THE RESPONSE OF ARCTIC VEGETATION TO CLIMATE WARMING IN AN UNGULATE GRAZING SYSTEM

A Dissertation in

Biology

by

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ABSTRACT

Ecologists have long been searching for the mechanisms that control the distribution and abundance of species. There are numerous examples of studies that have investigated the influence of local and regional climates, intra- and interspecific competition for limiting resources as well as predation. Recently, increased attention has been devoted to the effects of climate change on species distributions, abundance and community composition. Plants have been shown to respond to climate change in various ways. For instance, primary production, phenological progression, reproduction as well as plant community composition have all been shown to respond to a changing climate. However, herbivory has also been shown to have strong impact on plants and plant communities. But, the influence of herbivory has been excluded from the majority of published studies on climate change and the effects on ecosystem properties. This may have led to inaccurate predictions about how ecosystems respond to climate change. The Arctic is expected to experience the earliest and most pronounced changes due to increasing global temperatures. My research was conducted in a low-arctic ungulate grazing system in West-Greenland occupied by large ungulate grazers like caribou (Rangifer tarandus) and muskoxen (Ovibos moschatus). The goal of this research was to investigate the influence of herbivory on how arctic vegetation responds to a warmer climate.

Twelve pairs of permanent vegetation plots were randomly selected inside and outside of herbivore exclosures in 2003. An open top chamber (OTC) was randomly assigned to each pair of permanent plots, to simulate climate warming. I investigated the influence of ungulate herbivory on the biomass production of arctic vegetation to
simulated climate warming. By the use of the non-destructive point-intercept method (PIM) I acquired a biomass index that was converted to biomass values. By monitoring changes in aboveground biomass from 2003 until 2006 I investigated the potential effect of climate warming on plant biomass production in an arctic grazing system. I did not find any strong evidence of climate warming effects on the aboveground plant biomass production. Neither did I find any strong effects of ungulate herbivory on plant production although there was indications that large herbivores could mitigate the predicted increase in shrub biomass over graminoids and forbs. However, the effect of my treatments was probably concealed by intense caterpillar foraging during a population outbreak of the moth *Eurois occulta* in 2004 and 2005 that severely affected aboveground biomass in the study area.

In a related study, I investigated the effects of climate warming and ungulate herbivory on plant community composition and the abundance of shrubs, graminoids and forbs. By converting plant intercepts from the PIM to vegetation cover values, I monitored changes in abundance from 2003 until 2006. The intent was to investigate if ungulate herbivores could mitigate the predicted increasing dominance of shrubs in the Arctic as a response to a warmer climate. I did not detect any significant changes in the abundance of shrubs, graminoids or forbs to either the warming treatment or exclosure treatment. But, there appeared to be higher abundance of shrubs where ungulate herbivores were excluded and higher abundance of graminoids in grazed areas, suggesting potential negative effect of ungulates on shrub dominance. However, the lack of responses observed in plant abundance to the treatments was most likely affected by the caterpillar outbreak during 2004 and 2005.
Climate warming has been shown to affect plant reproduction. Also, theory suggests that if herbivory is predictable in time and space, plants have the ability to compensate for tissue lost. Several plant species have been shown to compensate for tissue lost to herbivory. I investigated the possible influence of ungulate herbivory and climate warming on the flower and fruit production of two co-occurring forb species, *Cerastium alpinum* and *Draba cana*. The objective was to investigate potential compensatory responses in these two forbs species to grazing exposure and climate warming that could lead to changes in interspecific competition. Forty eight ramets from each species were permanently marked in the vegetation plots. Biometric measurements were performed on each ramet throughout the growth season. Results indicate a reduced reproductive success in *D. cana* to climate warming when exposed to herbivory while *C. alpinum* experienced increased reproductive success when compared to ramets in plots excluded from herbivory. This suggests that climate warming could affect the competitive outcome between plant species and hence affect future community composition.

Finally, I investigated the effects of climate warming and ungulate herbivory on plant emergence and phenological progression of arctic plants during the 2004 and 2005 growth seasons. Higher air and soil temperatures have been shown to advance plant emergence and the phenological progression of arctic and alpine plants. It has also been shown that plants have the ability to compensate loss of tissue to herbivores by compensatory growth. However, such allocation of resources to compensatory growth responses has been suggested to delay phenological progression. By monitoring plant emergence and phenological progression of plants in the permanent vegetation plots in
2004 and 2005, I investigated if herbivory could mitigate an advanced phenological progression of arctic plants as a response to climate warming. In 2004, the results indicated that a warmer climate advances the emergence of arctic plants. Furthermore, ungulate herbivory delayed plant emergence, but it appeared that the plants compensated a later emergence with a faster phenological progression. However, during the caterpillar outbreak in 2005, the relationships found in 2004 were offset by severe plant defoliation that caused fewer plant species to emerge during that year.

The results found in this study did not find sufficient evidence that climate warming and the effects of herbivory have strong influence on aboveground plant production or plant community composition. However, the outbreak of the moth *E. occultata* severely affected aboveground biomass and plant cover and most likely concealed any treatment effects from the experiment. However, effects of both climate warming simulations and ungulate herbivory significantly affected plant reproduction, plant emergence and phenological progression. Based on the findings in this study, it is strongly advised that the influence of herbivory should be taken into account when effort is made to make prediction about how plants respond to a changing climate.

Throughout the development of my dissertation work, I have been involved in and contributed to research closely related to the issues investigated in this thesis. These publications are found in Appendix A-D.
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All my life I have been fascinated by the beauty and diversity of nature. From the first short exploratory expeditions in my parents back yard to the later scientific expeditions that finally led me to Greenland and the project presented on the pages below. On this journey from a romantic young naturalist towards a more professional scientist my appreciation for nature has grown. To be able to travel to Greenland four consecutive field seasons has been a tremendous adventure. Being able to work closely with the system you are trying to study is an important part of your research. I wish to thank my advisor Eric Post for letting me be part of this research project. I would especially thank him for bringing me to Greenland, a place so pristine and still largely untouched by humans. The experiences we have had together while developing this long-term project will be a major part of me for as long as I live.

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Chapter 1

Introduction

The distribution and abundance of species is partly a reflection of their adaptation to local and regional climates, intra- and interspecific competition for limiting resources, as well as predation, and has long been the focus of ecologists. To be able to understand and predict the behavior of populations it is important to understand what factors are regulating them. Over the last two decades the search for such mechanisms has been of increasing importance due to the rapidly changing global climate, which is predicted to have profound effects on species’ distributions and abundance.

Malthus (1798) recognized that any population, given an unlimited food source, has the intrinsic capacity for exponential growth. He argued that populations would grow exponentially if left unchecked, and eventually would exhaust their food source. Ever since then, ecologists have been searching for a single, general mechanism for controlling the density of populations. Historically, ecologists have argued for either a density-dependent mechanism or a density-independent mechanism of population control. Abiotic factors, such as weather, have been argued to influence animal populations (Davidson and Andrewartha 1948), whereas other studies have shown that density-dependent factors such as food availability is the most important regulating factor (Lack 1954). A controversial and influential paper, commonly known as HSS (Hairston, Smith and Slobodkin), argued that most studies focused on single species populations, and that the different mechanisms for population regulation depend on the trophic level in consideration (Hairston et al. 1960). They argued that decomposers, producers and predators are commonly regulated by density-dependent mechanisms, and that
herbivores are regulated by predation and not food availability. The HSS argumentation generated rebuttals and intense debate for years. Later critique pointed out that herbivore food supply could vary in availability and quality, especially in seasonal environments, which could lead to food limitation regulating herbivores (Murdoch 1966). This critique was further supported by Ehrlich and Birch (1967), who argued that herbivores can also regulate plant populations, and that the influence of weather cannot be ignored. These arguments have recently enjoyed renewed interest due to recent focus on climate change.

The influence of climatic variation on population densities and fluctuations has been argued ever since Andrewartha and Birch (1954) published their influential book “The distribution and abundance of animals”, where they presented several case studies arguing for density independent control of animal populations. Recently, increased attention has been given to large-scale climate systems and their influence on local populations (Post and Forchhammer 2002, Walther et al. 2002, Post 2003). As the global climate continues to change, there is increasing evidence that such changes will have profound effects on plant and animal populations and their distributions. A recent publication suggests that presently the global climate as a whole is within 1°C of the maximum temperature of the past 1.3 million years (Hansen et al. 2006). Over the past 100 years, the average global temperature has increased by approximately 0.6 °C (IPCC 2001), and within the last 3 decades the global temperature has risen approximately 0.2 °C per decade. It is this relatively rapid rise in global average temperature that is expected to have strong ecological effects on species distributions and abundance. This is especially important for ecosystems at higher latitudes that are strongly temperature limited. Recent reports show a strong increase in winter temperatures over northern
continents in the last 30-40 years (Serreze et al. 2000) that likely will have important ecological effects.

Arctic ecosystems have been a major focus of climate change studies, because they are expected to undergo a more rapid temperature increase than any other major ecosystem on earth and to experience the most pronounced changes due to these increasing temperatures (Maxwell 1992). The Arctic is considered to be relatively constant over time, compared to most other biomes, with little resilience to disturbance, and is therefore susceptible to rapid climatic changes. Ecosystem processes in the Arctic are strongly limited by temperature and permafrost and, as a consequence, a large amount of carbon has accumulated in the soil as frozen or buried organic deposits (Oechel et al. 1993). This strong temperature dependence makes the arctic susceptible to rapid temperature increase. Evidence from the paleoclimate records, such as tree rings, sediments and glaciers, show that the Arctic climate is at present warmer than at any time during the last 400 years (Overpeck et al. 1997). The frozen organic deposits that have accumulated in the Arctic are a potential carbon source if the permafrost melts and releases the stored carbon through increased decomposition rates. For example, it is reported that minimum temperatures increase at twice the rate of maximum temperatures causing a lengthening of the freeze free periods (Walther et al. 2002). The recent warming of the Arctic has already resulted in a net release of CO$_2$ and CH$_4$ and has the potential for a substantial feedback on climate as atmospheric carbon concentration increases (Oechel et al. 1993, Oechel et al. 2000). However, some of this carbon release might be mitigated by an increase in plant biomass.
The Arctic is generally nutrient limited and a warmer climate is expected to increase nutrient mineralization rates (Jonasson et al. 1999b). This increase in nutrient availability could positively influence net primary productivity (NPP), causing an increase in plant biomass of arctic vegetation (Jonasson et al. 1999b). This increase in NPP and plant biomass could, at least partly, mitigate the carbon release from arctic soils by sequestering carbon in plant biomass (Melillo et al. 2002). For example, it has been shown that plant aboveground biomass has increased as a response to nutrient fertilization in Alaskan tundra (Mack et al. 2004). However, a recent meta-analysis of experiments on nutrient fertilization and CO₂ enrichment studies revealed that elevated CO₂ only caused a sequestration of carbon in the soil if nitrogen were added at concentrations between 30 and 150 kg·ha⁻¹·yr⁻¹ compared to the maximum atmospheric nitrogen deposition in the USA and Europe of 30 kg·ha⁻¹·yr⁻¹ (van Groenigen et al. 2006).

Based on these results, it is evident that increasing plant growth and carbon sequestration in ecosystems limited by nutrient availability are dependent on nitrogen input from other sources. One ecological factor that could influence nutrient content and cycling is changes in plant community composition. There are recent observations of increasing abundance of shrubs in the Arctic ascribed to a warmer climate (Arft et al. 1999, Sturm et al. 2001b, Sturm et al. 2005). Such responses suggest an increase in the carbon storing potential of arctic vegetation because shrubs have a higher carbon sequestration potential than other plant functional groups such as graminoids and forbs (Shaver et al. 1998, Sturm et al. 2001b). A shift in composition and diversity may influence soil nutrient availability such that species with high quality litter input (forbs, graminoids) increase productivity, while litter input of lower quality shrubs may limit the productivity
response (Shaver et al. 2000) due to a slower turnover rate. This may again lead to higher biomass accumulation. Another factor influencing plant community composition and nutrient input is the effect of herbivores.

Historically, the effects of herbivory have been viewed as obligate negative for the plants. However, the evolution of herbivore-plant interactions has been under increasing interest since Fraenkel (1959) published a paper on plant chemical defenses, insect herbivory, and agriculture. He argued that if plants would have been entirely successful in defending themselves from herbivory there would be no insect problem. However, he suggested that there must be some sort of co-evolutionary mechanism that causes insects to overcome this anti-herbivory strategy from the plant. Frankel’s suggestions inspired systematic investigations of the interaction between insect herbivores and plant defenses (Ehrlich and Raven 1964). Ehrlich and Raven (1964) concluded that there appeared to be a reciprocal interaction between plant secondary compounds and butterfly caterpillar herbivory in a co-evolutionary relationship. Later evidence led to the conclusion that there exist two different strategies of plant responses to herbivory. Plants can either resist herbivory by chemical or structural defenses, or they can develop strategies that allow them to tolerate loss of plant tissue (Bryant et al. 1983, Strauss and Agrawal 1999, Juenger and Lennartsson 2000). Such differential responses to herbivory vary also between different plant functional groups, such as shrubs and graminoids. The vulnerability to herbivory depends largely on plant growth forms. Shrubs, with their apical meristems and relatively slow growth, are negatively affected by herbivore foraging, and usually depend on chemical or structural defenses. Graminoids,
on the other hand, are relatively tolerant of even repeated herbivory because basal meristems are located close to the ground (Wright and Illius 1995). The differential effect of herbivory on different plant growth forms can cause vegetational transitions leading to shifts in plant community composition. This is especially evident in the large herbivore grazing systems (van der Wal 2006).

The ecology of grazing ecosystems has been the focus of scientific attention for a long time, and is especially well-studied on the African savannah (McNaughton 1979, 1983, 1986), on American grasslands (Frank and Evans 1997, Frank et al. 2002), and in northern ecosystems like the Arctic (Skogland 1980, Thing 1984, Manseau et al. 1996). In these systems, woody species such as shrubs are usually reported to decrease in abundance in areas where large ungulate herbivores forage. Studies of grazing systems in Kenya and Tanzania indicate that the feeding behavior of these large groups of animals establishes extensive grazing lawns of low growing vegetation (McNaughton 1984). But such effects have also been found in more northern ecosystems. For example, studies of 30-year-old exclosures on reindeer pastures in Northern Norway (Olofsson et al. 2001, Olofsson et al. 2004b) suggest that grazing has the potential to constrain productivity and reduce standing biomass of shrubs, promoting development of grass-dominated tundra. Such effects also have been reported from West Greenland, where caribou grazing and trampling precipitates the dieback of the shrub *Betula nana*, and eventually led to the spread and domination of grasses (*Poa* sp.; (Thing 1984). As well, studies of caribou summer ranges in sub-Arctic Canada (Manseau et al. 1996) have revealed that grazing has the potential to constrain productivity and reduce standing biomass of shrubs in the
Arctic. Vertebrate herbivores can also promote growth of graminoids and forbs by reducing the depth of the moss layer through grazing and trampling (Olofsson et al. 2001, van der Wal et al. 2001, Olofsson et al. 2004b, Van der Wal and Brooker 2004). Studies of 40-year-old fences in northern Norway have revealed that reindeer grazing has produced a shift in tundra vegetation from moss-rich to graminoid dominated meadows (Olofsson et al. 2001), and resulted in increased soil temperatures, decomposition rates and nutrient availability (Olofsson et al. 2004b). Similar results have been found in exclosure experiments on Svalbard, where reduction of the moss layer has resulted in greater soil temperatures, increased litter decomposition, and enhanced primary production (Van der Wal and Brooker 2004).

In many of the grazing ecosystems worldwide, there exist long histories of plant-herbivore interactions. The sometimes positive effect of grazing on plant primary production has led authors to suggest that herbivore-plant interactions through ecological and evolutionary time have led to grazing optimization mechanisms or overcompensation or even plant–herbivore mutualism (Owen and Wiegert 1981, McNaughton 1983, Vail 1992, Jaremo et al. 1996, Nilsson et al. 1996, de Mazancourt et al. 2001). (Zimov et al. 1995) proposed a keystone herbivore hypothesis, suggesting that large mammalian herbivores can shift tundra plant communities into graminoid-dominated steppe with high rates of nutrient turnover and enhanced primary production. They even postulated that the large-scale transition of the extensive Beringian grasslands into an unproductive moss dominated tundra ecosystem was caused by the extinction of Pleistocene mega-herbivores.
Increased attention to tolerance mechanisms in plants, especially in grazing ecosystems, has revealed that plant primary production may increase in areas exposed to low or moderate grazing, compared to ungrazed areas (McNaughton 1979, 1983, Bråthen and Odasz-Albrigtsen 2000, Frank et al. 2002, McIntire and Hik 2002). Grazing by large ungulates seems to shift plant communities from shrub domination towards graminoid-dominated grazing lawns, with increased primary productivity. Enhanced nutrient cycling appears to be important for a shift towards graminoid domination (Stark and Grellmann 2002), and grazers deposit faeces and urine in areas where they forage, further increasing soil nutrient availability that can sustain the high productivity of graminoids in these systems. This actually gives the herbivores the ability to manipulate plant community composition, and hence their own food supplies (van der Wal 2006). Though this perspective is contentious, these findings have been supported by theoretical models that demonstrate increased primary production as a result of nutrient cycling due to herbivory, which could lead to grazing optimization (Loreau 1995, de Mazancourt et al. 1998, 1999).

The overall effect of vertebrate herbivory will depend on the balance between negative and positive feedback effects that herbivores exert on plant productivity and nutrient cycling (Augustine and McNaughton 1998), and may contribute to how vegetation productivity responds to climate change. Experiments addressing the effect of grazing or browsing in several ecosystems have revealed that vertebrate herbivores affect plant biomass, NPP, nutrient cycling and species composition (Pastor et al. 1988, McInnes et al. 1992, Kielland et al. 1997, Augustine and McNaughton 1998, Frank and
Groffman 1998, Bråthen and Oksanen 2001, Stark and Grellmann 2002). These influences may mediate the response of vegetation to climate change, and may be especially important in the Arctic, where productivity is generally nutrient limited (Chapin and Shaver 1996, Jonasson et al. 1999a). I propose that large ungulate grazers like caribou (*Rangifer tarandus*) and muskoxen (*Ovibos moschatus*) have the ability to mitigate the predicted increase in shrub abundance as a response to climate change, and promote the establishment of graminoids and forbs.

To address the effect of how ungulate grazing influences the response of climate warming on arctic vegetation, I conducted a full factorial experiment in the low-Arctic on the summer range of the Kangerlussuaq-Sisimiut caribou herd in West-Greenland (Fig. 1.1), where the grazing history from ungulate herbivores extends at least 4,500 years (Melgaard 1986). The study area is part of the low-arctic, and the plant community is defined as low shrub tundra that represents 24% of the vegetated area of the Arctic (CAVM Team 2003). The study site is occupied by caribou (Thing 1984, Bøving and Post 1997, Post et al. 2003) and muskoxen (Forchhammer and Boomsma 1995) from late winter throughout the summer. The experiments were conducted inside and outside of herbivore exclosures with the use of open-top chambers (OTCs) to simulate climate warming of the vegetation (Fig. 1.2).

Plant functional groups such as deciduous and evergreen shrubs, forbs, graminoids, lichens and mosses, have been widely used for investigating plant responses to changes in environmental conditions (e.g. nutrient additions and temperature manipulations), and ecosystem processes (e.g. nutrient cycling) as well as impacts of
herbivory (Chapin et al. 1996). Functional groups are more useful than single species as predictors of climate change because they influence many ecological processes such as primary production as well as nutrient cycling through litter quality (Chapin et al. 1996).

For chapters 2 and 3 of this thesis the focus will be on 3 main functional plant groups: deciduous shrubs, forbs and graminoids; whereas for chapters 4 and 5, I have distinguished among individual species.
Figure 1.1: Map of the study area near Kangerlussuaq, West Greenland. Blue line depicts the Arctic Circle. Map source: [http://maps.grida.no/arctic/](http://maps.grida.no/arctic/)
Figure 1.2: OTC’s inside one of the exclosure sites. These chambers passively warm the vegetation and soil, and have limited effect on precipitation and gas exchange.
Chapter two of this thesis addresses the influence of ungulate herbivory on how productivity of functional plant groups, such as shrubs, forbs and graminoids, respond to climate warming. I focused on aboveground biomass responses of these key functional plant groups in an ungulate grazing system in West-Greenland. Biological processes and plant productivity is considerably limited by low temperatures and the presence of permafrost. The arctic is generally nutrient limited and climate warming is expected to increase decomposition rates causing an increase in nutrient mineralization (Jonasson et al. 1999b). This increase in a limited resource is predicted to have a positive influence on net primary production (NPP) and cause an increase in plant biomass of arctic vegetation (Jonasson et al. 1999b). Productivity responses seem to depend on plant community composition of plant functional groups. An increase in abundance of shrubs in some parts of the arctic suggests an increasing dominance of shrubs over other functional plant groups as a response to climate change (Sturm et al. 2001b, Sturm et al. 2005). Experiments on climate change and vegetation responses support these observations of a change towards shrub dominance at the expense of forbs and graminoid species (Chapin et al. 1995, Shaver and Jonasson 1999).

Studies of the effects of herbivory, and ungulate grazing systems in particular, have revealed that large herbivores can shift the vegetation from initially high shrub domination toward graminoid dominated grazing lawns with relatively high productivity (Manseau et al. 1996, Olofsson et al. 2001, Stark et al. 2002). In West-Greenland, reduced biomass of Betula nana and increased biomass of graminoids was related to grazing by caribou (Thing 1984). In northern Norway reindeer reduce the biomass of shrubs and promote a biomass increase in grazing tolerant graminoids (Bråthen and
Oksanen 2001). In areas where large groups of ungulate grazers occur, the influence of herbivory may mitigate the expected accumulation of shrub biomass in the Arctic. By investigating the change in biomass of shrubs, forbs and graminoids exposed to climate warming and herbivory, I have tried to address the potential effects of herbivory on plant biomass production.

Whereas chapter two concerns plant productivity and biomass, chapter three investigates the effects of ungulate herbivory on the abundance, or percent cover, of shrubs, forbs and graminoids in response to climate warming. The increased abundance of shrubs observed in the Arctic is predicted to increase solar energy absorption in summer (Chapin et al. 2005) but also snow conditions and dynamics during winter (Sturm et al. 2005). This could further strengthen the increasing abundance of shrubs in several arctic ecosystems (Sturm et al. 2005) and reduce plant species diversity of the plant communities. Experimental studies of climate change report increased abundance of shrubs and reduced abundance of lower stratum growth forms such as forbs, graminoids, lichens and mosses (Chapin et al. 1995, Shaver and Jonasson 1999, Hollister et al. 2005, Wahren et al. 2005). Such changes could reduce productivity because species diversity and plant community composition is often correlated with vegetation productivity (Reich et al. 2001).

Herbivory has been shown to reduce the ground cover of shrubs and increase the cover of graminoids. For example, the ground cover of the dwarf birch Betula glandulosa was less in Rangifer grazed areas compared to areas with no herbivory (Manseau et al. 1996). Ericaceous shrubs in northern Norway also have almost disappeared in reindeer
grazed areas (Olofsson et al. 2001). Grazing and trampling from *Rangifer* in Svalbard have been reported to change plant community composition by reducing the moss layer to the benefit of graminoids (Van der Wal and Brooker 2004). By changing plant community composition and the abundance of plant functional groups, large ungulate herbivores have the potential to limit or even prevent the predicted increase in shrub abundance and domination in the Arctic where these animals occur. By measuring changes in the abundance of functional plant groups in relation to climate warming and ungulate herbivory I tried to quantify if herbivory has any influence on how plant communities respond to climate change.

Chapter four of this thesis investigates the influence of ungulate herbivory and climate warming on the flower and fruit production of two arctic forb species. There has been an increasing interest in the evolution of herbivore and plant interactions since Frankel (1959) published a paper on the interactions between insect herbivory and plant crops. A systematic investigation of butterfly caterpillar foraging and plant responses initiated a focus on a possible co-evolutionary process between plant and herbivore animals (Ehrlich and Raven 1964). Plants can either resist herbivory by chemical or structural defenses or they have evolved mechanisms that allow them to tolerate herbivory (Strauss and Agrawal 1999, Juenger and Lennartsson 2000). There is now an increasing interest in plant tolerance mechanisms that could lead to increased plant primary productivity (Frank et al. 2002, McIntire and Hik 2002). If herbivory is predictable in time and space, plant compensatory growth in response to herbivory could compensate for tissue lost (McNaughton 1983). Overcompensation is commonly defined
as increased plant productivity and/or reproductive effort in response to herbivory (Belsky et al. 1993). Increased reproductive effort in relation to herbivory has been reported (Paige and Whitham 1987, Paige 1992, Lennartsson et al. 1997), and others have suggested that there is a plant-herbivore mutualistic relationship (Owen and Wiegert 1981, de Mazancourt et al. 2001).

Arctic and alpine plant species are influenced by temperature and several experiments have found that plant reproductive effort and success increases for some plant species (Wookey et al. 1993, Totland 1997, Price and Waser 1998). However there are studies indicating that reproduction in some plant species has a neutral or negative response to a warmer climate (Stenstrom et al. 1997, Totland and Alatalo 2002, Saavedra et al. 2003). These studies suggest that the competitive balance between plant species can be altered due to climate warming. Such a response can further be affected by the presence of herbivory. I have in chapter four investigated the flower and fruit production of the two co-occurring species Draba cana and Cerastium alpinum in relation to simulated climate warming and ungulate herbivory. The intention was to find out if the competitive balance between these two species was affected by climate warming and if this effect was differentially influenced in the presence of ungulate herbivores.

Finally, in chapter five, I investigated the phenological development of plants in relation to climate warming and herbivory. Phenological events, such as growth initiation, leaf emergence and reproduction is dependent on temperature. Longterm monitoring of flowering dates show an advanced phenological progression in relation to a changing climate (Post and Stenseth 1999, Abu-Asab et al. 2001, Post et al. 2001, Hepper
Climate change projections suggest that arctic and alpine species may advance their phenological progression by as much as 2-3 weeks (Molau 1997). Advanced flowering phenology has been found among all functional plant groups; shrubs (Welker et al. 1997, Suzuki and Kudo 2000), perennial forbs (Molgaard and Christensen 1997, Stenstrom et al. 1997), and graminoids (Stenstrom and Jonsdottir 1997).

Several studies have found that herbivory can have profound effects on plant biomass and production (McInnes et al. 1992, Bråthen and Oksanen 2001, Frank et al. 2002, also see chapter 2). Furthermore, studies show that herbivory also can affect reproductive effort and success (Lennartsson et al. 1997, Paige 1999, Huhta et al. 2000a, also see chapter 4). However, it has been argued that the compensatory responses in plants to herbivory might cause delay in the phenological progression due to resource allocation to compensatory growth (Tiffin 2000). A delayed phenological progression could reduce seed germination and seedling survival rates in the fall due to frost damage. Hence, the expected phenological progression in arctic plant in response to a warmer climate might not be as prevalent in areas were ungulate grazers are present. In chapter five of this thesis I have investigated the phenological progression of plants during two growth seasons with emphasis on response to both simulated climate warming and ungulate herbivory.

To be able to understand the variation in the nutrient cycles and what factors influences them will provide important information about variations in the carbon cycle (Shaver and Jonasson 1999). As mentioned previously, changes in plant communities and ecosystem properties as a result of a changing climate have been reported from several
studies. Except for the work conducted by van der Wal et al. (2007) on goose grazing, few, if any, studies have investigated the influence of herbivores in how vegetation respond to climate change. Furthermore, most studies of climate change effects have investigated responses in biomass and productivity, changes in plant community composition, changes in reproductive effort and phenological changes. In this dissertation I have tried to make a connection among ungulate herbivores and plant aboveground biomass, community composition, flower and fruit production, and phenological development of Arctic vegetation. The intention has been to investigate several aspects of climate change effects on arctic vegetation at once and in the same system. It has been my aim that this research will further our knowledge of how climate change will affect the ecological interactions between plants and animals and ecosystem processes. Furthermore, results from this thesis will provide the basis for further empirical work on this topic as well as development of improved process models assigned to make predictions about future effects of climate change on the terrestrial biosphere.
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Chapter 2

The response in aboveground biomass of arctic vegetation to climate warming in an ungulate grazing system¹

Abstract

A major part of studies investigating the effects of global climate change have focused on arctic ecosystems. The Arctic is expected to undergo the earliest and most pronounced changes in response to increasing global temperatures because the ecosystems in these northern latitudes are considerably limited by low temperatures and permafrost. In these nutrient limited systems, a warmer climate is expected to increase decompositions rates and nutrient mineralization. An increase in a limiting resource is predicted to increase plant biomass production in the Arctic. These changes are expected to cause an increased dominance of shrub over graminoids and forbs. Woody species have a higher carbon storing potential than other functional plant groups, and an increase in shrub dominance suggest an increased ecosystem carbon storage potential in areas where shrubs are abundant. But, the influence of vertebrate herbivores have been largely absent in studies investigating the effects of climate change on vegetation responses. However, it is a well established fact that vertebrate herbivory can have a major influence on plant community composition, biomass and nutrient cycling. Neglecting the influence of vertebrate herbivores might bias estimates of ecosystem change in relation to climate change. In this paper I present results from a study investigating the effects of vertebrate herbivory on how plant biomass respond to simulated climate warming in the Arctic. The warming simulations were conducted by the use of open-top chambers (OTC’s) inside and outside of herbivore exclosures in West-Greenland. The results after four years of treatments did not give any clear evidence of increased abundance in shrubs as a response to climate warming. Neither did I find evidence suggesting that grazing mediated increased domination of shrubs over other functional plant groups in response to climate
warming. Intense caterpillar foraging from the moth *Eurois occulta* during two growing seasons may have concealed any treatment effects. However, there was some evidence suggesting that vertebrate herbivores constrain the biomass production of shrubs over graminoids and forbs. It is therefore advisable to consider the effect of vertebrate herbivores in studies investigating climate change effects on plant communities in areas where such animals forage.
Introduction

Arctic ecosystems have been a major focus of climate change studies because the biological processes in the northern high-latitude environments are considerably limited by temperature and permafrost. Records show that the winter temperatures over northern continents have increased considerably in the last 30-40 years (Serreze et al. 2000) while paleoclimate evidence (e.g. sediments, tree rings and glaciers) suggest that the Arctic has now warmed to the highest temperatures in the last 400 years (Overpeck et al. 1997). Arctic ecosystems are generally nutrient limited (nitrogen and phosphorus) and climate warming is expected to increase decomposition rates and nutrient mineralization (Jonasson et al. 1999b). This increase in a limited resource is predicted to have a positive influence on net primary production (NPP) and cause an increase in plant biomass of arctic vegetation (Jonasson et al. 1999b). Process models indicate that the NPP response of arctic vegetation to an increasing CO$_2$ concentration in the atmosphere is dependent on increased nitrogen mineralization due to climate warming (Melillo et al. 1993). Increased NPP might in turn compensate for carbon loss from arctic soils by sequestering carbon as increased plant biomass production stimulated by increased availability of mineral nitrogen (Melillo et al. 2002). In Alaskan tundra annual aboveground plant production has been shown to double during a fertilization experiment (Mack et al. 2004). Productivity responses at the community level are dependent on species diversity, plant community composition and plant growth forms (functional groups). Higher species diversity is often correlated with higher primary production and biomass accumulation (Reich et al. 2001). Several studies have reported differential effects of climate change on
biomass production of functional plant groups and hence plant community composition. In arctic Alaska, species diversity was lost due to the increasing dominance of shrubs at the expense of graminoids and forbs (Chapin et al. 1995, Shaver and Jonasson 1999). This might again affect the carbon balance in the arctic because the carbon storing potential of shrubs is higher than that of graminoids and forbs (Shaver et al. 1998, Sturm et al. 2001b). Recent observations of increased shrub abundance in arctic Alaska (Sturm et al. 2001b) as well as meta-analysis of warming experiments at 13 arctic research sites showing increasing dominance of shrubs over other functional plant groups (Arft et al. 1999) does suggest that there is a potential for increased ecosystem carbon storage. (But see Mack et al. 2004).

However, the influence of herbivory has been excluded from published process models and empirical work on climate change effects on ecosystem processes and may have led to inaccurate predictions about productivity responses and ecosystem carbon storage potentials. By understanding the variation in nutrient cycles and what influences them will give us important understanding of the variation in the carbon cycle (Shaver and Jonasson 1999). Experiments addressing the effect of grazing or browsing in several ecosystems have revealed that vertebrate herbivores have a considerable impact on plant biomass, NPP, nutrient cycling and species composition (Pastor et al. 1988, McInnes et al. 1992, Manseau et al. 1996, Kielland et al. 1997, Augustine and McNaughton 1998, Frank and Groffman 1998, Bråthen and Oksanen 2001, Stark and Grellmann 2002). These influences may mediate the response of vegetation to climate change, and may be especially important in the arctic where productivity is generally nutrient limited (Chapin
and Shaver 1996, Jonasson et al. 1999a). The observed increase in shrub biomass in some parts of the arctic might not be happening in areas where large vertebrate herbivores are present. In Greenland, grazing from caribou has been reported to cause die-back of dwarf birch (*Betula nana*) and spread of *Poa* sp. dominated grazing lawns (Thing 1984). Both studies of caribou summer ranges in sub-Arctic Canada (Manseau et al. 1996) and 30 year old exclosures on reindeer pastures in Northern Norway (Olofsson et al. 2001) suggests that grazing has the potential to constrain productivity and reduce standing biomass of shrubs in the Arctic. Vertebrate herbivores have also been shown to reduce the depth of the moss layer through grazing and trampling that could affect soil temperatures and nutrient cycling (Olofsson et al. 2001, van der Wal et al. 2001, Olofsson et al. 2004b, Van der Wal and Brooker 2004). Studies of almost 40 year old fences in northern Norway have revealed that reindeer grazing has produced a shift in tundra vegetation from moss-rich to graminoid dominated meadows (Olofsson et al. 2001) and resulted in increased soil temperatures, decomposition rates and nutrient availability (Olofsson et al. 2004b). Similar results have been found in exclosure experiments on Svalbard where reduced moss layers have resulted in higher soil temperatures, increased litter decomposition and subsequent enhanced primary production (Van der Wal and Brooker 2004). The overall effect of vertebrate herbivory will depend on the balance between negative and positive feedback effects that such herbivores exert on plant productivity and nutrient cycling (Augustine and McNaughton 1998). Herbivory could therefore make an important contribution to the productivity response of arctic vegetation in response to climate change due to the limited nutrient availability in these ecosystems. Neglecting the influence of vertebrate herbivores on plant productivity may bias
estimates of ecosystem changes in relation to global warming in areas where large vertebrate herbivores occur.

Here I present results from a five year field experiment conducted on the summer range of the Kangerlussuaq-Sisimiut caribou herd in West-Greenland. By the use of 800 m² herbivore exclosures and open-top chambers (OTCs), I have investigated the influence of caribou and musk ox grazing on how the arctic vegetation responds to simulated climate warming. I hypothesize that herbivory by caribou and muskoxen have the potential to suppress growth of shrubs and promote development of graminoid-dominated swards, thereby mediating the expected biomass accumulation where these herbivores occur.
Methods

Study area

The study was conducted on the summer range of the Kangerlussuaq-Sisimiut caribou herd in West-Greenland and located 10 km west of Kangerlussuaq (67°6.8’N, 50°20’W, 50-500 m.a.s.l). The area is occupied by caribou during and following parturition from early May until late June (Thing 1984, Bøving and Post 1997, Post et al. 2003) and by a residential musk ox population (Forchhammer and Boomsma 1995). The study site is located on non-carbonate mountain bedrock and the plant community is defined as low shrub tundra (CAVM Team 2003). The mean precipitation in my study area is relatively low during large parts of the growth season. For the months from May through August the mean precipitation is 8, 15, 24 and 33 mm, respectively (DMI; www.dmi.dk). The mean monthly temperatures for the same period are 2.5, 8.6, 10.7 and 8.2°C. The north facing and cooler slopes are dominated by Labrador tea (Ledum palustre) while xerophyllic plants (e.g. Kobresia myosuroides and Carex supine) characterize the warmer more south facing slopes with dense patches of dwarf birch (Betula nana) interspersed with blue-green willow (Salix glauca) at lower elevations. The moister valley floors are typically dominated by greens of Poa pratensis (Post et al. 2003).

Experimental design

The experiments were conducted inside and outside of two, 800 m², circular caribou and muskoxen proof exclosures that was erected in early June of 2002. The 6 ft. tall exclosures were constructed of woven wire and steel fence posts. Two comparable
areas of the same size, elevation and vegetation type were established as controls at the same time as the exclosures were erected. In early summer 2003 I initiated the climate warming experiment to investigate how Arctic vegetation responds to climate warming with and without ungulate herbivores. Warmer climate was simulated by the use of circular open-top chambers (OTC’s) with a basal diameter of 150 cm and with that passively warmed near surface temperatures. The OTCs were cone shaped, with a side angle of 60°, had a basal diameter of 150 cm and a height of 40 cm. These chambers were constructed according to the protocol for the ITEX program and are reported to increase near surface temperature by 3-4 °C (Marion et al. 1997). On both the exclosed and control areas six experimental plots, each of 0.25 m², were randomly selected for a total of 24 plots and OTCs were randomly assigned to three of the plots within each area. This resulted in a nested design where each experimental plot was nested within the corresponding exclosure or control area. There were four different treatment combinations: ungrazed and warmed (UW), ungrazed and ambient (UA), grazed and warmed (GW) and grazed and ambient (GA). The following rejection criteria were used for plot selection: all functional plant groups of interest had to be represented in each plot (shrubs, graminoids and forbs but also lichens and mosses), all shrubs had to be small enough to entirely grow within the plot, and plots had to be at least 2 m away from the fence. The warming manipulation lasted for 22 days in June 2003 (from June 4 until June 25) before the OTC’s were removed from all plots, both inside and outside the exclosures, allowing ungulate herbivores access to the un-exclosed plots. This was practiced for all the seasons to give the plots exposed to grazing and those excluded from grazing the same warming treatments. During the 2004 growth season the warming
treatment lasted from May 19 until July 11 before the OTC’s were removed from all plots. In 2005 warming lasted from May 23 until July 17 while the warming period in 2006 lasted from May 22 until July 29.

**Sampling**

To assess the effects of the OTC treatment on microclimate, I monitored soil and near-surface temperature in control and warmed plots from June 17 until July 12 2004. From mid July I left the study area to make any effects of my presence on animal grazing behavior as minimal as possible, and for that reason was not able to extend the temperature monitoring. Digital thermometers that logged max/min data for 6 consecutive days were used (Taylor Precision Products; www.taylorusa.com). The soil temperatures were measured by a probe inserted 10 cm into the soil, while the near surface temperatures were measured with the sensor placed approximately 5 cm above the ground in the vegetation. I made sure that the sensors were not directly exposed to sunlight.

Plant sampling was conducted using a non-destructive point-intercept method (Jonasson 1988, Bråthen and Hagberg 2003) since this study is part of a long-term experiment. An aluminum quadratic frame, 0.25 m², with adjustable steel legs was placed on each plot, with a 0.25 m² plexi-glass plate with 20 randomly drilled holes on top. A metal pin, 3 mm in diameter, was vertically lowered through each of the holes until it hit the ground or cryptogam layer. Dead plant tissue attached or on the ground was recorded as litter. Every encounter between the pin and the vegetation were recorded according to
different functional groups (shrubs, forbs, graminoids etc.). The number of intercepts gives an index of the biomass of each functional plant group in each plot. Each plot was permanently marked for repeated sampling. Measurements were conducted at the initiation and end of the warming treatment (usually at peak growth season) as well as at the end of the growing season in August.

*Biomass estimation*

To convert the intercept frequency to biomass values for the permanent vegetation plots, 20 plots were chosen during peak growth season in 2003 with emphasis on representing as many of the functional groups and as wide range of biomass as possible. The plots were chosen from the same area and vegetation types as the permanent plots. After the intercept frequency was recorded, the vegetation in each of the plots were clipped to the ground level, separated into functional groups and dried for 24 hours at 60°C before being weighed (Jonasson 1988, Bråthen and Hagberg 2003). For shrubs the leaf and stem biomass was parameterized separately. *B. nana* was the dominating species in my vegetation plots and is the only shrub species present in all the vegetation plots. In this investigation *B. nana* is the only shrub species considered. The point frequencies were then regressed against the biomass for each functional group with biomass as dependent variable and intercept frequency as independent variable. I compared an untransformed linear model, an exponential model with the dependent variable LN-transformed and a multiplicative model with both the dependent and independent variable LN-transformed, all of which had been previously considered (Jonasson 1988). The best regression model was chosen based on the highest value for the coefficient of
determination \((r^2)\). The multiplicative model \((y = ax^b)\) gave the best fit for graminoids and forbs (Graminoids, \(r^2 = 0.65, F = 33.79, p < 0.001\); Forbs, \(r^2 = 0.51, F = 15.39, p = 0.001\)) while the untransformed linear model \((y = bx + a)\) gave the best fit for \(B. nana\) leaves and stem (\(B. nana\) leaves, \(r^2 = 0.64, F = 32.43, p < 0.001\); \(B. nana\) stem, \(r^2 = 0.50, F = 17.92, p < 0.001\)). The resulting equations used to calculate biomass from intercepts were as follows: graminoids, \(y = 0.125x^{0.872}\); forbs, \(y = 0.478x^{0.491}\), \(B. nana\) leaves, \(y = 1.09x + 4.76\) and \(B. nana\) stem, \(y = 8.30x + 30.14\). All the regression based translations of the pin-intercepts are presented as g/m². The results are presented as biomass and not pin intercepts because biomass is a more biological relevant way of analyzing and presenting the data in this study. The intercepts were also analyzed and provided the same results as for analyzes of biomass.

**Analyses**

There was an outbreak of the moth *Eurois occulta* during the 2004 and 2005 growing seasons that altered the aboveground biomass of the functional groups analyzed in this paper. Although the influence of the caterpillars made a strong impact on the plants the effect on the biomass should be equal among the treatments and hence should not influence the between treatment comparisons presented here. The results presented here are from 2003, 2004, 2005 and 2006 with data collected during peak season biomass in July except data from 2003 that was collected at the end of June. This was done to minimize any effects that date of sampling would have on the between years comparisons.
Main effects of warming on mean near-surface and soil temperatures were evaluated by an ANOVA model with plot and Julian date as random factors to control for any between plot variation and time of measurement effects. The daily mean temperatures were calculated as the average between the maximum and minimum temperatures recorded in each plot. Due to the nested design of this experiment, a nested-ANOVA was used to analyze the effects of the warming and exclosure treatments on aboveground biomass of the main functional plant groups. All data are analyzed at the plot level and plot was included as a random factor in the model, to control for any between plot variations. Exclosure site was included as a random factor to control for any site variations, while year was included as a random factor to control for any year variations besides those controlled by the experiment. When changes in aboveground biomass were considered, I distinguished between “primary”, “secondary” and “cumulative” responses. The primary response was the change observed between 2003 and 2004, while the secondary response was between 2005 and 2006 and the cumulative response was the observed change between the initiation of the warming experiment in 2003 and 2006. The reason for focusing on these periods was to avoid most of the effects of the *E. occulta* outbreak that was initiated in 2004 and peaked in 2005 before reaching unnoticeable numbers in 2006. All statistical tests were performed using the statistical program SPSS version 10.0 for Windows.
Results

Temperature treatments

Mean daily near surface temperature (Fig. 2.1a) for warmed plots was on average 1.3 °C warmer than the control plots and significant ($F = 15.569, p < 0.001$) for the entire period of measurements. Mean daily soil temperatures, measured at 10 cm depth, were on average 1.0 °C higher on the warmed plots than on the control plots and significant ($F = 12.354, p = 0.001$) (Fig. 2.1b).

Responses in above ground biomass

When aboveground biomass was analyzed across all years, year turned out to be highly significant for all functional plant groups (Table 2.1) while there was a significant interaction between the exclosure and warming treatment for *B. nana* stems. As Figure 2.2 a-d illustrates, there was a strong reduction in biomass from 2003 until 2005 before there was a marked increase in biomass in 2006. This change appeared to depend on the treatments.

For *B. nana* leaves, on the plots exclosed from grazing, the biomass was significantly higher in 2003 and 2006 than in 2004 and 2005 (Figure 2.2a). However, on the plots exposed to grazing there appeared to be no significant differences between the years. For *B. nana* stems there were no significant differences between any of the years (Figure 2.2b).

For graminoids there appeared to be the same pattern for all treatment combinations with the biomass measured in 2006 significantly higher than all the previous years (Figure 2.2c).
The biomass of forbs was significantly lower in 2005 than any of the other years for all the treatment combinations except for the GA plots. For the GA plots the biomass observed in 2005 was only significantly lower than the 2006 biomass.

When the different temporal responses in biomass were analyzed few significant effects of the treatments occurred (Table 2.2). There was a marginally significant secondary ($\delta_p$) effect of the exclosure treatment for *B. nana* leaves while graminoids showed a significant primary ($\delta_p$) response to the exclosure treatment (Table 2.2).

During the primary response ($\delta_p$) the biomass change of *B. nana* leaves appeared not to be significantly different from zero (Table 2.3). However, for the secondary response ($\delta_s$) there were significantly positive changes in leaf biomass for all the treatment combinations. The change was lower on the grazed than ungrazed plots and significantly lower on the GA plots than the UA plots. The cumulative response ($\delta_c$) in *B. nana* leaf biomass was significantly positive on the ungrazed plots while none of the grazed plots had a change in biomass that was significantly different from zero.

For *B. nana* stems, the primary change ($\delta_p$) in biomass was significantly positive for all the different treatment combinations (Table 2.3). The change in stem biomass was more positive on the ungrazed plots and significantly higher on the UW plots than on both the GA and GW plots. During the secondary response ($\delta_s$) none of the treatment combinations produced any changes in stem biomass significantly different from zero, however the mean changes were more positive on the plots experiencing ambient temperatures. The cumulative change ($\delta_c$) in stem biomass was significant for all
treatment combinations. The changes were lower on the plots experiencing warming than compared to the plots experiencing ambient temperatures (Table 2.3).

None of the primary changes in graminoid biomass was significantly different from zero, however the change in biomass on the GA plots were significantly lower than for the other treatment combinations (Table 2.3). During both the secondary ($\delta_s$) and cumulative ($\delta_c$) periods the change in graminoid biomass was positive and significantly different from zero for all the treatment combinations.

For forbs, none of the biomass changes were significantly different from zero for the primarily (Table 2.3). However, during the secondary change ($\delta_s$) in biomass, all the treatment combinations produced positive changes in forb biomass that were significantly different from zero. The change in biomass was lowest on the grazed plots and highest on the UW plots (Table 2.3). The cumulative change, on the other hand, did not produce any changes in forb biomass that were significantly different from zero. But the plots experiencing warming had a slight negative change while the warmed plots produced a slight positive change in forb biomass (Table 2.3).

The cumulative change in biomass for all the functional plant groups was positive or not significantly different from zero. Moreover, there appeared to be differences in the primary and secondary response of the functional groups.
Discussion

The purpose of this experiment was to investigate the joint effect of ungulate herbivores and climate warming on the productivity response of key functional plant groups in a low shrub tundra ecosystem with emphasis on above ground biomass. However, my warming manipulations did not reflect all the possible environmental changes that are likely to happen as a consequence of increased greenhouse gas concentrations in the atmosphere e.g. increased precipitation, timing of snowmelt, length of growth season and winter warming. My intention was to focus on one climatic factor that is predicted to have both direct and indirect influence on aboveground biomass of arctic plants. Moreover, it is throughout the plant growth season that vascular plants are most exposed to ungulate grazing and were therefore chosen as the focus for this study. Furthermore, my OTC treatments resemble other studies of climate change in the arctic that will facilitate comparisons of results with the added dimension of herbivory.

Temperature treatments

The OTC treatments did not increase soil or near surface temperatures as much as reported from similar experiments elsewhere, where a warming effect of 3-4 °C have been achieved (Marion et al. 1997, Hollister et al. 2005, Jonsdottir et al. 2005, Wahren et al. 2005). Neither was the temperature increase measured in this study within the range of an additional arctic warming of 4–7 °C predicted by the ACIA for the next 100 years (Kattsov et al. 2005). The mean daily near surface temperature was on average only 1.3 °C higher in the OTC’s compared to the controls while mean daily soil temperature differed by only 1.0 °C on average. It is therefore questionable if these relatively small
differences in temperature could induce a change in plant production similar to what is expected during predicted climate warming. Several other studies (Chapin et al. 1995, Robinson et al. 1998, Jonasson et al. 1999b, van Wijk et al. 2003) have shown that increased nutrient availability has the strongest effect on plant production and that temperature has an indirect effect through increased mineralization rates in the soil. The relatively small increase in soil temperature observed in this study might not have been enough to stimulate mineralization rates in the plots comparable to nutrient concentrations added in those experiments. On the other hand, the warming effect achieved in this study was closer to the increase of 0.2 °C per decade in global average temperature observed during the last three decades (IPCC 2001), and might therefore have been a more realistic warming treatment compared to what is expected to occur during such a short term experiment.

Above-ground biomass production

Our results do not provide any clear indication that the warming and exclosure treatments alone or in concert had any effect on the above-ground biomass of any of the functional plant groups during the first 4 years of warming and 5 years of exclosure treatments. No significant difference in shrub (Betula nana), graminoid or forb biomass was found for any of the treatment combinations in any of the years. This result is somewhat surprising since several other studies have found clear indications of increasing shrub biomass and abundance at the expense of non-vascular plants to simulations of climate change (Arft et al. 1999, Walker et al. 2006). However, the majority of these experiments have found that it is the addition of nutrients alone or in
combination with warming that produce the strongest responses (Chapin et al. 1995, Hobbie and Chapin 1998, Shaver et al. 1998, Shaver and Jonasson 1999). The lack of responses found in this study do lend support to the hypothesis that it is the indirect effects of cold temperatures that limits plant production through low nutrient availability and not low temperatures per se (Hobbie and Chapin 1998). It has been shown that nutrient addition elicits a stronger response on plant biomass than increased temperature (Press et al. 1998) that does suggest a more limited response to warming. Long-term nutrient addition and temperature experiments in arctic ecosystems have revealed that elevated temperature can indirectly affect plant responses by increasing nitrogen and phosphorous availability through increased mineralization rates (Chapin et al. 1995) while nutrient addition directly increase biomass production and alter plant community composition (Chapin et al. 1995, Shaver et al. 2001). The small observed responses to the warming treatments presented here could be an indication that my study area is predominantly nutrient limited and are responsible for the lack of responses during the initial stages of this long term experiment. On the other hand, if my system is not nutrient limited increased availability of nutrients due to climate warming might not result in increased biomass. At present, I do not know how the nutrient availability in my system compares to that of other studies, nor do I know if plants in my study area are suffering from nutrient limitation or not. There might be other explanations for the limited response in biomass production as well. The largest short-term effects of warming might not appear as responses in biomass but rather in other important plant traits e.g. flower and seed production (Shaver et al. 1998). Furthermore, studies that found effects of warming treatments on biomass, produced temperatures that were 2-3 °C higher than what was
achieved in this study. Such a temperature difference could facilitate a much stronger effect in biomass.

The effect of the exclosures was expected to increase aboveground biomass on the ungrazed plots compared to the plots exposed to grazing, especially for shrubs that has been reported to be susceptible to herbivory (Thing 1984, Manseau et al. 1996, Bråthen and Oksanen 2001, Olofsson et al. 2001). Furthermore, the effect of grazing was expected to promote the production of graminoids and forbs. However, I have not found any detectable effects of the exclosure treatment so far in this experiment, except for a primary negative response in graminoids. The strongest effect found was an effect of year. There was a reduction in aboveground biomass from 2003 until 2005 for all of the functional groups followed by a strong increase in biomass from 2005 until 2006. Only the stem biomass of \textit{B. nana} did not show the same strong reduction from 2003 until 2005. This corresponds with the outbreak of the moth \textit{E. occulta} that first reached noticeable numbers in 2004 and reached even higher numbers in 2005. It is quite possible that the effect of the exclosures and OTC’s on biomass production may have been concealed by the biomass off-take of caterpillar foraging. However, there are some indications that the exclusion of ungulate grazing pressure did affect the biomass of the different plant functional groups. It is, as far as I can see, 3 competing explanations for the limited response in biomass of the major functional plant groups in my system. I observed a limited effect of the OTC treatment on near-surface and soil temperatures that could be partially responsible for the lack of responses observed. Furthermore, I do not at present have any knowledge on the nutrient availability in my system that could have
revealed why there are differences in the responses observed in this study compared to other similar studies. Finally, there was a caterpillar outbreak that clearly made a huge impact on the aboveground biomass of all the functional groups (Figure 2.2 a-d).

However, a closer look at the mean biomass for each treatment combination revealed that there were some differences suggesting some treatment effects. For the leaf or stem biomass of *B. nana* there was no differences between the treatment means. The strong reduction in leaf biomass and no effect on the stem biomass suggests that the shrub *B. nana* was more affected by caterpillar foraging than my manipulations. In 2003 plots that were exposed to grazing and ambient temperatures had a mean graminoid biomass higher than the other plots but no difference was evident in 2004. However, the mean biomass in the grazed and ambient plots was higher again in 2005. But this difference was not significant in 2006 although the mean biomass was still higher on the GA plots. This could indicate that graminoids are stimulated to produce more aboveground biomass on grazed plots than on ungrazed plots. The biomass estimates for forbs show that plots that were ungrazed and warmed in 2003 and 2004 had a mean biomass higher than the other plots. However, this relationship changes in 2005 where the plots exposed to grazing and ambient temperatures had a higher mean biomass. But in 2006 there is no significant difference in mean biomass between the treatments mainly due to a higher biomass on the ungrazed and warmed plots.

Although, my distinction between the primary and secondary responses is arbitrary due to the short duration of the experiment, these indications can still be useful to understand any effects on biomass production, especially when it comes to the
direction and magnitude of change. There were very few significant temporal effects found as a response to my treatments. There was a significant primary response in graminoid biomass while there was a marginally significant secondary response in leaf biomass for *B. nana* to the exclosure treatment. This could indicate that *B. nana* and graminoids are somewhat responsive to presence/absence of ungulate herbivores. However, there appears to be no response in graminoid biomass during the secondary and cumulative periods. Furthermore, no changes in stem biomass are evident for *B. nana* and no strong effects are observed in forbs to the different manipulations. During the primary response few of the changes in biomass are statistically different from zero, however there is a significant increase in stem biomass for *B. nana* for all the treatment combinations (Table 2.3). This change in biomass is larger in the plots located inside the exclosures and significantly so on the UW plots. This suggests that grazing has a limiting effect on biomass accumulation in shrubs in response to climate warming. During the secondary response there were significant positive changes in leaf biomass of *B. nana* for all treatment combinations, however none of my manipulations produced any changes in stem biomass. This difference in response between leaves and stem biomass could indicate a resource allocation strategy as a response to the relatively heavy defoliation these plants experienced during the 2004 and 2005 growth season. Plants have been shown to have such a compensational strategy in growth as a response to herbivory (McNaughton 1979, 1983, Bråthen and Odasz-Albrigtsen 2000, Frank et al. 2002, McIntire and Hik 2002), and what I have observed here could be a response to the limited photosynthetic ability they experienced during the caterpillar outbreak that removed nearly all the leaf biomass. Both for graminoids and forbs the secondarily change in
biomass was significant and positive for all treatment combinations. This is most likely a response to the relief in caterpillar grazing but might also be a response to the limited increase in *B. nana* stem biomass. When the cumulative change was examined the change in leaf biomass of *B. nana* was only significant on the ungrazed plots suggesting a negative effect of grazing. For the stem biomass there was a positive cumulative change for all treatment combinations. A similar pattern was observed for graminoids with no difference between the treatment combinations that suggest limited response to my manipulations. There were no significant cumulative responses observed for forbs indicating limited treatment effects.

Overall there were varying direction and magnitude of the different temporal responses in this experiment. The findings does lend support to other studies that have found that short-term responses are not good predictors of longer term trends (Chapin et al. 1995, Robinson et al. 1998, Hollister et al. 2005) To find a general conclusion about why these responses in biomass change direction and magnitude is difficult and complex. It is further complicated by the outbreak of the caterpillar *E. occulta* that most likely is the main reason why several of the plots showed a reversal from a neutral to a sometimes strong positive change in biomass. A more general conclusion can only be reached as this long-term experiment progresses and the effect of the caterpillar outbreak in further weakened.

My preliminary results do not provide clear evidence that herbivory constrains the biomass response of shrubs to warming or that grazing should promote establishment of
graminoids or forbs. However, I did find changes in the biomass of the functional plant groups suggesting that herbivory mediates the competitive dominance of shrubs over graminoids that is a predicted response to climate change. Furthermore, my results also indicate a limited response in forb biomass that could indicate that species of this functional plant group are more vulnerable than the other functional groups. I also found differences in the short-term and long-term responses that, due to the short duration of this study, prevent general conclusions to be made about the interacting effects of climate warming and grazing. However, as this experiment progresses, more of the mechanisms controlling the responses in the vegetation will hopefully be revealed.
Acknowledgements

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Literature cited


ecosystem level experiments at Toolik Lake, Alaska, and at Abisko, Northern Sweden: generalizations and differences in ecosystem and plant type responses to global change. Global Change Biology 10:105-123.


Figure 2.1: Mean daily temperatures for warmed (w) and control (c) plots measured during the warming treatments in summer 2004. (a) Near surface air temperature was on average 15.8 °C in the warmed and 14.5 °C in the control plots. (b) Soil temperature at 10 cm depth was on average 8.4 °C in the warmed plots and 7.4 °C in the control plots.
Table 2.1: Results from the nested analyses of variance of treatment effects on the biomass (g/m²) of plant functional groups in low shrub tundra, Kangerlussuaq, Greenland. W: warming treatment, E: exclosure treatment, Y: year. * marks significance level of p ≤ 0.05.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Source of variation</th>
<th>W F p</th>
<th>E F p</th>
<th>Y F p</th>
<th>E*W F p</th>
<th>E<em>W</em>Y F p</th>
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<td>1.051</td>
<td>0.332</td>
<td>1.677</td>
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<td>0.000</td>
<td>0.985</td>
<td>10.216</td>
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Figure 2.2: Mean biomass (g/m²) of major functional plant groups for each of the treatment combinations during the four years of warming treatments in low shrub tundra, Kangerlussuaq, Greenland. Biomass was estimated by calibration of the non-destructive point-intercept method with actual plant biomass measurements. Dark columns: ungrazed and ambient, clear columns: ungrazed and warmed, dotted columns: grazed and ambient and lined columns: grazed and warmed. Error bars are the 1±SE of the means.
Table 2.2: Results from the nested analyses of variance of treatment effects on the changes in biomass (g/m$^2$) of major plant functional groups in a low shrub tundra, Kangerlussuaq, Greenland. $\delta_p$: primary change 2003-2004, $\delta_s$: secondary change 2005-2006, $\delta_c$: cumulative change 2003-2006. W: warming treatment, E: exclosure treatment. a indicates significance at the $p \leq 0.05$ level.

<table>
<thead>
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<th>Response</th>
<th>P-values</th>
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<td></td>
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<td>B. nana leaf</td>
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<td></td>
<td>$\delta_s$</td>
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<td></td>
<td>$\delta_c$</td>
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<tr>
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<td></td>
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<tr>
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<td>$\delta_s$</td>
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<td></td>
<td>$\delta_c$</td>
<td>0.297</td>
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Table 2.3: Mean changes in biomass (g/m$^2$) of major functional plant groups in low shrub tundra, Kangerlussuaq, Greenland. CI: confidence intervals of the means for each treatment combination. *a* indicates that the mean is statistically different from 0 at $p \leq 0.05$. $\delta_p$: primary change (2003-2004), $\delta_s$: secondary change (2005-2006), $\delta_c$: cumulative change (2003-2006).

<table>
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<tr>
<th>Functional groups</th>
<th>Treatment combinations</th>
<th>$\delta_p$</th>
<th>95% CI [min,max]</th>
<th>$\delta_s$</th>
<th>95% CI [min,max]</th>
<th>$\delta_c$</th>
<th>95% CI [min,max]</th>
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<td>B. nana leaf</td>
<td>Ungrazed Ambient</td>
<td>-10.03</td>
<td>[-28.86, 8.80]</td>
<td>74.85$a$</td>
<td>[46.32, 103.38]</td>
<td>35.03$a$</td>
<td>[2.14, 67.91]</td>
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<td>Ungrazed Warmed</td>
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<td>56.61$a$</td>
<td>[28.08, 85.13]</td>
<td>35.75$a$</td>
<td>[2.87, 68.64]</td>
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<td>14.63</td>
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<td>[5.06, 58.03]</td>
<td>20.02</td>
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<td>[-16.50, 18.47]</td>
<td>46.37$a$</td>
<td>[19.88, 72.86]</td>
<td>9.49</td>
<td>[-21.04, 40.02]</td>
</tr>
<tr>
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<td>[124.71, 304.54]</td>
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<td>[-34.61, 241.42]</td>
<td>159.29$a$</td>
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<td>[175.07, 354.89]</td>
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<td>[-51.21, 224.82]</td>
<td>142.69$a$</td>
<td>[39.24, 246.15]</td>
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<td>102.722</td>
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<td>165.45$a$</td>
<td>[69.41, 261.50]</td>
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<tr>
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<td>132.25$a$</td>
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<td>6.46$a$</td>
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<td>6.00$a$</td>
<td>[1.93, 10.07]</td>
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<td>5.78$a$</td>
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<td>0.06</td>
<td>[-1.93, 2.06]</td>
<td>1.86$a$</td>
<td>[0.03, 3.69]</td>
<td>-0.12</td>
<td>[-2.28, 2.05]</td>
</tr>
</tbody>
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Chapter 3

The temporal effect of ungulate herbivory and climate warming on the community composition of functional plant groups in Arctic Greenland.
Abstract

Arctic plants are limited by low temperatures and a short growth season. The recent observed warming of the arctic climate is predicted to advance the onset of spring and hence prolong the growing season. This change in climatic conditions is expected to change species distributions and plant community composition. There are already observations of increased shrub abundance at the expense of graminoids and forbs in certain areas of the Arctic. Such changes in plant communities towards more shrub domination are predicted to also influence soil-temperatures, microbial activity and decomposition rates. However, several studies conducted in grazing systems have revealed that vertebrate herbivores can have strong influence on plant community composition. It has been shown that vertebrate herbivores have the ability to prevent domination of woody species and promote graminoid and forb establishment. Vertebrate herbivores may therefore prevent domination of shrubs as a response to climate warming in areas where they forage. Over four growth seasons, I investigated the effects of both herbivory, from caribou (*Rangifer tarandus*) and Muskoxen (*Ovibos moschatus*), and simulated climate warming on the plant community composition in West-Greenland. There were no unambiguous responses in the plant community composition to the warming simulation or vertebrate herbivory. However, there was some evidence suggesting a higher abundance of shrubs in plots excluded from herbivory and a higher abundance of graminoids in plots exposed to grazing. This suggests that herbivory should be included in studies investigating the influence of climate change on plant community composition.
Introduction

The recent observed warming of the arctic climate is predicted to have a strong influence in the distribution and abundance of species. For arctic plants a warmer climate is expected to cause changes in plant species distributions, plant community composition and hence ecosystem properties. Aerial photographs, with a 50 year interval, show an increasing abundance of shrubs at the expense of graminoids and forbs in certain areas of the arctic (Sturm et al. 2001b). These changes in plant functional types towards more woody species are predicted to increase the solar energy absorption in the summer (Chapin et al. 2005) but also affect snow conditions and dynamics in winter. Shrubs trap more of the drifting snow causing a thicker, more insulative snow-cover that will positively influence soil-temperatures, microbial activities as well as decomposition rates (Sturm et al. 2001a, Sturm et al. 2005). These effects are predicted to have a positive feed-back effect and with a continued warming of the arctic could further strengthen the increasing dominance of woody species in the arctic (Sturm et al. 2005). Several experiments designed to simulate the effects of climate change report changes in species diversity and plant community composition. In a long-term experiment at Toolik Lake, Alaska, species diversity declined and due to the increasing dominance of the deciduous shrub Betula nana at the expense of graminoids and forbs (Chapin et al. 1995, Shaver and Jonasson 1999). Another study conducted at Toolik Lake, investigated the effects of winter snow cover and summer air temperatures using snow fences and open-top chambers (OTC) (Wahren et al. 2005). It was found that species diversity was greatly reduced during the 8 years of treatments. Most of this change was contributed to the increase in the abundance of shrubs, especially Betula nana as well as a decrease in
lichens and bryophytes. Similar results were found in a study conducted in northern Alaska by the use of OTCs (Hollister et al. 2005). There was a general increase in the cover of woody species while the cover lower stratum plants such as bryophytes, lichens and some graminoids and forbs decreased. Furthermore there was also a decrease in species diversity. Such trends have also been observed in a dwarf shrub heath in Iceland where the cover of deciduous and evergreen shrubs increased at the expense of other functional plant groups (Jonsdottir et al. 2005). However, there was no significant change in species diversity. These findings have been further supported by a meta-analysis from 13 different arctic research sites investigating the effect of climate warming on plant performance (Arft et al. 1999). Such changes in plant community composition could have strong influence on biological processes in these communities. Plant productivity is often correlated with species diversity and community composition of functional plant groups (Reich et al. 2001).

Although there is strong evidence suggesting changes in the composition of plant communities towards a dominance of woody species, there is, to my knowledge, few, if any, studies examining the effects of herbivory in climate change studies. Several studies from different ecosystems have shown that vertebrate herbivores influence plant community composition and hence several biological processes such as plant biomass and production, species composition as well as net primary production (NPP) (Pastor et al. 1988, McInnes et al. 1992, Manseau et al. 1996, Kielland et al. 1997, Augustine and McNaughton 1998, Frank and Groffman 1998, Bråthen and Oksanen 2001, Stark and Grellmann 2002). I argue that the increased abundance of shrubs observed in some parts
of the arctic might not be as obvious in areas where ungulate herbivores are present in large numbers. For example, the reduced abundance of *Betula nana* in West-Greenland was ascribed to the grazing activity of caribou (Thing 1984). Furthermore, studies of caribou summer ranges in sub-Arctic Canada revealed that the biomass and cover of shrub tundra were greatly reduced due to caribou grazing (Manseau et al. 1996). Long-term exclosures on reindeer pastures in Northern Norway revealed that grazing promotes graminoid establishment at the expense of shrubs (Olofsson et al. 2001). As well, the grazing and trampling from ungulate herbivores have the potential to influence soil temperatures, decomposition and nutrient cycling by reducing the depth of the moss layer that again affects biomass production (Olofsson et al. 2001, van der Wal et al. 2001, Olofsson et al. 2004b, Van der Wal and Brooker 2004). These responses in plant community composition described above suggest that it is imperative to include the effects of herbivory in experiments addressing the effects of climate change on plant species responses and community composition.

In this study I present results from an ongoing field experiment addressing the joint influence of climate warming and herbivory on the community composition of plant functional groups in the arctic. I hypothesize that herbivory by caribou and muskoxen have the potential to suppress growth of shrubs and promote development of graminoid-dominated swards, thereby preventing the predicted dominance of woody species as a response to climate warming.
**Methods**

**Study area**

This field experiment was conducted in West-Greenland (67°6.8’N, 50°20’W, 50-500 m.a.s.l) in a plant community defined as low-shrub tundra (CAVM Team 2003). The shrub species are typically dominated by dwarf birch (*Betula nana*) and blue-green willow (*Salix glauca*) while the evergreen Labrador Tea (*Ledum palustre*) are more abundant in the north facing slopes (Post et al. 2003). The more dominant graminoid species are *Kobresia myosuroides, Carex supine* and *Poa pratensis*. Typical forb species are *Cerastium alpinum, Draba cana, Polygonum viviparum* and *Stellaria* spp. The study site was occupied by caribou from early May until the end of June (Thing 1984, Bøving and Post 1997, Post et al. 2003) as well as a more stationary musk ox population (Forchhammer and Boomsma 1995).

**Experimental design**

These climate warming simulations were conducted inside and outside of two herbivore exclosures at a long-term research facility outside Kangerlussuaq, West-Greenland. These 800m² exclosures were erected in early summer 2002 together with comparable control areas of the same size and location. Climate warming was simulated by the use of circular open-top chambers (OTC) (also see Chapter 2) that were constructed according to the ITEX-program protocol (Marion et al. 1997). Six permanent experimental vegetation plots, each of 0.25 m², were randomly selected inside the exclosures and on the adjoining control areas for a total of 24 plots. Three OTCs were randomly assigned to the vegetation plots inside the exclosures and on the control areas.
This experimental setup resulted in a nested design, where each vegetation plot was nested within the corresponding exclosure or control area. The different treatment combinations were: ungrazed and warmed (UW), ungrazed and ambient (UA), grazed and warmed (GW) and grazed and ambient (GA). The warming simulations were initiated in spring of each year and ended towards the peak of the growth season (for more details see chapter 2). To allow ungulate herbivores access to the vegetation plots the OTCs were removed simultaneously both inside and outside of the enclosures to achieve equal warming treatment on all experimental plots.

**Sampling**

To be able to measure cumulative changes over time I used a non-destructive point-intercept method as a sampling technique (Jonasson 1988, Bråthen and Hagberg 2003). An aluminum quadratic frame (0.25 m²) with a plexi-glass plate on top was placed on each plot. A metal pin of 3mm in diameter was vertically lowered through each of 20 randomly drilled holes in the plexi-glass plate until it hit the ground or cryptogam layer. Every intercept between the pin and the vegetation was recorded according to different functional groups: shrubs, forbs, and graminoids etc. For shrubs, intercepts with leaves and stems were recorded separately. Litter was defined as dead plant tissue attached or on the ground. The number of intercepts per functional group per plot gives an index of the cover or abundance in each plot and was converted to % cover values. For repeated measurements, each plot was permanently marked with aluminum stakes in the corners for accurate placement of the point frame. Measurements were performed at the time
when the OTCs were placed on and removed from the plots as well as at the end of the growing season in August.

**Analyses**

In this paper I present data from the first four years of the experiment collected during the growing seasons in 2003, 2004, 2005 and 2006. The analyses and results presented are based on measurements done in July at or near peak growth season. It must also be mentioned that during the 2004 growth season I observed increasing numbers of caterpillars of the species *Eurois occulta* that had not been noticed in 2003. The caterpillar reached very high numbers in 2005 and the foraging behavior of these insects made strong impact on the vegetation. However, no caterpillars were observed during the 2006 growth season. It is very likely that the impact of the caterpillars could have affected the measurements that were made and the effects of my treatments. I did not, however, observe any significant difference in caterpillar numbers between the plots. Due to the nested design of this experiment, a nested-ANOVA was used to analyze the effects of the warming and exclosure treatments on abundance (% cover) of the main functional plant groups. The abundance of the functional plant groups was calculated by recording the number of intercepts between the pin, when it was lowered vertically down through the vegetation, and each functional group in the plots. By taking the number of intercepts for each functional group and dividing it by the total number of intercepts per plot, the abundance was calculated. The cover calculations were converted to relative cover values such that the cover of the functional groups considered in this paper (shrubs, graminoids and forbs) equaled 100%. The dominant shrub in the study site was *B. nana* and is the
only shrub species included in the analyses. I analyzed differences in abundance between the treatments with year, exclosure site and individual plots as random factors to control for any variability between years or site and among plots. When changes in abundance for each treatment were analyzed I distinguished between “primary”, “secondary” and “cumulative” responses. A “primary” response was defined as the change between 2003 and 2004, “secondary” response as the change between 2005 and 2006 and “cumulative” change as the change between 2003 and 2006. These periods were chosen to limit the effect of the caterpillar outbreak as much as possible (also see chapter 2). All statistical tests were performed using the statistic program SPSS version 10.0 for Windows.
Results

When the abundance (% cover) of the functional plant groups was analyzed across all years, *B. nana* leaves did not respond significantly to any of the treatments (Table 3.1), however there was a significant effect over time (Fig. 3.1a). The abundance of *B. nana* stems changed significantly over time, but there was also a significant interactions term between the exclosure and warming treatment (Table 3.1). The abundance of *B. nana* stems on the UA plots (23.77 % ± 4.39 S.E.) and the GW plots (23.95 % ± 3.78 S.E.) were significantly higher than on the GA plots (15.74 % ± 3.78 S.E.) (Fig. 3.1b).

Graminoids did not respond significantly to any of the treatment combinations (Tab. 1), but for the abundance of graminoids there was a significant increase over time (Fig. 3.1c). For all plots there was a higher abundance in 2006 than in any of the other years.

The abundance of forbs showed no response to the exclosure or the warming treatments but the interaction term was significant (Table 3.1). The UW plots (14.30 % ± 3.02 S.E.) had a higher mean cover than the other plots (Fig. 3.1d). The abundance of forbs in the plots was significantly affected by year (Tab. 1), with a decrease until 2005 before increasing in 2006.

The effect of the warming treatment did not have a significant effect on the change in leaf or stem abundance of *B. nana* (Table 3.2), but the exclosure treatment had
an effect on the secondary response ($\delta_s$) in leaves. Neither did it occur to be a significant interaction effect between the two treatments. There was a tendency towards negative changes in *B. nana* leaf abundance during the primary response ($\delta_p$) except for the GA plots and only the change in abundance on the UA plots were significantly different from zero (Table 3.3). When the means of each treatment permutation were compared, the GA plots had a change in abundance that was statistically different from both the UA and UW plots (Table 3.3). During the secondary response ($\delta_s$) in *B. nana* leaf abundance there was a significant positive changes on the UA and UW plots but no significant changes were observed on the GA or GW plots (Table 3.3). However, the mean changes in leaf abundance on UA plots were statistically different from the changes in the GA and GW plots (Table 3.3). The cumulative change ($\delta_c$) in leaf abundance was negative for all treatment combinations but only significant on the GW plots (Table 3.3).

The changes in abundance of *B. nana* stems were not significant during the primary response ($\delta_p$) for any of the treatment combinations (Table 3.3), but the means were positive. However, during the secondary response ($\delta_s$), the changes in abundance were negative and significant for all treatments except the GA plots (Table 3.3). Furthermore, the change in abundance on the GA plots was statistically different from the UA plots. The cumulative change in *B. nana* stem abundance was negative for all treatment combination but none were significantly different from zero (Table 3.3).

The change in the abundance of graminoids did not respond significantly to the warming treatment but had a significant primary response ($\delta_p$) to the exclosure treatment
There was no significant interaction between the warming and exclosure treatments. Changes in graminoid abundance during the primary response ($\delta_p$) were not statistically different from zero but the means were positive inside the exclosures and negative on outside (Table 3.3). Furthermore, the mean change in abundance on the UA plots was statistically different the mean of the GA and GW plots (Table 3.3). During the secondary response ($\delta_s$), all mean changes in graminoid abundance were positive but statistically different from zero only on the UW plots (Table 3.3). The cumulative change ($\delta_c$) in abundance was positive for all permutations but statistically different from zero only on the UW and GW plots (Table 3.3).

Neither the warming treatment nor the exclosures produced any significant responses in forb abundance for any of periods considered (Table 3.2). The interaction between the main factors was also insignificant. None of the primary ($\delta_p$) mean changes for the different treatment permutations turned out to produce changes in forb abundance that were statistically different from zero (Table 3.3). However, the means of the ungrazed plots were positive while the changes on the grazed plots were negative. For the secondary response in forb abundance, all means were positive but only the changes on the UW plots were statistically different from zero (Table 3.3). The cumulative change ($\delta_c$) was not statistically different for any of the treatment combinations. However, the changes in abundance turned out to be negative inside the exclosures and positive on the outside (Table 3.3). Furthermore, the mean change on the UW plots was statistically different from the change in forb abundance on the GA plots.
Discussion

There was no significant difference in abundance of *B. nana* between the initiation of the experiment in 2003 and the abundance observed in 2006 as I expected based on predictions in regards to climate change (Sturm et al. 2001b, Sturm et al. 2005). However, the abundance of *B. nana* leaves and stems changed considerably from 2003 until 2005 before returning to similar abundance values in 2006 (Figs. 3.1 a, b) and was highly significant. The reduction in abundance for *B. nana* leaves corresponds well with the changes seen in biomass of *B. nana* leaves presented in chapter 2 (fig. 2.2 a), and is related to the outbreaks of *E. occulta* in 2004 and 2005 (see chapter 2). However, the increase in abundance of *B. nana* stem (Fig. 3.1 b) does not correspond to the lack of change found in biomass of *B. nana* stem (chapter 2, fig. 2.2 b). This can be explained by the reduction in abundance of *B. nana* leaves, graminoids and forbs. As they are reduced in abundance, the relative abundance of *B. nana* stem increased.

Except from the effect of year, there did not appear to be any effects of the experimental treatments on *B. nana* abundance. The lack of an exclosure effect contradict findings of others that have found that ungulate herbivores suppress shrub abundance (Thing 1984, Manseau et al. 1996). As well, the lack of response to the warming treatment is contrary to other similar studies where increases in shrub abundance have resulted from climate change simulation experiments (Chapin et al. 1995, Robinson et al. 1998, Hollister et al. 2005, Wahren et al. 2005). On the other hand, these experiments did not find strong effects of the warming treatments alone but rather in concert with nutrient additions and hence are in concordance with the results from this experiment were only temperature treatments were considered. But, there was a significant interaction observed
between the warming and exclosure treatment for *B. nana* stems for the full model (Table 3.1) which suggests some effect of warming depending on the grazing regime. When the means of each treatment combination were compared there was an indication that the plots excluded from grazing exposure had a higher abundance of *B. nana* leaves in 2006 and stems in 2005.

The cover of graminoids increased over time from 2003 until 2006 as seen in Fig. 3.1c. But the analysis across years showed no significant effect of the exclosures or the warming treatment on graminoid abundance (Table 3.1). That there was no apparent effect of herbivory on abundance of graminoids is contrary to other studies that have found that grazing might promote the establishment of graminoids (Olofsson et al. 2001, Van der Wal and Brooker 2004) and prevented shrub dominance similar to observations done in other studies (Thing 1984, Manseau et al. 1996). Although the abundance of graminoids was relative stable until 2006 (fig. 3.1 c), the biomass of graminoids was reduced between 2003 and 2005 before increasing in 2006 (chapter 2, fig. 2.2 c). The stable abundance of graminoids can be explained by a strong reduction in abundance of *B. nana* leaves and forbs (fig. 3.1 a, d) and an increase in abundance of *B. nana* stem (fig. 3.1 b). The changes in abundance of the other functional plant groups cause the abundance of graminoids to be relatively stable in the plots.

Forbs, on the other hand, showed a significant reduction in cover over time but with an increase in 2006. This is rather unexpected because a reduction in forbs is usually coupled with an increase in the cover of shrubs (Chapin et al. 1995), but I found no
evidence of increased shrub abundance or biomass. However, the decrease in forb abundance corresponds well with the caterpillar outbreak observed in 2004 and 2005, and is also supported by the significant reduction in forb biomass (chapter 2, fig. 2.2 d). Forb abundance seemed not to respond to any of the experimental factors, but the interaction term for the overall model was significant (table 3.1). The abundance on the UW plots had a much higher abundance compared to the other plots in all years except 2005, suggesting a positive effect of climate warming when ungulate herbivores are excluded.

The analyses of the temporal responses for each treatment permutation revealed no clear trend in how the abundance of different functional plant groups respond to changes in climate and grazing pressure. During the primary response ($\delta_p$) $B. nana$ leaves showed a tendency towards a reduction in abundance. The change in abundance on the UA plots was significant. But at the same time the abundance of $B. nana$ stems showed a slight positive change although not significantly different from zero. This negative change in leaf abundance could likely be ascribed to the defoliation from caterpillar foraging. The outbreak of $E. occulta$ was initiated in 2004 and could explain the observed negative change in abundance. There was a significant primary response ($\delta_p$) in graminoids to the exclosure treatment where the abundance increased inside the exclosures and decreased on plots exclosed to grazing. This is contrary to observations elsewhere where usually graminoids increase in abundance when grazers suppress shrubs (Olofsson et al. 2001, Van der Wal and Brooker 2004). However, this pattern might be affected by the moth caterpillars. On the plots exposed to ungulate herbivory from caribou and muskoxen, there was also intense grazing from caterpillars that could explain
why there is a significant difference inside and outside of the exclosures. Also, the change in abundance for each treatment combination was not significantly different from zero. Forbs did not respond significantly to any treatment combination. However, the means were negative on the ungrazed plots and positive on the grazing exclosed plots. On the exclosed plots the mean abundance change was more negative when experiencing warming than ambient temperatures. Such trends have also been found in other studies as a response to warming (Robinson et al. 1998) but appears to vary between communities (Hollister et al. 2005, Jonsdottir et al. 2005). But on the grazing exposed plots, the mean change in abundance inside the OTC’s experienced the strongest response.

During the secondary response ($\delta_s$) the B. nana leaf abundance increased significantly inside the exclosures while there was no change on the grazing exposed plots. At the same time, B. nana stem abundance decreased both inside and outside. It is probable that this could be a strategy of grazing compensation found in several other studies (McNaughton 1979, 1983, Bråthen and Odasz-Albrigtsen 2000, Frank et al. 2002, McIntire and Hik 2002). After 2 growth seasons of heavy caterpillar defoliation, there might have been a trade off between producing photosynthetic tissue at the expense of investing resources into woody biomass. The significant positive change in B. nana leaf abundance inside the exclosures while no change was observed on the grazed plots could also indicate a negative effect of ungulate grazing on shrubs. At the same time as B. nana experienced a reduction in abundance during the secondary period, both graminoids and forbs increased in abundance on all plots. Although not always significant there was a positive tendency. This does lend support to the notion that herbivory could prevent the
domination of shrubs at the expense of other functional plant groups that has been found in several other studies (Thing 1984, Manseau et al. 1996, Olofsson et al. 2001). Bear in mind that what was observed during the secondary period ($\delta_s$) happened after the caterpillar population outbreak crashed at the end of 2005. The differences observed between the treatment combinations during the secondary period is most likely a result of my manipulations.

However, when looking at the cumulative change in B. nana leaf and stem abundance, the change in abundance is overall negative both inside and outside of the exclosures although not significant for all treatment permutations. Graminoids on the other hand do increase in abundance and significantly on the UW and GW. This could indicate that graminoids respond more strongly to a warmer climate since a similar response was observed during the secondary period. However, the mean changes between the different treatment combinations were not statistically different and it is probably not obvious yet if this is a longer term trend. The cumulative change in forb abundance revealed the same trends as for the primary response, with negative means inside the exclosures and positive on the grazing exposed plots. Based on the observations and measurements done during the first few years of this long-term field experiments, the preliminary cumulative measurements did not give strong support to my initial hypothesis that plant community composition might respond differently to climate change depending on the grazing pressure. There are several factors that could partly be the reason why I did not observe the changes I expected:
There was an overall lack of unambiguous responses to the warming simulations and exclosure treatments among the different functional plant groups, which are not straightforward to explain. Moreover, there were differences in the primary and secondary responses suggesting that short-term effects are not good predictors of longer term responses in predicting plant community composition (Chapin et al. 1995, Robinson et al. 1998). There are, as far as I can see, 3 competing explanations that might have influenced, alone or in concert, the lack of significant results. I do not know how the nutrient availability in this system compares with that of systems in other similar studies (Robinson et al. 1998, Hollister et al. 2005, Jonsdottir et al. 2005) or if this system is nutrient limited at all. Moreover, the temperature treatments in this experiment did not produce those same effects as in other studies using the same OTC technology (Chapter 2). It is likely that the temperature increase in this experiment was not enough to affect nutrient mineralization rates in such a fashion that it was noticeable in my abundance measurements and observed elsewhere (Chapin et al. 1995). Moreover, I can not ignore the effects that the caterpillar outbreak had on both the aboveground vegetation but also on the nutrient availability in this system. The biomass of all the functional groups showed a strong decline from 2003 until 2005 (Chapter 2) and undoubtedly had an effect on this plant community. However, these issues can only be properly addressed as this long-term experiment continues with the added attention to the nutrient availability in the system. Although, there was no clear effect of the temperature treatments there was evidence suggesting that in the plots excluded from ungulate herbivory there was higher abundance of shrubs compared to the grazing exposed plots and that there was higher abundance of graminoids in the grazed plots. Based on these findings I do conclude that
the influence of herbivory, including insect herbivory, should be included in studies investigating the effects of climate change on plant community composition in the future.
Acknowledgements

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Literature cited


Table 3.1: Results from the nested analyses of variance of treatment effects on the abundance of plant functional groups in low shrub tundra, Kangerlussuaq, Greenland. W: warming treatment, E: exlosure treatment, Y: year. * marks significance level of $p \leq 0.05$.

<table>
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<th>Variable</th>
<th>Source of variation</th>
<th>W</th>
<th>E</th>
<th>Y</th>
<th>E*W</th>
<th>E<em>W</em>Y</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
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<td>F  p</td>
<td>F  p</td>
<td>F  p</td>
<td>F  p</td>
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Figure 3.1: Mean abundance of major functional plant groups for each of the treatment combinations during the four years of warming treatments in low shrub tundra, Kangerlussuaq, Greenland. Dark columns: ungrazed and ambient, clear columns: ungrazed and warmed, dotted columns: grazed and ambient and lined columns: grazed and warmed. Error bars are the 1±SE of the means.
Table 3.2: Results from the nested analyses of variance of treatment effects on the changes in abundance of plant functional groups in low shrub tundra, Kangerlussuaq, Greenland. $\delta_p$: primary change 2003-2004, $\delta_s$: secondary change 2005-2006, $\delta_c$: cumulative change 2003-2006. W: warming/ambient treatment, E: exclosure treatment. * depicts a significant effect of $P \leq 0.05$.

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Table 3.3: Mean changes in abundance of major functional plant groups in low shrub tundra, Kangerlussuaq, Greenland. CI: confidence intervals of the means for each treatment combination. * indicates that the mean is statistical difference from 0 at $p \leq 0.05$. $\delta_p$: primary change (2003-2004), $\delta_s$: secondary change (2005-2006), $\delta_c$: cumulative change (2003-2006).

<table>
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<td>Change % cover</td>
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Chapter 4

The effect of ungulate herbivory and climate warming on the flower and fruit production of two arctic perennials
Abstract

Studies of the effect of climate warming on the phenology of plants suggest an advanced phenological development as a response to earlier snowmelt and warmer air and soil temperatures. Furthermore, a warmer climate has also been shown to affect fruit maturation and hence reproduction in several plant species. If the effect of herbivory is predictable in time and space, theory suggests that compensatory growth responses in plants might alleviate the deleterious effect of tissue lost. A substantial body of evidence suggests that several plant species have the ability to compensate or even overcompensate from herbivory by replacing either lost somatic or reproductive tissue.

It is not yet understood how the interaction between ungulate herbivores and plants is affected by rapid climatic changes similar to what is observed at present time. I have investigated the effect of climate warming on the interaction between ungulate herbivory and flower and fruit production of the two perennials *Cerastium alpinum* and *Draba cana* in an arctic community in Greenland. My results indicate a significant effect of climate warming in areas where ungulate herbivores are present that reduced the flower and fruit production of *D. cana* compared to ungrazed areas. Grazing and warming negatively affected flower production in *C. alpinum* but had no effect on fruit production, compared to areas where ungulate herbivores were absent. These findings also suggest that climate warming could affect interspecific competition and community composition.
Introduction

The effects of changing climatic conditions on different ecosystems due to the increasing levels of “greenhouse” gases are difficult to predict and vary among biomes. The first and most pronounced changes are nevertheless predicted to occur in arctic and alpine areas where primary production is highly dependent on temperature, permafrost and a short snow-free growth season (ACIA 2004). Several authors have focused on direct and indirect effect of climate change on primary production and changes in the distribution and abundance of single or groups of similar species. The effect of a changing climate on the interaction between species at different trophic levels, such as the interaction between herbivores and plants, is less well known.

The evolution of herbivore and plant interactions has been of increasing interest ever since the seminal paper of Fraenkel (1959) and the systematic investigation of Ehrlich and Raven (1964) arguing for a co-evolutionary process between herbivores and plants. Investigations of plant/herbivore interactions have revealed that plants have evolved two general strategies to herbivory: They can either resist or reduce herbivory by the use of chemical defenses or structures like thorns or spines, or they have evolved mechanisms that allow them to tolerate loss of reproductive or somatic tissue (Bryant et al. 1983, Strauss and Agrawal 1999, Juenger and Lennartsson 2000). The traditional view has been that herbivory has an obligate negative effect on the forage plants. However, increased attention to tolerance mechanisms in plants has revealed that plant primary production may increase in areas exposed to low or moderate grazing compared to ungrazed areas (McNaughton 1979, 1983, Bråthen and Odasz-Albrigtsen 2000, Frank et al. 2002,
It is suggested that compensatory growth in plants exposed to grazing may alleviate the potential deleterious effect of tissue lost to herbivores. These findings have been supported by theoretical models that demonstrate increased primary production as a result of nutrient cycling as an indirect effect of herbivory that could lead to grazing optimization (Loreau 1995, de Mazancourt et al. 1998, 1999). In many of the grazing ecosystems worldwide there exist long histories of plant-herbivore interactions. The sometimes positive effect of grazing on primary production has led authors to suggest that herbivore-plant interactions through ecological and evolutionary time has lead to grazing optimization mechanisms and or overcompensation or even plant–herbivore mutualism (Owen and Wiegert 1981, McNaughton 1983, Vail 1992, Jaremo et al. 1996, Nilsson et al. 1996, de Mazancourt et al. 2001). However this view has also led to severe criticism from other authors claiming that the rapid regrowth or overcompensation is a response to any physical disturbance posing a selective pressure on the plants alone or in concert (e.g. frost, fire, wind, heat) and not a response to herbivory alone (Belsky 1986, Belsky et al. 1993, Mathews 1994).

Overcompensation is commonly defined as increased plant productivity and/or reproductive effort as a response to herbivory (Belsky et al. 1993). Several studies have found evidence of increased productivity and reproductive effort as a response to herbivory. Paige and Whitham (1987) found that the biennial herb scarlet gilia (Ipomopsis aggregata), when exposed to herbivory from mule deer (Odocoileus hemionus) and elk (Cervus elaphus), produced four times as many flowering stalks as unbrowsed plants. Furthermore, browsed plants produced 2.76 more flowers and 3.05
times more fruits than unbrowsed plants. A five year study found that secondarily browsed plants of *I. aggregata* produced 2.4 times more fruits and flowers than unbrowsed plants showing that this species can fully compensate for repeated browsing events (Paige 1992). This is further supported by a theoretical model considering repeated grazing (Nilsson et al. 1996). Evidence of overcompensation has also been found in geographically separate populations suggesting that this is also a geographically widespread phenomenon and not just a local adaptation to herbivory (Paige 1999). A comparison of several populations of field gentian (*Gentianella campestris*) with an evolutionary history of grazing and/or management compared to ungrazed/unmanaged populations showed differences in compensatory capacity when exposed to clipping (Lennartsson et al. 1997, Lennartsson et al. 1998). All overcompensating populations came from grazed or managed areas while none of the ungrazed or unmanaged populations showed any sign of overcompensation. If clipped, the overcompensating plants produced on average 8.9 fruits per plant while unclipped plants produced 15.0 fruits (Lennartsson et al. 1997). In comparison, the non-overcompensating plants produced 7.2 fruits when clipped and 10.9 when not clipped (Lennartsson et al. 1997). One mechanism causing growth compensation in plants to herbivory can be explained by the loss of apical dominance where apical damage causes a positive effect on plant biomass production, branching, and fruit production through the stimulation of dormant or basally located meristems. Clipping experiments of the herbs *Erysimum Strictum*, *Rhinanthus minor* and *Gentianella campestris* showed that apical damage had positive effects on biomass production, branching and fruit production with moderate levels of clipping (Huhta et al. 2000a, Huhta et al. 2000b). These empirical studies of grazing
induced compensation and overcompensation have found support in several theoretical models as well (Vail 1992, Tuomi et al. 1994, Vail 1994, Nilsson et al. 1996, Yamauchi and Yamamura 2004). There is now a substantial body of evidence suggesting that several plant species have the ability to compensate and even overcompensate from herbivory either by replacing lost somatic or reproductive tissue. If the effect of herbivory is predictable in time and space, and not a result of outbreaks in the herbivore population, compensatory growth responses in the damaged plants can alleviate the deleterious effect of tissue loss (McNaughton 1983).

In experiments simulating climate warming it is commonly found that warming significantly increases the reproductive effort and success of arctic and alpine plant species (Wookey et al. 1993, Wookey et al. 1994, Stenstrom and Jonsdottir 1997, Totland 1997, Price and Waser 1998, Totland and Nylehn 1998, Totland 1999). In a meta-analysis of experimental data of one to four years duration collected from 13 different sites, it was found that the reproductive effort and success increased in response to simulated climate warming (Arft et al. 1999). In high arctic studies, plant species showed a stronger response in reproductive effort than species found in low arctic sites. The warming simulations produced small to moderate responses in reproductive success but a trend towards greater responses over time. Still, there are some studies that have found few effects of climate warming on the reproductive performance of some plant species. A study of the widespread arctic and alpine herb *Saxifraga oppositifolia* revealed that climate warming had little effect on phenology and that a reduction in reproductive success was ascribed to competition for light from an increase in taller neighboring
species (Stenstrom et al. 1997). These findings are supported by a long-term study of the performance of *Ranunculus glacialis* to climate warming where no significant effects of the experimental warming treatments on reproduction, phenology or growth were found aside from an initial increase in seed weight (Totland and Alatalo 2002). Furthermore there are also studies that have found negative effects of climate warming on plant performance. In the forb *Delphinium nuttallianum* warming caused a reduction in both the abundance of flowering plants as well as the number of flowers per plant (Saavedra et al. 2003). These neutral or negative responses to climate warming could potentially make these species vulnerable to increased competition from other neighbouring species with higher phenotypic plasticity. Moreover, recent studies of species interactions have revealed that climate change might alter the competitive outcome and hence plant community composition (Kudo and Suzuki 2003, Dormann et al. 2004, Klanderud 2005).

Several of the studies mentioned above indicate that the competitive balance between plant species can be altered due to climatic changes. However, there are indications that herbivory and the grazing regime might mitigate such a response (Wada 1999, Dormann et al. 2004). The inclusion of herbivores in empirical studies and model predictions about climate change effects on plant performance and future community composition is urgently needed. Except for the work conducted by van der Wal et al. (2007) on goose grazing in tundra ecosystems, few, if any, studies have investigated the influence of herbivores on how vegetation responds to climate change.
In this study I investigate the effect of climate warming on the interaction between ungulate herbivory and the flower and fruit production of two perennial forbs, *Cerastium alpinum* and *Draba cana*. The study was conducted on the summer range of the Kangerlussuaq-Sisimuit caribou herd where the grazing history from ungulate herbivores is at least 4,500 years old (Melgaard 1986). I hypothesized that the flower and fruit production of *C. alpinum* and *D. cana* show a positive and stronger response to warming when exposed to grazing from ungulate herbivores compared to areas that are prevented from being grazed.
Materials and methods

Study site

The research site is part of the low-Arctic and is located 20 km west of Kangerlussuaq in south-west Greenland (67°6.8’N, 50°20’W, 50-500m a.s.l) on the summer range of the Kangerlussuaq-Sisimiut caribou herd. The climate is typically continental with low levels of precipitation in both summer and winter (see Chapter 2). The study site is located in moist tundra on noncarbonated mountain bedrock and the plant community is defined as low shrub tundra (CAVM Team 2003). Shrub species are typically dominated by *Salix glauca* and *Betula nana* on the south facing slopes and lower elevations, with Labrador Tea (*Ledum palustre*) dominating the cooler north facing slopes (Post et al. 2003). Forbs are dominated by *Cerastium alpinum*, *Melandrium sp.*, *Draba cana*, *Stellaria longipes* and *Polygonum viviparum*. The graminoids are typically dominated by *Kobresia myosuroides* and *Carex supine* in the drier slopes while *Poa pratensis* are abundant in the moister areas towards the valley floors. The only mammalian herbivores in West-Greenland are caribou (*Rangifer tarandus*), muskoxen (*Ovibos moschatus*) and arctic hare (*Lepus timidus*). Caribou are present in the study area during calving and post-calving until the end of June (Thing 1984, Bøving and Post 1997, Post et al. 2003) while the muskox population is residential (Forchhammer and Boomsma 1995).

Study species

*Cerastium alpinum* L. is a perennial herb of circum-polar distribution. The shoots are typically 10-30 cm and loosely mat-forming. The five-petalled flowers are white with stems and leaves densely covered with long white hairs. The *Cerastium* genus is difficult
to distinguish but the silvery, translucent hairs characterises *C. alpinum*, which is divided into 3 sub-species: ssp. *alpinum*, ssp. *lanatum* and ssp. *glabratum* (Lid and Lid 2005). *C. alpinum* is self-pollinating and typically blooms from early to mid-summer, depending on locality (Lid and Lid 2005). It has a wide habitat distribution and is typically found in dry, gravelly barrens and steppe-like communities, but is also found in scrub and scree (Böcher et al. 1978, Feilberg et al. 1996). It is found in subarctic North-America and Eastern Canada, Northern Europe and mountains in mid- and southern Europe, northwest Russia and Iceland. In Greenland it is found northward towards 78°N on the west-coast and towards 74°N on the east-coast.

*Draba cana* Rydb., also known as *D. lanceolata*, is a perennial herb with shoots typically 6-30 cm with a dense rosette of basal leaves and stems with 2-3 leaves. The flowers are white with lancet shaped and twined silicles (Böcher et al. 1978). This species grows in dry sun exposed areas and by salt-lake shores. Depending on locality, *D. cana* bloom from early to mid-summer (Lid and Lid 2005). In West-Greenland *D. cana* grows in the interior between Ameralik and Nugssuaq, while on the east-coast only in the interior of Scoresby Sund. This species is also found in the North American arctic, and south in the Rocky Mountains to Montana, Idaho, and Colorado. It is also found in Utah, Nevada, the eastern portion of North America, and Eurasia. Within the *Draba* genus some species have insect- and self pollination while others are strictly self-pollinators. Most of the species found within this genus are arctic or alpine. In Greenland there are 19 species of the genus *Draba* and 300 worldwide, and they are hard to distinguish (Feilberg et al. 1996). Based on locality and silicle shape my study species are most likely *Draba cana*. 
Experimental design

This study was conducted inside 2 experimental exclosures, each of 800 m², which were erected in summer 2002, and on 2 adjacent control areas. These exclosures were part of a long-term research program investigating the role of ungulate herbivores in the productivity response of arctic vegetation to climate warming (Chapter 1). Twelve pairs of permanent vegetation plots, each of 0.25 m², had been established inside and outside of the exclosed areas at the beginning the 2003 growth season as part of the long-term project. Six of these pairs were located inside the exclosures (3 in each exclosure), and 6 were located on the control areas. Twelve open-top chambers (OTCs) to simulate climate warming were randomly assigned to each pair of plots. These cones are reported to increase the near surface temperature by 3-4°C (Marion et al. 1997); however, my chambers did not achieve the same effects (Chapter 1). To expose the plots in the control areas to ungulate grazing during the growth season, the OTC’s were removed simultaneously inside and outside the exclosures (Chapter 1).

In summer 2004, I investigated the flower and fruit production of 48 ramets from each of the two species *C. alpinum* and *D. cana*. The ramets were chosen at random such that 12 ramets were located in plots exposed to grazing and warming, 12 ramets were exposed to grazing and ambient temperatures, 12 ramets were exclosed from grazing and experienced warming, while the final 12 ramets were exclosed from grazing and experienced ambient temperatures. Each individual ramet was permanently marked such that it would be possible to revisit each one for consecutive biometric measurements. The intention of this study was to investigate the flower and fruit production of *C. alpinum* and *D. cana* over several years starting during the 2004 growth season, during the third year of exclosure treatment and second year of
warming treatment. However, a population outbreak of the moth *Eurois occulta* that began in 2004 and persisted with even greater numbers in 2005 prevented biometric measurements during the 2005 growth season. The impact of these caterpillars was of such magnitude that none of the individual ramets that were permanently marked or any other in the area produced reproductive structures in 2005. I quantified the total number of flowers produced per ramet, the total number of fruits produced per ramet, and the fruit to flower ratio.

**Biometric analysis**

During the 2004 growth season, a series of biometric analyses were conducted on *C. alpinum* and *D. cana*. Every 3 days, from June 19 to July 12, the number of flower buds, bud scars, flowers blooming, flowers bloomed and number of mature fruits that had developed was counted and logged on each permanently marked individual ramet. By keeping track of all buds, flowers, fruits and bud scars, it was possible to quantify the total flower and fruit production for each single, permanently marked ramet. The counting and monitoring procedures were conducted until all flowers had developed into mature fruits, senesced or aborted, which occurred on July 12, 2004. The marking technique and counting procedures involved no damage to the plants. The fruit to flower ratio was calculated by dividing total number of fruits produced by total number of flowers produced. Flower was defined as all floral structures including buds, blooming flowers, bloomed flowers, fruits and flowers that did not successfully produce mature fruits.

**Statistical analysis**

Due to the nested design of this experiment, a nested-ANOVA was used to analyze the effects of the warming and exclosure treatments on flower and fruit production, using the
statistical program SPSS version 10.0 (SPSS 1999). The effects of the warming and exclosure treatments on the flower and fruit production were analysed based on the data collected on the final day of monitoring. The dependent variables tested were “total number of fruits”, “total number of flowers” and “fruit/flower ratios” with warming and exclosure treatments as fixed factors. To account for any between ramet, plot or exclosure site variation these variables were included in the analyses as random factors. None of the random factors turned out to be significant and were not included in the analysis presented here.
Results

*Cerastium alpinum*

On the exclosed plots the mean number of flowers produced per plant was significantly higher on the plots that experienced ambient temperatures compared to the warmed plots (Fig. 4.1a). Also, for the grazed plots fewest flowers were produced on the warmed plots. There was no difference in mean number of flowers produced between the ungrazed and warmed and grazed and ambient plots. Overall, the mean number of flowers produced was highest on the ramets exclosed from grazing and experiencing ambient temperatures, while it was lowest on the ramets exposed to grazing and elevated temperatures. The ANOVA model showed that the warming treatment and exclosure treatment had significant effects on the flower production but no significant interaction was observed (Table 4.1).

Among the ungrazed plots, the mean number of mature fruits produced did not turn out to be significantly different between the ambient plots compared to the warmed plots (Fig. 4.1b), although the warmed plots had a slightly lower mean than the ambient plots. On the plots exposed to grazing, the ramets on the warmed plots produced slightly more mature fruits than the ramets on the ambient plots, although not significantly so. The ANOVA model showed that none of the treatments produced significant effects on the fruit production (Table 4.1).

The fruit to flower ratio was not significantly different between the ramets on the warmed and ambient plots inside the exclosures (Fig. 4.1c). On the grazed plots, the fruit to
flower ratio was significantly higher among the ramets exposed to increased temperature compared to the ambient plots. Overall, the fruit to flower ratio was highest on the grazed and warmed plots and lowest among the ungrazed ramets. The ANOVA model revealed that both main effects were significant, but not the interaction term (Table 4.1).

*Draba cana*

On the ungrazed plots, the mean number of flowers per ramet was higher on the plots experiencing ambient temperatures compared to the warmed plots, but not significantly so (Fig. 4.2a). Ramets that were exposed to grazing produced significantly more flowers on the plots that experienced ambient temperatures (Fig. 4.2a). The highest number of flowers was observed on the ramets exposed to ambient conditions, with insignificant differences between grazed or exclosed plots. The lowest number of flowers was found on the warmed plots, with fewest flowers on the grazed and warmed plots. The ANOVA model revealed that the OTC treatment had a significant negative effect on the number of flowers produced (Table 4.1). None of the other parameters turned out to be significant.

A similar pattern to that for flower production was revealed in terms of fruit production (Fig. 4.2b). The use of OTC’s had a significantly negative influence on the number of mature fruits produced (Table 4.1). For both the ungrazed and grazed plots, the ramets experiencing warming produced significantly fewer mature fruits than the ramets experiencing ambient temperatures. Neither the exclosure treatment nor the interaction term turned out to be significant.
The fruit to flower ratio was high for all treatment combinations except for the ramets exclosed from grazing and experiencing warming, which had a fruit to flower ratio significantly lower than the other plots (Fig. 4.2c). Furthermore, the ramets exposed to grazing had a lower fruit to flower ratio on the warmed plots than the ambient plots, but this difference was not significant, as was the case on the ungrazed plots (Fig. 4.2c). The ANOVA model revealed that the warming treatment turned out to be significant (Table 4.1), as well as the interaction between the OTC and exclosure treatments.
Discussion

In an environment where herbivory is predictable in time and space and plants are not subject to outbreaks in the herbivore population, compensatory plant growth may develop as an adaptation to a long coexistence with herbivores (McNaughton 1983). This coexistence between plants and their herbivores could also evolve into a mutual or antagonistic relationship that is beneficial to the plants such that they overcompensate in response to being eaten (Owen and Wiebert 1981, Vail 1992, Jaremo et al. 1999, de Mazancourt et al. 2001). Several studies have shown that plants are sensitive to a changing climate in terms of phenological development and reproduction that could also be affected by ungulate grazing. This could be especially important in the arctic where temperature is a limiting factor for plant performance, and climate change is expected to be most pronounced.

For this study on flower and fruit production in plants, I chose two perennial plant species, *C. alpinum* and *D. cana*, that have circumpolar and alpine distributions and that are exposed to ungulate grazing throughout the growing season. Furthermore, my study site is on the calving grounds of the Kangerlussuaq-Sisimiut caribou herd, where the caribou return every spring and early summer year after year. Caribou have coexisted with vascular plants in south-west Greenland for more than 4500 years (Melgaard 1986). The grazing pressure exercised by these ungulate herbivores on the vegetation is predictable both in space and time, and should pose a potential selective pressure on the vegetation to develop mechanisms to resist or tolerate herbivory. I hypothesized that the flower and fruit production of both *C. alpinum* and *D. cana* would have a positive
response to climate warming and herbivory compared to areas where ungulate herbivores are absent. However, the results only partly supported this hypothesis.

Flower production

My results suggest that climate warming might reduce flower production in terms of number of flowers per ramet. For both grazed and ungrazed plots, *C. alpinum* and *D. cana* flower production was lower on the plots experiencing warming than on the plots experiencing ambient temperatures. Such trends have been found in other studies as well. In a 3-year study investigating the effects of OTCs on the performance of *Saxifraga oppositifolia*, simulated climate warming reduced the number of flowers per genet (Stenstrom et al. 1997). Some of this negative effect was ascribed to the increased shading effect from neighboring plants of other co-occurring species. In a 9-year study in the Colorado Rocky Mountains, climate warming had a negative effect on both the abundance of flowering plants as well as the total number of flowers produced per plant of *Delphinium nuttallianum* (Saavedra et al. 2003). The experimental warming resulted in a reduction in the abundance of flowering plants but also in the total number of flowers per plant compared to control plots. My results also indicate that flower production is to some extent influenced by ungulate herbivory. The lowest mean number of flowers produced by *C. alpinum* was on ramets that experienced grazing and warming, while the highest number of flowers were produced on the ungrazed plants that were experiencing ambient temperatures. For *D. cana* temperature seemed to be more important than grazing due to an insignificant exclosure effect and a highly significant warming treatment. In terms of flower production my results suggests that climate change in
combination with herbivory can reduce the total flower production in some arctic plants, in this case *C. alpinum*, but also that climate warming independent of grazing history could negatively affect flower production in other species as indicated here by *D. cana*.

Although my findings are supported by results from other studies, there might be other explanations for the fewer flowers observed in my warmed plots. Instead of allocating resources into several flowers per plant, the two species investigated in my study may instead put more resources into heavier fruits, heavier seeds or more seeds per fruit. Such responses have been observed elsewhere. In a 4-year study of the effect of temperature on the species *Ranunculus acris* flowering was lower in plots warmed by OTCs compared to control plots (Totland 1999). However, seed number, seed weight and seed to ovule ratio increased by 13, 22 and 14 % respectively, in response to simulated warming. The same response was found in the perennial herb *Leontodon autumnalis* that produced significantly more and heavier seeds inside OTCs compared to control plots (Totland 1997). Since this study is part of a larger and long-term project, I did not investigate and measure the fruit and seed weights as well as seed numbers due to the need for non-destructive sampling techniques. This has limited my ability to monitor how plants allocate resources between flowers produced and seed number or weight. Even so, my results still give important information about how climate change may affect plant reproduction in relation to herbivory.
Fruit production

For fruit production, warming had a significant effect on *D. cana*, with the lowest fruit maturation on the plots experiencing warming, while the highest number of mature fruits were found on the plots experiencing ambient temperatures. This suggests that the number of mature fruits of *D. cana* might be susceptible to climatic warming, while grazing regime did not appear to have any noticeable effect. Furthermore, the lack of a significant effect of grazing regime on both flower and fruit production indicates that *D. cana* could be grazing tolerant and perfectly compensating for the loss of reproductive tissue. For *C. alpinum* the pattern was different. There appeared to no effect of either the warming treatment or the exclosure treatment on the number of mature fruits produced. On the grazed plots, the ramets that experienced warming produced on average slightly more mature fruits than the plots experiencing ambient temperatures, suggesting a weak response to warming. Furthermore, on the ungrazed plots, fruit production was slightly lower on the ramets experiencing warming than on those exposed to ambient temperatures. Although I could not detect any significant interaction term, my findings suggest that warming in combination with grazing induces increased fruit maturation, while absence of herbivory results in fewer mature fruits. Hence, ignoring the effect of grazing when making predictions about how plants responds to climate change could lead to erroneous conclusions.

A possible explanation for the patterns observed here could be that ramets stimulated by grazing are likely to be more responsive to warming. It has been argued that herbivory can influence growth regulators in plants such that compensatory growth and
reproduction could be initiated following herbivore damage (McNaughton 1983). Such effects on the hormonal balance might also be susceptible to warmer temperatures, and could explain why I see significant interaction terms between the exclosure and OTC treatments in this study. Furthermore, release from apical dominance might also stimulate dormant or quiescent buds to develop and mature fruits, as found in the monocarpic herbs *Erysium strictum* and *Rhinanthus minor* (Huhta et al. 2000b).

Based on the differences seen in fruit production between these co-occurring species in response to both climate warming and herbivory, there are indications that the future reproductive success of at least some plant species in a changing climate might depend on the grazing regime. This again could affect competitive outcomes between species that, at least partly, depend on sexual reproduction and seedling recruitment and potentially could alter plant community composition. However, I did not investigate germination success and seedling survival in this study, which limited my ability to evaluate the recruitment to the populations of the two species investigated here. It has been shown that clipping experiments have reduced seed germination, possibly due to delayed flowering and reduced pollination success (Huhta et al. 2000b). This lack of germination effect could also have been an effect of the clipping treatment because it is argued that simulated herbivory, often through clipping, is a poor substitute for natural herbivory (Strauss and Agrawal 1999). In an investigation of the effect of natural herbivory, seedling survival of *Ipomopsis aggregata* was 2.4 times higher on plots grazed by mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) compared to controls (Paige and Whitham 1987).
Fruit to flower ratio

For *C. alpinum*, the fruit to flower ratio was highest on the grazed and warmed plots. The lowest ratio was observed on the plots that were ungrazed. Both grazing and warming significantly affected the total number of flowers produced, but had no marked effect on fruit production. Therefore the fruit to flower ratio was higher on the grazed and warmed plots compared to the grazed and ambient plots, and more of the flowers actually produced matured into fruits on the grazed plots relative to the ungrazed plots. Furthermore, the slightly negative warming effect on fruit production on the ungrazed plots compared to the slightly positive effect on the grazed plots further amplified the fruit to flower relationship. These findings suggest that exposure to grazing could cause reproduction in *C. alpinum* to be more responsive to climate warming than when ungulate herbivores are excluded. However, as mentioned above, I have not investigated the weight of the fruits, the number of seeds per fruit or the weight of the seeds.

The effect of warming turned out to significantly affect the fruit to flower ratio for *D. cana*. The highest fruit to flower ratio was observed on the ungrazed and ambient plots while the lowest ratio was found on the ungrazed and warmed plots. Also, the interaction term between the OTC and exclosures turned out to be significant. What these findings indicate is that when grazed, proportionally fewer of the *D. cana* flowers develop into mature fruits when exposed to elevated temperatures. However, this relationship is much stronger on the ungrazed plots. It seems that *D. cana* has a stronger negative response to warming when excluded from grazing.
For both species reproductive output depends on both the effect of temperature and the grazing regime. In my study area, where large ungulate herbivores are present during the growing season, a warmer climate seems to positively affect the reproductive performance of *C. alpinum* and negatively affect the performance of *D. cana*. My short-term results suggest that a continued warming of the Arctic could offset the competitive balance between these two co-occurring species in favor of *C. alpinum*. These findings also suggest that a continued warming of the Arctic could, over time, alter the species composition of plant communities.

In low- and sub-Arctic ecosystems, where dense vegetation cover is extensive, clonal life-forms are dominant and recruitment from seedlings is rare (Callaghan and Carlsson 1997). In the high-Arctic, with more barren ground, recruitment through seedling establishment is more important. However, recruitment through seedlings at lower latitudes is important in disturbed areas such as polygons and frost boils (Callaghan and Carlsson 1997). My study site is part of the low-Arctic with dense vegetation and little barren ground. However, I argue that recruitment through seedlings may be important in areas where large ungulate herbivores exist. Over the years, I have observed that the resident musk-ox population frequently disturbed the vegetation cover, and while doing so exposed relatively large areas of naked soil (Pers. obs.). This soil exposure could be important to those species that depend to some extent on seed production and seedling recruitment. The effects of climate warming and grazing observed in this study on flower and fruit production could offset the competitive balance between these two species and their establishment in the exposed soil patches.
The results presented here are data collected during just one field season. The intention was to track reproductive performance of these two species over several growth seasons, but the outbreak of the moth *E. occulta* prevented any reproductive parts to develop in 2005. However, the exclosures were established in spring and early summer of 2002 and the OTC treatment initiated in spring 2003, so the differences observed in the summer 2004 might be a result of these manipulations. Although caution should be taken when general conclusions and interpretations are made after just one season’s measurements, I do argue that the results presented here have important implications for how future studies of climate change and plant community responses are approached. As the results from this study show, there are differences in how *C. alpinum* and *D. cana* respond to climate warming depending on the grazing regime. This study was conducted in an area where ungulate herbivores have been present for over 4500 years (Melgaard 1986). This relatively long period of herbivore and plant interactions made my study site optimal for studying how plant and herbivore interactions are affected by climate warming. The higher fruit to flower ratio of *C. alpinum* in response to the exclosure treatment indicates that the species is performing better when exposed to grazing, and hence lends support to the hypothesis that some plants can benefit from the presence of herbivores (McNaughton 1983, Paige and Whitham 1987). *D. cana* on the other hand shows no significant response to the exclosure treatment alone. If grazing had a negative effect on plant performance, one would expect to see a difference in means between grazed and ungrazed plots. No such differences were found, which suggests that *D. cana* has the ability to tolerate grazing, and could also indicate that this species has the ability to compensate perfectly for tissue lost to herbivory. In the grazed plots, the fruit production
and fruit to flower ratio of *C. alpinum* was higher when experimentally warmed compared to *D. cana*, which performed less well when exposed to elevated temperatures. The responses presented here indicate that the competitive outcome between these two co-occurring species might be altered in a changing climate were *C. alpinum* seems to perform better, which could potentially affect community composition. But inside the exclosures where ungulate herbivores were absent, *D. cana* performed better than *C. alpinum* at elevated temperatures. Based on the results presented here, it is advised that the influence of herbivores is incorporated in empirical studies as well as model predictions about how individual species and plant communities respond to climate change.
Acknowledgements

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Figure 4.1: Mean number of a) flowers, b) fruits and c) fruit to flower ratios of the different treatment combinations for *Cerastium alpinum*. Different capital letters indicate that means are significantly different from each other at $p \leq 0.05$. Controls in the experiments are the plots that are grazed but experience ambient temperature. Error bars represent 1±SE of the means. Kangerlussuaq, Greenland.
Figure 4.2: Mean number of a) flowers, b) fruits and c) fruit to flower ratios of the different treatment combinations for *Draba cana*. Different capital letters indicate that means are significantly different from each other at $p \leq 0.05$. Controls in the experiments are the plots that are grazed but experience ambient temperature. Error bars represent $1\pm\text{SE}$ of the mean. Kangerlussuaq, Greenland.
Table 4.1: Results from the nested-ANOVA analyses of treatment effects on the different reproductive stages of the co-occurring species *Cerastium alpinum* and *Draba cana* in low shrub tundra, Kangerlussuaq, Greenland. Analyses were conducted when all flowers had set fruit or senced, which occurred on July 12, 2004. W: warming/ambient treatment, E: exclosure treatment.

<table>
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<tr>
<th>Species</th>
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Chapter 5

The effect of climate warming and ungulate herbivory on the phenological progression of arctic plant species.
Abstract

Studies of key phenological events in plants such as leaf emergence, flowering and reproduction suggest strong temperature dependence. Arctic and alpine plant species are exposed to extremely low temperatures as well as a short growth season. The length of the growth season is perhaps the most limiting factor on plant performance in these areas. The enhanced global temperatures are reported to advance spring snowmelt as well as postponing the onset of fall. The higher air and soil temperatures result in an earlier initiation of plant emergence and phenological progression of arctic and alpine plants.

However, studies of climate warming on plant phenology have, to my knowledge, not taken into account the influence of grazing animals such as ungulate herbivores. Several studies have revealed a strong impact of ungulate herbivores on several aspects of plant performance. Also, several plant species have the ability to compensate for herbivory by compensatory growth. However, it is likely that allocation of resources to compensatory growth may delay phenological progression as a response to ungulate herbivory. I investigated the effect of climate warming on the phenological progression of arctic plants during 2004 and 2005, in areas grazed by ungulate herbivores and areas relieved of grazing pressure. My results revealed that a warmer climate can promote earlier emergence of arctic plants and that ungulate herbivory has the potential to delay plant emergence. Moreover, I found that plants with later emergence have the potential to compensate with a faster phenological progression, especially on plots that are prevented from grazing. Furthermore, during a caterpillar outbreak in 2005, the relationships found in 2004 were offset by plant defoliation and fewer plant species that emerged during that
year. My results suggest that the influence of both ungulate and invertebrate herbivory should be taken into account when effort is made to predict the phenological response of plants to a changing climate.
Introduction

Key phenological events in plants such as growth initiation and leaf emergence, flowering phenology and reproduction, are strongly dependent on temperature. Long term monitoring of first flowering dates in several plant species and different geographical areas has revealed that the phenological progression of plants is affected by increasing temperatures caused by global climate change (Abu-Asab et al. 2001, Hepper 2003). Arctic and alpine plant species are exposed to extremely low temperatures, permafrost and limited nutrient availability as well a very short snow free growth season (Callaghan and Carlsson 1997). The length of the growth season is perhaps the most limiting factor on plant performance in these areas due to a very limited time for growth, flowering, fertilization, fruit maturation and seed set (Molau 1997). The phenological initiation and progression of these species are dependent on spring snowmelt as well as air and soil temperatures. Studies of the impact of snowmelt patterns on key phenological events such as growth initiation and maximum leaf length (Walker et al. 1995) but also timing of flowering (Inouye et al. 2003) has revealed that snowmelt date is a strong determinant of plant phenological progression. A snow removal and soil warming experiment near Toolik Lake, Alaska simulating lengthened growing season, resulted in advanced growth of the forb Polygonum bistorta ascribed to the advancement of soil thaw allowing for earlier growth initiation (Starr et al. 2000). The enhanced global temperatures caused by anthropogenic greenhouse gas emissions are predicted to cause a warming of the arctic by 4-7°C, advance snowmelt in the spring, and postpone the autumn frost, causing a longer growth season (ACIA 2004). Projection from a 3°C increase in air temperatures show a speed up of thawing that in turn will advance initiation of plant emergence and
phenological progression of arctic and alpine species by as much as 2-3 weeks earlier than present (Molau 1997). An 11 year study of 75 plant species in Iceland showed that the number of species in flower by the first week of July was strongly correlated with air temperatures in the preceding 5 weeks (Thorhallsdottir 1998). Several climate warming experiments have found evidence that such effects are likely to happen and are also likely to happen for the majority of plant growth forms. For both deciduous and evergreen shrubs (Suzuki and Kudo 2000) as well as perennial herbs (Molgaard and Christensen 1997) it has been found that experimental warming has advanced initiation of the plant growth season. As well, advanced flowering phenology has been found to be affected by increased climate warming. Flowering phenology was found to be advanced for both deciduous and evergreen shrubs (Welker et al. 1997, Suzuki and Kudo 2000), perennial forbs (Molgaard and Christensen 1997, Stenstrom et al. 1997) as well as graminoids (Stenstrom and Jonsdottir 1997), and suggests similar patterns across functional plant groups.

However, the climate warming experiments on plant phenology have, to my knowledge, not taken in to account the effect of grazing animals such as ungulate herbivores. Several studies of ungulate grazing have found that they can have profound effects on plant biomass and production (McInnes et al. 1992, Bråthen and Oksanen 2001, Frank et al. 2002), nutrient cycling and mineralization rates (Frank and Groffman 1998, van Wijnen et al. 1999, van der Wal et al. 2004), plant community composition (Augustine and McNaughton 1998, Olofsson 2001, Olofsson et al. 2004a) as well as reproductive effort and success (Lennartsson et al. 1997, Paige 1999, Huhta et al. 2000a) in areas where they forage. Hence, it is likely that the advanced phenological progression
of arctic and alpine species due to climate warming might be affected by grazing from ungulate herbivores. It has been shown that in areas where plants and herbivores have been co-existing for long periods of time, plants have evolved an ability to compensate for somatic and reproductive tissue loss (Lennartsson et al. 1997) (also see chapter 4). However, many of these studies of plant compensation on reproductive effort and success have not been able to investigate the possible effect of such compensation on the phenological progression of these species. It has been argued that the compensatory responses and resource allocation to such responses might cause phenological progression to be delayed (Tiffin 2000). If this is the case, a delayed progression of phenology might cause the plants to produce seeds so late in the growth season that successful germination and seedling survival might be limited. Furthermore, the predicted advancement of arctic plant phenology as a response to climate warming might be mitigated by grazing from e.g. ungulate herbivores. Disregarding such a potential effect on plant phenological response to climate change might lead to erroneous predictions about how arctic and alpine plants respond to a changing climate. In this study I wanted to investigate if grazing from ungulate herbivores such as caribou (Rangifer tarandus) and muskoxen (Ovibos moschatus) caused a phenological delay compared to areas that were excluded from grazing as well as investigating if grazing could potentially prevent the advanced phenological progression of arctic plant species due to climate warming in an Arctic field site in West-Greenland. I hypothesized that grazing from ungulates could cause a delay in the phenological progression of arctic plants due to tolerance and compensatory responses in the grazed plants. Herbivory would then mitigate enhanced phenological progression due to climate change.
Materials and methods

Study site

My observations of the phenological progression of arctic plant species were conducted in a long-term research site on the summer range of the Kangerlussuaq-Sisimiut caribou herd located 20 km west of Kangerlussuaq in south-west Greenland (67°6.8’N, 50°20’W, 50-500m a.s.l). The study area experiences a typically continental climate with low precipitation during summer and winter. The mean precipitation in summer is 8mm, 15mm, 24mm and 33 mm for May, June, July and August, respectively, while the mean monthly temperatures are 2.5°C, 8.6°C, 10.7°C and 8.2°C (DMI (www.dmi.dk)). The study site has been defined as low shrub tundra located on noncarbonated mountain bedrock (CAVM Team 2003). *Salix glauca* and *Betula nana* are the dominant shrub species in the south facing slopes and at lower elevations with Labrador Tea (*Ledum palustre*) dominating the cooler north facing slopes (Post et al. 2003). Forbs are dominated by *Cerastium alpinum*, *Melandrium sp.*, *Draba cana*, *Stellaria longipes* and *Polygonum viviparum*. The dominant graminoid species are *Kobresia myosuroides* and *Carex supine* in the drier slopes, while *Poa pratensis* is abundant in the moister areas towards the valley floors. Caribou are present in the study area during calving and post-calving until the end of June (Thing 1984, Bøving and Post 1997, Post et al. 2003) while the musk ox population is resident (Forchhammer and Boomsma 1995).
Experimental design

The observation of phenological progression was conducted inside 3 experimental exclosures, each of 800 m², erected in summer 2002, and on 3 adjacent control sites. These exclosures were part of a long-term research program investigating the role of ungulate herbivores on plant community changes and productivity response of arctic vegetation to climate warming (see Chapter 2). Twelve pairs of permanent vegetation plots, each of 0.25 m², had been established inside and outside of the exclosed areas at the beginning the 2003 growth season as part of the long-term project. Six of these pairs were located inside the exclosures (3 in each exclosure), and 6 were located on the control areas. Twelve open-top chambers (OTC’s) to simulate climate warming were randomly assigned to each pair of plots. These cones are reported to increase the near surface temperature by 3-4°C (Marion et al. 1997) to simulate climate warming, however my chambers did not achieve the same reported effects (see Chapter 2). This design of exclosures and climate chambers gave 4 different treatment combinations as follows: ungrazed and ambient temperatures (UA), ungrazed and warmed temperatures (UW), grazed and ambient temperatures (GA) as well as grazed and warmed temperatures (GW). To expose the plots in the control areas to ungulate grazing during the growth season, the OTC’s were removed simultaneously inside and outside the exclosures at the peak of the growth season (see Chapter 2). The reasoning behind the timing of OTC removal was a trade-off between maximizing temperature treatment effects and at the same time allowing for herbivore grazing. The effect of warming on plant performance is more important during the first part of the growth season than increased temperature throughout the growth season (Molgaard and Christensen 1997).
Collection and analysis of plant phenology data

The phenological state of the species in the permanent plots was monitored at 3 day intervals. This monitoring routine was performed to minimize human interaction with the caribou and muskoxen at the study site, but at the same time making sure that the phonological progression was recorded. However, on a few visits to the study site it was impossible access some of the plots due to presence of caribou or muskoxen immediately by the plots. I still decided to include the observations on those days in the data to be able to have enough observations for robust analyses. On each visit to the plots the number and names of the species in an emergent state were recorded. I defined a graminoid species as emergent when a green leaf was observed above ground. A forb species was defined as emergent when a leaf or stem was observed above ground and turning green. A shrub was defined as emergent when the buds broke and a green leaf was observed. In 2004 the phenological observations started on June 16 and ended on July 12, while the observations in 2005 started on May 26 and ended on June 17, with a final observation day on July 28. I used an ANOVA model to test for any differences in species numbers between the different treatment combinations with exclosure site as a random factor to account for any site differences. There was no significant difference in the final number of species emergent between the treatment combinations in the 2004 growth season (UA: 8.3 ± 0.9, UW: 7.3 ± 0.9, GA: 7.8 ± 0.9 and GW: 8 ± 0.9 (mean ± SE)) (ANOVA: F_{[1,18]} = 0.40, p = 0.54). Neither was there any difference between the treatments in the final number of species emergent in 2005 (UA: 4.9 ± 0.4, UW: 5.5 ± 0.4, GA: 5.3 ± 0.4 and GW: 5.7 ± 0.4 (mean ± SE)) (ANOVA: F_{[1,44]} = 0.12, p = 0.73). However the mean number of species emergent in the plots was lower in 2005 than in 2004 for all
treatments. The reason for this is most likely due to the outbreak of the moth *Eurois occulta* that reached noticeable numbers in 2004 but reached very high numbers in 2005 causing a huge impact on the vegetation (see chapter 2). To make my analysis comparable between treatments I transformed daily numbers of emergent species to daily proportions of the final number of species emergent on each plot. To analyze the progression of plant phenology in each treatment I used non-linear regression to estimate the date of 50% emergence and the number of days between 10% and 80% emergence. This approach has previously been used by Post and Klein (1999) and Post et al. (2003). Due to the non-linear relationship between the proportion of plant species emergent and time, I used a logit-transformation of the daily proportions of species emergent to estimate the slope of the relationship between species emergence and Julian date (day 1 = 1 January) of each treatment combination. Then I performed a regular linear regression on the transformed data, and compared the slopes of the regressions for each treatment combination. Because my analyses of the phenological progression might be sensitive to the length and number of days of the observation periods in 2004 and 2005 as well as the influence of *E. occulta* on species numbers emergent limited my comparisons of treatment effect to each year separately. All analyses were performed with SPSS version 10.0 (SPSS 1999).
Results

In 2004 the emergence of species on ungrazed sites commenced earlier in the plots experiencing warming than on the plots exposed to ambient temperatures: 50% of the final number of species observed were emergent on 13 June on the UW plots and on 17 June on the UA plots (Figure 5.1a). However, plant phenology progressed more rapidly in the UA plots (non-linear regression, $R^2 = 0.75$) with 8 days between 10% and 80% emergence compared to 12 days for the UW plots (non-linear regression, $R^2 = 0.71$).

On the grazed plots the emergence of plant species commenced earlier in the plots experiencing warming than the plots exposed to ambient temperatures: 50% of the final number of species were emergent on 14 June in the GW plots and on 21 June in the GA plots (Figure 5.1b). Also for the grazed plots plant phenological progression was more rapid on the plots experiencing ambient temperatures (GA) (non-linear regression, $R^2 = 0.73$) with 8 days between 10% and 80% emergence compared to 9 days for the GW plots (non-linear regression, $R^2 = 0.51$). When comparing the slopes of the regression lines of the logit-transformed relationship between plant species progression and Julian date, the UA plots ($r^2 = 0.57$, $F = 77.14$, df =1, $p < 0.001$) had a statistically significant lower slope than the UW ($r^2 = 0.59$, $F = 84.99$, df =1, $p < 0.001$) and GW ($r^2 = 0.42$, $F = 42.15$, df =1, $p < 0.001$) plots. However, there was no significant difference between the UA and GA plots ($r^2 = 0.52$, $F = 61.90$, df =1, $p < 0.001$) (Table 5.1, Figure 5.3a).

For 2005 the patterns were different between the treatments compared with 2004. On a few days, the proportion of plants emergent decreased. This pattern was caused by the presence of caribou and muskoxen at the some of the plots preventing observations at some of the plots (see materials and methods section). For the ungrazed plots, emergence
of plant species commenced earlier on the plots experiencing ambient temperatures compared with the warmed plots: 50% of the final number of species were emergent on 9 June for the UA plots and on 12 June in the UW plots (Figure 5.2a). There was no difference in the progression of plant phenology between the UW plots (non-linear regression, $R^2 = 0.84$) and the UA plots (non-linear regression, $R^2 = 0.74$) with 7 days passing between 10% and 80% emergence. In the grazed plots emergence of plant species commenced earlier on the plots that experienced warmer temperatures compared to the ambient plots: 50% of the final number of species were emergent on 7 June in the GW plots compared to 14 June in the GA plots (Figure 5.2b). Plant phenology progressed more rapidly on the GW plots (non-linear regression, $R^2 = 0.81$) with 7 days passing between 10% and 80% emergence compared to 12 days in the GA plots (non-linear regression, $R^2 = 0.69$). However, when comparing the slopes of the regression lines of the logit-transformed relationship between plant species progression and Julian date, there was no significant difference between the different treatments (Table 5.1, Figure 5.3b).
Discussion

The phenological progression of arctic plants is limited by the time of snowmelt in spring, low air and soil temperatures, and the short growing season (Callaghan and Carlsson 1997). A warmer climate has been predicted to alleviate, at least to some extent, all of these climatic constraints in a fashion that will advance the timing of key phenological events. However, such effects might be mitigated by herbivory by inducing compensatory growth responses in plants that could delay the phenological progression (Tiffin 2000). It is a scientifically well established fact that if an organism experiences an alteration or evolution in one trait or character it is often, if not always, at the expense of another related trait (Williams 1966). In this study I hypothesized that the selection for precocity as a response to climate warming might be mitigated due to the compensatory response to tissue lost to herbivory.

During the 2004 growth season the warming simulations advanced the commencement of plant species by 4 days compared to the plots that experienced ambient temperatures inside of the exclosures. This suggests that a warmer climate advances the phenological progression of arctic plants. This was also supported by the significantly higher slope of the regression lines. Natural selection should favor rapid phenological development in plants, or at least the ability to rapidly respond to favorable climatic conditions, because the more quickly a plant can reach its reproductive stage the more likely it is to reproduce successfully before the end of the growth season (Primack 1987). This is especially important in seasonal climates such as in the Arctic with a short growth season and very low temperatures. Similar results have been observed elsewhere for single species experiments. In a study investigating experimental warming and
consequent effects on *Papaver radicatum* on Disko Island outside the west coast of Greenland, it was found that warming resulted in an earlier onset of the growth period (Molgaard and Christensen 1997). This also resulted in an earlier onset of flowering which, for this species, was argued to be a greater advantage than increased temperature throughout the season. A snow-removal and soil warming experiment at Toolik Lake, Alaska, simulating earlier onset of spring resulted in an advanced termination of dormancy in the forb *Polygonum bistorta* L. (Starr et al. 2000). Although these experiments focused on single forb species, there is also evidence that such responses are found across functional plant groups. In this study I observed the phenological progression of all the species across functional groups that were growing in the permanent vegetation plots. Other studies have also investigated species with different growth strategies. A study of the effects of warming by OTCs on alpine deciduous and evergreen shrubs showed that warming advanced the time of leaf emergence for all species throughout the 3 year study although there were differences in how strongly each species responded to the OTC treatment (Suzuki and Kudo 2000). These findings are further supported by a meta-analysis from 13 different arctic and alpine sites investigating plant responses to experimental warming (Arft et al. 1999). It was found that deciduous and evergreen shrubs, forbs and graminoids all responded to climate warming by an advanced phenological progression.

Although I found that plant emergence was advanced on warmed plots, the progression of phenology was more rapid on the plots experiencing ambient temperatures. This could suggest that some species show a more advanced phenology while others are not responding as strong to a warmer climate. As a result I observed a
longer phenological development on the warmed plots than on the ambient plots, from the time of first emergence until the final species had emerged. Arft et al. (1999) found that evergreen and deciduous shrubs responded to warming within the 2 first years of warming simulations while forbs and graminoids did not show a clear response until the 3rd or 4th year. Moreover, a 3 year study of the forb Saxifraga oppositifolia in relation to climate warming was also found to have no immediate phenological response to a warmer climate (Stenstrom et al. 1997). On the other hand, the phenotypic plasticity in plants could allow them to respond to climatic conditions in a way that buffer the effects of a highly variable climate. Later growth initiation in the spring could initiate a faster phenological progression to allow the plants to reproduce and set seeds before the onset of winter. This might be a reason why I observed a faster progression in phenology on the later emerging plots.

Also for the plots exposed to grazing, the OTC treatment resulted in an earlier emergence of plant species compared to the controls. However, there was no significant difference in how rapidly the progression occurred between the two treatments. Although not significant, the coefficient for the earlier emerging grazed and warmed plants was smaller than the later emerging grazed and ambient plants. From my findings it seems that grazing does not delay the earlier progression on warmed plots. However, the emergence of plants on the grazed and ambient plots was on average 4 days later than the ungrazed and ambient plots, suggesting delayed phenological initiation when plants are exposed to ungulate grazing. As mentioned by Tiffin (2000), such a delay could result in reduced fitness if seedlings are not established by the onset of frost in the fall. It seems
that grazing speeds up the phenological progression of plants during warmer conditions, but delays emergence of plants during ambient temperatures.

The pattern observed in 2004 was not observed in 2005. For the ungrazed plots the plants experiencing ambient temperatures commenced earlier than the OTC treated plants. This is contrary to what was expected initially but also compared to what was observed in 2004. As well, later emerging plants in 2004 were observed to have a more rapid progression compared to the earlier emerging plants. There was no difference between the number of days between 10% and 80% emergence, nor was there a significant difference between the slopes of the regressions in 2005. It is not clear to me why there were such differences between years. The most likely explanation for this surprising result could be the outbreak of the caterpillars of the moth *E. occulta* that caused severe defoliation of plants in the study site. This defoliation could have had an effect on which species that emerged and the progression of the phenology. The analyses of the species numbers emergent in the permanent vegetation plots showed a significant lower number of species in the plots in 2005 compared to 2004 (see Materials and methods). It could very well be that the impact of caterpillar foraging affected the phenotypic progression in 2005 in such a way that it offset the treatment effects found in 2004. The grazed plots showed a pattern similar to 2004 with the warmed plots having the earliest emergence, but there was no difference in phenological progression. It is to my knowledge not clear what could cause these differences between the 2 years in terms of commencement and phenological progression. However, it seems likely that the lack of significant differences between the treatments in 2005 was caused by the foraging behavior of the caterpillars that could have concealed any clear treatment effects.
Based on the results observed from the 2004 growing season it seems clear that a warmer climate might advance the initiation of plant emergence of arctic plants by between 4-7 days after 2 years of warming simulations and 3 years of large herbivore exclusion. However, it seems that herbivory could delay such a response in time. My results also indicate that plants have the ability to compensate for delayed emergence with a more rapid phenological progression, but not when exposed to grazing. However, during a peaking invertebrate population outbreak the effects of climate and large herbivore grazing disappear, as observed in 2005. The long term effects of such outbreaks on plant phenology are not obvious and probably depend on the temporal nature of such an outbreak. But my results from 2004 illustrate that predictable herbivory, from caribou and muskoxen in this case, does affect the phenological progression of arctic plants in response to climate warming. Future investigations of climate change effects on plant phenology should acknowledge the effects of grazing in areas where large herbivores exist.
Acknowledgements

This project has received financial support from the U.S. National Science Foundation under grants to E.P. #DEB0124031 and #DEB0217259, and The Committee for Research and Exploration of the National Geographic Society under grant #7442-03. Invaluable support was given to us by the logistical support staff of VECO Polar Resources.
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Figure 5.1: a) Phenological progression of warmed (○) and ambient (●) plots excluded from grazing in 2004 expressed as the cumulative percentage plant species emergent versus Julian date. b) Phenological progression of the warmed (○) and ambient (●) grazed plots in 2004 expressed as the cumulative percentage plant species emergent versus Julian date. The fitted function is $Y = 1/(1 + e^{a-bX})$ for both a) and b) where $Y$ is percent plant species emergent and $X$ is Julian date.
Figure 5.2: a) Phenological progression of warmed (○) and ambient (●) plots excluded from grazing in 2005 expressed as the cumulative percentage plant species emergent versus Julian date. b) Phenological progression of the warmed (○) and ambient (●) grazed plots in 2005 expressed as the cumulative percentage plant species emergent versus Julian date. The fitted functions are the same as in Figure 5.1.
Table 5.1: Results from linear regressions of the logit-transformed proportions of emergent plant species for each treatment combination.

<table>
<thead>
<tr>
<th>Year</th>
<th>Treatment</th>
<th>Slope</th>
<th>S.E.</th>
<th>Estimate</th>
<th>S.E.</th>
</tr>
</thead>
<tbody>
<tr>
<td>2004</td>
<td>Ungrazed, warmed</td>
<td>0.025</td>
<td>0.003</td>
<td>-4.73</td>
<td>0.483</td>
</tr>
<tr>
<td></td>
<td>Ungrazed, ambient</td>
<td>0.035</td>
<td>0.004</td>
<td>-6.59</td>
<td>0.714</td>
</tr>
<tr>
<td></td>
<td>Grazed, warmed</td>
<td>0.025</td>
<td>0.004</td>
<td>-4.72</td>
<td>0.689</td>
</tr>
<tr>
<td></td>
<td>Grazed, ambient</td>
<td>0.029</td>
<td>0.029</td>
<td>-5.41</td>
<td>0.656</td>
</tr>
<tr>
<td>2005</td>
<td>Ungrazed, warmed</td>
<td>0.280</td>
<td>0.095</td>
<td>-52.25</td>
<td>15.70</td>
</tr>
<tr>
<td></td>
<td>Ungrazed, ambient</td>
<td>0.323</td>
<td>0.102</td>
<td>-60.72</td>
<td>16.97</td>
</tr>
<tr>
<td></td>
<td>Grazed, warmed</td>
<td>0.234</td>
<td>0.091</td>
<td>-43.97</td>
<td>15.16</td>
</tr>
<tr>
<td></td>
<td>Grazed, ambient</td>
<td>0.201</td>
<td>0.086</td>
<td>-37.97</td>
<td>14.33</td>
</tr>
</tbody>
</table>
Figure 5.3: Comparison of the coefficient determining the slope of the relationship between percent emergent species and Julian date for each treatment combination where a) 2004 and b) 2005. Error bars represent 1±SE for the regression coefficients.
Chapter 6

Conclusion

A key topic of ecological studies is the search for mechanisms that regulate abundance and distributions of populations. This is especially important in light of global climate change. The overall goal of my thesis research was to gain a better understanding of how the different components of the Arctic terrestrial ecosystem will respond to climate change. Most studies have either looked at how plant communities or single plant species respond to changes in climatic conditions (e.g. temperature, snow conditions, precipitation) or resource availability. My intention was to investigate the interaction between different trophic levels of the ecosystem and how this interaction is affected by climate warming. It is to my knowledge few, if any, studies that have incorporated the effects of herbivory on how plant communities respond to a warmer climate. Several of the process models designed to make predictions about how the ecosystems responds the global climate change have so far ignored the influence that herbivores have on the vegetation. This could lead to erroneous conclusion especially when making predictions about the carbon cycle and biomass accumulation because herbivores have shown to make considerable impact on plant biomass, community composition, nutrient cycling and biomass production. One of my goals has been to gather enough material and insight such that future modeling approaches and predictions can be more accurate and complete.

Throughout this study, I have tried to address some of the classical discussions in ecology concerning what mechanisms are regulating density and distribution of plants by investigating the joint influence of climate and herbivory on a plant community in West-
Greenland. It is essential to understand what factors are controlling plant communities to be able to predict the changes that might occur as a result of global climate change. But I have not only tried to look at two possible mechanisms that can regulate plant communities, I have also tried to investigate several possible responses of the plant communities to climate change. I have focused on possible changes in plant biomass and production, plant community composition, plant reproductive effort and success as well as timing of key phenological events. The intention has been to get as complete picture as possible during the course of my Ph. D. program.

In chapter two the focus was on possible changes in plant biomass and production of shrubs, graminoids and forbs. I did not find any significant effects of simulated climate warming or herbivore exclosures on aboveground biomass or productivity. However, there were indications that herbivory might limit increased biomass of shrubs as found by others (Thing 1984, Manseau et al. 1996, Bråthen and Oksanen 2001, Olofsson et al. 2001). But warming appeared to have no effect on the plant biomass and does not support findings from other similar studies (Arft et al. 1999, Walker et al. 2006). Therefore, my results do not lend support to my original hypothesis that there is an interacting effect of herbivory and warmer temperatures on biomass production. It appears that my data of biomass measurements lend more support towards plant biomass being controlled by herbivores more so than temperature or climate.

In chapter three, I investigated possible changes to the plant community composition as a response to herbivory and simulated climate warming. Also for the abundance measures there were no clear results supporting the hypothesis of an interacting effect between herbivory and warming. However, herbivory tended to
negatively affect shrub abundance as reported by other studies (Manseau et al. 1996, Olofsson et al. 2001). This supports the idea that herbivores have the ability to regulate vegetation. However, graminoids were positively affected by warming that also suggests that temperature can influence at least graminoid abundance.

In chapter four I investigated the effect of climate warming on the interaction between ungulate herbivory and the flower and fruit production of the two perennial forbs *Cerastium alpinum* and *Draba cana*. Ehrlich and Raven (1964) argued for a co-evolutionary interaction between herbivores and plants. It has later been argued that if herbivory is predictable in space and time compensatory growth can alleviate the negative effects of tissue removal from herbivores (McNaughton 1983). Co-evolutionary mechanisms have even been argued to increase plant productivity and/or reproductive effort as a response to herbivory (Belsky et al. 1993). The intention of the study presented in paper four was to investigate the reproductive success of two co-occurring species in an ungulate grazing system and how climate warming might affect the competitive balance between these two species. My results indicate that in a warmer climate *C. alpinum* has a higher reproductive success than *D. cana* when exposed to grazing suggesting a disrupted competitive balance in favor of *C. alpinum*. But when herbivores were excluded *D. cana* performed better than *C. alpinum*. This suggests an interacting effect of both herbivory and climate warming that could lead to changes in plant community composition.

Finally, in chapter five, I investigated the potential for interactions between herbivory and climate warming on key phenological events such as growth initiation and leaf emergence. It has been argued that a warmer climate will advance the phenological
progression of plants (Molau 1997). But it has also been argued that compensatory mechanisms in plants to herbivory might delay phenological progression (Tiffin 2000). I wanted to investigate a possible interacting effect between herbivory and climate warming on plant phenology. The results found in 2004 suggest that warming advance the emergence of plants but that later emerging species had a faster progression. It appears that climate warming cause earlier progression of some species that is better adapted to respond to changes in climatic conditions. Furthermore, grazing seemed to delay emergence of plants, especially in the ambient plots supporting my initial predictions. In 2005, intense caterpillar foraging offset the patterns seen in 2005 due mainly to fewer emerging species.

There was a general lack of unambiguous results in the responses found in biomass and abundance of the functional plant groups. However, there were significant treatment effects for both reproduction and phenological progression. This might suggest that the initial responses of the plants in this system to the treatments were observed in the reproductive parts of the plants as well as the phenological development, rather than in biomass and productivity. This is a plausible explanation considering the massive biomass off-take caused by the caterpillars in both 2004 and 2005. To be able test this further, the study needs to be extended until the effects of the caterpillar outbreak is minimized and the effects of the warming and exclosure treatments can clearly be measured.

*Improvements*
This study has been part of a long-term field experiment and the need for non-destructive sampling has put limitations on important aspects of such a complicated study. A limited budget also put limitations to what I was able to investigate during the course of my Ph. D. program. I measured responses of the warming treatment and herbivore exclosures on aboveground biomass. However, I was not able to quantify any effects on belowground biomass. There are several studies that report changes in root biomass, changes in NPP as well as carbon sequestration potential as responses to climate change (Chapin and Ruess 2001, Matamala et al. 2003, Majdi and Ohrvik 2004). Moreover, there are also studies showing that herbivory affects root dynamics and belowground community composition (McKendrick et al. 1980, Ruess et al. 1998, Bardgett and Wardle 2003). Even though I did not measure clear differences in aboveground biomass and cover as a response to my manipulations, there might have been changes in the belowground biomass. However, an improvement to this study would have been to look at changes in the root system. A useful tool for such an investigation could have been a minirhizotron that is commonly used for non-destructive studies of the root zone (Johnson et al. 2001).

I do not know if the system I have been working with is nutrient limited or not, and I do not know how the nutrient availability in this system compares to similar experiments in other systems. Therefore, I cannot ignore the fact that the nutrient availability could have affected the lack of clear responses found here. Furthermore, the warming effect found in this system was lower than reported from other similar studies and could partly be the reason why no strong effects from the warming treatment were found. Elevated temperature has been shown to indirectly affect nutrient availability and
hence biomass production (Chapin et al. 1995). An improvement of this study would be to measure changes in nutrient availability of the soil and in plant tissues to unravel any effects of the treatments on the nutrient contents.

As mentioned above, there are several factors outside my control that could have influenced the results from this study. However, the most likely explanation for the lack of treatment effects found is due to the *E. occulta* outbreak in 2004 and 2005 that had considerable impact on aboveground biomass as seen in Chapter 2 and abundance as seen in Chapter 3. Such unpredictable events are impossible to foresee and control and has unquestionably affected the results and conclusions of this thesis. However, the important experience gained from this is the importance of long-term studies. If a project is allowed to run for several years, it is less likely that such unpredictable events will affect the result to such an extent that the original hypothesis cannot be tested.

**Overall implication**

The object of my thesis research has been to incorporate the effects of herbivory into experiments addressing the effects of climate change on plant community responses. I focused on functional plant groups to be able to investigate the potential effects herbivory could have on the predicted increase in shrub abundance that could further lead to biomass accumulation. The intention was to gain insight into factors controlling plant responses to climate change such that process models used to predict consequences of a changing climate could be further developed. It is my understanding that the results found during my thesis research was not as clear as anticipated but I still think they gave
enough evidence arguing for the incorporation of herbivores in studies of climate change and its effect on terrestrial ecosystems.
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Appendix A

Synchrony between caribou calving and plant phenology in depredated and non-depredated populations
Synchrony between caribou calving and plant phenology in depredated and non-depredated populations

Eric Post, Pernille Sporon Boving, Christian Pedersen, and Megan A. MacArthur

Abstract: Two main hypotheses have been proposed to explain reproductive synchrony exhibited by many species of large herbivores: the predation hypothesis and the seasonality hypothesis. Although examples supporting both hypotheses have been presented, no study has compared the intraseasonal progression of parturition and plant phenology in depredated and non-depredated populations of large herbivores. We monitored, on a daily or near-daily basis, the progression of the caribou (Rangifer tarandus) calving seasons in two populations: the Caribou River population in Alaska, U.S.A., where predators of caribou are present and the Kangerlussuaq-Sisimiut population in West Greenland where such predators have been absent for approximately 4000 years. Simultaneously, we quantified directly the phenological progression of caribou forage plants on spatially replicated plots in both study sites. Parturition was significantly more synchronous in the West Greenland (predator-free) population than in the Alaskan (depredated) population. Progression of the calving seasons in both populations was highly synchronized to the progression of forage plant phenology, and the slopes of these relationships were statistically indistinguishable, with 50% of births having occurred when approximately 60%–70% of forage plant species were emergent. These results document clear synchronization of the timing of parturition by caribou to plant phenology, regardless of predation pressure.

Résumé : Deux hypothèses principales, celle de la prédation et celle de la saisonnalité, ont été mises de l’avant pour expliquer le synchronisme de la reproduction chez plusieurs espèces de grands herbivores. Bien qu’il existe des exemples à l’appui de chacune des hypothèses, aucune étude ne compare la progression de la parturition au cours de la saison et la phénologie des plantes chez des populations de grands herbivores, soumis ou non à la prédation. Nous avons suivi, sur une base journalière ou presque, la progression des saisons de vêlage chez deux populations de caribous (Rangifer tarandus), la population de la rivière Caribou en Alaska, États-Unis, où il existe des prédateurs, et la population de Kangerlussuaq-Sisimiut au Groenland occidental où il n’y a pas de prédateurs depuis environ 4000 ans. En même temps, nous avons quantifié directement l’évolution phénologique des plantes de fourrage du caribou sur des parcelles dédiées dans l’espace aux deux sites. La mise bas est significativement plus synchronisée chez la population du Groenland occidental (en l’absence de prédateurs) que chez celle d’Alaska (avec prédateurs). La progression de la saison de vêlage chez les deux populations est fortement synchronisée avec l’évolution de la phénologie des plantes de fourrage : les pentes des deux relations ne peuvent se distinguer statistiquement et 50 % des naissances ont eu lieu lorsque environ 60 % – 70 % des espèces de plantes de fourrage ont poussé. Ces données montrent une synchronisation claire du moment de la mise bas chez le caribou avec la phénologie des plantes, indépendamment de la pression de prédation.

[Traduit par la Rédaction]

Introduction

Early studies of reproductive synchrony in colonially nesting birds led to the hypothesis that such behavior had evolved through reduced risk of predation to individual offspring (Darling 1938). This “predator swamping” hypothesis was subsequently forwarded to explain the highly synchronous season of births in wildebeest (Connochaetes taurinus) in the Ngorongoro Crater, Tanzania (Estes 1976). Wildebeest born into large groups at the peak of the highly synchronized calving season were argued to be less likely to suffer predation than those born early or late (Estes 1976; Estes and Estes 1979). In part, advantages of being born during the peak of the birth season derive from the greater numbers of potential prey per predator during the peak, but benefits may also be derived from being born into groups of vigilant mothers congregating during the peak of calving (Rutberg 1987; Boving and Post 1997).

Great interest in the phenomenon of reproductive synchrony arose from the seminal studies by Estes (1976) and Estes and Estes (1979), with similar patterns of highly synchronous parturition having been documented in many species, including bighorn sheep (Ovis canadensis) (Festa-Bianchet 1988), white-tailed deer (Odocoileus virginianus) (McGinnis and Downing 1977), Dall’s sheep (Ovis dalli)
(Rachlow and Bowyer 1991), roe deer (Capreolus capreolus) (Gaillard et al. 1993), mule deer (Odocoileus hemionus) (Bowyer 1991), and caribou or wild reindeer (Rangifer tarandus) (Skogland 1989; Post and Klein 1999). Rutberg (1987) argued, however, that it is unlikely for synchronous parturition to have evolved from asynchronous parturition solely in response to predation on newborns. Rather, predation on early- and late-born individuals might, according to Rutberg (1987), increase synchrony of parturition in populations in which seasonal birth peaks are timed to coincide with seasonal peaks in resource availability.

The "seasonality hypothesis" predicts that selection acting through intraannual variation in weather and resource availability results in optimization of the timing of parturition by individuals to coincide with the seasonal peak of food availability (Sadleir 1969; Sekulic 1978). According to this hypothesis, synchrony within populations may result from selection on the timing of parturition by individuals and the consequent variation in their own reproductive success and that of their offspring as influenced by seasonal variation in resource availability (Rutberg 1987; Ims 1990). Indeed, the considerable degree of geographic variation within some species in the average timing of parturition among populations suggests that environmental factors, which also vary geographically, influence timing of reproduction. In Norwegian wild reindeer, for example, timing of parturition may vary among populations by as much as 2–3 weeks, presumably because of combined influences of environmental conditions on forage availability and physical condition of reproductive females (Reimers et al. 1983). In further support of the seasonality hypothesis, Skogland (1989) reported that the peak of parturition varied by 34 days among six populations of wild reindeer in Norway, with southern populations calving earlier than northern populations, and that the populations calving later also calved over a shorter period, i.e., more synchronously.

Many recent studies of reproductive synchrony in large mammals that have taken into account seasonal variation in resource availability have urged reevaluation of the predator swamping hypothesis. Evidence from multiannual studies of depleted populations of Dall’s sheep (Rachlow and Bowyer 1991) and moose (Bowyer et al. 1998) in Alaska, U.S.A., and of mule deer (Bowyer 1991) in California, U.S.A., indicate that, despite predation on newborns, timing and synchrony of parturition in the focal populations appear to relate to long-term climatic patterns, a predictor of temporal variability in resource availability, and their influence on offspring survival. In northern environments, in particular, the short season of plant growth results in a rapid peak in, and deterioration of, digestibility and nutrient content of plant tissues associated with the progression of plant phenology (Klein 1990). Mammalian herbivores inhabiting such environments are therefore faced with a brief season of peak forage quality in which they must maximize nutrient intake to support the costs of lactation. As a consequence, large herbivores adapted to reproducing in the far north, such as caribou and wild reindeer, display considerable selectivity and sensitivity to patterns of plant phenology in their use of calving sites (Eastland et al. 1989; Fancy and Whitten 1991; Nellmann and Thomsen 1994; Vistnes and Nellmann 2001). Here, we expand upon earlier work (Post and Klein 1999) in which we documented synchronous parturition in two populations of caribou in Alaska that were depredated by brown bears (Ursus arctos) and wolves (Canis lupus). Progression of the calving seasons in these depredated populations appeared to track closely progression of plant phenology in the two study sites, although relationships between synchrony of calving and plant phenology were not explicitly investigated by Post and Klein (1999). Using similar data on caribou calving and plant phenology in West Greenland, where natural predators of caribou have been absent for approximately 4000 years (Meldgaard 1986), we compare the timing and synchrony of calving, and their relationships to plant phenology, between depredated and non-depredated populations.

Materials and methods

Study sites

We observed congregations of calving caribou in the Caribou River (CR) population in Alaska in 1992 and in the Kangerlussuaq-Sisimiut (KS) population in West Greenland in 1993 and 2002; data from 1993 are presented here only for comparison with those from 2002. The CR population inhabits subarctic, mesic, and wet-sedge meadows at the southwesterly terminus of the Alaska Peninsula (55°45’N, 161°30’W) (Post and Klein 1999). The area is treeless with a strongly maritime climate, and calving sites are dominated by short-stalk sedge (Carex nesophila), marsh cinquefoil (Potentilla palustris), and field horsetail (Equisetum arvense) (Post and Klein 1996). During the calving season (late May – early July) on the CR calving range, daily minimum and maximum ambient temperatures average 5.8 and 14.6 °C, respectively (Boving and Post 1997). The KS population occupies low arctic coastal and inland ranges in West Greenland, in the area bounded by the Davis Strait to the west, the Inland Ice to the east, Nordre Isortoq River to the north, and the Sukkertoppen Ice cap to the south (66°–67°N, 50°–52°W) (Boving and Post 1997). During and following the calving season, the KS population occupies the farthest eastern inland portion of its range, at the western edge of the Inland Ice (Thing 1984; Boving and Post 1997). This area is characterized by a dry, continental climate with mean daily minimum and maximum temperatures during the calving and postcalving seasons (late May – late June) of 1.6 and 12.5 °C, respectively (Boving and Post 1997). The KS calving range comprises east–west running ridges with xerophytic plant species dominating the warm, dry south-facing slopes, including the graminoids Kobresia myosuroides and Carex supine, interspersed with patches of blue–green willow (Salix glauca) and dwarf birch (Betula nana) (Thing 1984; Boving and Post 1997). North-facing slopes on the KS calving range experience greater snow accumulation during winter and later snowmelt and are dominated by dense Labrador tea (Ledum palustre) heath, while mesic lowlands are characterized by Poa pratensis greens (Thing 1984; Boving and Post 1997). Whereas on the calving range of the CR population, large predators are common and include wolves, brown bears, lynx (Lynx conaensis), golden eagles (Aquila chrysaetos), coyotes (Canis latrans), and wolverines (Gulo gulo) (Post 1995; Post and Klein 1999), large predators of caribou have been absent from West Greenland for approxi-
imately 4000 years and no predation, human or otherwise, occurs on the KS calving range (Meldgaard 1986; Klein et al. 1987).

**Collection of calving data**

In both study sites, we observed groups of pa...calving range (Meldgaard 1986; Klein et al. 1987).

**Collection of calving data**

In both study sites, we observed groups of pa...calving range (Meldgaard 1986; Klein et al. 1987).

**Analysis of calving data**

Following methods in Caughley and Caughley (1974), Caughley (1977), and Skogland (1989), we converted our data from proportion calves versus date to cumulative percent births versus date. We used probit analysis (Finney 1947) to estimate mean dates of parturition (Caughley and Caughley 1974) and nonlinear regression to estimate the length of each calving season (i.e., its synchrony) as the difference between the dates of 10% and 80% births. Further details of methods of collecting and analyzing parturition data are given in Post and Klein (1999).

**Collection and analysis of plant phenology data**

We established 10 (CR) and 20 (KS) 0.5-m² phenology plots in each of the study sites and monitored them at regular intervals of 3 days (CR study site) or daily (KS study site). Plots were divided among two (CR) and four (KS) meadows of comparable species composition, aspect, and elevation within each study site; these meadows were chosen so as to be representative of, and adjacent to, the areas where parturient caribou were observed. Phenology plots were placed randomly within each meadow and spaced a minimum of 50 m apart; meadows containing the plots were separated by approximately 1 km within each study site.

On each visit to the phenology plots, we recorded the names and numbers of plant species emergent in each plot. The final numbers of plant species emergent differed between study sites, with the CR site being more speciose (18 ± 1.3 (mean ± SE) species per plot) than the KS site (6.8 ± 0.4 species per plot) (one-way ANOVA comparing means: \( F_{1,28} = 112.4, P < 0.001 \)). Within neither the CR nor the KS study site, however, did the final number of species emergent differ among plots between the meadows sampled (CR: \( F_{1,8} = 1.3, P = 0.29 \); KS: \( F_{1,16} = 2.9, P = 0.07 \)). Because of differences in species number between CR and KS, to make our analyses comparable between ranges, we transformed daily numbers of species emergent to daily proportions of the final number of species emergent in each plot on each range. Using the final number of species emergent in each plot at the end of monitoring, we back-calculated the percentage of this final number in an emergent state on each day of observation prior to the last day of monitoring. To analyze the progression of plant phenology on each study site, we used nonlinear regression to estimate the date of 50% emergence in each study site, the number of days between 10% and 80% emergence (i.e., synchrony), and the rate of forage species emergence in each study site as the slope of the relationship between percent emergent and Julian date (calculated from day 1 = 1 January). Further details on methods of monitoring and analyzing plant phenology data are given in Post and Klein (1999).

**Comparisons of parturition between populations and analysis of parturition in relation to phenology**

We compared the synchrony of calving between populations using an approximation of the Student’s *t* test for regression coefficients (Zar 1984). In this approximation, 95% confidence intervals of regression coefficients, in this case the slopes of the regressions of percent births versus Julian date, are compared against each other and the regression coefficients deemed to be significantly different (*P* < 0.05) if the confidence intervals do not overlap (Bjørnstad et al. 1995). The same analysis was applied to test for differences in the synchrony of plant phenology between study sites and for differences in the relationships between the progression of calving and plant phenology in the two populations. All analyses were performed with SPSS version 10.0 (SPSS Inc. 1999).

**Results**

First calves were observed on 31 May (1992) and 5 June (1993 and 2002) in the CR and KS populations, respectively (Fig. 1a). Progression of the 1993 and 2002 calving seasons in the KS population was comparable, although overall calf production was higher in 2002 (Fig. 1a). The mean date of calving in the CR population was 5 June (Post and Klein 1999), and the number of days between 10% and 80% births was estimated at 10 days (nonlinear regression, \( R^2 = 0.95 \)) (Post and Klein 1999). In the KS population, the mean date of calving was 8 June (probit, \( R^2 = 0.90 \)), and the number of days between 10% and 80% births was 5 days (nonlinear regression, \( R^2 = 0.98 \)). Hence, calving started later but was more synchronous by 5 days in the KS population than in the CR population (Fig. 1b). As with the seasons of calving, emergence of forage plants commenced earlier in the CR study site than in the KS study site; 50% of the final number of species observed were emergent on 24 May in the CR site and on 7 June in the KS site (Fig. 2a). Similarly, plant phenology progressed more rapidly in the KS site, with 8 days passing between 10% and 80% emergence (nonlinear regression, \( R^2 = 0.98 \)) compared with 43 days in the CR site (nonlinear regression, \( R^2 = 0.98 \)) (Post and Klein 1999). Because this analysis may be sensitive to differences in the lengths of observation periods in the two study sites, we repeated these analyses using the subset of CR data that overlapped the KS data. With this subset, 50% of the final number of species observed were emergent in the CR site on 26 May, and the number of days between 10% and 80% emergence was 21; hence, forage plant emergence commenced later and was more synchro-

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Fig. 1. (a) Progression of the caribou (*Rangifer tarandus*) calving seasons expressed as proportion of calves (calves/(cows + calves)) versus Julian date in the Kangerlussaqq-Sisimiut population in West Greenland (gray circles, 1993; black circles, 2002) and in the Caribou River population in Alaska (open circles, 1992). (b) Progression of the caribou calving seasons in the same populations expressed as cumulative percent births versus Julian date (see Materials and methods). The fitted function is $Y = \frac{1}{1 + e^{-\omega X}}$ where $Y$ is percent births and $X$ is Julian date.

Fig. 2. (a) Progression of plant phenology in the Kangerlussaqq-Sisimiut (●) and Caribou River (○) study sites expressed as the cumulative percent forage-species emergent versus Julian date. Also see Materials and methods. (b) Relationships between the progression of calving (cumulative percent births) and progression of plant phenology (cumulative percent forage-species emergent) in the populations and study sites. The fitted functions are the same as those in Fig. 1. Also see Materials and methods.

nous in the KS site even when the data from the two sites were constrained to overlap.

The progression of the calving season in both populations was closely related to the progression of plant phenology in the respective study sites (CR: $R^2 = 0.93$; KS: $R^2 = 0.96$) (Fig. 2b). Despite a significant difference in synchrony of calving between these populations, the slopes of the relationships between the progression of calving and plant phenology in the two populations were statistically indistinguishable (Fig. 3).

Discussion

Although synchronous parturition certainly reduces the risk of predation to individual offspring born at or near the
Fig. 3. Comparison of the coefficients quantifying the relationships between progression of caribou calving and Julian date (solid lines) and between progression of caribou calving and plant phenology (broken lines) in the Kangerrussuaq-Sisimiut (KS) and Caribou River (CR) populations. Bars indicate 95% confidence intervals for the regression coefficients (see Materials and methods).

peak of the season of births (Kruuk 1972; Estes 1977), we concur with Rutberg (1987) that it seems unlikely that synchronous parturition has evolved from an asynchronous state solely in response to predation pressure. Rather, synchrony, a population-level characteristic, must evolve as a consequence of the timing of reproduction by individuals to coincide with a common environmental cue (Rutberg 1987). Our data, and those of other studies (Rachlow and Bowyer 1991; Bowyer et al. 1998), suggest that the degree of synchrony of parturition relates to patterns of plant phenology rather than predation risk.

In a circumpolar comparison of calving times among populations of caribou and wild reindeer that included some with natural predators and some without, Skogland (1989) reported a close agreement between the onset of parturition and the onset of the plant growing season. Skogland (1989) also noted that parturition was more synchronous in northern populations that commenced calving later than in southern populations that calved relatively early and speculated that this difference may have been related to more rapid progression of the plant growing season in northern sites. Our results corroborate those observations.

Calving started later in arctic West Greenland, the more northern of our study sites, and progressed more rapidly (i.e., was more synchronous) than in our subarctic Alaskan site. This difference apparently reflects disparities in the progression of plant phenology, and the tracking of this phenological progression by female caribou in both populations, because plant growth started later but proceeded more rapidly in Greenland than in Alaska (Fig. 2a). Moreover, despite differences in the progression of calving through time in these two populations (Figs. 1 and 3), the progression of calving in relation to plant phenology was similar in the two areas (Figs. 2b and 3). Previous studies of calving site selection by caribou in North America have also shown that pregnant females track geographic variation in patterns of snowmelt immediately preceding parturition as a means of maximizing intake of highly nutritious, newly emergent forage plants (e.g., Eastland et al. 1989). Such individual-based studies have also shown that selection of calving sites with newly emergent forage plants by preparturient female caribou influences subsequent survival of neonatal calves (Fancy and Whitten 1991).

Early studies of timing of parturition in caribou concluded that the onset of calving was fairly invariant within populations from year to year (Bergerud 1975; Holthe 1975). Our data from West Greenland in 1993 and 2002 display remarkable agreement among years in both the timing and synchrony of parturition in the KS population (Fig. 1a). Without comparable data on plant phenology from West Greenland in 1993, however, it is not possible to determine whether this agreement reflects similar climatic conditions and patterns of plant phenology in those 2 years (i.e., 1993 and 2002). Given the close tracking of plant phenology by caribou evident in this study and others (Skogland 1989; Post and Klein 1999; Van der Wal et al. 2000), it seems plausible that interannual variation in plant phenology, induced, for example, by climatic variability (Post and Stenseth 1999), has the potential to induce variation in the timing of parturition within populations of caribou. Such variation would, undoubtedly, be constrained to some extent by gestation length.

Notably, however, the onset of calving by caribou in Denali National Park, U.S.A., for example, varied by 8 days over a 9-year period (Adams and Dale 1998). This variation matched closely interannual fluctuations in climatic conditions influenced by the Arctic Oscillation (Post 2003). Whether this reflects an indirect influence of climate on timing of parturition acting through plant phenology or a direct influence of climate acting through condition of pregnant females (Adams and Dale 1998) is, however, difficult to determine. Nonetheless, implications of potential climate change for reproductive synchrony in caribou and for synchrony between caribou parturition and plant phenology should be investigated. Of particular interest to us is the question of whether climatic influences on plant phenology may play a role in geographically widespread synchrony in population dynamics of herbivores, exemplified, for instance, by the correlated population dynamics of caribou throughout West Greenland (Post and Forchhammer 2002) and by synchrony among populations of Greenlandic caribou and Russian wild reindeer separated by thousands of kilometres (Post 2004).²

Acknowledgments

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²E. Post. 2004. Spatial synchrony as an indicator of Pleistocene faunal response to large-scale environmental change in the Holocene. Submitted for publication.

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Appendix B

Phenological sequences reveal aggregate life history response to climatic warming
PHENOLOGICAL SEQUENCES REVEAL AGGREGATE LIFE HISTORY RESPONSE TO CLIMATIC WARMING

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Abstract. Climatic warming is associated with organisms breeding earlier in the season than is typical for their species. In some species, however, response to warming is more complex than a simple advance in the timing of all life history events preceding reproduction. Disparities in the extent to which different components of the reproductive phenology of organisms vary with climatic warming indicate that not all life history events are equally responsive to environmental variation. Here, we propose that our understanding of phenological response to climate change can be improved by considering entire sequences of events comprising the aggregate life histories of organisms preceding reproduction. We present results of a two-year warming experiment conducted on 33 individuals of three plant species inhabiting a low-arctic site. Analysis of phenological sequences of three key events for each species revealed how the aggregate life histories preceding reproduction responded to warming, and which individual events exerted the greatest influence on aggregate life history variation. For alpine chickweed (Cerastium alpinum), warming elicited a shortening of the duration of the emergence stage by 2.5 days on average, but the aggregate life history did not differ between warmed and ambient plots. For gray willow (Salix glauca), however, all phenological events monitored occurred earlier on warmed than on ambient plots, and warming reduced the aggregate life history of this species by 22 days on average. Similarly, in dwarf birch (Betula nana), warming advanced flower bud set, blooming, and fruit set and reduced the aggregate life history by 27 days on average. Our approach provides important insight into life history responses of many organisms to climate change and other forms of environmental variation. Such insight may be compromised by considering changes in individual phenological events in isolation.

Key words: arctic; Betula nana; Cerastium alpinum; climate change; global warming; phenology; Salix glauca.

INTRODUCTION

The annual timing of reproduction by organisms inhabiting seasonal environments is characterized by a sequence of phenological events that constitute the individual’s life history as it relates to offspring production. In temporally varying environments, natural selection has shaped the timing of these events and relationships among them through their influences on offspring production, survival, and lifetime reproductive success (Primack 1987, Stearns 1992). Any of the life history events preceding and including offspring production may be constrained by a variety of factors, including density-dependent resource limitation, competition, herbivory, and abiotic conditions (Cole 1954, Silvertown et al. 1997, Post et al. 2001). Because of the consequences for offspring production and survival of variation in the timing of reproduction, individuals can be expected to adjust their reproductive phenology according to variation in the magnitude and importance of such constraints from year to year. Phenological responses to climatic variation and change represent some of the clearest examples of this environmental tracking by reproducing individuals, as Miller-Rushing and Primack (2008) have documented for data on hundreds of plant taxa spanning over a century. Because evolution in one trait rarely, if ever, proceeds independently of other associated traits (Williams 1966, Maynard Smith 1993), individuals might experience constraints on the extent of phenotypic plasticity they display in response to density-dependent resource limitation or environmental variation and change. As a consequence, organisms may display greater adaptive responses in some components of their life history to environmental change, such as changes attributable to climate warming, than in others. For instance, many recent studies have documented shifts in timing of key life history events related to reproduction, such as timing of arrival at breeding grounds by migratory birds.
Forchhammer et al. (1998, 2002, Root et al. 2003), but comparatively minor shifts in other life history events such as egg-laying (Both and Visser 2001, 2005). Hence, to improve our understanding of the manner in which organisms respond to climate change, it is important to begin to think in terms of the individual’s aggregate life history response, rather than changes in single events in isolation. For this more comprehensive approach, it is beneficial to consider the sequence of phenological events constituting the life history of an organism leading up to and including reproduction, and the timing of successive events in relation to one another. Such a perspective enables us to understand better organismal response to rapid environmental change as well as its potential demographic and fitness consequences (sensu Lewontin 1965).

We advocate an aggregate life history approach to understanding organism response to climate change because the timing of individual life history events may be independently advanced, delayed, or unchanged by warming. As an example, consider a series of life history events leading up to reproduction, which, in plants, might comprise emergence, flower set (the first appearance of a flower bud in the current growing season), and blooming. Any number of events comprising an aggregate life history may be considered, but the simplest case, and the one we will pursue for illustrative purposes, is a sequence of three events. Climatic warming could influence this phenological sequence in several ways, advancing or delaying the timing of all of the events together (Fig. 1a), or advancing or delaying individual events while leaving others unchanged (Fig. 1b–d). Warming might also influence changes in the timing of individual events in the sequence to different extents. Moreover, the duration of each life history event may increase, decrease, or remain constant with climatic warming (y-axis shifts in Fig. 1). Taking changes in both into account will give a more informative picture of where the greatest or least flexibility in life history response to warming occurs in the life cycle of organisms. Using this approach, we can observe sequences of life history events related to reproduction, and ask whether the aggregate life history of an organism has responded to warming.

Because natural selection favors precocity (Cole 1954, Williams 1966), we should expect alleviation of environmental constraints on early development to promote accelerated progression to reproduction. Indeed, according to Williams (1966), rapid development should always be favored by natural selection because the more quickly an organism matures to a given critical size for successful reproduction the less likely it is to perish before reproducing (see also Primack 1987). As well, if adult survivorship sets the limit on reproductive success, then investment in early reproduction should be favored (Sibly 1997). Similarly, we should expect the aggregate life history of an organism (the period encompassing development to reproduction) not only to shift toward earlier reproduction, but also to be minimized if existing constraints are lifted.
Organisms may also experience tradeoffs between adjustment of one life history event to climatic change and the timing of the subsequent life history event preceding reproduction. Such tradeoffs may determine the manner in which both the timing and duration of successive life history events respond to climate change. In migratory birds, for example, changes in the timing of arrival at breeding sites in response to climatic warming may alter the length of the interval between the timing of arrival and the timing of egg-laying (Both and Visser 2005). Similarly, changes in early stages of plant phenology in response to climatic warming may alter the interval between emergence and flowering or between flowering and fruit production or seed dispersal. As a consequence of variation in both the timing and duration of successive life history events, the organism’s aggregate life history may change. Alternatively, if only the timing but not the duration of life history events responds to climatic warming, the organism’s aggregate life history may remain unaltered despite shifting temporally (sensu Fig. 1a).

By recording the timing and duration of successive life history events related to, for example, reproduction, and their changes over time in response to climatic warming, or by comparing their differences between warmed and control plots in an experimental setting, we can quantify the aggregate life history response to climatic warming. An advantage of this approach lies in its ability to inform us of whether an organism’s investment of time in development preceding and including reproduction may be altered by climatic change. Furthermore, it allows us to determine whether the so-called aggregate life history of an organism remains constant despite shifts in response to warming, whether it changes but does not shift in response to warming, or whether it changes due to a shift in the timing of one or more life history events. Such information has the potential to furnish vital insights into species’ differences in their life history responses (or lack thereof) to climate change that may have consequences for reproductive success and population behavior.

**Methods**

To test the hypothesis that an organism’s aggregate life history may change in response to climatic warming, we conducted a controlled warming experiment in a low-arctic plant community near Kangerlussuaq, West Greenland (67°6’48” N, 50°20’ W). The area is characterized by non-carbonate mountain complexes dominated by low-shrub tundra (Circum-Arctic Vegetation Map Team 2003; see also Post et al. 2003). Beginning in June 2002, as part of a larger experiment designed to quantify the influences of herbivory and warming on primary productivity and plant community dynamics, we erected six 800-m² exclosures in a remote site utilized by caribou (Rangifer tarandus) and muskoxen (Ovibos moschatus). The exclosures were circular, and constructed of steel t-posts and woven-wire fence measuring 120 cm high. From 14–15 May 2003, we erected four open-topped passive warming chambers (OTCs) inside each of three of the exclosures. The OTCs were constructed of UV-neutral glazing material in 1 mm thickness (Sun-Lite HP, Solar Components Corporation, Manchester, New Hampshire, USA) according to the protocol of the International Tundra Experiment (ITEX); they were cone-shaped, with a 60° side angle, and measured approximately 150 cm in diameter at the base and stood approximately 40 cm high (Marion et al. 1997). The OTCs are designed to elevate passively near-surface temperatures while minimizing unwanted side effects, such as interfering with gas exchange and evaporation and precipitation (Molau and Møggaard 1996). In addition to elevating temperature, they may, however, alter the relative humidity at the soil surface within the chamber, in addition to reducing surface wind speed (Molau and Møggaard 1996). However, the suitability of OTCs as an analogue of climatic warming has been experimentally validated (Hollister and WEBER 2000), and so we assume that elevated temperature was the predominantly important abiotic alteration on our plots.

Upon erection of the OTCs, we also demarcated an adjacent control plot for each treatment plot. Within each exclosure, control and treatment plots were separated by a minimum of 3 m. We placed surface thermometers and hygrometers inside treatment and control plots. Although there was a thin cover (<1 cm) of patchy snow on the ground at the time the OTCs were erected on 14 May 2003, we recorded all visible species present and their phenological states at that time. We revisited the field site on 3 June 2003, when all snow was melted, and remained on-site until termination of the experiment on 19 June 2003, when all OTCs were taken down. The experiment resumed on 18 May 2004, when we revisited the field site and replaced all OTCs, thermometers, and hygrometers. As in 2003, there was a trace of snow on the ground upon reinitiation of the experiment in 2004, and we recorded all species present and their phenological states at that time. Observations in 2004 recommenced on 4 June and terminated on 20 June, following the procedures used in 2003. We visited all plots on a daily or near-daily basis, and recorded the phenological stages of all species present in each plot, as well as surface temperature and humidity. Average daily temperature on our plots was quantified as the mean of the minimum and maximum temperatures recorded on each plot within a 24-hour period. For each year, we compared mean minimum daily temperature, mean maximum daily temperature, and mean average daily temperature between treatment and control plots using an ANOVA with “treatment” as a fixed factor and “date” as a random factor.

To the best of our knowledge, all plots contained a single individual of the clonal gray willow (Salix glauca; Salicaceae) and/or a single individual of dwarf birch (Betula nana; Betulaceae), as well as one to several
individuals of many forb species (see Post et al. 2003). We recognize, however, that what we identified as individuals may be more accurately described as ramets rather than as genets. Therefore, we restricted our analyses to data on a single individual of each species for each plot. We were able to track phenological progression through at least three stages of development in individual willow, birch, and a single forb species, alpine chickweed (Cerastium alpinum). In both years of the experiment, however, chickweed emerged during our absence between erection of OTCs and recommencement of our observations in early June.

To quantify the aggregate life history of an organism, we may define it as a function of both the timing of key life history events related to reproduction and their duration. As well, as a result of selection on an organism’s fecundity schedule (Lewontin 1965), we can expect the duration of any particular life history event, or the total duration of all observed life history events, to be related to the timing of onset for any sequence of life history events. Hence, the aggregate life history of an organism may be quantified as the area of the polygon delineated in parameter space by the points representing, in our case, the duration of each phenological event plotted against the dates on which those events occurred, as in Fig. 1. It is the area of such a polygon that we will denote as the organism’s aggregate life history.

To derive polygons on which to base our analyses of changes in the aggregate life histories of the study organisms in response to warming, we plotted, for each individual, the date of each observed phenological event on the $x$-axis in Fig. 1, and the duration of each event on the $y$-axis. Because our observations concluded with the third phenological event observed for each species, its duration was recorded as zero; however, its actual duration could also have been included in the estimation of the aggregate life history if it had been observed. We then quantified, for each individual, the area of the polygon anchored by these points and extending downward to the $x$-axis, thereby estimating the aggregate life history (ALH) of the organism preceding production of offspring. Polygon areas were calculated by separating each polygon into a trapezoid and a triangle, calculating their respective areas, and summing them. In other applications of this approach, the method for quantifying the area of the polygon representing an organism’s ALH would, of course, vary according to the shape of the polygon. For each species, we then compared the mean ALH on warmed vs. ambient plots using a univariate ANOVA. It is important to stress that, in this approach, we are not analyzing the relationship between the $y$-axis variable (duration) and the $x$-axis variable (date), because, of course, the duration of any phenological interval is dependent upon the dates of the events defining the beginning and end of the interval. Rather, this approach is used as a means of depicting and quantifying the ALH as a two-dimensional polygon defined by the timing and duration of a series of phenological events (sensu Fig. 1).

For each species, we used the earliest observed phenological events as the start of the ALH, and the latest observed events as the end of the ALH preceding offspring production. These varied slightly among the three species observed because of differences in their phenological progression. The events comprising the ALH preceding offspring production in the three species were as follows: for alpine chickweed, emergence of vegetation, flower set (the date of first appearance of flower buds), and first bloom; for gray willow, opening of leaf buds, flower set (the date on which the catkin reached $\sim 1$ mm in size), and first bloom; and for dwarf birch, flower set (the date on which the catkin reached $\sim 1$ mm in size), bloom, and fruit set (the date on which more half of the visible stigmas had withered and initial swelling of the ovary was apparent). Because the phenological events observed differed among species, direct comparisons among them of their responses to warming are not possible. Nonetheless, the same events were observed within species on treatment and control plots; facilitating species-specific analyses of ALH response to warming.

 Aggregate life histories were estimated for three and two chickweed individuals on treatment and control plots, respectively, in 2003, and three and three chickweed individuals on treatment and control plots, respectively, in 2004; five and five gray willow individuals on treatment and control plots, respectively, in 2003; and seven and five dwarf birch individuals on treatment and control plots, respectively, in 2003. Chickweeds observed in 2003 and 2004 were not the same individuals, and data were pooled between years. All individuals were observed on different plots. Because we observed only 11 individual chickweed plants, 10 individual willows, and 12 individual dwarf birch, we urge caution in the interpretation of our results, but have no reason to believe that the plants we observed were not representative of the larger populations.

**Results**

Mean daily average temperature was significantly higher on treatment than on control plots by 2.02°C in 2003, and 1.4°C in 2004 (both $P$ values = 0.001; Table 1). In 2003, the mean daily minimum temperature recorded on our plots was 0.63°C warmer on treatment than on control plots ($P = 0.002$), whereas, in 2004, mean daily minimum temperature did not differ significantly between treatment and control plots ($P = 0.25$). In 2003, mean daily maximum temperature was higher on treatment than on control plots by 3.9°C, whereas, in 2004, this difference was only 2.6°C (both $P$ values < 0.001). We are unable to explain the differences in treatment means between years as being due to different ambient environmental conditions. Daily temperatures recorded by the Danish Meteorological Institute at Kangerlussuaq Airport were higher in 2004 than in 2003.
TABLE 1. Temperatures (mean ± SE) on treatment vs. control plots in the study site, and ambient environmental temperatures during the study as measured at Kangerlussuaq International Airport, Greenland, ~20 km from the study site.

<table>
<thead>
<tr>
<th>Conditions</th>
<th>Average (°C)</th>
<th>Minimum (°C)</th>
<th>Maximum (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2003</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Treatment</td>
<td>10.8 ± 0.17</td>
<td>-2.2 ± 0.16</td>
<td>23.1 ± 0.20</td>
</tr>
<tr>
<td>Control</td>
<td>8.78 ± 0.18</td>
<td>-2.88 ± 0.16</td>
<td>19.28 ± 0.20</td>
</tr>
<tr>
<td>Ambient</td>
<td>8.54 ± 0.11</td>
<td>2.63 ± 0.09</td>
<td>14.5 ± 0.13</td>
</tr>
<tr>
<td>2004</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Treatment</td>
<td>12.0 ± 0.16</td>
<td>3.18 ± 0.13</td>
<td>20.8 ± 0.26</td>
</tr>
<tr>
<td>Control</td>
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<td>18.29 ± 0.26</td>
</tr>
<tr>
<td>Ambient</td>
<td>9.95 ± 0.06</td>
<td>4.62 ± 0.06</td>
<td>15.3 ± 0.09</td>
</tr>
</tbody>
</table>

Notes: Within columns, and within years, lowercase letters denote comparisons between means on treatment and control plots. Different letters denote means that differ significantly (P < 0.05).

(Table 1); however, this weather station lies approximately 20 km from our study site at the end of a fjord, and may not represent weather conditions at our site, which is adjacent to the Inland Ice. One possible explanation for the differences between years on our plots is that average daily wind speed was higher in 2004 than in 2003, because the main mechanism of warming induced by OTCs is wind blockage. Average daily relative humidity was ~9% lower on treatment than on control plots in both years, but this difference was not significant in either year (both P values > 0.05).

For chickweed, the mean timing of emergence between treatment and control plots did not differ, presumably because individuals on both plots were emergent upon the first observation in June of each year. However, the duration of emergence (i.e., the number of days from the occurrence of emergence to the date of flower set) was shorter on warmed than on control plots because flower set occurred on average 2.5 days earlier on warmed than on control plots (F1,9 = 11.1, P < 0.01; Fig. 2a). The duration of flower bud set did not differ between warmed and control plots (F1,9 = 0.95). Blooming in chickweed did not occur significantly earlier on warmed than on control plots (F1,9 = 1.55, P = 0.25). Despite alteration of the duration of emergence and the timing of flower set by the warming treatment, the aggregate life history of chickweed was not significantly shorter on warmed (25.2 ± 9.0 days) than on control (37.4 ± 9.9 days) plots (F1,9 = 0.78, P = 0.40).

Hence, this species, while displaying a slight developmental shift suggestive of an advance in response to warming of phenological events preceding offspring production (Fig. 2a), similar to a rigid translation of the fecundity schedule (Fig. 1a), did not adjust its aggregate life history in response to warming. These results, may, however, have been influenced by the lack of observations of actual dates of emergence.

In gray willow, leaf opening occurred 3 days earlier on warmed than on control plots (F1,8 = 13.2, P < 0.01; Fig. 2b). As well, the duration of the leaf opening phase was shorter by 4 days on warmed than on control plots (F1,8 = 6.95, P = 0.03) because flower bud set occurred earlier by 7 days on warmed than on control plots (F1,8 = 10.6, P = 0.01; Fig. 2b). However, the duration of flower bud set did not differ between warmed and control plots (F1,8 = 0.18, P = 0.68). Nonetheless, blooming occurred 7 days earlier on warmed than on control plots (F1,8 = 10.1, P = 0.01). As a result, the aggregate life history of gray willow was not only advanced by warming, it was

![Fig. 2. Mean aggregate life history responses of multiple individuals of (a) alpine chickweed (Cerastium alpinum), (b) gray willow (Salix glauca), and (c) dwarf birch (Betula nana) to experimental warming in Kangerlussuaq, West Greenland, during the growing seasons in 2003 and 2004. For each species, each point represents the mean (±SE) timing of a phenological event in the sequence comprising the total observed life history preceding seed production, against which is plotted the mean (±SE) duration of that event. In chronological order from left to right, these were, for chickweed, emergence, flower set, blooming; for willow, leaf opening, flower set, blooming; for birch, flower set, blooming, fruit set. Dashed lines delineate boundaries of the polygons anchored by the means plotted in each panel; these polygons represent the mean aggregate life history of each species on warmed and ambient (control) plots.](image-url)
also reduced significantly on warmed (10.3 ± 6.6 days) compared to control (32.3 ± 6.7 days) plots ($F_{1,8} = 5.47$, $P = 0.048$; Fig. 2b).

Flower bud set in dwarf birch occurred on average 1.6 days earlier on warmed than on control plots ($F_{1,10} = 6.18$, $P = 0.03$; Fig. 2c). The duration of flower bud set in dwarf birch was on average 2 days shorter on warmed than on control plots, though this difference was only marginally significant ($F_{1,10} = 6.18$, $P = 0.052$). Blooming, in contrast, occurred nearly 4 days earlier ($F_{1,10} = 85.1$, $P < 0.001$) and was shorter in duration by 2 days on warmed than on control plots ($F_{1,10} = 14.6$, $P = 0.003$). Fruit set in dwarf birch occurred on average nearly 6 days earlier on warmed than on control plots ($F_{1,10} = 367.5$, $P < 0.001$). Hence, dwarf birch responded to warming by advancing all life history events monitored, as well as reducing the intervals between them. As a result, the aggregate life history of dwarf birch on warmed plots (20.4 ± 3.6 days) was less than half of that on control plots (47.0 ± 4.2 days; $F_{1,10} = 22.9$, $P = 0.001$).

**DISCUSSION**

Differences in responses of the individual life history events within each species studied here to experimental warming might be indicative of the extent to which phenological phases differ in their plasticity with respect to environmental constraints. In a long-term experiment conducted in a subalpine meadow, Price and Waser (1998) observed that warming advanced timing of reproduction in four of 10 forb species studied, whereas warming altered the duration of reproduction in only one of those species. Our study emphasizes that, when considered in sequence, differences in the timing and duration of individual events reveal which events are key to variation in the aggregate life history response to climatic warming. For example, even though the duration of emergence in chickweed was reduced by warming (Fig. 2a), its aggregate life history remained unchanged by warming (with the caveat that emergence was not observed and is assumed to have shifted in parallel to timing of flower set). In gray willow, by contrast, the reduction in the aggregate life history of individuals on warmed plots compared to ambient plots apparently related mainly to a reduction in the length of time spent in the leaf opening stage (Fig. 2b). In dwarf birch, however, the reduction of the aggregate life history by warming appeared to be driven mainly by a reduction in the length of time spent in the blooming stage (Fig. 2c). Similar analyses of sequential life history events in other species, or in similar species in different environments, may reveal not only the extent to which the total life histories of other organisms respond to climatic warming, but also which individual phenological events are key to such changes.

Each of the examples in this study reveals a shortening of at least one component of the aggregate life history in response to warming. In far northern or alpine environments, where early warming may also be followed by frost events, hastening development through at least one stage of the phenological sequence in response to warming may also reflect a strategy aimed at minimizing risk of floral tissue loss in highly variable environments. Inouye (2008), for instance, documented that earlier snowmelt in an alpine environment led to earlier blooming by many forb species, but also greater flower bud loss to frost kill. In some species, such as aspen sunflower (Helianthella quinquenervis), annual bud loss can be as high as 100%. Under such intense selection in highly seasonal environments where freezing occurs during the growing season, acceleration through the blooming stage should be favored, as we documented in dwarf birch (Fig. 2c).

The life history responses to warming observed in this study may have fitness consequences for reproducing individuals that extend beyond phenological dynamics. A meta-analysis of long-term warming manipulations across the Arctic and sub-Arctic revealed, for instance, increases in reproductive success of forbs but reductions in reproductive success of deciduous shrubs, including B. nana and Salix spp., following warming with OTCs (Arft et al. 1999). Moreover, experimental manipulation of germination timing in Arabidopsis thaliana influenced multiple life history characters related to reproduction, including rosette size, numbers of leaves, timing of flowering, and over winter mortality (Donohue 2003). Early-germinating individuals had more leaves and were larger at the time of reproduction than later germinants, whereas the interval between bolting and flowering was not related to germination timing, resulting in earlier flowering in early germinants (Donohue 2003). As well, Inouye (2008) reported an interesting threshold effect in the relationship between flowering date and date of snowmelt that has implications for demography and reproductive success. In years with late snowmelt, there is a positive relation between flowering date (which is determined by snow melt) and numbers of flowers produced; however, this relationship is absent in years with early snowmelt, suggesting greater loss of flower heads to frost by plants that bloom later in such years (Donohue 2000, 2008).

Whether the abbreviated aggregate life histories we observed in relation to experimental warming will be characteristic of the response of arctic plants to climate change is difficult to foresee. The main limitation of our study was the low numbers of individuals within each species studied. Furthermore, our experiment lasted only two years. Longer-term warming experiments have revealed disparate results. In one four-year manipulation in a subalpine meadow in Norway, the duration of flowering in Cerastium spp. was unaltered by warming (Totland and Schulte-Herbruggen 2003). As well, in other arctic sites, phenological responses of B. nana to experimental warming appear to attenuate after the first two years of warming (Arft et al. 1999), although productivity responses persist (Wahren et al. 2005).
Further insights into the manner in which the aggregate life history may vary with differential responses of individual phenological events to climatic warming may be gained by examining recent research on migratory birds. Many species of migratory birds are arriving earlier on breeding grounds, and initiating egg-laying earlier, in response to spring warming (Forchhammer et al. 1998, 2002, Walther et al. 2002, Root et al. 2003). Throughout Europe, for instance, flycatchers (Ficedula sp.) have advanced their laying dates in response to increases in local temperatures, and the magnitude of the advance in laying date scales with the increase in local temperatures (Both et al. 2004). Similar continental-scale analyses of breeding phenology of North American species have revealed that Tree Swallows (Tachycineta bicolor) advanced their laying date by nine days over a 32-year period in response to increasing temperatures (Dunn and Winkler 1999), though clutch sizes did not vary with advances in laying date (Winkler et al. 2002). The shift toward earlier egg-laying has not, however, matched the shift in arrival on breeding grounds in at least one population, suggesting a translation of Lewontin’s (1965) fecundity schedule similar to that depicted in Fig. 1b. Flycatchers in the Netherlands, despite having advanced their laying dates, have not advanced their arrival dates at breeding grounds (Both and Visser 2001). This disparity in the response of different phenological events to warming suggests that the interval between them has declined, as has, perhaps the aggregate life history of Flycatchers related to nesting. Moreover, in years when Pied Flycatchers (F. hypoleuca) nest late relative to the peak in abundance of their prime food source, caterpillars, they reduce the interval between laying and hatching by initiating incubation earlier (Both and Visser 2005).

Such an adjustment in the second event in the phenological sequence related to reproduction in flycatchers, and a consequent reduction in the interval between successive events in that sequence, is reminiscent of the response to warming shown by willows in this study (Fig. 2b), which led to a reduction in the individuals’ aggregate life histories.

Continental-scale analyses of plant phenology also indicate disparities in the response of distinct life history events to climatic warming. Across Europe, for instance, early phenological events such as leaf unfolding have advanced by several days while late events such as leaf senescence have been delayed by several days (Menzel and Fabian 1999). At individual sites in Germany, there is evidence that advances in early phenological events are mirrored by changes in later events, though early events appear to have advanced to a greater degree than later events (Menzel et al. 2001), again suggestive of the form of change shown in Fig. 1b. Similarly, in an analysis of plant phenology spanning 97 populations in Norway, four of 11 species showed an increase in the duration of flowering, in addition to flowering earlier, in response to climatic warming (Post and Stenseth 1999).

Although these studies relate patterns observed at the landscape scale, rather than changes in the life histories of individuals, they are nonetheless indicative of the flexibility and inequity displayed by the response of different life history events to warming.

**Conclusion**

Phenological responses of plants and animals to experimental warming or observed climate change have typically been studied in isolation. By considering changes in the sequence of key phenological events that comprise the life histories of organisms, and interactions among them, we may gain a better understanding of the implications of climate change for life history variation and its demographic consequences than is possible by considering only changes in isolated events. The approach we have developed and applied here is a first step in this direction. Although we were able to monitor responses to warming of just a few individuals and species over two growing seasons, the consequences of phenological shifts for aggregate life histories were clear. We urge the application of this approach, or at least the incorporation of this aggregate perspective, in future studies.

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**Literature Cited**


Appendix C

Warming, plant phenology and the spatial dimension of trophic mismatch for large herbivores
Temporal advancement of resource availability by warming in seasonal environments can reduce reproductive success of vertebrates if their own reproductive phenology does not also advance with warming. Indirect evidence from large-scale analyses suggests, however, that migratory vertebrates might compensate for this by tracking phenological variation across landscapes. Results from our two-year warming experiment combined with seven years of observations of plant phenology and offspring production by caribou (*Rangifer tarandus*) in Greenland, however, contradict evidence from large-scale analyses. At spatial scales relevant to the foraging horizon of individual herbivores, spatial variability in plant phenology was reduced—not increased—by both experimental and observed warming. Concurrently, offspring production by female caribou declined with reductions in spatial variability in plant phenology. By highlighting the spatial dimension of trophic mismatch, these results reveal heretofore unexpected adverse consequences of climatic warming for herbivore population ecology.

Keywords: caribou; climate change; global warming; life history; plant phenology; population dynamics

1. INTRODUCTION

The heterogeneous distribution of resources in time and space has long been recognized as an important factor in population dynamics (Roughgarden 1974; Levin 1976). Indeed, in many systems, successful survival and reproduction by individuals depends upon the strategies employed in coping with temporal and spatial variability in resources (Giesel 1976; Wiens 1976). In seasonal northern environments, migration confers a selective advantage related to maximization and prolongation of the intake of high-quality forage during the season of highest reproductive costs (Klein 1970; White 1983; Lundberg 1988; Kingsolver et al. 2002). Influences of climatic warming on the dynamics of resource availability in time and space may, therefore, pose important consequences for the reproductive success of migratory animals.

Primarily for this reason, the role of temporal shifts in resource availability associated with warming has received considerable attention in development of the trophic mismatch concept (Visser et al. 1998) and documentation of its consequences for reproductive success in migratory birds. For instance, flycatchers (*Ficedula sp.*) in Europe appear to time their migration to breeding areas on the basis of light cues, whereas the timing of emergence of their forage resources is cued by local temperatures on the breeding grounds; as springtime temperatures increase, resources emerge earlier and there is a consequent gap between resource availability and resource demand by breeding pairs (Both et al. 2004; Visser et al. 2004; Visser & Both 2005).

On the contrary, far less attention has been devoted to the spatial dimension of temporal shifts in resource availability associated with climatic warming. For large-bodied migratory herbivores, this dimension may be particularly important (Mårell et al. 2002). In the most seasonal environments, large herbivores display a migratory strategy that, whether it evolved in response to predation pressure or not, enables them to follow the spatial front of emerging vegetation, prolonging the period of intake of the most digestible, highly nutritious plants (Klein 1970; Skogland 1989; Gunn & Skogland 1997; Ferguson & Elkie 2004). Red deer (*Cervus elaphus*), for example, migrate upslope along elevational gradients in spring as green-up advances (Albon & Langvatn 1992), and the timing and synchrony of their offspring production is closely cued to the onset and progression of the plant growing season (Loo et al. 2005). Caribou (*Rangifer tarandus*) also time their spring migrations to coincide with the emergence of nutritious, highly digestible plant tissues to support the high costs of lactation (Klein 1970; White 1983). Indeed, among populations, variation in timing of parturition by caribou corresponds with variation in the onset of plant growth on the calving grounds of those populations (Skogland 1989; Post et al. 2003). In the context of climate change, however, a crucial consideration is whether advances in phenology at lower trophic levels related to climatic warming will be matched by the species at higher trophic levels that depend on them for successful reproduction (Both & Visser 2005). At least one multi-annual study of a large herbivore...
population suggests that this may not be the case, as advancement of the onset of the plant growing season in West Greenland has not been matched by advancement of the onset of calving by caribou there, and consequently productivity in that caribou population has declined (Post & Forchhammer 2008).

The manner in which spatial heterogeneity in the timing of plant growth responds to climatic warming is likely, therefore, to be of importance to the reproductive success of herbivores in highly seasonal environments. Considerable effort has been devoted to analysing large-scale spatial patterns of plant phenology in relation to climatic variation and change. Continental-scale analyses of normalized difference vegetation index (NDVI) data spanning thousands of kilometres from north temperate China, for instance, have revealed that large-scale spatial patterns of the onset of plant growth correlate with spatial patterns of variation in spring warming (Chen et al. 2005). Similarly, landscape-scale analyses of data on first flowering dates of plants spanning hundreds of kilometres in Norway revealed earlier onset of flowering following warm winters and springs (Post & Stenseth 1999), and an increase in spatial variability at the same scale following warming (Post & Stenseth 1999; Post 2003). As well, landscape-scale analyses of NDVI data from Norway have shown an increase in spatial variability in the timing of the onset of plant growth following warm winters, presumably owing to accentuation of terrain–snowmelt interactions (Pettorelli et al. 2005a,b).

Such analyses suggest that warming increases the spatial variability of timing of phenological events in plants. However, the results described above were based on analyses of coarsely resolved, landscape-scale, time-series data. In contrast to the patterns observed at the scale of the landscape, warming might not, at the local scale (i.e. metres to hundreds of metres), increase spatial heterogeneity of phenological events, but instead could reduce it. This might be the case for at least two reasons. First, at such small spatial scales there is less pronounced variation in aspect, slope and elevation, all of which interact with temperature and precipitation at the landscape scale; second, alleviation of temperature constraints on the timing of life-history events by warming at the local scale might be expected to hasten phenological development among individuals co-occurring at that scale (Post et al. 2008). Thus, our objectives were to conduct a plot-scale warming experiment designed to determine whether the relationships between warming and spatial dynamics of plant phenology observed at scales of hundreds to thousands of kilometres were mirrored by patterns at the much smaller scale of metres to hundreds of metres, at which individual herbivores forage; to determine whether the results of our experiment accorded with multi-annual observational data at the same spatial scales; and to examine the consequences of relationships between observed warming and spatial dynamics of plant phenology for herbivore productivity.

2. MATERIAL AND METHODS

(a) Plant phenological response to experimental warming

We conducted our warming experiment in a low-arctic plant community near Kangerlussuaq, West Greenland (67°6.8′ N, 50°20′ W). This area comprises non-carbonate mountain complexes with the dominant vegetation type characterized as low-shrub tundra (CAVM Team 2003; see also Post et al. 2003), and is inhabited by caribou and muskoxen (Ovibos moschatus). In June 2002, we erected six 800 m² enclosures as part of a large-scale experiment designed to quantify the influences of herbivory and warming on primary productivity and plant community dynamics. The enclosures were circular and constructed of steel T-posts and woven wire fence measuring 120 cm high. Our warming experiment was conducted inside three of these enclosures. The mean (±1 s.e.) distance among our enclosures was 621.4 ± 151 m.

In May 2003, before the onset of plant growth, we erected four open-topped passive warming chambers (OTCs) inside each of three of the enclosures. The OTCs were constructed of UV-neutral glazing material that was 0.10 cm thick (Sun-Lite HP, Solar Components Corporation). We followed the protocol of the International Tundra Experiment in designing our OTCs, which were cone shaped, with a 60° side angle, approximately 150 cm in diameter at the base, 1.77 m² in area and approximately 40 cm high (Marion et al. 1997). The OTCs elevate near-surface temperatures but minimize unwanted side effects, such as interfering with gas exchange and evaporation and precipitation (Marion et al. 1997). Use of the term ‘treatment plot’ hereafter refers to experimental plots warmed with OTCs. Adjacent to each treatment plot, but at least 3 m away, we also demarcated a control plot of the same dimensions; plots of both types were equipped with a surface thermometer and hygrometer. All plots were positioned at a minimum of 2 m away from the inside of enclosure fencing to minimize edge effects and at least 3 m away from the nearest treatment or control plot.

At the time of establishment of our treatment and control plots, we recorded all plant species present and their phenological states. We revisited the site on 3 June 2003 and remained onsite until termination of the experiment on 19 June 2003. All plots were visited on a daily or bi-daily basis, when we recorded the phenological stages of all species present in each plot, as well as surface temperature and humidity. On 19 June 2003 all OTCs were taken down. We revisited the site 18 May 2004, when all OTCs, thermometers and hygrometers were replaced on the original plots. At the time of re-establishment of the warming experiment in 2004, we recorded all species present and their phenological states. In 2004, observations recommenced on 4 June and terminated on 20 June, following the exact procedures used in 2003. In 2003, temperature and humidity were recorded on all plots for a total of 11 days; in 2004 they were monitored for 14 days. Mean daily temperature was calculated as the average of the daily maximum and minimum temperatures, and was compared between treatment and control plots using ANOVA with treatment effect as a fixed factor, and day of year as a continuous random covariate.

(b) Timing of phenological events and intervals between them

As a precursor to investigating influences of warming on spatial dynamics of plant phenology, first it was necessary to quantify influences of warming on timing of phenological events. We compared the timing of phenological events, including emergence in forbs and leaf opening (LO) in deciduous shrubs, flower set (FS), blooming (B) and fruit set (FR), within each species monitored, between treatment and
control plots. We used a univariate ANOVA with treatment effect and ‘year’ as fixed factors, and the June date of first observation of each event for each species observed on each plot as the response; the ANOVA included ‘site’ and ‘plot’ as random covariates, with plot nested within site.

We investigated the influence of warming on the progression of phenology by comparing the mean interval between successive phenological events on treatment and control plots. We calculated the number of days between first observation of successive events for each species within each plot and compared means for each phenological interval within each species among treatment and control plots in a univariate ANOVA. In contrast to our previous analysis (Post et al. 2008), we did not attempt to track phenology in individual plants. Although we did in fact record successive events observed on each plot for each species, we used the intervals between the first date for each event within species among all plots in this analysis. As stated, our intent was to compare the spatial heterogeneity of plant phenology between treatment and control plots. Because previous results from this experiment revealed that warming hastened phenological sequences in several species (Post et al. 2008), we expected warming to reduce spatial variability in plant phenology among plots. The relevance of this analysis to herbivore foraging ecology is that it quantifies the influence of warming on the progression of the plant growing season at local and intermediate spatial scales. This presumably reflects the resource state in space and time that herbivores might be exposed to in a warmer climate.

In all cases, ANOVAs included year as a fixed factor to test for between-year variation. A significant between-year effect was detected only for emergence in Stellaria longipes, and for blooming in Cerastium alpinum and Carex supina. For events for which there was no significant year effect, data from both years were pooled. For the events for which we detected a significant effect of year, means are reported after accounting for this effect. Results for the timing of phenological events are reported as the June date of the event.

The numbers of treatment and control plots on which we observed multiple phenological events within each species limited our analyses of phenological dynamics. The earliest phenological event observed in most cases was emergence in forbs and its analogue in deciduous shrubs, LO; this was observed for C. alpinum, Draba sp., C. supina, S. longipes and Salix glauca. Emergence and LO were also observed, but not on a sufficient number of plots for analysis, in Potentilla palustris and Betula nana. Following emergence, FS was observed for C. alpinum, S. longipes, S. glauca and B. nana. Blooming was observed in C. alpinum, Draba sp., C. supina, S. glauca, B. nana and P. palustris. Finally, FR was observed in B. nana, Draba sp. and C. supina.

(c) Spatial variability in phenological events

We examined spatial variability in phenological progression at two scales: an intermediate scale, with comparisons among plots over distances of hundreds of metres, and a local scale, with comparisons among plants within plots, over distances of 1 m or less. To quantify the influence of warming on spatial variability of plant phenology at the intermediate spatial scale, we used F-tests of variances around the means of each event observed for each species among all plots of each type (treatment or control). In quantifying the influence of warming on local-scale spatial dynamics of plant phenology, we calculated the coefficient of variation (CV) of the dates of all events observed within each plot and then used an ANOVA to test for differences between treatment and control plots. The ANOVA included plot and site as random effects, neither of which was significant, and year as a fixed factor.

(d) Observed spatio-temporal variation in plant phenology and herbivore reproduction

We monitored emergence of plant species on permanent plots within the calving area of caribou in our study site in 1993 and from 2002 to 2007 as described in detail previously (Post & Klein 1999; Post et al. 2003, 2008). We quantified the progression of the plant growing season using the nonlinear regression model,

$$ Y = \frac{1}{1 + \exp(-a + b \times X)} $$

in which $Y$ is the daily proportion of the final number of species emergent and $X$ is the Julian date. In this model, the intercept $a$ quantifies the date at which species begin emerging, and the slope $b$ quantifies the rate of species emergence. We used estimates of $a$ and $b$ from (2.1) to estimate the date of onset of plant growth in each year as the date at which 5% of species had emerged. Spatial variation in the progression of the plant growing season was quantified in two ways: first, as the standard error of the estimate of $b$ from (2.1) with data from all of our phenology plots pooled in each year; second, as the standard error of the mean of $b$ estimated for each plot individually each year. These approaches gave similar results, but we report results using both methods rather than choosing one set of results post priori.

Previously, we reported that offspring production by caribou in our study site was inversely related to an index of trophic mismatch quantified as the per cent of forage species emergent at the midpoint of the calving season each year (Post & Forchhammer 2008). This index of trophic mismatch quantifies the temporal state of the plant growing season, and hence resource availability, in relation to the timing of offspring production and hence peak resource demands for offspring provisioning. Here, we investigated the consequences for offspring production by caribou of spatial variation in timing and progression of the plant growing season. We focused on offspring production because declines in summer calf-to-cow ratios and calf proportions have been associated with declines in other caribou populations in Alaska and Canada (Klein 1968; Ferguson & Mahoney 1991; Collins et al. 2003; Haskell & Ballard 2004; Larner & Nagy 2004), and are presumably an important component of caribou population dynamics. Previously, we reported a positive association between trophic mismatch and early calf mortality in this population (Post & Forchhammer 2008), but did not focus on calf mortality here because that association was not statistically significant.

We performed a multivariate regression analysis of variation in annual offspring production, defined as the peak proportion of calves among the adult female segment of the population each year (Post & Forchhammer 2008), using our index of trophic mismatch and index of spatial variability in the progression of the plant growing season as predictor variables. This model was strictly density independent for two reasons: first, we were constrained by very low sample size ($n=7$ years of data) and second, our only estimates of population density for each year were our own counts of the total number of caribou observed in the study site each.
summer. We tested for a relationship between offspring production and caribou density using our estimates of the maximum daily number of caribou observed in the study site each year, and found a negative association suggestive of density-dependent limitation ($r = -0.63$, $p = 0.13$), but did not pursue a density-dependent model for the reasons stated above.

We began with generalized additive models to test for nonlinear relationships between offspring production and our predictor variables, but those analyses revealed no significant nonlinearity. Hence, we resorted to linear models, of which we report both overall model fit and significance, in addition to partial correlations and significance of each predictor variable. We compared candidate models of offspring production (including trophic mismatch only, spatial variability in phenology only, and both) using corrected Akaike's information criterion ($AIC_c$; Sakamoto et al. 1986) scores based on residual sums of squares, sample size and the number of parameters in the model.

3. RESULTS

(a) Experimental warming and timing of events

Mean daily temperature was significantly higher on treatment than on control plots by 2°C in 2003 and 1.4°C in 2004 (Post et al. 2008). Also, daily maximum temperatures were significantly higher on treatment than on control plots in both years (by 3.9°C in 2003 and by 2.6°C in 2004; Post et al. 2008). RH did not differ significantly between treatment and control plots in either year (Post et al. 2008).

Because our phenology results might have been influenced by the number of phenological events observed on treatment and control plots, we used a univariate ANOVA to compare the means of the total number of events observed on each type of plot in each year. The mean ($\pm$1 s.e.) number of phenological events observed in 2003 did not differ between treatment (8.92 $\pm$ 0.79) and control plots (10.9 $\pm$ 1.35 versus day 13.4 $\pm$ 1.48; $F_{1,45} = 3.1$, $p = 0.09$). Likewise, the mean number of events observed in 2004 did not differ between treatment (8.92 $\pm$ 0.79) and control plots (8.33 $\pm$ 0.96; $F_{1,45} = 2.7$, $p = 0.11$).

The timing of the earliest phenological events observed, emergence in forbs and LO in deciduous shrubs, occurred significantly earlier on treatment than on control plots for two species: S. longipes and S. glauca (figure 1). Emergence in S. longipes occurred on average on day 5.8 ($\pm$ 0.52) on treatment plots compared with day 7.4 ($\pm$ 0.49) on control plots ($F_{1,45} = 4.99$, $p = 0.03$). LO in S. glauca occurred on average on day 4.5 ($\pm$ 0.32) on treatment plots and on day 6.9 ($\pm$ 0.32) on control plots ($F_{1,45} = 28.3$, $p < 0.001$).

FS occurred earlier on treatment than on control plots only for S. glauca (figure 1). For this species, however, sufficient data on timing of FS were available only for 2003, when FS occurred earlier on treatment plots (day 6.33 $\pm$ 1.35 versus day 13.4 $\pm$ 1.48; $F_{1,9} = 12.4$, $p = 0.006$).

Blooming occurred earlier on treatment than on control plots for several species (figure 1), including C. alpinum (day 10.1 $\pm$ 0.53 versus day 14.5 $\pm$ 0.90; $F_{1,26} = 10.0$, $p = 0.004$), Draba sp. (day 5.82 $\pm$ 0.93 versus day 8.88 $\pm$ 0.96; $F_{1,31} = 5.26$, $p = 0.03$), B. nana

Figure 1. Timing of plant phenological events on treatment (warmed, black bars) and control (ambient, grey bars) plots at our study site near Kangerlussuaq, West Greenland, in 2003 and 2004. Endpoints of the bars represent the mean ($\pm$ 1 s.e.) dates of the events for each species listed along the l.h.s. of the figure. For each bar, the left endpoint represents the mean date of the first phenological event listed to the l.h.s. of the figure and the right endpoint represents the mean date of the second phenological event listed to the l.h.s. of the figure. The bars represent the mean interval between the pairs of events listed to the l.h.s. of the figure for each species. The events are emergence (E), flower set (FS), blooming (B), fruit set (FR) and leaf opening (LO). The species are listed in §2. Asterisks within the figure denote a significant ($p < 0.05$) difference between treatment and control means for the phenological event represented by the endpoint of the bar. Asterisks outside of the figure and in parentheses denote a significant ($p < 0.05$) difference between treatment and control means for the interval between successive phenological events listed to the l.h.s. of the figure. Events are portrayed in the order in which they occurred on control plots.
(day 7.31±0.54 versus day 11.3±0.61; $F_{1,21}=23.9, p=0.001$), *P. palustris* (day 6.5±1.99 versus day 15.4±1.26; $F_{1,5}=14.3, p=0.01$) and *C. supina* (day 10.1±0.88 versus day 13.4±0.89; $F_{1,26}=7.00, p=0.014$). As with FS for *S. glauca*, sufficient data on timing of blooming were available only for 2003, when blooming occurred earlier on treatment (day 9.14±1.1) than on control plots (day 15.8±1.2; $F=17.7, p=0.001$).

Fruit set occurred earlier on treatment than on control plots for *Draba* sp., *B. nana* and *C. supina* (figure 1). For *Draba* sp., mean date of FR on treatment plots was day 12.2 (±0.69), but averaged 5 days later on control plots (day 17.5±0.72; $F_{1,25}=28.2, p<0.001$). Similarly, FR in *B. nana* occurred on average almost 5 days earlier on treatment (day 12.4±0.48) than on control plots (day 17.4±0.45; $F_{1,19}=57.1, p<0.001$). For *C. supina*, sufficient data were available only for 2003, when FR occurred on average 6.5 days earlier on treatment (day 10.3±0.33) than on control plots (day 16.9±0.66; $F_{1,15}=51.4, p<0.001$).

(b) Phenological intervals among plots

In 5 out of 15 cases, the mean interval from one phenological event to the next successive event among plots was shortened by warming (figure 1). In *C. alpinum*, progression from emergence to blooming lasted 6.7±0.82 days on treatment plots and 9.8±0.67 days on control plots ($F_{1,26}=8.72, p=0.007$). In *B. nana*, progression from FS to bloom lasted 2.8±0.51 days on average on treatment plots compared with 4.8±0.66 days on control plots ($F_{1,14}=6.0, p=0.03$), whereas the interval between FS and FR lasted 7.1±0.48 days on treatment plots and 11.0±0.59 days on control plots ($F_{1,15}=26.3, p<0.001$). In *S. glauca*, the progression from LO to FS lasted 2.2±0.98 days on treatment plots and 6.2±1.1 days on control plots ($F_{1,9}=7.73, p=0.02$). In *C. supina*, the transition from blooming to FR lasted 3.7±0.66 days on treatment plots and 6.5±0.78 days on control plots ($F_{1,8}=7.58, p=0.03$). In only one case was progression delayed by warming: the interval between FS and bloom in *S. glauca* was shorter on control than on treatment plots, but this difference was not significant ($F_{1,8}=0.18, p=0.68$).

When arranged in order from earliest to latest occurring events as observed on the control plots, our results suggest that differences between treatment and control means amplified as the growing season progressed (figure 1). We tested for such an effect size using the ratio of control:treatment means for all events observed in an ANOVA with the mean dates of events observed on control plots and ‘start’ or ‘end’ as fixed factors, where these terms indicate whether each event represented the beginning or end of the phenological interval of interest (the endpoints depicted in figure 1). We detected a significant influence of control mean date on effect size ($F=8.93, p=0.007$), but no influence of start or end ($F=1.08, p=0.31$). To determine the direction of the influence of control mean date of events on the effect size of our warming treatment, we split the effect size results into groups of initial and terminal events according to the intervals depicted in figure 1. There was a significant relationship between the date of events and effect size for initial events ($r=0.65, p<0.02$), but no such relationship for terminal events ($r=0.06, p>0.50$). This suggests that there was a greater response to our warming manipulation among initial events in phenological sequences that occurred later in the growing season. This is also evident in the greater difference between treatment and control means later in the growing season depicted in figure 1.

(c) Spatial variability in plant phenology among and within plots in response to experimental warming

For 12 out of 17 phenological events recorded, warming reduced the spatial variability in the timing of events among plots; however, in only six cases was this reduction statistically significant ($p<0.05$, F-tests; figure 2). In 5 out of 17 cases, warming increased the spatial variability among plots in the timing of events, but in only two cases was this increase statistically significant (figure 2). Warming significantly reduced the spatial variability among plots in the timing of five of the six earliest events observed, including emergence in *C. alpinum*, *Draba* sp. and *S. longipes*; FS in *B. nana*, and LO in *S. glauca* (figure 2). In only one late event, FR in *C. supina*, did warming reduce spatial variability among plots. By contrast, increases in variability in timing of events among plots in response to warming were isolated to the two latest events observed: FR in *Draba* sp. and FS in *S. longipes* (figure 2). For all events that displayed a reduction in spatial variability in response to warming, warming reduced the spatial variability in timing of events among plots by an average of 57.2% (range: 4–86.7%; figure 2). By contrast, the average amount by which warming increased the spatial variability in timing of events among plots was 60.8% (range: 20.6–98.8%; figure 2).
In our analysis of spatial variability of phenological events within plots, we detected a significant effect of year ($F_{1,44}=14.2$, $p<0.001$) as well as of the warming treatment ($F_{1,44}=7.27$, $p=0.01$), but the interaction between warming and year was not significant ($F_{1,44}=2.00$, $p=0.16$). Averaged across both years, variability among all phenological events observed within plots was lower on treatment (mean ± 1 CV = 18.4 ± 1.76) than on control plots (25.1 ± 1.22). The same pattern was apparent in 2003 (treatment mean = 21.3 ± 2.49; control mean = 31.6 ± 2.50) and 2004 (treatment mean = 15.5 ± 2.49; control mean = 18.7 ± 2.51) when means were estimated for each year individually. Hence, within plots, warming reduced the spatial variability in timing of events by approximately 27% for the pooled data, and by 33 and 17% in the first and second years, respectively, of the experiment. The difference between years may have been due to differences in ambient temperature and precipitation (Post et al. 2008). There were no significant random effects of plot ($F=0.23$, $p=0.87$) or site ($F=0.04$, $p=0.97$).

**Figure 3.** Relationships between (a) the date of onset of the annual plant growing season, defined as the date at which 5% of plant species had emerged or (b) spatial variability in the date of onset of the plant growing season, defined as the standard error of the date of onset of the growing season each year at our study site near Kangerlussuaq, West Greenland, and mean April temperature in 1993 and from 2002 to 2007. Temperature was recorded at Kangerlussuaq International Airport. See §2 for details on estimation of the dependent variables in (a,b).

**Figure 4.** Relationships between annual offspring production by caribou (proportion calves in the population of adult females) and (a) the degree of trophic mismatch each year and (b) the spatial variability in timing of plant growth each year at our study site near Kangerlussuaq, West Greenland, in 1993 and from 2002 to 2007. Both plots show partial correlations from the best-fit regression model. See §2 for details on estimation of the dependent and independent variables.

**Observed spatio-temporal variation in plant phenology and herbivore offspring production**

From 1993 to 2007, there was a trend towards earlier onset of the plant growing season in warmer years. Annual dates of 5% emergence of plant species on our observational plots displayed a negative association with mean April temperature ($r=-0.59$, $p=0.17$; figure 3a). Furthermore, just as our warming experiment revealed a spatial compression in the timing of plant phenological events within and among experimental plots in comparison with control plots, our observational data revealed a negative association between natural variation in springtime temperatures and spatial variability in progression of the plant growing season across the local landscape. Both of our indices of spatial variability in progression of plant growth were negatively correlated with mean April temperature (s.c.h across plots: $r=-0.70$, $p=0.08$; s.c.mean h among plots: $r=-0.74$, $p=0.06$; figure 3b). Hence, spring warming not only advanced the onset of plant growth but it also led to spatial compression of the plant growing season.

Our index of trophic mismatch and spatial variation in progression of the plant growing season combined explained 90% of the observed variation in offspring production by caribou among years ($F_{2,4} = 17.8$, $R^2 = 0.90$, $p=0.01$). The overall best-fit model explaining interannual variation in offspring production included both predictor variables (AIC$_c = -44.35$, compared with $-30.14$ for the model with trophic mismatch only and $-30.86$ for the model with spatial variability in
The spatial dimension of trophic mismatch  E. Post et al.  2011

phenology only). Most of the variance in offspring production was explained by the index of trophic mismatch (partial $r = -0.89, p = 0.005$; figure 4a), while less of the remaining variance was attributable to spatial variability in progression of the plant growing season (partial $r = 0.75, p = 0.05$; figure 4b). Despite the fact that a simple correlation between offspring production and spatial variability in the progression of the plant growing season was not significant ($r = 0.31, p = 0.49$), our regression model indicates that this factor explains residual variation in offspring production after accounting for trophic mismatch. Hence, when plant growth occurs later and more variably in space across the local landscape, offspring production by caribou is higher than it is in years when the timing and progression of plant growth is compressed spatially across the local landscape.

4. DISCUSSION

Selective foraging by migratory herbivores reflects a strategy aimed at prolonging the intake of newly emergent, highly digestible and nutrient-rich plants (Senft et al. 1987). Selectivity in large ruminants occurs at multiple spatial scales, from the landscape and local scales (Märell & Edenius 2006; Hebblewhite et al. 2008) to the forage patch (Märell et al. 2002), and even to the scale of individual plants and plant parts (Bryant & Kuropat 1980; Trudell & White 1981). In far northern environments, this strategy is necessary for successful reproduction because resource availability is highly pulsed in time and heterogeneously distributed across the landscape and is visible precisely owing to the interaction between temporal and spatial dynamics of resource availability. Our results here and elsewhere (Post & Forchhammer 2008) emphasize that the mismatch not only in time but also in space, between peaks of resource availability and demand by reproducing individuals, are aspects of climate change that may have consequences for offspring production.

However, several cautionary notes are warranted. Our observations suggest that herbivore productivity was adversely associated with both the advancement of spring-time availability of forage resources and the compression of resource availability spatially (figure 4). Nonetheless, we acknowledge that the short-term nature of both the observational, and more especially, experimental components of our study must be taken into consideration in interpretation of our results. Moreover, we recognize that the spatial scale of both our experiment and observations do not match completely the scale of the entire calving range occupied by this caribou population. Although offspring production by caribou in this population declined with reductions in spatial variability in plant phenology on their calving range, this relationship was significant only after accounting for the adverse effect of temporal advancement of plant phenology (figure 4). Moreover, we were previously unable (Post & Forchhammer 2008) to link conclusively the temporal component of trophic mismatch to offspring mortality in this population, so the extent to which further changes in either temporal or spatial aspects of plant phenological response to climatic warming will influence caribou population dynamics remains unaddressed, but worthy, in our estimation, of further consideration. Finally, although the patterns of temporal advancement and spatial compression of plant phenological events by warming revealed by our experiment were both corroborated by patterns of temporal and spatial variation in plant phenology in response to natural spring warming at the larger scale of our 7-year observational study (figure 3), neither of these relationships in the observational data were significant at the rigorous 0.05 level. Therefore, we cannot conclusively state that future warming at this site will further exacerbate spatial and temporal aspects of trophic mismatch for caribou, or influence their population dynamics, but we believe this area of research deserves further attention.

Several recent studies have focused on spatial patterns of interaction between climate change, plant phenology and herbivore population ecology. Invariably, however, those studies have used a regional landscape-scale approach, comparing patterns among populations of herbivores, and in this regard we believe our approach constitutes an important complement to such studies. Mysterud et al. (2001), for instance, reported in a comparison of harvested red deer among 105 municipalities spanning hundreds of kilometres in Norway that body weight correlated positively with landscape heterogeneity, namely altitudinal variation. Mysterud et al. (2001) concluded that this relationship reflected interactions between landscape heterogeneity, abiotic conditions and spatial patterns of plant phenology, but did not include actual measures of plant phenology in their study. By contrast, Herfindal et al. (2006), despite having conducted a similar comparison of variation in moose body weights among seven regions spanning the same spatial scale in Norway, documented a negative relationship between altitude and body weights. Herfindal et al. (2006), however, incorporated an NDVI of plant phenology in their analysis and found a positive relationship between body weights and a composite measure of plant phenology.

In contrast to such studies, ours, focused on spatial dynamics of plant phenology at local and intermediate spatial scales, though admittedly not at the same scale as the entire calving range of the focal population. This study was explicitly designed to experimentally test relationships between warming and spatial dynamics of plant phenology documented in previous large-scale analyses (Post & Stenseth 1999; Pettereili et al. 2005a), and to determine whether those patterns were reflected at smaller spatial scales relevant to the foraging horizon of individual large herbivores. Our results indicate they were not.

In a broader ecological context, the spatial compression of plant phenology by experimental and observed warming documented here might represent a heretofore overlooked aspect of trophic mismatch induced by climate change. Most studies of the consequences of trophic mismatch for reproduction and population dynamics have focused on birds, where the emphasis has been on the temporal mismatch between resource availability and resource demand (Both et al. 2004). In migratory herbivores, however, arrival at the breeding grounds is not the end of the story. Herbivores track phenological progression of forage plants by moving across the local landscape to maintain intake of newly emergent species, individual plants or even tissues within plants (Klein 1970, 1990; Skogland 1989; Hebblewhite et al. 2008). Such observations suggest that any spatial
constriction of the plant growing season might constrain the ability of migratory herbivores to prolong intake of high-quality forage during peak resource demand. Furthermore, such a constraint might negatively affect physical condition (Mysterud et al. 2001) and offspring production and survival (Post & Forchhammer 2008).

Our results may have general significance to herbivores inhabiting seasonal environments. Large herbivores prefer newly emergent forage, presumably owing to the high digestibility and nutrient content of young plant tissues (Hebblewhite et al. 2008). Plants consumed by reindeer (R. tarandus) on tundra, for instance, can be as much as 10% more digestible than the average available foraging radius of 10 m (White & Trudell 1980). In a famous example of multiplier effects in ecology, White (1983) documented that selective foraging by female reindeer resulted in a 27% increase in dry matter intake, a 45% increase in digestible dry matter intake, a 45% increase in metabolizable energy intake, a 267% increase in net energy for production and a 268% increase in body weight gain over non-selective foraging. Such selectivity occurred within a foraging radius of 10 m (White & Trudell 1980; White 1983), relatively the same scale, ecologically, as that at which our experiment was conducted. Our experiment revealed that warming reduced the spatial variability of plant phenology at the plot scale (1.5 m or less) by approximately 27% and at the local scale (hundreds of metres) by over twice that amount. Furthermore, our multi-annual observations revealed an approximately 80% reduction in local-scale variability in plant phenology between the coldest and warmest years (figure 3b). Reductions of that magnitude associated with future warming could conceivably impair the ability of herbivores such as caribou to forage selectively, with adverse consequences for their productivity. We suggest, therefore, that it is highly relevant to herbivore ecology to consider the manner in which warming will alter spatial patterns of plant phenology at more immediate spatial scales than that of the regional landscape.

Procedures for observation of animals were approved by the Institutional Animal Care and Use Committee of The Pennsylvania State University.

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Appendix D

Opposing plant community responses to warming with and without herbivores
Opposing plant community responses to warming with and without herbivores

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If controls over primary productivity and plant community composition are mainly environmental, as opposed to biological, then global change may result in large-scale alterations in ecosystem structure and function. This view appears to be favored among investigations of plant biomass and community responses to experimental and observed warming. In far northern and arctic ecosystems, such studies predict increasing dominance of woody shrubs with future warming and emphasize the carbon (C)-sequestration potential and consequent atmospheric feedback potential of such responses. In contrast to previous studies, we incorporated natural herbivory by muskoxen and caribou into a 5-year experimental investigation of the plant community response to warming. In accordance with other studies, warming increased total community biomass by promoting growth of deciduous shrubs (dwarf birch and gray willow). However, muskoxen and caribou reduced total community biomass response, and responses of birch and willow, to warming by 19%, 46%, and 11%, respectively. Furthermore, under warming alone, the plant community shifted after 5 years away from graminoid-dominated toward dwarf birch-dominated. In contrast, where herbivores grazed, plant community composition on warmed plots did not differ from that on ambient plots after 5 years. These results highlight the potentially important and overlooked influences of vertebrate herbivores on plant community response to warming and emphasize that conservation and management of large herbivores may be an important component of mitigating ecosystem response to climate change.

Results

Plant Biomass Responses to Warming and Large Herbivores. In accordance with our previous results (C.P. and E.P., unpublished data; and E.P. wrote the paper).

The authors declare no conflict of interest.

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T he interplay between biotic and abiotic control over community composition and dynamics has been a favored topic of investigation in ecology for decades (1), well before its relevance to contemporary climate change received emphasis (2, 3). Both the abundance and distribution of species may be determined by interactions of individuals with competitors of their own or other species, with predators and parasites, and with the abiotic environment (4). In the context of ecosystem response to global climate change, considerable emphasis has been placed on the question of how plant community composition and productivity will respond to warming (5). Undoubtedly, this reflects the importance of the abundance and species diversity of primary producers to ecosystem function (6). A great deal of effort has been devoted to investigating, therefore, plant biomass and community responses to warming in experimental, observational, and analytical frameworks (7–12). The extent to which plant responses to warming may be constrained or even exacerbated by herbivory has, in contrast, received comparatively little attention (6, 13) and has largely been overlooked in experimental investigations.

Vertebrate herbivores in particular may be of key importance to plant community response to warming because they influence plant biomass, soil nutrient dynamics, and species composition of plant communities (14–16). In high latitude systems, experimental evidence indicates that both small and large mammalian herbivores play an important role in structuring plant communities through selective foraging that not only reduces the abundance of preferred species but also alters competitive interactions among plant species (17, 18). Such influences may mediate plant biomass response to climate change, especially in arctic and subarctic ecosystems, where vegetation is characteristically nutrient limited (9, 10), as is its potential response to increasing atmospheric CO₂ (7, 19, 20).

The influences of large herbivores on vegetation in arctic and subarctic ecosystems include biomass reduction of preferred species (21, 22) with extensive ecosystem consequences (23) that may even affect other herbivores (24). Caribou and reindeer (Rangifer tarandus), for instance, can promote expansion and productivity of graminoids while constraining biomass of deciduous shrubs such as dwarf birch (Betula nana) and willow (Salix glauca) (21, 22, 25–27). Such opposing responses to herbivory of plant species belonging to different functional groups may contribute to changes in plant community composition and C-sequestration potential of ecosystems in response to climate change.

Recent evidence from long-term warming experiments in the Arctic indicates that plant community responses to warming appear to oppose the responses to herbivory described above. The most notable and consistent vegetation response to experimental and observed warming in the Arctic is an increase in cover and canopy height of deciduous shrubs (11, 12). Such results appear to corroborate observations of warming-related increases in dwarf birch, willow, and white spruce (Picea glauca) cover and abundance in Alaska over the past 50 years (11). Increases in biomass and cover of woody plants in response to warming represent an important modification of the tundra biome because they may, in addition to reducing albedo, interact with snow-trapping during winter to further promote the expansion of shrubs in the Arctic (28, 29). The extent to which herbivores may interact with climate change to promote or constrain shrub dynamics in the Arctic remains, however, unexamined. Evidence from long-term studies in northern temperate elk-aspen (Cervus elaphus-Populus tremuloides) and moose-balsam fir (Alces alces-Alnus abies) systems implies that woody plant expansion in response to warming may be constrained by large herbivores (30, 31).

We suggest that herbivores have the potential to play an important role in community dynamics and biomass response of vascular plants to climate change. The objectives of this study were to investigate the influences of warming and herbivory on aboveground biomass and plant community composition in an experimental framework in which large herbivores interacted with the warming experiment. Midway through our experiment, however, there was an unexpected outbreak of larvae of a noctuid moth; the effect of this outbreak was thus incorporated opportunistically into our experiment.

Results

Plant Biomass Responses to Warming and Large Herbivores. In accordance with our previous results (C.P. and E.P., unpublished data; and E.P. wrote the paper)

The authors declare no conflict of interest.

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data), community composition did not vary between treatments and controls during the first 4 years of our experiment. However, by the fifth year, total community biomass was greatest on exclosed-warmed plots, and exceeded that on control (grazed-ambient) plots by 33.1% (Fig. 1A). This was due primarily to greater aboveground biomass (ABM, see Materials and Methods) of deciduous shrubs on exclosed-warmed plots, exceeding that on control plots by 84.7% (Fig. 1B). Within deciduous shrubs, total ABM of dwarf birch was highest on exclosed plots; although there was no difference between exclosed-warmed and exclosed-ambient plots, ABM on exclosed-warmed plots exceeded that on control plots by 98.7% (Fig. 1C). In contrast, willow ABM was highest on warmed plots, regardless of whether they were exclosed or grazed; however, ABM on exclosed-warmed plots exceeded that on control plots by 58.4% (Fig. 1D). Graminoid ABM was highest on grazed plots and lowest on exclosed plots; although there was no difference between warmed and ambient plots within these treatments, ABM on exclosed-warmed plots was lower than on control plots by 32.7% (Fig. 1E). Finally, forb ABM was greatest on exclosed-warmed plots and lowest on exclosed-ambient plots, but means after 5 years of treatment did not differ from those at the start of our experiment (Fig. 1F). Nonetheless, ABM of forbs on exclosed-warmed plots

![Fig. 1. Time series of ANOVA-estimated mean (± 1 SE) numbers of point-intercepts per 0.25 m² plot, according to treatments (red: exclosed, ambient; blue: exclosed, warmed; green: grazed, ambient; black: grazed, warmed). Means are shown for (A) the total plant community; (B) deciduous shrubs; (C) dwarf birch; (D) gray willow; (E) graminoids, and (F) forbs.](image-url)
exceeded that on control plots by 114.9% (Fig. 1F). Although not shown, ABM of litter did not differ among any of our treatment or control plots in any year of the experiment, except for 2005, the peak of a caterpillar outbreak (see below), when litter was lowest on exclosed-ambient plots by 28.3%.

Within dwarf birch and gray willow, leaves and stems displayed differential biomass responses to warming and herbivory [see supporting information (SI)]. By the fifth year of the experiment, birch leaf biomass was highest on exclosed plots, whether warmed or not, and greater on exclosed-warmed than on control plots by 133.1%. Birch stem biomass was highest on exclosed-ambient plots, but greater on exclosed-warmed plots than on control plots by 49.1%. Willow leaf biomass was highest on warmed plots, whether exclosed or grazed, but greater on exclosed-warmed plots than on control plots by 90.4%. Willow stem biomass was highest on exclosed-warmed and grazed-warmed plots, but greater on exclosed-warmed plots than on control plots by 9.32%.

**Percentage Reductions of Plant Biomass Response to Warming by Muskoxen and Caribou.** Herbivory by muskoxen and caribou reduced the biomass response to warming of the total community, total deciduous shrubs, total birch, birch leaves and stems, willow leaves, and forbs (Fig. 2A). The greatest percent reduction by herbivory of the biomass response to warming was for birch leaves (57.7% reduction) and forbs (48.2% reduction) (Fig. 2A).

In contrast, herbivory enhanced the biomass response to warming of willow stems (4.78%), graminoids (35.1%), and litter (4.22%) (Fig. 2A). There was a significant difference between muskox and caribou in the magnitude of the correlation between mean community size and effect size of the exclosure treatment on biomass response to warming (F = 8.03, P = 0.01), and a significant interaction between the herbivore species and plant functional group (F = 2.76, P = 0.02), with the mean correlation per plant functional group for muskoxen (r_mean = 0.41) exceeding that for caribou (r_mean = 0.18). For muskox, the highest correlations between the effect size ratio and mean daily herbivore density were found for responses to warming by the total community (r = 0.70, P < 0.05), total deciduous shrubs (r = 0.71, P < 0.05), total birch (r = 0.70, P < 0.05), birch stem (r = 0.30, P > 0.05), and litter (r = 0.42, P > 0.05). For caribou, the strongest correlation was found for graminoids (r = 0.22, P > 0.05). Hence, the effect of the exclosure treatment on biomass response to warming increased with presence of muskoxen in general but not with caribou.

**Reduction of Plant Biomass by the Caterpillar Outbreak.** Our ANOVA revealed significant effects of caterpillar density on ABM of the total community (F = 114.8, P < 0.001), total deciduous shrubs (F = 55.8, P < 0.001), total dwarf birch (F = 21.5, P < 0.001), total gray willow (F = 9.40, P < 0.001), graminoids (F = 54.5, P < 0.001), and forbs (F = 18.0, P < 0.001). For dwarf birch, caterpillars reduced leaf biomass (F = 42.2, P < 0.001), but not stem biomass (F = 1.25, P = 0.29). For gray willow, caterpillars reduced both leaf biomass (F = 10.3, P < 0.001) and stem biomass (F = 4.82, P = 0.009). The greatest percent reductions in ABM by caterpillars occurred with dwarf birch leaves (87.1%), gray willow leaves (97.8%), and forbs (90.5%) (Fig. 2B). In no case did we detect an interaction between the warming treatment and caterpillar density on aboveground biomass (P > 0.10 in all cases).

**Differential Alteration of Plant Community Composition by Warming and Herbivory.** Community composition changed during the course of the experiment according to the differential responses of ABM among functional groups to our warming and exclosure treatments. After 5 years, communities on both types of exclosed plots had shifted from graminoid-dominated to dwarf birch-dominated (Fig. 3A). Additionally, willow cover had declined on exclosed-ambient plots and increased on exclosed-warmed plots, while on exclosed-ambient plots, forb cover had declined compared with baseline composition, and on exclosed-warmed plots, moss cover had declined (Fig. 3B). In contrast, the grazed-warmed community increased in moss and willow cover, but declined in graminoid cover (Fig. 3C).

To estimate interaction effects of our warming and exclosure treatments on community composition, we compared ANOVA-estimated means of control plots in 2007 to those of each combination of treatment and control manipulations in 2007 (Fig. 3B). Warmed plots that were also exposed to herbivory by muskoxen and caribou did not differ in community composition from control plots that were exposed to herbivory but not warmed (Fig. 3B, black “warming” arrow). In contrast, warmed plots that were not exposed to herbivory displayed significantly greater dwarf birch cover, but lower moss and graminoid cover, than control plots (Fig. 3B, black “warming + exclosure arrow”). Similarly, plots released from herbivory, but not warmed, displayed greater dwarf birch cover but lower graminoid cover than grazed, ambient plots (Fig. 3B, black “exclosure” arrow). Sporadic exclosure plots, warmed plots that were released from herbivory displayed greater dwarf birch cover, but lower moss and graminoid cover, than warmed plots that were also grazed (Fig. 3B, green “outbreak” arrow). Plots released from herbivory but not warmed displayed less willow and forb cover than warmed plots released from herbivory (Fig. 3B, red “warming” arrow).
through changes in plant species composition and C-balance that Arctic ecosystems have been a major focus of climate change studies.

**Discussion**

Arctic ecosystems have been a major focus of climate change studies because they have the potential for substantial feedback on climate through changes in plant species composition and C-balance that might, in turn, influence atmospheric CO$_2$ concentration (7, 12, 19). Yet, most studies examining plant productivity and community responses to warming in the Arctic have not incorporated animal influences (but see ref. 33). The results of our study indicate an important role of insect outbreaks and large herbivores on plant biomass and community composition under warming.

The picture emerging within the first 5 years of this experiment is one of divergence between warmed plant communities with and without large herbivores. Although warming increased aboveground biomass of the entire plant community by 33%, and that of dwarf birch and gray willow by 98% and 58% respectively, herbivory by muskoxen and caribou reduced this warming response by 19%, 46%, and 11%, respectively (Fig. 2A). Moreover, community composition under warming with large herbivores shifted toward increased cover of graminoids and reduced cover of dwarf birch compared with community composition under warming alone. Such influences could substantially alter the C-sequestration potential of arctic vegetation over the long-term because woody shrubs have much greater C-sequestration capacity than do graminoids (34). That these differences were apparently due primarily to herbivory by muskoxen is noteworthy because they are less abundant than caribou at our site, and occur at much lower density here than elsewhere in Greenland (35–37), Canada (38), and Alaska (39).

The differences in responses among plant functional groups to experimental warming in the Arctic revealed by metaanalyses (8, 12) could have implications for the manner in which communities will respond to the combined effects of herbivory and warming (13). For instance, a common feature of warming experiments is an initially greater and more consistent response in forbs and graminoids than in shrubs (8). Productivity of forbs and graminoids tends to increase with the number of years of warming, while that of deciduous shrubs tends to decline with increasing number of years of treatment (8). The relationships we documented suggest herbivory may enhance the productivity response of herbaceous plants to warming and exacerbate the reduction in productivity of deciduous shrubs, mainly _B. nana_ (8), in response to warming, although not completely (Fig. 2B).

Shifts in plant community composition in response to warming may also influence soil nutrient availability and dynamics. For example, long-term warming of soil and vegetation in a subalpine meadow produced changes in litter input to the soil due to a shift in community composition from forbs (which produce labile litter) to shrubs (which produce more recalcitrant litter) (19). Also, community-level effects of herbivory are a potentially important component of biospheric feedbacks to climate in the Arctic because colonization by deciduous shrubs would allow greater biomass accumulation than that which is possible in a graminoid-dominated community (34), with important consequences for soil C and nitrogen (N) storage and gas exchange (40, 41).

Both the biomass and community composition responses to warming and herbivory we documented here likely extend to ecosystem functioning. Dwarf birch may retard N mineralization and perhaps litter decomposition in communities where it dominates, whereas graminoids may function as facilitators that accelerate N dynamics (23). Our experiment revealed that in the absence of herbivory, dwarf birch increased in response to warming while graminoids declined, whereas the reverse occurred where herbivory interacted with warming (Figs. 1 and 3). Graminoid biomass and cover were nearly twice as great on warmed plots also exposed to herbivory as on those that were only warmed (Figs. 1 and 3), suggesting that N mineralization rates were likely also higher on those plots. In addition, vertebrate herbivores deposit fecal and urinary N, which further enhances N availability and cycling where they occur (16). Moreover, regrowth of grazed graminoid shoots may contain higher tissue N concentrations than nongrazed shoots (27, 42).

The caterpillar outbreak midway through our experiment represents a highly pulsed event with presumably very low frequency (43). Nonetheless, it may have dramatic ecosystem consequences (44). In far northern ecosystems, insect outbreaks can influence
growth dynamics of woody plants for several years after the outbreak has passed (45) and are an important component of climate-tree line dynamics (46, 47). In addition to the effects of defoliation on aboveground biomass we documented (Fig. 2B), insect outbreaks may also influence ecosystem function through nutrient dynamics. Leaf tissues of dwarf birch and gray willow we collected at our site contained ~4 x greater N concentration at the peak of the caterpillar outbreak than before it (D. Eissenstat and E.P., unpublished data). By accelerating the turnover of N that would otherwise have remained in recalcitrant form as leaf tissue and litter, the caterpillar outbreak may have provided an N pulse to the system. This may, in part, explain the rapid biomass recovery that is apparently underway among all functional groups (Fig. 1).

Only by collection of additional data will we be able to determine the extent to which the divergence among our treatments in year 5 of this experiment relates to recovery from the caterpillar outbreak.

The results of this multiannual experiment illustrate that both insect outbreaks and continuous grazing pressure from large herbivores constrain—and in some cases even reverse—the biomass response of arctic vegetation to warming, with consequences for plant community composition. Two concerns remain, however, uncertainty about whether the plot-scale effects of herbivory on plant response to warming will scale up at the ecosystem level of plant response to warming. The second, related concern is how population dynamics in both invertebrate and vertebrate populations will interact with future ecosystem and biome-scale changes associated with warming. Although insect damage and defoliation may become more frequent at northern latitudes with future warming (43, 46, 47), as evidence from the Paleocene-Eocene Thermal Maximum suggests (48), whether abundance of caribou and muskoxen will increase or decline as a result of climate change is far more difficult to predict (49, 50). If the last two remaining large herbivores in this formerly mega-herbivore-rich biome (51) were to expand or go extinct, however, it appears likely that plant community composition would undergo rapid and dramatic changes (52). Even in the absence of long-term changes in abundance, however, both types of herbivores will undoubtedly play a role in ecosystem response to future climate change. The fact that plant community composition after 5 years of warming under continuous grazing pressure from muskoxen and caribou did not differ from plant community composition without warming (Fig. 3B) suggests that management and conservation of large herbivores may be an important aspect of mitigating ecosystem response to future climate change.

Materials and Methods

Study Site. Our study site lies in the inland area east of Kangerlussuaq Fjord, West Greenland (71.11°N, 50.37°W). Vegetation is low shrub tundra dominated by Betula nana, Salix glauca, and Poa sp. The study site comprises the 3 most common vegetation types in the Arctic that represent 39% of the vegetated area of the Arctic (CAVM Team 2003). The study area is occupied by caribou (53, 54) and muskoxen (55). Ptarmigan and Arctic hares both occur at very low densities, and small herbivorous mammals are absent in the study site (E.P., personal observation).

Exclosure and Warming Experiment. In late June 2002, at the peak of the growing season, we erected 6, 800 m² circular exclosures constructed of woven wire and steel fence posts and delimited control sites of the same size and dimensions adjacent to each exclosure within a distance of 40–100 m. Baseline measures of forbs, graminoids, willows, birch, moss, and lichens were made at 10-m intervals along permanently marked, 50-m transects on exclosed and standing ABM of forbs, graminoids, willows, and birch. We used a rigid, square sheet of Plexiglas (measuring 0.25 m x 0.25 m) with 20 randomly located holes drilled in it, secured to 4 adjustable legs. All holes in the Plexiglas sheet were numbered, and the corners of the sheet were labeled with the cardinal directions. When the frame was anchored in the corner pegs on each plot, a single pin 3 mm in diameter was lowered through each hole, and each contact of the pin with living and standing dead vegetation was recorded until the pin reached soil or moss substrate. Encounters were recorded to the species level, although data for forbs and graminoids were analyzed at the level of functional groups. We also recorded whether pits hit leaves or stems and whether they hit litter or bare soil. Biomass was sampled in three periods: early growing season (late May to early June), mid growing season (mid to late June), and at the end of the growing season (mid July to early August).

Abiotic Measurements. We monitored plot surface temperature using Taylor digital maximin thermometers and relative humidity using hygrometers daily while OTCs were in place. Mean daily temperature, the average of the minimum and maximum temperatures in a 24-h period, was significantly higher inside OTCs than outside by 1.5–3 °C (56), which accords with expected temperature increase over the next century according to some scenarios (57). Relative humidity was insignificantly lower inside vs. outside OTCs (58).

Assessing the Effect of Muskoxen and Caribou on Plant Biomass Response to Warming. Before and since erection of the exclosures, we recorded numbers of caribou and muskoxen seen feeding on adjacent control sites daily through 2007. Mean daily numbers of each species feeding in each site were incorporated into our analyses of the effect size of the exclosure treatment on vegetation response to warming. We used three approaches to analyzing the effect of muskoxen and caribou on plant biomass response to warming. First, we compared ANOVA means of ABM of each functional group, and leaf and stem tissue of birch and willow among grazed and exclosed plots; means for forbs and graminoids were not analyzed because their confidence intervals if they fell outside of the 95% confidence intervals of the means to which they were compared (32). The ANOVAs included treatments (warmed vs. ambient; exclosed vs. grazed) as fixed effects, with the warming treatment nested inside the exclosure treatment; year, sampling period (early, middle, or late), and site as random effects. Comparisons were made for each year to produce time series of differences among means according to treatments over the course of the experiment. Second, we quantified percentage alteration of the biomass response to warming by herbivory on caribou and muskoxen as the relative difference between ANOVA means for exclosed-warmed vs. grazed-warmed plots in the fifth year of the experiment. Third, to identify whether muskoxen and caribou exerted similar effects on plant biomass response to warming, we tested for correlations between the effect size (ln(experimental mean/control mean)) of the exclosure experiment for warmed plots and the mean daily number of muskoxen and caribou observed on each site in each year. Positive correlations indicate an increasing divergence between the response to warming of exclosed and grazed plots with greater mean densities of large herbivores on the grazed plots.

Assessing the Impact of Caterpillar Herbivory. In 2004, we realized a caterpillar outbreak was underway. To analyze the influence of what turned out to be a 2-year outbreak of caterpillars of a noctuid moth (Eurois occultus) on plant biomass response to warming, we counted caterpillars on all plots in 2005. The outbreak peak occurred in 2005, when caterpillar densities were conservatively estimated as being twice the levels we had observed in 2004. We estimated mean plot level caterpillar density across all sites in 2005 using an ANOVA with treatments as fixed effects (nonsignificant), and site, and Julian date as random effects. We estimated that caterpillar densities in 2004 were half the mean level of
for 2005. We tested for differences in plant biomass according to annual mean caterpillar density and our treatments using an ANOVA with treatment as a fixed factor and site and period as random factors. We conducted these ANOVAs for 2003 to obtain baseline mean proportions and for 2007 to obtain mean proportions at the end of the fifth year of the experiment. Means differed at the 0.05 level of significance if they fell outside of the 95% confidence intervals of the means to which they were compared (32).

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Assessing Changes in Plant Community Composition. We investigated whether plant community composition had changed after the first 5 years of our treatments. We calculated the proportion of the total community ABM comprising each functional group by dividing the number of pin holes per plot for each functional group by the total number of pin holes for each individual plot in each sampling period each year. We estimated mean proportions of each functional group across all treatments using an ANOVA with treatment as a fixed factor and site and period as random factors. We conducted these ANOVAs for 2003 to obtain baseline mean proportions and for 2007 to obtain mean proportions at the end of the fifth year of the experiment. Means differed at the 0.05 level of significance if they fell outside of the 95% confidence intervals of the means to which they were compared (32).

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