

Opposing plant community responses to warming with and without herbivores

Eric Post^{*†‡} and Christian Pedersen^{*}

^{*}Department of Biology, Penn State University, 208 Mueller Lab, University Park, PA 16802; and [†]Department of Arctic Environment, National Environmental Research Institute, University of Aarhus, DK-4000 Roskilde, Denmark

Edited by Stan Boutin, University of Alberta, Edmonton, Canada, and accepted by the Editorial Board June 9, 2008 (received for review March 17, 2008)

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

arctic | climate change | global warming | herbivory | species interactions

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

Vertebrate herbivores in particular may be of key importance to plant community response to warming because they influence plant biomass, soil nutrient dynamics, and species composition of plant communities (14–16). In high latitude systems, experimental evidence indicates that both small and large mammalian herbivores play an important role in structuring plant communities through selective foraging that not only reduces the abundance of preferred species but also alters competitive interactions among plant species (17, 18). Such influences may mediate plant biomass response to

climate change, especially in arctic and subarctic ecosystems, where vegetation is characteristically nutrient limited (9, 10), as is its potential response to increasing atmospheric CO₂ (7, 19, 20).

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

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

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

Results

Plant Biomass Responses to Warming and Large Herbivores. In accordance with our previous results (C.P. and E.P., unpublished

Author contributions: E.P. designed research; E.P. and C.P. performed research; E.P. analyzed data; and E.P. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission. S.B. is a guest editor invited by the Editorial Board.

[†]To whom correspondence should be addressed. E-mail: esp10@psu.edu.

This article contains supporting information online at www.pnas.org/cgi/content/full/0802421105/DCSupplemental.

© 2008 by The National Academy of Sciences of the USA

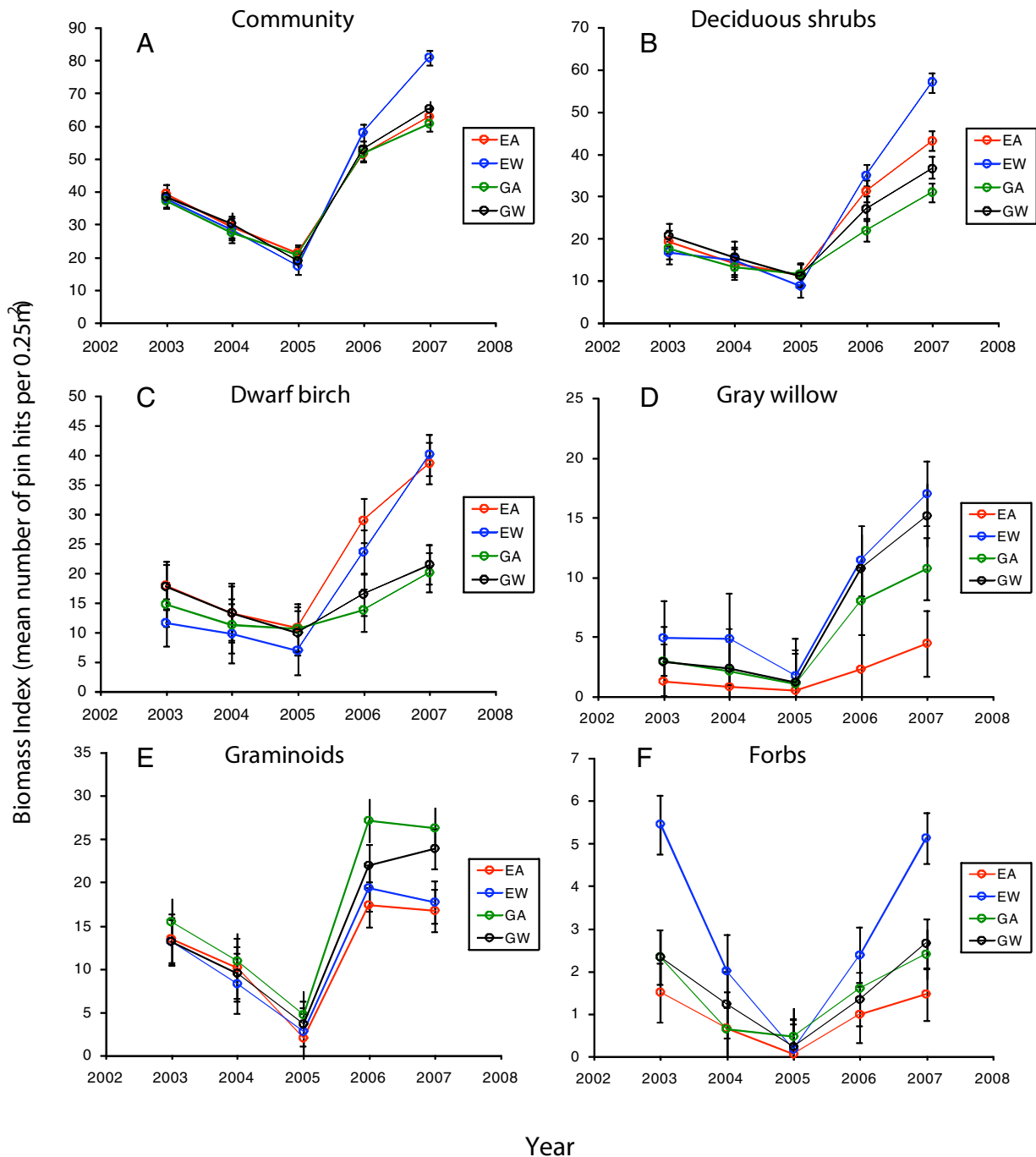


Fig. 1. Time series of ANOVA-estimated mean (± 1 SE) numbers of point-intercepts per 0.25 m² plot, according to treatments (red: excluded, ambient; blue: excluded, warmed; green: grazed, ambient; black: grazed, warmed). Means are shown for (A) the total plant community; (B) deciduous shrubs; (C) dwarf birch; (D) gray willow; (E) graminoids, and (F) forbs.

data), community composition did not vary between treatments and controls during the first 4 years of our experiment. However, by the fifth year, total community biomass was greatest on excluded-warmed plots, and exceeded that on control (grazed-ambient) plots by 33.1% (Fig. 1A). This was due primarily to greater aboveground biomass (ABM, see *Materials and Methods*) of deciduous shrubs on excluded-warmed plots, exceeding that on control plots by 84.7% (Fig. 1B). Within deciduous shrubs, total ABM of dwarf birch was highest on excluded plots; although there was no difference between excluded-warmed and excluded-ambient plots, ABM on excluded-warmed plots exceeded that on control plots by 98.7% (Fig. 1C). In

contrast, willow ABM was highest on warmed plots, regardless of whether they were excluded or grazed; however, ABM on excluded-warmed plots exceeded that on control plots by 58.4% (Fig. 1D). Graminoid ABM was highest on grazed plots and lowest on excluded plots; although there was no difference between warmed and ambient plots within these treatments, ABM on excluded-warmed plots was lower than on control plots by 32.7% (Fig. 1E). Finally, forb ABM was greatest on excluded-warmed plots and lowest on excluded-ambient plots, but means after 5 years of treatment did not differ from those at the start of our experiment (Fig. 1F). Nonetheless, ABM of forbs on excluded-warmed plots

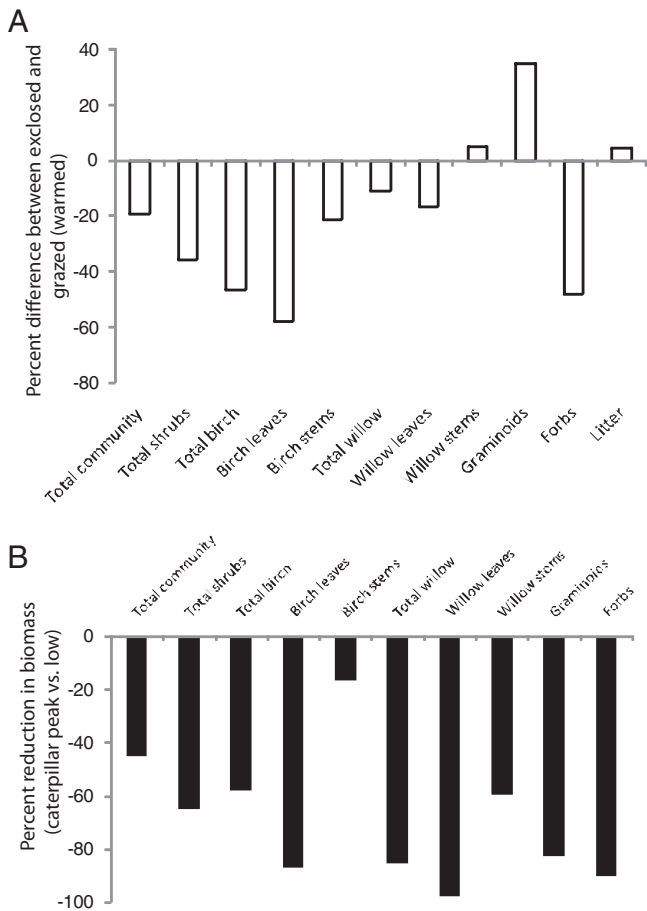


Fig. 2. Effects of (A) large herbivores (muskoxen and caribou) and (B) moth larvae on plant biomass response to the warming treatment. (A) Percent reduction or enhancement of the plant aboveground biomass response to warming by large herbivores. Percent difference is calculated as [(grazed mean – enclosed mean)/enclosed mean] × 100. (B) Percent difference per functional group or growth form between the peak of the caterpillar outbreak in 2005 and non-outbreak years, estimated across treatments. Percent difference is calculated as [(peak mean – non-outbreak mean)/non-outbreak mean] × 100.

exceeded that on control plots by 114.9% (Fig. 1F). Although not shown, ABM of litter did not differ among any of our treatment or control plots in any year of the experiment, except for 2005, the peak of a caterpillar outbreak (see below), when litter was lowest on enclosed-ambient plots by 28.3%.

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

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

herbivory of the biomass response to warming was for birch leaves (57.7% reduction) and forbs (48.2% reduction) (Fig. 2A). In contrast, herbivory enhanced the biomass response to warming of willow stems (4.78%), graminoids (35.1%), and litter (4.22%) (Fig. 2A).

There was a significant difference between muskoxen and caribou in the magnitude of the correlation between mean daily group size and effect size of the enclosure treatment on biomass response to warming ($F = 8.03, P = 0.01$), and a significant interaction between the herbivore species and plant functional group ($F = 2.76, P = 0.02$), with the mean correlation per plant functional group for muskoxen ($r_{\text{mean}} = 0.41$) exceeding that for caribou ($r_{\text{mean}} = 0.18$). For muskoxen, the highest correlations between the effect size ratio and mean daily herbivore density were found for responses to warming by the total community ($r = 0.70, P < 0.05$), total deciduous shrubs ($r = 0.71, P < 0.05$), total birch ($r = 0.70, P < 0.05$), birch stem ($r = 0.30, P > 0.05$), and litter ($r = 0.42, P > 0.05$). For caribou, the strongest correlation was found for graminoids ($r = 0.22, P > 0.05$). Hence, the effect of the enclosure treatment on biomass response to warming increased with presence of muskoxen in general but not with caribou.

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

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

To estimate interaction effects of our warming and enclosure treatments on community composition, we compared ANOVA-estimated means of control plots in 2007 to those of each combination of treatment and control manipulations in 2007 (Fig. 3B). Warmed plots that were also exposed to herbivory by muskoxen and caribou did not differ in community composition from control plots that were exposed to herbivory but not warmed (Fig. 3B, black “warming” arrow). In contrast, warmed plots that were not exposed to herbivory displayed significantly greater dwarf birch cover, but lower moss and graminoid cover, than control plots (Fig. 3B, black “warming + enclosure” arrow). Similarly, plots released from herbivory, but not warmed, displayed greater dwarf birch cover but lower graminoid cover than grazed, ambient plots (Fig. 3B, black “enclosure” arrow). Among treatment plots, warmed plots that were released from herbivory displayed greater dwarf birch cover, but lower moss and graminoid cover, than warmed plots that were also grazed (Fig. 3B, green “enclosure” arrow). Plots released from herbivory but not warmed displayed less willow and forb cover than warmed plots released from herbivory (Fig. 3B, red “warming”

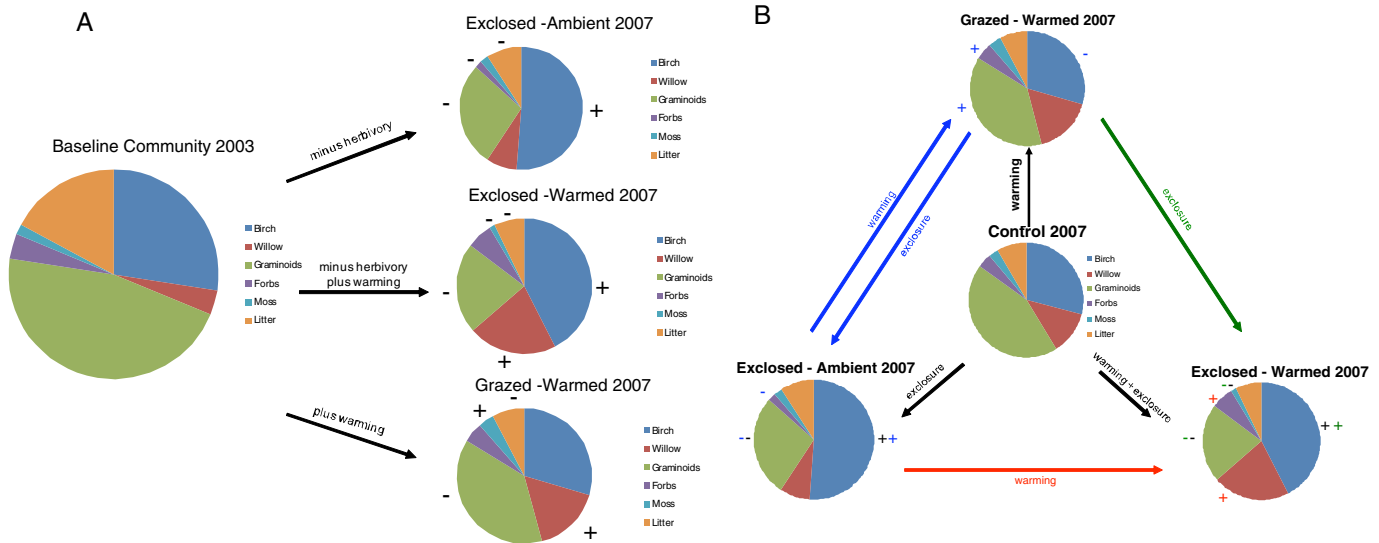


Fig. 3. (A) Changes in plant community composition from the baseline measures taken at the beginning of the experiment until the end of the fifth year of the experiment. Arrows identify the type of treatment applied to the baseline community. Signs (+ or -) adjacent to pie wedges indicate significant ($P < 0.05$) differences between treatment proportions and baseline proportions. (B) Differences in plant community composition between control and treatment plots in the fifth year of the experiment (2007). Arrows indicate treatments, and signs (+ or -, color-coded to treatment arrows) indicate significant ($P < 0.05$) differences between pie wedges in the direction of manipulations.

arrow). Finally, plots exposed to herbivory and warming displayed greater graminoid and forb cover, but lower birch cover, than plots not exposed to herbivory or warming (Fig. 3B, blue arrows).

Discussion

Arctic ecosystems have been a major focus of climate change studies because they have the potential for substantial feedback on climate through changes in plant species composition and C-balance that might, in turn, influence atmospheric CO_2 concentration (7, 12, 19). Yet, most studies examining plant productivity and community responses to warming in the Arctic have not incorporated animal influences (but see ref. 33). The results of our study indicate an important role of insect outbreaks and large herbivores on plant biomass and community composition under warming.

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

The differences in responses among plant functional groups to experimental warming in the Arctic revealed by metaanalyses (8, 12) could have implications for the manner in which communities will respond to the combined effects of herbivory and warming (13). For instance, a common feature of warming experiments is an initially greater and more consistent response in forbs and graminoids than in shrubs (8). Productivity of forbs and graminoids tends

to increase with the number of years of warming, while that of deciduous shrubs tends to decline with increasing number of years of treatment (8). The relationships we documented suggest herbivory may enhance the productivity response of herbaceous plants to warming and exacerbate the reduction in productivity of deciduous shrubs, mainly *B. nana* (8), in response to warming, although not completely (Fig. 2A).

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

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

The caterpillar outbreak midway through our experiment represents a highly pulsed event with presumably very low frequency (43). Nonetheless, it may have dramatic ecosystem consequences (44). In far northern ecosystems, insect outbreaks can influence

growth dynamics of woody plants for several years after the outbreak has passed (45) and are an important component of climate-tree line dynamics (46, 47). In addition to the effects of defoliation on aboveground biomass we documented (Fig. 2B), insect outbreaks may also influence ecosystem function through nutrient dynamics. Leaf tissues of dwarf birch and gray willow we collected at our site contained $\approx 4 \times$ greater N concentration at the peak of the caterpillar outbreak than before it (D. Eissenstat and E.P., unpublished data). By accelerating the turnover of N that would otherwise have remained in recalcitrant form as leaf tissue and litter, the caterpillar outbreak may have provided an N pulse to the system. This may, in part, explain the rapid biomass recovery that is apparently underway among all functional groups (Fig. 1). Only by collection of additional data will we be able to determine the extent to which the divergence among our treatments in year 5 of this experiment relates to recovery from the caterpillar outbreak.

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

Materials and Methods

Study Site. Our study site lies in the inland area east of Kangerlussuaq Fjord, West Greenland (67.11°N, 50.37°W). Vegetation is low shrub tundra dominated by *Betula nana*, *Salix glauca*, and *Poa* sp. The study site comprises the 3 most common vegetation types in the Arctic that represent 39% of the vegetated area of the Arctic (CAVM Team 2003). The study area is occupied by caribou (53, 54) and muskoxen (55). Ptarmigan and Arctic hares both occur at very low densities, and small herbivorous mammals are absent in the study site (E.P., personal observation).

Exclosure and Warming Experiment. In late June 2002, at the peak of the growing season, we erected 6, 800 m² circular exclosures constructed of woven wire and steel fence posts and delimited control sites of the same size and dimensions adjacent to each exclosure within a distance of 40–100 m. Baseline measures of standing ABM of forbs, graminoids, willows, birch, moss, and lichens were made at 10-m intervals along permanently marked, 50-m transects on exclosed and control sites in June 2002 using a linear point frame 1 m long with 10 intercept pins positioned at intervals of 10 cm. Measurements in 2002, however, preceded establishment of our permanent experimental and control plots. Beginning in 2003, with the establishment of permanent plots, and for the duration of the experiment, we switched to using a 0.5 m² Plexiglas point frame with 20 randomly located pin holes on all plots. With this point frame, biomass was estimated using the non-destructive canopy intercept method (see details below). On May 15, 2003, we established 12 experimental and 12 control plots in the study site by randomly locating plots for 3 passive warming open-top-chambers (OTCs) inside

and outside of each of 2 exclosures for a total of 12 OTCs. The number of OTCs was increased and expanded to 3 exclosures in May 2004, giving 25 warming and 25 control plots. The OTCs were constructed according to protocols of the International Tundra Experiment (56) from Sun-Lite HP (0.10 cm thick) fiberglass for solar applications (57), and measured 1.5 m in diameter at the base.

Within OTCs (treatment) and adjacent to them (control, at least 2.5–3 m away), we marked plots by sinking an aluminum peg measuring 7.5 cm into the soil at the center of each plot and at each of the 4 corners marking the cardinal directions. We assume that caribou and muskoxen, which were observed in May each year and daily throughout fieldwork, had access to vegetation outside the exclosures when OTCs were not present. It is possible that OTCs inhibited foraging by caribou and muskoxen, but we observed both species reaching into OTCs on two occasions, and one instance of a muskox attempting to lift the edge of an OTC with its nose.

Plant Aboveground Biomass Estimation. Dates of erection and dismantling of the OTCs in each year were reported (58). Upon establishment of plots, we quantified, to species level whenever possible, ABM of forbs, graminoids, willows, and birch. We used a rigid, square sheet of Plexiglas (measuring 0.25 m²) with 20 randomly located holes drilled in it, secured to 4 adjustable legs. All holes in the Plexiglas sheet were numbered, and the corners of the sheet were labeled with the cardinal directions. When the frame was anchored in the corner pegs on each plot, a single pin 3 mm in diameter was lowered through each hole, and each contact of the pin with living and standing dead vegetation was recorded until the pin reached soil or moss substrate. Encounters were recorded to the species level, although data for forbs and graminoids were analyzed at the level of functional groups. We also recorded whether pins hit leaves or stems and whether they hit litter or bare soil. Biomass was sampled in three periods: early growing season (late May to early June), mid growing season (mid to late June), and at the end of the growing season (mid July to early August).

Abiotic Measurements. We monitored plot surface temperature using Taylor digital max/min thermometers and relative humidity using hygrometers daily while OTCs were in place. Mean daily temperature, the average of the minimum and maximum temperatures in a 24 h period, was significantly higher inside OTCs than outside by 1.5–3 °C (58), which accords with expected temperature increase over the next century according to some scenarios (59). Relative humidity was insignificantly lower inside vs. outside OTCs (58).

Assessing the Effect of Muskoxen and Caribou on Plant Biomass Response to Warming. Before and since erection of the exclosures, we recorded numbers of caribou and muskoxen seen feeding on adjacent control sites daily through 2007. Mean daily numbers of each species feeding in each site were incorporated into our analyses of the effect size of the exclosure treatment on vegetation response to warming. We used three approaches to analyzing the effect of muskoxen and caribou on plant biomass response to warming. First, we compared ANOVA means of ABM of each functional group, and leaf and stem tissue of birch and willow, among grazed and exclosed plots; means differed at the 0.05 level of significance if they fell outside of the 95% confidence intervals of the means to which they were compared (32). The ANOVAs included treatments (warmed vs. ambient; exclosed vs. grazed) as fixed effects, with the warming treatment nested inside the exclosure treatment; and year, sampling period (early, middle, or late), and site as random effects. Comparisons were made for all years to produce time series of differences among means according to treatments over the course of the experiment. Second, we quantified percentage alteration of the biomass response to warming by herbivory by caribou and muskoxen as the relative difference between ANOVA means for exclosed-warmed vs. grazed-warmed plots in the fifth year of the experiment. Third, to identify whether muskoxen and caribou exerted similar effects on plant biomass response to warming, we tested for correlations between the effect size ($\ln[\text{experimental mean/control mean}]$) of the exclosure experiment for warmed plots and the mean daily numbers of muskoxen or caribou observed on each site in each year. Positive correlations indicate an increasing divergence between the response to warming of exclosed and grazed plots with greater mean densities of large herbivores on the grazed plots.

Assessing the Impact of Caterpillar Herbivory. In 2004, we realized a caterpillar outbreak was underway. To analyze the influence of what turned out to be a 2-year outbreak of caterpillars of a noctuid moth (*Eurois occulta*) on plant biomass response to warming, we counted caterpillars on all plots in 2005. The outbreak peak occurred in 2005, when caterpillar densities were conservatively estimated as being twice the levels we had observed in 2004. We estimated mean plot level caterpillar density across all sites in 2005 using an ANOVA with treatments as fixed effects (nonsignificant), and plot, site, and Julian date as random effects. We estimated that caterpillar densities in 2004 were half the mean level

for 2005. We tested for differences in plant biomass according to annual mean caterpillar densities and our treatments using an ANOVA with warming and enclosure treatments as fixed effects and caterpillar density in each year as a random effect. We also tested for interactions between our warming and enclosure treatments with caterpillar density. For 2003, 2006, and 2007, we coded caterpillar density as 0.01 per plot (0.25 m²). We observed only a few caterpillars in those years and assume their direct influence on ABM was functionally negligible. We used the ANOVA means from this analysis to estimate percent reduction in ABM by caterpillars across functional groups and treatments by comparing means in outbreak years (2004 and 2005) to means of non-outbreak years (all other years combined).

Assessing Changes in Plant Community Composition. We investigated whether plant community composition had changed after the first 5 years of our treatments. We calculated the proportion of the total community ABM comprising each functional group by dividing the number of pin hits per plot for each

functional group by the total number of pin hits for each individual plot in each sampling period each year. We estimated mean proportions of each functional group according to our treatments using an ANOVA with treatment as a fixed factor and site and period as random factors. We conducted these ANOVAs for 2003 to obtain baseline mean proportions and for 2007 to obtain mean proportions at the end of the fifth year of the experiment. Means differed at the 0.05 level of significance if they fell outside of the 95% confidence intervals of the means to which they were compared (32).

ACKNOWLEDGMENTS. We gratefully acknowledge help in the field from Tom Adams, Pernille Bøving, Toke T. Høye, Syrena Johnson, Megan MacArthur, Ieva Perkons, Mason T. Post, Taylor Rees, Henning Thing, Chris Wilmers, Tyler Yenter, Kangerlussuaq International Science Support, and VECO Polar Resources. We thank Mads C. Forchhammer, Oswald J. Schmitz, and three anonymous referees for useful comments on drafts of this article. This research was funded in part by grants to EP from National Science Foundation, the National Geographic Society, and the Penn State Institutes of Energy and the Environment.

- Hairton NG, Smith FE, Slobodkin LB (1960) Community structure, population control, and competition. *Am. Nat* 94:421–425.
- Schmitz OJ, Post E, Burns CE, Johnston KM (2003) Ecosystem responses to global climate change: Moving beyond color mapping. *Bioscience* 53:1199–1205.
- Johnston KM, Schmitz OJ (1997) Wildlife and climate change: Assessing the sensitivity of selected species to simulated doubling of atmospheric CO₂. *Glob Chang Biol* 3:531–544.
- Case TJ, Holt RD, McPeck MA, Keitt TH (2005) The community context of species' borders: Ecological and evolutionary perspectives. *Oikos* 108:28–46.
- Chapin FS, Hobbie SE, Shaver GR (1997) In *Global Change and Arctic Terrestrial Ecosystems*, eds Oechel WC, Callaghan T, Gilmanov T, Holten JI, Maxwell B, Molau U, and Sveinbjörnsson B (Springer Verlag, New York), pp 221–228.
- Chapin FS, et al. (1997) Biotic control over the functioning of ecosystems. *Science* 277:500–504.
- Shaver GR, Jonasson S (1999) Response of Arctic ecosystems to climate change: results of long-term field experiments in Sweden and Alaska. *Polar Research* 18:245–252.
- Arft AM, et al. (1999) Responses of tundra plants to experimental warming: Meta-analysis of the international tundra experiment. *Ecological Monographs* 69:491–511.
- Chapin FS, Shaver GR (1985) Individualistic growth-response of tundra plant species to environmental manipulations in the field. *Ecology* 66:564–576.
- Chapin FS, Shaver GR, Giblin AE, Nadelhoffer KJ, Laundre JA (1995) Responses of arctic tundra to experimental and observed changes in climate. *Ecology* 76:694–711.
- Sturm M, Racine C, Tape K (2001) Climate change—Increasing shrub abundance in the Arctic. *Nature* 411:546–547.
- Walker MD, et al. (2006) Plant community responses to experimental warming across the tundra biome. *Proc Natl Acad Sci USA* 103:1342–1346.
- Callaghan TV, et al. (2004) Effects on the structure of arctic ecosystems in the short- and long-term perspectives. *Ambio* 33:436–447.
- Pastor J, Dewey B, Naiman RJ, McInnes PF, Cohen Y (1993) Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. *Ecology* 74:467–480.
- McInnes PF, Naiman RJ, Pastor J, Cohen Y (1992) Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. *Ecology* 73:2059–2075.
- Frank DA, Groffman PF (1998) Ungulate vs. landscape control of soil C and N processes in grasslands of Yellowstone National Park. *Ecology* 79:2229–2241.
- Olofsson J, Hulme PE, Oksanen L, Suominen O (2004) Importance of large and small mammalian herbivores for the plant community structure in the forest tundra ecotone. *Oikos* 106:324–334.
- Rammul U, et al. (2007) Vole-vegetation interactions in an experimental, enemy free taiga floor system. *Oikos* 116:1501–1513.
- Shaver GR, et al. (2000) Global warming and terrestrial ecosystems: A conceptual framework for analysis. *Bioscience* 50:871–882.
- Melillo JM, et al. (1993) Global climate change and terrestrial net primary production. *Nature* 363:234–240.
- Bräthen KA, Oksanen J (2001) Reindeer reduce biomass of preferred plant species. *J Veg Sci* 12:473–480.
- Eskelinen A, Oksanen J (2006) Changes in the abundance, composition and species richness of mountain vegetation in relation to summer grazing by reindeer. *J Veg Sci* 17:245–254.
- Bräthen KA, et al. (2007) Induced shift in ecosystem productivity? Extensive scale effects of abundant large herbivores. *Ecosystems* 10:773–789.
- Ims RA, et al. (2007) Can reindeer overabundance cause a trophic cascade? *Ecosystems* 10:607–622.
- Ouellet JP, Boutin S, Heard DC (1994) Responses to simulated grazing and browsing of vegetation available to caribou in the Arctic. *Can. J Zool* 72:1426–1435.
- Manseau M, Huot J, Crete M (1996) Effects of summer grazing by caribou on composition and productivity of vegetation: Community and landscape level. *J Ecol* 84:503–513.
- Post ES, Klein DR (1996) Relationships between graminoid growth form and levels of grazing by caribou (*Rangifer tarandus*) in Alaska. *Oecologia* 107:364–372.
- Sturm M, et al. (2001) Snow-shrub interactions in Arctic tundra: A hypothesis with climatic implications. *J Clim* 14:336–344.
- Sturm M, et al. (2005) Winter biological processes could help convert arctic tundra to shrubland. *Bioscience* 55:17–26.
- Ripple WJ, Beschta RL (2004) Wolves, elk, willows, and trophic cascades in the upper Gallatin Range of Southwestern Montana, USA. *For Ecol and Manage* 200:161–181.
- Post E, Peterson RO, Stenseth NC, McLaren BE (1999) Ecosystem consequences of wolf behavioural response to climate. *Nature* 401:905–907.
- Sokal RR, Rohlf FJ (1995) *Biometry: The principles and practice of statistics in biological research* (Freeman and Company, New York), 3rd Ed.
- van der Wal R, van Lieshout SMJ, Loonen M (2001) Herbivore impact on moss depth, soil temperature and arctic plant growth. *Polar Biol* 24:29–32.
- Shaver GR, et al. (1998) Biomass and CO₂ flux in wet sedge tundra: Responses to nutrients, temperature, and light. *Ecol Monogr* 68:75–97.
- Born EW, Wiig O, Neve PB (1995) Observations of muskoxen (*Ovibos moschatus*) in central east Greenland International. *Z Saugtierkd* 60:373–379.
- Pedersen CB, Aastrup P (2000) Muskoxen in Anguartaortfup Nunaa, West Greenland: Monitoring, spatial distribution, population growth, and sustainable harvest. *Arctic* 53:18–26.
- Forchhammer M, Boertmann D (1993) The muskoxen, *Ovibos moschatus*, in north and northeast Greenland—population trends and the influence of abiotic parameters on population dynamics. *Ecography* 16:299–308.
- Miller FL (1991) Estimating Bathurst Island Peary caribou and muskox populations. *Arctic* 44:57–62.
- Reynolds PE (1998) Dynamics and range expansion of a reestablished muskox population. *J Wildl Manage* 62:734–744.
- Christensen TR, et al. (2000) Trace gas exchange in a high-arctic valley 1. Variations in CO₂ and CH₄ flux between tundra vegetation types. *Global Biogeochem Cycles* 14:701–713.
- Welker JM, Fahnestock JT, Henry GHR, O'Dea KW, Chimner RA (2004) CO₂ exchange in three Canadian High Arctic ecosystems: Response to long-term experimental warming. *Glob Chang Biol* 10:1981–1995.
- Hik DS, Jefferies RL (1990) Increases in the net aboveground primary production of a salt-marsh forage grass—a test of the predictions of the herbivore-optimization model *J Ecol* 78:180–195.
- Mjaaseth RR, Hagen SB, Yoccoz NG, Ims RA (2005) Phenology and abundance in relation to climatic variation in a sub-arctic insect herbivore-mountain birch system *Oecologia* 145:53–65.
- Lehtonen J, Heikkinen RK (1995) On the recovery of mountain birch after Epirrita damage in Finnish Lapland, with a particular emphasis on reindeer grazing. *Ecoscience* 2:349–356.
- Karlsson PS, Tenow O, Bylund H, Hoogesteger J, Weih (2004) M Determinants of mountain birch growth in situ: effects of temperature and herbivory. *Ecography* 27:659–667.
- Hagen SB, Jepsen JU, Ims RA, Yoccoz NG (2007) Shifting altitudinal distribution of outbreak zones of winter moth *Operophtera brumata* in sub-arctic birch forest: a response to recent climate warming? *Ecography* 30:299–307.
- Wolf A, Kozlov MV, Callaghan TV (2008) Impact of non-outbreak insect damage on vegetation in northern Europe will be greater than expected during a changing climate. *Clim Change* 87:91–106.
- Currano ED, et al. (2008) Sharply increased insect herbivory during the Paleocene-Eocene Thermal Maximum. *Natl Acad Sci USA* 105:1960–1964.
- Forchhammer MC, Post E, Stenseth NC, Boertmann D (2002) Long-term responses in arctic ungulate dynamics to variation in climate and trophic processes. *Popul Ecol* 44:113–120.
- Post E (2005) Large-scale spatial gradients in herbivore population dynamics. *Ecology* 86:2320–2328.
- Guthrie RD (1982) In *Paleoecology of Beringia*, eds Hopkins DM, Matthews JV, Jr, Schweger CE, Young SB (Academic, New York), pp 307–326.
- Zimov SA, et al. (1995) Steppe-tundra transition—a herbivore-driven biome shift at the end of the Pleistocene. *Am Nat* 146:765–794.
- Thing H (1984) Feeding ecology of the West Greenland caribou (*Rangifer tarandus*) in the Sisimiut-Kangerlussuaq region. *Danish Rev Game Biol* 12:1–53.
- Bøving PS, Post E (1997) Vigilance and foraging behaviour of female caribou in relation to predation risk. *Rangifer* 17:55–63.
- Forchhammer MC, Boomsma JJ (1995) Foraging strategies and seasonal diet optimization of muskoxen in West Greenland. *Oecologia* 104:169–180.
- Henry GHR, Molau U (1997) Tundra plants and climate change: the International Tundra Experiment (ITEX). *Glob Chang Biol* 3:1–9.
- Marion GM, et al. (1997) Open-top designs for manipulating field temperature in high-latitude ecosystems. *Glob. Change Biol* 3:20–32.
- Post E, Pedersen C, Wilmers CC, Forchhammer MC (2008) Phenological sequences reveal aggregate life history response to climatic warming. *Ecology* 89:363–370.
- Houghton JT, et al. eds (2001) *Climate change 2001: The scientific basis. Contribution of Working Group I to the Third Assessment Report of the IPCC* (Cambridge Univ Press, Cambridge).