High-Arctic Plant–Herbivore Interactions under Climate Influence

THOMAS B. BERG, NIELS M. SCHMIDT, TOKE T. HØYE,
PETER J. AASTRUP, DITTE K. HENDRICHSEN,
MADS C. FORCHHAMMER AND DAVID R. KLEIN

SUMMARY

This chapter focuses on a 10-year data series from Zackenberg on the trophic interactions between two characteristic arctic plant species, arctic willow *Salix arctica* and mountain avens *Dryas octopetala*, and three herbivore species covering the very scale of size present at Zackenberg, namely, the moth *Sympistis zetterstedtii*, the collared lemming *Dicrostonyx groenlandicus* and the musk ox *Ovibos moschatus*.

Data from Zackenberg show that timing of snowmelt, the length of the growing season and summer temperature are the basic variables that determine the phenology of flowering and primary production upon which the herbivores depend, and snow may be the most important climatic factor affecting the different trophic levels and the interactions between them. Hence, the spatio-temporal distribution of snow, as well as thawing events during winter, may have considerable effects on the herbivores by influencing their access to forage in winter. During winter, musk oxen prefer areas with a thin snow-cover, where food is most easily accessible. In contrast, lemmings seek areas with thick snow-cover, which provide protection from the cold

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and some predators. Therefore, lemmings may be affected directly by both the timing of onset and the duration of winter snow-cover.

Musk oxen significantly reduced the productivity of arctic willow, while high densities of collared lemmings during winter reduced the production of mountain avens flowers in the following summer. Under a deep snow-layer scenario, climate and the previous year's density of musk oxen had a negative effect on the present year's production of arctic willow. Previous year's primary production of arctic willow, in turn, significantly affected the present year's density of musk oxen positively. Climatic factors that affect primary production of plants indirectly, influenced the spatial distribution of herbivores. Additionally, snow distribution directly affected the distribution of herbivores, and hence, in turn, affected the plant community by selective feeding and locally reducing the standing biomass of forage plants.

Although only few moth larvae were observed at Zackenberg, these had in some cases important local effects owing to their foraging on up to 60% of the flower stands on individual mountain avens.

UV-B radiation induces plants to produce secondary plant metabolites, which protects tissues against UV-B damage. This results in lower production of anti-herbivore defenses and improves the nutritional quality of the food plants. Zackenberg data on the relationship between variation in density of collared lemmings in winter and UV-B radiation indirectly supports this mechanism, which was originally proposed on the basis of a positive relationship between UV-B radiation and reproduction in two sub-arctic species of hares (*Lepus timidus* and *Lepus americanus*).

I. INTRODUCTION

In snow-covered ecosystems, such as those in the High Arctic, the distribution of vegetation types is largely governed by clinal variation in snow-cover (Babb and Whitfield, 1977; Walker *et al.*, 2001). In addition to this, the distribution of snow affects the spatio-temporal pattern of flowering and primary production (Høye *et al.*, 2007a; Ellebjerg *et al.*, 2008, this volume). As a result, herbivores in this region are confronted with a spatially and temporally variable food resource, and they adjust their foraging behaviour accordingly. The manner and scale of these adjustments, however, may differ considerably between species. The patterns of dispersion of herbivores are also affected by the risk of predation (Lima and Dill, 1990) together with social interactions especially during the mating season.

Plant–herbivore interactions are reciprocal (Klein *et al.*, 2008, this volume). Herbivores not only depend on plants but also affect their growth and survival directly through grazing and by altering the physical environment by trampling and digging. Despite the relatively low densities of mammalian

herbivores in Northeast Greenland, herbivory by small rodents has been shown in other arctic areas to be able to significantly alter the relative abundance of many common plant species in the tundra ecosystem (Olofsson *et al.*, 2002, 2004). Heavy exploitation of the vegetation may, in some cases, result in a decrease in density of herbivores (e.g., Stenseth and Oksanen, 1987; Selås, 1997), and both herbivory and trampling may locally destroy the insulating moss layer, leading to an increase in soil temperature (van der Wal *et al.*, 2004) and hence, induce changes in the plant communities. Defecation by herbivores recycles important nutrients to the vegetation (e.g., van der Wal *et al.*, 2004), and ultimately carcasses of herbivores constitute a large localized source of nutrients for plant growth (Danell *et al.*, 2002).

This chapter concentrates on two mammalian herbivores, collared lemming *Dicrostonyx groenlandicus* and musk ox *Ovibos moschatus*, and their shared food resources, arctic willow *Salix arctica* and mountain avens *Dryas octopetala*, and on one invertebrate herbivore, the lepidopteran larvae of *Sympistis zetterstedtii*, which also feeds on mountain avens. The effects of climate and climate variation on these plant–herbivore systems as well as the interaction between plants and herbivores are here illustrated using data obtained from the long-term biological monitoring programme BioBasis running at Zackenberg Research Station (74°30′N, 20°30′W; Meltofte and Berg, 2006).

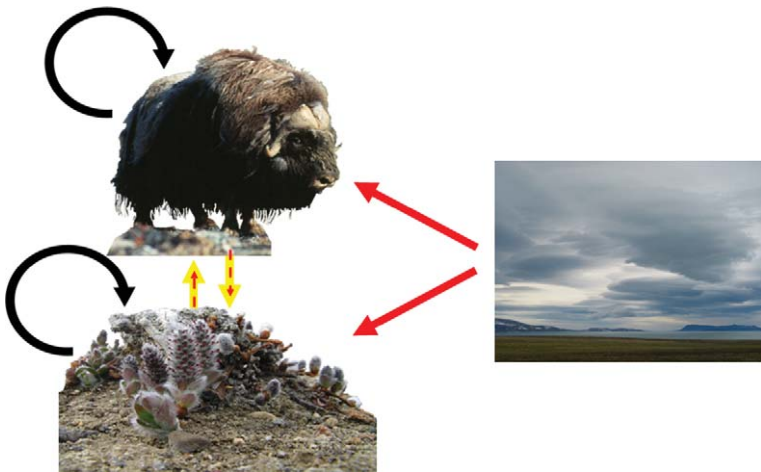## II. CLIMATIC PATHWAYS IN THE PLANT–HERBIVORE SYSTEM

There are basically three ways in which climate can influence the interactions between plants and herbivores (Box 1; see also Forchhammer *et al.*, 2008, this volume). All species may be affected directly by climatic variables though not necessarily in the same way or to the same extent. Alternatively, interacting species may be affected indirectly by climatic perturbations mediated through a climatic effect on adjacent or more distant trophic levels. Indirect climatic effects like these may act either bottom–up (i.e., soil–plant–herbivore) and/or top–down (i.e., predators–herbivore–plant). In addition, climate may affect the strength of the intra- and inter-specific interactions. For instance, a decrease in snow-cover will increase the synchrony of growth of arctic willow, which again, to a certain point, will increase the size of musk ox herds (Forchhammer *et al.*, 2005), thereby intensifying the plant–herbivore interaction on the site level.

Although arctic species are adapted to survive under extreme climatic conditions, both plants and herbivores may be directly affected by weather conditions. The annual phenology of flowering of the plants in the

Box 1

Climatic Influence in the Plant–Herbivore System

The influence of climate in a trophic system of interacting species may be either direct (full red arrows in Box Figure 1) or indirect, which is mediated via other adjacent trophic levels (broken red arrows in Box Figure 1). Additionally, climate may not only influence the way the individual trophic levels interact (yellow arrows in Box Figure 1) but also the way individuals of the same species interact (black arrows in Box Figure 1).

Box Figure 1   Conceptual model for the climatic pathways in the simple plant–herbivore system in the Arctic. Black arrows indicate intra-specific interactions, while yellow arrows indicate inter-specific interactions. The direct climatic influence on the various trophic levels is indicated by the full, red arrows, while the indirect climatic influences indicated by the broken, red arrows. See also Forchhammer (2001), Forchhammer and Post (2004) and Forchhammer *et al.* (2008, this volume). Photos: Niels Martin Schmidt.

The indirect climatic effects may be (a) bottom–up processes, where the climatic influence on lower trophic levels is mediated onto the higher trophic levels (Wilson and Jefferies, 1996; Callaghan *et al.*, 2005), for instance, via climate-induced changes in production of secondary

plant metabolites (Plesner-Jensen and Doncaster, 1999), (b) top–down processes, where the climatic effects onto the higher trophic levels are mediated onto the lower trophic levels, or (c) via a combination of bottom–up and top–down processes (Turchin *et al.*, 2000).

valley Zackenbergdalen varies widely between years, dependent largely on the date of snowmelt (Høye *et al.*, 2007b; Ellebjerg *et al.*, 2008, this volume). Likewise, the flower production shows large inter-annual variation (Høye *et al.*, 2007b; Ellebjerg *et al.*, 2008, this volume), indicating that climate directly affects not only the timing of and investment in reproduction but also the development of plant tissue.

Thawing events during winter may create ice crust directly hampering the access to food for the larger herbivores such as caribou and musk oxen (Vibe, 1967; Forchhammer and Boertmann, 1993), resulting in increased mortality and reduced fecundity. In contrast, predators may indirectly benefit from the ice crust effects on their prey.

Collared lemmings, by contrast, spend most of their time during winter beneath the snow (Stenseth and Ims, 1993). At Zackenberg, the number of lemming nests is positively correlated with the length of the winter season (Figure 1), indicating that the snow-cover functions as a protective layer against predators and extreme climate variability (Chernov, 1985).

Temperature and precipitation during the autumn movements between summer and winter habitats may influence collared lemming abundance. An early onset of snow accumulation has a positive effect on the winter density of lemming, while late onset of snow accumulation affects the winter population negatively (Figure 1) and expose the lemmings to both increased predation and low temperature (Scott, 1993). Predators also benefit from the increased exposure of lemmings during their spring movements from winter to summer habitats.

Late snowmelt in spring delays the emergence of caterpillars (Morewood and Ring, 1998) and may thus decrease their survival by reducing the time available for resource accumulation before returning to winter dormancy.

In the Arctic, climate influences the decomposition and mineralization of soils and thus the availability of nutrients (Flanagan and Bunnell, 1980; Webber *et al.*, 1980; Elberling *et al.*, 2008, this volume), and these climatic effects may be carried on to the herbivores. For instance, solar radiation influences soil temperature and the decomposition, mineralization and nutrient content of plants, which, in turn, has been found to influence the foraging behaviour of snow geese *Chen caerulescens* in Canada (Wilson and Jefferies, 1996).
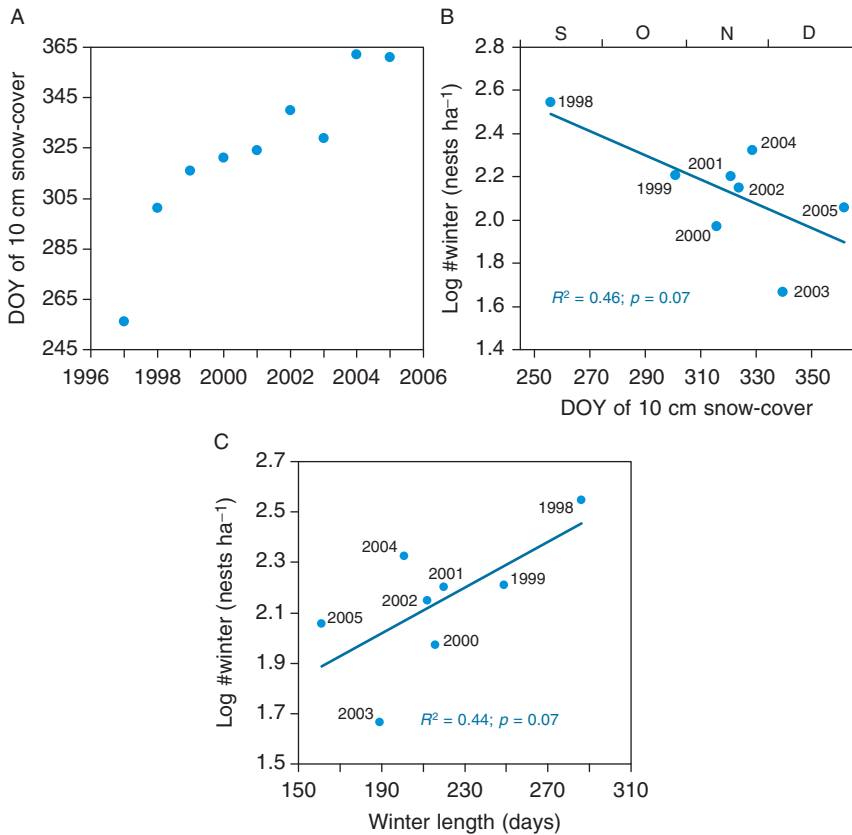
Figure 1 (A) Year to year variation in the onset of winter (defined as first day with >10 cm of snow at the Zackenberg meteorological station) during 1997–2005. (B) The relationship between the number of lemming winter nests and the onset of winter ($R^2 = 0.46$; $p = 0.07$). (C) The length of the winter season (from onset of winter until first day with <10 cm of snow) ($R^2 = 0.44$; $p = 0.07$).

High UV-B radiation may force the plant to allocate resources into UV-B protective secondary plant metabolites (SPM; see Box 2) at the expense of the anti-herbivory targeted SPM (Gwynn-Jones, 1999; Selås, 2006). One consequence of this is increased nutritional value (better assimilation of crude protein) to herbivores.

The climatic pathway in the arctic plant–herbivore system is complex, as different types of tundra respond differently to changes in the abiotic variables. The onset of the winter snow-cover and its duration are probably the most influential on the trophic interactions covered in this chapter both directly and indirectly.

III. PLANT–HERBIVORE INTERACTIONS AT ZACKENBERG

The herbivore system in Zackenbergdalen is relatively simple. The resident vertebrate community consists of one species of rodent (collared lemming), one species of lagomorph (arctic hare *Lepus arcticus*), one species of ungulate (musk ox) and one species of gallinaceus bird (rock ptarmigan *Lagopus mutus*). During summer, two species of geese (pink-footed goose *Anser brachyrhynchus* and barnacle goose *Branta leucopsis*) breed at Zackenberg. In contrast to vertebrates, the exact species composition of the invertebrate herbivore community in Zackenbergdalen is not known, but includes species of Lepidoptera and Hemiptera (Høye and Forchhammer, 2008, this volume).

The BioBasis monitoring programme at Zackenberg has concentrated on collared lemming, musk oxen and larvae of *S. zetterstedtii* and Tenthredinidae sp., but studies of plant–herbivore interactions have focused mainly on the interplay between collared lemmings and musk oxen and their forage.

A. Willow–Musk Ox Interactions

The spatiotemporal utilisation of plant forage by large-bodied and long-lived herbivores, such as the musk ox, is influenced by a range of factors such as variations in quantity and quality of plant forage, social structure, presence of predators and weather conditions (Clutton-Brock *et al.*, 1982; Clutton-Brock and Pemberton, 2004). The relationship between the musk ox and its food resources has been studied intensively in several populations in Greenland (Thing *et al.*, 1987; Klein and Bay, 1991; Forchhammer, 1995; Forchhammer and Boomsma, 1995). Musk oxen move over large ranges (Aastrup, 2004), and fluctuations in the number observed in Zackenbergdalen do not necessarily indicate fluctuations in population size. The actual size of the Zackenberg subpopulation is unknown, but air surveys in 1982–1989 and 2001 estimated the number of musk oxen within Wollaston Foreland and A.P. Olsen Land to be in the order of 500–800 (Boertmann and Forchhammer, 1992; Berg, 2003a). In all study years, musk ox herds at Zackenberg showed an apparent preference for grassland, which constitutes on average 35% of the area used by musk oxen but only 18% of the total available habitat in the valley (Figure 2).

In high-arctic Greenland, the temporal and spatial summer dynamics of musk oxen and one of its main summer food sources, the arctic willow, are linked (Forchhammer, 2003). The production of arctic willow in one year ($t - 1$) is positively associated with the abundance of musk oxen the following year (t) (Figure 3A). In contrast, increased numbers of musk oxen in year $t - 1$ reduce next year's (t) growth of arctic willow (Figure 3B). This high degree of
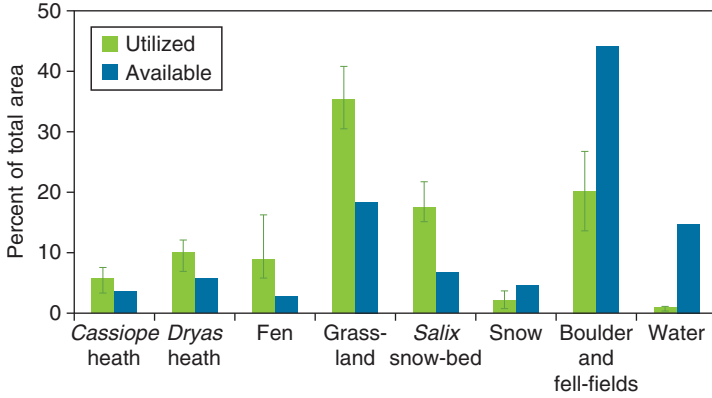
Figure 2 Summer habitat selection by musk oxen in Zackenbergdalen, showing the availability of different vegetation types in the area together with the average percentage musk ox utilisation of each vegetation type (1996–2005). Utilisation of vegetation types is calculated as the fraction of each habitat type within 100-m buffer zones of the herds (D.K. Hendrichsen, unpublished). By using buffer zones, water becomes part of their habitat use, which explains their utilisation of water. Bars indicate the minimum and maximum percentage over the same period of time.
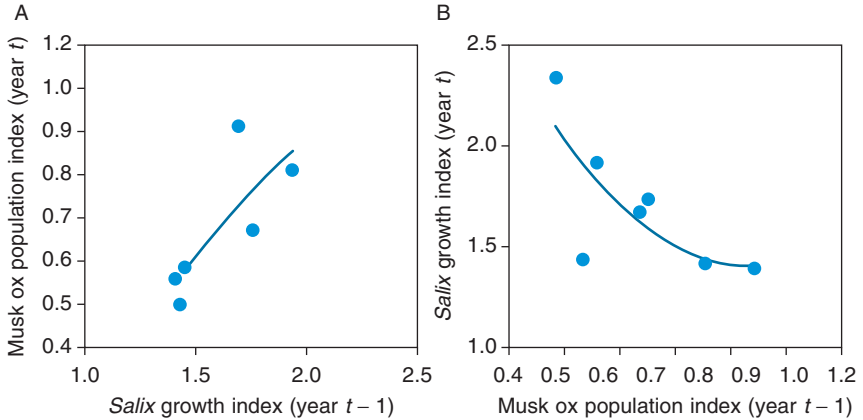

Figure 3 Temporal relationship between (A) current year (t) musk ox abundance and last year ($t – 1$) growth of *S. arctica* together with (B) current year growth (t) of *Salix arctica* and last year ($t – 1$) musk ox abundance at Zackenberg (modified from Forchhammer, 2003).

connectedness between trophic levels suggests that any direct climate-mediated change in the growth of arctic willow may in turn affect the herbivores, resulting in a significant indirect effect of climate on their abundance. Similarly, any direct climatic effect on the abundance of musk oxen is likely to influence the production of arctic willow (Forchhammer, 2001).

Full evaluations of the plant–herbivore interactions and, hence, of the relative role of climate require analyses performed in an ecosystem or in a community context that integrates all relevant effects simultaneously (Forchhammer, 2001). Hence, analysis of the interaction between musk ox and arctic willow in Zackenbergdalen needs to integrate possible interactive effects of the arctic wolf *Canis lupus arctos*. The dynamics of such a tri-trophic system may be analyzed using a three-dimensional autoregressive model (Post and Forchhammer, 2001), which integrates climatic effects with all intra- and inter-trophic interactions. Schmidt (2006) adopted this approach for the wolf–musk ox–willow system at Zackenberg/Wollaston Forland,

$$\begin{bmatrix} P_t \\ M_t \\ S_t \end{bmatrix} = \begin{bmatrix} a_0 \\ b_0 \\ c_0 \end{bmatrix} + \begin{bmatrix} a_1 & a_2 & 0 \\ b_1 & b_2 & b_3 \\ 0 & c_2 & c_3 \end{bmatrix} \cdot \begin{bmatrix} P_{t-1} \\ M_{t-1} \\ S_{t-1} \end{bmatrix} + \begin{bmatrix} a_4 \\ b_4 \\ c_4 \end{bmatrix} \cdot C_t \qquad (1)$$

where P_t and M_t is growth in the wolf abundance and musk ox abundance, respectively, from year $t - 1$ to year t; S_t is the annual growth of arctic willow, whereas C_t is the percent snow-cover on June 10 year t. The regression coefficients at the three trophic levels (a, b and c) express the effects of climate, density dependence and trophic interactions (Schmidt, 2006). For example, the annual change in musk ox abundance (M_t) is a result of the summed influence of changes in last year's wolf abundance (P_{t-1}), density dependence in the musk oxen (M_{t-1}), last year's growth in arctic willow (S_{t-1}) and current year percent spring snow-cover (C_t), that is, $M_t = b_0 + b_1 P_{t-1} + b_2 M_{t-1} + b_3 S_{t-1} + b_4 C_t$.

Dividing the data into two time periods (prior to and after the re-invasion of wolves), Schmidt (2006) found that wolves, at the present population density, seemingly did not influence the willow–musk ox system. However, the period prior to wolf reinvasion was also characterised by generally low snow-cover. In this period, musk ox dynamics were mainly governed by density dependence, whereas neither changes in musk ox abundance nor snow-cover influenced the growth of arctic willow (Figure 4A, B). In contrast, during the period after wolf reinvasion, the snow-cover was generally higher and increased growth of willow had a positive influence on the musk ox population (Figure 4C), whereas the arctic willow growth was negatively influence by both increased musk ox population and increased percent snow-cover (Figure 4D). These analyses indicate that changes in climate expressed by variation in snow-cover affect arctic willow directly, whereas the musk ox population at Zackenberg also is affected by climate indirectly through the climatic effects on one of its main food resource, arctic willow. In corroboration, large-scale studies of the dynamics of musk ox populations in North and Northeast Greenland revealed a 3-year delayed influence of the NAO, which is consistent with a climatic influence on fecundity (Forchhammer *et al.*, 2002, 2008, this volume).
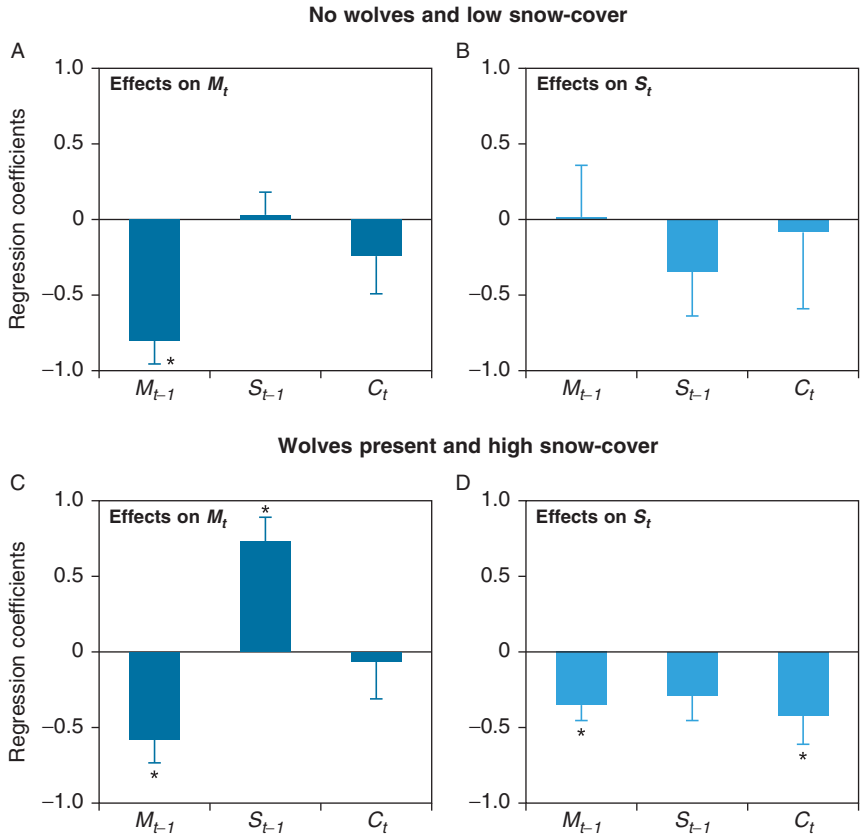
No wolves and low snow-cover

Wolves present and high snow-cover

Figure 4   Results from the three-dimensional model ([Eq. 1](#)) for musk oxen at Zackenberg. Effects (i.e., model regression coefficients) of last year's musk ox population (M_{t-1}), last year's growth in *S. arctica* (S_{t-1}) and current year percent snow-cover (C_t) on current year musk ox population (M_t) and current year growth of *S. arctica* (S_t) during climatic regimes characterised by low snow-cover (A, B) and high snow-cover (C, D), respectively. Asterisks indicate significant parameter estimates (data from Schmidt, 2006).

B. Plant–Lemming Interactions

The dynamics of the lemming cycle in Northeast Greenland are modulated chiefly by predation (Gilg *et al.*, 2003; Schmidt *et al.*, 2008, this volume), although probably also with a climatic component (Schmidt *et al.*, 2008, this volume) acting via changes in food quantity/quality (Berg, 2003b; Callaghan *et al.*, 2005). The collared lemming eat primarily shrubs and forbs (Batzli, 1993), and mountain avens and arctic willow are by far the most utilised food resource of collared lemmings at Zackenberg throughout the year
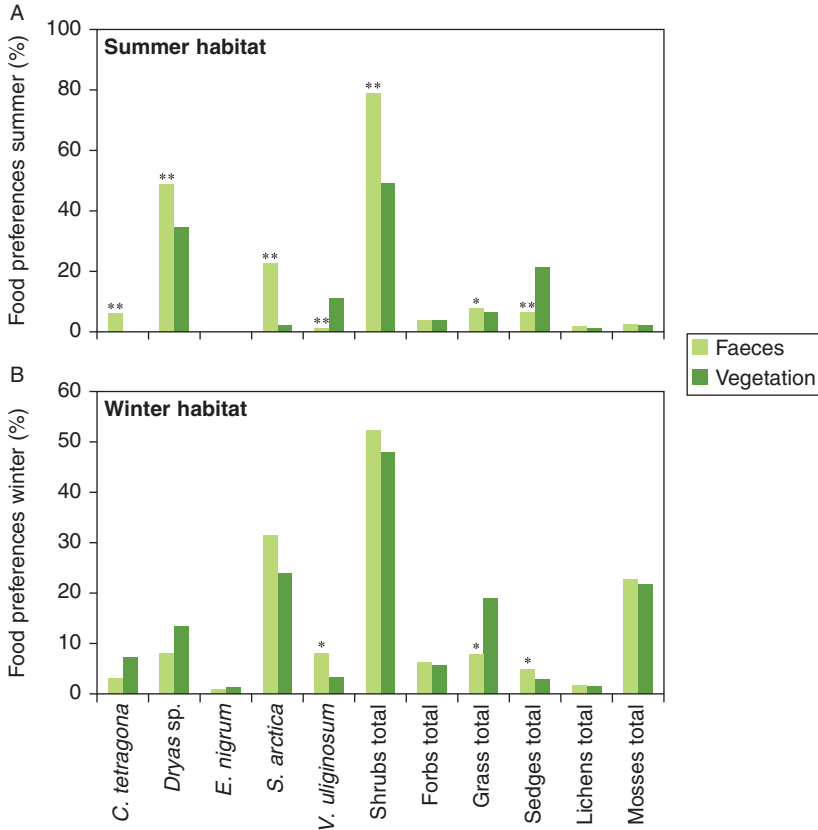
Figure 5 Collared lemming food preference at Zackenberg based on faeces analyses on droppings from nests and burrows compared with vegetation analysis around the respective nest (10 m radius) and burrow (1 m radius). (A) Food plant preferences around summer burrows. (B) Food plant preferences around winter nests. Asterisks indicate significant differences ($p < 0.05$ and $p < 0.01$) (modified from Berg, 2003b).

(Berg, 2003b). These plants are actively selected for during summer (Figure 5A). In winter, their diet reflects the availability of plants and includes a large amount of willow, which is common in their winter habitat (Figure 5B).

One central question is to what extent variation in the abundance of lemmings is influenced by variation in the abundance and quality of their forage. Quality in this perspective is defined as biomass rich in crude protein and modest in concentration of SPM targeted towards herbivory. Grasses are low in SPM (Rhoades and Cates, 1976; Berg, 2003c), and studies on grass–vole relations have not been able to document that the quality of grass is influencing vole abundance (Klemola et al., 2000). Collared lemmings forage, in contrast, contains higher levels of SPM than grasses (Rhoades and Cates, 1976) and, therefore, may negatively affect the herbivores that depend on them.

As in the case of the plant–musk ox interaction, high densities of small herbivores like collared lemmings can negatively affect their preferred food plants. Within the lemming winter habitat, there is an inverse relationship between the density of lemmings and the number of mountain avens flowers the following summer (Figure 6), illustrating that winter herbivory by lemmings may reduce the number of flowers of mountain avens. No such relationship was found for arctic willow. This may reflect the fact that at Zackenberg arctic willow are more evenly dispersed in the winter habitats and so are exposed to lower intensity of grazing per unit area, compared to the more patchily dispersed mountain avens. Despite the few study years, data on plant–lemming interaction in summer suggest that there is a positive relation between the rate of flowering of arctic willow and mountain avens and the density of lemmings in summer habitat. The lack of such positive relation in the winter habitat may relate to differences in the intensity of herbivory in winter and summer habitats. The estimated total area of foraging in winter habitats is on average 18 times greater than the corresponding area in summer (Berg, 2003b). Additionally, the inter-annual overlap in summer forage areas is 25.2% ± 0.02 SE, and within five consecutive years 86.2% of the summer forage area has been reused (T.B. Berg, unpublished analyses). The corresponding figure of inter-annual overlap in winter forage area is expected to be an order of magnitude lower, but no exact field data exists (Berg, 2003b). The intensive foraging during summer is linked to the high predation risk forcing lemmings to forage within 1 m of their summer burrows (Berg, 2003b; Kyhn, 2004; Schmidt *et al.*, 2008, this volume). Consequently, we hypothesise that the concentrations of herbivore-induced SPM is likely to be higher around a
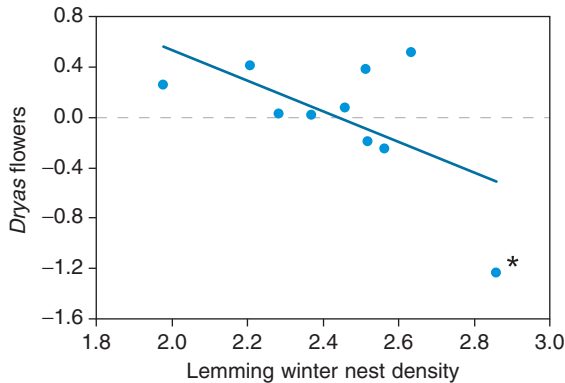

Figure 6   Numbers of *Dryas* flowers at Zackenberg (corrected for the previous year's number of flowers, given as residuals) versus present winter log-transformed lemming density. The outlier (marked with an asterisk) represents the only distinct population peak within the 10-year data ($R^2 = 0.347$, $F_9 = 4.25$, $p = 0.07$).

given summer burrow than around a given winter nest. High concentrations of SPM decrease the digestibility of the forage and the protein uptake by the lemmings and hence, increase their need for compensatory food intake (Seldal *et al.*, 1993), which increases their vulnerability to predators.

Not all SPM are targeted towards herbivores (see Box 2). Some of them are aimed for protection against UV-B. Production of this type of SPM takes up resources for production of SPM aimed for protection against herbivory. Indeed, Selås (2006) demonstrated increased fecundity of both mountain hare *Lepus timidus* and snowshoe hare *Lepus americanus* in response to increased sun screening SPM during high UV-B 2 years earlier. In Zacken-bergdalen, Albert *et al.* (2008, this volume) showed an increase in the UV-B-absorbing flavonoids following increased UV-B exposure. Like the hare-UV-B correlation, we found a positive correlation between winter lemming densities at Zackenberg and the UV-B radiation during July and August 2 years earlier (Figure 7), suggesting that a similar relation may exist between UV-B radiation and the reproductive success of lemmings, but more knowledge on the role of SPM on the reproductive success of lemmings is needed, as well as knowledge on how long the effect of these UV-B screening SPM lasts.

Scott (1993) found that low lemming abundance was associated with low temperatures and high levels of precipitation (rain) during freeze-up in October followed by low temperatures and precipitation during November and December. This combination of weather during early winter will lead to high risk of icing events and poor snow-cover and hence, reduced survival of lemmings (extended period of vulnerability to predation by arctic fox and avian predators). At Zackenberg, we found that a late buildup of a deep winter snow layer was coupled to a low winter population of lemmings, and
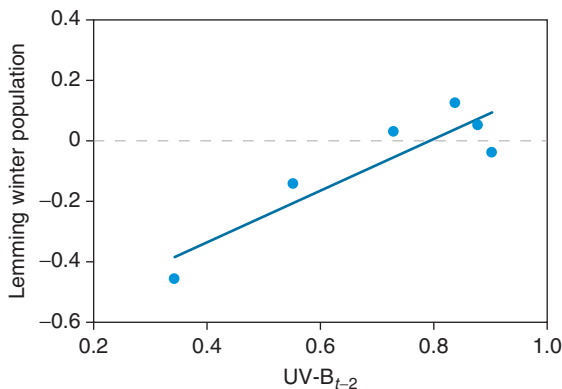

Figure 7   Lemming winter density at Zackenberg adjusted for last year's density (residuals of log-transformed winter nest densities) as a function of the UV-B radia-tion (during July–August) 2 years earlier.

that a long lasting snow-cover (late onset of snowmelt) was positively related with lemming density (Figure 1). Thawing events during winter, which create icy horizons in the snow pack, prevent the access by herbivores to their forage. On areas with thin snow-cover, severe thawing events destroy the vegetation cover. These effects may eventually lead to a crash of the herbivore population (Callaghan *et al.*, 2005) and disrupt the cyclic dynamics of small rodent populations (Aars and Ims, 2002). The number of days during winter with temperature above 0°C decreases the survival rate of tundra voles (Aars and Ims, 2002), and data from Zackenberg suggest that a similar relationship exists for the collared lemming in Northeast Greenland (Figure 8).

In conclusion, besides the effects of predation (see Schmidt *et al.*, 2008, this volume), data from Zackenberg show that the timing and duration of the snow-cover and positive winter temperatures affect the plant–lemming interaction both directly and indirectly and that these effects act through both bottom–up and top–down pathways. Additionally, UV-B radiation seems to affect the lemming density indirectly with a 2-year delay through food quality as has been found in a hare study by Selås (2006), but more studies are needed.

C. Insect Herbivory

Population dynamics of herbivorous invertebrates in the tundra biome is poorly known due to the lack of long-term data series (Callaghan *et al.*, 2005), but cyclic outbreaks by geometrid moths are know to occur with 10-year intervals in the subarctic hemisphere (Callaghan *et al.*, 2005).
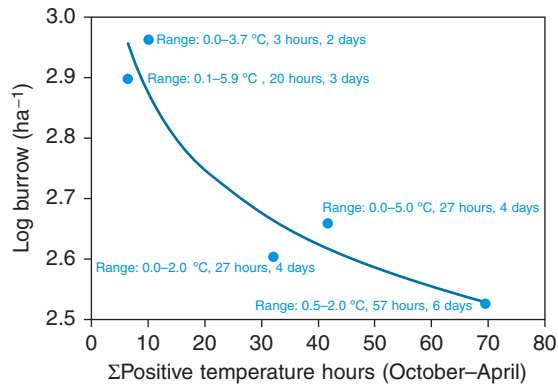

Figure 8 Effect of the sum of positive temperatures measured per hour during winter (October–April) at Zackenberg on the number of active burrows the following summer, $y = 3.3467x^{-0.0659}$, $R^2 = 0.89$. The numbers at each dot show the corresponding temperature range and the number of thawing hours and days. The number of active summer burrows is taken as an index of lemming summer density, which is linked to the winter survival of the lemming population.

No outbreaks of the lepidopteran moth *S. zetterstedtii* occurred during the 10-year time series from Zackenberg. Indeed, only seven larvae of *S. zetterstedtii* were found in all the mountain avens plots. The emergence of *S. zetterstedtii* larvae from winter dormancy takes place the same day their hibernacula become snow-free. Larvae become active by the time mountain avens have begun to flower and therefore can be exploited. The intensity of ovary predation by larvae of *S. zetterstedtii* was recorded as the highest proportion of depredated flowers among open and senescent flowers recorded at weekly checks. Flower ovary predation occurred in those plots that became snow-free in a period of 3 weeks between late-May and mid-June, with an optimum around June 10. Plants that became snow-free after July 1 showed no ovary predation.

From the maximum predation rate and total flower counts, we estimate that a total of 1761 flowers were depredated by *S. zetterstedtii* within the study plots through the study period. Although this is only 4.6% of the total number of flowers produced in the plots during the same period, the distribution is not uniform, and plants in some plots were strongly predated in some years. For instance, flower predation rate exceeded 60% in at least one section of an early snow-free study plot in both 1998 and 1999, meaning that the influence of *S. zetterstedtii* on reproductive success can be substantial on a local scale. It is known from West Greenland that in some years, ovary predation by *S. zetterstedtii* can reach rates of 60–70%, but not what factors may be controlling outbreaks (Philipp *et al.*, 1990).

At Zackenberg, two mountain avens study plots are situated 100 m a.s.l. and 2 km further inland from the other study plots at an average altitude of 35 m a.s.l. The two inland plots had the highest average rates of herbivory, but with considerable variation across years (Figure 9). On the contrary, two late snow-free plots situated in the lowland snow-beds had the lowest average predation rates ($<5\%$ in all years), and no more than three flowers were depredated by *S. zetterstedtii* in any year and plot. Dividing observations into a set of early snowmelt seasons and a set of late snowmelt seasons, both of equal range in terms of the date of onset of flowering, the predation rate was largest early in the season ($\text{mean}_{\text{early}} = 4.67$; $\text{SE}_{\text{early}} = 0.93$; $\text{mean}_{\text{late}} = 0.39$; $\text{SE}_{\text{late}} = 0.23$). In this calculation, we excluded the two uphill plots, since data on onset of flowering is available only for 2 years in these plots.

In conclusion, flower herbivory by *S. zetterstedtii* varies considerably from year to year and takes place mainly in areas of early flowering. We did not find any relation between predation rates and flower abundance nor between predation rates and timing of 50% flowering (GLM, $F_{22} = 1.51$, $R^2 = 0.06$, $p = 0.23$). The substantial spatial variability in herbivory rates seems to indicate that the risk of flower herbivory is small and is governed more by local conditions like suitable over-wintering habitats for *S. zetterstedtii* than by climatic effects on a bigger scale as recorded at the metrological station.
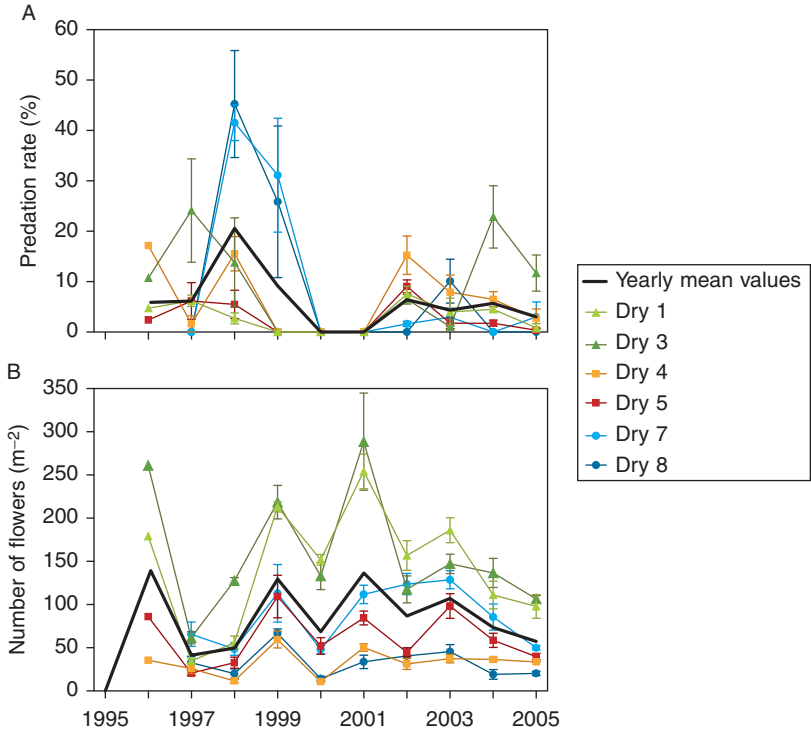
Figure 9 Year to year variation in predation rates on flowers of mountain avens and the corresponding abundance of flowers of mountain avens. (A) Average predation rates of insect flower herbivores in different plots. (B) Density of flowers (flowers m^{-2} in different plots) for mountain avens at Zackenberg. Error bars are one standard error. Data from plots that never exceeded 5% average predation are omitted (Dry 2 and Dry 6). Black lines indicate yearly mean values. The two inland plots (Dry 7 and Dry 8) had the highest average rates of herbivory, but with considerable variation across years.

IV. THE ROLE OF SECONDARY PLANT METABOLITES

Many plants produce various compounds, often referred to as SPM, which may act as anti-herbivore substances or in other ways help protect the plant (Box 2).

In a study conducted at Zackenberg, concentrations of anti-herbivore SPM in arctic willow and mountain avens have been shown to affect the consumption rate (amount eaten/hour) by collared lemming, with more plant material eaten from plants with less concentration of anti-herbivore SPM (Berg, 2003c). Such selective feeding by herbivores may likely affect the plant

Box 2

Secondary Plant Metabolites and Their Role in Plant–Herbivore Interaction

Plants exposed to various stress factors like nutrient shortage, drought, UV-B radiation, climatic extremes, herbivory and parasitism respond by changing their content of secondary plant metabolites (SPM). Some SPM reduces the degree of herbivory, as previously reported for lagomorphs (Bryant, 1987; Robbins et al., 1987; Selås, 2006), small rodents (Batzli, 1983; Seldal et al., 1993; Berg, 2003c; Laitinen et al., 2004) and large cervids (Robbins et al., 1987).

The SPM concentration changes during the growing season in relation to not only the amount of nutrients and energy available but also the reproductive investments of the plant (Batzli, 1983; Lindroth and Batzli, 1986; Laine and Henttonen, 1987; see Fig. 10A). The production of SPM is energetically costly (Soloman and Crane, 1970; Koricheva et al., 1998), and reduction in incoming solar radiation presumably decreases the energy available for production of SPM (see Figure 10B). UV-B is harmful to the plant and therefore plants respond to increased UV-B radiation by allocating amino acids into sun screening on the expenses of herbivore-protective phenolics, resulting in increased levels of leaf nitrogen content (Gwynn-Jones, 1999; Selås, 2006). Hence, the plants increase their nutritional value to herbivores. This is indicative of a climatic influence on the quality of plant tissues as food for herbivores.

Sexual differences may occur in those species having separate sexual individuals like arctic willow (Klein et al., 1998; see Figure 10A). In species of willow, poplar and birch, non-reproducing individuals contained more SPM than reproducing ones, and hence, were less preferred as food items by voles (Danell et al., 1987). The reason is that non-reproducing individuals are able to invest more in SPM than reproducing individuals (Danell et al., 1987). Among reproductive arctic willow, female plants tend to have higher concentration of SPM than male plants, since seed production is more costly than pollen production (Cornelissen and Stilling, 2005), which also has been observed in Zackenbergdalen (see Figure 10A). The reason may be that female plants need more photosynthetically active tissue for seed production than males do for pollen production and hence, females need to protect their tissues more than males.

Food plants with low digestibility increase the time needed for digestion, which escalate the nutritional stress, as stomach size becomes a limiting factor. Hence, food quality may play an important role in

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Box 2 *(continued)*

lemming ecology as well as in ruminant ecology, where the time for rumination is the limiting factor of food passage. For microtine rodents, consumption of food plants with high levels of proteinase-inhibiting SPM decreases the protein intake significantly, thereby increasing the time needed for foraging and ultimately affecting their condition. In extreme cases, lemmings have been found to die of malnutrition when fed with food plants high in proteinase-inhibiting SPM (Seldal *et al.*, 1993). In general, the quality of a food plant is a trade-off between the SPM content, energy content and the quantity of the given plant (Robbins *et al.*, 1987).
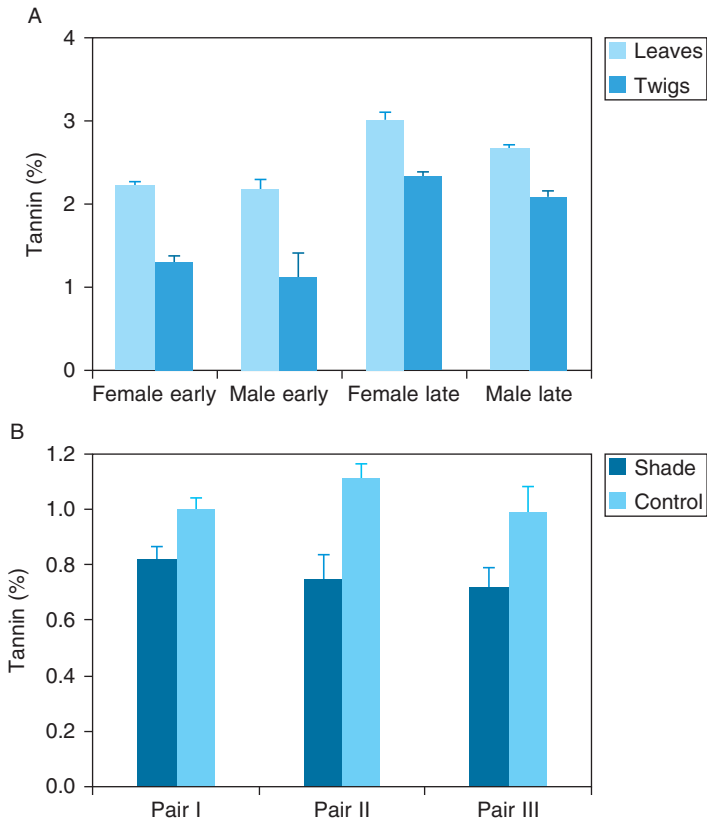

Figure 10 Tannin content in Arctic willow *Salix arctica*. (A) Sexual differences in tannin content and changes in tannin content during the growing season (D. Klein, unpublished data). (B) Three replicate pairs of shaded and unshaded arctic willow plots (1 month of 50% reduction in incoming solar radiation during the growth season) (modified from Klein *et al.*, 1998).

composition in favouring those individuals within a species that have the highest concentration of SPM.

In arctic willow, female-biased sex ratios are found in Zackenbergdalen (Klein *et al.*, 1998) and in arctic Canada (Crawford and Balfour, 1990). Seeds from arctic willow collected in the valley germinate and grow to flowering with a sex ratio close to unity. Nonetheless, the sex ratio of reproducing arctic willow plants in Zackenbergdalen is 60% female biased (Klein *et al.*, 1998). In the valley, female arctic willow plants contain higher concentrations of tannins (an anti-herbivore SPM; Swain, 1979) than male arctic willow plants, especially in late summer (Figure 10A, Berg, 2003c). Similar inter-sexual differences in SPM content have been observed elsewhere in the Arctic (Dawson and Bliss, 1989). Females of arctic willow may thus be better defended against tissue loss to herbivores than male plants, especially during the summer reproductive period (Klein *et al.*, 1998). Arctic willow makes up a large fraction of the diet of musk oxen and lemmings in summer and even in the winter diet of the collared lemming (Figure 11; Klein and Bay, 1991, 1994; Klein, 1995; Berg, 2003c). At Zackenberg, female arctic willow was eaten at significantly lower rates (amount eaten by lemmings per hour) than males (Berg, 2003c). This difference was positively related to the generally higher tannin concentration (mg/g) found in female leaves over the summer (39.28 $\pm$ 5.01SE) compared to males (25.87 $\pm$ 2.96) (Berg 2003c). Hence, inter-sexual differences in tannin levels may make female willow plants less prone to herbivory than male plants. Cantina experiments conducted at Zackenberg have documented that consumption rates of arctic willow and
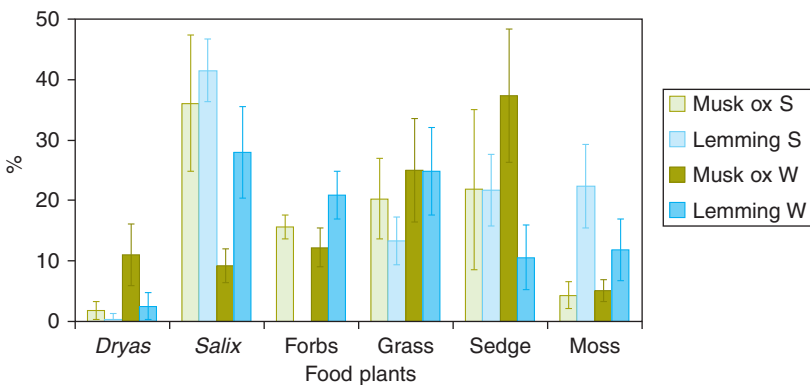

Figure 11 Comparison of fragments of different genera of plants in summer (S) and winter (W) faeces of lemmings and musk oxen in Nansen Land (North Greenland) (modified from Klein and Bay, 1994).

mountain avens by collared lemmings are negatively related to their content of anti-herbivore SPM (Berg, 2003c).

Several small rodent species have been shown to prefer plants with low SPM concentration over plants with high SPM concentrations (Dearing, 1997; Berg, 2003c; Laitinen *et al.*, 2004). Selective feeding on arctic willow genders, that is, sex-biased herbivory, may thus be an important factor in shaping the biased sex ratios observed in arctic willow (Elmquist *et al.*, 1988; Boecklen *et al.*, 1990; Hjältén, 1992; Ueno and Seiwa, 2003). The dietary intake of herbivores is, however, balanced between several elements, and in Zackenbergdalen, the preference of collared lemmings for arctic willow and mountain avens seems to reflect a trade-off between the crude protein content and the content of SPM (Berg, 2003b).

V. CONCLUSIONS AND FUTURE PERSPECTIVES

Beside the impact of predation, climate in terms of timing and duration of the snow-cover is one of the most important variables affecting the plant–herbivore system. Positive winter temperatures that create thawing events with ice horizons in the snow and icing on bare ground can have catastrophic effects on both vegetation and herbivores. Additionally, UV-B radiation seems to be yet another candidate that indirectly affects the herbivore population that depends on plants that produce UV-B-protective SPM, but more studies are needed. At least within the plant–musk ox and the plant–lemming systems, interactions can follow both bottom–up and top–down pathways. Herbivores respond to changes in primary production and plants respond to changes in the intensity of herbivory, with both pathways being affected by climate. Data on plant–insect interaction were able to illustrate only a top–down effect on a small local scale.

The expected future climatic changes in Northeast Greenland are outlined in detail by Stendel *et al.* (2008, this volume). As discussed by Ellebjerg *et al.* (2008, this volume), increased length of the growing season and more precipitation during summer will lead to increased plant biomass. Not all habitat types will be equally affected by the predicted climate change scenario, and climate may affect herbivore-specific winter and summer habitats differently. Wet tundra will be less affected by increased precipitation compared to dry tundra, which most likely will experience a relatively greater increase in biomass compared to the wet tundra (Heal *et al.*, 1998). Dry tundra is intensively used by lemmings during summer and may to great extent be regarded as a bottleneck in terms of survival and population growth. Hence, increased standing plant biomass will have a positive effect on lemmings, not only as an increased amount of forage but also as an

increased shelter against avian predators. Increased snow-cover will in general benefit the lemmings, if the snow-covered period stays unchanged. Contrarily, the positive effect of increased snow-cover will be hampered if the buildup of the snow pack is delayed. Musk oxen, in contrast, will benefit from a delayed buildup of the snow-cover, through the prolonged season with relative easy access to forage, if no icing occurs during the freeze-up period. Severe thaw events during winter will destroy the plant cover by ice crust formation on exposed vegetation or prevent the herbivores, like musk oxen and arctic hares, from reaching the vegetation through ice layers in the snow.

Another strong abiotic parameter affecting living species is UV-B radiation. UV-B radiation induces the plants to allocate more resources into UV protection, which does not at the same time protect against herbivores. Hence, higher UV-B radiation will be an advantage for all herbivores as will increased cloud cover, which in general reduces SPM production in plants (Figure 10B).

The well-known lemming cycle will most likely be affected during the expected climate change scenarios (Callaghan *et al.*, 2005; Schmidt *et al.*, 2008, this volume). During the present 10-year data period from Zackenberg, the lemming population has only experienced one well-defined peak (1998). Since this peak, the lemming population peaks have not reached equally high densities. The same holds for the population on Traill Ø, 220 km south of Zackenberg (see Figure 1 in Schmidt *et al.*, 2008, this volume). These two lemming scenarios coincide with the fact that since 1997 the buildup of the snow-cover in Zackenbergdalen and likely also on Traill Ø has been delayed by about 80 days, and seemingly the cyclic fluctuation in lemming numbers has been disturbed. A breakdown of the lemming cycles will probably lead to chaotic fluctuation pattern known from rodent populations under more southerly climates.

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