

Simulating the effects of soil organic nitrogen and grazing on arctic tundra vegetation dynamics on the Yamal Peninsula, Russia

This article has been downloaded from IOPscience. Please scroll down to see the full text article.

2009 Environ. Res. Lett. 4 045027

(<http://iopscience.iop.org/1748-9326/4/4/045027>)

View [the table of contents for this issue](#), or go to the [journal homepage](#) for more

Download details:

IP Address: 137.229.80.114

The article was downloaded on 08/07/2010 at 23:35

Please note that [terms and conditions apply](#).

Simulating the effects of soil organic nitrogen and grazing on arctic tundra vegetation dynamics on the Yamal Peninsula, Russia

Qin Yu¹, Howard Epstein¹ and Donald Walker²

¹ Department of Environmental Sciences, University of Virginia, Charlottesville, VA 22903, USA

² Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775, USA

Received 30 July 2009

Accepted for publication 1 December 2009

Published 17 December 2009

Online at stacks.iop.org/ERL/4/045027

Abstract

Sustainability of tundra vegetation under changing climate on the Yamal Peninsula, northwestern Siberia, home to the world's largest area of reindeer husbandry, is of crucial importance to the local native community. An integrated investigation is needed for better understanding of the effects of soils, climate change and grazing on tundra vegetation in the Yamal region. In this study we applied a nutrient-based plant community model—ArcVeg—to evaluate how two factors (soil organic nitrogen (SON) levels and grazing) interact to affect tundra responses to climate warming across a latitudinal climatic gradient on the Yamal Peninsula. Model simulations were driven by field-collected soil data and expected grazing patterns along the Yamal Arctic Transect (YAT), within bioclimate subzones C (high arctic), D (northern low arctic) and E (southern low arctic). Plant biomass and NPP (net primary productivity) were significantly increased with warmer bioclimate subzones, greater soil nutrient levels and temporal climate warming, while they declined with higher grazing frequency. Temporal climate warming of 2 °C caused an increase of 665 g m⁻² in total biomass at the high SON site in subzone E, but only 298 g m⁻² at the low SON site. When grazing frequency was also increased, total biomass increased by only 369 g m⁻² at the high SON site in contrast to 184 g m⁻² at the low SON site in subzone E. Our results suggest that high SON can support greater plant biomass and plant responses to climate warming, while low SON and grazing may limit plant response to climate change. In addition to the first order factors (SON, bioclimate subzones, grazing and temporal climate warming), interactions among these significantly affect plant biomass and productivity in the arctic tundra and should not be ignored in regional scale studies.

Keywords: soil organic nitrogen, grazing, ArcVeg, modeling, multi-factor analysis

1. Introduction

Arctic tundra vegetation dynamics are affected by various environmental factors such as climate, soil nutrients, and animal grazing (Chapin 1992, Callaghan *et al* 2004, Epstein *et al* 2008). These controlling factors have been individually studied in the field (Arft *et al* 1999, Hansen *et al* 2006, Epstein

et al 2008, Gough *et al* 2008). However, few studies have collectively examined the combinations of these factors and can provide insights as to how these factors may interact and affect tundra vegetation communities (Richardson *et al* 2002, Gough *et al* 2007).

Temperature is a key factor that regulates plant community distribution and biomass in arctic tundra (Walker *et al* 2005,

Epstein *et al* 2008). Across a climatic gradient, aboveground shrub biomass was found to increase substantially with summer warmth index (SWI—sum of mean monthly temperatures $> 0^{\circ}\text{C}$) (Walker *et al* 2003a, Epstein *et al* 2008). A global temperature increase of $0.76^{\circ}\text{C} \pm 0.19^{\circ}\text{C}$ from 1850–1899 to 2001–2005 (IPCC, 2007) may be amplified in the arctic (Serreze and Francis 2006) and be responsible for a recent increase in arctic vegetation in general as well as an increase in the abundance of shrubs (Myneni *et al* 1997, Sturm *et al* 2001, Jia *et al* 2003, Forbes *et al* 2009). Warming effects on tundra vegetation growth are generally believed to be positive but may vary across climatic zones over time (Arft *et al* 1999).

Soil substrate and nutrient levels in arctic tundra are also determinants of species richness, vegetation growth and productivity (Nadelhoffer *et al* 1991, Gough *et al* 2000, Knoepp *et al* 2000, Walker *et al* 2003a, 2003b). In nitrogen limited arctic ecosystems, soil organic matter quality may be more important in controlling N mineralization rates than temperature, since during the growing season, temperatures typically stay between 0 and 10°C (Nadelhoffer *et al* 1991). Observations from N fertilization experiments in the arctic have shown increases in plant biomass of several plant species as well as increases in litter decomposition with increasing available N (Shaver and Chapin 1995, Jonasson *et al* 1999, Aerts *et al* 2006, Shaver *et al* 2006, Kelley and Epstein 2009).

In the arctic, herbivores can have positive or negative effects on plant growth and yield various tundra vegetation community shifts depending on the grazing intensity and frequency (Jefferies *et al* 1992, Olofsson *et al* 2001, Herder *et al* 2003, van der Wal 2006, Susiluoto *et al* 2008). Grazing can also interact with soils to affect plant biomass. This was explored by Gough *et al* (2007) who manipulated soil nutrient levels in two arctic Alaskan tundra sites to study plant–herbivore interactions at the species level. Their results suggested that herbivores may cause reductions in plant biomass and shifts in competitive relationships in plant communities. Such relationships among soils, herbivores and vegetation can be further examined using vegetation modeling approaches.

Vegetation modeling has been widely used to improve our understanding of potential impacts of changing environmental variables on vegetation structure and function, e.g. Clein *et al* 2000, Sitch *et al* 2003, van Wijk 2007, Wolf *et al* 2008. ArcVeg is a dynamic vegetation model of arctic tundra that has been applied to various tundra communities in Alaska and Canada (Epstein *et al* 2000, 2001, 2004, 2007). Soils are parameterized essentially as the mass of soil organic nitrogen (SON), and grazing is an important disturbance parameterized in the model. Climate warming can be applied in the model simulation based on a subzonal approach. In other words, a summer warming of 2°C for an initial subzone is essentially a replacement by the climate at the adjacent southern subzone. Prior simulations using ArcVeg have shown increases in shrub biomass and reductions in moss biomass with summer warming of 2°C ramped over 50 years. This is consistent with field observations, indicating the applicability of this model for projecting vegetation responses to climate warming (Epstein *et al* 2004, 2007).

The Yamal Peninsula is a large area of arctic tundra in northwestern Siberia, Russia that encompasses landscape to regional gradients of each of these three environmental factors: climate, soil nutrients, and grazing (Forbes 1999). The Yamal is not only the source of much of Europe's current and future energy resources, and as a result is of enormous strategic importance to Russia, but it is also the world's largest area of reindeer husbandry (Stammler 2005, Forbes and Kumpula 2009). Sustainability of tundra vegetation under changing climate is of special importance to the people who rely on reindeer husbandry for their livelihood (Forbes *et al* 2001) and requires a good understanding of the interactions among soils, grazing, and warming (Kryazhinskii and Danilov 2000).

In this study, we use ArcVeg to address the effects of climatic subzones, soil organic nitrogen, grazing, and warming on the tundra vegetation of the Yamal Peninsula. We aim to answer the following research questions. (1) How do SON levels affect tundra vegetation in terms of total biomass and net primary productivity (NPP) responses to warming? (2) How does grazing affect tundra vegetation in terms of total biomass and NPP? (3) How do SON, grazing and climate interact to affect tundra vegetation?

2. Methods and materials

2.1. Study area

The study encompasses locations along a bioclimatic transect on the Yamal Peninsula, northwestern Siberia. Figure 1 shows the relative locations of the field sites in this study: two sites near Laborovaya ($67^{\circ}42' \text{N}$, $68^{\circ}01' \text{E}$), three sites near Vaskiny Dachi ($70^{\circ}17' \text{N}$, $68^{\circ}54' \text{E}$), and two sites near Kharasavey ($71^{\circ}19' \text{N}$, $66^{\circ}95' \text{E}$). The most southern site Laborovaya lies about 100 km north of treeline within the southern tundra subzone, dominated by *Carex bigelowii*, *Betula nana*, *Aulacomnium palustre* sedge, moist dwarf-shrub, moss tundra on moist silt loamy soils (site 1) and *Betula nana*, *Vaccinium vitis-idaea*, *Sphaerophorus globosus*, *Polytrichum strictum*, prostrate dwarf-shrub, lichen tundra on more sandy site (site 2). Vaskiny Dachi is to the southeast of the main Bovanenkovo gas field in the central part of the Yamal Peninsula. Soils in each site vary from silt loam (site 1), silt loam and sandy loam (site 2), and sand (site 3) and different soils are associated with different vegetation covers. For site 1, the dominant vegetation is *Carex bigelowii*, *Vaccinium vitis-idaea*, *Hylocomium splendens* sedge, dwarf-shrub, moss tundra; site 2 is dominated by *Betula nana*, *Calamagrostis holmii*, *Aulacomnium turgidum* dwarf-shrub, graminoid, moss tundra; and site 3 is *Vaccinium vitis-idaea*, *Cladonia arbuscula*, *Racomitrium lanuginosum* prostrate dwarf-shrub, sedge, lichen, tundra. Kharasavey is the most northern region in this study and is located on the northwestern coast of the peninsula. Vegetation in this region includes *Carex bigelowii*, *Calamagrostis holmii*, *Salix polaris*, *Dicranum elongatum*, *Cladonia spp.* graminoid, prostrate dwarf-shrub, and moss tundra on silt loamy soils (site 1) and *Carex bigelowii*, *Salix nummularia*, *Dicranum sp.*, *Cladonia spp.* graminoid, prostrate dwarf-shrub, and moss, lichen tundra on

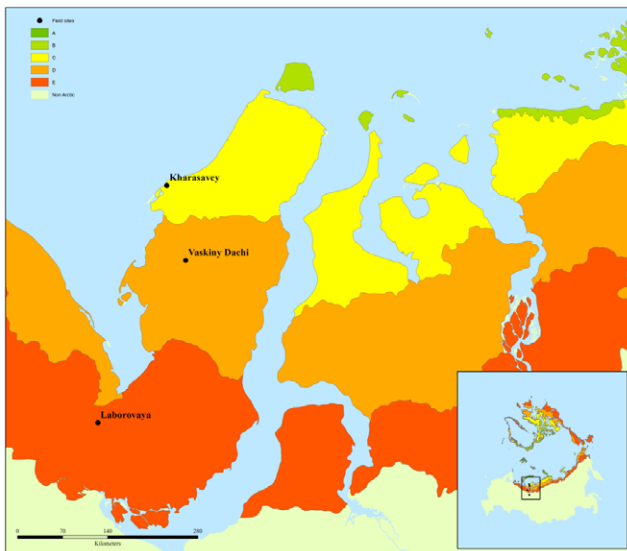


Figure 1. Locations of field sites along the Yamal Arctic Transect (YAT).

the sand loamy soils (site 2). These three regions are used as summer and autumn pasture for reindeer. More detailed information on each site can be found in the data report of the 2007 and 2008 Yamal expeditions (Walker *et al* 2009a), and studies associated with the sites along the Yamal transect can be found in the following: Goetz *et al* 2009, Walker *et al* 2009b, 2009c.

2.2. Model description

2.2.1. *ArcVeg*. *ArcVeg* is a nutrient-based, transient vegetation dynamics model, which was originally developed with a set of detailed plant functional types (PFT) to simulate how tundra vegetation represented by these PFTs responds to climate change. Since plant-available nitrogen can be a strongly limiting nutrient for tundra plants (Chapin *et al* 1995, Shaver *et al* 2000), the model functions essentially with nitrogen mass balance, redistributing nitrogen among soil organic matter, plant-available nitrogen, and plant pools. The current version of *ArcVeg* comprises 12 plant types, including mosses, lichens, forbs, and several categories of graminoids and shrubs (Epstein *et al* 2007). *ArcVeg* has been parameterized for the five arctic bioclimate subzones (Walker *et al* 2005) that range from the polar desert (subzone A) to the low arctic tundra at the southern extent of the tundra biome (subzone E). Soil conditions are expressed as different levels of soil organic nitrogen. A key assumption of the model is that with higher temperatures, decomposition rates increase, thus increasing the availability of soil nitrogen, which facilitates plant growth.

In addition, grazing as a major disturbance to tundra vegetation is parameterized as the removal of a specified percentage of plant biomass with different interannual frequencies. In other words, grazing intensity is represented by the combination of frequency and per cent removal. For example, (0.1, 25) indicates that there is a 0.1 annual

probability of a grazing herd (i.e. every 10 years frequency) and a maximum of 25% biomass will be removed. One of the model assumptions is that selectivity of grazing is determined by foliage nitrogen concentration.

2.2.2. *Model input data and simulation procedures*. Soil samples from each of the Yamal field sites have been collected and analyzed for bulk density, soil organic carbon, and soil organic nitrogen to the depth of the active layer. Each of the three field locations had two or three separate sampling grids to capture the variability of soil properties. The soil organic nitrogen data are used to drive the simulations in *ArcVeg* (table 1).

Other input data include: bioclimate subzone, grazing intensity, and climate warming. Two sites near Laborovaya (LV-1, LV-2) are located in the southern low arctic (subzone E). Three sites at Vaskiny Dachi (VD-1, VD-2 and VD-3) are within bioclimate subzone D, and two sites at Kharasavey (KH-1, KH-2) are in subzone C. The Yamal region is home to the indigenous Nenets people. Reindeer population increases have been documented by various authors (Golovnev and Osherenko 1999, Baskin 2000), and the drivers are quite complex as noted in Forbes and Kumpula (2009). Grazing patterns are quite heterogeneous and have been observed and modeled in various rangelands (Pickup and Chewings 1988, Stammer 2005). For managed reindeer herds on the Yamal, grazing is most intense near migratory Nenets camps and dissipates outward from the camps (Forbes and Kumpula 2009). We conducted a comparison study of grazing and soil effects across sites in different bioclimate subzones within a model simulation. The control grazing regime was set as (0.1, 25), indicating reindeer herds will graze on the same site every ten years and each visit a maximum of 25% of total biomass will be removed. A more frequent grazing regime is set as (0.5, 25), 25% of plant biomass will be removed every two years. These grazing scenarios are within the reasonable ranges that can be typically found in the Yamal region. Model simulations were conducted for 1500 years in total with a ‘spin-up’ to equilibrium conditions for the first 1000 years. A warming scenario was implemented in the model by beginning a temperature increase of 2 °C (essentially a shift of one subzone) in year 1000, ramped linearly over a 50 year period. Then the system was simulated under the new warmer climate for another 450 years.

All parameter combinations (including subzone (3), SON (7), grazing regime (2) and warming or non-warming) were simulated with 20 replicate runs. Plant total biomass and NPP were compared and evaluated across all sites on the Yamal Peninsula under the different grazing regimes and one subzone climate warming as discussed above. We calculated the mean total biomass and NPP for 100 years before the warming (year 901 to year 1000) and for 100 years after warming (year 1401 to year 1500).

2.3. Statistical analyses

Simulated total biomass and NPP with 20 replicates were used as dependent variables in ANOVA (analysis of variance). The

Table 1. Site name, bioclimate subzone, and soil parameters on the Yamal Arctic Transect.

Subzone	Sites	C%	N%	%sand	%silt	%clay	Bulk density (g m ⁻³)	Active layer depth (cm)	SON (g m ⁻²)
E	LV-1	1.72	0.06	18.00	59.32	22.68	1.21	81.20	570
E	LV-2	0.59	0.01	93.60	3.60	2.80	1.29	114.60	148
D	VD-1	1.25	0.03	28.90	60.80	10.30	1.34	71.75	271
D	VD-2	1.46	0.04	38.28	53.88	7.84	1.37	68.60	202
D	VD-3	1.31	0.05	92.80	4.64	2.56	1.18	113.80	498
C	KH-1	1.10	0.06	24.47	52.07	23.47	1.47	56.33	484
C	KH-2	1.18	0.07	65.60	26.60	7.80	1.22	75.50	599

main effects were soil organic nitrogen (continuous variable), climate subzones, climate warming, and grazing (categorical variables). The interactions of the main effects were also included in the ANOVA. LSMEANS (least square means) and Type III SS (Type III sums of squares) were used to account for the unbalanced data. All statistics were performed in SAS version 9.1 for Windows (SAS institute Inc.).

3. Results

The statistical analyses show that bioclimate subzones, SON, warming, and grazing have significant effects on total biomass and NPP individually (see appendix). SON is the most important factor with the highest *F* value, suggesting the most significant effects on total biomass and NPP. All interactions were also significant.

3.1. Soil organic nitrogen effects on biomass and NPP across climate subzones (figure 2—before warming)

Soil organic N significantly affected plant total biomass and NPP. In each bioclimate subzone, lower soil organic N supported less vegetation than higher soil organic N (figure 2). In particular, in the high SON site in subzone E (Laborovaya, LV-1), both total biomass and NPP were approximately 148% and 143% higher than those of the low SON site (LV-2) before warming. In LV-1 (SON = 570 g m⁻²), the soil supported nearly 831 g m⁻² biomass while only 336 g m⁻² biomass was simulated in LV-2 (SON = 148 g m⁻²). Effects of SON on total biomass and NPP changed with different climate subzones. With a similar amount of SON, warmer bioclimate subzones (e.g. subzone E) supported more vegetation and higher plant growth rates than colder subzones (e.g. subzone C) (figure 2). For example, total biomass and NPP at LV-1 were around 831 g m⁻² and 146 g m⁻² year⁻¹ whereas in KH-2 (SON = 599 g m⁻²), total biomass and NPP were 554 g m⁻² and 70 g m⁻² year⁻¹ respectively. With similar amounts of SON (LV-1 versus KH-2), each gram of SON can support 0.79 g m⁻² more biomass and 0.14 g m⁻² year⁻¹ greater NPP in subzone E than in subzone C.

3.2. Warming effects on total biomass and NPP across sites (figure 2—before and after warming comparison)

Temporal warming from our simulations with low grazing frequency showed an absolute increase in total biomass of 665 g m⁻² (absolute change will be shown following any

relative change in parentheses: 80%) in the high SON site (LV-1) and about 298 g m⁻² (89%) in the low SON site (LV-2). The absolute and relative increase in NPP in subzone E was found to be 95 g m⁻² year⁻¹ (65%) in LV-1 and 46 g m⁻² year⁻¹ (77%) in LV-2. For the set of sites in subzone D, the increases in biomass and NPP were 351 g m⁻² (63%) and 57 g m⁻² year⁻¹ (56%) in VD-3, 214 g m⁻² (75%) and 35 g m⁻² year⁻¹ (64%) in VD-2, and 246 g m⁻² (70%) and 40 g m⁻² year⁻¹ (61%) in VD-1 respectively, with higher relative increases in both total biomass and NPP in low SON sites compared to in high SON sites.

3.3. Grazing effects on total biomass and NPP (figure 3)

Grazing generally caused total plant biomass and NPP to decrease. Under the same climate conditions (here we used the data before climate warming), the absolute decline in total biomass caused by increased grazing frequency varied with SON levels. For example, comparing the sites in Vaskiny Dachi (subzone D), declines in biomass were found when grazing frequency increased from every ten to every two years: a decline of 191 g m⁻² in the high SON site (VD-3), 114 g m⁻² in VD-2 (the low SON site) and 135 g m⁻² in VD-1 (figure 3). This was also true for NPP, where we simulated a decrease of 18 g m⁻² year⁻¹ in VD-3, 15 g m⁻² year⁻¹ in VD-1 and 13 g m⁻² year⁻¹ in VD-2.

3.4. Grazing and warming interactions on total biomass and NPP (figure 4)

Grazing also interacted with climate warming, suppressing plant biomass and NPP response to warming. The suppression was stronger in sites with higher SON content than in the sites with lower SON content. The positive response of total biomass to warming was reduced from 665 g m⁻² in LV-1 to 369 g m⁻² due to higher grazing frequency (figure 4). In comparison, the total biomass increase due to warming in LV-2 site was decreased from 298 to 194 g m⁻². The NPP response decreased from 95 to 83 g m⁻² year⁻¹ in LV-1 and from 46 to 41 g m⁻² year⁻¹ in LV-2. Greater response declines in the high SON site (KH-2—8 g m⁻² year⁻¹) than the low SON site (KH-1—6 g m⁻² year⁻¹) were also found in subzone C.

4. Discussion

The results of this study demonstrate how tundra vegetation on the Yamal Peninsula in northwestern Siberia may respond

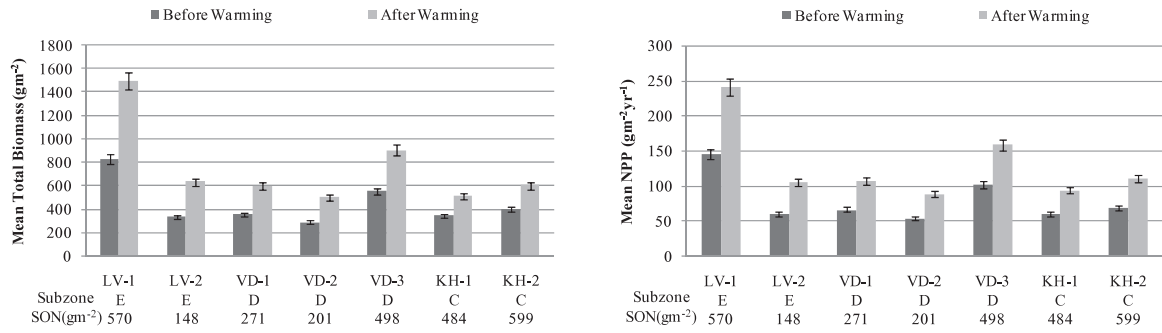


Figure 2. Comparison of mean total biomass (left) and NPP (right) (error bars show the 95% confidence intervals) before and after warming along the YAT for the low grazing frequency regime for each site. Subzone and soil organic nitrogen (SON, g m⁻²) are noted on the x-axis.

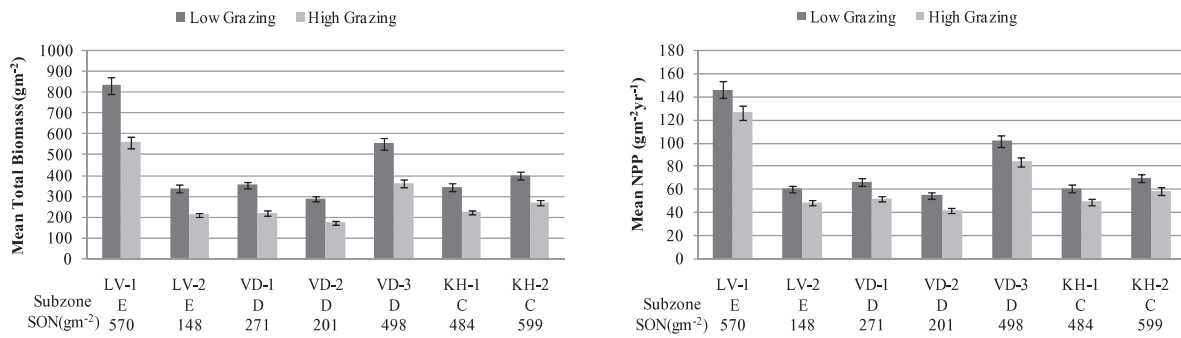


Figure 3. Comparison of change in mean total biomass (left) and NPP (right) (error bars show the 95% confidence intervals) for each site under two grazing regimes (low frequency grazing: (0.1, 25%) and high frequency grazing: (0.5, 25%).

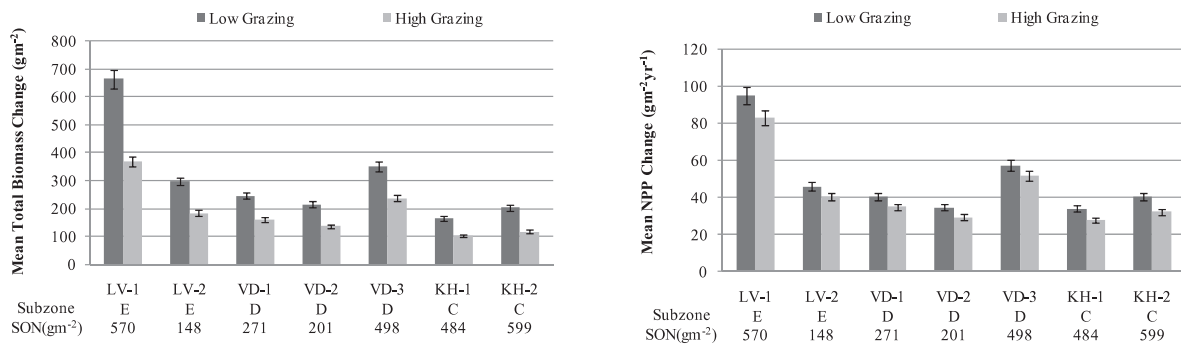


Figure 4. Comparison of absolute increase in mean total biomass (left) and NPP (right) (error bars show the 95% confidence intervals) caused by climate warming for each site under two grazing regimes (low frequency grazing: (0.1, 25%) and high frequency grazing: (0.5, 25%).

to warming and grazing with different soil nutrient levels associated with different soil substrates across a climatic gradient. Climate and soil nutrient levels (especially nitrogen) in arctic soils determine how much vegetation a site can support. Our results of total biomass and NPP being intimately coupled with arctic temperature gradients are consistent with field studies, where above ground biomass increased exponentially or linearly across a temperature gradient (Walker *et al* 2003a, Epstein *et al* 2008).

Soil organic nitrogen as a major limiting nutrient to arctic vegetation is found to be conspicuously important. High SON levels which tend to occur on clayey soils can facilitate plant growth and have a large impact on tundra vegetation (Chapin 1992). In high SON sites, simulated absolute increases

in NPP with warming are greater than those in low SON sites (sandy soil substrates), which is consistent with N fertilization experiments (Chapin and Shaver 1996, Shaver and Jonasson 1999, Shaver *et al* 2006). However, with the same grazing regime, nutrient-poor sites generally have higher SON efficiency (defined as model-simulated NPP divided by SON) than nutrient-rich sites. For example, SON efficiency calculated before warming was about 0.26 in LV-1 (SON = 570 g m⁻²) and 0.40 in LV-2 (SON = 148 g m⁻²). With climate warming, SON efficiency increased to 0.42 in LV-1 and to 0.72 in LV-2. The simulation results suggested that plants tend to make better use of SON in nutrient-poor sites than nutrient-rich sites, probably due to more intense resource competition in nutrient limited sites.

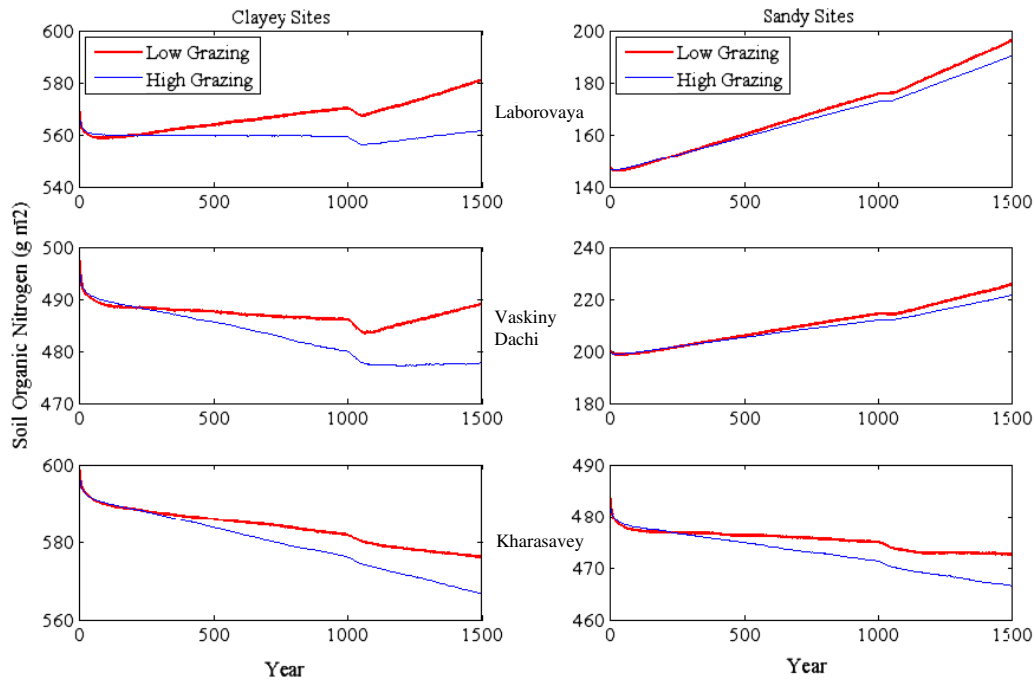


Figure 5. Grazing effects on soil organic nitrogen pool in each site over time.

One of the assumptions of ArcVeg is that climate warming increases soil organic matter decomposition rates (Epstein *et al* 2000). In the arctic, growth of tundra vegetation is limited by extreme low temperatures and short growing seasons, which result in low decomposition rates and low nutrient availability to plants (Chapin 1992, Hobbie and Chapin 1998). Increasing temperature may increase nitrogen mineralization rates in the arctic and provide plants with more nutrients, thus increasing plant biomass and productivity (Nadelhoffer *et al* 1991, Hobbie 1996, Rustad *et al* 2001, Jonasson *et al* 2006). A meta-analysis of the results from 32 research sites across the arctic region show an increase of net N mineralization rates by 46% (with a 95% confidence interval of 30–64%), and plant productivity by 19% (with a 95% confidence interval of 15–23%) in response to experimental ecosystem warming in the range 0.3 °C for 2–9 years (Rustad *et al* 2001). Toolik Lake in Alaska was included in the meta-analysis, and the responses of soil respiration to warming were found to be larger than the grand mean of the 32 sites. Some field warming experiments in the arctic can however show an increase in net N immobilization rather than net N mineralization, but this may be due to the short observation period (Aerts *et al* 2006). The climate gradient and warming scenarios were treated as separate factors that affect vegetation growth in ArcVeg. In both, temperature is positively related to total plant biomass and NPP. Climate warming effects on tundra vegetation communities have been addressed in several field experiments and the effect size of climatic warming is generally the greatest in the southern low arctic (Arft *et al* 1999). Our model simulations are consistent with these results. The warming stimulation effects decrease for colder subzones. In LV-1 (subzone E), the relative increase in NPP caused by warming is about 65%, while in KH-2 (subzone C, SON = 599 g m⁻²) the increase is only 58%.

Reindeer grazing was evaluated in this study by comparing a control grazing regime (0.1, 25) with an increased grazing frequency (0.5, 25). Soil nutrient conditions interact with grazing to yield complex effects on vegetation (Virtanen 2000, Gough *et al* 2007, Eskelinen 2008). Sites with high SON levels were generally more affected by disturbance from higher grazing frequency than the low SON sites. For instance, the absolute difference in total biomass between low and high grazing frequency is about 271 g m⁻² in LV-1 (SON = 570 g m⁻²) while only 125 g m⁻² in LV-2 (SON = 148 g m⁻²) in subzone E. The difference in NPP between low and high grazing frequency is 19 g m⁻² year⁻¹ in LV-1 and 12 g m⁻² year⁻¹ in LV-2. The interpretation can be that the site with high SON levels can support more vegetation, and hence more is eaten by grazing herds (Gough *et al* 2007, Eskelinen 2008, Olofsson *et al* 2009). A study conducted in northernmost Fennoscandia by Eskelinen (2008) showed that nutrient-rich sites are more intensively grazed than nutrient-poor sites. Gough *et al* (2007) measured weekly growth of dominant tundra plants under fertilized and unfertilized conditions. In their nine year manipulations, plants with herbivore exclusion grew better than those without exclusion, and plants were more grazed in fertilized sites than ambient sites without fertilization, indicating a negative effect of herbivory in the fertilized sites. Their results also corroborate our findings that absolute decrease in total biomass and NPP due to herbivory is significantly greater in sites with higher SON levels under the same grazing regime (figure 3), in that animals tend to graze more on the abundant vegetation patches. This can also be interpreted as spatial effects of grazing due to soil heterogeneity, and as temporal effects of N fertilization; the fertile sites can support more vegetation and tend to be grazed more often than the control sites (Gough *et al* 2007).

Increasing grazing frequency caused a greater decline in plant response to climate warming (in terms of total biomass and NPP) in sites with higher SON levels, suggesting again that herbivory generally becomes more important under higher nutrient conditions. This is supported by recent work documenting long-term effects of herbivory on tundra plant growth (Virtanen 2000, Grellmann 2002, Olofsson *et al* 2004a, 2004b). A grazing suppression effect is evaluated in our model by comparing the absolute increases in total biomass and NPP between two grazing regimes. In subzone E, the suppression effect in terms of total biomass and NPP was 296 g m⁻² and 12 g m⁻² year⁻¹ in LV-1 versus 113 g m⁻² and 5 g m⁻² year⁻¹ in LV-2 respectively. When comparing low grazing to high grazing effects on soil organic nitrogen pools over time (figure 5), higher grazing frequency led to either slower SON accumulation rates or more rapid SON depletion rates. Warming accentuated these differences caused by grazing, suggesting the interaction between grazing and warming may yield greater differences in SON levels across sites.

Appendix

5. Conclusion

This study has offered insights into the interactions among soil nutrients, climate, and grazing on arctic tundra vegetation on the Yamal Peninsula. Soil nutrients are a limiting factor to plant growth, and also limit the plant responses to climate warming. Long-term projections of how SON levels affect tundra vegetation responses to warming and grazing can be assessed using the ArcVeg model. Numerous studies have suggested that climate warming is an essential factor for promoting tree and shrub expansion in arctic tundra, however grazing may limit this response (Olofsson *et al* 2009). Research conducted in the neighboring Nenets Autonomous Okrug has shown that shrubs already above the reindeer browsing line have increased their growth significantly in response to current climate warming of the last few decades (Forbes *et al* 2009). A better understanding of soil organic nitrogen and grazing effects on tundra vegetation growth is crucial for determination of the rate of shrub expansion in the arctic.

Acknowledgments

This study was supported by NASA/NEESPI Land Cover Land Use Change Initiative, Grant No NNG6GE00A, NSF Grant

Table A.1. Statistics of total biomass and NPP as influenced by subzone, soil organic nitrogen, climate warming and grazing. Analysis of variance (ANOVA) was applied to the simulated datasets, where subzone, warming, grazing are independent categorical variables. DF is the degrees of freedom. Type III sum of squares assesses at the unbalanced data, since our variables are of different DFs. Mean square is the square root of Type III SS. *F* values measure the distance between individual distributions; as *F* values increase, *P* values decrease. *P* values < 0.05 indicate a statistically significant effect of that independent variable on the dependent variable.

Source of variations	DF	Type III SS	Mean square	<i>F</i> value	<i>P</i> > <i>F</i>
Total biomass					
Subzone	2	109 625.712	54 812.856	471.08	<0.0001
SON	1	3572 898.163	3572 898.163	30 706.5	<0.0001
Warming	1	28 548.129	28 548.129	245.35	<0.0001
Grazing	1	25 105.281	25 105.281	215.76	<0.0001
SON*subzone	2	531 677.655	265 838.828	2 284.70	<0.0001
Subzone*warming	2	14 999.054	7 499.527	64.45	<0.0001
Subzone*grazing	2	872.427	436.213	3.75	0.0242
SON*warming	1	178 326.428	178 326.428	1 532.59	<0.0001
SON*grazing	1	124 979.964	124 979.964	1 074.11	<0.0001
Warming*grazing	1	10 964.736	10 964.736	94.23	<0.0001
SON*subzone*warming	2	55 304.044	27 652.022	237.65	<0.0001
SON*subzone*grazing	2	47 219.928	23 609.964	202.91	<0.0001
SON*subzone*warming*grazing	3	191 960.578	63 986.859	549.92	<0.0001
NPP					
Subzone	2	3112.0345	1 556.0172	1 634.69	<0.0001
SON	1	128 213.4283	128 213.4283	134 696	<0.0001
Warming	1	1 126.0711	1 126.0711	1 183.00	<0.0001
Grazing	1	495.5042	495.5042	520.56	<0.0001
SON*subzone	2	16 647.3388	8 323.6694	8744.51	<0.0001
Subzone*warming	2	554.2940	277.1470	291.16	<0.0001
Subzone*grazing	2	21.0443	10.5222	11.05	<0.0001
SON*warming	1	5 786.5652	5 786.5652	6 079.13	<0.0001
SON*grazing	1	262.6218	262.6218	275.90	<0.0001
Warming*grazing	1	70.7726	70.7726	74.35	<0.0001
SON*subzone*warming	2	998.1921	499.0961	524.33	<0.0001
SON*subzone*grazing	2	75.8446	37.9223	39.84	<0.0001
SON*subzone*warming*grazing	3	157.0791	52.3597	55.01	<0.0001

No ARC-0531180, part of the Synthesis of Arctic System Science initiative and NSF Grant No ARC-0902152, part of the Changing Seasonality of Arctic Systems initiative.

References

- Aerts R *et al* 2006 Nitrogen supply differentially affects litter decomposition rates and nitrogen dynamics of sub-arctic bog species *Oecologia* **146** 652–8
- Arft A M *et al* 1999 Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment *Ecol. Monogr.* **69** 491–511
- Baskin L 2000 Reindeer husbandry/hunting in Russia in the past, present and future *Polar Res.* **19** 23–9
- Callaghan T V *et al* 2004 Effects on the function of Arctic ecosystems in the short-and long-term perspectives *AMBIO: J. Human Environ.* **33** 448–58
- Chapin F S 1992 *Arctic Ecosystems in a Changing Climate: an Ecophysiological Perspective* (New York: Academic)
- Chapin F S and Shaver G R 1996 Physiological and growth responses of arctic plants to a field experiment simulating climatic change *Ecology* **77** 822–40
- Chapin F S *et al* 1995 Responses of Arctic tundra to experimental and observed changes in climate *Ecology* **76** 694–711
- Clein J *et al* 2000 Modelling carbon responses of tundra ecosystems to historical and projected climate: a comparison of a plot-and a global-scale ecosystem model to identify process-based uncertainties *Glob. Change Biol.* **6** 127–40
- Epstein H E *et al* 2000 A transient nutrient-based model of arctic plant community response to climatic warming *Ecol. Appl.* **10** 824–41
- Epstein H E *et al* 2001 Analyzing the functional type concept in arctic plants using a dynamic vegetation model *Oikos* **95** 239–52
- Epstein H E *et al* 2004 Detecting changes in arctic tundra plant communities in response to warming over decadal time scales *Glob. Change Biol.* **10** 1325–34
- Epstein H E *et al* 2007 Simulating future changes in arctic and subarctic vegetation *Comput. Sci. Eng.* **9** 12–23
- Epstein H E *et al* 2008 Phytomass patterns across a temperature gradient of the North American arctic tundra *J. Geophys. Res.* **113** G3
- Eskelinen A 2008 Herbivore and neighbour effects on tundra plants depend on species identity, nutrient availability and local environmental conditions *J. Ecol.* **96** 155–65
- Forbes B and Kumpula T 2009 The ecological role and geography of reindeer (*Rangifer tarandus*) in Northern Eurasia *Geogr. Compass* **3** 1356–80
- Forbes B *et al* 2001 Anthropogenic disturbance and patch dynamics in circumpolar Arctic ecosystems *Conserv. Biol.* **15** 954–69
- Forbes B *et al* 2009 Russian Arctic warming and ‘greening’ are closely tracked by tundra shrub willows *Glob. Change Biol.* **13** 2486
- Forbes B C 1999 Land use and climate change on the Yamal Peninsula of north-west Siberia: some ecological and socio-economic implications *Polar Res.* **18** 367–73
- Goetz S J *et al* 2009 Vegetation productivity and disturbance changes across arctic northern Eurasia: satellite observations and simulation modeling *Arctic Land Cover and Land Use in a Changing Climate: Focus on Eurasia* ed G Gutman and C Justice (Berlin: Springer)
- Golovnev A and Osherenko G 1999 *Siberian Survival: the Nenets and their Story* (Ithaca, NY: Cornell University Press)
- Gough L *et al* 2000 Vascular plant species richness in Alaskan arctic tundra: the importance of soil pH *J. Ecol.* **88** 54–66
- Gough L *et al* 2007 Plant-herbivore interactions in Alaskan arctic tundra change with soil nutrient availability *Oikos* **116** 407–18
- Gough L *et al* 2008 Long-term mammalian herbivory and nutrient addition alter lichen community structure in Alaskan dry heath tundra *Arct. Antarct. Alpine Res.* **40** 1–21
- Grellmann D 2002 Plant responses to fertilization and exclusion of grazers on an arctic tundra heath *Oikos* **98** 190
- Hansen A H *et al* 2006 Long-term experimental warming, shading and nutrient addition affect the concentration of phenolic compounds in arctic-alpine deciduous and evergreen dwarf shrubs *Oecologia* **147** 1–11
- Herder M *et al* 2003 Growth of reindeer lichens and effects of reindeer grazing on ground cover vegetation in a Scots pine forest and a subarctic heathland in Finnish Lapland *Ecography* **26** 3–12
- Hobbie S 1996 Temperature and plant species control over litter decomposition in Alaskan Tundra *Ecol. Monogr.* **66** 503–22
- Hobbie S E and Chapin F S III 1998 The response of tundra plant biomass, aboveground production, nitrogen, and CO₂ flux to experimental warming *Ecology* **79** 1526–44
- Jefferies R *et al* 1992 Tundra grazing systems and climatic change *Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective* ed F S Chapin III, R L Jefferies, J F Reynolds, G R Shaver and J Svoboda (San Diego, CA: Academic) pp 391–412
- Jia G J *et al* 2003 Greening of arctic Alaska, 1981–2001 *Geophys. Res. Lett.* **30** 2067
- Jonasson S *et al* 1999 Responses in microbes and plants to changed temperature, nutrient, and light regimes in the arctic *Ecology* **80** 1828–43
- Jonasson S *et al* 2006 Interactions between plants, litter and microbes in cycling of nitrogen and phosphorus in the arctic *Soil Biol. Biochem.* **38** 526–32
- Kelley A and Epstein H 2009 Effects of nitrogen fertilization on plant communities of nonsorted circles in moist nonacidic tundra, northern Alaska *Arct. Antarct. Alpine Res.* **41** 119–27
- Knoepp J D *et al* 2000 Biological indices of soil quality: an ecosystem case study of their use *Forest Ecol. Manag.* **138** 357–68
- Kryazhinskii F V and Danilov A N 2000 Reindeer in tundra ecosystems: the challenges of understanding system complexity *Polar Res.* **19** 107–10
- Myneni R B *et al* 1997 Increased plant growth in the northern high latitudes from 1981 to 1991 *Nature* **386** 698–702
- Nadelhoffer K *et al* 1991 Effects of temperature and substrate quality on element mineralization in six arctic soils *Ecology* **72** 242–53
- Olofsson J *et al* 2001 Effects of summer grazing by reindeer on composition of vegetation, productivity and nitrogen cycling *Ecography* **24** 13–24
- Olofsson J *et al* 2004a Importance of large and small mammalian herbivores for the plant community structure in the forest tundra ecotone *Oikos* **106** 324
- Olofsson J *et al* 2004b Reindeer influence on ecosystem processes in the tundra *Oikos* **105** 386–96
- Olofsson J *et al* 2009 Herbivores inhibit climate-driven shrub expansion on the tundra *Glob. Change Biol.* **15** 2681–93
- Pickup G and Chewings V 1988 Estimating the distribution of grazing and patterns of cattle movement in a large arid zone paddock. An approach using animal distribution models and Landsat imagery *Int. J. Remote Sens.* **9** 1469–90
- Richardson S J *et al* 2002 How do nutrients and warming impact on plant communities and their insect herbivores? A 9-year study from a sub-Arctic heath *J. Ecol.* **90** 544–56
- Rustad L E *et al* 2001 A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming *Oecologia* **126** 543–62
- Serreze M and Francis J 2006 The Arctic amplification debate *Clim. Change* **76** 241–64
- Shaver G and Chapin F 1995 Long-term responses to factorial, NPK fertilizer treatment by Alaskan wet and moist tundra sedge species *Ecography* **18** 259–75

- Shaver G and Jonasson S 1999 Response of Arctic ecosystems to climate change: results of long-term field experiments in Sweden and Alaska *Polar Res.* **18** 245–52
- Shaver G R et al 2000 Global warming and terrestrial ecosystems: a conceptual framework for analysis *BioScience* **50** 871–82
- Shaver G R et al 2006 Carbon turnover in Alaskan tundra soils: effects of organic matter quality, temperature, moisture and fertilizer *J. Ecol.* **94** 740–53
- Sitch S et al 2003 Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model *Glob. Change Biol.* **9** 161–85
- Stammler F 2005 *Reindeer Nomads Meet the Market: Culture, Property and Globalisation at the 'End of the Land'* (Berlin: Lit Verlag)
- Sturm M et al 2001 Climate change: increasing shrub abundance in the Arctic *Nature* **411** 546–7
- Susiluoto S et al 2008 Effects of grazing on the vegetation structure and carbon dioxide exchange of a fennoscandian fell ecosystem *Arct. Antarct. Alpine Res.* **40** 422–31
- van der Wal R 2006 Do herbivores cause habitat degradation or vegetation state transition? Evidence from the tundra *Oikos* **114** 177–86
- van Wijk M T 2007 Predicting ecosystem functioning from plant traits: results from a multi-scale ecophysiological modeling approach *Ecol. Modelling* **203** 453–63
- Virtanen R 2000 Effects of grazing on above-ground biomass on a mountain snowbed, NW Finland *Oikos* **90** 295
- Walker D A et al 2003a Vegetation-soil-thaw-depth relationships along a low-arctic bioclimate gradient, Alaska: synthesis of information from the ATLAS studies *Permafrost Periglacial Processes* **14** 103–23
- Walker D A et al 2003b Phytomass, LAI, and NDVI in northern Alaska: relationships to summer warmth, soil pH, plant functional types, and extrapolation to the circumpolar Arctic *J. Geophys. Res.* **108** 8169
- Walker D A et al 2005 The circumpolar arctic vegetation map *J. Veget. Sci.* **16** 267–82
- Walker D A et al 2009a *Data Report of the 2007 and 2008 Yamal Expeditions* Alaska Geobotany Center, Institute of Arctic Biology, University of Alaska Fairbanks, AK: 121
- Walker D A et al 2009b Spatial and temporal patterns of greenness on the Yamal Peninsula, Russia: interactions of ecological and social factors affecting the Arctic normalized difference vegetation index *Environ. Res. Lett.* **4** 045004
- Walker D A et al 2009c Cumulative effects of rapid land-cover and land-use changes on the Yamal Peninsula, Russia *Arctic Land Cover and Land Use in a Changing Climate: Focus on Eurasia* ed G Gutman and C Justice (Berlin: Springer) at press
- Wolf A et al 2008 Future changes in vegetation and ecosystem function of the Barents region *Clim. Change* **87** 51–73