmeans and multcomp package in R were used for comparison. Significant differences between groups if group number is different between a row.

site	BS	Month	lsmean	SE	df	lower.CL	upper.CI	.group
high	Buried	MAY	2.90	0.10	12	2.67	3.12	1
low	Buried	MAY	3.08	0.06	14	2.97	3.20	1
low	Surface	MAY	3.29	0.05	14	3.18	3.41	12
low	Buried	AUGUST	3.37	0.05	14	3.26	3.48	23
low	Surface	AUGUST	3.51	0.05	14	3.40	3.62	34
high	Surface	MAY	3.62	0.05	12	3.51	3.73	345
medium	Surface	MAY	3.67	0.05	12	3.56	3.79	45
medium	Buried	MAY	3.75	0.07	12	3.60	3.90	456
high	Buried	AUGUST	3.78	0.04	12	3.68	3.87	56
high	Surface	AUGUST	3.79	0.05	12	3.67	3.91	456
medium	Surface	AUGUST	3.80	0.05	12	3.69	3.91	56
medium	Buried	AUGUST	3.91	0.05	12	3.80	4.01	6

Table A.3.5. Results of linear mixed model for %C difference between sites and harvest dates. Plot was treated as the random effect.

	% Carbon			
		DF	F	P
Overall	Site	2,12	6.56	**0.01**
	Collection Date	1,196	9.73	**0.002**
	Bag Type	1,196	0.17	0.67
	Site x Collection Date	2,196	0.18	0.84
	Site x Bag Type	2,196	22.72	**<0.0001**
	Collection Date x Bag Type	1,196	7.13	**0.008**
	Site x Collection Date x Bag Type	2,196	7.92	**0.0005**
Surface Bags	Site	2,12	1.3	0.30
	Collection Date	1,95	14.2	**0.0003**
	Site x Collection Date	2,95	5.1	**0.008**
Buried Bags	Site	2,12	9.70	**0.003**
	Collection Date	1,89	8.16	**0.005**
	Site x Collection Date	2,89	6.01	**0.004**
May Collection	Site	2,12	4.22	**0.04**
	Bag Type	1,67	2.40	0.12
	Site x Bag Type	2,67	23.06	**<0.0001**
August Collection	Site	2,12	3.77	0.05
	Bag Type	1,117	1.47	0.22
	Site x Bag Type	2,117	10.32	**0.0001**

Table A.3.6 TukeyHSD pairwise comparison where ANOVA from Table A.3.5 were significant. The lsmeans and mlutcomp package in R were used for comparison. Significant differences between groups if group number is difference between a row.

site	BS	Month	lsmean	SE	df	lower.CI	upper.CI	.group
high	Buried	MAY	44.04	0.79	12	42.32	45.76	1
high	Buried	AUGUST	48.98	0.29	12	48.34	49.62	2
low	Surface	MAY	49.05	0.38	14	48.24	49.86	2
high	Surface	MAY	49.46	0.36	12	48.67	50.24	23
medium	Surface	AUGUST	49.50	0.36	12	48.71	50.28	2
medium	Surface	MAY	49.57	0.38	12	48.75	50.39	2
low	Surface	AUGUST	49.76	0.36	14	48.98	50.53	23
low	Buried	MAY	49.90	0.40	14	49.04	50.76	23
medium	Buried	MAY	50.04	0.52	12	48.90	51.19	23
low	Buried	AUGUST	50.09	0.37	14	49.29	50.89	23
high	Surface	AUGUST	50.13	0.39	12	49.29	50.97	23
medium	Buried	AUGUST	51.31	0.33	12	50.60	52.02	3

Table A.3.7. Results of linear mixed model for C:N difference between sites and harvest dates. Plot was treated as the random effect.

		DF	F	P
Overall	Site	2,12	60.46	**<0.0001**
	Collection Date	1,196	72.95	**<0.0001**
	Bag Type	1,196	23.37	**<0.0001**
	Site x Collection Date	2,196	4.19	**0.016**
	Site x Bag Type	2,196	12.77	**<0.0001**
	Collection Date x Bag Type	1,196	9.86	**0.002**
	Site x Collection Date x Bag Type	2,196	8.21	**0.0004**
Surface Bags	Site	2,12	64.42	**<0.0001**
	Collection Date	1,95	33.17	**<0.0001**
	Site x Collection Date	2,95	0.96	0.387
Buried Bags	Site	2,12	37.56	**<0.0001**
	Collection Date	1,89	33.12	**<0.0001**
	Site x Collection Date	2,89	5.87	**0.004**
May Collection	Site	2,12	102.2	**<0.0001**
	Bag Type	1,67	52.97	**<0.0001**
	Site x Bag Type	2,67	17.75	**<0.0001**
August Collection	Site	2,12	25.64	**<0.0001**
	Bag Type	1,117	1.54	0.22
	Site x Bag Type	2,117	5.94	**0.004**

Table A.3.8 TukeyHSD pairwise comparison where ANOVA from Table A.3.7 were significant. The lsmeans and mlutcomp package in R were used for comparison. Significant differences between groups if group number is difference between a row.

site	BS	Month	lsmean	SE	df	lower.CI	upper.CL	.group
high	Buried	AUGUST	12.96	0.15	12	12.63	13.29	1
medium	Surface	AUGUST	13.03	0.17	12	12.65	13.40	12
medium	Buried	AUGUST	13.14	0.16	12	12.78	13.49	12
high	Surface	AUGUST	13.24	0.18	12	12.84	13.64	123
medium	Buried	MAY	13.42	0.24	12	12.90	13.94	123
medium	Surface	MAY	13.51	0.18	12	13.12	13.90	123
high	Surface	MAY	13.70	0.17	12	13.32	14.08	23
low	Surface	AUGUST	14.18	0.17	14	13.81	14.55	34
low	Surface	MAY	14.90	0.18	14	14.51	15.28	5
low	Buried	AUGUST	14.91	0.18	14	14.52	15.29	5
high	Buried	MAY	15.36	0.35	12	14.60	16.13	456
low	Buried	MAY	16.23	0.19	14	15.82	16.63	6

Table A.3.9 Litter mass loss TukeyHSD pairwise comparison where ANOVAs were significant in Table 8. Significant differences between groups if group number are different between a row.

Overall Difference	Comparison	lsmean	SE	df	95% CI	Group
	Low Buried August	64.99	1.16	14	[62.51, 67.47]	1
	Medium Buried August	65.04	1.07	12	[62.69, 67.39]	12
	High Surface August	67.51	1.29	12	[64.69, 70.32]	123
	High Buried August	67.81	0.96	12	[65.73, 69.89]	123
	Low Surface August	71.12	1.26	14	[68.41, 73.82]	2345
	Medium Buried May	71.24	1.62	12	[67.69, 74.77]	1234 6
	Medium Surface August	72.26	1.26	12	[69.51, 75.00]	34 6
	Low Buried May	73.12	1.41	14	[70.11, 76.14]	34567
	High Buried May	73.19	2.81	12	[67.06, 79.31]	1234567
	High Surface May	74.71	1.26	12	[71.96, 77.45]	4567
	Low Surface May	76.92	1.26	14	[74.22, 79.62]	67
	Medium Surface May	78.17	1.26	12	[75.42, 80.91]	5 7
Surface	Low August	71.12	0.95	14	[69.99, 72.16]	1
	Medium August	72.26	0.95	12	[70.17, 74.34]	1
	High August	67.47	0.97	12	[65.35, 69.59]	2
	Low May	76.92	0.95	14	[74.87, 78.97]	3
	Medium May	78.16	0.95	12	[76.08, 80.25]	3
	High May	74.71	0.95	12	[72.63, 76.79]	23

Buried	Low August	64.97	1.49	14	[61.77, 68.17]	1
	Medium August	65.06	1.39	12	[62.02, 68.11]	1
	High August	67.77	1.25	12	[65.04, 70.50]	12
	Low May	73.15	2.07	14	[66.67, 75.69]	12
	Medium May	71.18	1.79	12	[69.31, 77.01]	2
	High May	73.56	3.57	12	[65.76,81.35]	12
May	Low Buried	73.05	1.48	14	[69.87, 76.24]	12
	Medium Buried	71.31	1.71	12	[67.57, 75.05]	1
	High Buried	73.13	2.97	12	[66.66, 79.60]	12
	Low Surface	76.92	1.32	14	[74.07, 79.77]	12
	Medium Surface	78.17	1.32	12	[75.27, 81.06]	12
	High Surface	74.71	1.32	12	]71.81, 77.60]	2
August	Low Buried	65.04	1.08	14	[62.72, 67.35]	1
	Medium Buried	65.01	1.00	12	[62.82, 67.18]	1
	High Buried	67.51	1.21	12	[65.89, 69.73]	12
	Low Surface	71.11	1.18	14	[68.57, 73.65	2
	Medium Surface	72.23	1.18	12	[69.67, 74.83]	2
	High Surface	67.82	0.88	12	[64.86, 70.15]	12

A.4. Soil nutrient ANOVA results

Table A.4.1. Results of a single factor ANOVA for site differences between Soil nutrient characteristics between sites. Each site had n=3 soil pits dug.

	Site Differences			
		DF (num, den)	F value	P value
Nitrogen	0-2.5	2,18	15.78	**<0.01**
	5-7.5	2,16	161.18	**<0.01**
	10-12.5	2,16	20.85	**<0.01**
	15-17.5	2,16	11.75	**<0.01**
	20-22.5	2,14	2.99	0.08
	25-27.5	2,15	7.51	**<0.01**
	30-32.5	2,14	9.15	**<0.01**
	40-42.5	2,9	3.61	0.07
Carbon	0-2.5	2,18	5.99	**0.01**
	5-7.5	2,16	114.0	**<0.01**
	10-12.5	2,16	38.52	**<0.01**
	15-17.5	2,16	12.72	**<0.01**
	20-22.5	2,14	28.94	0.12
	25-27.5	2,15	4.48	**0.03**
	30-32.5	2,14	1.28	0.31
	40-42.5	2,9	1.71	0.23
C:N	0-2.5	2,18	4.03	**0.03**
	5-7.5	2,16	1.42	0.27
	10-12.5	2,16	4.55	**0.03**
	15-17.5	2,16	43.3	0.35
	20-22.5	2,14	0.25	0.78
	25-27.5	2,15	0.37	0.70
	30-32.5	2,14	2.18	0.15

	40-42.5	2,9	2.12	0.17
Bulk Density	0-2.5	2,13	4.5	**0.03**
	5-7.5	2,13	2.93	0.08
	10-12.5	2,13	8.49	**<0.01**
	15-17.5	2,13	5.45	**0.01**
	20-22.5	2,13	2.87	0.09
	25-27.5	2,13	1.00	0.39
	30-32.5	2,11	0.14	0.86
	40-42.5	2,11	0.004	0.99
Soil Organic Carbon (kg m^{-2})	0-20	2,6	9.348	**0.0143**
	0-40	2,6	740.21	0.235
Soil Organic Nitrogen (kg m^{-2})	0-20	2,6	8.65	**0.017**
	0-40	2,6	3.81	0.283

Table A.4.2 Tukey HSD Pairwise comparisons for significant ANOVA (from linear mixed model) in Table A.4.1 Differences in Group number indicate significant difference between rows. The lsmeans and multcomp package in R were used to determine differences.

	Depth	Pair	95% CI	P value
Soil % Nitrogen	0-2.5	Low – Medium Low – High Medium - High	[0.42, 1.45] [0.45, 1.49] [-0.53,0.61]	**<0.0001** **0.0004** 0.985
	5-7.5	Low – Medium Low – High Medium - High	[-0.24, 0.32] [1.45, 2.03] [1.42, 1.99]	0.932 **<0.0001** **<0.0001**
	10-12.5	Low – Medium Low – High Medium - High	[-0.757, 0.804] [0.96, 2.52] [0.91, 2.53]	0.9967 **<0.0001** **<0.0001**
	15-17.5	Low – Medium Low – High Medium - High	[-0.89, 1.02] [0.67, 2.57] [0.56, 2.54]	0.981 **0.001** **0.002**
	20-22.5	Low – Medium Low – High Medium - High	[-0.03, 0.37] [-0.07, 0.38] [-0.25, 0.21]	0.09 0.21 0.096
	25-27.5	Low – Medium Low – High Medium - High	[0.01, 0.07] [-0.03, 0.04] [-0.07, -0.001]	**0.0053** 0.895 **0.0413**
	30-32.5	Low – Medium Low – High Medium - High	[0.007, 0.06] [-0.045, 0.011] [-0.085, -0.019]	**0.0143** 0.273 **0.0026**
	40-42.5	Low – Medium Low – High Medium - High	[-0.011, 0.072] [-0.045, 0.022] [-0.087, 0.002]	0.152 0.608 0.059
Soil % Carbon	0-2.5	Low – Medium Low – High Medium - High	[-0.21, 29.82] [3.73, 33.76] [-12.51, 20.38]	0.053 **0.013** 0.816
	5-7.5	Low – Medium Low – High Medium - High	[[-6.43, 6.12] [26.24, 38.79] [26.16, 39.18]	0.997 **<0.0001** **<0.0001**

	10-12.5	Low – Medium Low – High Medium - High	[-9.88, 9.16] [19.04, 38.09] [19.05, 38.82]	0.994 **<0.0001** **<0.0001**
	15-17.5	Low – Medium Low – High Medium - High	[-13.82, 15.70] [11.26, 40.78] [9.76, 40.39]	0.986 **0.0009** **0.0017**
	20-22.5	Low – Medium Low – High Medium - High	[-1.02, 8.94] [-2.24, 8.98] [-6.34, 5.19]	0.130 0.289 0.962
	25-27.5	Low – Medium Low – High Medium - High	[0.08, 1.25] [-0.53, 0.80] [-1.23, 0.17]	**0.026** 0.86 0.16
	30-32.5	Low – Medium Low – High Medium - High	[-0.35, 1.06] [-0.83, 0.58] [-1.31, 0.35]	0.41 0.89 0.31
	40-42.5	Low – Medium Low – High Medium - High	[-0.14, 0.59] [-0.29, 0.29] [-0.61, 0.16]	0.24 0.99 0.27
Soil C:N	0-2.5	Low – Medium Low – High Medium - High	[-9.19, -0.22] [-7.91, 1.07] [-3.62, 6.20]	**0.039** 0.155 0.784
	5-7.5	Low – Medium Low – High Medium - High	[-17.35, 3.63] [-13.61, 7.38] [-7.13, 14.64]	0.24 0.73 0.65
	10-12.5	Low – Medium Low – High Medium - High	[-14.16, -0.89] [-8.44, 4.84] [-1.16, 12.61]	**0.025** 0.77 0.11
	15-17.5	Low – Medium Low – High Medium - High	[-14.10, 3.82] [-10.82, 7.10] [-6.01, 12.58]	0.33 0.86 0.64
	20-22.5	Low – Medium Low – High Medium - High	[-10.33, 6.66] [-9.03, 10.11] [-7.48, 12.23]	0.84 0.98 0.805
	25-27.5	Low – Medium Low – High Medium - High	[-10.64, 5.37] [-10.33, 7.82] [-8.19, 10.95]	0.67 0.93 0.92

	30-32.5	Low – Medium Low – High Medium - High	[-13.24, 6.07] [-4.27, 15.03] [-2.39, 20.32]	0.61 0.34 0.13
	40-42.5	Low – Medium Low – High Medium - High	[-73.9, 46.61] [-19.31, 75.97] [-21.04, 105.89]	0.81 0.27 0.21
Bulk Density	0-2.5	Low – Medium Low – High Medium - High	[-0.28, 0.04] [-0.35, -0.02] [-0.23, 0.09]	0.16 **0.027** 0.50
	5-7.5	Low – Medium Low – High Medium - High	[[-1.14, 0.31] [-1.53, 0.08] [-1.12, 0.50]	0.31 0.08 0.59
	10-12.5	Low – Medium Low – High Medium - High	[-0.56, 0.53] [-1.30, -0.21] [-1.28, -0.19]	0.9972 **0.0069** **0.0079**
	15-17.5	Low – Medium Low – High Medium - High	[-0.74, 0.16] [-1.03, -0.12] [-0.74, 0.16]	0.356 **0.01** 0.255
	20-22.5	Low – Medium Low – High Medium - High	[-0.70, 0.19] [-0.94, 0.06] [-0.69, 0.31]	0.318 0.084 0.594
	25-27.5	Low – Medium Low – High Medium - High	[-0.447, 0.138] [-0.435, 0.219] [-0.280, 0.374]	0.37 0.669 0.92
	30-32.5	Low – Medium Low – High Medium - High	[-0.53, 0.36] [-0.46, 0.43] [-0.42, 0.56]	0.86 0.99 0.91
	40-42.5	Low – Medium Low – High Medium - High	[-0.435, 0.424] [-0.444, 0.415] [-0.479, 0.461]	0.999 0.996 0.998
Soil Organic Carbon	0-20cm	Low – Medium Low – High Medium - High	[-9.67, 9.29] [1.20, 20.97] [2.19, 21.16]	0.997 **0.023** **0.022**
	0- 40cm	Low – Medium Low – High Medium - High	[-65.90, 70.42] [-29.95, 106.36] [-32.21, 104.11]	0.99 0.27 0.31

Soil Organic Nitrogen	0-20cm	Low – Medium Low – High Medium - High	[-0.51, 0.70] [0.15, 1.35] [0.05, 1.26]	0.875 **0.020** **0.035**
	0- 40cm	Low – Medium Low – High Medium - High	[-4.64, 5.13] [-2.33, 7.45] [-2.57, 7.20]	0.99 0.31 0.37

Table A.4.3. Results from mixed linear models for bulk nutrient differences (measured by PRS probes) that treated plot as the random effect.

		DF	F	P
P	SITE	2,12	0.81	0.46
	TIME	1,12	4.60	0.05
	SITE X TIME	2,12	0.53	0.60
NH4	SITE	2,12	0.47	0.64
	TIME	1,12	0.29	0.59
	SITE X TIME	2,12	2.60	0.12
Total N	SITE	2,12	0.55	0.59
	TIME	1,12	0.47	0.51
	SITE X TIME	2,12	2.95	0.09
S	SITE	2,12	0.25	0.78
	TIME	1,12	43.7	**<0.001**
	SITE X TIME	2,12	3.08	0.08
Mn	SITE	2,12	0.28	0.76
	TIME	1,12	2.87	0.12
	SITE X TIME	2,12	6.11	**0.01**
Fe	SITE	2,12	0.37	0.69
	TIME	1,12	4.72	0.05
	SITE X TIME	2,12	2.67	0.11
Ca	SITE	2,12	0.93	0.42
	TIME	1,12	0.12	0.74
	SITE X TIME	2,12	3.4	0.07
Mg	SITE	2,12	0.57	0.58
	TIME	1,12	0.15	0.71
	SITE X TIME	2,12	3.42	0.07
K	SITE	2,12	0.44	0.65

	TIME	1,12	11.5	**0.005**
	SITE X TIME	2,12	2.62	0.11

Table A.4.4. Tukey HSD pairwise comparison where ANOVA were significant in Table A.4.3. The lsmeans and multcomp package were used. Differences in Group number indicate significant difference between a row.

Nutrient	Test	Test	lsmean	SE	DF	95% CI	Group
Phosphorous	Spring	Low Medium High	4.86 2.00 3.50	0.62 0.62 0.62	14 12 12	[3.54, 6.18] [0.655, 3.344] [2.155, 4.844]	1 12 2
Sulfur	Time	Spring Low Spring Med Spring High Summer Low Summer Med Summer Hig	3.96 6.54 2.96 11.0 9.60 11.6	1.15 1.15 1.15 1.15 1.15 1.15	14 12 12 12 12 12	[1.47, 6.44] [4.01, 9.06] [0.44, 5.48] [8.47, 13.52] [7.07,12.12] [9.07, 14.12]	1 12 1 2 2 2
	Spring	Low Medium High	3.96 6.54 2.96	0.93 0.93 0.93	14 12 12	[1.95, 5.96] [4.50, 8.57] [0.92, 4.99]	12 1 2
Calcium	Summer	Low Medium High	304.0 137.2 187.4	43.5 43.5 43.5	14 12 12	[210.6, 397.4] [42.3, 232.1] [92.5, 282.3]	1 2 12

A.5. Linear mixed model and ANOVA results from laboratory mass loss and leaching studies

Table A.5.1. Linear mixed model results from laboratory leaching experiment testing differences between temperature treatments and time where cup was treated as the random effect.

DOC and SUVA Analyses				
		DF	F	P
Total N	TEMP	2,9	0.85	0.46
	DAY	1,117	2.73	0.10
	TEM x DAY	2,117	4.6	**0.01**
DOC	TEMP	2,9	0.17	0.85
	DAY	1,117	30.34	**<0.0001**
	TEM x DAY	2,117	0.17	0.85
$SUVA_{254}$	TEMP	2,9	0.71	0.52
	DAY	1,117	8.2	**0.005**
	TEM x DAY	2,117	1.2	0.30
$a_{365/250}$	TEMP	2,9	6.2	**0.02**
	DAY	1,117	155.1	**<0.0001**
	TEM x DAY	2,117	7.6	**0.0008**
Mass loss	TEMP	2,9	64.08	**<0.0001**

Table A.5.2 Tukey HSD pairwise comparison where ANOVA were significant in Table A.5.1. The lsmeans and multcomp package were used. Differences in Group number indicate significant difference between a row.

Test		lsmean	SE	DF	95% CI	Group
SUVA	T2 T5 T20	4.97 4.27 4.57	0.41 0.41 0.41	11 9 9	[3.64, 5.51] [3.34, 5.21] [3.64, 5.51]	1 1 1
TN	T2 T5 T20	0.43 0.48 0.43	0.03 0.03 0.03	11 9 9	[0.36, 0.50] [0.41, 0.55] [0.36, 0.50]	1 1 1
Suva 250/365 ratio	T2 T5 T20	2.81 2.94 4.26	0.32 0.32 0.32	11 9 9	[2.09, 3.52] [2.21, 3.67] [3.53, 4.99]	1 1 2

Table A.5.3 Tukey HSD for significant ANOVA result for litter mass loss in Table A.5.1

	Comparison	95% CI	P value
Lab loss	T20- T2 T5 – T2 T5 – T20	[-7.89, 13.49] [-0.49, 5.05] [-11.16, -5.62]	**<0.0001** 0.107 **<0.0001**

Table A.5.4. Single factor ANOVA result for laboratory mass loss experiment. No repeat sampling of cups occurred, therefore no random effect.

	DF	F	P
Day	1,28	5.100	**0.0319**
Temperature	1,28	0.4573	0.5044
Day X Temperature	1,28	0.0969	0.7579

Table A.5.5 Tukey HSD for significant ANOVA results from Table A.5.4

	Day	Comparison	95% CI	P
Lab loss	Day 2	Twenty-five	[-9.51, 12.62]	0.61
	Day 7	Twenty-five	[-25.84, 23.64]	0.866
	Day 14	Twenty-five	[-11.60, -0.16]	**0.047**
	Day 21	Twenty-five	[-6.63, -1.97]	**0.015**
	Day 30	Twenty-five	[-24.05, 15.25]	0.437

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