# HOW HERBIVORES AFFECT PLANT GROWTH, COMMUNITY STRUCTURE AND LITTER DECOMPOSITION IN ALASKAN TUNDRA: IMPLICATIONS FOR RESPONSES TO CLIMATE CHANGE

by

DAVID R. JOHNSON

Presented to the Faculty of the Graduate School of
The University of Texas at Arlington in Partial Fulfillment
of the Requirements
for the Degree of

DOCTOR OF PHILOSOPHY

UNIVERSITY OF TEXAS AT ARLINGTON
AUGUST 2008

# ACKNOWLEDGEMENTS

First and foremost, I am extremely grateful for my major professor, Laura Gough, for guiding me through this work. It has truly been a great privilege to have the opportunity to work with her. I am also grateful for our co-PI John Moore for the opportunity to work on this project. Thanks also to my committee members Howard Arnott, Daniel Formanowicz, James Grover, and Ellen Pritham. I am also thankful for Thomas Chrzanowski for much help obtaining and interpreting CHN data, as well as many thought provoking science discussions.

I am very grateful for the establishment and maintenance of the Arctic LTER study plots by Gus Shaver, Jim Laundre, and the many fence builders in 1996. Jim Laundre was also very helpful in providing and interpreting climate data. Thanks also to the many LTER scientists and staff at Toolik for providing a great atmosphere of scientific discovery. In particular, Donie Bret-Harte and Peter Ray were very helpful in identifying plant species. Sarah Hobbie was helpful in designing litterbags, and George Batzli provided advice regarding small mammal trapping. In the field, Elizabeth Ramsey, Brian Moon, Kanchan Shrestha, and Jef Knight were very valuable assistants, and thanks to Theo Varnes and Karl Wyant for collecting litterbags when I was away from Toolik. Statistical advice was provided by D. L. Hawkins, Nathan Dong, and Richard Ferim of the Statistics Lab, Department of Mathematics, UT Arlington. Cymbre Weatherly, Abby Stubbs, Rima Lucardi, and Christi Hull were helpful at entering and proofreading data. I am also grateful for the support of great current and former labmates, many of whom read copies of various chapters, including: Marnie Rout, Amie Treuer, Matt Watson, Carol Moulton and Sherri van der Wege.

I am greatly indebted to my wife and love of my life, Jennifer Davis. She has offered constant encouragement, been a great proofreader, and an overall wonderful support while doing this work. I am also thankful for my mother-in-law, Dee Covici, as well as my parents, Robert and Karin Johnson, and siblings for their continual support.

The Arctic LTER has been maintained through multiple grants from the National Science Foundation to the Marine Biological Laboratory. Logistic support was provided by Toolik Field Station (Univ. of Alaska Fairbanks). This work was supported by NSF grants OPP-0137832 and OPP-0435827 to Laura Gough.

May 9, 2008

# ABSTRACT

# HOW HERBIVORES AFFECT PLANT GROWTH, COMMUNITY STRUCTURE AND LITTER DECOMPOSITION IN ALASKAN TUNDRA: IMPLICATIONS FOR RESPONSES TO CLIMATE CHANGE

David R. Johnson, Ph.D.

University of Texas at Arlington

Supervising Professor: Laura Gough

Increasing atmospheric carbon dioxide ($CO_2$) concentrations have caused higher air temperatures in the Arctic. Because arctic organisms are temperature limited, warmer conditions lead to higher decomposition and nutrient cycling rates by soil microorganisms resulting in positive feedbacks; more $CO_2$ is released from warmer soils thus increasing global atmospheric $CO_2$ concentrations. Higher decomposition and nutrient cycling rates increase soil nutrient availability for plants resulting in increased net primary productivity (NPP) and shifts in community structure. If these “warmer” communities contain more woody shrubs, they may store more carbon in plant tissue, potentially offsetting increases in $CO_2$ from decomposition. However, little is known about how higher trophic levels affect plants under these conditions. I studied how mammalian herbivores affect individual plant growth, community structure and decomposition in two common arctic plant communities in northern Alaska that experienced ten years of experimental fertilization and herbivore exclosures in a factorial design. While fertilization increased growth of individual plants, increased community NPP and shifted species composition, the effects of herbivores were different in each community. In moist acidic tussock (MAT) tundra, long-term fertilization and herbivory decreased the growth of individual graminoids and increased deciduous shrub growth. Indeed, the graminoid *Eriophorum vaginatum* in MAT was not tolerant of herbivory regardless of fertilization. In contrast, graminoid growth in dry heath tundra (DH) increased with fertilization and was not affected by herbivores, while herbivores suppressed increases from fertilization in deciduous shrub growth. The DH graminoid *Hierochloe alpina* growing with fertilization was tolerant of and not strongly affected by herbivores. Additionally, I found evidence that the effects of fertilization and herbivores on individual growth scaled up to affect community structure in both communities. With higher soil nutrients and herbivore exposure in MAT, deciduous shrub abundance increased and graminoids decreased, while at DH the opposite was true. Lastly, I found no difference in *E. vaginatum* and *H. alpina* leaf decomposition due to herbivore processing with only minor changes attributed to fertilization. These results show that herbivores may play an important role in shaping plant responses to warmer temperatures in arctic ecosystems ultimately effecting feedbacks to the global carbon cycle.

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# CHAPTER 1

# PLANTS, HERBIVORES AND ECOSYSTEMS IN A WARMER ARCTIC

## 1.1 Climate Change and the Arctic

Increases in global temperatures have been causally linked to increases in atmospheric greenhouse gas concentrations, in particular to increasing levels of carbon dioxide ($CO_2$; I.P.C.C., 2007). Because the increase of $CO_2$ is forecast to continue into the indefinite future, global temperatures are also expected to continue to rise (McCarty 2001). Individual species and communities within ecosystems may in turn respond to both increased temperatures and $CO_2$ (Vitousek, 1994). These responses often vary widely with respect to specific ecosystems (Woodwell et al. 1978; Shaver et al., 2000) because of spatial heterogeneity of both energy and resource availability (Gates, 1965; Hairston and Hairston, 1993). Though patterns and generalizations have been difficult for ecologists to elucidate, understanding and predicting how ecosystems will respond to warmer temperatures is of prime importance because of the significant role ecosystem processes play in the global carbon cycle (Shaver et al. 1992; Vitousek, 1994). Primarily through photosynthesis and decomposition, ecosystem processes move significant amounts of $CO_2$ between the atmosphere and the living and dead biota within ecosystems (Post et al. 1982; Schimel, 1995; Schimel et al. 2000; Shaver et al. 2000). Thus ecosystems may be either a net source or sink of $CO_2$ depending on the specific rates of these processes.

Evidenced by a wide variety of data, temperatures in the Arctic are increasing at a rate faster than other, more temperate ecosystems (Serreze et al. 2000; Alley et al. 2003). Both atmospheric and surface temperature measurements in the region have been increasing by about 2 °C per decade since 1970 (Serreze et al. 2000), and Overpeck et al. (1997) suggest the current Arctic is the warmest in 400 years. Higher temperatures have been observed concurrent with other environmental phenomenon including reduced sea-ice (Overpeck et al. 2005), higher runoff in rivers emptying into the Arctic Ocean (Prouse et al. 2006), and increased glacial and permafrost melting (Lachenbruch and Marshall, 1986; Osterkamp et al. 2000; Prouse et al. 2006). Also associated with increased temperatures, the Arctic has experienced a shift in vegetation cover, where shrub expansion northward has occurred in the Scandinavian, Russian and North American Arctic (Sturm et al. 2002; Tape et al. 2006), suggesting changes in ecosystem processes with continued warming (Hinzman et al. 2005). Because of these observations, the Arctic is seen as a key region in understanding how increased temperatures will affect the global carbon cycle (ACIA, 2004).

Arctic ecosystems are characterized by a number of abiotic factors, such as low temperatures, short growing seasons and the presence of permafrost, which limit the growth of organisms (Bliss, 1956; Billings and Mooney, 1968). Due to these limiting factors, plant communities within terrestrial arctic ecosystems generally have low diversity and net primary productivity (NPP) in comparison with more temperate ecosystems (Bliss, 1962; Bliss and Matveyeva, 1992). The composition of species in these plant communities is often characterized by low-growing evergreen and deciduous shrubs, a variety of often clonal graminoids, perennial forbs, mosses and lichens (Billings and Mooney, 1968; Walker et al. 1994). Arctic plant species are considered nutrient limited because the decomposition rates of organic matter are also limited by temperature in the Arctic (Schimel et al. 1997; Hobbie et al. 2002). Because overall decomposition rates are low, the mineralization of both carbon (C) and nitrogen (N) has historically been slower than the net accumulation of these elements. Thus, the Arctic has been considered a net C sink relative to more temperate ecosystems (Shaver et al. 2000; Mack et al. 2004). Indeed, arctic and boreal ecosystems together are estimated to contain up to one-third of the global pool of C tied up in organic matter (Oechel and Billings, 1992; Callaghan et al. 2004; Shaver et al. 2006).

Higher arctic temperatures can alter the abiotic conditions important for ecosystem processes (Hinzman, et al. 2005). For example, warmer temperatures have been shown to increase the number of snow-free days per year, soil temperature, and depth to permafrost

(Osterkamp et al. 2000; Sturm et al. 2001, Stone et al. 2002). These factors all increase temperature dependent soil decomposition and nutrient cycling rates (Nadlehoffer et al. 1991; Schimel et al. 1996), which may result in increased $CO_2$ entering the atmosphere from arctic ecosystems (Shaver et al. 2006). Additionally, increased decomposition and nutrient cycling rates increase the availability of soil nutrients, particularly N, to plants (Nadelhoffer et al., 1992). Because arctic plant communities are considered nutrient limited, plants respond to elevated soil nutrients by increasing growth leading to higher ecosystem NPP (Chapin et al. 1996) often with an associated shift in community composition (van Wijk et al. 2003; Walker et al. 2006). However, the magnitudes of these responses vary because of both underlying differences in other abiotic factors (e.g. precipitation; Bliss, 1971) and plant species-specific traits governing ecosystem processes that differ among specific ecosystems (Shaver, 1995). While some plant growth forms have been shown to have generalized responses to increased soil nutrients (e.g. higher NPP of graminoids and deciduous shrubs, van Wilk et al. 2003), species living close geographically but in different communities often differ in response to increased soil nutrients (e.g., Gough et al. 2007). Because plant growth forms differ in response to higher nutrients (Chapin et al. 1996), the overall extent to which increases in arctic ecosystem NPP will function to remove $CO_2$ from the atmosphere is unknown. Thus to predict how the net $CO_2$ flux in the Arctic affects future global carbon balance, it is important to understand how higher amounts of $CO_2$ fixed by plants through photosynthesis, because of increased soil nutrients and higher NPP, offset higher amounts of $CO_2$ released to the atmosphere through decomposition (Shaver et al. 1992).

Ecologists are becoming increasingly aware that to understand the relative importance of both productivity and decomposition in a warmer Arctic, terrestrial food webs and higher trophic levels must be considered (Ims and Fuglei, 2005) as these have been shown to change as well (e.g. Forchhammer et al. 2005). For the remainder of this chapter, I will review current understanding of arctic trophic structure and the theoretical relationship between trophic structure and gradients of NPP. I will pay specific attention to herbivores and plant-herbivore interactions, as well as experimental studies conducted in an effort to understand how plants, communities and ecosystem processes are expected to change in a warmer Arctic. This chapter will conclude with a discussion of how elucidation of plant-herbivore interactions in arctic ecosystems will increase our understanding of how the Arctic will respond to warmer temperatures and the role the Arctic will play in the future global carbon cycle.

## 1.2 Trophic structures in exploitation ecosystems

Food web ecology involves characterizing the movement of matter and energy cycling through organisms and ultimately ecosystems (Gates, 1965). The evolutionary and life history strategies of organisms often explain the relative importance of different trophic components (Pimm, 1980), as well as feedbacks and linkages among trophic components of ecosystems (Paine, 1980). While theoretical and empirical understanding of food webs has advanced (Odum, 1969; May, 1973), applying this understanding to specific ecosystems has been difficult because of increased complexity that arises when considering different interactions governing food web topology in often dynamic unstable ecosystems (de Ruiter et al. 2005; Fox, 2006). Species identity and resource availability often vary among ecosystems (Chase et al. 2000), thus affecting the relative strength of one trophic level on another (Borer et al. 2005). However, some general patterns have emerged.

Hairston et al. (1960) proposed that ‘the world is green’ because the effect of herbivores on plants is controlled by the presence of carnivores, thus plants are able to grow limited only by light energy, water and nutrients. These food webs are thought to be governed top-down, as higher trophic levels have a disproportionate affect on immediately lower levels. The natural or experimental removal or addition of carnivores can have cascading effects on plant communities because of changes in herbivore abundance or behavior (e.g. Schmitz et al. 2000; Breyer et al. 2007). Overall, the interactions among trophic levels, though, are more complex because of positive feedbacks that often exist between adjacent trophic levels. For example, by returning nutrients and organic matter to soils through urination and defecation, herbivores increase decomposition of plant matter often increasing rates of nutrient and energy flow in ecosystems (Pastor and Cohen, 1997). Others propose that defense strategies, primarily for plants, circumvent relationships among trophic levels. Herbivore biomass is directly related to lack of sufficient forage in low NPP systems often because of high amounts of secondary metabolites in plant tissue (Strong, 1992). Indeed, plants in arctic ecosystems with low NPP often contain phenolic and tannin compounds in leaves (Haapasaari, 1988; Graglia et al. 1999), though concentrations are lower than in tropical plants. These food webs are thought to be governed bottom-up by environmental resource availability and resource allocation by plants (Polis and Strong, 1996), rather than top-down. However, there is much heterogeneity in trophic complexity among ecosystems because of differences in both resources and energy availability as well as differences in the identity of ecosystem biota (Chase et al. 2000). Thus, it appears that for most ecosystems the relative importance of top-down or bottom-up effects in terrestrial food webs vary, and for specific ecosystems both effects may be simultaneously important (Powers, 1992).

The Arctic has a long tradition of study in the theoretical development of food webs in terrestrial ecosystems. Early work by Summerhayes and Elton (1925) in the High Arctic produced one of the first holistic descriptions of the interactions among plants, herbivores and carnivores in a terrestrial ecosystem. While the work has since been shown to be overly simplistic (Hodkinson and Coulson, 2004), Summerhayes and Elton provided one of the first conceptual models of the movement of N through ecosystems. More recent work in the Arctic has been an attempt to explain observations of trophic structure in low NPP ecosystems with both top-down and bottom-up effects and has resulted in the hypothesis of exploitation ecosystem hypothesis (EEH; Oksanen et al. 1980). EEH describes patterns among trophic levels along gradients of NPP. At low NPP, herbivores are absent because there is insufficient plant biomass to support herbivore populations. As NPP increases along the gradient, a threshold is reached where NPP is high enough to support herbivores, and herbivores visit top-down effects upon plants. Herbivore biomass and their top-down effects on plants intensify as NPP further increases until another threshold is reached. Here herbivore biomass is high enough to support a secondary consumer (carnivore), thus imposing a constraint on herbivores and a subsequent relaxation of top-down effects of herbivores cascading to plants. Thus both direct effects between adjacent trophic levels and cascading effects arise along the NPP gradient, and top-down and bottom-up dynamics alternate in importance also with changes in NPP. The EEH appears to work well to describe patterns of plant and animal biomass patterns in low productivity ecosystems, such as those in the Arctic (Oksanen, 1983; Moan and Oksanen, 1993, Oksanen and Oksanen, 2000). Indeed, spatial patterns of NPP have been shown to govern patterns in herbivore impacts on plants in an arctic ecosystem (Aunapuu et al. 2008). How well the EEH can be applied to more temperate ecosystems remains to be seen, as explicit tests of EEH have not been conducted in more temperate ecosystems with much higher NPP (Oksanen and Oksanen, 2000). Regardless, theoretical understanding of low NPP food webs garnered from EEH provides a framework for understanding how arctic food webs will respond to increased NPP arising via increased temperatures and climate change. Because in many arctic ecosystems carnivores are often only transient, the interactions between plants and herbivores are considered the primary descriptors of food webs (Lindeman, 1942; Oksanen et al. 1996; Bardgett et al. 1998; Oksanen and Oksanen, 2000; Moore et al. 2004). Understanding how herbivores respond to increased NPP, and how understanding the strength of their interactions with plants in a warmer arctic, will be important in predicting future plant populations and community composition governing ecosystem photosynthesis. Thus, vertebrate herbivores in particular are an important consideration for predicting the degree to which arctic plants will function as C sinks in future global carbon cycling (Ims and Fuglei, 2005).

### 1.3 Herbivores and plant-herbivore interactions: examples from the Arctic

Herbivores of a wide variety can have strong effects on plant populations, plant communities and ecosystems (Huntly, 1991). Through the removal of biomass, herbivores directly affect the growth of individual plants. Depending on the severity of herbivory and tissue consumed, plants may respond to biomass removal by herbivores by increasing growth, called compensatory growth or tolerance (McNaughton et al. 1983). Tolerance often varies according to life history traits and resource availability (Wise and Abrahamson, 2002, 2007). Plant species with high growth rates and basal meristems, such as graminoids, often tolerate biomass removal better than species with lower growth rates (Strauss and Agrawal, 1999). Variation in tolerance within plant species is often governed by resource availability (Leriche et al. 2001). Plants with higher resources are generally able to withstand herbivory better than those with lower resources. Additionally, some plants respond to herbivory by increasing the production of secondary compounds in leaves as defense against herbivory (Rosenthal and Janzen, 1979). While this is an inherent trade-off, using energy and C and N for defense rather than growth and reproduction, the overall result may be increased fitness for plants with higher secondary compounds than those with lower amounts (Karban and Meyers, 1989). Because of these responses and others, herbivory has the potential to affect many aspects of plant metabolism and performance (Crawley, 1983). However, it has been difficult to use these responses and scale up and make predictions at higher levels of organization, such as communities and ecosystems (Crawley, 1983; 1987).

Because many herbivores selectively forage, some herbivores can modify the genetic structure of plant populations by choosing certain genets and removing biomass of preferred plant species (Crawley, 1983). Additionally, non-preferred plant biomass in close proximity to preferred forage may be removed in communities resulting in apparent competition (Holt, 1977, Holt and Kotler, 1987). Also via selective foraging, herbivores may shape plant community composition by removing biomass of preferred plant species (de Mazancourt and Loreau, 2000, Cingolani et al. 2005), thus altering competition for shared resources among plant species within communities. Changes in species composition often lead to changes in structural properties of ecosystems such as diversity (e.g. Rambo and Faeth, 1999; Manier and Hobbs, 2007), which vary among ecosystems according to NPP and herbivore size (Bakker et al. 2006). In some ecosystems, such as grasslands, herbivores typically increase plant community diversity (Olff and Ritchie, 1998), or have no effect (Huntly, 1991). Effects on diversity are often dynamic both temporally and spatially (Huntly, 1991) and often can be directly related to differences in NPP (e.g. Gough and Grace, 1998). While there are cases where herbivores function to decrease ecosystem NPP by removing plant biomass (Olff and Richie, 1998), they may effectively increase ecosystem NPP through feedbacks including increases in nutrient cycling (McNaughton et al. 1989; de Mazancourt and Loreau, 2000). Primarily through defecation and urination, herbivores may increase the decomposition rates of plants (McNaughton et al. 1989) and also function to spatially redistribute nutrients within and among communities (e.g Sirotnak and Huntly, 2000). In heavily grazed ecosystems, herbivores can have pronounced effects on plant communities, which can be positive, negative or both (McNaughton et al. 1989).

Much work and synthesis is needed however, to fully understand the role herbivores will have on arctic plants in the future. Thus, after first discussing arctic herbivores, in the remainder of this section I will review our current understanding of plant responses to herbivory in arctic ecosystems.

### *1.3.1. Arctic Herbivores*

Arctic ecosystems support a number of both large and small vertebrate (Batzli et al. 1980) as well as insect herbivores (MacLean and Jensen, 1985). While vertebrate arctic herbivores are considered generalists with respect to the plants they prefer to eat (Batzli et al. 1980), there is ample evidence of selective herbivory among plant growth forms (Batzli and Lesieutre, 1991, 1995; Post and Klein, 1996). Herbivores tend to prefer plant species with low C to N ratios and low secondary compounds. The abundance of plant species with these traits is often spatially and temporally heterogeneous in arctic landscapes, and often herbivore abundances vary both spatially and temporally as well (reviewed by Mulder, 1999). For example, some small mammals, such as voles and lemmings (or microtine rodents: *Lemmus* spp., *Dicrostonyx* spp., *Microtus* spp., *Clethrionomys* spp.), are local residents of various arctic plant communities year-round and do not hibernate. Alternatively, other small mammals, such as arctic ground squirrels, also are year-round residents but hibernate and are only active during the summer (Buck and Barnes, 1999). Additionally, microtine rodent populations are well known to experience wide fluctuations in locations through time. In a classic work using a twenty year dataset, Pitelka (1973) showed that populations of lemmings near Barrow, Alaska had wide inter-annual fluctuations in population sizes governed by timing of stochastic events, such as timing of snowmelts with life history events. Additionally, populations of arctic microtine rodents have been shown to cycle in a delayed density dependent manner possibly due to temporal variation in the quality and quantity of forage (Hornfeldt, 1994). However, the theoretical understanding of these population cycles has been difficult to reconcile with observational data. Population cycles can vary locally among different habitats (Oksanen et al. 1999), and between species of microtines (Oksanen and Oksanen, 1992). Indeed, populations of microtines in arctic tundra often explode and then crash, appearing much more chaotic than cyclic. The current view is that differences in cycles seem to be regulated by the abundance of carnivores, particularly mustelids (Oksanen and Oksanen, 1981; Oksanen, 1990; Hanski et al. 1993), however inherent differences in both NPP and forage quality appear to be important predictors of herbivore abundance (Batzli et al. 1980; Oksanen et al. 1999; Hamback et al. 2002).

Large mammalian herbivores that utilize arctic habitats include both caribou (*Rangifer tarandus*, called reindeer in Eurasia) and muskoxen (*Ovibus moschatus*; Forchhammer et al. 2002). These animals, particularly caribou, are often very transitory in many arctic ecosystems, with abundance and density of animals dependent on migration and annual reproductive cycles (Batzli et al. 1980). Often caribou populations vary according to availability of suitable habitat consisting of digestible forage (White et al. 1975). Predatory carnivores may also influence behavior of caribou; animals in predator-free environments may maximize intake of energy from plants (Loe et al. 2007). Ultimately, the population patterns of large mammals, and small mammals discussed above, suggest a relationship to NPP in support of EEH.

Before discussing the effects of these herbivores on arctic plants, one additional group warrants mention. There is a large body of work on the importance of birds, particularly *Branta* spp., in coastal salt marshes in the Arctic (Bazely and Jefferies, 1986; 1989). Snow geese are migratory visitors to these systems, though they often congregate in large numbers during arctic summers, which can have great impacts on composition, NPP and nutrient cycling in arctic salt marsh communities (e.g., Cargill and Jefferies, 1984).

### *1.3.2. Herbivory and plant-animal interactions in arctic ecosystems*

Historically, herbivores have not been thought to be as important to plants as other factors in the Arctic primarily because NPP is low relative to more temperate ecosystems (Jefferies et al. 1994). Arctic plants face harsh abiotic conditions as well as often low soil nutrient availability (Billings and Mooney, 1968), resulting in communities with low NPP that support few herbivores. However, herbivores have been shown to affect growth of individual plants, plant populations and communities as well as ecosystem processes in many arctic tundra ecosystems (reviewed by Mulder, 1999). These effects may be extreme (e.g. snow geese in salt marshes, Jefferies, 1988, Ngai and Jefferies, 2004; Abraham et al. 2005), but often are more subtle (e.g. Grellman, 2002). Variation in plant responses to herbivory often seems to be determined by local climate as well as soil resource availability, which may constrain NPP (Eskilenin, 2008). Thus responses of individual plants, and the scaling up of these to populations, communities and ecosystems, may be controlled ultimately by NPP as predicted by EEH (Oksanen and Oksanen, 2002).

Arctic plant species can have a wide variety of responses to herbivory, such as tolerance or the induced production of secondary metabolites, often differing among growth form (Archer and Tieszen, 1980; Chapin, 1980). While there is limited knowledge of tolerance for arctic plants in general, there is some evidence of herbivore tolerance in some graminoid species (Archer and Tieszen 1983; Wegener and Odasz, 1997; Brathen and Odasz-Albrigtsen, 2000). For example, graminoids often respond to above ground biomass removal by altering nutrient allocation among tissue types, such that aboveground biomass may seem unaffected by biomass removal (Chapin, 1980). A number of graminoids shift nutrient allocation to leaf growth from roots following defoliation and increasing nutrient absorption and respiration in root tissue (Chapin et al. 1986). These effects often vary seasonally (Chapin et al. 1980), thus the timing of herbivory is important for different plant species (e.g. Hamback et al. 2002). While responses in other growth forms are less well characterized, deciduous shrubs recover more rapidly from biomass removal than evergreen shrubs, perhaps due to large below ground reserves and higher leaf turnover rates (Mulder, 1999). However, the trade-off between growth and higher levels of secondary compounds may explain reduced tolerance in evergreen shrubs (Shevtsova et al. 2005). While these generalizations often can be applied to species within plant communities, there is some evidence of variation in tolerance for plant species within growth form (Tolvanen, 2001). Growth responses to herbivory have also been shown to differ within growth form depending on community context (Gough et al. 2007) and NPP (Grellman, 2002; Gough et al. 2007). Finally, while there is some evidence that herbivores may induce secondary metabolites in some growth forms (e.g. lichens, Hyvarinen, et al. 2002), this response does not seem generalizable (e.g. Lingren et al. 2007). There is some speculation that the increased production of these compounds may interact in a dynamic way with microtine population cycles (Oksanen and Oksanen, 1981). Explicit tests of this pattern have not produced sufficient data in support of this conjecture (Jonasson, et al. 1986); abiotic factors seem to govern the production of secondary compounds for many arctic plants.

Through selective herbivory herbivores can structure the population of arctic plants (Mulder, 1999). Herbivores often select inflorescences among plant tissue types for consumption (e.g. Cooper and Wookey, 2003). Additionally, herbivores may select individual genotypes within populations that are relatively more palatable than their con-specifics (e.g. Pusenius et al. 2002), thus may structure plant populations (e.g. Prittenen et al. 2006). Ultimately, herbivores may suppress plant sexual reproduction because of nutrient and biomass allocation for regrowing removed tissue (Tolvanin and Laine, 1999). However, it is yet unclear how variable population responses to herbivory are among arctic plant species, and how these might scale up to community effects (Mulder, 1999).

Herbivores can alter a variety of competitive interactions among plants in some arctic tundra ecosystems (Olofsson, et al. 2002), and effects may be mediated partially by nutrient availability and NPP (Eskelinen, 2008). Grazer presence can influence competitive interactions between species within communities. For example, large mammals can reduce moss cover through trampling, which subsequently changes in abiotic conditions (e.g. temperature) resulting in an increase in graminoid species (van der Wal et al, 2001a; van der Wal, 2004). Primarily though, herbivores alter community composition through selective foraging. Biomass of palatable species is removed from communities reducing the competitive pressure on less-palatable species for resources (Olofsson et al. 2001, Virtenen et al. 1997). In particular, caribou may influence the abundance of lichen species within communities (van der Wal et al., 2001a; Gough et al. 2008; Vistnes and Nellemann, 2008). Additionally, community composition in some ecosystems may be affected more intensely by small herbivores than large ones because of more localized selective herbivory and the transient nature of species such as caribou (Fox, 1985; den Herder et al, 2004; Oloffson et al. 2004). Direct tests of the effect of herbivore grazing pressure on community diversity have shown mixed results (Olofsson and Oksanen, 2005; Olofsson, 2006), and it is still unclear if or how herbivores affect plant community resilience to disturbance (Olofsson et al. 2005; van der Wal, 2005).

Although recent evidence suggests that herbivores may be suppressing plant biomass over large spatial scales by both small and large mammalian herbivores (Jonssdottir et al., 1999; Brathen et al. 2007), the majority of studies have focused on herbivore effects on NPP through altering nutrient cycling (Mulder, 1999). Herbivore presence tends to increase both N and phosphorus (P) in soils available to plants (Batzli, 1978; McKendrick et al. 1980), and has been shown to increase nutrient mineralization and decomposition rates (Stark et al. 2002; Oloffson et al. 2004). Van der Wal et al. (2004a) suggest that through feces alone, large mammals are able to increase the biomass of their own food sources. Alternatively, herbivores have been shown to slow soil microbial processes in some instances (Stark and Grellman, 2002). Stark and Grellman postulate that unless herbivore migrations are timed with the highest plant demand for soil nutrients, herbivores may function to remove nutrients from the system. Herbivores may also alter relationships between plants and soil microorganisms directly through herbivory. Because herbivory often results in C and nutrient reallocation from plant roots to shoots (Chapin et al. 1986), grazing may reduce C flux from plants to soils (Stark and Kytoviita, 2006). The result may be reduced microbial growth and N immobilization, which functions to increase N available to plants. Finally, herbivores can increase the decomposability of plant tissues by inducing changes in plant chemistry (Olofsson and Oksanen, 2002). Plant biomass from heavily grazed areas may have higher C:N than that from lighter grazed areas, resulting in increased decomposition in plants from heavily grazed areas. Although all these effects may be important ecosystem determinants at different temporal and spatial scales, it has been difficult to generalize effects among arctic ecosystems (Mulder, 1999).

## 1.4 Plant responses to simulated climate change: Experimental studies

There is some evidence that arctic plants are already responding to climate change (Tucker et al. 2001). Remote sensing of vegetation of the Alaskan Arctic comparing past aerial photography with current photographs (Sturm et al. 2002; Tape et al. 2006),as well as satellite images collected during the 1980s (Myneni et al. 1997), has shown that plant communities are becoming shrubbier. Additionally, there is evidence that the interface between boreal forest and tundra, or tree-line, is progressing northward in a number of circumpolar locations (Chapin et al. 2005; Lescop-Sinclair and Payette, 1995). Through a variety of studies designed to simulate the abiotic affects of climate change on arctic ecosystems, mechanisms describing these and other phenomenon are starting to emerge (van Wijk et al. 2003). In the following section I will first describe the general understanding regarding how plants, communities and ecosystems are constrained by extreme abiotic factors, then elaborate on our current understanding of how climate change may affect these abiotic factors and biotic responses to those changes.

### *1.4.1. Abiotic constraints on arctic plants, communities and ecosystems*

Arctic plants have been well characterized as being limited by a variety of abiotic factors such as low temperatures, short growing seasons and the presence of permafrost (Bliss, 1956; Bliss, 1962; Billings and Mooney, 1968; Chapin and Shaver, 1985). Arctic plants must utilize a short temporal window in summer for growth (Pielou, 1994), and often recovery from disturbance events is slow for many plant communities (Bliss and Wein, 1971; Vavrek et al. 1999). Most arctic species also occur at lower latitudes, and uniquely arctic adaptations have rarely been found

(Sonesson and Callaghan, 1991). Species, such as $C_3$ grasses, with traits for relatively high $CO_2$ uptake at low temperatures and high light intensity are common (Tieszen, 1973; Ellis and Kummerow, 1982; Kummerow et al. 1980). Because of nutrient limitation, arctic plants show similarity among species in C and nutrient allocation to specific plant tissues (Chapin, 1989), often with increased allocation to root tissue relative to shoots (van Wijk, 2003). These differences in patterns often reflect soil nutrient availability (Sorensen et al. 2008). Soil nutrient availability can affect timing of life history events, such as initial growth and senescence of plants (Shaver and Laundre, 1997), although site characteristics have been shown be important determinants of foliar nutrients as well (Hobbie and Gough, 2002).

While there are similarities among plant growth forms in response to the extreme abiotic conditions in the Arctic, species assemblages are determined in Arctic communities by both positive and negative interactions among plants as they are in other ecosystems (Bertness and Calloway, 1994; Shaver et al. 1994; Walker, 1995). Carlsson and Callaghan (1991) propose that associations between species ameliorate the abiotic stresses by providing shelter, particularly for dwarf shrubs on graminoids (Olofsson, 2004). Similar interactions have been found between evergreen and deciduous shrub species, though exclusion of species within growth form may occur (Shevtsova et al. 1995). Neighborhood removal experiments have also shown that competitive interactions can be important for some species in these nutrient limited ecosystems (Bret-Harte et al. 2004; Gough, 2006; Hobbie, 1996). Associations and co-existence may be possible due to differential uptake of different forms of nutrients, in particular N, among species (Nadelhoffer et al. 1996; McKane et al. 2002, van Wilk et al. 2003). Additionally, associations between species have been shown to vary among communities depending on abiotic differences such as exposure (Olofsson, 2004).

Abiotic factors also strongly structure plant community composition, structure and function (Shaver, 1995; Walker, 1995). Underlying differences in abiotic factors seem to determine species composition in a given community (Walker et al. 1994). For example, differences in species composition and community diversity have been found between communities in close proximity with differing soil pH and differential loess deposition, ultimately controlled by the geologic age since deglaciation for substrates in each community (Walker and Everett, 1991; Gough et al., 2000; Oechel et al. 2000). Species composition in arctic communities also strongly reflects nutrient availability, and ultimately NPP (Shaver et al. 1996). One interesting finding seems to be that relationships between leaf area index, foliar N, and NPP are highly constrained among different tundra plant communities (Williams et al., 1999; Street et al. 2007). Different combinations of plant species in widely spatially separated locally show a relationship where canopy leaf area predicts well gross primary production, though the relationship seems to weaken with increased soil nutrients (Street et al. 2007). These patterns suggest that arctic plants are constrained by nutrient availability, and ultimately NPP in any one community is controlled by local abiotic conditions and nutrient availability (Shaver, 1995).

Other ecosystem processes, such as decomposition and nutrient mineralization are largely controlled primarily by temperature (Miller et al., 1994; Nadelhoffer et al. 2001), however soil moisture, plant species identity and quality, as well as diversity of soil microorganisms are important (Hobbie, 1996; Robinson, 2002). Low arctic temperatures limit the decomposition of plant matter, resulting in a net ecosystem build up of C in soils (Miller et al. 1994). Additionally, community context can influence decay rates of plants biomass (Hobbie and Gough, 2004), although differences in plant tissue quality within plant species appear to be relatively unimportant to litter decomposition (Hobbie and Gough, 2002). Differences between plant species can highly influence decomposition rates (Nadelhoffer et al. 1991; Hobbie, 1996; Dorrepaal et al. 2007). Plant litter with higher C:N ratios (i.e. high lignin or secondary metabolites) decomposes slower than plant litter with lower C:N values. In general, decomposition has been better characterized as being primarily temperature and substrate limited than has N mineralization (Robinson, 2002). Nitrogen mineralization is generally thought to be nutrient limited (Sjogersten and Wookey, 2005; Aerts et al.2006), however recent work has shown that N fixation can be a very important process in some tundra systems (Weiss et al. 2005; Hobaru et al., 2006). Overall, biological processes are temperature limited in Arctic ecosystems; thus, higher temperature patterns have the potential to have substantial consequences on these systems.

### *1.4.2. Simulating a warmer Arctic: experimental efforts*

Because global $CO_2$ concentrations are predicted to continue to increase, arctic temperatures are also predicted to continue to increase (IPCC, 2007). Further, the magnitude increase may be larger than in more temperate regions (ACIA, 2004). This suggests that changes in arctic ecosystem processes, particular NPP and decomposition, may be major determinants in future global $CO_2$ balances (Shaver et al. 2006). Because of this, there has been much effort to understand the relative importance of processes and how these may change with increased temperatures. The overarching theme of research is to best understand the C fluxes among biota within ecosystems and the atmosphere primarily through whole ecosystem experimental studies (Shaver and Jonasson, 1999). Often research is coordinated among different ecosystems in the Arctic in an attempt to determine if the Arctic will respond holistically to increased temperatures (Shaver et al. 2000). Two field sites, near Abisko, Sweden and the Arctic Long-Term Ecological Research (LTER) site at Toolik Lake, AK, have established replicated experiments (Shaver and Jonasson, 1999; van Wijk et al., 2003). Experiments include the manipulation of both the direct effects of warming, such as increased $CO_2$ concentrations and air temperature, and indirect effects, such as decreased light availability due to greater cloud cover predicted by some climate models (Serreze and Francis, 2006). Because soil microbial processes, such as decomposition and nutrient mineralization, are known to be sensitive to increased temperature, fertilization experiments have been established to understand how ecosystems function with higher soil nutrient availability (Shaver et al. 1991). Based on data from these and other sites, the following summarizes our current understanding of how the direct and indirect effect of increased temperatures affect arctic plants, plants communities and ecosystems.

The International Tundra Experiment (ITEX) has conducted passive warming, using open-top chambers, across 20 sites to determine plant and ecosystem responses to warming (Arft et al. 1999; Oberbauer et al. 2007). Individual plant responses to direct warming experiments vary among species, though there are some general patterns (Arft et al. 1999). Increased air temperatures tend to cause phenological shifts such as earlier budburst and flowering for most growth forms (Aerts et al. 2006; Borner et al. 2008), although there is little support for changes in nutrient allocation (Aerts et al. 2007). Additionally, graminoids respond to higher soil temperatures (Brooker and van der Wal, 2003) more strongly and consistently than woody species (Starr et al. 2008). Although often deciduous shrubs can respond more positively to warmer temperatures relative to evergreen shrubs (Wahren et al. 2005). Thus, it is no surprise that experimental warming has resulted in changes in composition at the community level (Jonsdottir et al. 2005). However, for some growth forms the indirect effects of warmer temperatures, such as higher soil nutrients, may be more important than direct effects (Arft et al. 1999). For example, non-vascular plant species may respond negatively to fertilization (Jonasson, 1992), while deciduous shrubs appear to respond positively to increased soil nutrients (Bret-Harte et al. 2002). Because of these patterns, research at the community and ecosystem levels has used growth form to make predictions at those levels (Chapin et al.1996; Walker et al. 2006). There is speculation, however, that functional groups may not be as effective predictors as thought; species may not respond similarly in all ecosystems and circumstances (Doormann and Woodin, 2002; Dorrepaal, 2007).

Increased soil nutrients arising via climate change have the potential to affect species-species interactions in arctic plant communities (Bret-Harte et al. 2004). Bret-Harte et al. found that vascular growth forms tend to increase growth with fertilization in the absence of competitors, while non-vascular plants did not. Additionally, dominant species responded positively more often than sub-dominant ones. For example, fertilized plots in moist acidic tussock tundra (MAT) near Toolik Lake have become dominated by the dwarf shrub, *Betula nana*, after 15 years (Chapin et al. 1995; Shaver et al. 2001). Interestingly, dry heath tundra (DH) and heath communities nearby and near Abisko, which have *B. nana* and other species in common with MAT, did not see similar dominance by *B. nana* after similar time; all growth forms responded positively to fertilization and there were no major shifts in species composition (Gough et al. 2002; van Wijk et al, 2003). Generally, experimental fertilization has resulted in an overall decrease in both species richness and evenness in some plant communities (Press et al. 1998; van Wilk et al. 2003). The magnitude of responses of composition and diversity may vary among sites with similar species composition according to differences in other abiotic factors such as underlying geology (Hobbie et al. 2005).

Long-term fertilization of these communities results in increase NPP, particularly through the addition of both N and P, though the magnitude often varies among communities (Shaver et al. 2001; Gough et al. 2002; Hobbie and Gough, 2002, Gough and Hobbie, 2003, van Wijk et al. 2003). This result has increased speculation as to the role that arctic plants may have as potential C sinks through increased NPP (Shaver et al. 2000). This potential negative feedback may offset large C fluxes from soils through increased decomposition of the large soil C pool in the Arctic (Cornelissen et al. 2007). Additionally, there may be positive feedbacks to increased microbial activity because of higher soil nutrients themselves (Nadelhoffer et al. 2002) as well as the direct effect of increased temperatures (Schmidt et al. 2002). While there is some speculation of the relative importance and magnitude of these mechanisms, arctic ecosystems have the potential to be a large source of $CO_2$ to the atmosphere providing a net positive feedback on global atmospheric $CO_2$ concentrations and global temperatures (Shaver et al. 2006).

## 1.5 Plant-herbivore interactions in a warmer Arctic: research objectives and dissertation overview

One consistent criticism of climate research in arctic ecosystems has been the lack of investigative efforts studying the effects of increased temperatures on higher trophic levels (Ims and Fuglei, 2005, but see Jefferies et al.1994). This fact has long been acknowledged among arctic researchers, however efforts have to date been prioritized to understand the relationships among higher temperatures, NPP, and feedbacks to the global carbon cycles (Shaver et al. 1992; 2000). As arctic climate research has matured, it has become apparent that the effects of climate change on higher trophic levels and interactions among trophic levels and ecosystem processes need consideration (Ims and Fuglei, 2005). EEH predicts that increased NPP will have an impact on higher trophic levels, which have the potential to have cascading effects on other processes (Oksanen et al. 1980; Oksanen and Oksanen, 2000). To this end, I have focused my dissertation research with the broad goal of understanding how higher NPP, arising from increased soil nutrients, affects plant-herbivore interactions in two different tundra communities in the Alaskan Arctic.

While EEH predicts that herbivore populations should increase as NPP increases due to higher soil nutrient availability (Oksanen et al. 1980), to date there have been no published data showing population increases attributed to higher temperatures in the Arctic. However, there have been a number of studies which have causally linked changes in climate to changes in plant and herbivore populations (Forchammer et al. 2005; Cebrian et al. 2008; Tyler et al. 2008). Using long-term datasets and modeling techniques, these studies have shown that changes in climate patterns have effects on plant phenology and chemistry which in turn may have short-term effects on herbivore populations. More often, research has focused on indirect effects of increased nutrients on plant-herbivore and plant-soil-herbivore interactions. Efforts in the European Arctic have shown that the importance of herbivores on soil nutrient cycling with higher NPP may be hard to detect if the timing of herbivory is not synchronized with plant need for increased nutrients (Grellman, 2002; Stark and Grellman, 2002). Studies in plant-herbivore interactions have revealed that responses to NPP and herbivory often depend on plant species identity (Gough et al. 2007; Eskelinen, 2008). For example, interspecific competition for resources increases greatly with experimental fertilization among growth forms, and in such conditions herbivory may strongly limit growth of preferred species to the advantage of less-preferred species (Eskilenen, 2008). Similarly, long-term fertilization experiments and herbivore exclusion in MAT in Alaska has resulted in suppression of the graminoid *E. vaginatum* in fertilized plots exposed to herbivores (Gough et al. 2007). However, Gough et al. also found that other graminoids, *Carex bigelowii*, at MAT and *Hierochloe alpina* in DH, did not have similar suppression after nine years of fertilization and herbivore exclusion. These results reinforce the variation of individual plant responses to both resource availability and herbivory (Hawkes and Sullivan, 2001). Finally, there has been some work on community aspects regarding the relationship between plant-herbivore interactions and changes in NPP. Gough et al. (2008) showed that herbivores function to control lichen community composition and structure in DH tundra, and herbivores may exacerbate the negative response of lichens to fertilization.

My dissertation research used four studies to further investigate plant-herbivore interactions in both DH and MAT tundra communities, taking advantage of long-term manipulations of soil nutrient availability and mammalian herbivore activity at the Arctic LTER near Toolik Lake (Figure 1.1). DH and MAT are two common plant communities in northern Alaska which differ in species composition, NPP and herbivore abundance (Table 1.1). Experimental nutrient addition and fences to exclude herbivores were established in a factorial design in 1996, and it appears that herbivores may be preferentially utilizing fertilized plots in these communities (Table 1.2). Thus, DH and MAT offered an opportunity to study individual plant, plant community and plant decomposition responses in common but differing communities. In the following four chapters I explore how higher soil nutrients and herbivores affect these communities. In Chapter Two I explore a legacy of herbivory on individual growth and relative abundance of five common tundra species in the ninth, tenth and eleventh years of experimentation following the experimental design of Gough et al. (2007). In Chapter Three, I focus on the tolerance of herbivory with higher soil nutrients in two graminoids, *E. vaginatum* in MAT and *H. alpina* in DH, using the structural framework of a recent hypothesis explaining the relationship between plant tolerance to herbivory and resource availability (Wise and Abrahamson, 2002; 2007). I scale up to the community level in Chapter Four; exploring changes among growth form with respect to soil nutrient availability and herbivory. Specifically I test the null hypothesis that herbivores have no impact on both MAT and DH when soil nutrients are higher early and late in the growing season among the ninth, tenth and eleventh years of experimentation. Additionally in Chapter Four, I ask if signs of herbivores are more common in fertilized plots and are more evident early in the growing season than at peak seasonal growth. Finally in Chapter Five I explore how herbivores may be affecting the growth and decomposition of *E. vaginatum* leaves in MAT and *H. alpina* leaves in DH. Small mammals routinely create haypiles of leaves from *E. vaginatum* tussocks in MAT. Additionally, caribou are thought to denude *H. alpina* tussocks of standing leaf litter in fertilized plots in DH, resulting in abundant loose litter in fertilized plots. Using a litterbag experiment, I explore how these activities are affecting the decomposition of these leaves in both ambient and fertilized conditions. While I do not address direct effects of increased soil nutrients on herbivore populations, I did find interesting patterns in plant-herbivore dynamics with higher soil nutrients in both communities. Together these four studies add to our understanding of how plant-herbivore interactions may be influenced by increased soil nutrients from climate change and how changes in both DH and MAT may affect future arctic feedbacks to the global carbon cycle.

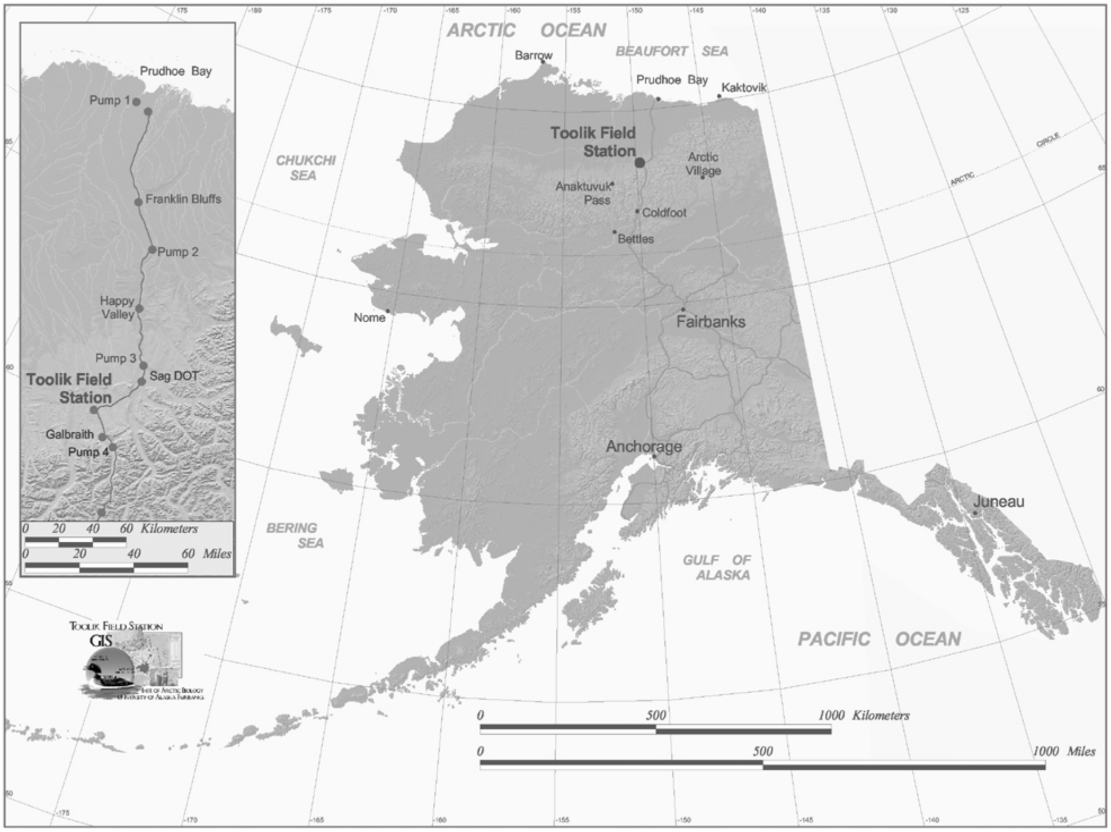

Figure 1.1. The Arctic Long Term Ecological Research station at Toolik Lake, Alaska (68°38’ N, 149°36’W 760 m a.s.l.). Figure taken from: http://www.uaf.edu/toolik/gis.

Table 1.1 Characteristics of moist acidic tussock (MAT) and dry heath (DH) tundras near the Arctic LTER at Toolik Lake, AK. Control plots represent natural conditions, NP plots represent nitrogen and phosphorus added yearly beginning in 1996 (see text for details). Species density (NP only), NPP, and aboveground biomass are from Gough et al. (2000), Gough et al. (2002) and Hobbie et al. (2005). Species density data for control plots are unpublished. Nomenclature follows Hultén (1968).

| Community | Plots | Species Density (# $m^{-2}$) | NPP (g $m^{-2}$ $yr^{-1}$) | Aboveground biomass (g $m^{-2}$) | Species composition |
|---|---|---|---|---|---|
| MAT | Control | 11 | 145 | Vascular only: 500<br>Total: 800 | Dwarf evergreen shrubs, dwarf deciduous shrubs, graminoids, mosses |
| | NP | 5 | 250 | Vascular only: 780<br>Total: 800 | Dwarf deciduous shrubs (*Betula nana*) |
| DH | Control | 6 | 60 | Vascular only: 370<br>Total: 600 | Dwarf evergreen shrubs, Lichens |
| | NP | 8 | 200 | Vascular only: 320<br>Total: 390 | Graminoid dominant (*H. alpina*) |

Table 1.2 A summary of small mammals trapped and released moist acidic tussock (MAT) and dry heath (DH) tundras near the arctic LTER at Toolik Lake Alaska during summers 2004 and 2005

| Site | Year | Treatment or trapline | # of animals caught | Species |
|---|---|---|---|---|
| MAT | 2004 | trap line near old NP | 4 | *M. oeconomus* |
| | | NFNP | 3 | *M. oeconomus* |
| | | NFCT | 0 | - |
| | 2005 | trap line near old NP | 2 | *M. oeconomus* |
| | | NFNP | 1 | *M. oeconomus* |
| | | NFCT | 0 | - |
| DH | 2004 | trap line east of site | 0 | - |
| | | trap line west of site | 6 | *M. microtus* |
| | | NFNP | 0 | - |
| | | NFCT | 0 | - |
| | 2005 | trap line east of site | 1 | *M. microtus, L. sibericus* |
| | | trap line west of site | 3 | *M. microtus* |
| | | NFNP | 0 | - |
| | | NFCT | 0 | - |

# CHAPTER 2

# INDIVIDUAL PLANT GROWTH RESPONSES TO A TEN YEAR LEGACY OF MAMMALIAN HERBIVORY AND INCREASED NUTRIENTS

## 2.1 Abstract

Historically, herbivores have been considered of little importance to plant growth in ecosystems with low net primary productivity (NPP), such as the Arctic, because herbivore populations are generally low. However, future climate scenarios for the Arctic predict that NPP may be higher and perhaps will support more herbivores as temperatures increase causing soil nutrients to become more available to plants. As plant communities respond to increased nutrient availability, the effect of herbivores on individual plant growth is only beginning to be understood. Here we explore how the growth and abundance of five species of arctic plants in two communities, moist acidic tussock (MAT) and dry heath (DH) tundras, are affected by long-term herbivore exclusion and experimental nutrient addition. We predicted that herbivory would be more important in ambient plots than in fertilized plots at MAT, because currently both NPP and herbivore presence are relatively higher than at DH. For plants at DH, we predicted the opposite response because fertilization increases the presence and abundance of preferred animal forage. We found that relative abundance of species largely reflected individual growth; while all species grew better when fertilized and overall growth varied among years, herbivore exclusion affected plants in each community differently. For example, *Hierochloe alpina*, a tussock forming graminoid that greatly increases growth when fertilized, grew even better with higher soil nutrients and herbivores present in DH. Alternatively, the graminoid *Eriophorum vaginatum* in MAT grew less with long-term herbivore exposure even when fertilized. Interestingly, the dwarf deciduous shrub *Betula nana*, measured in both communities, grew larger when fertilized but this increase in growth was suppressed by herbivore exposure in DH. In MAT, the opposite was true; *B. nana* increased growth when fertilized and herbivore presence intensified this effect. These results

suggest that herbivores may be at least partially responsible for shifts in plant community structure, which has long been associated solely with competition for soil nutrients, when soil nutrients become more available. Thus, generalizations regarding the importance of herbivores may differ among communities and growth forms as both NPP, and potentially herbivore abundance, increase with climate warming.

## 2.2 Introduction

Plant-herbivore interactions are often complex and difficult to study. In the Arctic, herbivory has historically been considered of little importance primarily because net primary productivity (NPP) is low relative to more temperate regions, and communities are often not able to support large populations of herbivores (Jefferies et al. 1994). However, this conjecture has been based largely on theoretical assumptions of trophic structure in systems with low NPP (e.g. Oksanen et al. 1981) and has only recently been tested in some arctic ecosystems where large herbivores have been shown to modify and homogenize vegetation and alter primary productivity (Bråthen et al. 2007). There are few well-studied Arctic ecosystems where mammalian herbivore abundance has been experimentally manipulated. Herbivore exclusion studies in Fennoscandian heath tundra have shown that herbivores may have a wide range of consequences for arctic plants (reviewed by Mulder, 1999). In addition to affecting individual plants through biomass removal, herbivores may affect plant community composition and diversity (Fox, 1985). Herbivores may also affect ecosystem processes such as decomposition and nutrient cycling by changing the quantity and quality of plant litter and spatially redistributing nutrients within communities (Stark and Grellman, 2002; Olofsson and Oksanen, 2002; McKendrick et al. 1980). Thus, although herbivory has not been considered for many arctic plant communities, further investigation into the potential importance of herbivores is warranted (Mulder 1999) especially as communities in the Arctic respond to an increase in global temperature (Serreze et al. 2000).

Much research in the recent past has focused on understanding how arctic plant communities are and will be affected by increased temperatures and concomitant changes in soil nutrient availability (Shaver and Jonasson, 1999; Tape et al. 2006; Walker et al. 2006).

Experimental temperature manipulations have shown that nutrient availability in tundra soils increases with increasing temperatures (Nadelhoffer et al. 1991, 1992; Hobbie 1996). Increased soil nutrients result in increases in NPP, with shifts in community structure as well as other ecosystem processes. As the region warms, these changes seem to be occurring, at least locally, and are predicted to continue to occur throughout the Arctic (Hinzman et al. 2005). Theory predicts that as higher soil nutrient availability increases NPP, plant communities may support more herbivores than currently (Oksanen et al. 1981). Many predictive ecosystem studies have not included plant-herbivore interactions (one exception being the role of warming and insect herbivory in Richardson et al. 2002). Thus, it is unclear if changes in herbivore abundance as well as potential feedbacks to plant communities may become more important in the future as the arctic warms.

Gough et al. (2007) showed how increased soil nutrients alter plant-herbivore interactions in two Alaskan tundra communities: moist acidic tussock (MAT) and dry heath (DH) tundras. These two communities differ in species composition, diversity, NPP and herbivore abundance (Table 1.1, 1.2). Both DH and MAT have been well studied and have long-term experimental manipulations as part of the Arctic Long Term Ecological Research (LTER) research sites. Further, when nitrogen (N) and phosphorus (P) are added to plots, DH and MAT respond differently to increased nutrient availability. At DH, NPP increases and community structure shifts from one dominated by dwarf evergreen shrubs and lichens to one dominated by graminoids, particularly *Hierochloe alpina* (Gough et al. 2002; 2008). Alternatively at MAT, while overall biomass does not change, NPP increases as this plant community shifts from a diverse community of dwarf evergreen and deciduous shrubs, graminoids, forbs and mosses to one dominated by dwarf shrubs, particularly *Betula nana*. Gough et al. (2007) found that when plants were subjected to nine years of experimental fertilization and herbivore exclusion, plants with similar growth forms responded differently in the two communities. While all species increased growth with fertilization, the effect of herbivore exclosures differed between the two communities: the magnitude of the effect of herbivores was greater for plants at DH when plants were fertilized.

In contrast, at MAT herbivores had somewhat less of an overall effect on fertilized plants in that community.

Presented here is a continuation of Gough et al. (2007), which examined the responses of three species in each tundra community (MAT and DH) in 2004, the ninth year of experimental nutrient addition and mammalian herbivore exclusion. Here we explore the response of these same individual plants across 2004, 2005 and 2006. Herbivore abundance in these communities is patchy (Batzli and Lesieutre 1995; Table 1.2), and we were uncertain if all measured plants had been directly consumed by herbivores when plants were initially marked in 2004. Because of this we used exclosures to capture a temporal description of the ‘legacy of mammalian herbivory’ of nine, ten and eleven years of fertilization for plants potentially exposed to herbivory compared to those protected from mammalian herbivores. Plants in unfenced plots may be in various stages of recovery from herbivory or alternatively may have stimulated growth due to the presence of herbivores at the onset of measurements in 2004 and throughout 2005 and 2006.

We chose plant species based on growth form similarity between DH and MAT as well as the known positive responses of all species to fertilization (Table 1.1). Thus, we formulated predictions regarding how fertilized plants would respond to herbivore exclusion among the ninth, tenth and eleventh years of treatments. We predicted that among years the individual growth and magnitude of herbivory of species growing with added nutrients would reflect individual growth patterns reported for these five tundra species in the ninth year (Gough et al. 2007). *E. vaginatum* in MAT and *C. microchaeta* in DH should be higher within fertilized-fenced treatments, while when fertilized *C. bigelowii* in MAT and *H. alpina* in DH should show no effect of herbivory. We predicted that fertilized *B. nana* would show the opposite responses in each community: a positive effect of herbivores in MAT and negative effect of herbivores in DH. Lastly scaling up to the community level, we predicted that the relative cover of all species in fertilized plots should reflect growth measurements. For fertilized *E. vaginatum* and *C. microchaeta*, we predicted cover to be negatively affected by herbivore exposure, while we predicted *C. bigelowii* and *H. alpina* to show no effect of herbivores. Similarly, we predicted that fertilized *B. nana* cover would be negatively affected by herbivore exposure in DH and positively affected in MAT. Together, these predictions allow better understanding of how these species respond to herbivory and higher soil nutrients in different community contexts, and increase our understanding regarding the role of herbivores on plants in a warmer Arctic.

## 2.3 Methods

### *2.3.1 Study sites*

The location of this research was the Arctic Long Term Ecological Research (LTER) site at Toolik Lake Alaska (68.2° N, 149.6° W, 760 m a.s.l.). Both MAT and DH have been subjected to experimental manipulation since 1989 as part of the terrestrial component of the Arctic LTER. These two communities of focus differ in diversity, NPP, species composition and response to experimental nutrient additions (Table 1.1). A factorial design was incorporated to test plant responses to the exclusion of herbivores along with the addition of both N and P ($10 g/m^2/yr$ as $NH_4NO_3$ and $5 g/m^2 /yr$ as $P_2O_5$) within blocks of 5 x 20 m plots in both communities beginning in 1996. One plot within each block was randomly assigned N and P addition (NP) and another as control (CT). Fertilizer treatment to NP plots began following snowmelt in June 1996 in the form of pellets, and was repeated yearly as part of long-term maintenance of terrestrial LTER experiments.

Half of each 5 x 20 m plot is unfenced (NF), while the remaining area consists of the combination of small and large mammal exclusion fences. To exclude large mammals such as caribou, 5 x 10 meters of a random half of each plot was enclosed in a large mesh fence (LF: 15.2 x 15.2 cm openings, approximately 1.2 m in height). A smaller mesh fence (SF: 1.3 x 1.3 cm openings, approximately 0.8 m in height) was built within a random 5 x 5 meters of the larger fence to exclude small mammals such as ground squirrels, voles and lemmings. The small-mesh fence was buried in the soil at least 10 cm at construction to prevent animals from burrowing into the plots.

Plots were replicated within four blocks at MAT and three blocks at DH. For this study, I did not consider the effects of small mammals and large mammals separately, thus all data were collected from unfenced areas and areas with both small and large mammal exclusion (SF). Therefore, each block contained plots with four possible combinations of fence and fertilization treatment at each site: unfenced control (natural herbivory + CT), fenced control (no herbivory + CT), unfenced N + P (natural herbivory + NP), and fenced N + P (no herbivory + NP). While there are herbivorous insects in these communities, their effect on leaf biomass appeared to be minimal compared to that of mammalian herbivores (personal observation). These plots may retain snow on the immediate northern edge of fences for 2-3 days early in the season relative to unfenced areas (C. Moulton, personal communication). To avoid this snow accumulation, all sampled plants were at least 0.5 m from the edge of the fence.

#### *2.3.2 Mammalian herbivores*

Five species of microtine rodents have been recorded on the north slope of Alaska (Batzli et al., 1980). These include three species of voles (*Microtus oeconomus*, *M. miurus*, and *Clethrionomys rutilis*) and two lemming species (*Dicrostonyx rubricatus* and *Lemmus sibericus*). Of these, the tundra vole (*M. oeconomus*) and singing vole (*M. miurus*) are common in communities near the Arctic LTER at Toolik Lake (Batzli and Lesieutre, 1995). Specifically at MAT, tundra voles are commonly seen (personal observation) as is evidence of their presence (hay piles, trails and fecal deposits) during cyclical outbreak years. Additionally, singing voles and collared lemmings (*D. rubricatus*) have been found in rocky areas very near DH (Batzli and Henttonen, 1990; pers. obs.). Batzli and Henttonen (1990) suggested that rodent densities in these tundra communities are limited by plant food availability, and animals seem to show strong preference for preferred plant species particularly *E. vaginatum* and *Carex* spp. Additionally, these authors suggest small mammals in these communities may be limited top-down by predator abundance similar to lemmings in coastal tundra (Batzli et al. 1980).

While transient, caribou are commonly sighted near the Arctic LTER at Toolik Lake (pers. obs.). Although Toolik Lake lies within the range of the Central Arctic Herd (D. Klein, personal communication; Lenhart 2002), their primary calving grounds lie far to the north. Thus caribou are not thought to be common foragers of plants in MAT. At DH however, caribou feces are frequently seen following snowmelt. Thus, DH may be an important winter habitat for caribou as snow cover is often less here than in other communities (Cheng et al. 1998).

### *2.3.3 Plant species*

#### 2.3.3.1 *Eriophorum vaginatum*

*E. vaginatum* is a tussock-forming sedge common in northern Alaska. This species is an important component of MAT, and is thought to be an important food source for microtine rodents (Batzli and Lesieutre, 1995). Following snowmelt in early June in years when voles are abundant, whole tussocks of *E. vaginatum* have extensive biomass removed by small mammals. Large portions of tussocks, including inflorescences, are clipped. In addition to a direct food source, voles create haypiles of *E. vaginatum* litter associated with fecal deposits, and may use these haypiles for shelter (personal observation).

#### 2.3.3.2 *Hierochloe alpina*

*H. alpina* is a grass species found at low abundance in many heath communities in northern Alaska (Walker et al. 1994). When nutrients experimentally become more available, *H. alpina* increases dramatically in growth, forming tussocks and becoming much more common in this community (Gough et al. 2002). Additionally, *H. alpina* has been shown to be a preferred forage plant for caribou (Boertje, 1984).

#### 2.3.3.3 *Carex microchaeta*

*C. microchaeta* is a rhizomatous sedge also found in low abundance in ambient nutrient plots. While eight years of nutrient addition did not show any significant increase due to fertilization (Gough et al. 2002), more recent data suggest that it increases in abundance after longer time scales following increased nutrient addition (Gough et al. 2008). The palatability of this species is unknown, however other con-genera in the area are preferred forage of animals near Toolik Lake (Batzli and Henttonen, 1990). We chose this species as a direct comparison to *C. bigelowii* in MAT, which has a similar growth form and is known to be a favored plant of voles.

#### 2.3.3.4 *Carex bigelowii*

At MAT, the second most common graminoid is the rhizomatous sedge *Carex bigelowii*, a preferred food of tundra voles in communities near Toolik Lake (Batzli and Lesieutre, 1991). Additionally, *C. bigelowii* is a common food source for mammals throughout its range in northern Europe (Brooker et al. 2001). At MAT, *C. bigelowii* has a slight increase in abundance in fertilized plots relative to ambient conditions (Shaver and Chapin 1986, Hobbie et al. 2005).

#### 2.3.3.5 *Betula nana*

Although more abundant at MAT than DH, the dwarf shrub *Betula nana* is common at both sites under ambient nutrient conditions. However the response to fertilization of *B. nana* differs at each site. At MAT, under fertilization and warming conditions, this species becomes dominant (Shaver et al. 2001, Bret-Harte et al. 2002). At DH *B. nana* also increases biomass in fertilized plots, though its distribution is patchier and does not come to dominate species composition as it does at MAT (Gough et al. 2008). This response at DH is similar to European tundra communities where fertilization of *B. nana* does not cause it to dominate communities (e.g., van Wijk et al. 2004). Whether or not animals eat this plant often throughout the Arctic is unclear. Tundra voles have been shown to consume *B. nana* in some Alaskan studies (Chapin et al. 1986, Batzli and Lesieutre, 1991), while results from the European Arctic have shown conflicting results. Reindeer were shown to use this species in one study (Olofsson and Oksanen, 2002), while animals had no effect in another (Grellman, 2002). Additionally, *B. nana* produces numerous secondary compounds, which have been shown to be affected by climate change (Graglia et al. 2001). Thus interactions between *B. nana* and herbivores are likely to be complex.

### *2.3.4 Data collection*

In June 2004, we randomly selected three individuals of each species in each block of each treatment at MAT and DH (n = 9, N = 36 at DH, and n = 12, N = 48 at MAT). Our measurements of each species differed based on species-specific growth form. For *E. vaginatum* and *H. alpina*, the two tussock-forming graminoids, we selected and tagged six tillers on each marked individual tussock. For NF treatments at MAT, we purposefully selected plants that had obvious visible vole damage and assumed that this damage occurred during spring snowmelt just prior to selection. Similarly, in NFNP plots at DH, all *H. alpina* tillers and associated plant litter had indication of animal activity. Because *H. alpina* in DH occurs in very low abundance and does not form tussocks under ambient conditions, we tagged all tillers (maximum number: 4) on each plant in CT plots. For both species, we measured the length of all leaves on each tagged tiller and recorded the total number of inflorescences per tussock/plant at each sampling date. To assess growth of the two rhizomatous-forming graminoids (*C. microchaeta* and *C. bigelowii*), we measured all leaves and assessed flowering on each individual ramet. Unlike the tussock forming species, these plants were randomly selected within NF plots as no detectable signs of herbivory were evident at the onset of this experiment. We selected and marked three individual live stems on each *B. nana* plant in all treatments in both sites. We chose stems that had one long individual terminal shoot from the previous year and tagged each stem at the bud scar. We measured total length of new stem production, and counted the total number of leaves, long shoots, short shoots and inflorescences on each stem at each sampling date. At the onset of this experiment, no visible signs of herbivory were evident on any *B. nana* in NF plots, thus these plants were randomly selected.

We conducted weekly sampling beginning on 14 June, 2004 at MAT and 16 June, 2004 at MAT. *H. alpina* and *E. vaginatum* growth was followed for six weeks, and *B. nana*, *C. microchaeta*, and *C. bigelowii* growth was followed for eight weeks. We repeated measurements weekly beginning on 13 June 2005 at MAT and 15 June, 2005 at DH, and continued for all species for eight weeks. Measurements were taken once during 2006 on 17 July, 2006 at MAT and 19 July at DH. In one NFCT plot at DH, *C. microchaeta* lacked one individual, while *B. nana* lacked four total plants in SFCT plots at DH. Thus there were only 35 *C. microchaeta* and 32 *B. nana* plants at DH included in this study, while all other species at DH had 36 plants, and all species at MAT had 48 plants. Additionally, several plants died of unknown causes, that did not appear to be unrelated to herbivory, during the course of this study including: one *C. microchaeta* ramet in 2005, two *H. alpina* tussocks in 2006, and three *C. bigelowii* ramets in 2006.

To estimate relative cover of the five species, we conducted non-destructive sampling of the plant community in all treatment combinations and replicates at both MAT and DH during peak plant growth during July 22-26 in 2004, and during July 22-29, 2005. We randomly selected locations of starting points in each treatment for 1 x 1 m quadrats with 20 x 20 cm subquadrats which were marked to aid in estimations. At each starting point, eight adjacent 1 x 1 m were censuses by relative aerial cover of each vascular plant species. Vascular plant species were recorded according to nomenclature found in Hultén (1968). We regularly standardized cover value estimates among observers to minimize bias. Within each treatment combination and replicate, 8 adjacent quadrats were censused. Cover was then relativized to generate relative cover for each individual sample plot.

### *2.3.5 Statistical analysis*

To meet parametric model assumptions, we natural log-transformed all growth measurements prior to analysis. For the four graminoids, to determine patterns of growth over years we used repeated measures ANOVA with fertilization and fence as main effects using growth at peak biomass in late-July (week 6) of each year. The lone exception to this was *C. microchaeta* in 2005, for which we used week 5 as plants began to senesce at week 6. Because *B. nana* is at both sites, we used a similar repeated measures ANOVA with site as an additional main effect (creating a three-way factorial model) for this species along with those described above. To determine if herbivory effects were the same in fertilized and non-fertilized plots, we calculated a response ratio for each species based on the growth measurements described above. We averaged the value of peak growth at week six (see exception for *C. microchaeta* noted above) in each year and calculated the following ratios:

$\ln RRCT = \ln(SFCT/NFCT)$

$\ln RRNP = \ln(SFNP/NFNP)$

where SFCT = small-mesh fence, ambient nutrients; NFCT = no fence, ambient nutrients; SFNP = small-mesh fence, amended nutrients; and NFNP = no fence, amended nutrients. A positive value indicated that plants grew more when protected from herbivory, a value of zero indicated that herbivory had no effect on growth, and a negative value indicated that herbivory actually increased growth. We ran a repeated measures ANOVA comparing this response ratio among years with community, species nested in community, and fertilization as main effects. Because the designs for two species at DH are unbalanced, we used LSMEANS and Type III SS for all analysis. To compare among means within groups post-hoc we used Tukey's HSD, and normality and homogeneity of variance were examined for all repeated measures ANOVAs.

To compare differences in the relative cover of all five species between early and peak seasons in the 2004 and 2005, we conducted a nested repeated measures ANOVAs with early and peak seasons nested within year (Scheiner and Guruvich, 1999) on the relative cover of each species for each site. For each repeated measures ANOVA, census measurements were compared between early and late nested within year, and differences between years were tested as within-subjects effects. Fertilization and fencing treatments were tested as main effects, and differences among treatments were compared post-hoc using Tukey's HSD. All cover estimates were arcsine square-root transformed prior to analysis to insure normality and homogeneity of variance. SAS Version 9.1 for Windows was used for all analyses (SAS institute, Cary, NC).

## 2.4 Results

### *2.4.1 Graminoid growth responses to fertilization and herbivory at DH*

In 2004, after nine years of fertilization, *H. alpina* plants in NP plots were significantly larger in terms of total tiller size than those in CT plots (Table 2.1; Figure 2.1a.). However, plants outside fences (NF) were not different from plants protected from herbivores (SF) as supported by a non-significant main effect of fence (Table 2.1), despite the trend of smaller plants in NFNP compared with SFNP in all three years. While *H. alpina* plants grew less in 2005 and 2006 (significant within-subjects effects of year: $F_{2,42} = 29.46$, $p < 0.001$; and significant within-subjects interactions of year*block: $F_{2,42} = 4.16$, $p = 0.006$; and year*fertilization: $F_{2,42} = 3.97$, $p = 0.03$), the overall pattern seen in 2004 was maintained. Fertilized plants were always larger than ambient nutrient plants, and exposure to herbivory did not significantly affect plant size for this tussock-forming graminoid. Similarly, the ramet-forming sedge *C. microchaeta*, was larger in NP plots relative to CT plots, but was significantly smaller when exposed to herbivores (Figure 2.1b., Table 2.1). This overall pattern was maintained in 2005 and 2006 although fertilized plants grew less in these years than in 2004 (significant within-subjects effect of year: $F_{2,42} = 5.44$, $p = 0.008$).

### *2.4.2 Graminoid growth responses to fertilization and herbivory at MAT*

*E. vaginatum* growth was affected by increased nutrients and herbivory uniquely relative to the other species studied here. Plants grew significantly more when fertilized and protected from herbivores in all three years (Figure 2.2a) compared to other treatments (significant fence*fertilization interaction, Table 2.1). Additionally, plants in SFCT plots were significantly larger than either fertilized or unfertilized exposed plots in 2004. Like *H. alpina*, plants in most treatments grew less in 2005 and 2006 than in 2004 (significant within-subject effect of year: $F_{2,66} = 22.28$, $p < 0.001$), though in these years SFNP plants were significantly larger than any other treatment. Unlike 2004, SFCT plants were not different from either NFCT or NFNP plants in 2005 and 2006. Thus, *E. vaginatum* in fertilized plots that were exposed to herbivores seem suppressed to similar levels as controls regardless of increased soil nutrients, suggesting a long-term legacy of exposure to herbivores.

*C. bigelowii* also responded to treatments differently from the other species. Although fertilized plants were significantly larger in NP plots in 2004 (Table 2.1), there were no overall significant effects or interaction for either fencing or fertilization. *C. bigelowii* individuals in NFNP plots were the largest followed by SFNP plants in 2004, with both SFCT and NFCT being the smallest. This general pattern held in 2005, although all plants were smaller and there was no difference among treatments. However, the overall large growth of *C. bigelowii* ramets in NFNP plots in 2004 was affected by biomass removal in 2006 and perhaps in 2005 (significant within subjects interaction of year*fence*fertilization). Several marked plants grew less in 2006 (Figure 2.2b), and indeed showed signs of biomass removal by herbivores (all leaves clipped above the meristem).

### *2.4.3* B. nana *growth responses at DH and MAT*

As stated above, we analyzed *B. nana* at both sites simultaneously (Table 2.2) to determine if the pattern was different in response to added nutrients and herbivore exposure at both sites (significant year*community*fertilization interaction). Growth in all years for plants in both sites was based on a marked point in 2004 at the 2003 bud scar. At DH, *B. nana* consistently grew bigger, with more new growth per marked shoot, in plots with nutrient addition (Figure 2.3a; Table 2.2). However, the exclusion of herbivores (SF plants) allowed individual *B. nana* to grow even larger than unprotected plants (NF). This may not be a direct result of consumption by herbivores, however, as we documented no obvious signs of herbivory on any *B. nana* individuals.

Like those at DH, individual *B. nana* plants grew more at MAT when fertilized (Figure 2.3b, Table 2.2). Unlike those at DH, however, plants grew more when herbivores were present. In 2004, NFNP plants were on average larger but not significantly different from SFNP plants. In 2005, this difference was significant, although there was no difference between plants in these two treatments in 2006. These results suggest that *B. nana* is in some way facilitated by the presence of herbivores in fertilized plots at MAT, as there was no direct evidence of biomass removal by herbivores on *B. nana* in this study.

### *2.4.4 The magnitude of herbivory response at DH and MAT*

Testing the response ratio allows for a direct comparison of the magnitude of herbivory growth responses among species and between tundra communities and fertilization treatments. Overall, there was a significant between subjects community and fertilization interaction ($F_{1,29}$ = 5.01 p = 0.03), and a significant between subjects fertilization by species (nested within community) interaction ($F_{4,29}$ = 3.5, p = 0.02). This supports the conjecture that plants with similar growth form (or the same species, as with *B. nana*) respond to increased soil nutrient availability and the presence of herbivores differently in each community. During all three years for NP plants at DH, the lnRR was significantly larger than zero (mean = 0.38 p = 0.01 in 2004, and mean = 0.24, p = 0.03 in 2005, mean = 0.39 p = 0.03 in 2006) indicating that these plants were negatively affected by herbivory when fertilized. Alternatively, the lnRR for CT plants at DH were not different from zero during any year, and the values for NP and CT plants at MAT were also not different from zero in both 2004 and 2005. Interestingly, at MAT plants in both NP and CT plots the lnRR values were significantly larger than zero (mean of NP = 0.34, $p = 0.04$, and mean of CT = 0.33, $p = 0.04$) in 2006. These results suggest that the magnitude of response to herbivory is variable year to year and from community to community.

The lnRR of individual species also varied among years and between species (Table 2.3). The lnRR of *C. microchaeta* showed that herbivory had a significant negative effect for plants in NP plots in 2004 and 2005, and a marginally significant effect in 2006. *E. vaginatum* was also significantly affected by herbivory for NP plants only suggesting that for both *C. microchaeta* and *E. vaginatum*, herbivory is negatively impacting growth when plants are grown with increased nutrients. Other plants in other treatments had different responses. The lnRR value for *C. bigelowii* in NP plots was different in all three years (Table 2.3). While the value was not different from zero in 2004, the herbivory effect on *C. bigelowii* was marginally significantly positive in 2005 and marginally significantly negative in 2006. The lnRR values for *B. nana* were also somewhat contradictory. In CT plots the response ratio was not different from zero at either site in any year. However, in NP plots at DH the herbivory was marginally significantly negative for *B. nana* in 2004 and 2006, while being significantly positive in 2005. At MAT, the presence of herbivores for *B. nana* varied in all three years; marginally so in 2004, significant in 2005, though there was no difference in 2006. This suggests that although *B. nana* is not believed to be directly eaten in either of these communities, the presence of herbivores is detrimental to *B. nana* growth at DH, while seemingly beneficial at MAT.

### *2.4.5 The relative cover of species in the ninth and tenth years in DH and MAT*

In DH, the graminoid *H. alpina* increased more seasonally in fertilized plots compared to ambient plots in both years, although the increase was greater in 2005 than 2004 (within subjects effects year*fertilization $F_{1,69} = 12.77$, $p < 0.001$; season*fertilization $F_{1,69} = 36.66$, $p < 0.001$). Relative cover was higher in fertilized plots compared to ambient plots, and herbivores enhanced this effect (Table 2.4, Figure 2.4). NFNP plots had the highest *H. alpina* relative cover followed by SFNP plots. *H. alpina* occurred at very low abundances in both fenced and unfenced ambient plots. Overall, the effect of fertilization on *H. alpina* relative cover supports the growth results presented above, while the significant effecting of fencing did not as *H. alpina* growth was not affected by fencing.

*C. microchaeta* also increased seasonally much more in fertilized plots compared to ambient plots (within subjects effects season*fertilization $F_{1,69} = 19.95$, $p < 0.001$), however fencing marginally increased this seasonal effect (Figure 2.4), within subjects effects season*fence F = 3.3, p = 0.07). Thus *C. microchaeta* responded positively to fertilization and marginally to fencing (Table 2.4), and this effect was more pronounced in 2005 than in 2004 (Figure 2.4, within subjects effect year*season*fertilization $F_{1,69} = 8.11$, $p = 0.005$). Supporting the individual growth response results, SFNP plots consistently had the highest *C. microchaeta* relative cover followed by NFNP plots, the inverse of the pattern seen with *H. alpina*. Like *H. alpina*, however, the cover in both ambient treatments was very low in both years (Figure 2.4).

For *B. nana* cover in DH, no seasonal or year differences were detected statistically. There was a strong positive fertilization response and no significant fence effect (Table 2.4). These results did not fully support the growth results which had a significant interaction between fertilization and fencing. *B. nana* was more abundant in fertilized plots compared to ambient plots, and was higher in SFCT plots compared to NFCT plots (Figure 2.4). However, in 2004 and 2005 there was no difference between NFNP and SFNP plots.

### 2.4.6 Fertilization and herbivory on relative cover in 2004 and 2005 in MAT

In MAT, *E. vaginatum* increased relative cover through growth in both 2004 and 2005, although there were differences detected between fencing treatments (within subjects season*fence $F_{1,93} = 22.19$, $p < 0.001$). Fencing increased the relative cover of *E. vaginatum* in both fertilized and ambient conditions (Figure 2.5) in both years. Indeed, the graminoid was most abundant in SFCT plots as fertilization herbivore exposure significantly decreased relative cover (Table 2.4). Interestingly, NFCT and SFNP treatments were not different in 2004; however cover in NFCT plots was higher than SFNP plots in 2005. NFNP plots consistently had the lowest *E. vaginatum* cover in both years and in each season (Figure 2.5). These results are somewhat opposite the growth response which showed higher growth in fertilized plots and a negative effect of herbivore exposure.

Like *E. vaginatum*, *C. bigelowii* also increased relative cover over both growing seasons (within subjects effects season $F1,_{93} = 12.35$, $p = 0.001$). However, cover increased seasonally more in 2005 than 2004, and a different pattern was detected with respect to fencing and fertilization might be predicted based on the individual growth data (Figure 2.5, Table 2.4). This species increased in all treatments seasonally, and was consistently more strongly affected by fertilization although fencing was important. *C. bigelowii* relative cover was the highest in NFCT plots (Figure 2.5) in both years. SFNP plots had the second highest *C. bigelowii* cover, and NFNP and SFCT plots had the lowest cover in 2004. However, there was no difference among these treatments in 2005.

*B. nana* in MAT increased cover slightly seasonally, although not significantly, and the pattern was opposite *B. nana* cover in DH. Cover was greater in 2005 than 2004 (within subjects effects year $F_{1,93} = 9.49$, $p < 0.01$), and patterns among treatments were consistent among seasons and years (Figure 2.5). Fertilization greatly increased *B. nana* cover, and herbivore exposure exacerbated this effect in this community (Table 2.4) supporting the individual growth results. NFNP plots had the highest *B. nana* cover, followed by SFNP plots. This effect was seen in ambient plots as well where NFCT plots had more *B. nana* than SFCT plots.

## 2.5 Discussion

### *2.5.1 Climate factors affected growth in 2005 and 2006*

All graminoids in most treatments in this study grew less in 2005 and 2006 than in 2004. Additionally, growth of *B. nana* at MAT in NP plots was less in 2006 than might be anticipated based on the difference between 2004 and 2005. These results may be due to climate factors as growth of some arctic species (specifically *C. bigelowii* and *E. vaginatum*) is thought to be predicted by the previous year's temperature and precipitation (Shaver and Laundre, 1997).

Temperatures were on average higher during the summer of 2004 and precipitation was on average lower month to month in 2005 than the long term average for sites at the Arctic LTER (Table 2.6). Some tundra species have been shown to have reduced growth when treated with higher temperatures (Tieszen, 1973). Thus, particularly warm and dry conditions during these two growing season may have contributed to reduced growth of these species.

### *2.5.2 Graminoid legacy of herbivory and increased soil nutrients*

The general patterns for the graminoids *E. vaginatum*, *H. alpina*, and *C. microchaeta* in 2005 and 2006 were similar to 2004 supporting our hypothesis regarding these species. These results support conjectures of Gough et al. (2007) that herbivory may become more important for plants in DH and less in MAT when soil nutrients become available through warmer temperatures. The decreased growth of fertilized *E. vaginatum* in particular has important consequences for small mammal populations that currently thrive there. Additionally, our predictions for C. bigelowii were incorrect. While, Gough et al. (2007) found no effect of herbivory on *C. bigelowii*; rather the overall pattern was that plants in NFNP plots were larger than SFNP plots in 2004. However, there was direct evidence of consumed *C. bigelowii* leaves in SFNP plots in two blocks in 2006 contributing to the decreased size of plants in that treatment in that year. This observation conflicts with the overall response ratio results which suggest that herbivory was the least severe among species overall in 2006. We believe that 2004 was a peak year in small mammal production, as estimated from evidence of animal presence in this community. The *C. bigelowii* results may underscore the idea that herbivory by small mammals may be important at small spatial scales in communities even if small mammal populations are not at peak condition. Mammals seem to be attracted to fertilized plots (Johnson, data unpublished), presumably because plants contain higher nutrients than control plots. Thus, the effect of increased soil nutrients and exposure to herbivory has resulted in *E. vaginatum* completely excluded from plots with longer term fertilization (17-year treatments) concurrent with the increased dominance of the presumably less preferred dwarf shrub *B. nana*. If this trend were to occur to the community as a whole, the shift to a dwarf shrub community may reduce the availability of graminoid forage for small mammals in this community.

Alternatively, at DH, the transition from a dwarf evergreen shrub community to a grassland may cause the increase of both large and small mammals in this area. *H. alpina* greatly increases growth when soil nutrients are higher, thus potentially providing greater forage for animals. Additionally, although *C. microchaeta* growth is reduced by herbivory in fertilized plots, its abundance in these plots is much greater than in control plots further supporting the idea that DH may support more herbivores in the future than it currently does.

### *2.5.3* B. nana *legacy of herbivory and increased nutrients*

Our prediction that B. nana would increase growth with fertilization but be affected in opposite ways in each community was supported. In DH, *B. nana* seems to be negatively impacted by exposure to herbivores. However, reduced growth in NFNP plots may be a result of trampling by caribou, as several broken stems on individual marked *B. nana* shrubs were seen in early June 2005. Thus, growth of these plants in NFNP plots may be limited purely by attraction by more palatable species such as *H. alpina* or *C. microchaeta*, rather than direct consumption of plant tissue by herbivores.

At MAT, however, the growth of fertilized individual *B. nana* plants seems to be facilitated by the presence of herbivores. This result is supported by community census and biomass harvest data, which show that *B. nana* is more abundant in NFNP plots than SFNP plots (Gough, unpublished data). While the paradigm describing the increase of *B. nana* in fertilized plots at MAT has been ascribed solely to competition for resources (Shaver et al. 2001), these results suggest otherwise. Neighborhood removal studies have shown that removal of potential resource competitors; in particular, removal of *Sphagnum* spp. allows *B. nana* to increase abundance at MAT (Hobbie et al., 1999). Additionally, recent work by Mack et al. (2004) has documented a net ecosystem loss of soil carbon storage in fertilized plots at MAT after 20 years of experimental nutrient addition. Thus, this decrease in soil carbon may be offsetting carbon storage in secondary tissues of deciduous shrubs associated with the shift at MAT to *B. nana*. While the mechanism of this loss is yet unknown, herbivores may be acting in an integral way with their ability to preferentially remove tissues from preferred plants such as graminoids and redistribute nutrients within this community. As graminoids respond to fertilization in many tundra ecosystems by increasing growth, herbivores may be responding to these increased nutrients in their preferred food sources. Thus, in MAT animals may be functioning to remove graminoids as potential competitors with shrubs, such as *B. nana*, for soil resources as well as redistributing soil nutrients away from fertilized plots.

### *2.5.4 Species abundance respond differently to increased soil nutrients and herbivory*

Supporting our predictions regarding scaling these species up to the community level, the relative cover of species overall reflected the individual growth data for species in each communities, with only a few exceptions. The relative cover of individual species increased seasonally in all treatments in both communities during 2004 and 2005 reflecting the seasonal growth of all five species. In DH, the graminoid *H. alpina* abundance was highest in fertilized unfenced areas. We predicted that there would be no difference in abundance due to herbivory when soil nutrients were higher for this species. Thus, not only is *H. alpina* more tolerant of herbivory when fertilized (Chapter 3, this volume), it seems that *H. alpina* may be facilitated by herbivory perhaps by decreasing attached litter associated with *H. alpina* tussocks in fertilized plots. *C. microchaeta* abundance was highest in fertilized plots when protected from herbivores. This result is similar to *E. vaginatum* and supports individual ramet growth data reported by Gough et al. (2007) and above. *C. microchaeta* may not be as tolerant of herbivory as *H. alpina* when growth is greater due to higher soil nutrient availability.

*E. vaginatum* abundance was lowest in fenced and fertilized plots, supporting Gough et al. (2007) and the individual growth results. Additionally, this species is relatively intolerant of herbivory (Chapter 3, this volume) and largely reflects the graminoid growth form results presented in Chapter 4 (this volume). However, *C. bigelowii* relative cover did not respond as predicted. Abundance was highest in non-fenced ambient conditions, and fertilization did not increase abundance of this species in either year nine or ten. However, herbivore exposure did decrease the abundance of *C. bigelowii* when fertilized suggesting that herbivores are selectively removing this species with higher soil nutrients.

*B. nana* relative abundance reflected the overall growth form responses to treatments for deciduous shrubs reported above in each community supporting our predictions. In MAT, it appears that the dominance of *B. nana* in fertilized plots may be partially explained by the selective removal of competitors for soil nutrients by herbivores. In DH, while *B. nana* increases in fertilized plots relative to ambient plots, the effect of herbivores was insignificant.

## 2.6 Conclusion

While traditionally herbivory has been historically seen as being of little importance to tundra plant communities with low NPP, these data and other recent work has shown that this conjecture may be unfounded (e.g. Bråthen et al., 2007, Eskilenen, 2008). Increased soil nutrients arising via warmer temperatures may add an additional dynamic to plant-herbivore interactions in the Arctic. Arctic plants respond differentially to herbivory and increased soil nutrient availability in species specific ways (Grellman, 2002) often depending on community context. The results presented here show how plants with similar growth forms respond differently to increased nutrients and herbivory. When soil nutrients are higher, graminoid growth and abundance, such as that of *H. alpina* in DH, were unaffected by herbivores. Alternatively *E. vaginatum* growth and abundance may be strongly reduced by herbivores in spite of increased soil nutrients. Additionally, *B. nana* showed opposite responses, in both growth and abundance, in each site. Herbivore presence seems to facilitate *B. nana* growing with higher soil nutrients in MAT, while in fertilized plots at DH herbivore presence has a negative effect. Thus, plant-herbivore interactions may be different for various communities as primary productivity and community composition change and respond differently to increased soil nutrients (Shaver et al. 2001). Further, as higher temperatures increase soil nutrient availability, herbivores may ultimately be able to affect changes in species composition and increases in NPP long attributed to simply to competition among plant species for higher soil nutrient. Herbivores may be facilitating shifts in MAT tundra towards deciduous shrubs increasing the ability for this community to offset increases in $CO_2$ from arctic soils through an increase in long-term carbon storage in secondary tissue. In DH, the opposite may be true; herbivores may be facilitating a shift in this community towards a grassland, decreasing the ability of DH tundra for long-term carbon storage. Thus, to understand the role plant communities will have when soil nutrient availability is higher due to warmer temperatures, herbivores must be considered.

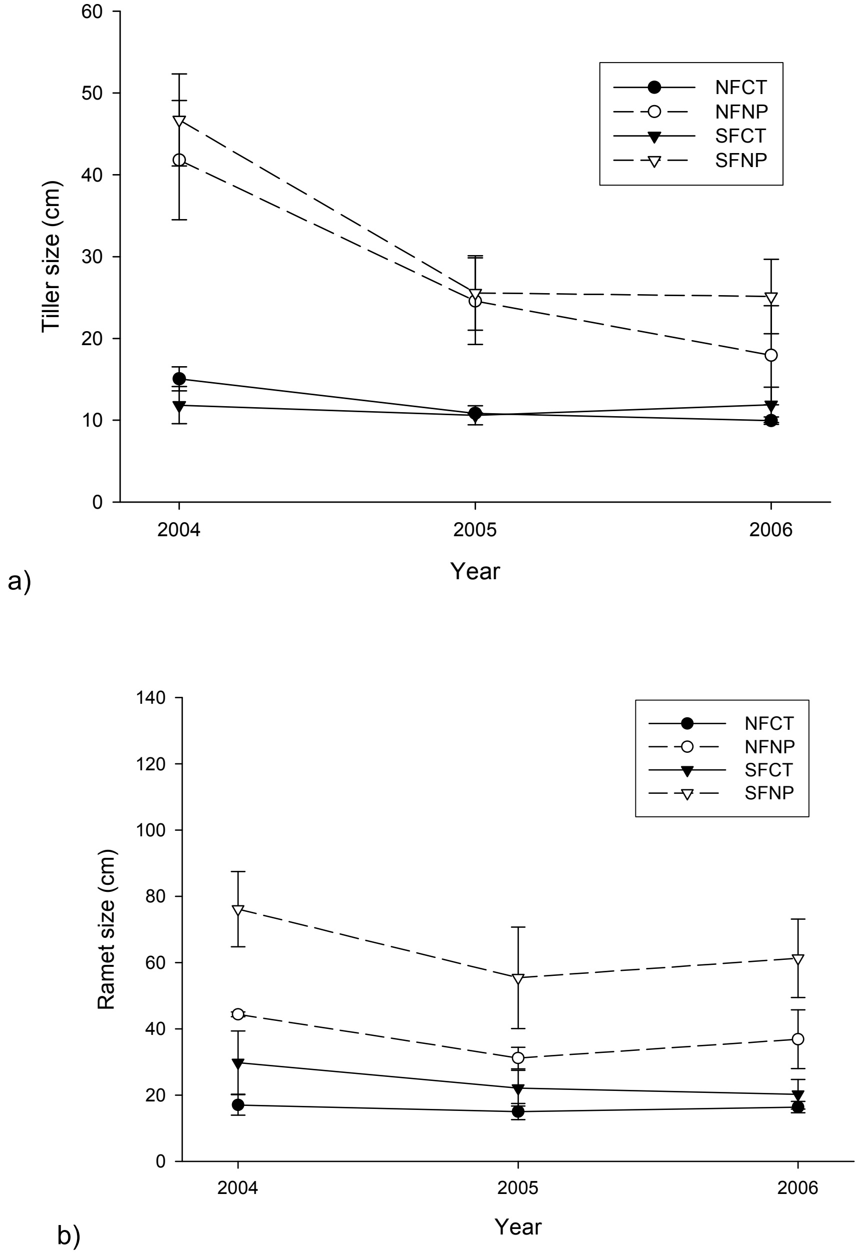

Figure 2.1 Yearly growth of two graminoid species in dry heath tundra at peak biomass in late-July 2004, 2005 and 2006: (a) *Hierochloe alpina* measured as mean tiller size (sum of all leaves within each tiller, then averaged within each tussock; n = 9), (b) *Carex microchaeta* measured as mean ramet size (sum of all leaf lengths with each ramet; n = 9 except n = 8 in NFCT),. 2004 represents the ninth year of treatments. Error bars indicate ± SE. Treatment abbreviations: NFCT = no fence control; NFNP = no fence, N + P; SFCT = small fence, control; SFNP = small fence, N + P.

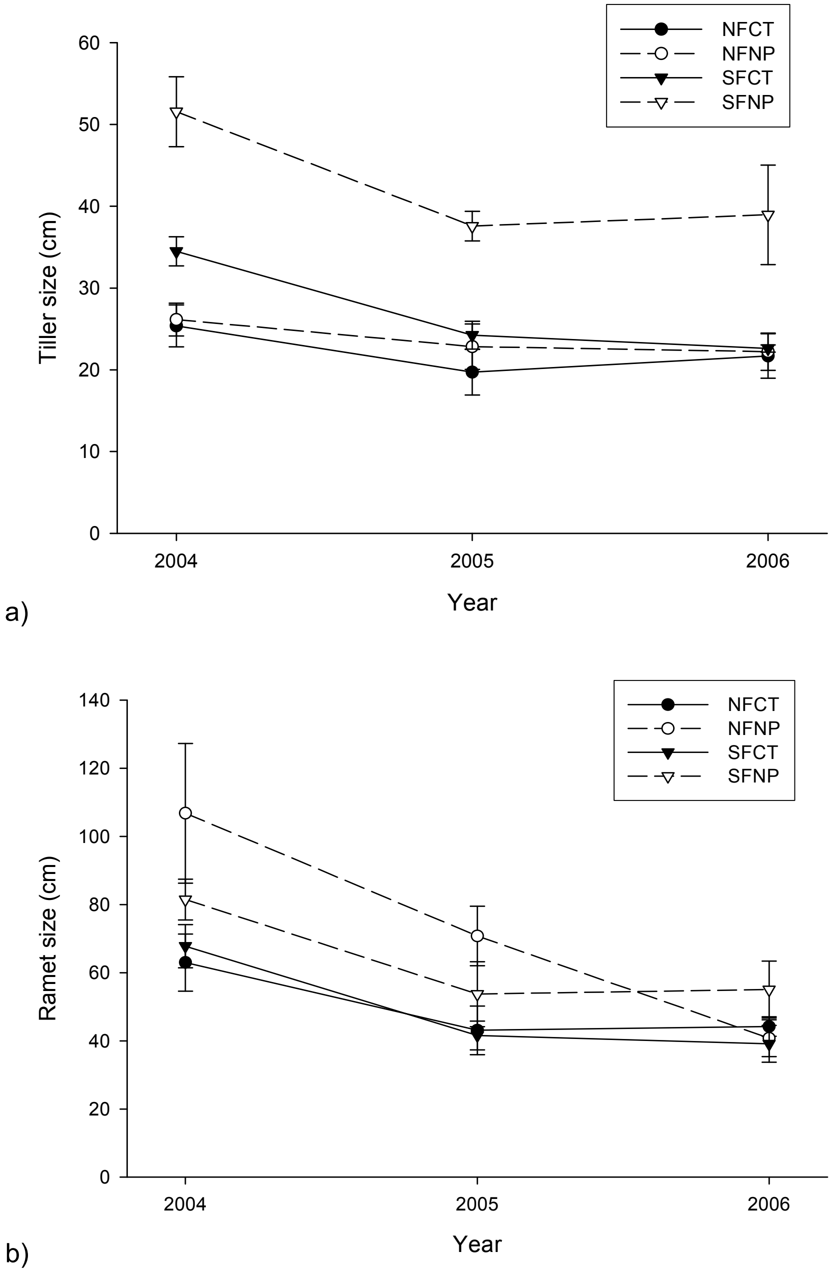

Figure 2.2 Yearly growth of three species moist acidic tussock tundra at peak biomass in late-July 2004, 2005 and 2006: (a) *Eriophorum vaginatum* measured as mean tiller size (sum of all leaves within each tiller, then averaged within each tussock; n = 12), (b) *Carex bigelowii* measured as mean ramet size (sum of all leaf lengths with each ramet; n = 12). 2004 represents the ninth year of treatments. Error bars indicate ± SE. Treatment abbreviations as in Figure 2.1.

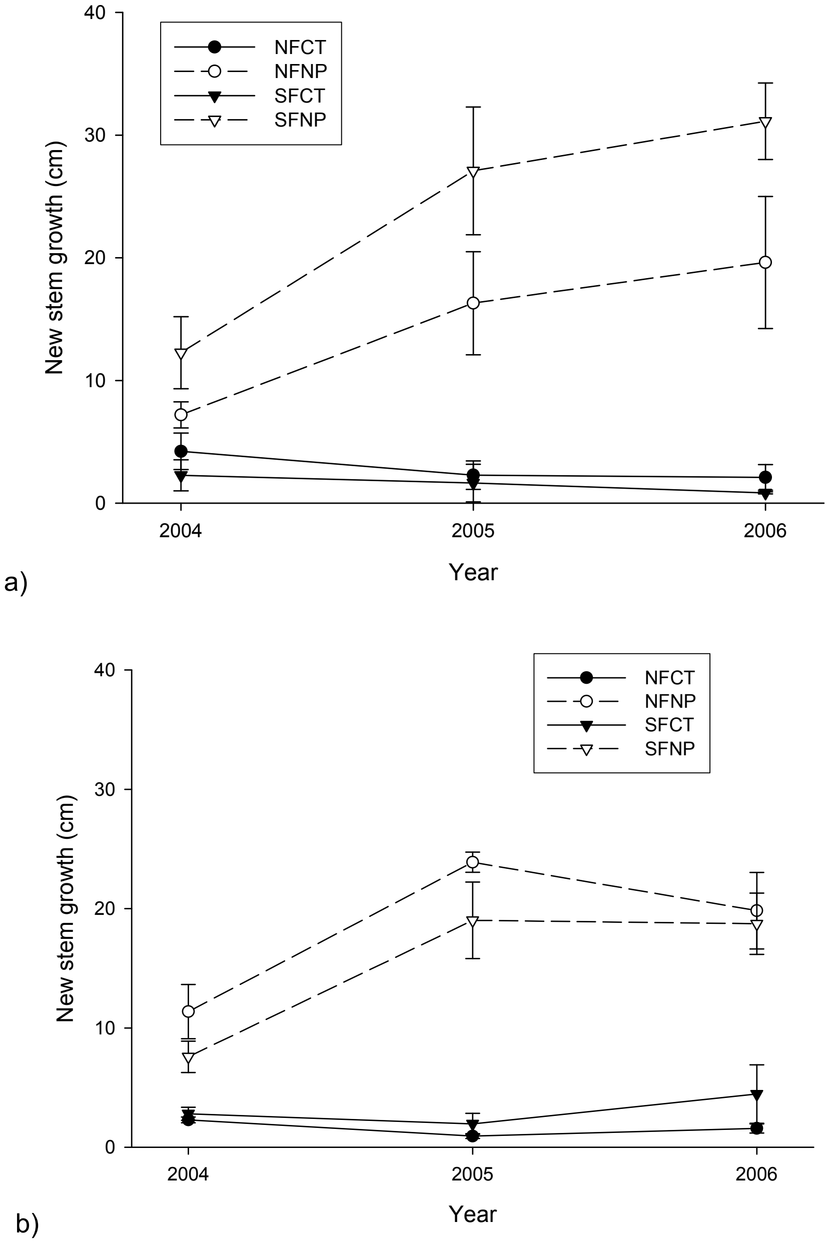

Figure 2.3 Yearly growth of *Betula nana* in dry heath (a) and moist acidic tussock tundra (b) at peak biomass in late-July 2004, 2005, and 2006 measured as mean new shoot length (n = 12 in MAT; n = 9 except n = 5 in SFCT in DH). 2004 represents the ninth year of treatments. Error bars indicate ± SE. Treatment abbreviations as in Figure 2.1.

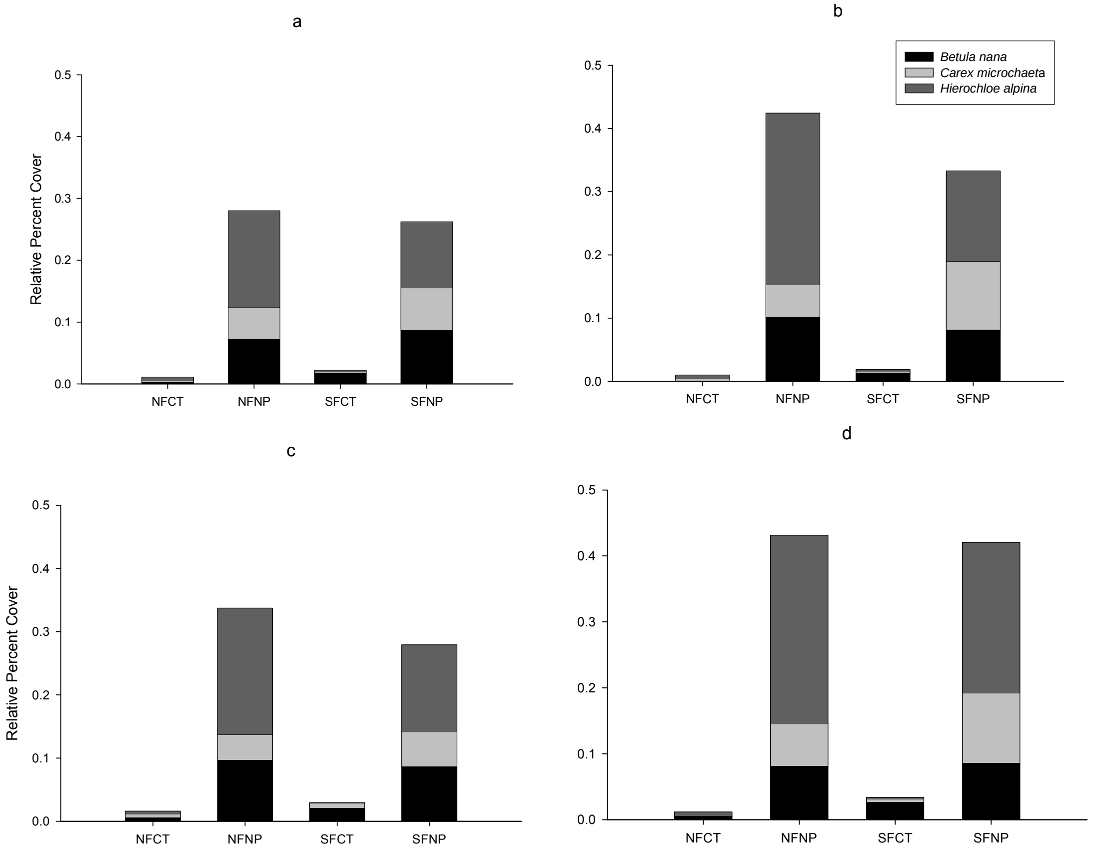

Figure 2.4 Relative percent cover of three species at DH in June 2004 (a) July 2004 (b), June 2005 (c) and July 2005 (d).

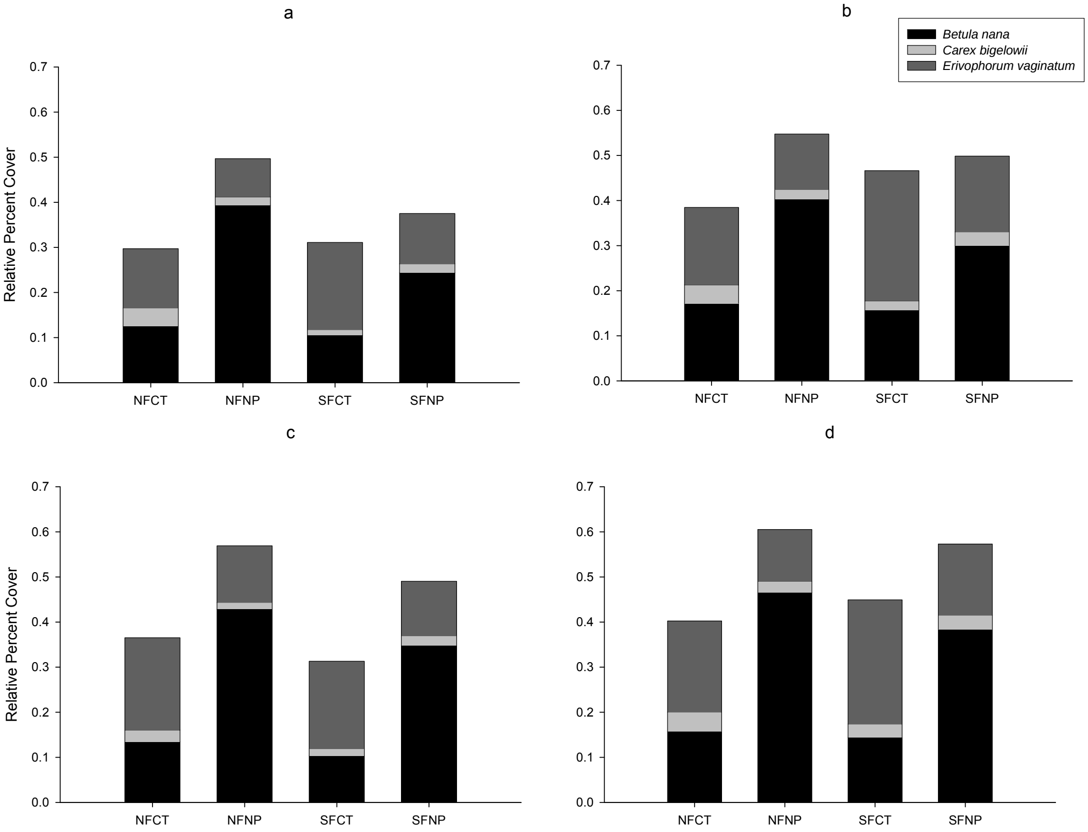

Figure 2.5 Relative percent cover or three species at MAT in June 2004 (a) July 2004 (b), June 2005 (c) and July 2005 (d).

Table 2.1 F-values for repeated measures analysis of between-subjects factor tests for growth in 2004, 2005, and 2006 for four tundra graminoids. See text for within-subjects effects results. Significant levels indicated by ***p<0.001, **0.001<p<0.01, *0.01<p<0.05, †0.05<p<0.1.

| Community | Species | DF | Fence | Fertilization | Fence x Fertilization |
|---|---|---|---|---|---|
| DH | *H. alpina* | 1, 21 | 0.02 | 77.99*** | 0.38 |
| | *C. microchaeta* | 1, 22 | 12.66** | 45.42*** | 0.24 |
| MAT | *E. vaginatum* | 1, 33 | 42.65*** | 17.38** | 9.62* |
| | *C. bigelowii* | 1, 30 | 0.94 | 2.82 | 0.3 |

Table 2.2 Source table for a repeated measures analysis of between-subjects factor tests for growth in 2004, 2005, and 2006 for *Betula nana* in two tundra communities. Individual plant was nested within block. Significant effects are bold for emphasis. See text for within-subjects effects results.

| Source | DF | MS | F | P |
|---|---|---|---|---|
| block | 3 | 0.895 | 1.36 | 0.26 |
| plant(block) | 8 | 0.571 | 0.87 | 0.55 |
| site | 1 | 1.63 | 2.49 | 0.12 |
| fence | 1 | 0.175 | 0.27 | 0.61 |
| site*fence | 1 | 0.014 | 0.02 | 0.88 |
| fert | 1 | 223.26 | 340.43 | < 0.0001 |
| site*fert | 1 | 2.416 | 3.68 | 0.06 |
| fence*fert | 1 | 1.088 | 1.66 | 0.20 |
| site*fence*fert | 1 | 5.602 | 8.54 | 0.005 |
| error | 61 | 0.656 | | |

Table 2.3 Mean response ratio (CT: ln(SFCT/NFCT); NP: ln(SFNP/NFNP)) ± SE for five tundra species. Significant levels indicated by ***p<0.001, **0.001<p<0.01, *0.01<p<0.05, †0.05<p<0.1.

| Species | Site | Treatment | 2004 | 2005 | 2006 |
|---|---|---|---|---|---|
| *B. nana* | DH | CT | - 0.33 ± 0.31 | 0.0 ± 0.26 | - 0.23 ± 0.37 |
| | | NP | 0.50 ± 0.25† | 0.48 ± 0.21* | 0.52 ± 0.3† |
| *C. microchaeta* | | CT | 0.63 ± 0.25* | 0.36 ± 0.21† | 0.21 ± 0.3 |
| | | NP | 0.52 ± 0.25* | 0.5 ± 0.21* | 0.53 ± 0.3† |
| *H. alpina* | | CT | - 0.26 ± 0.25 | -0.04 ± 0.21 | 0.14 ± 0.3 |
| | | NP | 0.12 ± 0.25 | 0.05 ± 0.21 | 0.12 ± 0.3 |
| *B. nana* | MAT | CT | 0.17 ± 0.22 | 0.06 ± 0.18 | 0.72 ± 0.26 |
| | | NP | - 0.39 ± 0.22† | - 0.39 ± 0.18* | - 0.05 ± 0.26 |
| *C. bigelowii* | | CT | 0.09 ± 0.22 | - 0.01 ± 0.18 | 0.23 ± 0.26 |
| | | NP | - 0.22 ± 0.22 | - 0.3 ± 0.18† | 0.5 ± 0.26† |
| *E. vaginatum* | | CT | 0.34 ± 0.22 | 0.23 ± 0.18 | 0.06 ± 0.26 |
| | | NP | 0.68 ± 0.22** | 0.52 ± 0.18** | 0.54 ± 0.27* |

Table 2.4 Summary of between subjects effects from nested repeated measures ANOVAs, conducted on five tundra species individually. Early and peak censuses are nested within 2004 and 2005, the ninth and tenth year of the study.

| Community | Species | DF | Fence | Fertilization | Fence x Fertilization |
|---|---|---|---|---|---|
| DH | *B. nana* | 1, 69 | 1.3 | 18.63*** | 0.5 |
| | *C. microchaeta* | 1, 69 | 3.12† | 26.81*** | 2.32 |
| | *H. alpina* | 1, 69 | 9.36** | 269.99*** | 3.11† |
| MAT | *B.nana* | 1, 93 | 23.18*** | 357.37*** | 8.25** |
| | *C. bigelowii* | 1, 93 | 4.84* | 349.92*** | 0.13 |
| | *E. vaginatum* | 1, 93 | 14.67*** | 54.21*** | 1.8 |

Table 2.5 Climate summaries for temperature and precipitation from the central weather station of the Arctic LTER at Toolik Lake. The long-term average (1988-2007) is bolded for comparison. Measurements in 2005 began in June with replacement of bad data loggers from the previous winter. These data are found at http://ecosystems.mbl.edu/ARC/weather/tl/index.shtml.

| | Precipitation (mm) | | | | | Temperature (°C) | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| year | May | June | July | August | September | May | June | July | August | September |
| 1988 - 2007 | 16.6 | 42.5 | 73.5 | 63.4 | 34.2 | -1.0 | 8.6 | 11.2 | 7.3 | -0.3 |
| 2003 | 24.6 | 20.3 | 154.2 | 102.1 | 42.7 | -3.3 | 8.6 | 8.7 | 5.9 | -3.0 |
| 2004 | . | 32.3 | 138.2 | 65.0 | 20.8 | . | 13.3 | 12.9 | 10.6 | -2.9 |
| 2005 | 5.1 | 22.4 | 66.6 | 17.3 | 18.5 | 0.4 | 9.2 | 8.6 | 8.7 | 1.8 |
| 2006 | 28.7 | 60.7 | 85.1 | 64.3 | 31.3 | -4.7 | 9.6 | 10.3 | 5.7 | 4.7 |

# CHAPTER 3

# WILL CLIMATE CHANGE AFFECT HERBIVORE TOLERANCE IN TWO COMMON ARCTIC GRAMINOIDS?

## 3.1 Abstract

Understanding plant tolerance of herbivory has proved to be difficult, as many factors, both intrinsic and extrinsic, contribute to any particular plant species' ability to respond to biomass removal by herbivores. In the Arctic, as temperatures continue to rise, tolerance of herbivory may change for plant species as soil nutrient conditions change. We studied how two Alaskan arctic graminoids tolerate both natural (by mammals) and manual (clipping) biomass removal when grown with artificially increased soil nutrients. The grass species *Hierochloe alpina* growing in dry heath tundra was able to tolerate biomass removal well when soil nutrients were more available. *H. alpina* size, with natural biomass removal, did not differ from plants with no biomass removal after only two months. Further, *H. alpina* with manual biomass removal recovered after one year. In contrast, the sedge *Eriophorum vaginatum*, growing in moist acidic tussock tundra, was less tolerant of biomass removal when soil nutrients were more available. While *E. vaginatum* plants with both natural and manual biomass removal were larger when grown with higher soil nutrients than those in ambient conditions, these plants were consistently smaller than plants with no biomass removal for two years following manipulation. These results support ideas posited by Wise and Abrahamson (2005) that plant tolerance of herbivory is dependent upon species specific intrinsic factors governing access to limiting resources. Thus, as the abiotic conditions in the Arctic change and soil nutrients become more available with warmer temperatures, species with similar growth forms and position in arctic food webs may differ with respect to herbivore tolerance.

## 3.2 Introduction

Plant tolerance is defined as the ability to regrow or compensate following biomass removal by an herbivore (Strauss and Agrawal 1999, Juenger and Lennartsson 2000). Tolerance involves interactions with herbivores that are often complex, and though extensively studied in agricultural monocultures, has only recently been documented in natural systems (Hjalten et al. 1993, Houle and Simard, 1996, Gonzalez-Teiber and Gianoli 2007). With the exception of grasses in grazing ecosystems (Ferraro and Oesterheld 2002), tolerance in many plant lineages has not been thoroughly explored (Juenger and Lennartsson 2000).

The evolutionary mechanisms of plant tolerance involve intrinsic factors, often associated with specific species, such as high relative growth rate, increased net photosynthetic rate following damage, and the ability to shift carbon and nutrient stores from root to shoot tissue following damage (Strauss and Agrawal 1999, Tiffin 2001). Also important are extrinsic factors: abiotic and biotic environmental factors such as soil nutrient availability, the timing of herbivore damage, and type of herbivore preying on the plant (Gavloski and Lamb 2000, Strauss and Agrawal 1999). Often interactions among these make elucidation of the relative importance of the individual factors difficult. However, some tolerance of herbivores is believed to be important ecologically and evolutionarily for many plant species (Crawley 1997), especially graminoids (Ferraro and Oesterheld 2002).

The intrinsic factors allowing for tolerance of mammalian herbivory have been studied for some common arctic plant species (e.g., Archer and Tieszen 1980, Archer and Tieszen 1983, Chapin and Slack 1979, Chapin 1980). Because nutrient allocation following biomass removal varies among arctic plant growth forms, plant tolerance may vary as well. Species such as graminoids and deciduous shrubs that have high rates of nutrient uptake and growth as well as large below-ground reserves are not thought to be negatively affected by biomass removal by herbivores. Alternatively, other growth forms, such as evergreen shrubs, lack these traits and are negatively affected by herbivory (Chapin 1980). However, among graminoids in other ecosystems, tolerance of herbivory has been shown to vary (Guitian and Bardgett, 2000). A recent meta-analysis suggests that while total plant biomass often seems negatively affected, the relative growth rate of graminoids often increases after defoliation events depending on plant recovery time and soil nutrient conditions (Ferraro and Oesterheld 2002). Thus, tolerance in arctic plants growing in different soil nutrient conditions may also vary both among and within species.

In the Arctic, while graminoids in general have been thought to be tolerant of herbivores (Archer and Tieszen 1980), studies of specific species growing in different tundra types have shown conflicting results. For example, biomass removal did not affect shoot growth in the sedges *Eriophorum vaginatum* and *Carex* spp. in ambient nutrient conditions as plants were able to shift nutrient resources from roots to shoots as well as increase soil nutrient uptake into root tissue following experimental biomass removal (Chapin and Slack 1980). More specifically, *E. vaginatum* growing in Alaskan coastal tundra seems very tolerant of biomass removal; growth was only reduced after four defoliation events within one season. Interestingly, seasonal leaf growth of *E. vaginatum* plants, with long-term experimental nutrient addition in moist acidic tussock tundra (MAT) in inland Alaska, was reduced when plants were exposed to herbivores compared to fertilized plants protected from herbivores (Gough et al. 2007). Additionally, fertilized exposed plants were the same size as exposed plants in ambient plots, suggesting herbivores consumed the additional biomass produced by the plants in response to greater soil nutrient availability. This may support the assertion that plant tolerance of biomass removal differs between low and high nutrient conditions (Ferraro and Oesterheld 2002), and may even be lower with higher nutrient conditions (Strauss and Agrawal 1999). Thus, the tolerance of arctic graminoids remains unclear for many reasons, including how tolerance may vary as plants respond to changes in soil nutrient availability expected with regional increases in temperatures (Hinzman et al., 2005).

Arctic ecosystems are often considered to be nutrient limited because decomposition rates are restricted by cold temperatures and thus soil nutrient input rates from decomposition are low relative to more temperate ecosystems (Schimel et al. 1997). However, this condition may be changing as temperatures in the Arctic are increasing at a faster rate than most other locations on

Earth and are predicted to continue to increase in the future (Lachenbruch and Marshall, 1986; Overpeck et al. 1997; Serreze et al. 2000; Sturm et al. 2002; Alley et al. 2003). Higher arctic temperatures can alter the abiotic conditions controlling nutrient availability for plants (Hinzman, 2005). For example, warmer temperatures have been shown to increase the number of snow-free days per year, soil temperature, and the depth to permafrost (Osterkamp et al. 2000; Sturm et al. 2001). Higher temperatures also increase soil decomposition and soil nitrogen mineralization rates, potentially increasing the pool of soil nitrogen available to plants (Nadelhoffer et al. 1991; Schimel et al. 1996). More soil nutrients often lead to increases in net primary productivity (NPP) and changes in plant species composition (Chapin et al. 1996; Shaver et al. 2001; Hinzman et al. 2005). Indeed, experimental warming studies in various arctic ecosystems have shown that plant communities respond to increased temperature with changes in individual species abundance (e.g., Hollister et al., 2005; Wahren et al., 2005; Jonsdottir et al., 2005; Walker et al., 2006). Frequently, warming favors some plant species, such as graminoids or deciduous shrubs, that have higher growth rates and nutrient uptake ability than other members of the plant community (Dormann and Woodin, 2002).

While the vegetation response to increased nutrients is well studied in several arctic communities, the effects of increased soil nutrients on herbivores and plant tolerance of herbivores is less understood. The vole species *Microtus oeconomus* and *Microtus miurus* are thought to be important predators of plants in MAT, eating primarily the tussock forming sedge *Eriophorum vaginatum* (Batzli and Lesieutre, 1991, personal observation). In Alaskan dry heath tundra (DH), voles and caribou (*Rangifer* sp.) are thought to be important consumers of lichens and the grass *Hierochloe alpina*, especially following experimental fertilization of this community (Batzli and Henttonen, 1990; personal observation). Voles and to a lesser degree caribou are known to selectively forage on tundra plants (Batzli and Henttonen, 1990; Batzli and Lesieutre, 1991; Olofsson, 2005). These arctic herbivores will select plant species with lower secondary compounds for food (Batzli and Lesieutre, 1991; Hamback et al., 2002). Plants at both DH and MAT commonly show biomass removal presumably by herbivores (personal observation), although the exact timing of this biomass removal is unknown. Because of this unknown, experimental herbivory studies may be able to capture plant responses to biomass removal and estimate plant tolerance of natural herbivory (Baldwin, 1990). Experimental herbivory studies have been used in the past for arctic graminoids (e.g. Chapin and Slack, 1979; Archer and Tieszen, 1993). Additionally, experimental herbivory studies in general have been shown to be fairly accurate in estimating plant growth (Lehtila and Boalt, 2004) and are especially useful in finding true estimates of tolerance when the timing of natural herbivory events is not known (Tiffin and Inouye, 2000).

Because many arctic plant species are known to respond differently to increased nutrient availability (Press et al., 1998), preferred plant species abundance and quality, e.g. plant forage with higher nutrient content, may change as well (Graglia et al. 2001, Aerts et al., 2007), thus changing the relationship between plants and their herbivores. Therefore, as NPP increases, communities may support more animals, increasing the amount of herbivory plants experience (Oksanen et al., 1980). How might plant tolerance of herbivores change when plants have greater access to soil nutrients?

To begin to answer this question, we conducted research in two different arctic plant communities in northern Alaska: moist acidic tussock (MAT) and dry heath (DH) tundra, where the graminoids *E. vaginatum* at MAT and *H. alpina* at DH respond differently when fertilized. While both species increase individual plant size with higher soil nutrients, *H. alpina* has come to dominate fertilized plots at DH while *E. vaginatum* becomes less dominant than in control plots as deciduous shrubs also increase with fertilization at MAT. To address how tolerance of these two arctic graminoids differs with increased soil nutrients, we conducted a manual herbivory experiment in which we clipped biomass (once or multiple times within one growing season) of fertilized *E. vaginatum* and *H. alpina* plants in MAT and DH, respectively. we compared these to fertilized plants that were protected from herbivores by fences as well as fertilized plants that experienced natural herbivory by herbivores, primarily small mammals. At MAT, we selected plants from both ambient nutrients plots and fertilized plots, however, at DH, because *H. alpina* is rare in ambient plots, we only performed this experiment on plants in fertilized plots. We specifically addressed three predictions. First, because we did not know if experimental clipping fully captures the effect of a natural herbivory event and also did not know the actual timing of biomass removal by actual herbivores, we explored the null hypothesis that the magnitude of tolerance, measured in leaf size and flowering, is the same for plants experiencing manual herbivory and those with natural herbivory. Second, because tolerance of *E. vaginatum* specifically has been shown to be reduced only following repeated biomass removal (Chapin and Slack 1979, Archer and Tieszen, 1983), and regrowth response may only be detected following repeated natural herbivory events. Thus, we predicted that plants receiving multiple experimental clippings would be less tolerant, having smaller leaves and fewer flowers, than plants experiencing only one experimental clipping. And lastly, we hypothesized that *E. vaginatum* and *H. alpina* growing with increased nutrients have high tolerance of herbivores. More specifically, we predicted that leaf size and flowering of these species would be greater for plants following biomass removal than plants with no biomass removal, perhaps showing evidence for overcompensation. Testing these three hypotheses together will begin to explain how graminoid tolerance to herbivory may be affected by higher soil nutrient availability in a warmer Arctic.

## 3.3 Methods

### *3.3.1 Study sites*

The location of this research was the Arctic Long Term Ecological Research (LTER) site at Toolik Lake Alaska (68.2° N, 149.6° W, 760 m a.s.l.). Both MAT and DH have been subjected to experimental manipulation since 1989 as part of the terrestrial portion of the Arctic LTER. These two communities of focus differ in diversity, NPP, species composition and response to experimental nutrient additions (Table 1.1). A factorial design was incorporated to test plant responses to the exclusion of herbivores along with the addition of both N and P (10g/m$^2$/yr as $NH_4NO_3$ and 5g/m$^2$ /yr as $P_2O_5$) within blocks of 5 x 20 m plots in both communities beginning in 1996. One plot within each block was randomly assigned N and P addition (NP) and another as control (CT). Fertilizer treatment to NP plots began following snowmelt in June 1996 in the form of pellets, and was repeated yearly as part of long-term maintenance of terrestrial LTER plots.

Half of each 5 x 20 m plot is unfenced (NF), while the remaining area consists of the combination of small and large mammal exclusion fences. To exclude large mammals such as caribou, 5 x 10 meters of a random half of each plot was enclosed in a large mesh fence (LF: 15.2 x 15.2 cm openings, approximately 1.2 m in height). A smaller mesh fence (SF: 1.3 x 1.3 cm openings, approximately 0.8 m in height) was built within a random 5 x 5 meters of the larger fence to exclude small mammals such as ground squirrels, voles and lemmings. The small-mesh fence was buried in the soil at least 10 cm at construction to prevent animals from burrowing into the plots.

Plots were replicated within four blocks at MAT and three blocks at DH. For this study, we did not consider the effects of small mammals and large mammals separately, thus all data were collected from unfenced areas and areas with both small and large mammal exclusion (SF). Therefore, each block contained plots with four possible combinations of fence and fertilization treatment at each site: unfenced control (natural herbivory + CT), fenced control (no herbivory + CT), unfenced N + P (natural herbivory + NP), and fenced N + P (no herbivory + NP). While there are herbivorous insects in these communities, their effect on leaf biomass appeared to be minimal compared to that of mammalian herbivores (personal observation). These plots may retain snow on the immediate northern edge of fences for 2-3 days early in the season relative to unfenced areas (C. Moulton, personal communication). To avoid this snow accumulation, all sampled plants were at least 0.5 m from the edge of the fence.

### *3.3.2 Mammalian herbivores*

Five species of microtine rodents have been recorded on the north slope of Alaska (Batzli et al., 1980). These include three species of voles (*Microtus oeconomus*, *M. miurus*, and *Clethrionomys rutilis*) and two lemming species (*Dicrostonyx rubricatus* and *Lemmus sibericus*). Of these, the tundra vole (*M. oeconomus*) and singing vole (*M. miurus*) are common in communities near the Arctic LTER at Toolik Lake (Batzli and Lesieutre, 1995). Specifically at

MAT, tundra voles are commonly seen (personal observation) along with evidence of their presence (hay piles, trails and fecal deposits) during cyclical outbreak years. Additionally, singing voles and collared lemmings (*D. rubricatus*) have been found in rocky areas very near DH (Batzli and Henttonen, 1990; pers. obs.). Batzli and Henttonen (1990) suggested that rodent densities in these tundra communities are limited by plant food availability, and animals seem to show strong preference for preferred plant species, particularly *E. vaginatum* and *Carex* spp. Additionally, these authors suggest small mammals in these communities may be limited top-down by predator abundance similar to lemmings in coastal tundra (Batzli et al. 1980).

While transient, caribou are commonly sighted near the Arctic LTER at Toolik Lake (pers. obs.). Toolik Lake lies within the range of the Central Arctic Herd (D. Klein, personal communication; Lenhart 2002); their primary calving grounds are far to the north. Thus caribou are not thought to be common foragers of plants in MAT. At DH however, caribou feces are frequently seen following snowmelt. Thus, DH may be an important winter habitat for caribou as snow cover is often less here than other communities (Cheng et al. 1998).

### *3.3.3 Plant species*

#### 3.3.3.1 *Eriophorum vaginatum*

*E. vaginatum* is a tussock-forming sedge common in northern Alaska. This species is an important component of MAT, and is thought to be an important food source for microtine rodents (Batzli and Lesieutre, 1995). Following snowmelt in early June in years when voles are abundant, whole tussocks of *E. vaginatum* have extensive biomass removed by small mammals. Large portions of tussocks, including inflorescences, are clipped. In addition to a direct food source, voles create haypiles of *E. vaginatum* litter associated with fecal deposits, and may use these haypiles for shelter (personal observation).

#### 3.3.3.2 *Hierochloe alpina*

*H. alpina* is a grass species found at low abundances in many heath communities in northern Alaska (Walker et al. 1994). When nutrients experimentally become more available, *H. alpina* increases dramatically in growth, forming tussocks and becoming much more common in this community (Gough et al. 2002). Additionally, *H. alpina* has been shown to be a preferred forage plant for caribou (Boertje, 1984).

### *3.3.4 Manual herbivory*

To test tolerance of *E. vaginatum* at MAT at two levels of nutrients, we established a 2 x 4 factorial design with fertilization (added N and P or control) and herbivory type (no herbivory, natural herbivory, manual once, and manual repeated) as treatments. We compared plants located in fences and protected from natural herbivores (no herbivory) to plants with two different levels of experimental clipping (manual once and manual repeated) and also to plants randomly located in unfenced plots that had natural herbivory. At DH to test tolerance of *H. alpina*, we had a simpler 1 x 4 design where we compared tolerance among the same four herbivory types growing with added soil nutrients, because there were too few individual *H. alpina* plants in ambient nutrient plots to replicate manual herbivory.

To begin manual herbivory treatments, we randomly selected undamaged tussocks within SF plots. We then removed (clipped to moss layer within tussocks) half of the leaves of six *E. vaginatum* tussocks in each SFNP and SFCT plots at MAT on 15 June 2004, and six *H. alpina* tussocks in SFNP plots at DH on 16 June 2004. Three of these tussocks were labeled "manual once." To determine the effect of repeated biomass removal on these species, we repeated clipping two additional times on the other three tussocks in each plot (June 29th and July 13th, 2004 at MAT; and June 29th and July 12th at DH). These we labeled "manual repeated". Six tillers on each tussock were tagged at clipping in June 2004. We selected six tillers on three tussocks from inside fences with no evidence of herbivory and labeled these "no herbivory", and six tillers on three tussocks outside fences with obvious signs of herbivory and labeled these "natural herbivory". For each species, tillers consisted of between two and four leaves which were measured repeatedly to estimate regrowth following biomass removal. We measured regrowth as the sum length of all leaves on each tiller bi-weekly from late June to early August 2004, repeating these measurements three times during 2005 (late June, mid-July, and early August), and once in mid-July 2006. To determine how sexual reproduction was affected by biomass removal, we counted the total number of inflorescences on each tussock of both species concurrent with tiller measurements.

### *3.3.5 Statistical analysis*

To meet parametric model assumptions, we natural log-transformed tiller length prior to analysis. For *H. alpina*, we used repeated measures ANOVA to test regrowth over time within 2004 with individual plants nested within block, and herbivory type (none, manually clipped once, manually clipped repeatedly, natural) as the main effect. For *E. vaginatum*, we also used repeated measures ANOVA for 2004 with individual plants nested within block, and both fertilization and herbivory type as factorial main effects. To determine patterns of regrowth over years, we used a repeated measures ANOVA of plant growth at peak biomass (mid-July of each year) with main effects the same as described above. To compare among means within groups post-hoc we used Tukey's HSD. Because of multiple zeros in flower data sets, we used PROC GENMOD and a Poisson distribution with a log-link function to determine differences among treatments for each species in each site. SAS Version 9.1 for Windows was used for all analyses (SAS institute, Cary, NC).

## 3.4 Results

### *3.4.1* Hierochloe alpina

#### 3.4.1.1 Seasonal response to biomass removal in 2004

Two weeks after the start of this experiment, patterns among treatments seemed established with the main effect of herbivory significantly reducing *H. alpina* size (Figure 3.1, $F_{3,24} = 49.05$, $p < 0.0001$). While fertilization increased size (relative to non-fertilized plants with no herbivory, Figure 3.1) natural herbivory significantly reduced *H. alpina* size at week two compared to protected plants. Similarly, plants in both fertilized manual herbivory treatments (manual once and manual repeated) were significantly smaller than those with no herbivory over the course of measurements in 2004 although these experimentally clipped plants did not differ from each other at week two. Manual repeated plants, reclipped at week two, were significantly smaller than all other fertilized plants at week four, and remained similar to plants that had not been fertilized

(Figure 3.1) for the remainder of 2004. A few patterns did vary among treatments within weeks as shown by a significant week*herbivory interaction ($F_{6,48} = 12.25$, $p < 0.0001$). For example, plants with natural herbivory recovered and were not different from plants with no herbivory at the end of 2004. Also, natural herbivory and manual once plants were not different from each other at week four; however, manual once plants were smaller than natural herbivory plants by the end of 2004. Additionally, in the statistical analysis, block was a significant effect ($F_{2,24} = 5.01$, $p = 0.02$), likely reflecting poor growth of fertilized manual repeated plants in block 3 compared to the other two blocks at DH.

### 3.4.1.2 Recovery from biomass removal

Supported by a significant year effect ($F_{2,42} = 11.53$, $p < 0.0001$), all fertilized *H. alpina* plants were approximately half as large in 2005 and 2006 than in 2004 (Figure 3.2). However, the pattern seen among herbivory treatments at the end of 2004 was similar in 2005 and 2006. Plants with manual once and natural herbivory did not differ from those with no herbivory measured at peak growth in late July of both 2005 and 2006 suggesting *H. alpina* is tolerant of herbivory when fertilized. Manual repeated plants remained significantly smaller in 2005 than all other treatments (significant herbivory effect: $F_{3,21} = 4.92$, $p = 0.01$, Figure 3.2). However, by 2006, these plants recovered and were not different from other herbivory treatments.

### 3.4.1.3 Effects of biomass removal on flowering

There were marginally more *H. alpina* flowers for most treatments (excluding natural herbivory) in 2005 than in 2006 (Table 3.1; $\chi^2_1 = 2.61$, $p = 0.11$). However, there were no significant differences in total number of inflorescences among herbivory treatments for either 2005 or 2006 ($\chi^2_3 = 2.36$, $p = 0.5$). Because of substantial variation among treatments within years, there was no discernible pattern with respect to flowering among herbivory categories for this species.

### *3.4.2* Eriophorum vaginatum

#### 3.4.2.1 Seasonal response to biomass removal in 2004

Similar to *H. alpina*, size patterns among treatments of *E. vaginatum* at MAT were established by week three of the experiment and remained consistent for the duration of 2004. There was a significant interaction between fertilization and herbivory ($F_{3,77} = 3.61$, $p = 0.02$, Figure 3.3a and b), suggesting that *E. vaginatum* tolerance of herbivory may be affected by nutrient availability. This interaction is driven by a greater magnitude of response to biomass removal for fertilized tillers relative to ambient plants. Fertilized tillers with no herbivory were significantly larger than all other treatment combinations (Figure 3.3b) and substantially larger than fertilized plants with herbivory. Further, while smaller than fertilized plants with no herbivory, ambient nutrient plants with no herbivory were larger than any plants with biomass removal (Figure 3.3a). Natural herbivory reduced size of both fertilized and ambient nutrient plants to the same extent, and these plants were larger than experimentally clipped plants. Interestingly, ambient manual repeated plants were larger than fertilized manual repeated plants and not different from fertilized manual once plants for most of 2004 (Figure 3.3a and b). Fertilized manual once plants were significantly larger than ambient manual once, and plants in both these treatments were larger than manual repeated plants in fertilized plots throughout 2004 (Figure3.3a and b). Herbivory type varied within weeks as well (significant week*herbivory interaction, $F_{6,154} = 18.37$, $p < 0.0001$), perhaps reflecting the fact that manual repeated tillers in both fertilized and ambient conditions were reclipped at week two and four.

#### 3.4.2.2 Recovery from biomass removal

As with *H. alpina*, almost all *E. vaginatum* plants were smaller in 2005 and 2006 than in 2004. However, the general pattern seen among treatments in 2004 continued in 2005 and 2006. There was a significant fertilization and herbivory interaction over the three years ($F_{3,77} = 3.06$, $p = 0.03$). While all plants were affected by biomass removal, the relative decrease in size was greater for fertilized plants (Figure 3.4b). Fertilized plants with no herbivory were significantly larger than ambient no herbivory plants and all herbivory treatments across all three years (Figure

3.4a and b). Additionally, in 2005 and 2006 there was no difference between fertilized natural herbivory and fertilized manual once plants. Further, manual once plants increased in size over all three years in both fertilized and ambient plots suggesting a gradual recovery from low intensity herbivory (as supported by a significant year*herbivory interaction, $F_{6,154} = 5.99$, $p < 0.0001$). While there was no difference between ambient manual once and ambient manual repeated in 2004, there was a significant difference between these in both 2005 and 2006 suggesting that multiple biomass removal suppressed plant size in the long term (Figure 3.4a).

#### 3.4.2.3 Effects of biomass removal on flowering

Although there was a slight tendency for *E. vaginatum* to produce fewer flowers when fertilized (Table 3.1), no differences could be detected statistically among herbivory treatments in 2005 or 2006 ($\chi^2_3 = 3.69$, $p = 0.3$). However, year was a significant factor as *E. vaginatum* plants produced more flowers in 2005 than 2006 (Table 2, $\chi^2_1 = 76.51$, $p < 0.0001$).

## 3.5 Discussion

### *3.5.1 Climate factors affecting growth in 2005 and 2006*

Both *E. vaginatum* and *H. alpina* plants in most treatments grew less in 2005 and 2006. Climate factors may explain this reduction in growth, as tundra species in general are thought to be affected by previous year's temperature and precipitation (e.g. Shaver and Laundre, 1997). Both average daily temperature and precipitation for the years of this study deviated from the average values for climate factors (Table 2.5). While 2003 was a particularly wet year with average temperatures, 2004 temperatures were much warmer than average. Further, 2005 was particularly dry and slightly warmer than average. Both *H. alpina* and *E. vaginatum* have been shown to have reduced physiological capacity for growth when grown in temperatures above 15 °C (Tieszen 1973, Kummerow et al. 1980, Ellis and Kummerow 1982). While the daily average temperatures did not reach 15°C during any one year (Table 2.5), daily maximum temperature often did. Thus, higher temperatures in 2004 and much lower precipitation in 2005 may explain the smaller size for most plants in this study in both 2005 and 2006.

### *3.5.2 Response to natural and manual herbivory differ*

Contrary to our null prediction that there would be no observable differences between natural and manual herbivory, we found that growth and recovery among natural and experimental treatments varied among years for both species. This may reflect the timing of biomass removal events. While the timing of experimental clipping in this study is known, natural herbivory events occurred prior to clipping in the spring 2004 and were not witnessed. Thus, perhaps plants with natural herbivory had additional time to grow before measurements began than manual plants. With this caveat stated, *E. vaginatum* and *H. alpina* responded differently to manual herbivory and natural herbivory. Both experimental treatments affected *E. vaginatum* more so than *H. alpina*. Fertilized *H. alpina* plants with experimental clipping recovered and were not different from plants with no herbivory: manual once plants recovered by 2005 and manual repeated plants recovered by 2006. However, while manual once *E. vaginatum* plants in both fertilized and ambient conditions were not different from fertilized plants with natural herbivory by 2005, fertilized plants clipped repeatedly never regrew to levels similar to those with natural herbivory. Although not statistically different from plants with natural herbivores, fertilized manual once plants seemed to be increasing growth with each successive year following biomass removal. This suggests that plants with natural herbivores may suffer from a ‘legacy of herbivory’ where these plants have experienced natural herbivory often enough that overall growth through time may be suppressed.

### *3.5.3 Multiple biomass removal effects on tolerance*

We predicted that tolerance of plants receiving multiple experimental clippings would be less than those experiencing only one clipping event. Results differed between the two study species, with repeated biomass removal decreasing *H. alpina* size in only the short term. In 2004, manual repeated plants were the smallest and comparable in size to plants with no herbivory in ambient nutrient conditions. In 2005 these plants remained smaller than other fertilized plants, but by 2006 manual repeated plants were not different from fertilized plants with no herbivory. This suggests that *H. alpina* is tolerant of multiple repeated herbivory events when soil nutrients are higher. This lends additional support that herbivores may be ameliorating intra-plant competition for an alternative resource such as space to grow within a tussock (Wise and Abrahamson, 2005).

*E. vaginatum* growth has previously been shown to be negatively affected by repeated biomass removal events (Chapin and Slack 1980, Archer and Tieszen, 1983). Interestingly, in this study repeated experimental biomass removal decreased *E. vaginatum* in fertilized, but not in ambient conditions in 2004. Although smaller than ambient plants with natural herbivory, manual repeated *E. vaginatum* plants in ambient conditions were larger than manual once plants. Ambient manual once plants recovered slowly by 2005; however, ambient manual repeated did not. The relative decrease in size was greatest for fertilized manual repeated plants, relative to plants with no herbivory. This also supports the notion that *E. vaginatum* is less able to respond to biomass removal by herbivores when soil nutrients are more available, perhaps because herbivory is affecting competition for an alternative resource (Wise and Abrahamson, 2005).

### *3.5.4 Tolerance of* H. alpina *and* E. vaginatum *grown with higher nutrients*

We predicted that tolerance would be higher for both species when grown with increased nutrients: this was only supported for *H. alpina*. Fertilized *H. alpina* plants with biomass removal were the same size as plants with no herbivory after one year, while leaves of *E. vaginatum* plants in herbivory treatments were half as large as no herbivory plants. Additionally, the magnitude of the negative response to biomass removal initially was much greater for fertilized *E. vaginatum* than for fertilized *H. alpina* suggesting that *H alpina* is more tolerant than *E. vaginatum* in both the short and long term.

A recent review by Wise and Abrahamson (2007) compares three different models of herbivory tolerance in plants. These authors suggest that their model, the limiting resource model or LRM (Wise and Abrahamson, 2005), is more flexible with respect to differences along resource gradients than older models of tolerance and compensation. The results of tolerance in *H. alpina* and *E. vaginatum* may be addressed by LRM. *H. alpina* growth is greatly increased by fertilization (Figure 3.1 and 3.2; Gough et al. 2002, 2007), and thus was able to quickly replace biomass lost to herbivory when grown with increased soil nutrients. This suggests that herbivores are not affecting the ability of *H. alpina* to access increased nutrients, but rather may be affecting another important abiotic factor. Because tolerance seems to be higher when fertilized, perhaps herbivory is ameliorating the effect of intra-plant competition for leaf access to light for photosynthesis among *H. alpina* plants as predicted by LRM (Wise and Abrahamson, 2007). Alternatively, *E. vaginatum* seems less tolerant of herbivory when fertilized because the magnitude of response to protection from herbivores was greater for fertilized plants than ambient plants. Fertilized protected plants were approximately twice as large as the mean of all fertilized herbivory treatments, while ambient plants were only 20% larger. This suggests that when this species is released from soil nutrient limitation, herbivores have a stronger effect on plants and may be affecting acquisition of an alternative resource according to LRM (Wise and Abrahamson, 2007). Further, *E. vaginatum* at MAT, while performing well when fertilized, is excluded by the dwarf shrub *Betula nana* after 17 years of experimental fertilization (Shaver et al. 2001). Herbivores may be partially responsible for this change, as they may be negatively affecting the growth of *E. vaginatum*. Herbivores may be attracted to *E. vaginatum* in fertilized plots, and by consuming fertilized individuals preferentially they may by exacerbating the limitation of an alternative resource, such as light, in the presence of increased growth of *B. nana* when fertilized.

### *3.5.5 Plant tolerance of herbivory with increased temperatures*

Soil nutrient limitation for arctic plants is expected to change in the future as the Arctic continues to warm (Schimel et al. 1997, Hinzman et al. 2005). While plant responses to increased nutrients is beginning to be understood in both MAT and DH (e.g. Shaver et al. 2001, Gough et al. 2002), it is only beginning to be known how herbivore populations may respond to increased nutrients in the plants they eat and how tolerant plants may be affected by these changes (Grellman, 2002). While tolerance may be determined by the evolutionary history of species (Núñez-Ferán et al. 2007, Foroni et al. 2003), tolerance of plants in this study varied with resource availability. As plants respond to increased nutrient availability from higher temperatures, tolerance may differ for other graminoids as well depending on species-specific context. Graminoids such as *H. alpina* that seem to have evolutionary mechanisms to respond positively to increased nutrients in spite of herbivory may become more common in tundra communities. While those, such as *E. vaginatum*, that may not have the ability to sufficiently increase growth to offset biomass removal by herbivores may become less common or extinct within plant communities. This may especially be true if different herbivore populations themselves change in response to increased nutrients in the preferred plants they eat. Different herbivores, for example voles and caribou, have been shown to affect arctic plants differently in species-specific ways (e.g., Batzli et al. 1980, Grellman, 2002). Thus, the species-specific context of evolutionary tolerance of herbivores should play a role in determining future plant community structure as soil nutrients become more available. How different plants respond to herbivores should be considered along with other biotic interactions, such as competition, to fully understand how these communities are to change under future climate scenarios.

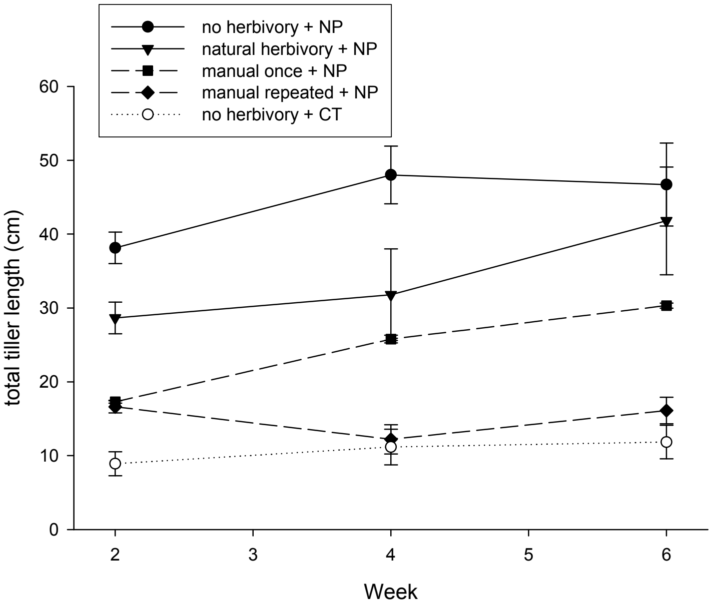

Figure 3.1. *Hierochloe alpina* growth in 2004 following biomass removal by experimental clipping and natural herbivory. Week 0 represents the week of June 14, 2004. See text for description of treatments. Plants grown without fertilization but with protection from herbivores (no herbivory + CT) are shown here for comparison, but not included in statistical analysis.

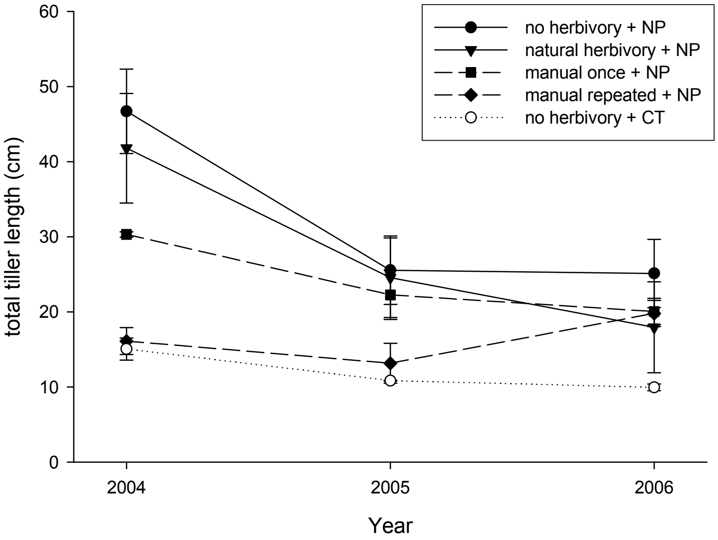

Figure 3.2. *Hierochloe alpina* growth recorded in mid-July 2004, 2005, and 2006 following biomass removal by experimental clipping and natural herbivory in mid-June 2004. Treatments as in Figure 3.1.

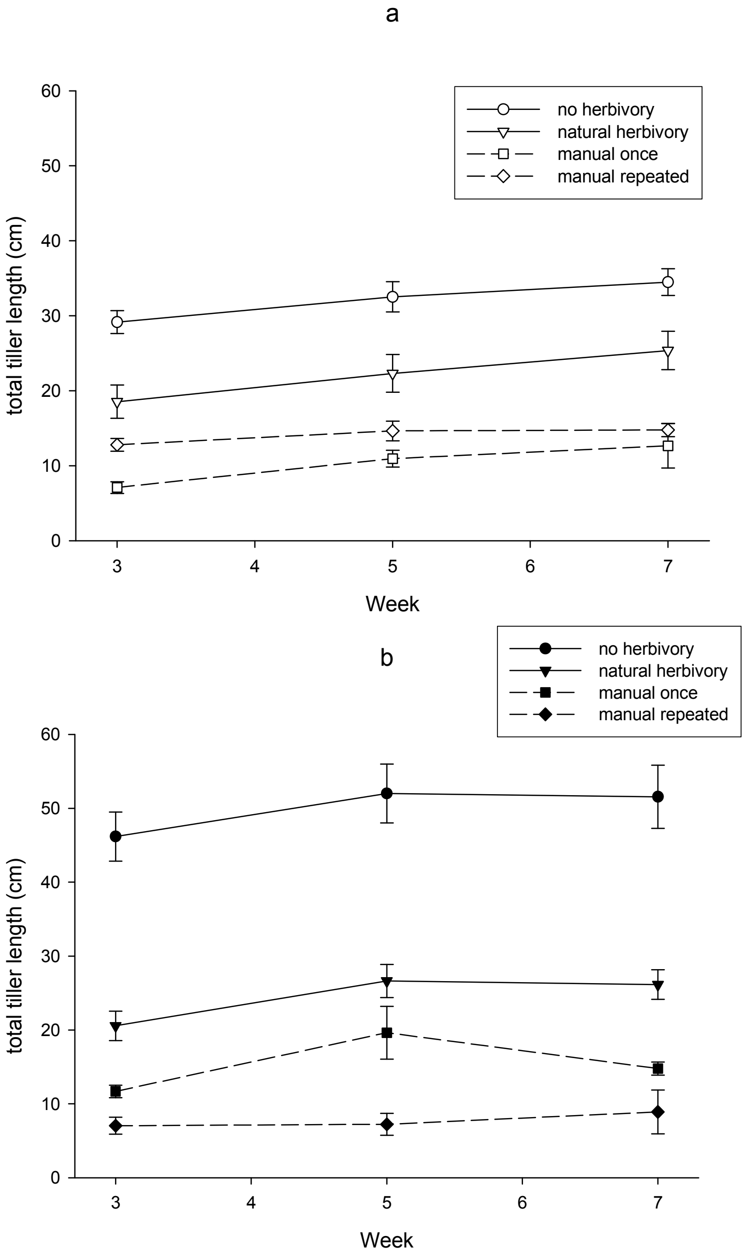

Figure 3.3. *Eriophorum vaginatum* regrowth in ambient nutrient (a) and fertilized (b) plots following biomass removal in mid-June 2004 by experimental clipping and natural herbivory. Week 0 represents the week of June 14, 2004. Treatments include plants with natural herbivory, no herbivory, plants with leaves manually removed once, and plants with leaves manually removed repeatedly.

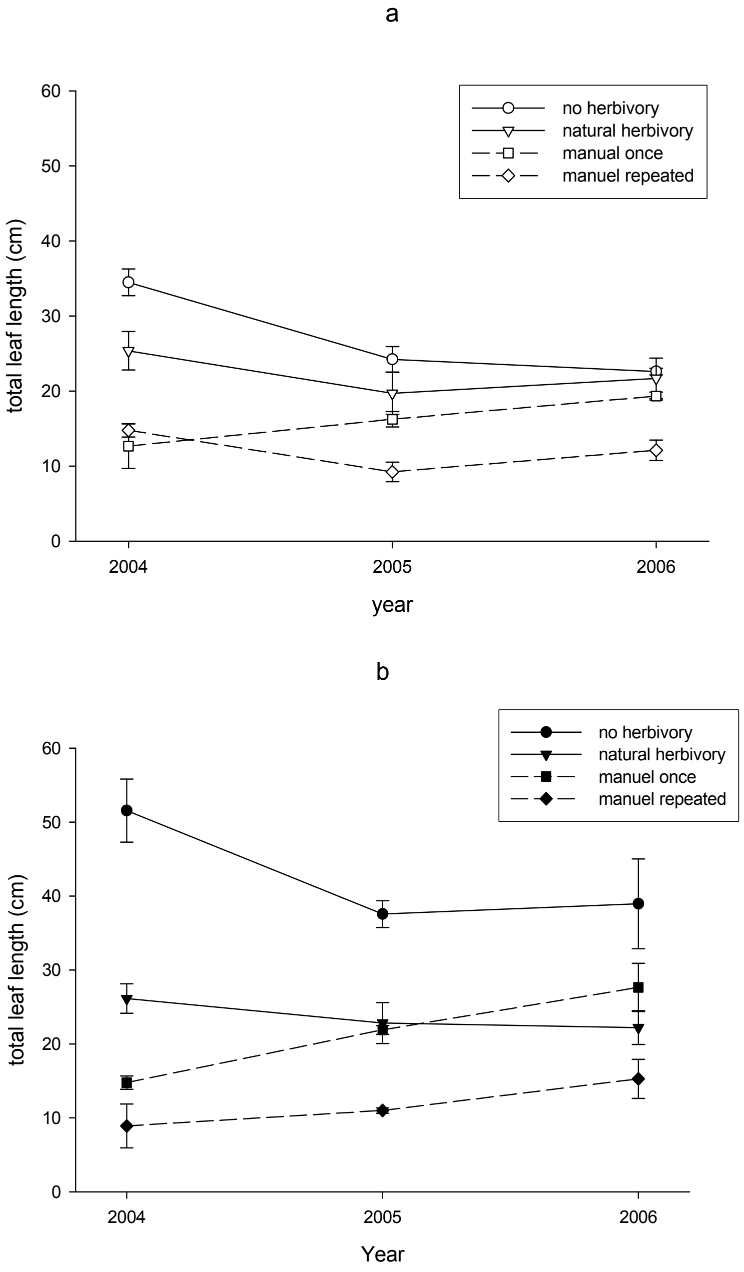

Figure 3.4. Growth of *Eriophorum vaginatum* tillers in ambient nutrient (a) and fertilized (b) plots following biomass removal in June 2004. Treatments include plants with natural herbivory, plants with no herbivory, plants with leaves manually removed once, and plants with leaves manually removed repeatedly.

Table 3.1 Mean number of flowers per tussock ± SE. (DH: n = 0, MAT: n = 12) for *E. vaginatum* in MAT and *H. alpina* in DH growing with added soil nutrients (NP) and ambient nutrients (CT) and four different levels of herbivory (plants with no herbivory, natural herbivory, leaves manually clipped once and repeatedly). Herbivory treatments were conducted in June 2004 for natural and once, while manual repeated leaves were clipped in June and July 2004.

| | | NP | | | | CT | | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | Year | no herbivory | natural herbivory | manual once | manual repeated | no herbivory | natural herbivory | manual once | manual repeated |
| *Eriophorum vaginatum* | 2005 | 0.8 ± 0.4 | 2.1 ± 0.5 | 2.3 ± 1.5 | 3.1 ± 0.1 | 4.8 ± 1.9 | 2.2 ± 0.9 | 9.3 ± 1.4 | 3.0 ± 1.2 |
| | 2006 | 1.1 ± 1.0 | 2.4 ± 1.7 | 3.2 ± 0.8 | 3.8 ± 2.6 | 1.6 ± 0.6 | 1.9 ± 1.3 | 2.8 ± 0.4 | 0.7 ± 0.4 |
| *Hierochloe alpina* | 2005 | 23.6 ± 15.2 | 9.9 ± 1.5 | 39.8 ± 3.1 | 27.6 ± 10.2 | 0.00 | | | |
| | 2006 | 15.8 ± 6.6 | 16.8 ± 11.1 | 22.0 ± 9.7 | 8.6 ± 3.0 | 0.1 ± 0.1 | | | |

# CHAPTER 4

# HERBIVORES AND INCREASED SOIL NUTRIENTS STRUCTURE COMPOSITION AND DIVERSITY IN DIFFERENT WAYS IN TWO ALASKAN ARCTIC TUNDRA COMMUNITIES

## 4.1 Abstract

Through a variety of mechanisms, herbivores can play key roles in shaping the plant communities within which they live. In the Arctic however, the roles of herbivores have historically not been considered as important as in temperate or tropical regions, primarily because net primary productivity is too low to support large populations. While this conjecture is largely based on theoretical assumptions with little Holarctic experimental testing, recent studies suggest that herbivores may become important as soil nutrient availability to plants increases. Increased temperatures arising via climate change may cause herbivores to have more pronounced effects on plant communities. As the Arctic warms, soil nutrients become more available to plants as microbial processes such as decomposition and nutrient mineralization increase. Increased soil nutrients lead directly to an increase in NPP and shifts in community structure. We studied how long-term experimental nutrient addition and herbivore exclosures in a factorial design affected plant community dynamics in moist acidic tussock (MAT) and dry heath (DH) tundras.  We used plant community censuses conducted twice during 2004 and 2005, and once during 2006 (the ninth, tenth and eleventh years of experimental manipulations) to determine how herbivores and increased soil nutrients were shaping these two communities. We found that growth form responses to fertilization and herbivore exclosures differed for each community. In MAT, while fertilization increased the relative cover of deciduous shrubs, and herbivores intensified this effect allowing deciduous shrubs to further dominate fertilized plots. Other growth forms showed strong responses to fertilization (with the direction of response differing with growth form), and herbivores were less important. While both graminoids and deciduous shrubs increased in relative abundance in fertilized plots in DH, herbivores decreased deciduous shrub abundance in

fertilized plots while graminoid cover was greater with herbivore exposure. Additionally, patterns of plant diversity differed between the two communities in response to treatments. Fertilization lowered diversity in MAT and herbivores had transient effects on diversity only in the eleventh year, while in DH there were no significant treatment effects on plant diversity, even after 11 years. Overall, differences between DH and MAT show that when soil nutrients are higher, herbivores may differentially affect the competitive interactions between species and growth forms, suggesting that they may be affecting other factors. As the Arctic warms and soil nutrient availability and NPP increase, herbivores will play a more important role in the Arctic than has been historically thought, though their effects on growth forms will differ depending on community contexts.

## 4.2 Introduction

Herbivores can be key biotic factors shaping plant communities through a variety of mechanisms (Huntly, 1991). By selectively removing biomass from preferred plants, herbivores affect growth of these plants. By attraction to preferred plants, herbivores may also affect growth of nearby less palatable species, resulting in apparent competition (Holt, 1977; Kotler and Holt, 1987). Herbivory often results in changes in community composition as non-preferred plants may increase when preferred plant abundance is reduced or extirpated. Thus, by decreasing the abundance of dominant plants, herbivores can increase plant community diversity (Fox, 1985; Virtanen et al. 1997; Olff and Richie, 1998). Additionally, herbivores may be important in redistribution of nutrients within communities thus changing spatial patterns of nutrients available for plants (Jonasson, 1992; Sirotnak and Huntly, 2000). Plant-herbivore interactions may also differ for different types and sizes of herbivores (Olofssen et al. 2004a; McNiel and Cashmann, 2005). Additionally, the overall effects of herbivores on plant communities may vary greatly in magnitude and can be either positive or negative in ways that are often very specific depending on measured variables or specific communities in different ecosystems. Plant-herbivore interactions often vary temporally (Olofsson et al. 2001; Bakker et al. 2006; Vistnes and Nellemann, 2008) and spatially (Aunapuu et al. 2008), and are frequently hard to elucidate. Thus, an overarching theory describing how herbivores affect plants and how these interactions in turn affect plant community dynamics and trophic structure among all ecosystems has eluded ecologists.

Plant-herbivore dynamics may interact with other plant community processes such as competition and facilitation (e.g. Eskilenin, 2008). The relative importance of these biotic processes often varies along gradients of resources and community net primary productivity (NPP). Thus, unraveling the interplay between herbivory, competition, and facilitation, and the relative importance of these along gradients of NPP, has given insights into understanding the importance of herbivores to plant communities that differ in NPP (Eskelinen, 2008). For example, numerous studies have shown how the responses of plant species and functional traits to herbivory differ between areas of high and low NPP (e.g., Hawkes and Sullivan, 2001; Osem et al. 2002; Leriche et al. 2004). When NPP is high, species that have higher growth rates and a greater intrinsic ability to access nutrients, such as graminoids, respond positively to herbivory by increasing growth following herbivory events. Alternatively, when NPP is low, graminoids may be negatively affected by herbivores, and plants with other traits, such as forbs and woody eudicots with secondary compounds, maintain competitive ability and persist within communities (Hawkes and Sullivan 2001). Thus, NPP may determine the response to herbivory of species and functional groups within communities (Pakeman, 2004), which may affect competitive interactions among plants themselves. Indeed, theoretical models with differing predictions regarding the plant-herbivore dynamics in ecosystems may be reconciled by considering the successional state of the community and resource availability or NPP (Cingolani et al. 2005).

In the Arctic, herbivores have historically been seen as unimportant to plant communities because NPP is low relative to communities at lower latitudes and direct effects of herbivores are often difficult to quantify (Jefferies et al. 1994). However, numerous studies have shown that herbivores may strongly affect these plant communities (reviewed by Mulder, 1999). In arctic salt marshes, snow geese limit plant growth and spatially redistribute nutrients (Bazely and Jefferies, 1986; 1989). In the Fennoscandian Arctic, the best studied arctic plant-mammalian herbivore system, both large and small mammals have been shown to affect plants in a variety of differing plant communities (Grellmann, 2002; Olofsson et al. 2004a; Olofsson et al. 2004b; Hamback et al. 2004; Hansen et al. 2007). Community composition in these European tundra ecosystems can be determined by herbivore densities, particularly large mammals such as caribou (Brathen et al. 2007). Additionally, the direction and magnitude of tundra plant community responses to herbivory may be predicted by differences in NPP among communities as theory predicts (Oksanen et al. 1981; Oksanen and Oksanen, 2000; Aunapuu 2008). This theory, the Exploitation Ecosystem Hypothesis (EEH), predicts that trophic structure and the importance of herbivores in communities change along gradients of NPP (Oksanen et al. 1981). In areas of very low NPP, herbivores are absent because the plant community does not produce enough biomass to support them. As NPP increases, a threshold is reached where herbivores may be supported (Oksanen and Oksanen, 2002). As NPP continues to increase, plant biomass remains constant as herbivore productivity increases until a second threshold is reached, whereby the system may support a third trophic level. The EEH has been experimentally supported in numerous arctic ecosystems with low NPP (recent examples include: Hansen et al. 2007; Eskelinen, 2008; Aunapuu et al. 2008), however it has not been explicitly tested in temperate ecosystems with higher productivity. Aunapuu et al. (2008) suggest that in high NPP ecosystems, niche trade-offs and specialization occur among both plants and herbivores resulting in increased trophic complexity. This may explain the often complex and species-specific plant-herbivore interactions reported in ecosystems with high NPP, and suggests the interaction between herbivory and competition is governed proximally by NPP and ultimately by resource availability.

As the Arctic warms, higher soil nutrient availability is expected to increase NPP (Hinzman et al. 2005). Historically, soil nutrient availability is limited in the Arctic by cold temperatures, which limit decomposition of dead plant matter (Nadelhoffer et al. 1991). Warmer temperatures increase the availability of water needed by soil microorganisms for metabolic processes such as decomposition (Schimel et al. 2005). Because decomposition rates are higher, warmer temperatures arising via climate change are predicted to result in higher amounts of soil nutrients, such as nitrogen and phosphorus, available for plants. Many arctic tundra communities respond to increased soil nutrient availability with shifts in community composition and/or higher NPP (e.g., Shaver et al. 2001; Grellmann 2002; Gough et al. 2008). How plant-herbivore interactions change as NPP increases in these arctic communities is largely unknown, though increases in herbivore populations may be predicted.

In Alaska, long-term experimental manipulations of tundra communities were experimentally established to understand the effects of increased soil nutrient availability. In dry heath (DH) tundra, higher soil nitrogen and phosphorus (NP) increased NPP over threefold, and community composition shifted from an evergreen shrub and lichen community to grassland (Gough et al. 2002, 2008, Table 1.1). In nearby moist acidic tussock (MAT) tundra, soil NP fertilization shifted community composition from a diverse community of graminoids, evergreen and deciduous shrubs, mosses and lichens to one dominated by deciduous shrubs, particularly *Betula nana* (Shaver et al. 2001, Table 1.1), and NPP increased less dramatically than in DH (by 170%). Concurrent with these soil fertilization experiments, fencing treatments were established to understand the effect of herbivores in both DH and MAT. Differences in responses to herbivory and increased soil nutrients within and among plant functional groups were found in the 9th year of the experiment (Gough et al. 2007). With higher soil nutrients, the tiller growth of the graminoid *Eriophorum vaginatum* was affected negatively by herbivore presence in MAT, while the graminoid *Hierochloe alpina* in DH was not affected. *B. nana* growth had opposite responses in each community with respect to fertilization and herbivory. While interesting, to date these effects on individual plants have not been shown to scale up to affect community structure in either the DH or MAT.

To examine the effects of increased soil nutrients and herbivory on DH and MAT community properties, we conducted censuses of the plant communities at peak plant biomass in late-July 2004, 2005 and 2006, the ninth, tenth and eleventh years of this study, respectively. Additionally, to explore seasonal differences, plant censuses were also conducted shortly following snowmelt in the ninth and tenth years. We had three hypotheses exploring community responses to increased nutrients and herbivory. First, because herbivores selectively prefer plants with higher nutrients (Batzli and Hentonnen, 1990) and herbivore activity has been shown to vary seasonally (Olofssen et al. 2001; Vistnes and Nellemann, 2008), herbivore activity and effects on plants in fertilized plots may not be easily detected when community data are historically collected because plants are able to outgrow early season biomass removal by herbivores (personal observation). Thus, we hypothesized that the herbivore activity and effects on both DH and MAT in fertilized plots would be more apparent early in the season, particularly in fertilized plots.

Second, we explored the null hypothesis that herbivores have no effect on DH and MAT plant communities in either ambient nutrient conditions or when soil nutrients are higher. The responses of growth forms to fertilization are well known (Shaver et al. 2001; Gough et al. 2002, 2008). In MAT, dwarf shrubs greatly increase in abundance, while graminoids, evergreen shrubs, lichens and mosses decrease. While in DH, fertilization greatly increases graminoid relative abundance, with a smaller magnitude increase in deciduous shrubs. Similarly to MAT, both lichens and evergreen shrubs decrease with fertilization, while moss relative abundance increases. By comparing differences among these growth forms in plant communities between plots with fences to exclude herbivores and those without, we tested the null hypothesis that herbivores have no effect.

Lastly, we explore the null hypothesis that herbivores have no effect on community diversity in either ambient nutrient conditions or when soil nutrients are higher. While fertilization has been shown to decrease diversity in these communities (Chapin et al. 1995; Gough et al. 2002), the overall effect of herbivores on plant diversity has been harder to detect (Gough et al. 2008). By comparing species density (number of vascular plant species per $m^2$) and the Shannon-Wiener Index of diversity between fenced plots and unfenced plots we tested the hypothesis that herbivores had no effect on diversity in both MAT and DH when soil nutrients availability is higher.

## 4.3 Methods

### *4.3.1 Study sites*

The location of this research was the Arctic Long Term Ecological Research (LTER) site at Toolik Lake Alaska (68.2° N, 149.6° W, 760 m a.s.l.). Both MAT and DH have been subjected to experimental manipulation since 1989 as part of the terrestrial component of the Arctic LTER. These two communities of focus differ in diversity, NPP, species composition and response to experimental nutrient additions (Table 1.1). A factorial design was incorporated to test plant responses to the exclusion of herbivores along with the addition of both N and P (10g/m$^2$/yr as $NH_4NO_3$ and 5g/m$^2$ /yr as $P_2O_5$) within blocks of 5 x 20 m plots in both communities beginning in 1996. One plot within each block was randomly assigned N and P addition (NP) and another as control (CT). Fertilizer treatment to NP plots began following snowmelt in June 1996 in the form of pellets, and was repeated yearly as part of long-term maintenance of terrestrial LTER plots.

Half of each 5 x 20 m plot is unfenced (NF), while the remaining area consists of the combination of small and large mammal exclusion fences. To exclude large mammals such as caribou, 5 x 10 meters of a random half of each plot was enclosed in a large mesh fence (LF: 15.2 x 15.2 cm openings, approximately 1.2 m in height). A smaller mesh fence (SF: 1.3 x 1.3 cm openings, approximately 0.8 m in height) was built within a random 5 x 5 meters of the larger fence to exclude small mammals such as ground squirrels, voles and lemmings. The small-mesh fence was buried in the soil at least 10 cm at construction to prevent animals from burrowing into the plots.

Plots were replicated within four blocks at MAT and three blocks at DH. For this study, I did not consider the effects of small mammals and large mammals separately, thus all data were collected from unfenced areas and areas with both small and large mammal exclusion (SF). Therefore, each block contained plots with four possible combinations of fence and fertilization treatment at each site: unfenced control (natural herbivory + CT), fenced control (no herbivory + CT), unfenced N + P (natural herbivory + NP), and fenced N + P (no herbivory + NP). While there are herbivorous insects in these communities, their effect on leaf biomass appeared to be minimal compared to that of mammalian herbivores (personal observation). These plots may retain snow on the immediate northern edge of fences for 2-3 days early in the season relative to unfenced areas (C. Moulton, personal communication). To avoid effects of this snow accumulation, all sampling was done at least 0.25 - 0.5 m from the edge of the fence.

### *4.3.2 Mammalian herbivores*

Five species of microtine rodents have been recorded on the north slope of Alaska (Batzli et al., 1980). These include three species of voles (*Microtus oeconomus*, *M. miurus*, and *Clethrionomys rutilis*) and two lemming species (*Dicrostonyx rubricatus* and *Lemmus sibericus*). Of these, the tundra vole (*M. oeconomus*) and singing vole (*M. miurus*) are common in communities near the Arctic LTER at Toolik Lake (Batzli and Lesieutre, 1995). Specifically at MAT, tundra voles are commonly seen (personal observation) as is evidence of their presence (hay piles, trails and fecal deposits) during cyclical outbreak years. Additionally, singing voles and collared lemmings (*D. rubricatus*) have been found in rocky areas very near DH (Batzli and Henttonen, 1990; pers. obs.). Batzli and Henttonen (1990) suggested that rodent densities in these tundra communities are limited by plant food availability, and animals seem to show strong preference for preferred plant species particularly *E. vaginatum* and *Carex* spp. Additionally, these authors suggest small mammals in these communities may be limited top-down by predator abundance similar to lemmings in coastal tundra (Batzli et al. 1980).

While transient, caribou are commonly sighted near the Arctic LTER at Toolik Lake (pers. obs.). Toolik Lake lies within the range of the Central Arctic Herd (D. Klein, personal communication; Lenhart 2002), their primary calving grounds lie far to the north. Thus caribou are not thought to be common foragers of plants in MAT. At DH however, caribou feces are frequently seen following snowmelt. Thus, DH may be an important winter habitat for caribou as snow cover is often less here than other communities (Cheng et al. 1998).

### *4.3.3 Plant community survey*

To estimate community structure, we conducted non-destructive sampling of the plant community in all treatment combinations and replicates at both MAT and DH. We randomly selected locations of starting points located 0.25-0.5 m away from the edge of the plot in each treatment for 1 x 1 m quadrats with 20 x 20 cm subquadrats which were marked to aid in estimations. At each starting point, eight adjacent 1 x 1 m plots were censused for relative aerial cover of each vascular plant species, mosses, lichens, bare ground, and “animal categories.” Vascular plant species were recorded according to nomenclature of Hultén (1968). Because of differences in animal use at each site, animal categories differed slightly between MAT and DH. At MAT, animal categories consisted of caribou and vole feces, vole holes, vole litter (litter removed and processed by voles), vole trails. At DH, animal categories consisted of caribou and vole feces, caribou litter, vole litter, vole holes, and vole trails. Caribou litter consisted of loose litter that appeared removed from *H. alpina* tussocks and was associated with caribou feces. We regularly standardized cover value estimates among observers to minimize bias. We subsequently grouped vascular plant species into growth forms and cover was then relativized to generate relative cover for each individual sample plot.

To capture differences in animal activity within the growing season, this process was conducted during early and peak plant growth in 2004 and 2005, the ninth and tenth years of the study. Early census dates were from June 17-24 in 2004, and between June 17-21 in 2005. Peak census dates were from July 22-26 in 2004, and from July 22-29, 2005. In 2006, the eleventh year of the study, we conducted an additional peak census during July 13-18.

### *4.3.4 Statistical analysis*

Plant community composition was analyzed separately for 1) the two years that had both early and late census dates (the ninth and tenth years) and 2) the eleventh year, which had only a peak census date. To compare differences between early and peak seasons in the 9th and 10th years, we conducted a nested repeated measures ANOVAs with early and peak seasons nested within year (Scheiner and Gurevitch, 1999) on each growth category for each site. For each repeated measures ANOVA, census measurements were compared between early and late nested within year, and differences between years were tested as within-subjects effects. Fertilization and fencing treatments were tested as main effects, and differences among treatments were compared post-hoc using Tukey's HSD. Data in the following growth categories were analyzed, each in a separate ANOVA: deciduous shrubs, evergreen shrubs, forbs, graminoids, lichens, litter, moss. All cover estimates were arcsine square-root transformed prior to analysis to insure normality and homogeneity of variance.

In the eleventh year, MANOVA was used to analyze differences among growth forms in response to fertilization and fencing treatments for the peak cover estimates. A separate MANOVA was used for each community. We used the following growth forms as dependent variables: bare ground, deciduous shrubs, evergreen shrubs, forbs, graminoids, lichens, litter and mosses, and animal categories. Animal categories consisted of the sum of all evidence of animal activity described above within each treatment. Reflecting the experimental design, a block design was used and the main effects of fencing and fertilization were examined with Wilks' Lambda as the test statistic for these between-subjects effects. All cover estimates were arcsine square-root transformed prior to analysis to achieve normality and homogeneity of variance. We used Tukey's HSD for pairwise comparisons and probability values at 0.05 or below were considered significant.

Finally, to compare community diversity among fertilization and fencing treatments among years we performed repeated measures ANOVAs on species density (the total number of species per $m^2$ plot) and Shannon Weiner indices (McCune et al. 2002) at peak census in each community. All statistical analyses were performed using SAS 9.1 for Windows (SAS Institute, Cary, North Carolina).

## 4.4 Results

### *4.4.1 Responses in MAT*

#### 4.4.1.1 Seasonal changes in relative cover in the ninth and tenth years

At MAT, animal categories, analyzed together, were lower in fenced plots (Figure 4.1, Table 4.1). Animal presence in the tenth year was even lower within fences than in the ninth year due to increased diligence in fence maintenance; small mammals readily burrow under the fence if they can find areas that have moved due to winter frost heaving. Regardless, these cover categories showed a strong fertilization effect that varied between seasons and years (within subjects year*season*fence*fertilization $F_{1,93} = 7.36$, $p = 0.007$). Generally, NFNP plots showed much more activity than NFCT plots (Figure 4.1). When considered separately, vole litter tended to increase seasonally in the ninth and decrease seasonally in these plots in the tenth year. In addition, vole trail tended to decrease seasonally in both years.

The relative percent cover of deciduous shrubs increased between early and peak census in the ninth year, reflecting growth of the canopy throughout the summer (significant within subjects effect of season $F_{1,93} = 12.17$, $p < 0.001$; Figure 4.2). There was significantly more deciduous cover in fertilized plots than ambient plots reflecting the strong effect of fertilization (Table 4.1), and there appeared to be no significant effect of fencing for this group although NFCT showed the least change in growth in the ninth year. In the tenth year, there was a significantly greater seasonal change in deciduous cover in fertilized plots than ambient plots, and the absolute magnitude difference between fertilized and ambient plots was greater for unfenced plots (0.09) than for fenced plots (0.03; within subjects year*fence*fertilization $F_{1,93} = 4.28$, $p = 0.02$). This suggests that herbivores may be facilitating deciduous shrubs in some way when soil nutrients become more available at the expense of other growth forms.

Similar to deciduous shrubs, graminoids showed an increase in cover between the beginning and end of the growing season during both the ninth and the tenth years, however the pattern differed slightly between years (within subjects year*season $F_{1,93} = 4.4$, $p = 0.04$), and there were differences due to significant fencing and fertilization effects (Table 4.1). At peak census, there were consistently more graminoids in SFCT than all other treatments (Figure 4.2). NFNP consistently had the least amount of graminoid cover, while NFCT consistently had more graminoids than SFNP. This pattern was reflected in the seasonal change in cover. In the ninth year however, there was no difference in the change of relative cover between NFCT and NFNP, while there was a significant larger change in cover between SFCT than SFNP (within subjects year*fence $F_{1,93} = 25.98$, $p < 0.001$), showing that in the absence of herbivores graminoids were able to increase in relative abundance during the season. In the tenth year, there was significantly more graminoid cover in fenced than in unfenced plots, and a smaller magnitude of change in fertilized (0.04) compared with unfertilized plots (0.09). This pattern suggests herbivores are having larger negative effect on graminoid density in fertilized conditions.

There were significantly fewer evergreen shrubs in fertilized plots than ambient plots in all treatments, in both early and peak census, in both years (Table 4.1; Figure 4.2). Additionally, with the exception of the early census in the tenth year, there were consistently more evergreens in unfenced areas than fenced areas. There was a significant within-subjects year*season*fence*fertilization interaction ($F_{1,93} = 7.36$, $p < 0.01$) supporting differences in relative change in evergreen shrubs seen between seasons and between the ninth and tenth years. In the ninth year, in only fertilized plots, evergreen shrubs decreased in relative abundance over the growing season, while in the tenth year evergreens decreased in all treatments, though not equally.

For mosses, there was a strong negative fertilization effect and a less strong positive fence effect (Table 4.1). Consistently in both seasons in both years, the relative cover of mosses was greatest for SFCT plots followed by NFCT plots, and there was much less moss in SFNP and NFNP plots. There were seasonal changes, however, with mosses generally decreasing abundances in treatments during the growing season with the effect being greatest in ambient plots (within subjects season*fertilization $F_{1,93} = 14.05$, $p < 0.001$). Similar to mosses, lichen relative cover showed a strong decrease due to fertilization (Table 4.1). However, lichens were also negatively affected by fencing. Lichens tended to decrease in abundance for all treatments seasonally, which was exacerbated by both fencing and fertilization (within subjects season*fertilization $F_{1,93} = 17.98$, $p < 0.001$; season*fence $F_{1,93} = 15.76$, $p < 0.001$). These seasonal decreases were expected as the relative growth rates for lichens and mosses are much lower seasonally than vascular plant growth forms and also are less apparent below canopy at peak plant growth. Lastly forbs, in these years, were largely absent in fertilized plots with no difference due to fencing.

#### 4.4.1.2 Relative cover at peak biomass in the eleventh year

In the eleventh year at MAT, the overall response across all growth forms was a strong fertilization x fence interaction (Figure 4.3a, Wilk's Lambda $F_{10,84} = 3.29$, $p = 0.001$). Individually, growth forms responded differently to treatments (Table 4.2), and with patterns that were similar to the ninth and tenth years (Figure 4.1). Deciduous shrub relative cover was highest in NFNP plots, followed by SFNP, NFCT, and SFCT plots. Thus, deciduous shrubs were more common in fertilized plots compared to ambient plots, however herbivore exclusion lowered deciduous shrub cover regardless of fertilization (Table 4.2). Graminoids also responded similarly in the eleventh year, although the response continued to be opposite that of deciduous shrubs. Graminoid cover was highest in SFCT plots, followed by NFCT, then SFNP, with NFNP having the least amount of graminoids (Figure 4.3a). Thus, graminoids decreased in relative abundance in fertilized plots, and exposure to herbivory exacerbated this effect (Table 4.2). Evergreen shrubs, lichens and mosses had a similar response to fertilization as graminoids in the eleventh year, although the response to fencing varied among these groups (Figure 4.3a, Table 4.2). Unlike the ninth and tenth years evergreen shrubs were significantly lower in unfenced plots. Also in the eleventh year, lichens, and mosses marginally so, showed no significant difference due to fencing. Forbs in the eleventh year were similar to lichens, largely absent in fertilized plots with no difference due to fencing.

The relative cover of animal categories in the eleventh year, analyzed together, had similar patterns as those seen in ninth and tenth years. Although there was no significant statistical fertilization effect, there was a strong fencing effect (Table 4.2). Animal sign was absent in fenced treatments, and there appeared to be greater activity in NFNP plots relative to NFCT plots, although this difference was smaller than that seen in the ninth and tenth years and was not statistically significant (Figure 4.4a). In the eleventh year, both vole litter and vole trails were higher in NFNP plots than NFCT plots, and caribou feces were censused in NFNP plots for the first time in this study in MAT.

### *4.4.2 Responses in DH*

#### 4.4.2.1 Seasonal changes in relative cover in the ninth and tenth years

There was animal activity in unfenced plots throughout the experiment (Figure 4.5), and there was much more activity in fertilized plots (Table 4.1). Additionally, animal categories were much more apparent in unfenced plots early in the season (Figure 4.5; within subjects season*fertilization*fence $F_{1,69} = 35.66$, $p < 0.001$), and also greater in the tenth year than in ninth year (within subjects year*season $F_{1,69} = 14.74$, $p < 0.001$). Both caribou feces and “caribou litter” were higher in the tenth than in the ninth. Interestingly, caribou feces cover was higher in ambient plots than in fertilized plots in the ninth, but the same in both treatments early in the tenth year. Evidence of animals other than caribou include squirrel feces seen early in the tenth year in NFNP plots, and vole trails in NFNP plots in both years.

Unlike in MAT where the unfenced fertilized plots had the highest relative cover of deciduous shrubs, SFNP had the highest proportion of deciduous shrubs, followed by NFNP, while SFCT had fewer still, and NFCT had the fewest in DH (Figure 4.6). This pattern was consistent between early and peak season and between years. However, the magnitude of response to treatments differed between years (within-subjects year*fertilization*fence $F_{1,69} = 24.45$, $p < 0.001$). There were slight decreases over the course of the season for this growth form (Figure 4.6; within-subjects year*season $F_{1,69} = 4.7$, $p = 0.03$) to a great extent in the ninth and to a lesser extent in tenth year. Although this decrease may be due to large increases seasonally in graminoids particularly in fertilized plots, it appears that herbivores are negatively affecting deciduous shrub growth in DH as the relative cover of these shrubs is lower in unfenced plots (Table 4.1).

Graminoid cover greatly increased with long-term fertilization at DH (Figure 4.6, Table 4.1). Also, graminoids increased growth seasonally in fertilized plots relative to ambient plots (Figure 4.6; within-subjects season*fertilization $F_{1,69} = 70.09$, $p < 0.001$) to a large extent in the ninth and an even larger extent in tenth year (within-subjects year*fertilization $F_{1,69} = 51.63$, $p <$

0.001). However, effects of herbivore exclusion were more subtle (Table 4.1). Herbivore exclusion decreased the relative cover of graminoids in both ambient and fertilized conditions (Figure 4.6).

Evergreen shrubs decreased greatly in long-term fertilized plots, though the magnitude differed between fenced and unfenced areas in opposite ways in the two years (Figure 4.6, within-subjects year*fence*fertilization $F_{1,69} = 4.02$, $p = 0.05$). In both years, there were fewer evergreen shrubs at peak growth in fenced treatments. However, early in the ninth year abundance was greater in SFNP plots compared to NFNP plots, and in the tenth year the opposite was true (within subjects year*season*fertilization $F_{1,69} = 7.21$, $p < 0.009$).

The pattern for lichens was similar to evergreen shrubs, where this group largely decreased in fertilized plots (Figure 4.6, Table 4.1). Additionally, this fertilization effect was exacerbated by herbivore exclusion such that there were fewer lichens in unfenced areas. Alternatively, mosses greatly increased abundance in fertilized plots (Figure 4.6, Table 4.1). This effect varied seasonally, between the ninth and tenth years and between fenced and unfenced areas (within-subjects year*season*fertilization*fence $F_{1,69} = 4.68$, $p = 0.05$). In the ninth year moss relative cover decreased seasonally in NFNP plots while all other treatments did not change seasonally. In the tenth year, however, mosses increased in NFNP plots seasonally and decreased seasonally in SFNP plots.

#### 4.4.2.2 Relative cover at peak biomass in the eleventh year

In the eleventh year like in MAT, the relative cover of growth forms when analyzed collectively showed a strong fertilization x fence interaction in DH (Figure 4.3b, Wilk's Lambda $F_{9,61} = 4.3$, $p < 0.001$). However, the pattern was somewhat different for individual growth forms relative to MAT (Table 4.3). Deciduous shrub cover increased in fertilized plots, but the response to fencing was different depending on fertilization. In ambient conditions, fenced plots had more deciduous shrubs than unfenced plots, while in fertilized plots, fenced areas had slightly less than unfenced areas. Graminoids also increased in fertilized plots; however, relative cover was much greater in unfenced compared to fenced plots (Figure 4.3b) in the eleventh year. Fertilization decreased cover of evergreen shrubs and lichens, and there was no significant effect of fencing for these two growth forms (Figure 4.3b, Table 4.3). Mosses showed the opposite pattern, with increases in fertilized plots but with marginally significant increases in SFNP plots relative to NFNP plots. Forbs were seen very infrequently at very low abundance, thus are not included here due to lack of statistically meaningful numbers.

Analyzed collectively, animal categories responded significantly to both fertilization and fencing (Table 4.3). These categories were absent in fenced plots, and were significantly greater in fertilized treatments in the eleventh year (Figure 4.7). There were vole trails seen only in NFNP treatments, and 'caribou litter' was at much greater abundance in NFNP plots relative to NFCT plots. However, caribou feces was much greater in ambient compared to fertilized plots.

### *4.4.3 Effects of fertilization and herbivory on diversity at MAT and DH*

Vascular plant species density in DH and MAT responded differently to fertilization and fencing (Table 4.4, within subjects effect year*community*fertilization*fence $F_{2,370} = 3.12$, $p = 0.045$). In DH, there were no significant differences among treatments or among the ninth, tenth, and eleventh years (Figure 4.8). However, important patterns were evident in MAT: fertilization significantly decreased species density in this community. Marginally significant effects were also seen in years nine and eleven between fence treatments in MAT. In year nine, there were fewer species in SFNP plots compared to NFNP plots, and the opposite pattern was detected in year eleven.

Results for the Shannon-Weiner diversity index in DH were very similar to species density (Figure 4.9). Only one difference was detected among treatments during any of the three years: in year ten, SFCT plots had a higher diversity estimate than NFCT plots. Also similar to species density, there were differences in Shannon-Weiner values between the communities with respect to treatments that varied among years (Table 4.5, within subjects effect year*community*fertilization*fence $F2_{,370} = 8.74$, $p = 0.002$). During all three years fertilization significantly decreased diversity estimates in MAT with respect to ambient plots. While there were no differences in Shannon-Weiner values due to fencing in the ninth and tenth years, NFNP plots had a lower average value in year eleven compared to SFNP plots. Thus, both estimates of diversity responded strongly to fertilization in all years, however, it seems that herbivores may only have transient effects on diversity which varied year to year.

## 4.5 Discussion

### *4.5.1 Herbivore activity more evident early in fertilized plots*

In general, there was significantly more animal activity in fertilized plots and early in the season compared to ambient plots in both DH and MAT, supporting our first hypothesis. At MAT, both vole trails and vole litter were more abundant in NFNP plots compared to NFCT plots in the ninth, tenth and eleventh years. Additionally, during the eleventh year caribou feces was seen in fertilized plots in this community. Because we do not know precisely the small mammal population in MAT, it is difficult to determine temporally when animals are important to plants. However, we believe the ninth year was a peak year for animal activity (Table 2.1), which would explain the increase in vole litter in both ambient and fertilized plots during this year. Thus, our prediction that animal activity would be detected early in the season more so than at peak season was incorrect in the ninth year but correct in the tenth year at MAT. There were more vole trails and vole litter in both nutrient conditions in the early census during this year. This may explain why individual plants in these communities appear to be suffering from a ‘legacy of herbivory’ in this community (Chapter 2, this volume), while herbivore impacts have been not been often seen at the community level. Censuses and biomass harvests have historically been conducted during peak seasonal growth (e.g., Shaver et al. 2001) and may have not captured herbivory effects, particularly if these data were collected during non-peak small mammal population years. It has historically been difficult to completely remove herbivores from plots in MAT because of differential thawing of the active layer among micro-sites within this community causing the fences to bend and buckle each winter and spring. Thus, continual maintenance of fences has been needed to insure that small mammals are kept out of fenced areas, which has not always been effective and explains the evidence of animals within fenced areas in this community. Regardless, evidence of animal activity was more common in unfenced areas compared to fenced areas, thus we are confident that the fences significantly reduced animal activity, even if they did not entirely eliminate it.

In DH, herbivore evidence was much higher in the early census than the peak census in both the ninth and tenth years. However, responses were different among types of herbivore evidence with respect to treatments in all three years. Caribou feces were encountered more often in ambient plots, while caribou litter was encountered more often in fertilized plots. This litter comes primarily from *H. alpina* tussocks, which is much more abundant in fertilized plots, explaining this result. Regardless, it may be that caribou are attracted to this community first because of high amounts of lichens in DH, but also due to the increased nutrients available in palatable plants in fertilized plots (Gough et al. 2002, 2007).

### *4.5.2 Growth form responses to long-term fertilization and herbivory*

The null hypothesis that herbivores would not affect the relative abundance of growth forms in either fertilized or ambient conditions was rejected for some growth forms in both communities. The relative cover of all plant growth forms changed seasonally in both communities reflecting the relative growth rates of species within those growth forms, particularly in fertilized plots. Evergreen shrubs, lichens and mosses with slower growth rates decreased, while deciduous shrubs and graminoids tended to increase presumably because of higher growth rates. Community census estimates were taken by observing a canopy view of plots, and thus the slower-rate growth forms did not necessarily decrease in absolute abundance. Regardless, these estimates highlight the competition for light seasonally among species within these communities, especially when soil nutrients are more available to plants.

Growth forms responded more strongly to fertilization than to herbivory in both communities supporting previous studies which have shown shifts in community structure in both communities with experimental nutrient addition (Shaver et al. 2001, Gough et al. 2002, 2008). Gough et al. (2008) report results from a similar MANOVA analysis conducted on relative abundance of the plant community in DH in 2005, the tenth year, although their results include data collected from a large fence to exclude only caribou. There are subtle differences between those results and results presented here. In the tenth year, Gough et al. report a significant interaction between fencing and fertilization for all growth forms. In the eleventh year, only graminoids showed such an interaction, while all other growth forms had no fence effect or were affected by fencing regardless of fertilization. For example, in the data presented here, mosses, lichens and evergreen shrubs were not affected by fences, while there was not a significant interaction for deciduous shrubs. Evergreen shrubs and lichens decreased greatly or were absent in fertilized plots in DH, as was seen in MAT. This effect has largely been explained by competitive disadvantages for soil nutrients in the face of the higher growth rates of competing graminoids and deciduous shrubs (Shaver and Chapin, 1980). The decrease of these growth forms with increased soil nutrients was further exacerbated by herbivory. For unpalatable evergreen shrubs, this may be due to apparent competition as herbivores are attracted to higher nitrogen content in preferred plants in fertilized plots. Several growth forms had different responses to treatments in each community. Mosses decreased in relative abundance with fertilization in MAT and increased in DH, while herbivores seemed to also exacerbate this effect. In MAT increased animal activity in fertilized plots may explain this, as mosses as a group have been shown to be affected by herbivores primarily by trampling in European tundra (van der Wal and Brooker, 2004). In DH, increases in moss may be explained if water availability increases with increased soil organic matter associated with changes in plant species composition in fertilized plots.

Graminoids and deciduous shrubs also showed different responses to increased soil nutrients and herbivory in each community. In MAT, graminoid abundance decreases with long-term fertilization; an effect long associated with competition with deciduous shrubs for soil nutrients (Shaver et al. 2001). However, there was an overall decrease in graminoid density with fertilization may not entirely explain the complete exclusion of graminoids in older plots with 17 years of experimental fertilization (personal observation). In our experiment, the decrease in graminoid abundance in fertilized plots was lessened when herbivores were excluded. These graminoids, particularly *E. vaginatum* are preferred forage for voles, which seem to preferentially frequent fertilized plots (Batzli and Hentonnen, 1990; Batzli and Lesietre, 1991). This suggests that herbivores may selectively remove graminoids from fertilized plots because of higher nutrient content in these plant tissues, regardless of increased growth seen with fertilized graminoids in MAT (Gough et al. 2007). In DH, alternatively graminoids greatly increased abundance when fertilized; an effect that was higher in the presence of herbivores. This result may seem counterintuitive, as herbivore pressure on palatable graminoids was predicted to be higher in fertilized plots. A variety of graminoids increase when fertilized (Gough et al. 2002, 2008). However, *H. alpina* greatly increases in these fertilized plots and has been shown to be tolerant of herbivores when grown with higher soil nutrients (Chapter 3, this volume). Given these differing results in MAT and DH, graminoid responses to herbivory may be a function of both species identity and abiotic community characteristics.

Like graminoids, deciduous shrubs increased with fertilization in both communities, however they responded oppositely to herbivore exclusion in each community. We have seen no evidence of herbivory on the primary dwarf shrub in these communities, *B. nana*. In MAT, increase in deciduous shrub abundance was greater when exposed to herbivores, perhaps because herbivores are removing potential competitors for soil nutrients such as graminoids. Alternatively, in DH the increase in deciduous shrub abundance was greater within fenced areas. This may be due to increased caribou activity causing trampling in fertilized plots.

Overall, the abundance of growth forms with negative responses to fertilization may be generalized between MAT and DH. However, growth forms which respond positively to fertilization by increasing growth and abundance showed very different responses in each community. These results are supported by biomass harvest estimates conducted in the eleventh year (Gough, unpublished data), which suggests that herbivores are functioning in structuring these two communities when soil nutrients are more available.

### *4.5.3 Fertilization decreases diversity in MAT but not DH*

We rejected our null hypothesis that herbivores would not affect diversity in either soil nutrient condition in only one instance; herbivores increased diversity in fertilized plots in MAT in the eleventh year, relative to ambient plots. While both estimates of diversity overall showed similar results, herbivores had no effect on diversity in the ninth and tenth years in MAT or in DH in any year. In MAT, while there were small effects seen due to herbivory, fertilization strongly decreased both species density and Shannon-Weiner estimates. This result is supported by other fertilization experiments in other ecosystems (Clark et al. 2007; Clark and Tilman, 2008; Mittelbach et al. 2001), where species often disappear from long term fertilization experiments, particularly nitrogen addition. The current understanding is that higher soil nutrients may alter conditions important for species with specialized traits for dealing with low levels of fertilization (Suding et al. 2005). These characteristics may apply to many tundra plant species (Chapin, 1989). Interestingly in DH, there was no pattern in either species density or Shannon-Wiener Index detected with respect to treatments among the ninth, tenth and eleventh years. These results contradict earlier species density patterns found in longer-term fertilization in DH (Gough et al. 2002). Fertilization had decreased species density at this site after ten years of N and P addition. We found no such relationship for plots in this study. This community may reflect similar patterns found in polar desert communities, where fertilization has shifted species composition without an effect on diversity (Robinson et al. 1998). This may be because bare ground in DH is available for immigrating species which take advantage of increased soil nutrient availability. Indeed, longer-term fertilization treatments have experienced an immigration of fireweed (*Epilobium angustifolium*) that is not naturally found locally. Ultimately though the results for both DH and MAT together highlight that as NPP increases due to soil nutrient availability in these communities, differences in overall diversity are not generalizable among tundra plant communities.

## 4.6 Conclusion

Historically, herbivores have not been thought to be important biotic factors shaping arctic plant communities (Jefferies et al. 1994). However, our results suggest that herbivores can be important determinants of plant community composition in ways that may be very community specific. They may especially become more important as temperatures continue to warm and soil nutrients become more available, and NPP increases as is predicted by theory (Oksanen et al.1980). Herbivores appear to be affecting species in both DH and MAT primarily by reducing growth (Gough et al. 2007) and abundance of preferred species and altering the competitive interactions between growth forms, particularly between graminoids and deciduous shrubs. The inverse responses of graminoids and deciduous shrubs in each community are intriguing, and determining precisely why these results occurred warrants further work. In addition to preferentially feeding on certain palatable species reducing their biomass in fertilized plots, herbivores may be directly altering soil nutrient availability . For example, herbivores may also be functioning to redistribute soil nutrients as has been shown in other systems (Sirotnak and Huntly, 2000) although this has not been studied for either DH or MAT. Regardless, future predictions need to consider plant responses to increased nutrients and plant-herbivore interactions concurrently to effectively understand how different tundra communities function with warmer temperatures.

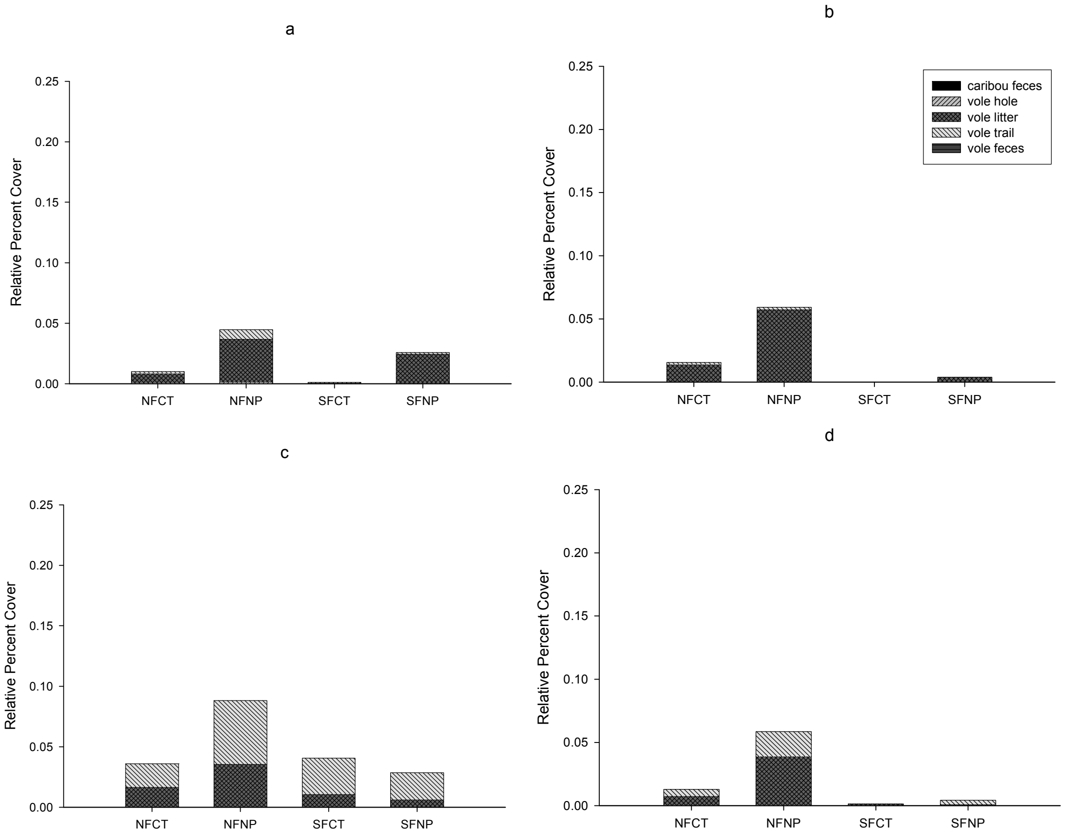

Figure 4.1. Relative cover of various animal categories in MAT in the ninth and tenth year of the study: (a) mid-June, 2004, (b) late July, 2004, (c) mid-June, 2005, and (c) late July 2005 in four treatments in a factorial design. NFCT refers to no fence with ambient nutrients, NFNP refers to no fence with N and P addition, SFCT refers to small fence with ambient nutrients, and SFNP refers to small fence with N and P addition. Categories described in text.

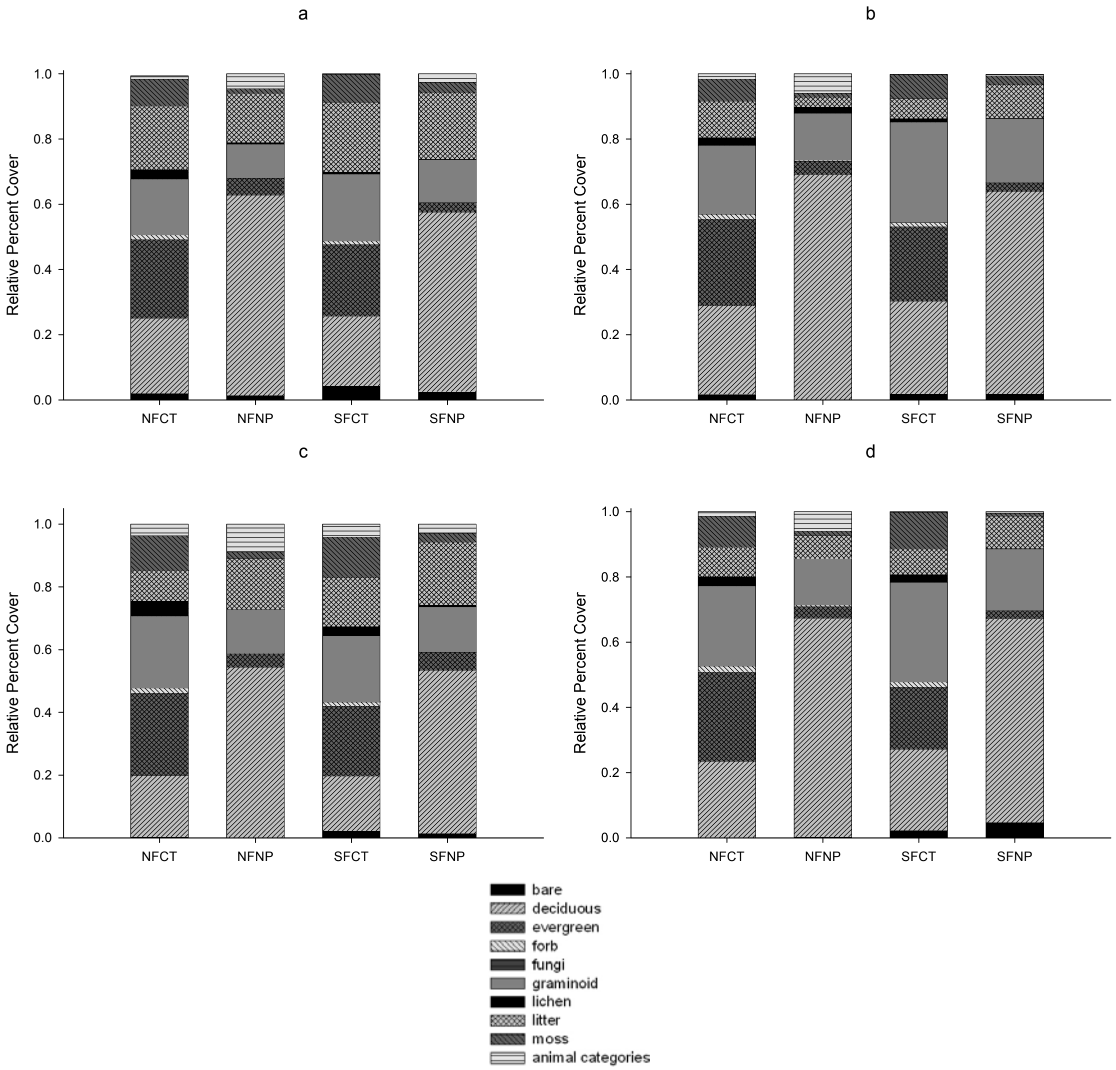

Figure 4.2 Relative cover of vegetation types at MAT in the ninth and tenth year of the study: (a) mid-June, 2004, (b) late July, 2004, (c) mid-June, 2005, and (c) late July 2005 in four treatments in a factorial design. Treatments as in Figure 4.1., and categories are described in detail in the text.

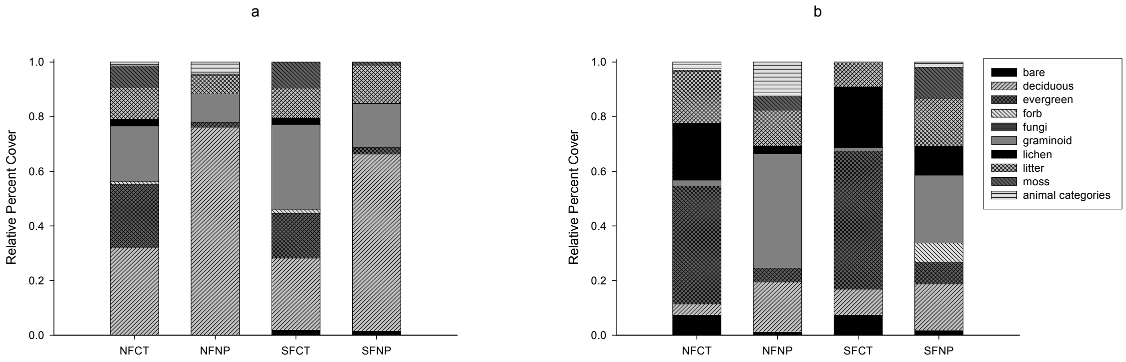

Figure 4.3. Relative cover of vegetation types at (a) MAT, and (b) DH at peak seasonal plant growth in July 2006, the eleventh year of the study. Treatments described in Figure 4.1., and categories described in text.

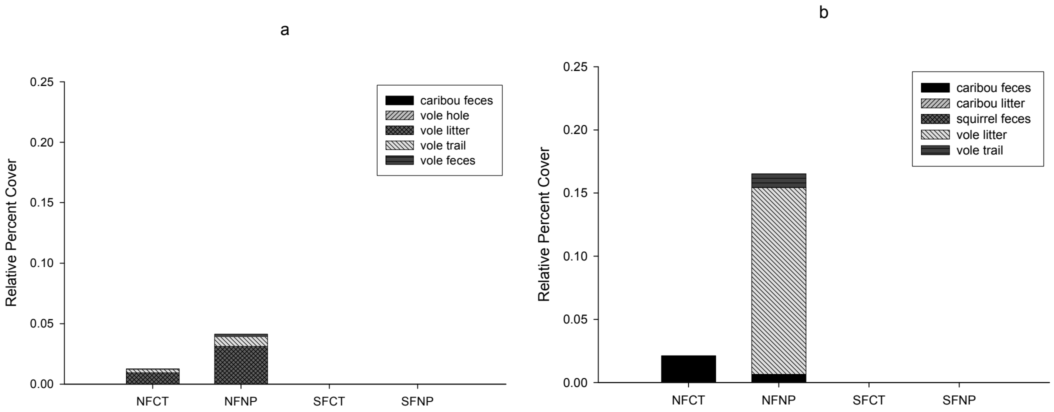

Figure 4.4. Relative cover of various animal categories at (a) MAT, and (b) DH at peak seasonal plant growth in July 2006, the eleventh year of the study. Treatments described in Figure 4.1., and categories described in text.

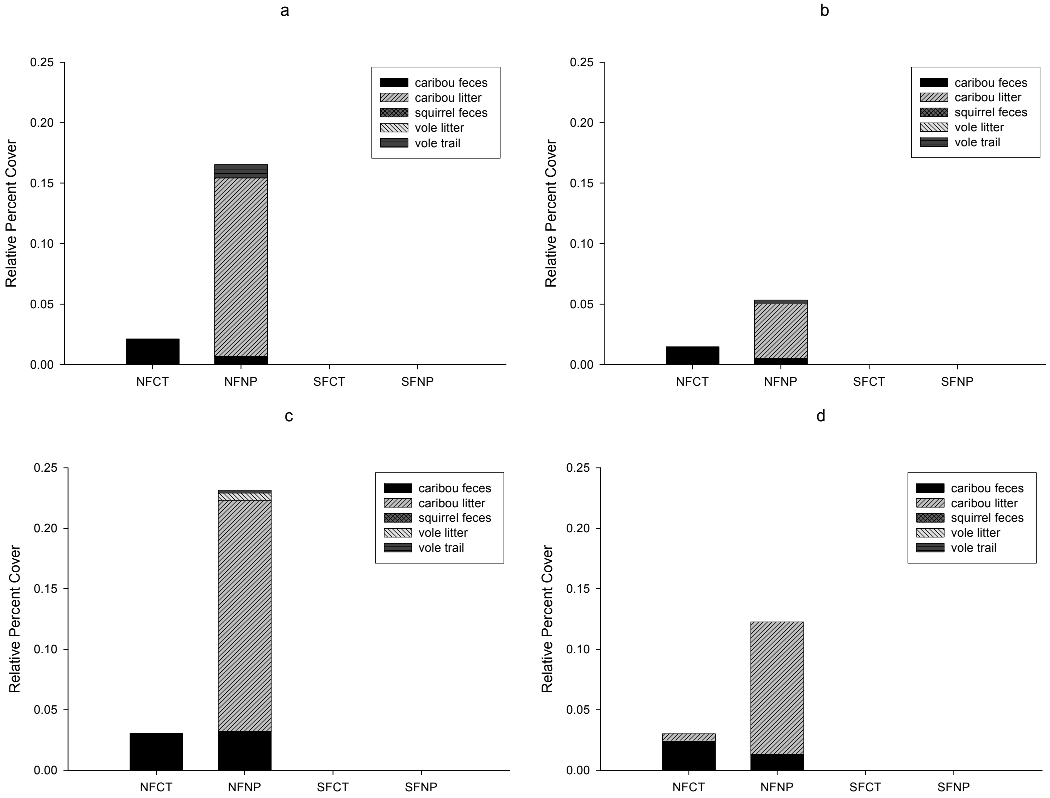

Figure 4.5. Relative cover of various animal categories in DH in the ninth and tenth year of the study: (a) mid-June, 2004, (b) late July, 2004, (c) mid-June, 2005, and (c) late July 2005 in four treatments in a factorial design. Treatments as in Figure 4.1, and categories are described in detail in the text.

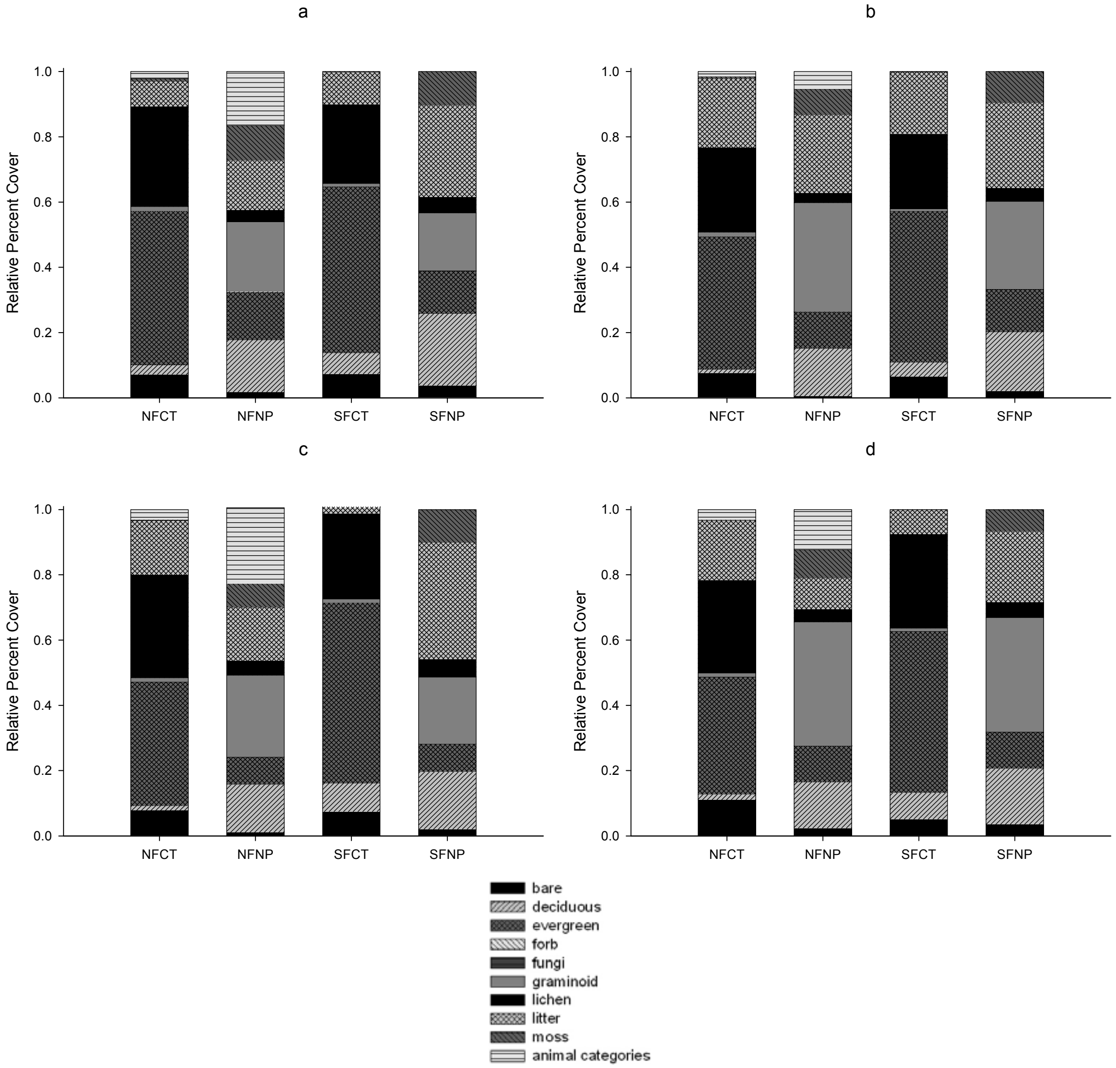

Figure 4.6. Relative cover of vegetation types at DH in the ninth and tenth year of the study, (a) mid-June, 2004, (b) late July, 2004, (c) mid-June, 2005, and (c) late July 2005 in four treatments in a factorial design. Treatments described in Figure 4.1.

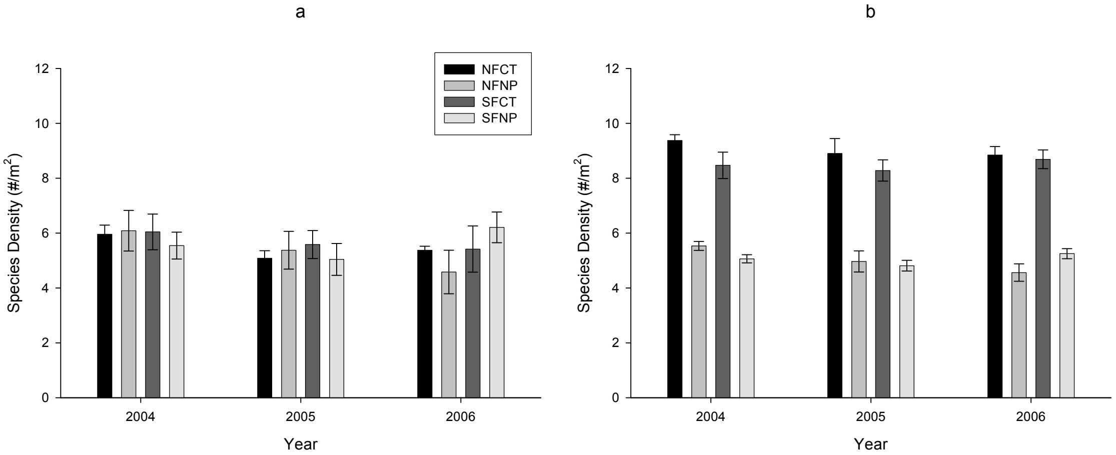

Figure 4.7. Species density (# species/m2) for DH (a) and MAT tundra at peak seasonal plant growth. Treatments as in 4.1.

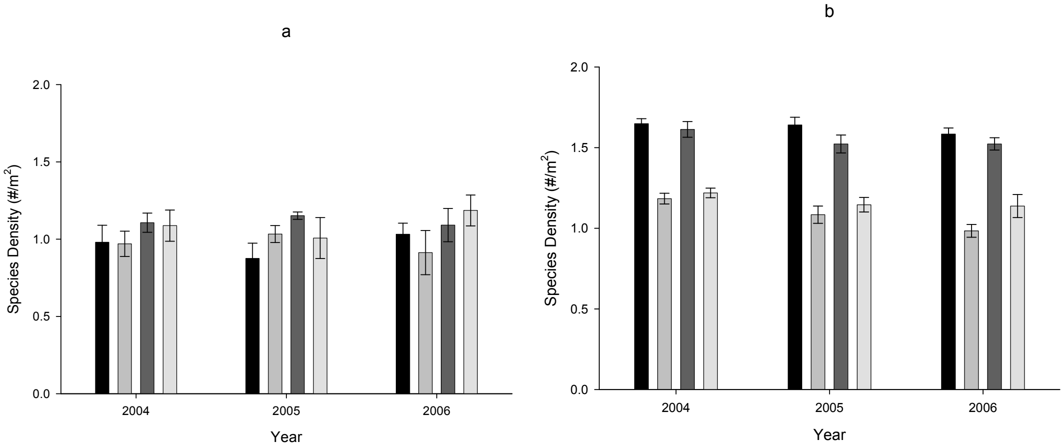

Figure 4.8. Shannon-Weiner Indices of diversity (H’) for DH (a) and MAT (b) tundras at peak seasonal plant growth. Treatments as in 4.1.

Table 4.1. Summary of between subjects effects from nested repeated measures ANOVAs, conducted on each growth form individually. Early and peak censuses are nested within 2004 and 2005, the ninth and tenth year of the study. Degrees of freedom for MAT = 1,93 and DH = 1, 69. Significant levels indicated by ***p<0.001, **0.001<p<0.01, *0.01<p<0.05, †0.05<p<0.1.

| Community | Vegetation Category | Fence | Fertilization | Fence x Fertilization |
|---|---|---|---|---|
| MAT | deciduous | 2.53 | 561.26*** | 2.37 |
| | animal categories | 92.26*** | 66.31*** | 26.31*** |
| | evergreen | 15.33*** | 943.14*** | 1.67 |
| | forb | 1.93 | 124.74*** | 0.2 |
| | graminoid | 10.26** | 65.69*** | 0.04 |
| | lichen | 15.01*** | 179.32*** | 6.44* |
| | litter | 9.14*** | 0 | 17.74*** |
| | moss | 4.84* | 349.92*** | 0.13 |
| DH | deciduous | 9.49** | 2.27 | 1.65 |
| | animal categories | 177.17*** | 50.09*** | 49.92*** |
| | evergreen | 0.19 | 311.29*** | 7.44** |
| | forb | 8.68** | 143.54*** | 17.84*** |
| | graminoid | 3.25† | 347.74*** | 0.45 |
| | lichen | 0.46 | 519.44*** | 7.53** |
| | litter | 4.59* | 20.78*** | 21.68*** |
| | moss | 1.03 | 286.5*** | 1.52 |

Table 4.2 Univariate results for plant growth form relative abundance censused at peak growth in 2006, the eleventh year of the study, in MAT tundra.

| | fence | | fertilization | | fence*fertilization | |
|---|---|---|---|---|---|---|
| Growth Form | F1,93 | p | F1,93 | p | F1,93 | p |
| ancat | 21.06 | < 0.0001 | 1.35 | 0.25 | 1.35 | 0.25 |
| bare | 26.05 | < 0.0001 | 0.38 | 0.54 | 1.44 | 0.23 |
| deciduous | 12.43 | 0.007 | 307.71 | < 0.0001 | 2.04 | 0.16 |
| evergreen | 4.36 | 0.04 | 326.2 | < 0.0001 | 5.59 | 0.02 |
| forb | 0.75 | 0.39 | 91.24 | < 0.0001 | 0.03 | 0.86 |
| graminoid | 31.16 | < 0.0001 | 79.62 | < 0.0001 | 1.51 | 0.22 |
| lichen | 0.42 | 0.52 | 117.91 | < 0.0001 | 0.08 | 0.78 |
| litter | 13.33 | 0.0004 | 4.63 | 0.034 | 20.15 | < 0.0001 |
| moss | 2.95 | 0.089 | 202.85 | < 0.0001 | 0.25 | 0.62 |

Table 4.3 Univariate results for plant growth form relative abundance censused at peak growth in 2006, the eleventh year of the study, in DH tundra.

|  | fence |  | fertilization |  | fence*fertilization |  |
|---|---|---|---|---|---|---|
| Growth Form | F1,69 | p | F1,69 | p | F1,69 | p |
| ancat | 48.86 | < 0.0001 | 18.01 | < 0.0001 | 4.64 | 0.035 |
| bare | 0.54 | 0.46 | 89.81 | < 0.0001 | 0.38 | 0.54 |
| deciduous | 7.17 | 0.009 | 34.37 | < 0.0001 | 0.92 | 0.34 |
| evergreen | 1.76 | 0.19 | 398.98 | < 0.0001 | 1.83 | 0.18 |
| forb | . | . | . | . | . | . |
| graminoid | 3.58 | 0.063 | 319.63 | < 0.0001 | 2.76 | 0.101 |
| lichen | 2.36 | 0.129 | 306.43 | < 0.0001 | 0.7 | 0.4 |
| litter | 0.26 | 0.61 | 4.46 | 0.038 | 29.06 | < 0.0001 |
| moss | 1.25 | 0.27 | 63.57 | < 0.0001 | 0.62 | 0.44 |

Table 4.4 Between subjects effects from a repeated measures ANOVA for species density (number of plant species per m2) in MAT and DH tundras in a factorial design of long-term fencing and fertilization treatments recorded in 2004, 2005 and 2006, the ninth, tenth and eleventh year of the study.

| Source | DF | MS | F | p |
|---|---|---|---|---|
| community | 1 | 245.44 | 83.20 | < 0.001 |
| fence | 1 | 0.07 | 0.02 | 0.82 |
| fertilization | 1 | 604.57 | 204.94 | < 0.001 |
| community*fence | 1 | 540.64 | 183.27 | 0.06 |
| community*fertilization | 1 | 10.29 | 3.49 | < 0.001 |
| fence*fertilization | 1 | 4.02 | 1.36 | 0.24 |
| community*fence*fertilization | 1 | 3.02 | 1.02 | 0.31 |
| Error | 185 | 2.95 |  |  |

Table 4.5 Between subjects effects from a repeated measures ANOVA for Shannon-Wiener Index of diversity (H’) in MAT and DH tundras in a factorial design of long-term fencing and fertilization treatments recorded in 2004, 2005 and 2006, the ninth, tenth and eleventh year of the study.

| Source | DF | MS | F | p |
|---|---|---|---|---|
| community | 1 | 14.93 | 253.52 | < 0.001 |
| fence | 1 | 0.85 | 14.41 | 0.93 |
| fertilization | 1 | 9.08 | 154.17 | < 0.001 |
| community*fence | 1 | 0.72 | 12.16 | 0.006 |
| community*fertilization | 1 | 8.57 | 145.47 | < 0.001 |
| fence*fertilization | 1 | 0.16 | 2.64 | 0.12 |
| community*fence*fertilization | 1 | 0.36 | 6.17 | 0.01 |
| Error | 185 | 0.05 | | |

# CHAPTER 5

# DOES HERBIVORE PROCESSING INCREASE GRAMINOID LEAF LITTER DECOMPOSITION IN ARCTIC TUNDRA?

## 5.1 Abstract

As atmospheric carbon dioxide concentrations increase, arctic temperatures are also increasing and affecting ecosystem processes. Higher decomposition rates in particular are expected, potentially raising the amount of carbon entering the atmosphere from arctic soils. Net primary productivity (NPP) is also expected to increase along with shifts in plant species composition because of higher soil nutrient concentrations arising through faster decomposition, potentially affecting the net carbon dioxide exchange between arctic ecosystems and the atmosphere. Because plant species respond differently to higher soil nutrients and differ in tissue composition, understanding factors effecting plant tissue decomposition is important for accurately predicting the relative importance of decomposition and NPP in the Arctic to future the global carbon cycle. Mammalian herbivores may be able to affect both of these processes through a variety of mechanisms. In particular, voles in moist acidic tussock (MAT) tundra create haypiles of *Eriophorum vaginatum* leaves, and caribou often remove leaves from *Hierochloe alpina* tussocks in dry heath (DH) tundra potentially increasing the decomposition of these graminoids. Using a litterbag experiment, I studied the decomposition of litter processed by animals compared to senesced plant leaves in plots with ambient and increased soil nutrient levels. In MAT, litter mass loss, litter C, and decomposition constants all showed that vole litter decomposed more slowly than senesced plant litter, while there were no direct effects of fertilization. Additionally, while caribou litter in ambient plots in DH had a lower decomposition rate than in fertilization treatments, no overall effects were detected between caribou and plant litter on mass loss or litter C. In both communities there were clear differences in litter quality between litter types as estimated by C:N ratios. Litter N was also immobilized at different time periods for various litter

types and fertilization treatments in each community. These differences likely reflect the timing of leaf removal between litter types as vole and caribou litter may have lost labile C in the interim between removal by animals and collection for this experiment. While these results suggest that herbivores might decrease decomposition of graminoid litter, more study is necessary to determine if litter processing by animals indeed affects graminoid decomposition.

## 5.2 Introduction

Increased carbon dioxide ($CO_2$) concentrations in the recent past have caused global temperatures to increase (IPCC, 2007). While all terrestrial ecosystems have experienced warming, the magnitude of increase has been greatest in the Arctic (Serreze et al. 2000). Increased temperatures can impact ecosystem processes (Rustad et al. 2001; Shaver et al. 2006), particularly decomposition (Robinson, 2002) and nutrient mineralization (Schmidt et al. 2002), which are temperature limited in arctic ecosystems (Nadelhoffer et al. 1991). Additionally, the flux of carbon (C) from the atmosphere into organic matter via plant photosynthesis has historically been greater than the release of $CO_2$ to the atmosphere via decomposition (Shaver et al. 2000), and has resulted in a buildup of organic matter in arctic soils. Thus the Arctic has functioned as a net C sink in the global carbon cycle (Post et al. 1992). Indeed, when one includes boreal forests, northern terrestrial ecosystems are estimated to contain up to one-third of the planet's soil organic matter (Schimel, 1995).

As the Arctic warms, decomposition and nutrient mineralization rates in arctic soils are predicted to increase (Shaver et al. 2006), and a warmer Arctic may result in ecosystems switching from a net C sink to a source in the global carbon cycle (Nowinski et al. 2008). While the major concern is a potential positive feedback to atmospheric $CO_2$ concentrations, higher decomposition and nutrient mineralization rates are also predicted to increase soil nutrient availability to plants (Shaver et al. 2001). Arctic plants in a variety of communities increase net primary productivity (NPP) and shift species composition with experimental increases in soil nutrient availability (van Wijk et al. 2004). However, changes in plant species composition may increase the abundance of species with leaf litter that is more recalcitrant, resulting in a negative feedback to climate change (Cornelissen et al. 2007). Tissue decomposition of arctic plant species differs widely according to growth form (Hobbie, 1996), and species responding positively to increased nutrients may not be as decomposable as others (Robinson, 2002). Thus, it is unclear how increases in NPP will offset increases in $CO_2$ mineralization from higher decomposition, and understanding factors affecting the decomposition of different plant species is essential to predict how arctic ecosystems will affect future global carbon balance (Shaver et al. 1992; 2000).

Through a variety of mechanisms, herbivores can alter decomposition and nutrient cycling in arctic ecosystems (Mulder, 1999). Herbivore presence tends to increase both nitrogen (N) and phosphorus (P) in soils available to plants (Batzli, 1978; McKendrick et al. 1980), and often urination and defecation can increase nutrient mineralization and decomposition rates (Stark et al. 2002; Oloffson et al. 2004b). van der Wal et al. (2004a) suggest that through feces alone, large mammals can increase the biomass of their own food sources by returning nutrients to soils (Ngai and Jefferies, 2004). Alternatively, arctic herbivores can reduce the rates of soil microbial processes in some instances (Grellman, 2002), because peak herbivore activity is not always timed with the highest plant demand for soil nutrients (Stark and Grellman, 2002). Hence herbivores can remove nutrients from ecosystems. Herbivores can also alter relationships between plants and soil microorganisms through direct herbivory on plants. Because herbivory often results in carbon and nutrient reallocation from plant roots to shoots (Chapin et al. 1986), grazing may alter the C flux from plants to soils (Stark and Kytoviita, 2006), resulting in reduced microbial growth and N immobilization. Additionally, herbivores can increase the decomposability of plants (Olofsson and Oksanen, 2002). Plant biomass from heavily grazed areas may have lower C:N than that from lighter grazed areas, resulting in increased decomposition in plants from heavily grazed areas (Semmartin and Ghersha, 2006). Indeed, plant digestibility has been shown to be correlated with decomposition for a number of subarctic species because plant traits, such as lignin:N ratios, affect both processes (Cornelissen et al. 2004). Although all these effects may be important ecosystem determinants at different temporal and spatial scales, it has been difficult to generalize herbivore effects on decomposition among arctic ecosystems (Mulder, 1999).

To better understand how higher soil nutrients that arise through warmer temperatures affect ecosystem processes, experimental fertilization experiments have been established in plant communities at the Arctic Long-Term Ecological Research (LTER) near Toolik Lake, Alaska (Shaver and Jonasson, 1992). In moist acidic tussock (MAT) tundra, fertilization resulted in higher NPP and shifts in community composition from a diverse community of deciduous and evergreen shrubs, graminoids, forbs, mosses and lichens to a community dominated by deciduous shrubs, particularly the dwarf shrub *Betula nana* (Shaver et al. 2001). Higher soil nutrients may cause higher decomposition rates because changes in species composition alter litter quantity and quality (Hobbie 1996), but also because fertilization in MAT has resulted in increased decomposition of C located in deeper organic and mineral soils (Nowinski et al. 2008). Thus, while warmer temperatures directly increase decomposition rates (Moorhead and Reynolds, 1993), higher soil nutrients may ultimately result in a net loss of C from arctic ecosystems (Mack et al. 2004). Similar fertilization experiments have been conducted in nearby dry heath (DH) tundra also resulting in a shift in plant species composition (Gough et al. 2002; 2008). However, in DH, the shift has been from evergreen shrubs and lichens to a grassland dominated by *Hierochloe alpina*, with an increase in NPP (Gough et al. 2008). While *H. alpina* is present but at very low abundance in ambient nutrient plots in DH, it forms tussocks in under fertilized conditions. Soils in DH are dry, rocky and not as well developed as MAT; thus, decomposition rates are thought to be lower than in MAT (Shaver and Chapin, 1991). However, neither overall decomposition rates at the ecosystem or individual plant species levels have been well characterized in this community.

In both MAT and DH, animals process graminoid litter (personal observation, Batzli and Hentonnen, 1990). In particular, voles living in MAT chew through tussocks of the graminoid *Eriophorum vaginatum*, leaving loose piles of leaf litter. These haypiles are most evident in early summer following snowmelt, tend to disappear over the course of the summer, and may be absent after two full years (personal observation). It is unclear if these *E. vaginatum* haypiles serve a function for voles, as has been shown for herbivore haypiles in other ecosystems (e.g., Aho et al. 1998). Some herbivores have the ability to affect decomposition of plant litter in haypiles either through specific placement (Karban et al. 2007) or through selective addition of different plants with higher secondary compounds (Dearing, 1997a, 1997b), as combinations of plant species with different compounds are often difficult for microorganisms to decompose (Ball et al. 2008). In DH, caribou remove standing dead leaf litter from *H. alpina* tussocks in fertilized plots, which essentially spatially distributes litter away from tussocks (personal observation).

Litter removal and processing by mammals may affect the decomposition of both *E. vaginatum* and *H. alpina* in MAT and DH, respectively. To understand if this is so, I performed a litterbag experiment (Wieder and Lang, 1982) where I clipped senesced standing leaf litter from both species and compared the decomposition of these with litter that had been processed by animals under both ambient nutrient and fertilized conditions. Because animal processing breaks apart leaves into smaller pieces, I predicted that mass loss and decomposition would be faster for litter processed by animals than senesced plant litter. In addition, I predicted that fertilization and processing would interact such that this magnitude difference would be greater for litterbags in fertilized plots than for those in ambient plots. I also analyzed all samples for C and N content, and examined patterns reflecting litter quality and C and N loss over time. I predicted that C loss would reflect overall mass loss for all treatments. However, while I predicted that N loss would not be different among litter categories, I predicted that N loss would be greatest in ambient plots because of greater microbial demand for N in these plots compared to fertilized plots.

## 5.3 Methods

### *5.3.1 Study sites*

The location of this research was the Arctic LTER site at Toolik Lake Alaska (68.2° N, 149.6° W, 760 m a.s.l.). MAT and DH differ in diversity, NPP, species composition and response to experimental nutrient additions (Table 1.1). Beginning in 1996, experiments were established to test plant responses to the the addition of both N and P ($10 g/m^2/yr$ as $NH_4NO_3$ and $5 g/m^2/yr$ as

$P_2O_5$) within blocks of 5 x 20 m plots in both communities beginning in 1996. Treatment plots were replicated within four blocks at MAT and three blocks at DH. One plot within each block was randomly assigned N and P addition (NP) and another as control (CT). Fertilizer treatment to NP plots began following snowmelt in June 1996 in the form of pellets, and was repeated yearly.

### *5.3.2 Mammalian herbivores*

Five species of microtine rodents have been recorded on the north slope of Alaska (Batzli et al., 1980). These include three species of voles (*Microtus oeconomus*, *M. miurus*, and *Clethrionomys rutilis*) and two lemming species (*Dicrostonyx rubricatus* and *Lemmus sibericus*). Of these, the tundra vole (*M. oeconomus*) and singing vole (*M. miurus*) are common in communities near the Arctic LTER at Toolik Lake (Batzli and Lesieutre, 1995). Specifically at MAT, tundra voles are commonly seen (personal observation) as is evidence of their presence (hay piles, trails and fecal deposits) during cyclical outbreak years. Additionally, singing voles and collared lemmings (*D. rubricatus*) have been found in rocky areas very near DH (Batzli and Henttonen, 1990; pers. obs.). Batzli and Henttonen (1990) suggested that rodent densities in these tundra communities are limited by plant food availability, and animals seem to show strong preference for preferred plant species particularly *E. vaginatum* and *Carex* spp. Additionally, small mammals in these communities may be limited top-down by predator abundance similar to lemmings in coastal tundra (Batzli et al. 1980).

While transient, caribou are commonly sighted near the Arctic LTER at Toolik Lake (personal observation). Toolik Lake lies within the range of the Central Arctic Herd (D. Klein, personal communication; Lenhart 2002), their primary calving grounds lie far to the north. Thus caribou are not thought to be common foragers of plants in MAT. At DH however, caribou feces are frequently seen following snowmelt. Thus, DH may be an important winter habitat for caribou as snow cover is often less here than other communities (Cheng et al. 1998).

### *5.3.3 Plant species*

#### 5.3.3.1 *Eriophorum vaginatum*

*E. vaginatum* is a tussock-forming sedge common in northern Alaska. This species is an important component of MAT, and is thought to be an important food source for microtine rodents (Batzli and Lesieutre, 1995). Following snowmelt in early June in years when voles are abundant, whole tussocks of *E. vaginatum* have extensive biomass removed by voles. Large portions of tussocks, including inflorescences, are clipped. In addition to a direct food source, voles create haypiles of *E. vaginatum* litter associated with fecal deposits, and may use these haypiles for shelter (personal observation).

#### 5.3.3.2 *Hierochloe alpina*

*H. alpina* is a grass species found at low abundances in many heath communities in northern Alaska (Walker et al. 1994). When nutrients are experimentally added, *H. alpina* increases dramatically in growth, forms tussocks and becomes much more common in this community (Gough et al. 2002). Additionally, *H. alpina* has been shown to be a preferred forage plant for caribou (Boertje, 1984).

### *5.3.4 Litterbag construction*

I collected two types of litter from each plant species: litter processed by mammals and standing dead leaves that I clipped from plants. In MAT, I collected *E. vaginatum* litter processed by voles (VL) and *E. vaginatum* plant litter (PL) from an area near the main LTER treatments in August 2004. In DH, I collected loose *H. alpina* litter removed from tussocks by caribou (CL) and *H. alpina* litter clipped from senesced plants (PL) from areas near fertilized treatments in June 2005. Vole litter was sorted to remove vole feces and a small amount of other species' plant tissue. Litter types were homogenized, dried in an oven at 60 ºC to a constant weight, and stored at room temperature until litterbags were constructed. Additionally, I set aside a portion of the original homogenized sample for each litter type as a reference for C and N content before litterbags were placed in the field. In June 2005, I constructed 10 x 10 cm mesh litterbags from fiberglass black window screening (largest holes were approximately 1 mm in diameter). I placed approximately 1 g of litter into each bag, then sealed and marked the bags according to litter type. On 14 June, 2005 *E. vaginatum* PL and VL bags were placed in fertilized and ambient plots in MAT underneath the moss layer. *H. alpina* CL and PL bags were placed in treatments in DH on 30 June, 2005 on the surface of plots. In both communities, litterbags were placed in areas exposed to herbivores. I placed two replicate sets (set = 3 bags) of bags in each treatment plot in each block (n = 3) of each community (n = 6 litterbags per treatment per collection date). Bags were left in the field until collection dates: 5 August, 2005, 7 June, 2006, and 28 August 2006. These dates represent day 52, 358, and 438 for bags in MAT, and days 38, 342, and 422 for bags in DH. At each collection date, one bag from each set was collected, and the entire bag was dried to a constant weight at 60 C. Bags were opened and examined for fungi by looking for the presence of visible hyphae. Bag contents were then weighed and ground in a Wiley mill using a 0.6 mm screen. Ground samples were analyzed in triplicate for CHN using a Perkins-Elmer CHNS-O elemental analyzer. I also ground and analyzed the initial samples of each litter type set aside at litterbag construction for CHN using these same methods.

### *5.3.5 Statistical analysis*

To determine mass loss, I calculated the percent of initial mass remaining by dividing the initial weight into the final weight of samples placed in bags. I calculated litter C by dividing the initial C in litterbags into the C remaining in litterbags at each sample date. I calculated litter N in a similar manner. I also calculated the molar C:N ratio by multiplying the molar ratio of C:N (12:14) by the ratio of total percent C to total percent N in bags at each sample date. All values were arcsine square-root transformed to insure normality. Additionally, because percent N had values greater than 1.0, I multiplied these values by 0.1 in order to perform an arcsine square-root transform.

Differences among collection dates were determined as within-subjects effects in repeated measures ANOVAs. To determine differences among four variables (% initial mass remaining, litter C, litter N, and C:N) in each community, I used a separate two-way ANOVA for each variable with fertilization and litter type as main effects, and significant differences among treatments were determined using Tukey's HSD.

To determine differences in the decomposition rates among treatments, I calculated decay constants, *k*, for each treatment in each site using the following equation (from, Wieder and Lang, 1982, Hobbie 1996, Hobbie and Gough, 2004):

$M_t = M_0e^{-kt}$

where $M_t$ is litter mass at time *t*, and $M_0$ is initial mass. I used the linear model because I wanted to compare differences in overall decomposition between treatments rather than understand the precise shape of the decomposition curve. I then compared differences in decay constants using a two-way ANOVA for each site. Fertilization and litter types were main effects and significant differences among treatments were determined using Tukey's HSD. All statistical analyses were performed using SAS 9.1 for Windows (SAS Institute, Cary, North Carolina).

## 5.4 Results

### *5.4.1 Mass loss and decomposition constants among treatments in MAT and DH*

In MAT, litter mass (% initial weight) changed over time primarily according to litter type (within subjects effect of time*litter type $F_{2,30} = 26.16$, $p < 0.001$) but also due to fertilization (within subjects effect of time*fertilization $F_{2,30} = 3.67$, $p = 0.04$). Additionally, the overall pattern over time reflected seasonal changes in temperature. Between field placement and 52 days there was significant loss of litter among all treatments, followed by a long lag with little loss between 52 days and 358 days reflecting the autumn, winter and spring in northern Alaska (Figure 5.1a). Mass loss then resumed for PLCT and PLNP treatments between 358 and 438 days reflecting the second summer of this experiment, although VLNP and VLCT treatments did not lose mass during this interval. Overall, litter from senesced plants in both fertilization and ambient conditions lost significantly more mass at each collection date than vole litter in either fertilization condition (Figure 5.1a, Table 5.1). There was a marginally significant litter type by fertilization interaction (Table 5.1) supporting transient differences between fertilization treatments at specific collection dates. After 52 days, significantly more mass was lost in PLNP and PLCT litterbags, although this pattern disappeared by 358 days. Also after 358 days, significantly more mass was lost in VLCT plots than VLNP plots, but this effect was absent after 438 days. The decomposition constants (*k*), reflected the percent of initial mass loss for treatments in MAT. Plant litter had significantly higher decomposition constants than vole litter (Figure 5.2a, Table 5.2) and there was no effect of fertilization on decomposition of either litter type.

The overall pattern among litterbag treatments changed over time in much the same manner in DH as MAT reflecting the seasonality of northern Alaska, although differences more strongly reflected fertilization treatments rather than litter type (within subjects effect time*fertilization $F_{2,30} = 6.06$, $p = 0.006$). There were no differences among any treatments after 38 days. After 342 days, there was significantly more mass loss in CLNP plots compared to CLCT plots although PLNP and PLCT were not different than any other treatment (Figure 5.1b.). This pattern was pronounced after 422 days. In DH the decomposition constants for both PLNP and PLCT were not statistically different from each other or any other treatment (Figure 5.2b, Table 5.3). However, caribou litter types differed according to fertilization treatment. CLNP had a significantly higher decomposition constant than CLCT.

### *5.4.2 Litter carbon and nitrogen*

#### 5.4.2.1 MAT

In MAT, litterbag C decreased over time with differences seen between litter types, while there were no patterns detected with respect to fertilization (within subjects effect time*litter type $F_{2,30} = 5.93$, $p = 0.007$). After 52 days, more C was lost in plant litterbags compared to vole litterbags (Figure 5.3a, Table 5.1), though there were no differences among treatments at 358 days. The pattern seen at 52 days was again evident after 438 days as both PLNP and PLCT had lower C than vole litter in both fertilization treatments.

Litterbag N changed only marginally over time for litterbags in MAT, and some litterbags gained N (within subjects effect time $F_{2,30} = 2.75$, $p = 0.08$, Figure 5.4a). After 52 days, N was immobilized in PLNP litterbags, and there was significantly more litter N in these than all other treatments (Figure 5.4, Table 5.1). After 358 days, PLCT and VLNP litterbags immobilized N and were not different than PLNP, while there was a loss in litter N in VLCT litterbags. After 438 days, the pattern was similar to the first collection date as VLCT, PLCT, and PLNP all immobilized N between 358 and 438 days.

In MAT, no patterns in C:N over time were detected statistically. However there were differences in C:N with respect to litter type and fertilization as supported by a marginally significant litter type x fertilization interaction (Figure 5.5a. Table 5.1). Although plant litter did not differ significantly between fertilization and ambient plots, with one exception plant litter C:N was always significantly lower than vole litter C:N. After 58 days, there was no difference in C:N between PLCT and VLNP litterbags. However, this effect disappeared at the second collection date, never to return.

#### 5.4.2.2. DH

Litterbag C also decreased over time for litter in DH. However, this was due to fertilization at the final collection date rather than litter type (within subjects effect time*fertilization $F_{2,30}$ = 6.08, p = 0.006, Figure 5.3b). While there were no differences in litterbag C among treatments at either 38 or 342 days, differences emerged after 422 days. There was significantly greater C loss in CLNP than CLCT litterbags (Table 5.1).

The pattern of litterbag N was quite different in DH, as there were no significant within subjects effects. There was a strong initial N loss for caribou litterbags compared to plant litterbags (Figure 5.4b, Table 5.1) after 38 days which stayed consistent for the remainder of the experiment. Additionally there were no differences in litter N detected between ambient and fertilized plots for either litter type.

In DH, the C:N ratio of both litter types changed over time in both treatments (within subjects effect of time $F_{2,30}$ = 29.88, p < 0.001). Caribou litter C:N increased between placement of the bags and 38 days, while the C:N of plant litter declined at the first date and continued to do so throughout the experiment (Figure 5.5b.). Thus, at 38 and 342 days, the C:N was significantly higher in caribou litterbags than plant litterbags. After 422 days, the pattern was evident for plant litter in both fertilization treatments and CLCT. However, there was no difference between CLNP and any other treatment.

## 5.5 Discussion

### *5.5.1 Litter type determined mass loss and decomposition constants*

Animal processing slowed decomposition in MAT but not in DH. In MAT, litter type was the most important determinant of mass loss and governed patterns in the decomposition constants, but the results were opposite of my prediction. *E. vaginatum* litter from senesced plants had a much higher decomposition constant and greater mass loss than vole litter. There was also no difference in decomposition between fertilized and ambient nutrient plots which did not support my second hypothesis. Although there were transient effects of fertilization at two collection dates for both litter types, there were no strong overall fertilization effects seen in other studies (e.g. van Heerwaarden et al. 2003). Interestingly, higher nutrients have been shown to have negligible effects on *E. vaginatum* decomposition (Aerts et al. 2006). Regardless, litter processed by voles had slower decomposition. One explanation for this is that, through processing, voles deposit feces and probably urine within haypiles, which may increase decomposition (van der Wal et al. 2004a). Vole feces were removed from samples before litter was placed in bags to avoid the confounding plant and feces decomposition effects. The lack of feces in vole litterbags may explain the lower decomposition rates seen for vole litter in this study. Additionally, there was a large number of senesced plant litterbags which had obvious signs of fungal hyphae in fertilized plots (25 of 36 litterbags), while there was only one vole litterbag in a fertilized plot that had obvious fungi. There seemed to be no pattern of hyphae presence with respect to collection date. The experimental design did not allow for statistical testing of the presence of fungi, nor did I quantitatively analyze litterbags for fungi. However, there were slightly more senesced plant litterbags from fertilized plots (n = 14) with visible signs of fungi than unfertilized plots (n = 11) suggesting a shift towards fungal decomposers with fertilization consistent with other studies (Clemmensen et al. 2006; Rinnen et al. 2007). The lack of fungi in vole litter litterbags suggests that perhaps processing by voles somehow inhibits fungal growth on

*E. vaginatum* plant litter. Alternatively, there may have been no fungal growth on vole litter because C in forms accessible to fungi may have already been depleted before litter was collected for this experiment.

In DH my hypothesis, that processing by caribou increases *H. alpina* leaf litter decomposition, was also not supported, but patterns were somewhat different than in MAT. Litter type interacted with fertilization in a subtle way for both mass loss and decomposition constants. While there was no difference between plant and caribou litter over the entire experiment, differences in caribou litter decomposition emerged between ambient and fertilized plots sometime between the first and second collection dates. During this interval, caribou litter in fertilized plots lost more mass than caribou litter in ambient plots. This was also reflected in the decomposition constant, and suggests that for at least processed caribou litter, higher intrinsic soil nutrients allowed greater decomposition in fertilized plots (van Heerwaarden et al. 2003). Thus, my second hypothesis was supported for caribou litter only, as there was no difference in decomposition of senesced plant litter between ambient and fertilized plots. This may reflect the timing of collection between caribou litter and plant litter, as presumably caribou litter was removed from *H. alpina* tussocks by caribou sometime in the winter or early spring prior to beginning this experiment. As with vole litter discussed above, this may have allowed soil microorganisms more time to deplete litter of more labile C prior to litter collection for this experiment ultimately affecting the differences found in caribou litter in fertilized and ambient plots.

### *5.5.2 Litter C and N differ between litter types*

Patterns in litter C loss reflected mass loss in both communities, while patterns in litter N were much different between the two sites. Thus, my initial hypothesis that C loss would reflect overall litter mass loss for species in both communities was supported; patterns in litter C over time were consistent with litter mass. However, my hypothesis that litter N loss would be greatest in ambient plots was only supported vole litter at 358 days in MAT and there were no differences in litter N due to fertilization in DH. Overall there was a trend of increasing N in litter in MAT, as soil microorganisms may have immobilized N similar to results seen in other nutrient limited arctic ecosystems (e.g., Jonasson et al. 1996, Aerts et al. 2006) as well as other more temperate N limited systems (Barrett and Burke 2000; Fisk and Fahey, 2001; Knorr et al. 2005). Fertilization seemed to increase N retention of both plant and vole *E. vaginatum* litter in MAT, although this pattern was not seen for either plant or caribou *H. alpina* litter in DH. This result may be partially explained by the presence of fungal hyphae in *E. vaginatum* litter and lack thereof in *H. alpina* litter. In MAT, fertilization may cause a shift in soil conditions favoring fungal organisms (Doles, 2000), which have a higher capacity for N immobilization than the biota in ambient conditions (Moore et al. 2008). Additionally, the initial loss in N from caribou litter in DH may be explained by timing of caribou litter following fertilization two weeks prior. Because loose caribou litter was collected near fertilized plots, it is possible that this caribou contained residue from recent fertilization. This would explain the initial N loss for caribou litter between field placement of the bags and the first collection date, as residual N from fertilization may have rapidly been lost from this litter.

In this study, I did not determine quantitatively differences in litter quality, or form of C, in litter samples. However, the C:N ratio may be used as an approximation of litter quality (Nicolardot et al. 2001) as plant leaves with higher N content generally decompose faster (Robinson et al. 1995, Kochy and Wilson, 1997). Additionally, high C:N indicate more C may be tied up in more recalcitrant compounds, while lower C:N values indicate that the C in samples is more labile and may also decompose faster (van Veen et al. 1984). Theoretically, plants growing in fertilized plots should decompose faster because %N is generally increases in graminoid leaf tissues with fertilization (Dormann and Woodin, 2002). Interestingly, there are no overall patterns in C:N with respect to fertilization for either community signifying that fertilization did not affect decomposition regardless of litter quality. In MAT, vole litter had consistently higher C:N ratios than plant litter, suggesting that litter quality differences existed when both plant and vole litter were collected from the field, affecting overall decomposition of samples. While vole litter C:N ratios were not different from initial values over time, senesced plant litter C:N tended to decrease over time suggesting loss of more labile forms of C. In DH, there were also differences between initial C:N ratios, also suggesting differences in litter quality. At 38 days caribou litter C:N ratios sharply increased, which could indicate a decrease in labile C during this time period. However, following this anomaly, the patterns with respect to differences in C:N between litter types were established and C:N in all treatments tended to decrease for the duration of the experiment suggesting a decrease in recalcitrant forms of C. Alternatively, as stated above, this pattern of decreasing C:N in caribou litter may be simply due to the timing of caribou litter collection, which may have contained residual N from the fertilization treatment just prior to collection. Overall, differences in decomposition between litter types in both communities can be explained by differences in initial litter quality, which has been shown to be of a primary factor determining leaf decomposition rates in arctic ecosystems (Hobbie, 1996; Hobbie et al. 2002).

### *5.5.3 Herbivores may have the potential to decrease graminoid leaf decomposition*

Understanding how warmer temperatures affect plant decomposition in arctic ecosystems is crucial to understanding future global carbon balance (Cornelissen et al. 2007). Changes in community structure can indirectly affect the net contribution of $CO_2$ from the Arctic to the atmosphere because different species vary widely in decomposability (Hobbie, 1996) as litter quality largely affects the temperature sensitivity of soil microorganisms. With the exception of forbs, graminoids decompose faster than all other arctic growth forms (Cornelissen et al. 2007). Thus communities that experience shifts towards graminoids from more recalcitrant growth forms, such as DH (Gough et al. 2002; 2008), may have higher decomposition than communities experiencing other shifts. Alternatively, communities such as MAT shift away from graminoids towards more recalcitrant deciduous shrubs (i.e. *B. nana*; Shaver et al. 2001), suggesting a lower net contribution of $CO_2$ from decomposition from this community. However, because *B. nana* leaves are somewhat recalcitrant, warming may still stimulate decomposition of deeper buried C in MAT (Mack et al. 2004). Regardless, differences in litter quality among plant species may ultimately affect subsequent resource availability for plants (Dorrepaal et al. 2007).

It is possible that processing by mammals, voles in particular, may have the potential to affect these changes in plant litter quality by decreasing decomposition of graminoid plant leaves in communities similar to DH and MAT. By removing leaves early in the season and piling leaves on top of one another voles may delay decomposition. The primary mechanism by which herbivores in general are thought to affect leaf decomposition is through changes in leaf nutrient allocation patterns following biomass removal (Wardle et al. 1998; Guitian and Bardgett, 2000). Biomass removal by herbivores often decreases labile forms of C in leaf tissue decreasing the overall decomposition rate of leaves (Stark and Kytoviita, 2006). *E. vaginatum* is reported to reapportion C and nutrients from roots to leaves with biomass removal (Chapin et al. 1980; 1986). Ultimately, I did not know precisely when voles created haypiles of *E. vaginatum* leaves or when caribou removed litter from *H. alpina* tussocks; thus the timing of their formation and clipping of senesced leaves likely differed. Clear differences in C:N ratios suggest that litter quality was higher for senesced plant litter. Additionally, because patterns of nutrient and carbon allocation in arctic plants differ seasonally (Shaver and Chapin, 1986), a full understanding of processing would be possible only by knowing more precisely the timing of processing by herbivores. Although litter processed by herbivores decomposed more slowly than plant litter, the quality of processed litter and senesced plant litter did differ at the beginning of the experiment suggesting that processed litter had been leached of labile carbon before the experiment. Thus, I conclude that more investigation is needed to understand if decreased decomposition and difference in litter quality is due to processing itself or due to a difference in the timing of leaf removal from plants.

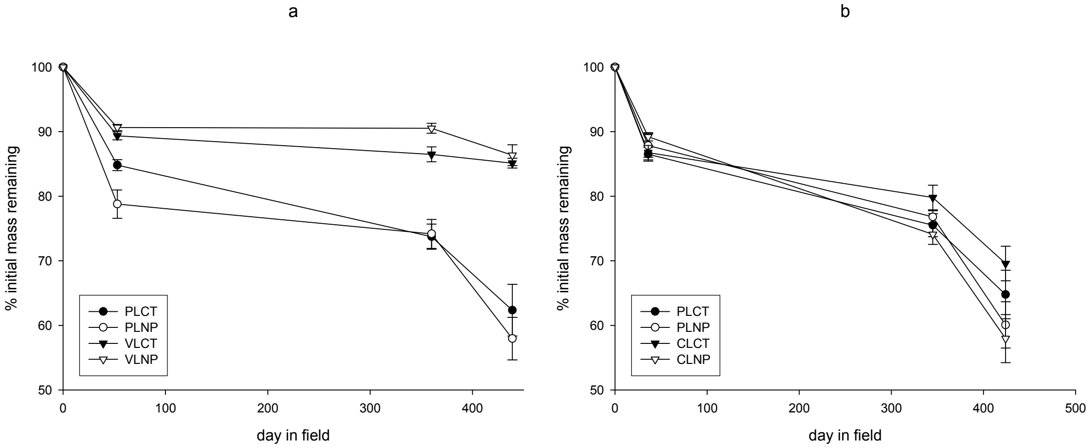

Figure 5.1. Percent initial mass remaining in litterbags in MAT (a) and DH (b) tundras placed in the field on 14 June, 2005 in MAT and 30 June, 2005 in DH. In MAT, treatments include, plant litter in ambient plots (PLCT), plant litter in fertilized plots (PLNP), vole litter in ambient plots (VLCT) and vole litter in fertilized plots (VLNP). In DH, treatments include: plant litter in ambient plots (PLCT), plant litter in fertilized plots (PLNP), caribou litter in ambient plots (CLCT) and caribou litter in fertilized plots (CLNP).

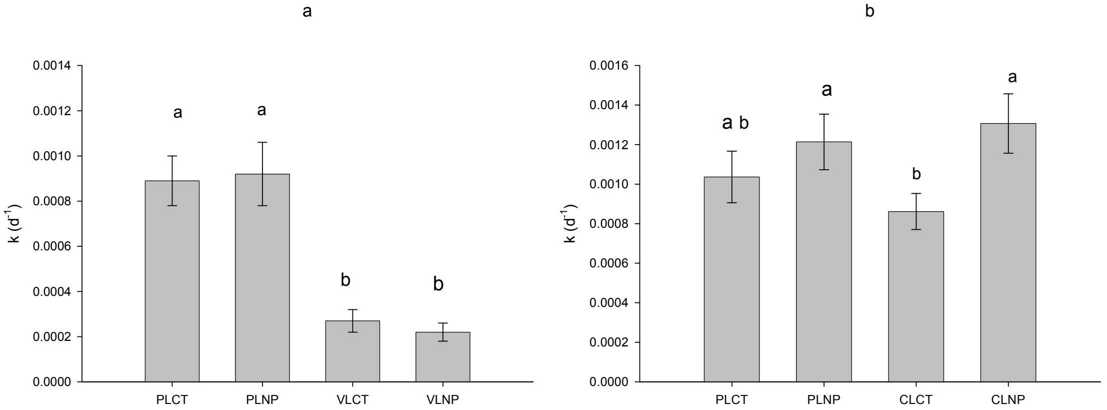

Figure 5.2. Decomposition constants (k) of litter in litterbags in MAT (a) and DH (b) tundras placed in the field on 14 June, 2005 in MAT and 30 June, 2005 in DH. constants were calculated determined from least squares regressions following Hobbie and Gough (2004), in MAT (a) and DH (b) tundras. Letters indicate significant differences between treatments (Tukey's HSD) Treatments as in Figure 5.1.

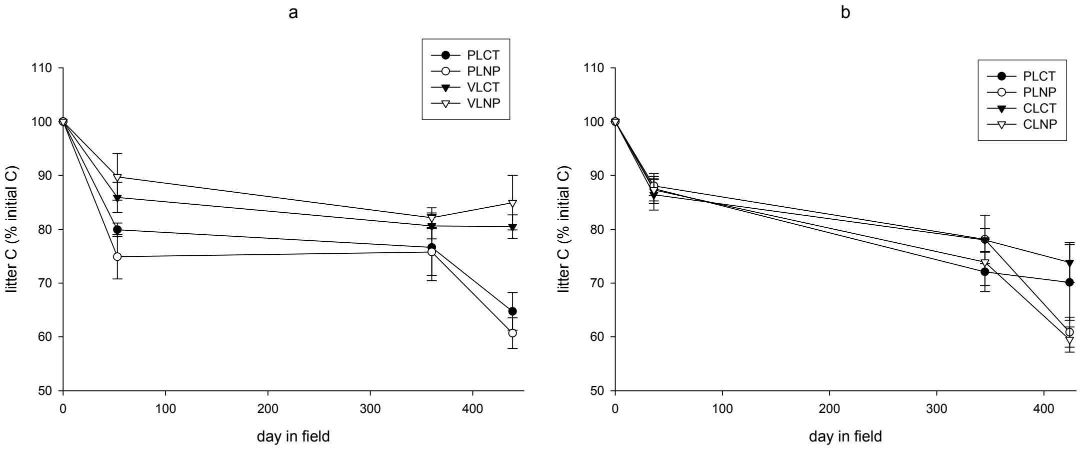

Figure 5.3. Percent initial C remaining in litter from litterbags in MAT (a) and DH (b) tundras placed in the field on 14 June, 2005 in MAT, and 30 June, 2005 in DH. Treatments as in Figure 5.1.

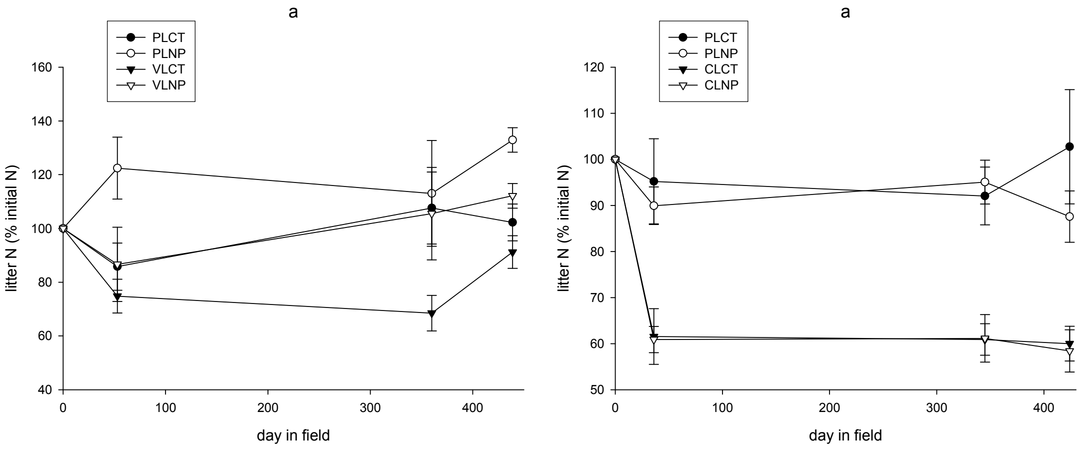

Figure 5.4 Percent initial N remaining in litter from litterbags in MAT (a) and DH (b) tundras placed in the field on 14 June, 2005 in MAT, and 30 June, 2005 in DH. Treatments as in Figure 5.1.

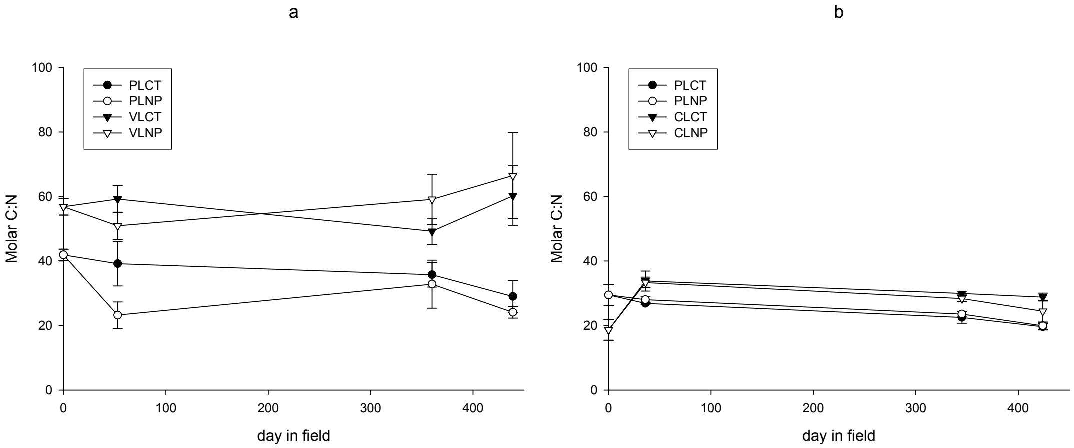

Figure 5.5. Molar C:N of litter from litterbags in MAT (a) and DH (b) tundras placed in the field on 14 June, 2005 in MAT, and 30 June, 2005 in DH. Treatments as in Figure 5.1.

Table 5.1. Summary of between subject F statistics from repeated measures ANOVAs conducted on different decomposition metrics. F-statistic degrees of freedom = 1, 15. Significant levels indicated by ***p<0.001, **0.001<p<0.01, *0.01<p<0.05, †0.05<p<0.1.

| Community | Species | Metric | Litter type | Fertilization | Litter type x Fertilization |
|---|---|---|---|---|---|
| MAT | *E. vaginatum* | % initial mass remaining | 131.07*** | 0.01 | 4.44† |
| | | % initial C remaining | 19.22*** | 0.01 | 1.36 |
| | | % initial N remaining | 8.0* | 9.9** | 0.001 |
| | | C:N | 88.85*** | 1.41 | 3.87† |
| DH | *H. alpina* | % initial mass remaining | 0.6 | 3.03 | 2.18 |
| | | % initial C remaining | 22.16*** | 0.15 | 7.99* |
| | | % initial N remaining | 125.48*** | 0.49 | 0.28 |
| | | C:N | 28.27*** | 0.26 | 1.58 |

Table 5.2 ANOVA source table examining treatment effects on the decomposition constant k for MAT

| Source | DF | MS | F | p |
|---|---|---|---|---|
| litter type | 1 | $4.05 \times 10^{-6}$ | 119.12 | < 0.001 |
| fertilization | 1 | $2.88 \times 10^{-8}$ | 0.85 | 0.37 |
| litter type*fertilization | 1 | $6.24 \times 10^{-8}$ | 1.84 | 0.2 |
| error | 15 | $4.05 \times 10^{-8}$ | | |

Table 5.3 ANOVA source tables examining treatment effects on the decomposition constant k for DH.

| Source | DF | MS | F | p |
|---|---|---|---|---|
| litter type | 1 | $1.01 \times 10^{-8}$ | 0.15 | 0.7 |
| fertilization | 1 | $5.82 \times 10^{-7}$ | 8.78 | 0.01 |
| litter type*fertilization | 1 | $1.08 \times 10^{-7}$ | 1.62 | 0.22 |
| error | 15 | $4.05 \times 10^{-8}$ | | |

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# BIOGRAPHICAL INFORMATION

David R. Johnson was born and raised in a small town in southeastern Idaho called Soda Springs. Early on, he went on many excursions into ‘the hills’ of eastern Idaho with his father and brother where a great love of nature was conceived. In high school, a great biology teacher reinforced this love of nature with the science of biology. David attended Idaho State University where he graduated in 2000 with a B.Sc. in Biology. Following this, David was part of an interdisciplinary project called the Lower Alaska Peninsula Project, which sought to understand how the prehistoric Aleut functioned to affect contemporary ecological systems in Southwest Alaska. He fell in love with Alaska, and earned a M.S. degree from Idaho State University in 2003 under Dr. Nancy Huntly and documented vegetation changes on long-abandoned Aleut village sites. David joined Dr. Laura Gough’s lab at UT Arlington in 2003 to continue working in the Alaskan Arctic. David’s research interest is in plant ecology; more specifically plant-plant and plant-animal interactions, herbivory, the ecology of prairie, desert, alpine and arctic ecosystems, and climate change. Most recently, he has become aware of the need of a paradigm shift among the general public regarding how persons understand the natural world around them. Thus, David has become very interested in urban and suburban ecology. David is married to a wonderful woman, Jen, and they are parents of one dog and two cats.