

First results from an experiment excluding three sizes classes of herbivores from tundra vegetation in southern Yamal, Russia

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Abstract

Plant-herbivore relationships are important for the functioning of tundra ecosystems. Here, we report the first results from an enclosure experiment that, something very few studies have done, separated the impact of three sizes of herbivores (small, medium and large) on nine functional groups of plants in the low arctic tundra of the Yamal Peninsula (Russia). Herbivore faeces counts in the enclosures and pictures from automatic cameras proved that the experimental setup worked. The majority of plant groups did not respond to exclusion of herbivores, supporting our expectation that vegetation responses in tundra are generally too slow to be measured during one growing season. The plant groups with highest growth rates and palatability (forbs and grasses) increased their biomass in meadows associated to tall willow shrubs when reindeer were excluded. This result was expected based on studies from other arctic regions. Our results also suggested that willow meadows and forb tundra, which are focal habitat for herbivores, are resilient and have the capacity to increase their biomass over a short term. We expect this experiment to provide valuable information on how different plant functional types and habitats with different growing conditions and importance to herbivores respond to relaxed grazing pressure from a variety of tundra herbivores.

Key words: plant-herbivore relationship, enclosures, point intercept method, Yamal

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Introduction

Herbivory is a significant driver of tundra vegetation change (Oksanen *et al.* 2000). Herbivores differ in body size, feeding mode, diet composition, morphology, digestive system, and ability to migrate (Davidson 1993). As a consequence, they have distinct impacts on the vegetation. The impact of herbivores can be cumulative when different animals tend to feed on the same plants. The more animals feed on certain plants, the more the plants are affected. When herbivores feed on different plants, different life-stages of plants or different parts of the plants, their impact can be complementary (Bryant 1987, Ravolainen *et al.* 2014). Thus, separating the effect of herbivores with different feeding modes is important to elucidate herbivore community level impacts and how this may change in time and space. The most powerful means for doing this are experimental studies with herbivore exclosures. Such studies have been conducted earlier in tundra ecosystems, but often with low resolution in terms of separating herbivore of different sizes and feeding modes (*e.g.* Ravolainen *et al.* 2011, Olofsson *et al.* 2009). More elaborate exclosure experiment designs to achieve better resolution will, however, first need to be validated with respect to how well they exclude/in-

clude the herbivores relative to the planned design.

To amend this knowledge gap, we set up an exclosure experiment in the shrub tundra of the southern Yamal Peninsula. Like most other low-arctic tundra food webs (Ims *et al.* 2013), this area hosts a variety of plant groups that are of differing palatability, growth rate and habitat preference, alongside with a diverse arctic herbivore community. We designed our exclosures so that they separate the impact of three size categories of herbivores on nine functional groups of plants. Because context-dependency is often strong in tundra vegetation response to herbivory (*e.g.* Bernes *et al.* 2015), we included three habitats as an additional experimental factor in the design. These habitats differ in growing conditions (soil type and moisture, placement in the landscape) and importance to the focal herbivores. The long-term goal of this experiment is to investigate whether the impact of different-sized herbivores on biomass and diversity of the plant communities is cumulative or complementary. Here, however, we focused on an assessment of the adequacy of the experimental setup by using information obtained on the response of both herbivores and the plants from the first year of the study.

Material and Methods

This study has been carried out since 2014 in the southern part of Yamal Peninsula in Russia (68.2° N, 69.2° E), in the Erkuta Tundra Monitoring site, situated close to Payutayakha and Erkutayakha rivers (Sokolova *et al.* 2014). The area is situated in the bioclimatic subzone E of the arctic tundra (Walker *et al.* 2005). Mean temperatures are -24.1°C in January and 11.4°C in July, and mean precipitation is 355 mm per year (averages from 1950 to

2000, [WP1]). We studied three size groups of vertebrate herbivores: (1) large herbivores: reindeer (*Rangifer tarandus*), (2) medium-sized herbivores: willow ptarmigans (*Lagopus lagopus*) and mountain hares (*Lepus timidus*), and (3) small herbivores, mostly narrow-headed voles (*Microtus gregalis*), Middendorff's voles (*Microtus middendorffi*) and collared lemmings (*Dicrostonyx torquatus*).

We focused on three habitat types: Willow Meadows, Forb Tundra, and Mesic Tundra. Willow Meadows (WM) were defined as the meadows surrounding willow thickets on slopes with sediment soils. They host a wide diversity of palatable plants in high quantities and are described by Pajunen et al. (2010). Forb Tundra (FT) was dominated by plants belonging to the Fabaceae and found on the upper slopes or on the top of sandy hills. FT is also characterized by significant patches of sandy substrate without any higher plants. These two habitat types (WM and FT) were ex-

pected to be focal habitats for all the herbivores as many faeces were present, indicating an intensive use by herbivores. Moreover, WM has been shown to be the preferred habitat of the narrow-sculled vole, one of the dominant vole species in the area (Sokolova et al. 2014). The third habitat, Mesic Tundra (MT), is a very common habitat type in the low Arctic and is characterized by high numbers of dwarf shrubs, sedges and a thick moss layer (Walker et al. 2005). This type was included because it is the most widespread habitat in the study area.

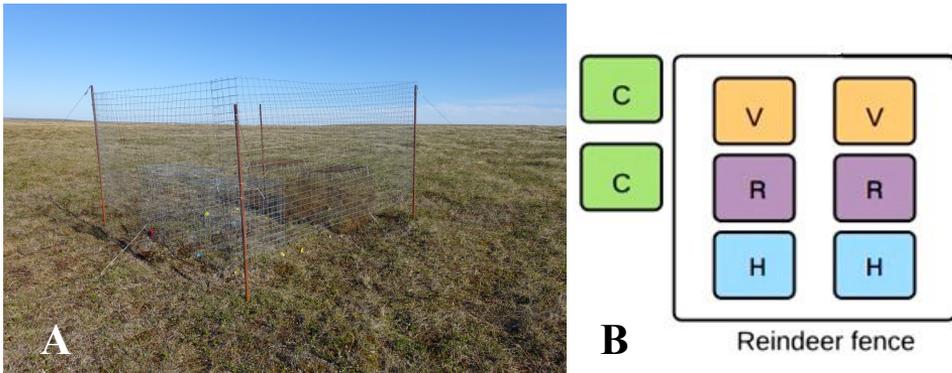


Fig. 1. A. Photography of an enclosure. The reindeer fence surrounds the small plots. The large mesh enclosures are hare plots. The fine mesh enclosures are all-excluded plots. Reindeer plots are not marked but are situated between hare plots and all-excluded plots.

B. Design of an enclosure. Each enclosure has 2 reindeer plots (R), 2 hare plots (H), 2 all-excluded plots (V). There are also 2 control plots (C) outside the enclosure.

The enclosures were erected in summer 2014. Each enclosure consisted of a 2.5 x 2.5 m fence, which was elevated and had a 40 cm gap above the ground (Fig. 1 A, B). Within this large enclosure, that excluded reindeer, but allowed hare and ptarmigan to enter below the fence, we established 6 small plots of 0.6 x 0.6 m. Two of them were protected by a 0.6 m high cage made of fence with 1 cm mesh size that was dug 10 cm deep into the ground and excluded all herbivores including small rodents. Two

other plots were enclosed by a fence with 5 cm mesh size to exclude medium sized herbivores, but not small rodents. The last two plots could be grazed by all herbivores except reindeer. In addition, there were two control plots outside the large fence. These enclosures and open plots formed 18 experimental blocks (3 habitats * 3 units * 2 replicates), allocated within three spatially replicated units, separated by 6 km, for a total of 144 sampling plots.

During the winter seasons 2014/2015 and 2015/2016, we visited all exclosures to assess to what extent they were covered by snow, and registered signs of presence of herbivores, such as faeces of hares, ptarmigans and reindeers. In order to assess whether medium sized herbivores passed below the large fence, all herbivore faeces were removed from the large exclosures in June 2016. In the end of July 2016, we counted fresh faeces in the exclosures. In addition, automatic cameras (Reconyx™) with a motion sensor programmed to high sensitivity were placed for 10 days close to two exclosures in June 2016.

For each plot, biomass was measured using the point intercept method (Bråthen et Hagberg 2004). We used a 50 x 50 cm frame with 15 pins to record the number of

hits. These measurements were done in summer 2014, before setting up the exclosures and in summer (July / August) 2015. A total of 90 species of vascular plant species were identified.

The point intercept counts were converted to biomass according to the equation of Bråthen et Hagberg (2004). For this conversion, we separated the species into biomass groups based on their growth form and leaf characteristics that influenced the hit-biomass relationship. While the conversion coefficient (b) for most plants was extracted from Ravolainen et al. (2010), for *Betula nana*, erect *Salix* shrubs and *Veratrum lobelianum*, the conversion factor was calculated from calibrations done in Yamal during summer 2015 (see Table 1).

Type	<i>B. nana</i>		<i>Salix</i>		<i>Veratrum</i>
	Wood	Leaves	Wood	Leaves	Leaves
b	126.9828	15.11911	216.9286	25.3898	52.93476
SD ²	0.0975667	0.03169931	0.02865975	0.08007821	0.06943706
CV	0.07982967	0.08890306	0.1265725	0.07745029	0.1176982
n	32	32	32	30	33

Table 1. Results from the calibration for *Betula nana*, *Veratrum lobelianum* and erect *Salix* spp. Results were obtained by fitting a regression between point intercept counts and dry weight biomass obtained from clipping the plants on 30-33 plots displaying a wide range in species cover and plant height. SD² is the variance, b is the regression coefficient (also called conversion coefficient), CV is the coefficient of variation and n is the number of plot for each category. *Veratrum* was chosen for calibration because it is present in large numbers in the study area and differs clearly in growth form from the other large forbs. For the two shrubs, the previous calibration had been done pooling branches and leaves. As these plant parts are affected differently by herbivory, we calibrated the relationship between point intercept counts and biomass for wood and leaves separately.

For the analysis of the effect of herbivore exclusion, the plant species were assembled into nine functional groups based on Chapin et al. (1996), Quested et al. (2003), Bråthen et al. (2007), Diaz et al. (2007) and Cornelissen et al. (2004): nitrogen-fixing forbs/hemiparasites (N-fix), *Betula*, *Salix*,

evergreen ericoids (ericoids), nitrogen-non-fixing forbs (forbs), grasses, sedges, deciduous shrubs and semi-evergreen forbs (evergreen forbs). Functional groups, which were absent from more than 20% of the plots in one habitat, were excluded from the analysis of this habitat.

The biomass estimates for each functional group in each plot were analysed using linear mixed models performed with the function lmer from the lme4 package (Bates et al. 2015) in R (R Core Team 2016). The response variable was log of plant biomass + 1, and explanatory variables were treatment and year (as factor, *i.e.*

2014: before; 2015: after the construction of exclosures), as well as the interaction between treatment and year. Exclosure and plot identity were included as random factors. A separate analysis was performed for each habitat and results were reported with 95% confidence intervals (CI).

Results

During winter visits, we regularly observed fresh signs of presence of hares (faeces and urine marks) inside the reindeer fences in FT and some MT exclosures. WM exclosures, which were situated on slopes, were completely covered by snow from December to the middle of May, excluding the possibility of foraging by other herbivores than small rodents. Hare and ptarmigan faeces were observed

in the large exclosures also in summer. On average, 10.2 (SD = 10.8) fresh hare faeces and 0.5 (SD = 0.8) ptarmigan faeces were counted in the exclosures in July 2016 (11 exclosures), clearly showing that these herbivores entered the fences. This was confirmed by the automatic camera observations, which showed how a hare entered one of the exclosures in WM.

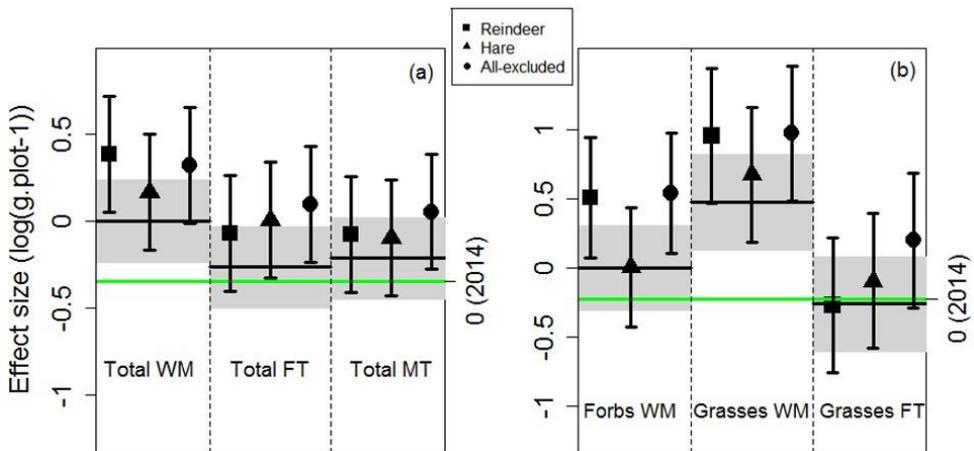


Fig. 2. Biomass change (in log(g).plot⁻¹) for total biomass (total), forbs and grasses. Results are presented for the habitat types Willow Meadows (WM), Forb Tundra (FT) and Mesic Tundra (MT). The treatment Reindeer, Hare and All-excluded are represented by the different shaped points (see legend) and contrasts to the control in 2015 are depicted on the Y-axis (log scale). The black lines indicate the control of 2015 for each habitat and plant group, and the green line is the control of 2014. Total biomass was higher in 2015 than in 2014, which was a cold and late summer. For each value, a confidence interval is presented. The confidence interval for the control of 2015 is represented by the grey area.

In WM plots excluding reindeer, total biomass increased 1.40 times compared to the control plots (CI = 1.01 – 1.93; Fig 2a). For the other treatments in WM, effects were not significant, but general tendencies were positive. Total biomass increased 1.42 times compared to the control in all-excluded plots of FT (CI = 1.03 – 1.96; Fig 2a), but there was no increase for the other treatments. Mesic tundra showed the least increase in total biomass. Considering only forbs, the reindeer plots and the all-excluded plots showed significant increases

in WM compared to the control (increased 1.65 times, CI = 1.06 – 2.59 and 1.71 times, CI = 1.09 – 2.68 respectively; Fig 2b), but not in FT (forbs were too rare to be analysed in MT). These increases were, also, not different from each other. For grasses, as well, there was a non-significant increase in biomass in WM when reindeers were excluded and when all herbivores were excluded (Fig 2b). In FT, biomass of grasses increased only in all-excluded plots (Fig 2b), but there was no response in MT.

Discussion

The first results from our experiment planned to distinguish effects of different sized herbivores on a variety of tundra plants indicated that the experimental design worked according to our expectations. We observed an increase in biomass for plant groups with high inherent growth rates and those that were preferred forage for several of the herbivores; *i.e.* in forbs and grasses. From other low-arctic areas, similar results have been reported (Ravolainen *et al.* 2011). Importantly, the experiment seems to have worked according to its aim and excluded the large, the medium-sized and the small herbivores successfully. Medium-sized and small herbivores have entered the exclosures that were designed to keep out only the largest animals.

Only few experiments on a global basis have looked at impact of different-sized herbivores, and majority of them have separated two size categories (Olofsson *et al.* 2009, Ravolainen *et al.* 2011, 2014, Lagendijk *et al.* 2012, Wigley *et al.* 2014; but *see* Hagenah *et al.* 2009 for more categories). The first experiences we have with an experimental design that separates three size categories are promising for the follow-up studies. Our solution to raise the fence material keeping reindeer excluded up from the ground worked at least in part

because hares and some ptarmigans entered the exclosures, although ptarmigans have done so to a lesser extent. It may still prove challenging to design a set-up for other herbivores and particularly birds such as geese that can be shy to human made structures.

The plant responses observed after one year agreed largely with our expectations. In WM, there was an increase in total biomass when the reindeer were excluded and when all herbivores were excluded. This can be explained by the fact that the dominating groups of plants were affected in the same way. Indeed, in the same habitat, there was a significant increase in forb biomass and an almost significant increase in grass biomass when reindeer were excluded and when all herbivores were excluded. Forbs and grasses are fast-growing plants (Aerts *et al.* 2000), they are considered very palatable for herbivores due to their high nitrogen content (Quesada *et al.* 2003) and are easily digestible (Cornelissen *et al.* 2004). With such characteristics, they are likely to be heavily grazed by reindeers (Skogland 1980, White *et al.* 1980) and small rodents (Soininen *et al.* 2013) and, therefore, can respond rapidly to herbivore exclusion. The same reasoning can be applied for FT as the significant increase of total biomass in the all-

excluded plot matches the significant increase in grass biomass. These results also support our assumption that fast-growing habitats such as WM and FT are focal habitats for the studied herbivores.

However, the results of this first year of the experimental set up showed that the experimental design caused some unexpected effects. One of them can be seen in the results from WM. While total biomass, forbs and grasses increased by excluding reindeer or all herbivores, it was not higher than in the control for the treatment, excluding both large and medium-sized herbivores. One possible explanation for this could be that rodents might prefer to feed in hare/ptarmigan cages either because there is no competition with hares nor with ptarmigans (Bakker et al. 2009), or because they can perceive the cages as shelter. WM is indeed the main habitat for *Microtus gregalis*; therefore, they are present there in large numbers (Sokolova et al. 2014). In these plots, plants are liberated from the

hare/ptarmigan and reindeer herbivory and, therefore, their biomass would increase. Rodents might be more numerous in these plots and could feed more on these plants, causing a decrease in biomass. This effect could be enhanced if ptarmigans are shy to man-made structures and forage less in the enclosures than on the controls. We, therefore, need also to monitor the prevalence of herbivores in the different plots, verifying that the different fences do not cause undesired side-effects that impinge on the results.

In conclusion, this is one of the very few experiments that separates the impact of three size categories of herbivores. As the experiment will proceed, we should be able to address the question whether the impact of herbivores of different sizes is cumulative and complementary on low-arctic plant biomass. We will also investigate the responses in plant diversity and community composition that take longer to appear.

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Web sources

- [WP1] WorldClim - Global Climate Data, Free climate data for ecological modeling and GIS, <http://www.worldclim.org>