Exclusion of brown lemmings reduces vascular plant cover and biomass in Arctic coastal tundra: resampling of a 50+ year herbivore exclosure experiment near Barrow, Alaska

D R Johnson¹, M J Lara¹, G R Shaver², G O Batzli³, J D Shaw⁴ and C E Tweedie¹

¹ Systems Ecology Laboratory, Department of Biology, The University of Texas at El Paso, 500 West University Avenue, El Paso, TX 79968, USA
² Ecosystem Center, Marine Biology Laboratory, 7 MBL Street, Woods Hole, MA 02543, USA
³ Department of Animal Biology, University of Illinois at Urbana-Champaign, 505 South Goodwin Avenue, Urbana, IL 61801, USA
⁴ Australian Antarctic Division, Department of Sustainability, Environment, Water, Population and Communities, 203 Channel Highway, Kingston, Tasmania 7050, Australia

E-mail: drjohnson2@utep.edu

Received 1 August 2011
Accepted for publication 24 October 2011
Published 17 November 2011
Online at stacks.iop.org/ERL/6/045507

Abstract

To determine the role lemmings play in structuring plant communities and their contribution to the ‘greening of the Arctic’, we measured plant cover and biomass in 50+ year old lemming exclosures and control plots in the coastal tundra near Barrow, Alaska. The response of plant functional types to herbivore exclusion varied among land cover types. In general, the abundance of lichens and bryophytes increased with the exclusion of lemmings, whereas graminoids decreased, although the magnitude of these responses varied among land cover types. These results suggest that sustained lemming activity promotes a higher biomass of vascular plant functional types than would be expected without their presence and highlights the importance of considering herbivory when interpreting patterns of greening in the Arctic. In light of the rapid environmental change ongoing in the Arctic and the potential regional to global implications of this change, further exploration regarding the long-term influence of arvicoline rodents on ecosystem function (e.g. carbon and energy balance) should be considered a research priority.

Keywords: lemmings, Arctic warming, climate change, tundra greening, herbivory, Arctic plant communities

1. Introduction

Multiple lines of evidence suggest that Arctic terrestrial ecosystems are sensitive to climate change (Post et al 2009) and that the amplified warming ongoing in the Arctic (IPCC 2007) may be resulting in large-scale and rapid changes in many Arctic ecosystems (ACIA 2005, Hinzman et al 2005, Callaghan et al 2011b). While these changes have the potential to affect both the cryospheric (Hinzman et al 2005) and hydrologic (Rowland et al 2010) properties of Arctic
landsca. The boom–bust population dynamics of the brown lemming (*Lemmus trimucronatus*) has long intrigued researchers in northern Alaska (Thompson 1955a, Pitelka and Batzli 2007). Early observers of periodic outbreaks of lemmings noted that lemmings could denude the landscape of graminoids, resulting in the depletion of their food supply and increased rates of predation (Thompson 1955b). Thus, lemmings were thought to have an important role in regulating many tundra ecosystem properties and processes (Pitelka 1957). This view formed the foundation of the Nutrient-Recovery Hypothesis (Schultz 1964), which described ecosystem responses following peak lemming years. This hypothesis proposed that during interim years between population highs, vegetation recovers, standing dead biomass accumulates, and gross primary production returns to levels that support increased lemming densities (Schultz 1964). To assess the impact of lemmings on the tundra ecosystem near Barrow, Alaska, exclosures were built in various plant communities among different land cover types (Thompson 1955b, Schultz 1964, 1969). During periods with lemming population highs, graminoid biomass in control plots was greatly reduced relative to that of the exclosures in the short-term (Thompson 1955b). However, resampling of these plots 15 years after establishment showed that long-term exclusion of lemmings resulted in higher, rather than lower, graminoid biomass in control plots relative to exclosures (Batzli 1975), thus highlighting the difference between long-term and short-term plant community responses to lemming outbreaks.

As a contribution to the International Polar Year—Back to the Future (Proj. No. 512) project (Callaghan et al 2011a), we revisited the exclosures established by Schulz in 1959 and collected data during the 2002 and 2010 growing seasons. We used 12 of the original exclosures that remain intact and have effectively excluded lemmings for the past 50+ years (figure 1). Biomass data were collected in 2002 from these plots, and we repeated biomass sampling and estimated cover for vascular and nonvascular plant species in 2010. Unfortunately, historic biomass data collected in 1974 no longer exist in their raw format. However, we qualitatively

---

**Figure 1.** An example of an historic lemming exclosure and control plot in wet tundra near Barrow, Alaska.
compare mean biomass measured in 1974 by Batzli (1975) to data collected in 2002 and 2010. This study represents what we believe to be the longest herbivore exclosure experiment in the Arctic. Specifically, we examine the effects of sustained herbivory on plant community composition and the degree to which lemming herbivory may have contributed to the regional greening signal detected by Bhatt et al. (2010). Thus, we asked: (i) how has long-term herbivore exclusion altered community composition and diversity?; (ii) how did this change between 1974, 2002 and 2010?; and (iii) did effects differ among exclosures in dry, moist and wet tundra?

2. Methodology

2.1. Site descriptions

All experimental plots used in this study are located within 5 km of Barrow, Alaska (71°18′N, 156°40′W) on the Arctic Coastal Plain of northern Alaska (Brown et al. 1980). Mean annual temperature, precipitation, and snowfall are −12°C, 11 cm and 69 cm respectively (1971–2000); (NCDC 2005). While there has been a slight warming trend in the Barrow area over the past ten years (Shiklomanov et al. 2010), neither the study years presented here, nor the year preceding, were exceptionally warm or wet. The landscape is underlain by continuous permafrost and active layer depth rarely exceeds 40 cm. The region’s low topographic relief (0–10 m a.s.l.) results in a fairly ‘waterlogged’ environment, 65% of which is polygonized tundra (Brown et al. 1980). Vegetation varies according to microtopography and soil moisture, where drier heath-like tundra with more shrubs and forbs dominates slightly elevated areas, such as old beach ridges, high-center polygons and the rims of some low center polygons; and graminoids dominate wetter areas with poor drainage, such as lower troughs, meadows and marshes. Brown lemmings are fairly common in this ecosystem, eating primarily graminoids and bryophytes in winter, and have periodic population outbreaks with very high densities every 3–5 years (Batzli et al. 1980). While the brown lemming is the primary herbivore in this system, collared lemmings (Dicrostonyx groenlandicus) live at very low abundances (Batzli et al. 1980). Caribou also occur in coastal tundra but they are rare at this study site due to hunting pressures from the local Barrow community.

In 2002 and 2010 we resampled twelve pairs of control and enclosure plots that discharged to the Barrow community. Sampling efforts in 2002 and 2010 occurred two years following lemming population outbreaks in 2000 and 2008 respectively (Holt 2010). Enclosures were situated in dry, wet and intermediate (moist) land cover types (n = 4 in all cases, figure 1) and consisted of a 2 m × 2 m plot with posts driven to permafrost surrounded by 1.27 cm² wire mesh buried 10–15 cm into the soil and extending ca. 75 cm above the ground. Control plots were established within 5 m of each enclosure and consisted of a 2 m × 2 m plot marked with wooden pegs. We quantitatively determined the land cover type for each site by measuring soil moisture with at Spectrum Time Domain Reflectometer probe, and categorized sites as dry below 30% volumetric water content (VWC), moist between 30% and 60% VWC, and wet above 60% VWC.

2.2. Plant cover and biomass

In 2010, during the final week of July and close to peak growing season, we measured plant species cover by visually estimating the cover of each vascular and nonvascular species present in the center 1 m² of the exclosure and control plots. We also estimated the cover of bare ground, vascular plant litter and animal sign (lemming clippings, burrows, and trails and feces).

Close to peak growing season in 2002 and 2010, we randomly located two 10 cm × 10 cm quadrats within all 1 m² plots described above and collected biomass samples by cutting through surface vegetation to below root depth and removing all plant and soil within the quadrat. An individual plant was considered ‘within’ the sample if the meristems were within the quadrat. All live, aboveground biomass (green material and woody stems) were sorted manually and vascular and nonvascular plants were assigned to various functional groups. We also combined standing and loose dead material as litter. All material was then oven dried at 70°C for 48 h and weighed.

2.3. Statistical analysis

We calculated species richness and the Shannon–Wiener index of diversity using 2010 cover estimates for individual species. To determine how herbivore exclosures affected diversity among land cover types with different plant communities, we applied a two-factor ANOVA using treatment and plant community as main factors. We examined differences among groups using least significant differences (LSD) in a post hoc test. To see how plant functional types as a whole differed with treatment and land cover type, we combined specific data for covering the following classes: lichens, bryophytes, forbs, deciduous shrubs, and graminoids. To calculate relative cover, which adjusts community composition for varying total cover in different samples and allows for better comparison among land cover types, we included categories for animal sign, litter, and bare ground. We only used six plant functional types; five living categories plus litter, for analysis of biomass. To determine the effect of treatment (exclosure) and land cover types on species composition, we used MANOVA with cover of plant functional types as the multiple variables and with exclosure or control (EX/C) and land cover type (LCT) as main factors. We used a two-way repeated-measures MANOVA to test for differences in biomass among plant functional types (treatment and plant community as main factors, and year, 2002 or 2010 as the repeated factor). We examined differences among functional types using univariate ANOVAs within the MANOVAs and post hoc LSD tests. All data were checked for normality and homogeneity of variance, and to meet these assumptions cover and biomass data were arcsine and natural log transformed respectively. All statistical analyses were performed using JMP V.8.0 (Cary, NC).

3. Results

3.1. Diversity

Exclusion of lemmings for over 50 years did not result in overall differences in species richness between enclosure and control plots (table 1). Species richness differed among

Environ. Res. Lett. 6 (2011) 045507

D R Johnson et al
land cover types, with dry communities having the most species and wet communities the fewest, but no statistical difference occurred between exclosures and control plots. This pattern generally held for the Shannon–Wiener index (which mathematically incorporates evenness and richness) of diversity, except that an interaction occurred so that exclosure plots had higher diversity than control plots at dry and moist sites, but controls had slightly higher diversity at wet sites (table 1).

### 3.2. Cover

Unlike diversity, exclusion of lemmings resulted in strong changes in the response of functional types to land cover type (figure 2; EX/CT main effect, Wilks’ $\lambda = 0.05$, $F_{7.12} = 9.0$, $p < 0.001$; LCT main effect. Wilks’ $\lambda = 0.03$, $F_{14.24} = 8.1$, $p < 0.001$; EX/CT*LCT Interaction Wilks’ $\lambda = 0.1$, $F_{14.24} = 3.73$, $p = 0.002$). Univariate analysis revealed greater animal sign and bare ground in control plots than in exclosures (no animal sign was observed in the exclosures), which did not vary with land cover type (table 2). Interestingly, bryophytes, deciduous shrub and forb cover did not show treatment effects, only land cover type effects. Cover of bryophytes and forbs generally increased as soil moisture increased, whereas more deciduous shrubs occurred in drier tundra (figure 2). Graminoids increased as soil moisture increased, and decreased in exclosures, particularly in wet tundra (figure 2, table 2). Lichens showed the opposite response, decreasing in cover with soil moisture and increasing in cover in exclosures, particularly at drier sites. More litter occurred inside lemming exclosures than in control plots, particularly in wet tundra.

### 3.3. Biomass

The distribution of biomass among functional types differed with year (figure 3; Wilks’ $\lambda = 0.44$, $F_{6.31} = 2.3$, $p = 0.06$), land cover type (Wilks’ $\lambda = 2.2$, $F_{6.31} = 11.38$, $p < 0.001$) and treatment (Wilks’ $\lambda = 0.26$, $F_{12.62} = 4.97$, $p < 0.001$), however, there were no significant interactions among main effects. Similar to cover, bryophyte biomass increased with soil moisture, however, year and treatment also influenced results (figure 3, table 3). Bryophyte biomass increased as sites increased with soil moisture in 2010, but not in 2002 (year*LCT interaction), and it was higher in exclosures than in controls in 2010, but not in 2002 (year*EX/CT interaction). Similar to results for cover, deciduous shrub biomass was higher at drier sites, no shrubs occurred in wet sites, and no significant effect of treatment was observed. Forb biomass, although never large, was generally greatest inside exclosures and in moist tundra (figure 3). Graminoid biomass increased as soil moisture increased and was lower inside exclosures than control plots in all land cover types. Lichen biomass showed opposing trends to those for graminoids (figure 3).

---

**Table 1.** Mean (±s.e.) species richness and the Shannon–Wiener Index of Diversity for herbivore exclosures (EX) and control plots (CT) in the three land cover types (LCT). ANOVA results revealed that richness differed among land cover types ($F_{2,18} = 26.2$, $p < 0.0001$), but exclosures and controls did not differ significantly ($F_{1,18} = 8.2$, $p = 0.5$). The ANOVA results for the Shannon–Wiener Index revealed a significant treatment*land cover type interaction ($F_{2,18} = 4.6$, $p = 0.02$).

| LCT     | CT  | EX  | CT  | EX  | Shannon–Wiener index |
|---------|-----|-----|-----|-----|----------------------|
| Dry     | 23.1 (±2.3) | 24.9 (±3.3) | 2.1 (±0.1) | 2.4 (±0.1) |                     |
| Moist   | 16.7 (±2.2) | 17.7 (±1.9) | 1.8 (±0.1) | 2.0 (±0.2) |                     |
| Wet     | 12.3 (±1.1) | 10.5 (±1.7) | 1.7 (±0.1) | 1.4 (±0.2) |                     |

**Table 2.** Probability values describing the results of univariate ANOVAs within a MANOVA for relative cover estimates of plant functional types in herbivore exclosures and control plots (EX/CT) among three land cover types (LCT) near Barrow, Alaska in 2010. Factors that were at or near statistical significance ($P = 0.05$) are indicated in bold type (n = 4 pairs of EX/CT plots per LCT). Mean values for categories are shown in figure 2.

| Univariate responses | EX/CT | LCT | EX/CT*LCT |
|---------------------|-------|-----|-----------|
| Animal sign         | 0.005 | 0.21| 0.25      |
| Bare ground         | 0.09  | 0.56| 0.56      |
| Bryophyte           | 0.6   | 0.05| 0.46      |
| Deciduous shrub     | 0.42  | 0.01| 0.67      |
| Forb                | 0.81  | 0.05| 0.75      |
| Graminoid           | 0.03  | 0.03| 0.02      |
| Lichen              | <0.001| <0.001| 0.01    |
| Litter              | 0.03  | 0.15| 0.005     |
Figure 3. Mean biomass of plant functional types in control plots and herbivore exclosures in three land cover types near Barrow, Alaska. Top panel gives results for 2002 and bottom panel for 2010. For summary of significant differences between years, treatments, and land cover types as indicated by univariate ANOVAs, see table 3.

Table 3. Probability values describing the results of univariate ANOVAs within a MANOVA of the biomass of plant functional types in herbivore exclosures and control plots (EX/CT) among three land cover type (LCT) near Barrow, Alaska in 2002 and 2010 (Year). Factors at or near statistical significance ($P = 0.05$) are indicated in bold type ($n = 4$ pairs of EX/CT plots per LCT). Mean values for categories are shown in figure 3.

| Univariate responses | Year | EX/CT | LCT | Year*EX/CT | LCT | Year*EX/CT*LCT |
|----------------------|------|-------|-----|------------|-----|----------------|
| Bryophyte            | 0.04 | 0.03  | <0.001 | 0.12       | 0.06 | 0.66           |
| Deciduous shrub      | 0.41 | 0.90  | 0.01  | 0.13       | 0.52 | 0.83           |
| Forb                 | 0.66 | 0.03  | <0.001 | 0.87       | 0.74 | 0.25           |
| Graminoid            | 0.21 | 0.07  | <0.001 | 0.20       | 0.59 | 0.53           |
| Lichen               | 0.54 | 0.04  | <0.001 | 0.30       | 0.21 | 0.72           |
| Litter               | 0.16 | 0.09  | 0.59  | 0.69       | 0.52 | 0.32           |

Litter biomass did not differ with land cover type or between exclosures and controls in either year.

Although Batzli (1975) sampled 20 sets of exclosures in 1974 (4 wet, 9 mesic and 7 dry) and we only sampled a subset of those (4 in each land cover type) due to many exclosures falling into disrepair, qualitative comparisons of biomass can be made for two functional components of the vegetation with the same sampling and classification procedures. At dry sites, lichen in control plots averaged ca. 40 g m$^{-2}$ in 1974, 50 g m$^{-2}$ in 2002, and 30 g m$^{-2}$ in 2010, whereas excursion plots averaged ca. 80 g m$^{-2}$ in 1974, 260 g m$^{-2}$ in 2002, and 150 g m$^{-2}$ in 2010. Thus, while control plots showed no trend over the years, lichen biomass increased two-fold in excursion plots. In moist plots, lichen biomass increased during the three sampling years in both controls and exclosures, but was greater within exclosures (30, 40 and 75 g m$^{-2}$, respectively for controls, and 40, 80 and 150 g m$^{-2}$ for exclosures, respectively). Less consistent changes in lichen biomass occurred at wet sites (5, 30 and 0 g m$^{-2}$, respectively for controls, and 10, 15 and 25 g m$^{-2}$, respectively for exclosures). Graminoids showed the opposite result with greater and more consistent increases in controls than in exclosures, except at dry sites (120, 175 and 160 g m$^{-2}$, respectively, for controls and 100, 135 and 70 g m$^{-2}$, respectively, for exclosures at wet sites; 40, 110 and 90 g m$^{-2}$, respectively, for controls and 25, 40 and 40 for exclosures at moist sites; 20, 40 and 40 g m$^{-2}$, respectively for controls and 10, 20 and 35 g m$^{-2}$, respectively, for exclosures at dry sites). No comparisons could be made for bryophytes because the two studies used different methods to determine bryophyte biomass.
4. Discussion and conclusion

The 50+ year exclusion of lemmings from the coastal tundra near Barrow resulted in dramatic changes to plant community structure, but the specific effects varied with vegetation type. Results are largely consistent with prior studies that suggest herbivores can have a positive effect on graminoids (e.g. van der Wal and Brooker 2004); although for an exception see (Virtanen 2000) and may control transitions between moss and lichen dominated tundra and graminoid tundra states (e.g. Zimov et al 1995). As expected, animal signs only occurred in the control plots, verifying the sustained effectiveness of the enclosures. Sampling methods also appeared to be coherent, indicated by the generally close agreement between data for cover and biomass. Although cover data showed some interactions between land cover type and treatment that biomass data did not, the exclusion of lemmings resulted in substantial changes to the plant communities investigated. In dry tundra enclosures, a lichen dominated community has developed, similar to that seen with the exclusion of other mammalian herbivores (e.g. van der Wal 2006, Gough et al 2008). Vegetation changes in wet tundra enclosures resulted in a moss-dominated community with higher amounts of standing litter and a lower abundance of graminoids, an effect similar to that reported by van der Wal and Brooker (2004). Exclusion in moist tundra appeared to produce an intermediate response with increases in lichens, forb and bryophyte biomass, and a decrease in the abundance of graminoids. Despite these shifts in functional types, enclosures had little effect on species diversity, a result that largely masks shifts in the species pool away from a diverse vascular flora toward a lichen and bryophyte dominated flora within the enclosures. However, there was a significant land cover type by treatment interaction for the Shannon–Wiener Index of Diversity. Exclusion of lemmings resulted in higher Shannon–Wiener values in dry, generally low productive, plots and lower values in wet, generally higher productive, plots is consistent with the grazer-reversal hypothesis (sensu Proulx and Mazumder (1998)). The increasing difference between controls and enclosures from 1974 to 2002/2010 indicated a continuing impact from the enclosure treatments almost 50 years after their construction. Differences in the distribution of biomass among functional plant groups in 2002 and 2010 suggests that changes in vegetation in response to removal of grazers are still occurring, but whether this reflects continuing development of treatment effects after 50 years or interannual variability remains unknown.

In work previously published on these enclosures and control plots, Batzli (1975) reported more graminoids in the moist and dry tundra control plots relative to enclosures, more litter in moist site enclosures, and more lichen in dry site enclosures. We found more graminoids in control plots than enclosures for all land cover types, suggesting that brown lemmings facilitate the production of their preferred forage, which includes several common species of graminoids in such as Carex spp., Eriophorum spp. and Dupontia fisherii (Batzli and Pitelka 1983). Herbivores usually influence vegetation through direct removal of biomass of palatable species (Diaz et al 2007), but many graminoid species with evolutionary histories closely tied to those of herbivores have compensatory growth strategies (Ferraro 2002). Although this seems to be rare in Arctic graminoid species (e.g. Elliot and Henry (2011)), tolerance (Brätten and Odasz-Albritsgen 2000) may be more common among graminoids at Barrow (Chapin et al 1980). While intensive grazing by lemmings may reduce production over short time scales of a few years (Thompson 1955b), sustained episodic herbivory appears to increase graminoid biomass over much longer time scales (Batzli 1975). Schultz (1969) noted that production and decomposition inside enclosures steadily declined with the age of the herbivory enclosures studied, whereas organic matter decomposed faster in the presence of lemmings outside the enclosures. As a result of these and other studies, Batzli (1975) concluded that extensive clipping of monocot shoots by episodic lemming outbreaks increased rates of nutrient cycling, and that this accounted for a greater production of graminoid biomass over long time periods. Batzli also noted that lemmings disrupt moss and lichen vegetation, particularly when they grub for rhizomes when population densities are high, which could account for the low abundance of moss and lichen cover documented for control plots in this study. Lemmings also eat large amounts of moss, particularly in winter (Batzli and Pitelka 1983), which may partially explain the decline of mosses in control plots.

The distinction between short-term and long-term effects highlights the importance of addressing the timing of vegetation sampling in relation to episodic changes in lemming population densities. Thompson (1955a, 1955b) and Schultz (1964) showed that lemmings reduce the production of graminoids during growing seasons with high lemming population densities, but that graminoids largely recover during the following growing season. As a result, vegetation in control plots reflects the phase of the lemming cycle. Thus, sampling for long-term effects, as in this study, should occur at least one and preferably two seasons after the year of a lemming high. Our sampling occurred in 2002 and 2010, both during the second growing season following lemming population highs in 2000 (Holt 2010) and 2008 (Villarreal et al 2011). Batzli’s (1975) sampling occurred in 1974, the third year after a lemming high in 1971. Thus, this and Batzli’s 1974 (Batzli 1975) study do not reflect a temporary depression of biomass associated with high lemming populations, but rather consistent long-term patterns.

A review of the effects of experimental warming on tundra plants concluded that higher temperatures leads to increased cover of deciduous shrubs and graminoids and to decreased cover of mosses and lichens (Walker et al 2006). Our results indicate that the activity of lemmings near Barrow facilitates three of those four effects, the exception being shrubs, which brown lemmings largely ignore. A considerable challenge remains in understanding the spatial and temporal extent of lemming effects on vegetation. Although brown lemmings appear to reach very high densities only within a 100 km or so of Barrow, other herbivorous arvicoline rodents become more abundant at other sites where up to five sympatric species
can be found (Pitelka and Batzli 1993). Several species of arvicoline consume deciduous shrubs, and in winter they may even eat bark and girdle shrubs (Batzli and Jung 1980, Batzli and Henttonen 1990). Of course, consumption and girdling of deciduous shrubs would reduce, rather than increase the prevalence of shrubs, an effect already reported for large herbivores (Post and Pedersen 2008, Olofsson et al 2009). In any event, a significant impact of arvicoline rodents probably occurs in a variety of habitats and geographic areas. Because functional attributes of ecosystems appear to be strongly affected by the timing and duration of the lemming cycles near Barrow (Lara et al 2011), we urge greater attention to sampling of ecosystem properties and processes with respect to arvicoline rodent populations in general.

In conclusion, our resampling of the historic herbivore enclosures in the coastal tundra near Barrow, Alaska revealed that lemming exclusion decreases the cover and biomass of graminoids markedly and increases the biomass of lichens and bryophytes, particularly in wet tundra. Because these plants respond similarly to warming, lemmings may have partially contributed to the recent greening of Arctic landscapes. Exploring these relationships in more depth over a range of spatio-temporal scales, including more mechanistic experiments detailing the responses of plants to arvicoline rodents in other tundra communities, examining the response of tundra to warming with and without herbivores, and assessing response of herbivores to climate change is much needed.

Acknowledgments

We would like to thank Andrew Johnson and all the other 2002 biomass pluckers. Additionally, we are grateful to the Ukpéaŋvik Iupiat Corporation (UIC) for permitting land access and the Barrow Arctic Science Consortium for logistical support. This work was funded by grants from the National Science Foundation (NSF-ANS-0732885, OPP-9906692). M J Lara is partly supported through a NSF GK-12 student scholarship. Any opinions, findings, conclusions, or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation.

References

ACIA 2005 Impacts of a Warming Arctic: Arctic Climate Impact Assessment Overview Report (Cambridge: Cambridge University Press)

Batzli G O 1975 The influence of grazers on tundra vegetation and soils Proceedings of the Circumpolar Conference in Northern Ecology, Ottawa (Ottawa: Natural Research Council of Canada) pp 1217–25

Batzli G O and Henttonen H 1990 Demography and resource use by microtine rodents near Toolik Lake, Alaska Arct. Alp. Res. 22 51–64

Batzli G O and Jung H J C 1980 Nutritional ecology of microtine rodents: resource utilization near Akasook, Alaska Arct. Alp. Res. 12 483–99

Batzli G O and Pitelka F A 1983 Nutritional ecology of microtine rodents: food habits near Barrow, Alaska J. Mammal. 64 648–55

Batzli G O et al 1980 The herbivore based trophic system An Arctic Ecosystem: The Coastal Tundra at Barrow, Alaska ed J Brown, P C Miller, L L Tieszen and F L Bunnell (Stroudsburg, PA: Dowden, Hutchinson and Ross) pp 335–410

Bhatt U S et al 2010 Circumpolar Arctic tundra vegetation change is linked to sea ice decline Earth Interact. 14 1–20

Bråthen K A and Odaasz-Albrigtsen A M 2000 Tolerance of the arctic graminoid Luzula arcuata ssp. confusa to simulated grazing in two nitrogen environments Can. J. Bot. 78 1108–13

Brown J, Miller P C, Tieszen L L and Bunnell F L (ed) 1980 An Arctic Ecosystem: The Coastal Tundra at Barrow, Alaska (Stroudsburg, PA: Dowden, Hutchinson and Ross)

Callaghan T V, Tweedie C E and Webber P J 2011a Multi-decadal changes in tundra environments and ecosystems: the International Polar Year-Back to the Future Project (IPY-BTF) Ambio 40 555–7

Callaghan T V et al 2011b Multi-decadal changes in tundra environments and ecosystems: synthesis of the International Polar Year-Back to the Future Project (IPY-BTF) Ambio 40 705–16

Chapin F S III, Tieszen L L, Lewis M C, Miller P C and McCown B H 1980 Control of tundra plant allocation patterns and growth An Arctic Ecosystem: The Coastal Tundra at Barrow, Alaska ed J Brown, P C Miller, L L Tieszen and F L Bunnell (Stroudsburg, PA: Dowden, Hutchinson and Ross) pp 140–185

Díaz S et al 2007 Plant trait responses to grazing—a global synthesis Glob. Change Biol. 13 313–41

Elliot T L and Henry G H R 2011 Effects of simulated grazing in ungrazed wet sedge tundra in the high Arctic Arct. Antarct. Alp. Res. 43 198–206

Ferraro D O 2002 Effect of defoliation on grass growth. A quantitative review Oikos 98 125–33

Gough L, Shrestha K, Johnson D R and Moon B 2008 Long-term mammalian herbivory and nutrient addition alter lichen community structure in Alaskan dry heath tundra Arct. Antarct. Alp. Res. 40 65–73

Hinzman L D et al 2005 Evidence and implications of recent climate change in northern Alaska and other Arctic regions Clim. Change 72 15251–98

Holt D 2010 personal communication

IPCC 2007 Climate Change 2007: Synthesis Report. The Fourth Assessment Report of the Intergovernmental Panel on Climate Change (Geneva: IPCC)

Lara M J, Villarreal S, Johnson D R, Hollister R H, Webber P J and Tweedie C E 2011 Change in tundra ecosystem function near Barrow Alaska 1972–2010 Environ. Res. Lett. submitted

Madsen J, Jaspers C, Tamstorf Mortensen C E and Rigét F 2011 Long-term effects of grazing and global warming on the composition and carrying capacity of graminoid marshes for moulting geese in East Greenland Ambio 40 638–49

McKendrick J D, Batzli G O, Everett K R and Swanson J C 1980 Some effects of mammalian herbivores and fertilization on tundra soils and vegetation Arct. Alp. Res. 12 565–78

Mulder C P H 1999 Vertebrate herbivores and plants in the Arctic and subarctic: effects on individuals, populations, communities and ecosystems Perspect. Plant Ecol. Syst. 2 29–55

NCDC 2005 Monthly Station Climate Summaries, 1971–2000 (Asheville, NC: National Climatic Data Center) (http://cdi.ncdc.noaa.gov/climatenormals/)

Oksanen L, Fretwell S D, Arruda J and Niemelä P 1981 Exploitation assessment Overview Report (Stroudsburg, PA: Dowden, Hutchinson and Ross)

Oksanen L, Fretwell S D, Arruda J and Niemelä P (Cambridge: Cambridge University Press) (Geneva: IPCC) IPCC 2007 Climate Change 2007: Synthesis Report. The Fourth Assessment Report of the Intergovernmental Panel on Climate Change (Geneva: IPCC) IPCC 2007 Climate Change 2007: Synthesis Report. The Fourth Assessment Report of the Intergovernmental Panel on Climate Change (Geneva: IPCC)

Perspect. Plant Ecol. Syst. 2 29–55
Olofsson J, Moen J and Oksanen L 2002 Effects of herbivory and competition intensity in two Arctic-Alpine tundra communities with different productivity Oikos 96 265–72

Olofsson J, Oksanen L, Callaghan T, Hulme P E, Oksanen T and Suominen O 2009 Herbivores inhibit climate-driven shrub expansion on the tundra Glob. Change Biol. 15 2671–93

Pajunen A, Virtanen R and Roininen H 2008 The effects of reindeer grazing on the composition and species richness of vegetation in forest-tundra ecotone Polar Biol. 31 1233–344

Pitelka F A 1957 Some characteristics of microtine cycles in the Arctic Arctic Biology ed H P Hansen (Corvallis, OR: Oregon State University Press) pp 57–88

Pitelka F A and Batzli G O 1993 Distribution, abundance and habitat use by lemmings on the North Slope of Alaska The Biology of Lemmings (Linnaean Society Symposium Series vol 15) ed N C Stenseth and RA Ims (London: Academic) pp 213–36

Pitelka F A and Batzli G O 2007 Population cycles of lemmings near Barrow, Alaska: a historical review Acta Theriol. 52 326–36

Post E and Pedersen C 2008 Opposing plant community responses to warming with and without herbivores Proc. Natl Acad. Sci. USA 105 12353–8

Post E et al 2009 Ecological dynamics across the Arctic associate with recent climate change Science 325 1355–8

Proulx M and Mazumder A 1998 Reversal of grazing impacts on plant richness in nutrient-poor vs. nutrient-rich ecosystems Ecology 79 2581–92

Rowland J C et al 2010 Arctic landscapes in transition: responses to thawing permafrost EOS, Trans. AGU 91 229–30

Schultz A M 1964 The nutrient-recovery hypothesis for Arctic microtine cycles Grazing in Terrestrial and Marine Environments: A Symposium of the British Ecological Society (Bangor, 11–14 April 1962) ed D J Crisp (Oxford: Blackwell) pp 57–68

Schultz A M 1969 A study of an ecosystem: the Arctic tundra The Ecosystem Concept in Natural Resource Management ed G M van Dyne (New York: Academic) pp 57–68

Shilkomanov N I et al 2010 Decadal variations of active-layer thickness in moisture-controlled landscapes, Barrow Alaska J. Geophys. Res. 115 G00104

Tape K, Lord R, Marshall H P and Rueß R W 2010 Snow-mediated ptarmigan browsing and shrub expansion in Arctic Alaska Ecoscience 17 186–93

Thompson D Q 1955a The 1953 lemming emigration at Point Barrow, Alaska Arctic 8 37–45

Thompson D Q 1955b The ecology and population dynamics of the brown lemming (Lemmus trimucronatus) at Point Barrow, Alaska PhD Thesis University of Missouri, p 138

van der Wal R 2006 Do herbivores cause habitat degradation or vegetation state transitions? Evidence from the tundra Oikos 114 177–86

van der Wal R and Brooker R W 2004 Mosses mediate grazer impacts on grass abundance in Arctic ecosystems Funct. Ecol. 18 77–86

van der Wal R, van Lieshout S M J and Loonen M J J E 2001 Herbivore impact on moss depth, soil temperature and Arctic plant growth Polar Biol. 24 29–32

Villarreal S, Hollister R D, Johnson D R, Lara M J, Tweedie C E and Webber P J 2011 Tundra plant community change near Barrow, Alaska (1972–2010) Environ. Res. Lett. submitted

Virtanen R 2000 Effects of grazing on above-ground biomass on a mountain snowbed, NW Finland Oikos 90 295–300

Walker M D et al 2006 Plant community response to experimental warming across the tundra biome Proc. Natl Acad. Sci. USA 103 1342–6

Wookey P A et al 2009 Ecosystem feedbacks and cascade processes: understanding their role in the responses of Arctic and Alpine ecosystems to environmental change Glob. Change Biol. 15 1153–72

Zimov S A et al 1995 Steppe-tundra transition: a herbivore-driven biome shift at the end of the Pleistocene Am. Naturalist 146 765–93