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Long-Term Mammalian Herbivory and Nutrient Addition Alter Lichen Community Structure in Alaskan Dry Heath Tundra

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Abstract

Mammalian herbivores in arctic tundra often alter plant species composition and lichen abundance, with effects dependent on grazing season and herbivore preference. We investigated how long-term mammal exclosures designed to exclude large mammals (caribou) alone, large and medium-sized mammals (e.g., ground squirrels), or all mammals (including voles and lemmings) affected lichen abundance and species composition as well as the vascular plant community. The exclosures were partly established in combination with long-term soil nutrient additions to investigate the interaction between mammal activity and nutrient availability. Our study was conducted in dry heath tundra in northern Alaska, dominated by dwarf evergreen shrubs and lichens. Excluding mammals for 17 years allowed the lichen community to increase in biomass, particularly within the genus *Cladonia*, which also had more intrageneric diversity in the exclosures; after 10 years, results were subtler. Fertilization, however, almost eliminated the lichens, regardless of herbivore treatment. This coincided with a dramatic shift in vascular vegetation toward a more palatable grass-dominated community, similar to studies of other arctic heaths. Our results suggest that with greater soil nutrient availability that occurs with climate warming, lichens will decrease in abundance, and this effect may be exacerbated by increased mammalian herbivory.

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Introduction

In arctic tundra communities where soil nutrients are limited, the growing season is short, and precipitation is low, lichens often play an important role in the ecosystem. Some species of arctic lichens can fix nitrogen (Alexander, 1974; Weiss et al., 2005) and thus contribute to increased net primary productivity (NPP) of the plant communities. They may be a major component of carbon fixation in some tundra ecosystems with low NPP (e.g., Shaver and Chapin, 1991) and thus may affect ecosystem nutrient cycling of several elements. Lichens also provide an important forage source for mammals, particularly caribou in the winter (Jefferies et al., 1994), which may also comprise an economic resource for people in the region (Cornelissen et al., 2001).

As arctic ecosystems continue to warm (Chapin et al., 2005; Hinzman et al., 2005), soil conditions will improve for microbial activities such as decomposition. Consequently, soil nutrient availability will increase (Nadelhoffer et al., 1992; Hobbie, 1996). As vascular plants, particularly deciduous shrubs, increase in abundance with both experimental (e.g., Chapin et al., 1995) and regional warming (Sturm et al., 2005; Tape et al., 2006), lichens frequently decline (Cornelissen et al., 2001). The exact mechanism responsible for this decline is unclear, and several factors may be involved. For example, the role of herbivores in this lichen decrease remains relatively unexamined and has not been separated from the negative effects of increased competition with vascular plants. The potential subsequent effects of this lichen decline on herbivores have only been infrequently observed in manipulative experiments, because arctic herbivores have not been well studied (Callaghan et al., 2004). These interactions may be quite complex, affecting mammalian predators as well if the herbivore populations are altered.

Caribou (*Rangifer tarandus*, used synonymously with reindeer in this paper) have been documented to cause dramatic shifts in tundra vegetation composition with long-term activity, including creating grasslands (Klein, 1987; Olofsson et al., 2004; van der Wal et al., 2004) or shrublands (e.g., Manseau et al., 1996). Several of these studies compared plant communities on islands that had caribou populations altered by hunting or other means to islands without caribou or with existing populations, or followed vegetation changes after caribou grazing had ceased. Results from *in situ* experiments restricting caribou abundance are relatively few, but do suggest that herbivory may have dramatic effects on the plant community, both directly by selectively removing plant material and indirectly by altering litter decomposition and soil nutrient availability (e.g., Stark and Grellmann, 2002; Olofsson et al., 2004). By reducing lichen abundance, caribou may affect invertebrate populations that rely on lichens for suitable habitat (Suominen et al., 2003). Small mammals are also known to affect tundra vascular plant and lichen communities (e.g., Batzli et al., 1980), but their activity may be more variable in time with herbivore and predator population fluctuations.

The purpose of this study was to understand the long-term effects of herbivory on the lichen community in an Alaskan dry heath ecosystem. We examined mammal exclosures that had been maintained for 17 and 10 years prior to data collection, as well as 10-year fertilization experiments designed to test how increased soil nutrients affect this ecosystem in combination with reduction of animal activity. Most warming and fertilization experiments in the Arctic allow access to herbivores, so determining how mammals may be affecting the community under increased nutrient conditions is essential to properly interpreting results of such studies. To accomplish our objective, we examined treatment

effects on lichen relative abundance, biomass, and species richness as well as vascular plant community structure and biomass. Because the fencing treatments excluded different sizes of mammals, we also hoped to determine the relative importance of groups of mammals in driving any changes we detected.

Methods

STUDY SITE

This research was conducted at the Arctic Long-Term Ecological Research (LTER) site at Toolik Lake, Alaska (68°38'N, 149°36'W, 760 m a.s.l.), on the North Slope of the Brooks Range. This dry heath community receives little precipitation and retains thin snow cover in winter. The organic layer is only a few centimeters thick, overlying rocky mineral soil that thaws deeply in summer (Shaver and Chapin, 1991; Gough et al., 2002). The dominant plants are dwarf deciduous shrubs including *Arctostaphylos alpina* and dwarf evergreen shrubs such as *Empetrum nigrum* and *Loiseleuria procumbens* (vascular plant nomenclature follows Hultén, 1968). Graminoid species are only sparsely interspersed. Lichens comprise up to one-third of the aboveground community biomass (Shaver and Chapin, 1991).

Mammalian herbivores in the area include caribou (*Rangifer tarandus*), ground squirrels (*Spermophilus parryi*), voles (*Microtus* spp.), and lemmings (including *Lemmus sibiricus* and *Dicrostonyx rubricatus*) (Batzli and Henttonen, 1990). Previous trapping studies in the vicinity of the study site have indicated that singing voles (*M. miurus*) are the most abundant mammalian herbivores in the dry heath tundra studied here ("Rocky Flat" site in Batzli and Henttonen, 1990). In recent years, increasing signs of caribou presence (primarily feces) have been noted (Gough, unpublished data). The animals are likely being attracted to the long-term fertilizer plots (described below) that have become dominated by a palatable grass.

Two sets of experiments were sampled in this dry heath community. In 1989, two replicate herbivore exclosures were established at the site (17-year exclosures; Fig. 1). The large portion of the exclosure (10 × 10 m) was fenced by a large-mesh fence designed to exclude caribou (LF treatment, 15.2 × 15.2 cm openings). Within that fence was a medium-size-mesh treatment (MF treatment, 2.5 × 2.5 cm openings, 5 × 5 m) to also exclude ground squirrels, and within that fence was a small-mesh fence (SF treatment, 1.3 × 1.3 cm openings, 2.5 × 2.5 m) to additionally exclude smaller mammals including voles and lemmings. The second set of study plots examined here was established in the same community in 1996 (10-year exclosures) within three blocks of replicate 5 × 20 m plots set up in 1989 (Fig. 1). The experimental design incorporated a factorial design of fencing to exclude mammalian herbivores with annual application of both N (10 g m⁻² as NH₄NO₃) and P (5 g m⁻² as P₂O₅). Within each block, two plots were used for this experiment, with each plot randomly assigned as control (CT) or fertilized (NP). Within each plot, a fence was constructed on a randomly determined half (5 × 10 m); the half of the plot without a fence was designated as the no fence (NF) treatment. The outer wire fence (LF) excluded caribou while the inner smaller mesh wire fence (SF) was established inside each LF on an inner 5 × 5 m plot to exclude caribou along with small mammals including ground squirrels, voles, and lemmings. Beginning in 1996, fertilizer was annually added in pellet form to the appropriate plots in June immediately following snowmelt. Snow accumulation increases slightly immediately adjacent to the northern edge of the fences because of the winds coming from the south, resulting in snowmelt occurring 2–3 days later there than in

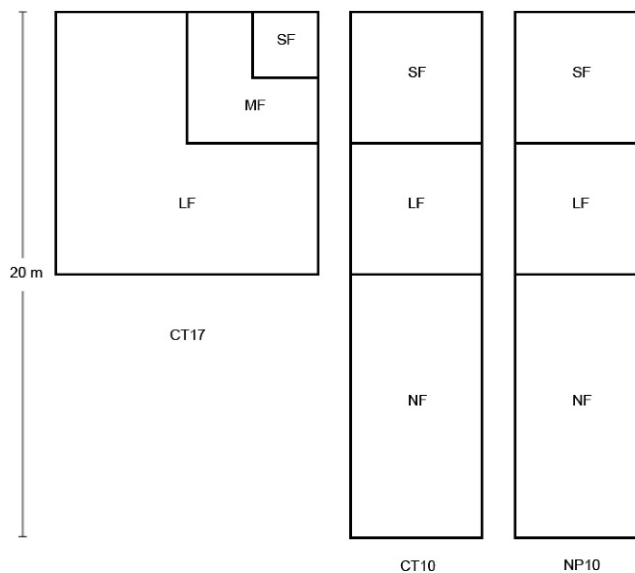


FIGURE 1. The experimental design. The 17-year plots (CT17) were replicated twice, while the 10-year plots (CT10 and NP10) were paired within each of three blocks. All plots were located at the same study site. Abbreviations as follows: CT: control (ambient nutrients), NP: added nitrogen and phosphorus, NF: no fence, LF: large-mesh fence, MF: medium-mesh fence, SF: small-mesh fence. NFCT10 plots were used as the non-manipulated controls for analysis of both experiments. See methods for details of treatments.

the rest of the plots (J. Laundre, personal communication). We avoid this artifact by sampling at least 0.5 m from the edge of the fence.

PLANT COMMUNITY SURVEY

Between 22 and 27 July 2005, non-destructive sampling of the plant community was conducted in each treatment plot using randomly located 1 × 1 m quadrats with 20 × 20 cm subquadrats marked to aid in estimates. Relative aerial cover of each vascular plant species, mosses, lichens, bare ground, and litter (designated as simply litter or "animal litter" if it had been noticeably processed by mammals) was recorded. To minimize bias, we consistently standardized cover value estimates across observers. Within each treatment combination and replicate, 8 quadrats were censused in the 10-year experiment and 4 quadrats in the 17-year experiment (the small size of the 17-year SF plots only allowed a sample area of 4 m²). Vascular plant species were subsequently grouped into growth forms. Cover was then summed within each plot and relativized to generate relative percent cover for each sample plot individually.

BIOMASS HARVEST AND LICHEN SPECIES RICHNESS

Between 2 and 22 July 2005, 10 × 10 cm quadrats randomly located along a transect running the length of each plot were harvested from each treatment: 3 quadrats were removed from each 10-year treatment plot and 4 from each 17-year treatment plot (to attempt to compensate for the smaller replication at the scale of the exclosures) for a total of 78 samples. The samples were brought to the lab, and aboveground biomass was separated into vascular plant growth forms (deciduous shrub, evergreen shrub, graminoid), moss, litter, and lichens. Four genera of lichens were separated out: *Cladonia/Cladina*, *Cetraria*, *Stereocaulon*, and *Sphaerophorus*, while all others were lumped together. The two

genera of *Cladonia* and *Cladina* (as distinguished in Brodo et al., 2001) were lumped into one category indicated here as *Cladonia*, based on the recent phylogeny for this group (Stenroos et al., 2002). Samples were then dried at 60°C to a constant weight. In the fall of 2005 each genus of lichen was identified to species (if possible) using an aggregate sample for each treatment following Brodo et al. (2001) with the exception of *Cladonia* species, as noted above, and two species of *Flavocetraria* which were included in *Cetraria*.

STATISTICAL ANALYSIS

Plant community composition was analyzed separately for the 10-year experiment and the 17-year experiment. The 10-year plots that were not fenced and did not receive fertilizer (NFCT10) were used as the non-manipulated control in both sets of analyses. We used a MANOVA with the following growth forms as dependent variables to analyze changes in relative abundance: lichen, moss, evergreen shrub, deciduous shrub, graminoid, litter, animal litter, and bare ground. For the 10-year analysis, main effects were fencing and fertilization and their interaction, while for the 17-year analysis fencing was the only main effect, with four levels (NF, SF, MF, LF). In both cases a block design was used, reflecting the experimental design at the site. Wilks' Lambda was reported as the test statistic for between-subjects effects. All cover data were arcsine square-root transformed to achieve normality and homogeneity of variances prior to analysis, and Type III sums of squares were examined to account for the unbalanced design in the 17-year analysis. Tukey's HSD was used for pairwise comparisons, and alpha levels of 0.05 or lower were considered significant.

Lichen and vascular plant biomass were analyzed similarly for the two separate data sets, one for the 10-year treatments (examining effects of fencing and fertilization) and the other for the 17-year treatments (examining the four levels of fencing by including NFCT10), for each growth form, vascular biomass, live biomass, and total aboveground biomass (including litter and lichens). The same univariate analysis was performed for each growth form and the following lichen genera: *Cladonia*, *Cetraria*, *Stereocaulon*, and *Sphaerophorus*. All biomass data were natural log transformed prior to analysis.

A chi-squared analysis was used to determine if lichen species richness was affected by the five treatments in which it was examined (NFCT10, NFNP10, LFCT17, MFCT17, SFCT17). All statistical analyses were conducted in SAS Version 9.1 for Windows (SAS Institute, Cary, North Carolina).

Results

PLANT COMMUNITY RELATIVE ABUNDANCE

Ten years of manipulation of herbivores and soil nutrient availability significantly affected the relative abundance of plant growth forms in this dry heath ecosystem (Fig. 2). The interaction between fencing and fertilization was significant ($F_{16,258} = 8.36$, $P < 0.0001$), as were the main effects of fencing ($F_{16,258} = 7.92$, $P < 0.0001$) and fertilization ($F_{8,129} = 187.92$, $P < 0.0001$). The significant interaction across the entire community was driven by significant interactions for evergreen shrubs, graminoids, litter, animal litter, and bare ground (Table 1, Fig. 2). Evergreen shrubs had less relative cover with fencing in fertilized plots and slightly more cover with fencing in ambient plots, with cover significantly less in fertilized plots (Table 1). Graminoids responded to fertilization in the opposite manner, with much greater relative abundance in fertilized plots. A significant interaction was caused

by slight pairwise differences among fertilized treatment plots along with consistently low abundance in control plots (Fig. 2, Table 1). Litter and animal litter were both greater in fertilized plots than control plots, and both had significant interactions between fertilization and fencing (Fig. 2, Table 1). If the two categories were examined simultaneously, however, the total amount of litter across fertilized plots was the same, except that in plots exposed to herbivory much of that litter had been processed by animals; almost no animal litter was detected in plots that were not fertilized (Fig. 2). Less bare ground was present in fertilized plots than control plots, with significantly more bare ground present in NFCT10 plots than other treatment combinations (Fig. 2, Table 1).

Fencing was significant as a main effect for mosses, deciduous shrubs, animal litter, and bare ground (Table 1). Deciduous shrubs, especially *Arctostaphylos alpina* and *Vaccinium uliginosum*, had significantly greater relative cover inside the herbivore enclosures than in open plots (NF10 significantly less than both LF10 and SF10 in pairwise comparisons; Table 1, Fig. 2), suggesting deciduous species were preferred forage for herbivores under ambient and nutrient-enriched conditions. This growth form, particularly *Betula nana*, had greater relative cover under fertilized conditions, although *A. alpina* was less abundant in these plots relative to ambient plots. Mosses also had greater relative cover in fertilized plots, but less inside fences (Table 1, Fig. 2). Finally, the fences marginally affected lichen relative cover, with the greatest cover in the LF10 treatments. Across all fencing treatments fertilization caused significantly lower lichen relative cover (Fig. 2, Table 1).

After 17 years of treatment, there was also a significant effect of fencing on community composition ($F_{24,102.11} = 1.76$, $P = 0.03$). This was caused by significant changes in relative abundance in three categories: lichen, litter, and bare ground. Lichen relative abundance was significantly greater in SFCT17 and LFCT17 than NFCT10 (main effect of fence $F_{3,42} = 3.91$, $P = 0.01$; Fig. 2). Litter accumulated significantly more in the exposed plots than the three fenced treatments ($F_{3,42} = 8.74$, $P = 0.0001$), while bare ground was also greater in the open plots ($F_{3,42} = 3.75$, $P = 0.02$; Fig. 2). Although other shifts in relative abundance appeared, they were not significant in pairwise comparisons (e.g., less deciduous cover in open plots).

VASCULAR PLANT AND LICHEN BIOMASS

The treatments had less of an effect on aboveground biomass than on relative abundance. After 10 years, fertilization caused significantly greater total community biomass (including vascular plants, mosses, lichens, and litter; $F_{1,40} = 4.51$, $P = 0.04$; Fig. 3) compared with plots that were not fertilized. This overall response was driven by significantly more plant litter with fertilization ($F_{1,40} = 62.85$, $P < 0.0001$), which offset the lower live biomass in NFNP and LFNP (main effect of fertilization on live biomass: $F_{1,40} = 5.30$, $P = 0.03$). Significantly lower lichen biomass ($F_{1,40} = 58.49$, $P < 0.0001$) caused the lower live biomass in fertilized plots. The significantly greater graminoid biomass ($F_{1,40} = 80.91$, $P < 0.0001$) with less evergreen shrub biomass ($F_{1,40} = 10.83$, $P = 0.002$; Fig. 3) with fertilization resulted in no net effect of fertilization on vascular plant biomass.

The lichen genera examined individually exhibited the same pattern of dramatically less biomass in fertilized plots (Fig. 4). Although fencing did not significantly affect total lichen biomass, *Cladonia* biomass was somewhat lower in plots exposed to mammals after 10 years ($F_{2,40} = 3.10$, $P = 0.06$) because of

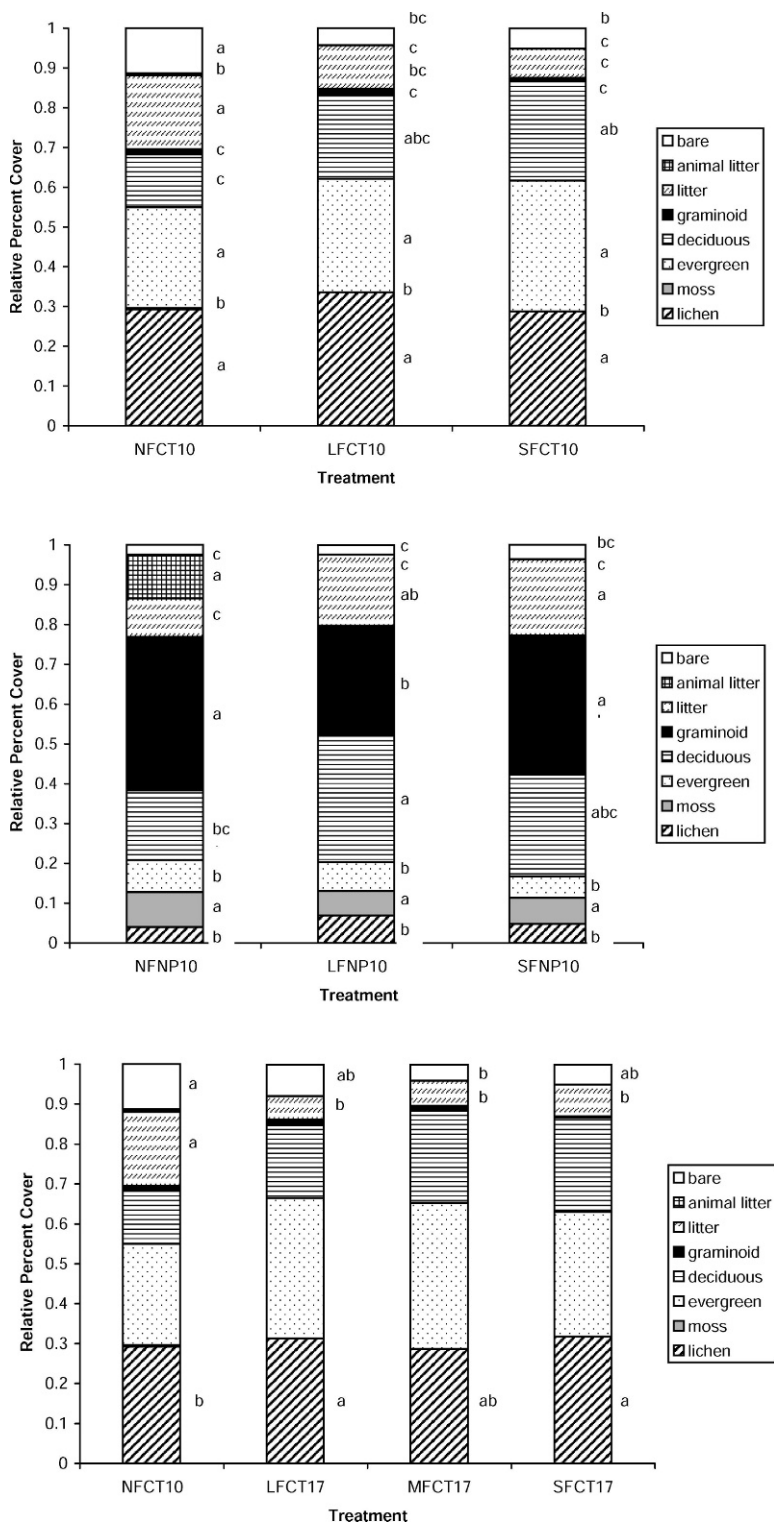


FIGURE 2. Relative percent cover for all plant growth forms in dry heath tundra for four levels of fencing (treatment abbreviations as in Fig. 1). The three panels represent two levels of fertilization in plots that had been maintained for 10 years, and ambient nutrient plots that had been maintained for 17 years. Different letters represent statistically significant pairwise differences within growth forms across all six treatment combinations within the 10-year experiment or the four fencing levels within the longer-running experiment.

slightly lower biomass values in the open plots when compared with the two fenced treatments (Fig. 4).

Vascular plant biomass was significantly affected by herbivory ($F_{2,40} = 4.27$, $P = 0.02$; Fig. 3), with significantly more biomass accumulating inside SF10 compared to NF10. This same pattern was noted with live biomass ($F_{2,40} = 3.53$, $P = 0.04$), suggesting similar, though non-significant, trends in moss and lichen biomass. In contrast, evergreen shrub biomass was marginally significantly less in open areas ($F_{2,40} = 2.86$, $P = 0.07$), with the least amount of biomass in NFNP plots.

After 17 years a different response was noted as fencing significantly affected total community biomass ($F_{3,19} = 3.99$, $P = 0.02$; Fig. 3), with greater biomass inside the fences. Also unlike after 10 years, no effect of fencing was noted on live or vascular plant biomass. The unbalanced design comparing the NFCT10 plots with the 17-year plots likely reduced our power to detect significant differences, given the suggested differences in the means. However, mosses were significantly affected by fencing level ($F_{3,19} = 9.09$, $P = 0.0006$; Fig. 3). Fencing had a marginally significant effect on total lichen biomass with the greatest lichen biomass in the SF17 plots,

TABLE 1

Univariate results for plant growth form relative abundance analysis of 10-year manipulations of herbivory and soil nutrient availability. Only effects with p -values < 0.10 were included in the table.

Growth Form	Fence * Fertilization		Fence		Fertilization	
	$F_{2,136}$	P	$F_{2,136}$	P	$F_{1,136}$	P
Lichen			2.67	0.07	487.89	<0.0001
Moss			3.57	0.03	120.58	<0.0001
Evergreen Shrub	5.58	0.005			287.13	<0.0001
Deciduous Shrub			8.57	0.0003	6.32	0.002
Graminoid	3.40	0.04			344.65	<0.0001
Litter	25.31	<0.0001			4.83	0.03
Animal Litter	25.37	<0.0001	40.42	<0.0001	25.37	<0.0001
Bare Ground	8.84	0.0002	6.64	0.002	44.94	<0.0001

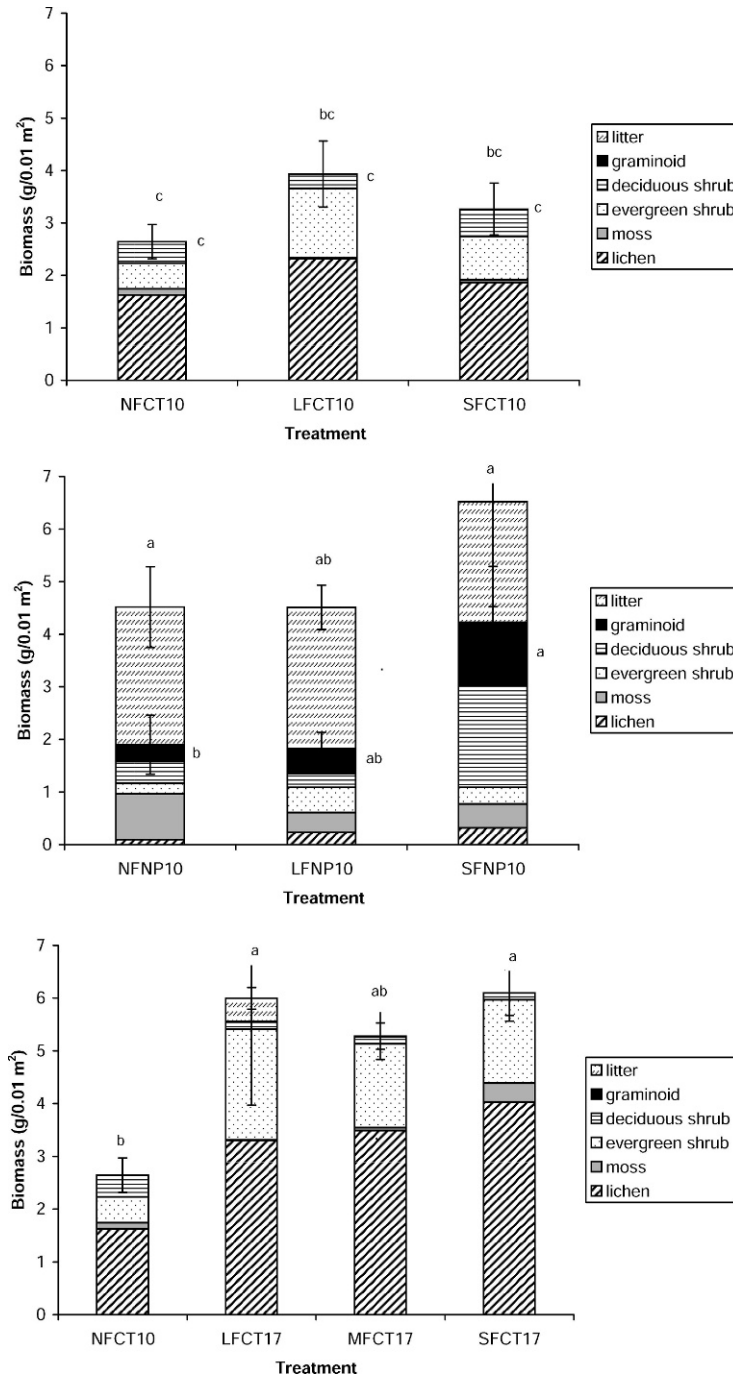


FIGURE 3. Aboveground biomass ($\text{g } 0.01 \text{ m}^{-2}$) for all plant growth forms in dry heath tundra for four levels of fencing (treatment abbreviations as in Fig. 1). The three panels represent two levels of fertilization in plots that had been maintained for 10 years, and ambient nutrient plots that had been maintained for 17 years. Different letters on the top of the bars represent statistically significant pairwise differences based on total biomass across all six treatment combinations within the 10-year experiment in the top two panels, or within the 17-year experiment in the bottom panel. Letters to the side of the bars in the top two panels indicate pairwise differences for graminoid biomass. Error bars represent ± 1 S.E. for live biomass as well as for total biomass (including litter).

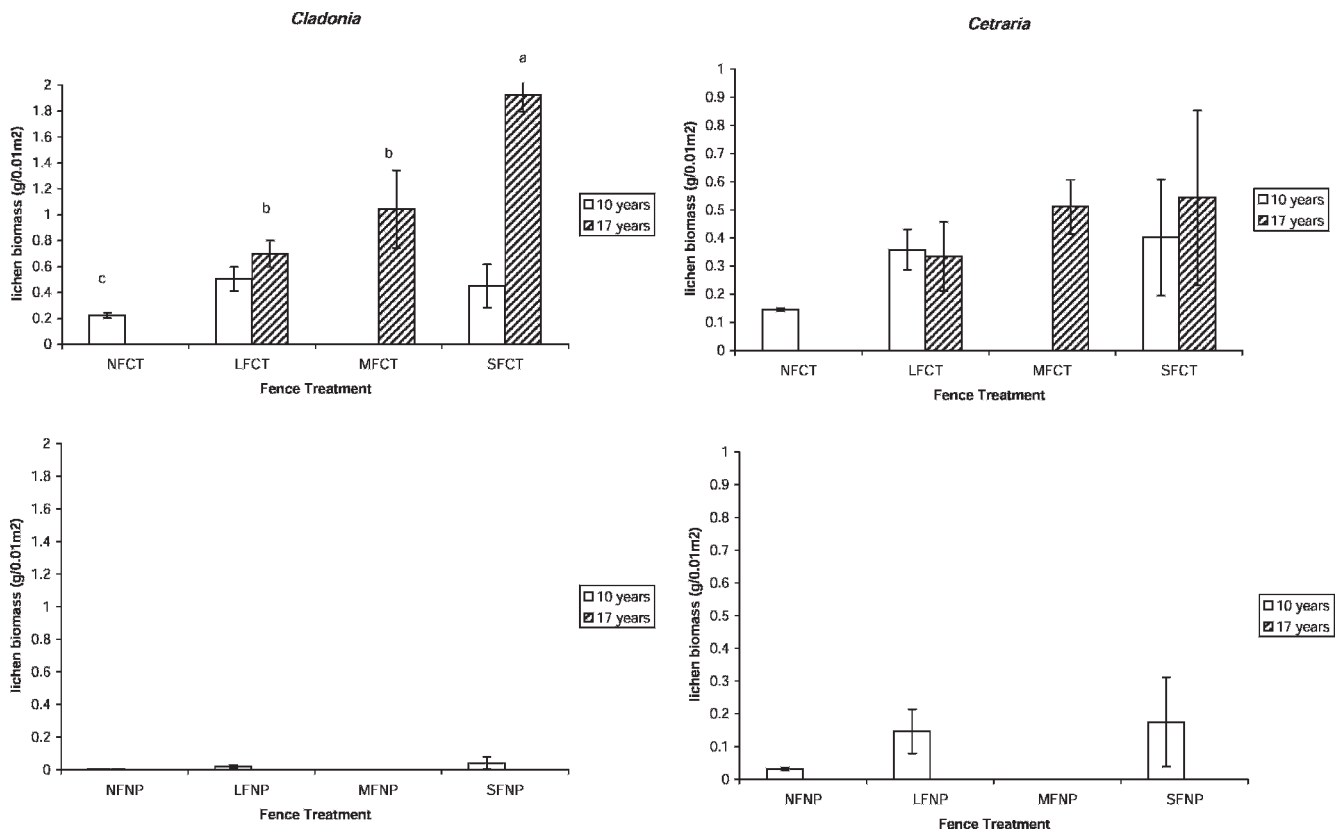


FIGURE 4. Lichen biomass ($\text{g } 0.01 \text{ m}^{-2}$) from all treatment plots for the lichen genera *Cladonia* (on left) and *Cetraria* (on right). Upper panel figures represent biomass from ambient nutrient plots in both the 10-year and 17-year experiments, while lower panel figures include data from fertilized plots, thus only from the 10-year experiments. Fencing treatment abbreviations as in Figure 1. Error bars represent ± 1 S.E. Different letters represent significant pairwise differences within that experiment.

and the lowest in the NF10 plots ($F_{3,19} = 2.79$, $P = 0.07$; Fig. 3). This was caused to some extent by significantly more *Cladonia* inside the fences ($F_{3,19} = 19.78$, $P < 0.0001$; Fig. 4). *Cetraria* also had a marginally significant response to fencing ($F_{3,19} = 2.80$, $P = 0.07$), again caused by less biomass accumulating in exposed plots. The other two genera examined, *Stereocaulon* and *Sphaerophorus*, were not significantly affected by fencing (data not shown).

LICHEN COMMUNITY COMPOSITION

More lichen species occurred in the older mammal exclosures than in exposed and fertilized plots (Table 2). The richness values for the five treatments in which they were determined were significantly different from the expected response ($\chi^2 = 9.31$, d.f. = 4, $P = 0.05$), with the fewest species in NFNP10 and the most in SFCT17. In particular, species richness within the genus *Cladonia* was dramatically lower in plots exposed to mammals or fertilized. There were three species unique to the SFCT17 plots, and one unique to MFCT17, perhaps suggesting species-specific herbivory by the small mammals.

Discussion

Hampering our interpretation of the results presented here is the fact that our understanding of mammal abundance in this community is quite limited. Based on studies conducted in the 1980s (e.g., Batzli and Henttonen, 1990), singing voles are likely the most abundant rodents in this area. Evidence of vole activity appeared greater in the fertilized plots, but we have not been able to adequately quantify their numbers (Gough and Johnson, un-

published data). Lichens were not noted in studies of vole stomach contents from animals trapped at this site, nor were they included in relevant feeding trials (Batzli and Lesieutre, 1991). Rather, these animals consumed mostly vascular plants, particularly dicots (Batzli and Henttonen, 1990). Caribou also appear to use the area, most likely more commonly in the winter when this site is relatively exposed compared to other nearby communities, although they have also been observed migrating through occasionally in summer (personal observation). Greater herbivore activity in winter may have contrasting effects on the plant communities and nutrient cycling when compared with summer grazing (Grellmann, 2002).

MAMMALIAN HERBIVORES HAD SUBTLE EFFECTS AFTER LONG-TERM EXCLOSURE

Under ambient nutrient conditions, herbivory somewhat decreased lichen biomass and relative abundance after 10 and 17 years relative to plots from which herbivores were excluded, with more marked effects in the longer-term experiments. No effect of grazing on lichen cover was noted after five years in similar small and large-mesh exclosures in a Norwegian heath tundra (Grellmann, 2002). In our study, several lichen species in the genus *Cladonia* were only recorded in the 17-year small mammal exclosures where biomass of this genus was significantly greater than in the other fencing treatments. *Cladonia* is known to provide valuable forage to mammals, particularly caribou (Brodo et al., 2001), although vole use of this species, as suggested here, is less understood. The small mammal exclosures also had the greatest lichen community biomass, although it was not significantly different from the other long-term fencing treatments.

TABLE 2

Lichen species identified from biomass harvest from aggregate samples within each treatment combination. Treatments indicated by fencing (NF: no fence, LF: large-mesh fence, MF: medium-mesh fence, SF: small-mesh fence), fertilization (CT: control, NP: N+P added), and duration (10 or 17 years).

Genus	Species	LFCT17	MFCT17	SFCT17	NFCT10	NFNP10
<i>Alectoria</i>	<i>nigricans</i>	X	X	X	X	
	<i>ochroleuca</i>	X	X	X	X	
	subtotal	2	2	2	2	0
<i>Cetraria</i>	<i>cucullata</i>	X	X	X	X	X
	<i>delisei</i>	X	X	X		X
	<i>islandica</i>	X	X	X	X	
	<i>laevigata</i>	X	X	X		
	<i>nivalis</i>	X	X	X	X	X
	subtotal	5	5	5	3	3
	<i>Cladonia</i>	<i>carneola</i>			X	
	<i>chlorophaea</i>	X	X	X		
	<i>cornuta</i>		X			
	<i>ecmocyna</i>			X		
	<i>gracilis</i>	X	X	X		
	<i>mitis</i>	X	X	X	X	X
	<i>rangiferina</i>	X	X	X	X	X
	sp.	X	X	X	X	
	<i>squamosa</i>			X		
	<i>stygia</i>	X	X	X		
	<i>uncialis</i>	X	X	X		
	subtotal	7	8	10	3	2
<i>Dactylina</i>	<i>arctica</i>	X	X	X	X	X
<i>Masonhalea</i>	<i>richardsonii</i>	X	X	X	X	X
<i>Sphaerophorus</i>	<i>globosus</i>	X	X	X	X	
<i>Stereocaulon</i>	<i>tomentosum</i>	X	X	X	X	
<i>Thamnomia</i>	<i>vermicularis</i>	X	X	X	X	
Total genera		8	8	8	8	4
Total species		19	20	22	13	7

Live and vascular plant biomass increased relative to open plots after 10 years of fencing while total community biomass was significantly greater inside 17-year exclosures. However, there were no significant differences in biomass among fencing treatment levels in either set of experiments, implying that the effect of herbivory on the plant community as a whole was driven by caribou that were excluded from all fenced plots. The relative cover results suggest that herbivory had a negative effect on moss abundance, although this was not detected in the biomass harvest. Similarly, deciduous shrub relative abundance (but not biomass) was greater inside the exclosures.

Thus, as a result of the reduction of animal activity, the vascular community and lichens increased in biomass. This is counter to previous experimental manipulations in which an increase in the vascular community was accompanied by a decrease in lichen abundance (Cornelissen et al., 2001). The increases in vascular plant biomass in our study were relatively small, and light competition was likely not intensified. Most of these vascular plant species are low in stature so light reaches the soil surface easily. Under fertilized conditions when the vascular plant community shifts toward grass dominance, however, light availability does appear to decrease (see next section).

FERTILIZATION DRAMATICALLY REDUCED LICHENS, ALTERED COMMUNITY

Ten years of nutrient addition drastically reduced lichen abundance relative to plots with ambient nutrient levels. The amount of fertilizer added in this study was quite high and was greater than the expected increases in mineralization rates with

atmospheric and soil warming; thus, these results must be interpreted cautiously. However, this method suggests an endpoint for the lichens and plant community along a trajectory of change caused by greater nutrient availability.

Several mechanisms may be responsible for the drop in lichen biomass in the fertilized plots after 10 years of treatment. Lichen biomass was slightly greater inside fences when plots were fertilized, but the numbers were too small for patterns related to mammal effects to be determined. Similar tundra fertilization studies have also noted lichen declines (e.g., McKendrick et al., 1980; Grellmann, 2002) along with increases in relative abundance of graminoids, and speculated the lichens were reduced by competition. Here, a tussock-forming grass, *Hierochloa alpina*, that is normally rare, was responsible for the increase in graminoid abundance (Gough et al., 2002, 2007). This species not only comes to dominate the plots, reducing space for lichens, but also contributes most of the increased litter that may further limit light availability to low-growing species. It is more palatable than the normally abundant evergreen shrubs, and may be the prime attraction to the fertilized plots for the herbivores. Dead tillers of *Hierochloa* are found cut into pieces by voles and assembled into haypiles (personal observation), so some of the attraction for the small mammals may be for shelter as well as higher quality forage. This increase in grass biomass was greatest inside the small-mesh exclosures, suggesting an important interaction between herbivory and nutrients. Because grass tissues senesce and decompose more readily than the normally dominant evergreen shrubs (Hobbie, 1996), nutrient cycling in fertilized plots may be accelerated and may be further altered by herbivore consumption and redistribution (Olofsson et al., 2004).

Another possible explanation for the lichen response is that the fertilizer is toxic to the lichens (e.g., Kellner, 1993), and thus directly reduces their abundance. Even if that is the case, however, the shifts in the plant community, reduction of bare space, and slow growth rates of lichens relative to vascular plants likely prevent any subsequent re-colonization by lichens.

Herbivory also interacted with fertilization at the community level in the 10-year experiments. In an earlier study, Gough et al. (2002) posited that fertilization did not increase live biomass because the dramatic losses of lichens and evergreen shrubs (particularly wood biomass) from fertilized plots were not offset by the increased production of graminoids. However, in this study, when fertilized plots were protected from herbivory by small and large mammals (SFNP), live biomass was greater than in open, fertilized plots, suggesting the mammals were consuming fertilized plant biomass, particularly graminoids. This also suggests that caribou alone did not affect plant biomass under enriched conditions because there was little difference between NFNP10 and LFNP10, although there were several differences in relative abundance of particular growth forms (e.g., greater deciduous cover and litter accumulation in LFNP10). Thus increased nutrient availability may not be detected in overall community biomass changes when herbivores are present, although effects on community composition may be significant (Gough et al., 2002).

LONG-TERM EFFECTS OF INCREASED SOIL NUTRIENT AVAILABILITY AND HERBIVORY ON LICHEN ABUNDANCE

Determining the importance of herbivores in arctic communities requires examination of animal activity levels under ambient as well as warmed or nutrient-enriched conditions to adequately predict effects in the future. Our results suggest that increased soil nutrient availability will interact with mammalian herbivory to cause negative effects on the lichen community. Caribou grazing has been negatively associated with lichen cover, biomass, and richness in other tundra studies (e.g., Manseau et al., 1996; van der Wal et al., 2001; Cooper and Wookey, 2001). Twenty-two years following intense caribou grazing in Alaska, lichens had only recovered to 10% of control values (Klein, 1987), and on Svalbard in northern Norway a similar slow recovery was noted 20 years after cessation of grazing (Cooper and Wookey, 2001). Implications of the loss of lichens for the vascular plant community also require further study. Lichens alone have been found to negatively affect germination of evergreen shrubs (Hawkes and Menges, 2003) and reduce germination of several arctic vascular plant species in combination with mosses (Gough, 2006).

As arctic Alaska becomes shrubbier with climate warming (Chapin et al., 2005), herbivore grazing patterns will undoubtedly be affected. Our study supports the previously documented decreases in lichen abundance as nutrient availability increases (Cornelissen et al., 2001), suggesting that lichens will suffer from these changes. Our results demonstrate that herbivores, including voles, will interact with the temperature and shrub increases to potentially further decimate lichen populations. This in turn can be expected to alter herbivore grazing patterns by affecting forage availability, particularly in winter for caribou. Any change in herbivore patterns may cause changes in predator abundance (Callaghan et al., 2004), and may alter the historical nutrient cycling patterns in these areas where herbivores are known to transform and transport nutrients across the landscape (e.g., Oloffson et al., 2004). These complex trophic interactions require further study in multiple regions of the Arctic.

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