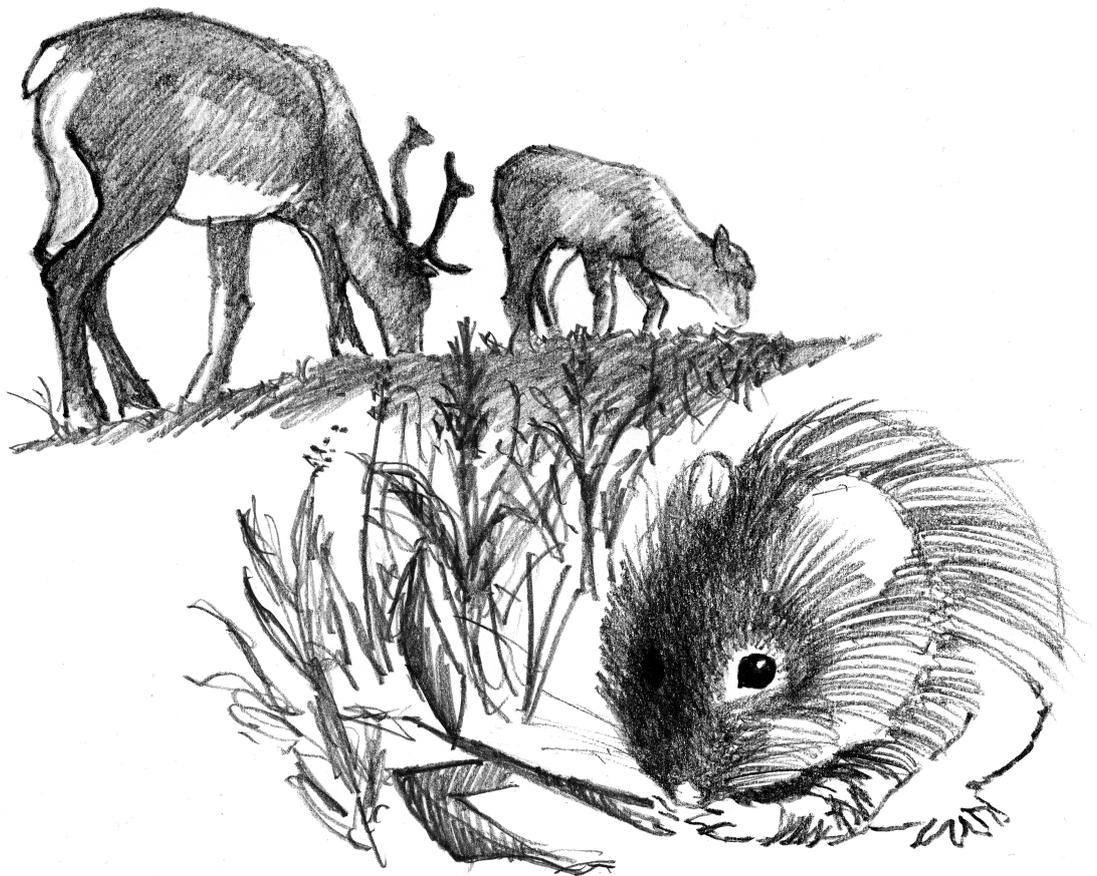


Herbivores modify palatability of Silica-rich grasses

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Katarina Inga

*BIO-3950 Master thesis in Biology, Northern Populations and Ecosystems
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#Orusjohkalevererar

Abstract

Silica-rich grasses are often abundant in pastures. The silica content causes these grasses to have low palatability, yet to what extent herbivores themselves modify the silica-content and the nutrient content of these grasses is uncertain.

Here we ask to what extent small rodents and reindeer can modify Silicon (Si), Nitrogen (N) and Phosphorous (P) contents in Si-rich grasses over a summer season in the sub-arctic tundra. We established an enclosure experiment, excluding mainly reindeer, in meadow habitats clearly impacted by small rodents winter activity and in meadow habitats with no visible impacts of small rodents. Within this experimental setup, we studied impacts of small rodents or reindeer or the combined effect of the two different sized herbivores on the nutrient responses in Si-rich grasses in meadow habitats. Leaves of three common Si-rich grasses, *Nardus stricta*, *Calamagrostis spp.* and *Deschampsia cespitosa*, were sampled every second week, from late June to mid September in 2015, after which samples were analysed for their Si, N and P content.

The small rodents winter activity significantly improved the N and P content in the Si-rich grasses and had no effect on the Si content, whereas reindeer summer grazing significantly decreased the Si content late in the season, but with no effect on N and P content. However, the combined effect of small rodents winter activity and summer reindeer activity showed the opposite pattern, with lower N and P leaf content and a higher Si content in the Si-rich grasses.

Results from this study indicates the effect of one herbivore alone improves the palatability of Si-rich grasses, whereas the combined effect of two herbivores, possibly through their combined prolonged activity in the meadow habitats over winter and summer, causes a reduction in Si-rich grass palatability. Consequently, herbivores create a mosaic of forage with different quality depending on if either one or both herbivores are active in the habitat.

Keywords: Silicon, Nitrogen, Phosphorous, herbivore-plant interaction, sub-arctic, reindeer, small rodent, Silica-rich grasses, NIRS

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Introduction

The availability of Nitrogen (N) and Phosphorous (P) are limited to plant growth and reproduction in most terrestrial ecosystems, and even more limited to consumers (Güsewell 2004; Elser et al 2007). As such, N and P represent important explanatory variables in ecological studies of vegetation. Lately the focus in research has increased on Silicon (Si) in plants for its importance to ecosystem functioning (Vicari & Bazel 1993; Schoelnyck et al 2014). Both N and P are essential nutrients to both plants and animals, while Si is not essential to either. However, plants are likely to gain strong benefits from Si, increasing plant growth and reproduction, through increased stress tolerance (e.g. Schoelnyck et al 2014; Epstein 2009). High Si-content can also cause plant material to be unavailable to decomposers (Schaller et al 2012), potentially impacting plant–soil feedbacks. Hence, the Si in vegetation may have a different role to consumers and decomposers.

The common understanding is that Si provides a defence against herbivores (e.g. McNaughton et al 1985; McNaughton & Tarrants 1983; Massey & Hartley 2006; Gali-Muhtasib, Smith & Higgins 1992; Massey et al 2008), and that herbivores promote an increased abundance of Si-rich grasses (e.g. McNaughton & Tarrants 1983; Birzuela, Delting & Cid 1986). However, the response of Si in the vegetation in relation to herbivore–plant interactions at a short-term basis have shown to differ between ecosystems (e.g. Soininen et al 2013b; McNaughton et al 1985; McNaughton & Tarrants 1983; Garbuzov, Reidinger & Hartley 2011; Massey et al 2008). As such, depending on ecosystem, herbivores may play different roles for the Si content in the vegetation.

Herbivores are capable of modifying the nutrient contents in plants, such as N, P and Si, either direct or indirect. Direct impacts of herbivores are defoliation or damage to the plants, such as grazing, cutting or trampling (e.g. McNaughton 1983; Nystuen et al 2014; Güsewell 2004). These impacts can restrict the plants phenological development, potentially affecting the plants' nutrient absorption capacity or orientation of nutrient deposition in the tissue (e.g. McNaughton 1983; Mysterud et al 2001; Kaufman et al 1981). Indirect impacts by the herbivores can be their modifications of the soil conditions for plants or microorganisms, in turn affecting the decomposition rates,

plant–soil feedbacks and nutrient availability to the plants (Güsewell 2004; Schimel, Bilbrough, & Welker 2004; Schaller et al 2012; Berendse & Jonasson 1992; Quedsted et al 2003; Hamilton & Frank 2001). Herbivore activities impacting the soil conditions can be trampling that creates bare soil patches (Faust 2011), mixing the soil, removing or adding litter (e.g. Nystuen et al 2014; Hamilton & Frank 2001), or nutrient addition to the soil via faeces and urine (McKendrick et al 1980; Jonasson 1992). As such, the herbivores have several potential ways to impact the quality of their forage.

Herbivore activity, i.e. mainly by rodents, have been shown to increased Si contents in grasses in the end of the growing season (Massey & Hartley 2006; Massey et al 2008). Such increased Si accumulation in grasses has been found in other studies of mammal and insect feeding (McNaughton & Tarrants 1983; Massey, Ennos & Hartley 2006; Massey, Ennos & Hartley 2007). Yet, weekly artificial herbivore defoliation of grasses has been showed to reduce the grass Si content (Bañuelos & Obeso 2000). This is likely if the grazing keeps the grasses in younger phenological stages, because young plants accumulate Si slower, independent of Si availability (Bañuelos & Obeso 2000; Rafi & Epstein 1999). However, most studies suggest Si content in vegetation to be related to grazing history (e.g. McNaughton & Tarrants 1983; Brizuela, Delting & Cid 1986). In England, Massey et al (2008) found a synchrony between rodent population cycles and Si content in grasses, suggesting the Si content in grasses to be the driving factor for small rodent population cycles. However, whether the Si content in grasses is herbivore induced or not is debated (e.g. Brizuela, Delting & Cid 1986; Soininen et al 2013b; Massey et al 2009). Previous studies showing herbivores to promote grasses to increased Si accumulation are conducted in areas with longer grazing season or in laboratories with constant environmental conditions (e.g. McNaughton & Tarrants 1983; Massey & Hartley 2006; Brizuela, Delting & Cid 1986; Massey, Ennos & Hartley 2007). The indications in the north sub-arctic area are that there is no herbivore induced Si accumulation (Soininen et al 2013b). Also, apart from grazing, other factors such as species identity of both plant and herbivore, plant genotype and environmental conditions for plant growth, and other factors associated with forage quality, also determine Si content (Soininen et al 2013b; Massey et al 2009). Here we ask to what extent herbivores, both small and large, and their impact alone or in combination can induce Si content in sub–arctic.

Due to the limited availability of N and P in most ecosystems (Güsewell 2004; Schimel, Bilbrough, & Welker 2004), any increase in N or P are likely to improve productivity, as well as the palatability of plants, improving herbivores digestibility (e.g. Sterner & Elser 2002; Elser et al 2007). As such, the herbivore can maximize their nutrient intake with less biomass (Massey et al 2009; Van der Wal et al 2000). In turn this can improve the herbivores reproduction and survival rates, affecting the herbivore population abundance and dynamic (White 1984; Huntly 1991; Massey et al 2008). Hence, the diet choice of herbivores should to a large extent reflect N and P contents in plants (e.g. Albon & Langvatn 1992; Sterner & Elser 2002; Van der Wal et al 2000). Moreover, the herbivores interactions with plants can promote nutrient content by keeping grasses in younger phenological stages (Albon & Langvatn 1992; Mysterud et al 2001; Hebblewhite et al 2008). However, whereas increased N and P contents have the potential to speed up nutrient cycling rates and increase plant palatability, an increased Si content has the potential to slow down these processes (e.g. Schoelnyck et al 2014; Schaller et al 2012; Vicari & Bazel 1993; Sterner & Elser et al 2002; Elser et al 2007). Hence, because of the nutrients different roles, the link between N, P and Si in the same tissue, especially in Si-rich plants, is essential to fully understand ecosystem processes.

Among plant groups, grasses are the group containing most Si (Voronkov 1975; Epstein 1994; Hodson et al 2005). Si mineral, e.g. quartz, is dissolved in the soil via weathering, and effectively accumulated by grasses as biogenic Si (hydrated amorphous Si) (Struyf & Conley 2012). The grasses accumulate Si either passively or actively, and deposit it as silica bodies or opal phytoliths within or between the cell walls (Parry & Smithson 1964; Cooke & Leishman 2011). Active accumulation of Si results in higher Si leaf content (Cooke & Leishman 2011). The characteristics of Si-rich grasses are their high Si content and distinctive abrasiveness, often with Si deposited as spines on the leaf surface (e.g. Kaufman et al 1981; McNaughton & Tarrant, 1983; Richmond and Sussman, 2003; Currie and Perry, 2007; Hartley et al 2015). This reduces the palatability and digestibility (Gali-Muhtasib, Smith & Higgins 1992; Massey, Ennos & Hartley 2006). Consequently, Si-rich grass species are less preferred as forage for herbivores, e.g. reindeer and small rodents (Bråthen & Oksanen 2001; Soininen 2013a). However, the Si-rich grasses are grazed when the Si content is low and the herbivores can maximize

their energy- and N-intake (e.g. Warenberg 1982; Massey et al 2009; Aagnes, Blix & Mathiesen 1996).

In the tundra, the guild of small rodents, Norwegian lemming (*Lemmus lemmus*), Grey-sided Vole (*Myodes rufocanus*) and Root Vole (*Microtus oeconomus*), are considered as keystone species (Killengreen et al. 2007). The populations in Scandinavia have cyclic fluctuations, with high impacts on the vegetation at high densities (Ims & Fuglei 2005; Stenseth 1999; Olofsson, Tømmervik & Callaghan 2012). The creation of bare soil patches in grasslands, via herbivore activities, e.g. soil mixing and trampling, is important for seedling establishment and dispersal (Faust et al 2011). Such patches have a higher abundance of plants established from seeds in the beginning of the season (Nystuen et al 2014; Faust et al 2011). During winter the small rodents are residing in the space between the snow cover and the ground, and impacts the vegetation via grazing, trampling, cutting and burrowing (Hambäck et al 1998; Turchin & Batzil 2001). Trampling in small rodent's paths mix both dead and live standing crops, with organic soil and humus (Nystuen et al 2014). This impacts both the soil's upper layer, and the plant's parts, aboveground and potentially underground, such as shallow roots. Additionally, rodent faeces and urine contribute to increased availability of N in the soil (McKendrick et al 1980; Jonasson 1992). Potentially the mixing can speed up the decomposition rates and release more nutrients to the soil (e.g. Berendse & Jonasson 1992; Quested et al 2003; Cornelissen et al 2000 & 2007; Weintraub & Schimel 2005).

The semi-domesticated reindeer (*Rangifer tarandus*) is another keystone species present in the tundra. Reindeer are dependent on different seasonal grazing pastures and migrate over large areas (e.g. Iversen et al 2014). Plant quality and digestibility are important factors for the reindeer's performance, e.g. growth and lactation during summer (Skogland 1988; White 1983), and a driving factor of their migratory pattern (Iversen et al 2014). Because of reindeer management, the reindeer density is somewhat constant between years in the seasonal grazing ranges. Trampling and grazing by reindeer can impact the plant directly via defoliation of plants, potentially keeping them in younger stages, and indirect impact the vegetation through altering competitive interactions and nutrient cycling (Bernes et al 2015). Hence, the reindeer is capable to impact vegetation patterns in the Arctic tundra (Oksanen & Virtanen 1995; Bernes et al

2015). However, reindeer and small rodents have different potentials to impact the vegetation, partly because of their difference in size, behaviour and population dynamics.

In the sub-arctic ecosystem in northern Norway, hotspots of herbivore–plant interactions can be found in the riparian sediment plains, where moisture and nutrients are sufficient to sustain meadows and willow thickets (Bråthen et al 2007). The Si-rich grasses are often abundant in these habitats due to long history of grazing reindeer (e.g. Ravolainen et al 2011; Soininen et al 2013b). Grasses respond fast in growth because of their capacity to effectively absorb and reabsorb nutrients (Von Numers & Van Der Maarel 1998). This makes the riparian meadow a subject to explore the short-term nutrient responses in Si-rich grasses to herbivore activity.

We established an experiment in order to explore to what extent small rodents and larger ungulates, i.e. mainly reindeer, can modify Si as well as N and P contents in the three common Si-rich grasses *Nardus stricta*, *Calamagrostis spp.* and *Deschampsia cespitosa*. As a replacement for chemical nutrient analyses, we applied Near Infrared Reflectance Spectroscopy (NIRS) methodology developed in Tromsø (Smis et al 2014). The method provides contents of Si, N and P in the same plant leaf, and therefore opens the possibility to simultaneously assess plant quality in terms of defence and nutrients.

We hypothesise small rodents winter activity (SRA) to impact the vegetation to be dominated by younger plants (Faust et al 2011; Nystuen et al 2014) and to modify the abiotic environmental conditions, such as indirect addition of N to the soil (McKendrick et al 1980; Jonasson 1992), and increase the P release to the soil via decomposition rates (e.g. Berendse & Jonasson 1992; Quested et al 2003; Hamilton & Frank 2001). This will in turn have a positive impact on the grasses potential to absorb limited nutrients as P and N (e.g. Schoelnyck et al 2014; Chapin, Shaver & Kedrowski 1986; Berendse & Jonasson 1992; Quested et al 2003), causing (i) Si-rich grasses N and P contents in SRA impacted vegetation to be greater than in vegetation not impacted by SRA. Ramets and younger plants, are likely to accumulate Si less effectively than older or mature plants (Rafi and Epstein 1999; Bañuelos & Obeso 2000), and younger plants are likely to contain more N and P (Albon & Langvatn 1992; Mysterud et al 2001; Hebblewhite et al

2008), causing (ii) the Si-rich grasses in vegetation impacted by SRA, to contain less Si in the beginning of the season, compared to non-SRA impacted vegetation. Further, we assume larger ungulates activity (LUA), such as trampling and defoliation of the vegetation to cause Si-rich grasses to be at younger phenological stages and hence (iii) to contain less Si, and (iiii) more N and P, especially early in the season. Finally, we hypothesise that the herbivores combined effect of both SRA and LUA is additive, (iv) causing plants in LUA and SRA impacted vegetation to contain more N and P and less Si.

Material and Method

Study area

The reindeer manager district in Ifjordfjellet located in Northern Norway was chosen as the study site. Ifjordfjellet (70025°N, 27020°E) is located on Laksefjordvidda west of the Varanger peninsula in Northern Norway. The area is classified as sub-arctic mountain tundra (Moen 1999). The mean temperatures in July has a range from 7,9 °C to 11,1 °C, and annual precipitation ranging from 365 mm to 460 mm (Norwegian-Metereological-Institute). The bedrock consists of sedimentary rocks, mainly sandstone and mudstone, with a thin humus and vegetation layer (Siedlecka & Roberts 1992, Moen 1999). The riparian meadow areas are dominated by graminoids and forbs with some willow patches (Ravolainen 2009). Our studied meadow sites were situated in two river catchments above the tree line. The vegetation consists of Si-rich grass species (e.g. *Nardus stricta*, *Deschampsia cespitosa*, *Calamagrostis spp.*) and other more palatable graminoids, sedges and forbs, such as *Avenella flexuosa*, *Poa spp.*, *Carex spp.*, *Viola spp.*, *Bistorta vivipara*, *Rumex acetosa* etc.

The study site is used as summer and migratory grazing pastures for semi-domesticated reindeer (*Rangifer tarandus*). A fence divides the area into two different seasonal land uses, i.e. the summer reindeer range and the migratory reindeer range. Hence the stimuli by ungulates are season regulated. However, the small rodent guild of Norwegian lemming (*Lemmus lemmus*), Grey-sided Vole (*Myodes rufocanus*) and Root Vole (*Microtus oeconomus*), are present on both sides of the fence the whole year (Killengreen et al 2007). Thus, potential impact to the plants in the beginning of the sampling period, on the summer reindeer range, would not be caused by reindeer activity. Consequently the migratory reindeer range should have lower reindeer

abundance during summer. However, during the sampling period reindeer was observed at both reindeer ranges, and faeces were found in and between our experimental plots. Accordingly the experimental predictor variables (for LUA) can be evaluated as equally independent of reindeer range.

The experiment was established with two sites in the summer reindeer range and two sites in the migratory reindeer range. The sites were located in close proximity to study sites established within the Climate Observatory for Arctic Tundra (COAT) science plan – where monitoring of herbivore densities is already taking place. Additional data of small rodent abundance in the area is gained from the COAT–project (COAT).

Experimental design and sampling

Wooden frames of 70 x 70 cm were glued and assembled together, to which netting of metal with 0.8 mm mesh size was attached with thumbtacks. The lid of the enclosure had netting with a mesh size of 11 mm, and the height of the enclosure was 50 cm. A criteria for site selection was that its area should be big enough to fit all plots, and the vegetation of the meadow should be somewhat homogenous, and include either or all of the Si–rich grass species *Nardus stricta*, *Calamagrostis spp.* and *Deschampsia cespitosa*.

Pairs of vegetation impacted by winter activities of small rodents (SRA) were subjectively selected in field where the vegetation was clearly impacted by SRA, such as rodent paths, bare soil and cut plants. To avoid aggregated nutrient addition in plots, we avoided large aggregation of reindeer and rodent faeces. In each site, six pairs of vegetation impacted by SRA, and six pairs with no visible SRA impact to the vegetation were marked, i.e. a total of 24 plots per site.

Within the pair the vegetation should have somewhat similar grass and herb distribution, and the degree of SRA impact should be similar, i.e. equal amount of visible paths, bare soil patches and cut plants (SRA impacted) or the absence of it (not impacted by SRA). The distance between the plots within the pair was 0.5–4 meters. Within the pair, one of the plots was randomly chosen for an enclosure treatment, excluding mainly larger ungulates activity (LUA), such as reindeer (Figure 1). The plots were then marked diagonal in two corners with a wooden stick, with plot identification, and the enclosure was attached to the ground with tent pegs. In total we established 96 plots within 48

pairs, equally distributed in four sites, Iešjohka (IE-1 & IE-2) in the summer reindeer range, and Stuurajohka (ST-4) and Aesturjohka (AE-3) in the migratory reindeer range (see Figure 1).

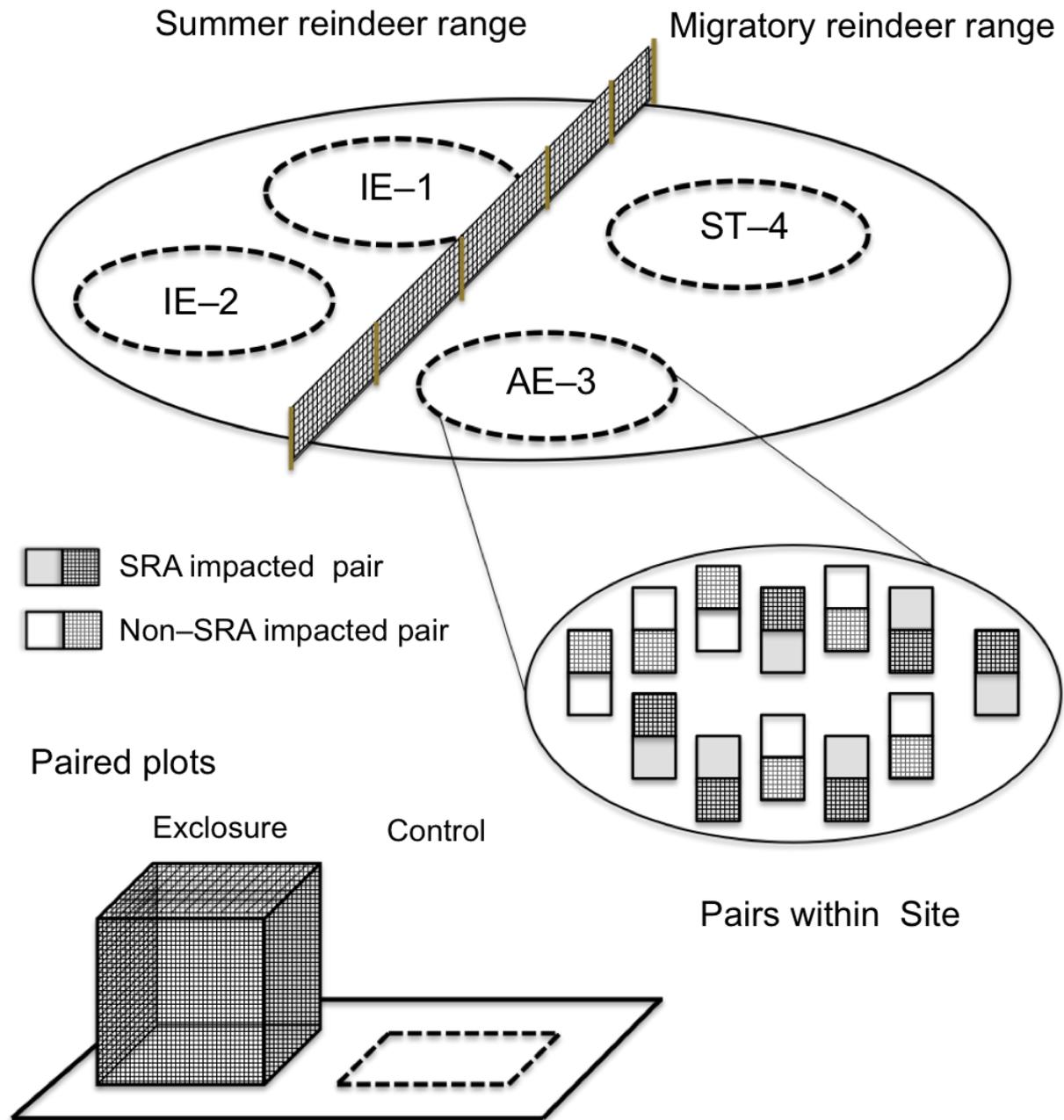


Figure 1 Study design. The summer and migratory reindeer range with the sites Iešjohka (IE-1 & IE-2), Stuurajohka (ST-4) and Aesturjohka (AE-3). Within each site, six SRA impacted pairs (grey paired boxes) and six non-SRA impacted pairs (white paired boxes) with two plots each were established (total of 24 plots per site). One of the plots within the pair was randomly chosen for an exclosure treatment, excluding mainly larger ungulates (LUA), such as reindeer.

The sampling was conducted at seven instances (**Table 1**). In order to have a relevant temporal scale the sampling started when the experiment was established, i.e. at the brink of the end of the spring season and onset of the summer season. Further sampling occurred every second week throughout the summer season, and was finalised in early autumn.

Table 1 Overview of sampling dates, period and season.

Period	Sampling dates	Season
1	28 - 30 June	Early
2	10 - 12 July	Early
3	23 - 25 July	Mid
4	3 - 5 August	Mid
5	13 - 15 August	Mid
6	26 - 28 August	Late
7	8 - 10 September	Late

We sampled the plants using point intercept with nine pins. Each leaf first touching the pin was noted, and for each noted species one leaf was collected, or enough biomass to cover a 4 mm in diameter area (NIRS adapter). Additionally, within each plot, sampling of leaves of common Si-rich grasses; *Deschampsia cespitosa*, *Nardus Stricta* and *Calamagrostis spp.* were always conducted if they were present in the plot. Each leaf was collected and put into a teabag and pressed flat the same day. When we arrived back from field, all leaf samples were dried in 60°C for 24 hours and stored in paper bags in room-temperature. For analyses of the samples' nutrient content (% of dry weight) we used the NIRS methodology developed in Tromsø and NIRS calibrated calculation models for Silicon (Si) content (Smis et al 2014), and corresponding models for Nitrogen (N) and Phosphorous (P) contents by Bråthen & Murguzur (*Unpublished*), Appendix A.

Abiotic factors

Soil moisture was taken as an abiotic factor variable since soil moisture can improve the nutrient uptake (e.g. Schoelynck et al 2014). We measured the soil moisture with an electrical soil-moisture instrument (SM150 2014) at each sampling period, in each plot with three replicates. The mean Volt-value for each plot was calculated with polynomial conversion for generalised organic soil (SM150 2014). We used the calibration coefficients for organic soil (SM150 2014) and calculated the apparent soil moisture $m_{H_2O}^3/m_{soil}^3$ (water volume in soil volume).

At the fifth sampling we collected soil with a soil sample cylinder, for pH-measurement and soil N content analyses. We collected the soil from all control plots and half of the enclosure plots, equally balanced between the reindeer ranges, except pair 5 because of a wasp nest. Before the cylinder was pushed down into the ground, litter was removed to avoid confounding pH measurement. In each plot, we attempted to collect three soil samples of 50 mm, with a minimum of 30 mm. If the minimum of 30 mm could not be sampled, e.g. due to stones in the ground, a total amount of minimum 90 mm was sampled. The soil was sampled the last day in field and transported in a styrofoam box to Tromsø, where we stored the soil in a refrigerator.

Within two weeks after the soil sampling, the soil was prepared for pH analysis in the lab, following the instructions of the soil protocol provided by the Herbivory network (2015). We mixed 15 mL of soil with 25 mL of distilled water, and let the samples soak over night in room temperature. The next day, we shook the samples vigorously for 5 minutes before measuring the pH. Each soil sample was measured three times with an electrical pH detector (pH/Cond340i). The remaining soil samples were dried for 24 hours at 60 °C for N content analyses conducted with NIRS (Bråthen & Murguzur, *Unpublished*).

NIRS plant data

Before laboratory scanning by NIRS, the samples were dried in 60°C for two hours to make sure that no moisture was left in the leaf, confounding the nutrient calculation (Smis et al 2014). The samples were kept in a desiccator after drying for consistent aridity, and were scanned when they had cooled down. When scanning the samples it is important to cover the whole adapter's area. Some of our samples were very small, e.g. *Nardus stricta*, and therefore the 4 mm in diameter adapter (referred to as 4 mm adapter) was preferred, compared to the 16 mm in diameter adapter (referred to as 16 mm adapter). The leaves in small samples were put close together and overlapping to cover the whole 4 mm area when scanned. Each sample was scanned 2–5 times, with two replicates per scan. The NIRS calibrated model for predicting nutrient content (% of dry weight) for the 16 mm adapter was used for our 4 mm adapter scans and then corrected for the downscaling to 4 mm (Appendix A).

The predicted nutrient values were merged with the information file, i.e. species, sampling period, pair, herbivore treatment and site, via the leaf ID. Negative nutrient content values were converted to the lowest detected value within the nutrient, to minimize loss of data. To verify that the plant species in our dataset was correct, we ran the whole data-set through a species discrimination model (Appendix A). The final distribution of species in our data-set can be seen in Table 2.

Table 2 Overview of sampling frequency in sites over the growth season with season and period division of final Si-rich grass species, based on the species identification-model (Appendix A).

Variable distribution			Season			Period						
Range	Site	Species	Early	Mid	Late	1	2	3	4	5	6	7
Summer	IE-1	Cal_spp	31	51	33	13	18	14	13	24	16	17
Summer	IE-2	Cal_spp	15	43	23	7	8	13	16	14	14	9
Migr.	ST-4	Cal_spp	16	37	24	6	10	9	13	15	12	12
Migr.	AE-3	Cal_spp	5	4	4	3	2	1	1	2	1	3
Summer	IE-1	Des_ces	6	11	4	4	2	3	4	4	2	2
Summer	IE-2	Des_ces	6	7	2	3	3	2	1	4	1	1
Migr.	ST-4	Des_ces	10	17	1	5	5	13	3	1	0	1
Migr.	AE-3	Des_ces	0	1	0	0	0	1	0	0	0	0
Summer	IE-1	Nar_str	28	47	38	16	12	13	18	16	20	18
Summer	IE-2	Nar_str	22	33	23	13	9	9	10	14	10	14
Migr.	ST-4	Nar_str	1	0	0	0	1	0	0	0	0	0
Migr.	AE-3	Nar_str	0	0	1	0	0	0	0	0	1	0

Spatial and temporal distribution of data

The time series over the summer season was treated both as a continuous variable and as a categorical variable representing sub-seasons, the latter supported by the method applied in Iversen et al (2014). The growth season was divided into early season, extending from late June (28–30 June) to mid of July (10–12 July), mid season extending from late July (23–25 July) to mid of August (13–15 August), and late season extending from the end of August (26–28 August) until September (8–10 September). Visual exploration of the nutrients seasonal fluctuation of the raw data, showed a similar pattern of a non-linear development for all studied grass species over the season (see Figure 2), indicating that the model with season represented as three distinct periods, early, mid and late, would be more appropriate for a good model-fit. The time units are hereafter referred to as period and treated as a continuous variable and the sub-season is treated as a non-continuous variable referred to as early-, mid- or late season.

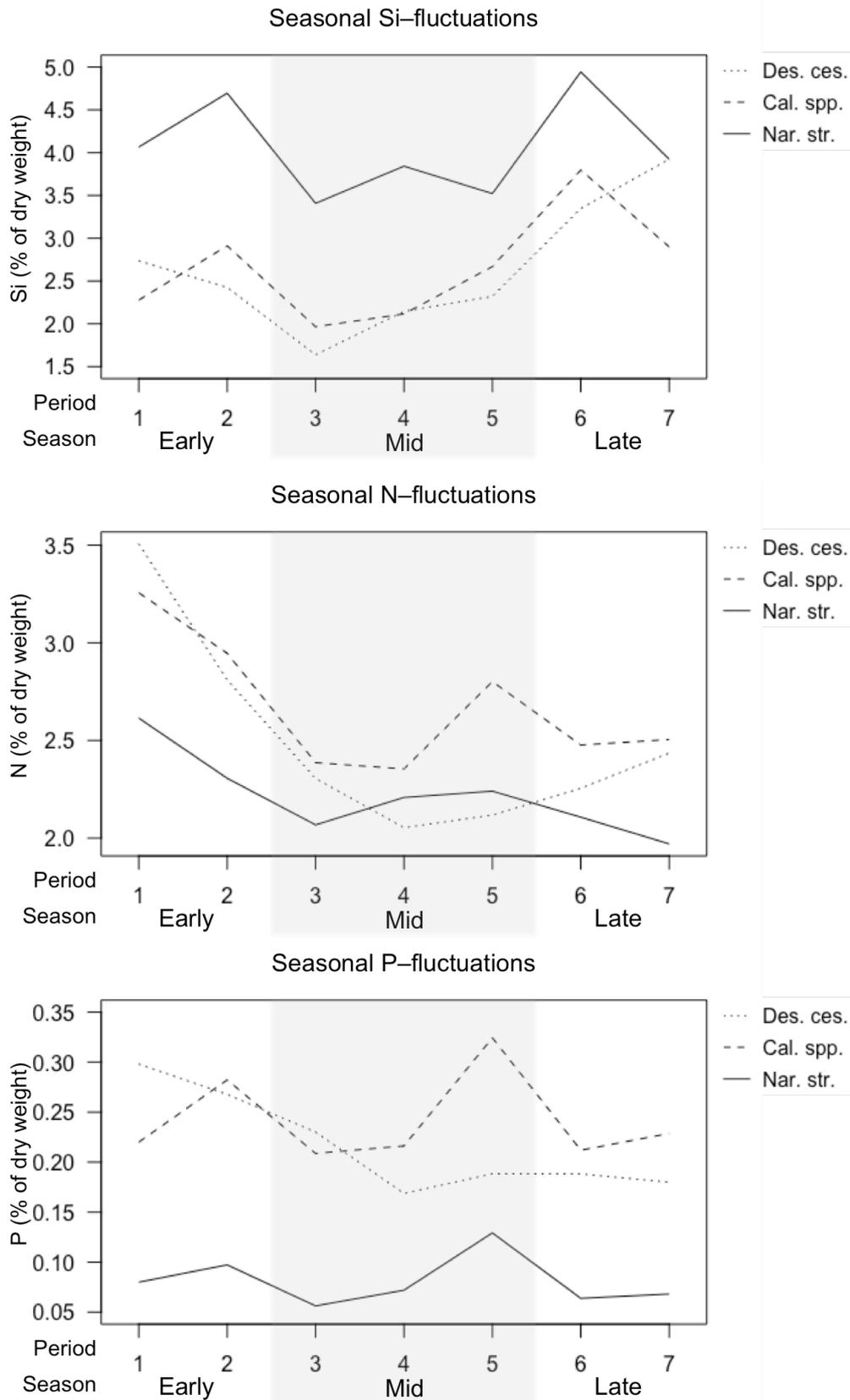


Figure 2 Species-specific seasonal mean nutrient fluctuation of raw-data over the seasons, see **Table 1** for date-specifics of periods.

Statistical analyses

All statistical analyses were conducted using the R statistical environment (R Core Team 2016). Considering the range of parameters, the nested study design and the repeated measurements, we used Linear Mixed Effect models, allowing us to specify multiple fixed effects and random effects (Crawley 2005).

We tested how the nutrient content response in the community of three common Si-rich grass species, was related to small rodents winter activity (SRA) and larger ungulates activity (LUA) over the growing season. The two herbivore treatments of the study design, SRA and LUA, and their interaction were applied in all models as fixed effects. Further, because of the non-linear development of nutrient content over the season, as indicated in the visual inspection of the raw data (Figure 2), we modelled the seasonal change in nutrient content using season as predictor, as opposed to period.

To account for potential variability in nutrient content between the reindeer ranges, we included reindeer range as a fixed effect. However, because we only had one contrast of reindeer range, and the distribution of samples in the migratory reindeer range was uneven and few, compared to the summer reindeer range (Table 2), we only included reindeer range as an additive fixed effect. The response pattern of the nutrient content obtained in the analysis of the summer reindeer range was strengthened when we included all sites.

Hence, we used N, P and Si as the response variables and SRA, LUA, season and species and their interactions as fixed effects, reindeer range as an additive fixed effect, and with Period nested in Site and Pair as the random factors. Because of the species variability in absolute nutrient content, we scaled N, P and Si in order for model estimates to be comparable between species.

We also tested if the abiotic factors influenced the model by adding them as covariates in the model. Accordingly, we tested models including both herbivore treatments LUA and SRA, all three seasons of early- mid- and late, the Si-rich grass species *Nardus stricta*, *Deschampsia cespitosa* and *Calamagrostis spp.* and both summer and migratory reindeer range, with and without their interactions and with and without the abiotic factors of

pH, soil moisture and N content in soil, as covariates (Appendix C, Table C1–C3). Further, we also ran models of the abiotic factors responses to LUA and SRA, to explore their behaviour within the study design. Season was only included in the model with soil moisture, because both pH and N content in soil were measured only once.

Model outcomes of leaf Si, N and P responses to LUA, SRA and their interaction were highly consistent (Appendix C, Table C2 & C3). Hence, results are based on the model including all the Si-rich grass species and where only significant interactions were retained in the model: The interaction of SRA, LUA and season and additive explanatory variables of species and reindeer range. The results are presented with the extracted estimated standardized coefficients from the most parsimonious model.

Results

Overall we found that both larger ungulates activity (LUA) and small rodents winter activity (SRA) have effect on the Nitrogen (N), Phosphorous (P) and Silicon (Si) leaf content (% of dry weight) of the Si-rich grasses *Nardus stricta*, *Deschampsia cespitosa* and *Calamagrostis spp.*, and we found the Si-rich grasses P and N contents to respond differently to the interaction of LUA and SRA, compared to the effect of LUA or SRA alone.

Silicon (Si)

All Si-rich grass species show the same pattern of higher leaf Si contents (% of dry weight) late in the season compared to early in the season, and with the lowest leaf Si contents in the mid-season (Figure 2). *Deschampsia cespitosa* had higher Si contents in the summer reindeer range, compared to in the migratory reindeer range.

Over the season there was no significant difference in leaf Si content between SRA- or non-SRA impacted pairs (Figure 3). Hence, the winter SRA did not impact the Si-rich grasses Si content to be significant lower early in the season (hypothesis ii). LUA had significant lower leaf Si content late in the season (Figure 3). Hence, LUA partly impacted the grass to contain less Si (hypothesis iii).

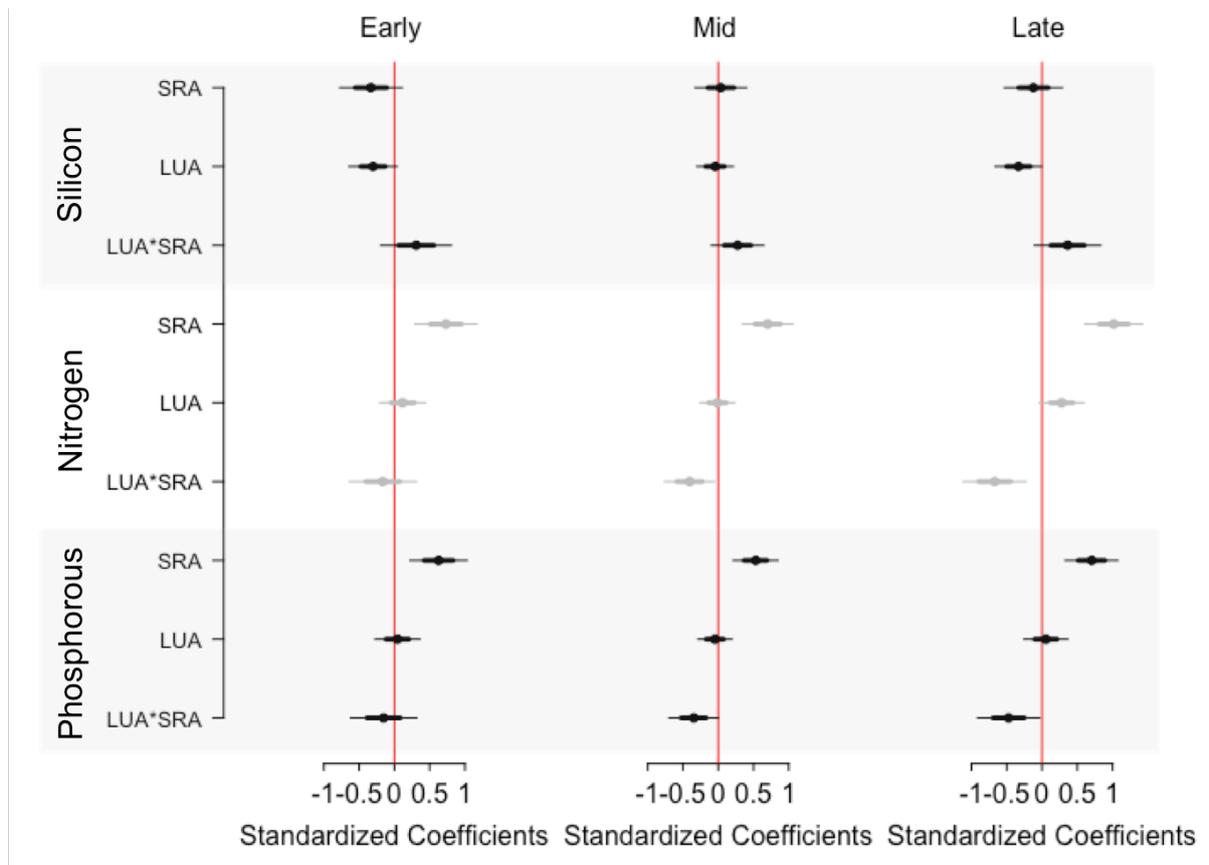


Figure 3 Herbivore activity effects on leaf Silicon, Nitrogen and Phosphorous content for Si-rich grass community of *Nardus stricta*, *Calamagrostis spp.* and *Deschampsia cespitosa*. The response relationship is presented with standardized coefficient estimates extracted from the model (see method chapter). The red central line is the intercept of non-SRA and non-LUA within the specific season. The middle point gives the model estimate, the thick lines give ± 1 SE (approximately $\pm 68\%$ CI) and the thin lines give ± 2 SE (approximately 95% CI). Predictor variables not crossing the red central line have a significant relationship to nutrient content response. Negative standardized coefficients indicate lower nutrient content and the positive standardized coefficients indicate higher nutrient content. For model specifics see Appendix C.

Nitrogen (N)

All Si-rich grass species had the same pattern of leaf N content (% of dry weight) variation over the season (Figure 2). Over all three seasons the SRA impacted pairs had significantly higher leaf N content (hypothesis i; Figure 3). The species-specific leaf N contents ranged from low to high in the order of *Nardus stricta*, *Deschampsia cespitosa* to *Calamagrostis spp.* there was trends for LUA impact to higher leaf N content late in the season (hypothesis iii; Figure 3; Appendix C: Table C2). The combined effects of LUA and SRA significantly decreased the Si-rich grasses N content in mid- and late season (Figure 3).

Phosphorous (P)

The variation of the leaf P content (% of dry weight) over all the seasons was similar in all Si-rich grass species (Figure 2). The leaf P content responded similar as the leaf N content response to the herbivore activity. The SRA impacted pairs had significant higher leaf P content through the whole season (hypothesis i; Figure 3). The interaction of SRA and LUA caused the Si-rich grasses to have significantly lower leaf P contents in mid- and late season (Figure 3).

Abiotic factors

We could not detect any significant impact of abiotic factors, i.e. soil N content, soil moisture and pH, on the response pattern of the nutrients in our model, when we included the abiotic factors as additive covariates (Appendix C, Table C3). However, the abiotic factors themselves differed between the herbivore treatments (LUA, SRA and LUA*SRA).

The SRA impacted meadow habitats contained significantly more N in the soil (total observations: 74, $SRA_{d.f.} = 27$, standard coefficient estimate $\pm 2SE$ [an approximation of the 95 % confidence interval]: 0.782 ± 0.591), whereas both SRA and LUA impacted meadow habitats were significantly moister (total observations: 450; $LUA_{d.f.} = 255$, standard coefficient estimate $\pm 2SE$: 0.079 ± 0.085 and $SRA_{d.f.} = 35$, standard coefficient estimate $\pm 2SE$: 0.412 ± 0.284) with SRA having a higher estimated impact on moisture than LUA.

However, when we analysed the soil moisture over the season, i.e. interaction of LUA, SRA and season, with reindeer range and species as additive variables, the soil moisture was only significant greater in the SRA impacted vegetation in the mid of the season (total observations: 450 ($226_{mid\ season}$); $SRA_{d.f.} = 35$, standard coefficient estimate $\pm 2SE$: 0.521 ± 0.390).

Discussion

We found that both small rodents and larger ungulates have a positive effect on the forage quality of the Si-rich grasses, with small rodents winter activity (SRA) increasing the Nitrogen (N) and Phosphorous (P) content (% of dry weight), and larger ungulates activity (LUA) to lowering the Silicon (Si) content (% of dry weight) late in the season. However, the interaction of the two different sized herbivores had a negative effect on the Si-rich grass quality, with lower N and P contents in the mid and late season (Figure 3; Appendix C)

The Si-rich grasses in our study site were most abundant in the summer reindeer range (Table 2), where the historical land use is greater during summer as opposed to the migratory reindeer range. This indicates the same pattern as Ravolainen et al (2011) presented, where the Si-rich grasses decreased in abundance when reindeer were excluded, and shows the capacity of reindeer to contribute to the promoting of Si-rich grasses in the landscape. The same pattern of long-term impact of herbivore activity to facilitate the Si-rich grasses abundance has been found in other ecosystems (e.g. McNaughton & Tarrant 1983; Birzuela, Delting & Cid 1986). However, when we compared the nutrients responses within the summer reindeer range to the responses with migratory reindeer range, the nutrients response (i.e. negative or positive) to herbivore activity was similar (Appendix C: Table C3). This indicates the Si-rich grasses short-term nutrient response to herbivore activity to be independent of historical herbivore activity.

Winter storage of N and P is of importance in Arctic tundra ecosystems, since their spring growth is dependent on the winter storage (Chapin, Shaver & Kedrowski 1986). As the growing season proceeds, graminoids are more supported by the current resource availability of N and P than stored reserves (Chapin, Shaver & Kedrowski 1986). Grasses gain most of their nutrients directly from the soil. The increased grass N and P contents (% of dry weight) we found in the SRA impacted vegetation (Figure 3), indicates increased current availability of N and P. The effect of increased N and P contents in the grasses was significant positive over the whole season in the SRA impacted meadow habitat (Figure 3; Appendix C), despite the low density of the small rodent population over the summer season (Appendix B, Figure B1). This demonstrates

the small rodents potential to impact the conditions of N and P availability for the Si-rich grasses, as suggested by others (e.g. Hambäck et al 1998; Turchin & Batzli 2001; McKendrick et al 1980; Jonasson 1992), corroborated by results on higher N content and higher soil moisture in soil in SRA impacted meadow habitats. Hence, the vegetation impacted by SRA is beneficial for the N and P availability, which benefits both grasses and herbivores. Potentially the Si-rich grasses increased N and P contents contribute to locally increased herbivore intensity.

Previous studies of P and N contents in grasses in relation to sheep grazing pressure, found the P content to peak at low sheep densities while N content increased at high sheep densities (Mysterud et al 2011). However, we could not detect any significant effects of N and P contents in relation to LUA in our study. The reasons can be many, 1) the sheep density could be higher than the reindeer density, and 2) the sheep grazing can have been more locally concentrated than the reindeer grazing in our study, which possible causes 3) the grazing to more easily keep the grasses in younger stages, and 4) the addition of nutrients via faeces and urine the soil to be more concentrated to the grazed area. However, Mysterud et al (2011) did not include the Si-rich grasses we examined in this study. Nevertheless, we found the LUA to increase the Si-rich grasses quality by decreasing the Si content late in the season (mean leaf Si content (% of dry weight) of raw data in late season in *Cal. spp.*= 3.7[no LUA & no SRA] and 3.3[LUA]; *Des. ces.*= 5.0[no LUA & no SRA] and 1.9[LUA]; *Nar. str.*= 4.2[no LUA & no SRA] and 3.7[LUA]; Appendix C: Table C4 & Figure C1). This corresponds to experiments by Bañuelos & Obeso (2000) showing that weekly artificial herbivore defoliation (clipping) of grasses decreases the grass leaf Si content. Yet, when the clipping intensity was lower, i.e. more than two weeks between the clippings, the Si content increased or did not change (Bañuelos & Obeso 2000). As such, the potential short-term impact of grass clipping by herbivores should partly be dependent on the herbivores density, affecting the potential rate of clipping by herbivores. Moreover, grazing that keeps the grasses in younger stages should cause the grass to accumulate Si less effectively (Bañuelos & Obeso 2000; Rafi & Epstein 1999). This in turn causes the Si-rich grasses to contain less Si late in the season.

Other studies (e.g. Massey et al 2007 & 2008) found grasses to increase leaf Si content when impacted by SRA over the growing season. However, our results did not correspond to previous studies of increased Si absorption in grasses promoted by SRA. Nevertheless, we found trends of increased Si contents in the Si-rich grasses when they were impacted by both SRA and LUA (e.g. mean leaf Si content (% of dry weight) of raw data in mid season for *Nar. str.* = 3.7 [no LUA & no SRA] and 4.1[LUA], Appendix C). In a study by Cid et al (1998) they found grasses with higher Si content to contain more N as well. Suggesting the high N content in the grasses to be the reason for herbivores to return to the same grazing areas (Cid et al 1998). In contrast, we found the N and P content to decrease in mid and late season in vegetation when impacted by both SRA and LUA (Figure 3; Appendix C). This result is controversial to that grazing keeping grasses in younger stages should contain more N and P (Albon & Langvatn 1992; Myrsterud et al 2001; Hebblewhite et al 2008). However, reindeer are selective feeders and graze grasses of high quality (e.g. Iversen et al 2014; Warenberg 1982). Consequently, the grass individuals with high N and P content and low Si content should be subjects for grazing to a larger extent, which potentially could leave behind Si-rich grass individuals with lower N and P contents and higher Si content. Indeed, N, P and Si content is dependent on the individual's phenological stage, i.e. older grasses accumulate Si more effectively (Bañuelos & Obeso 2000; Rafi & Epstein 1999), and have lower content of N and P. This could explain the low N and P content and the trends of increased Si contents in the Si-rich grasses in the interaction of SRA and LUA (Appendix C).

In a study conducted in the sub-arctic by Soininen et al (2013b) of herbivore induced Si contents in grasses, the responses to herbivore activity differed among grasses. They suggested the Si content determinants in grasses to be the combined effects of environmental factors, grazing pressure, grass species and their intraspecific genotypic differences (Soininen et al 2013b). In our study the effect size (standardized coefficient estimates $\pm 2SE$ [approx. 95% CI] extracted from Linear Mixed Effect model, Appendix C) of lower Si content in the Si-rich grasses had greater variation in the summer reindeer range (Appendix C, Table C3: M4 & M5), compared to when all sites were included, and smaller when the abiotic factors were included (Appendix C, Table C3: M6). This indicates the environmental factors to be important for the grasses Si accumulation.

Further, the species-specific analyses differed in effect size (standardized coefficient estimates $\pm 2SE$ (95% CI) extracted from Linear Mixed Effect model) between the species (Appendix C, Table C2). Indicating the species-specific differences to be important factors to determine the level of Si accumulation. As such, our findings indicate the importance of the combined effects of both environmental factors as species-specific characteristics, as Soinen et al (2013b) suggested.

Small rodents have the potential to increase the N availability in the soil (McKendrick et al 1980; Jonasson 1992). Likewise, the N content in the soil and the soil moisture are conditions potentially improving the plants nutrient absorption (e.g. Güsewell 2004; Schimel, Bilbrough, & Welker 2004). However, we cannot exclude the possibility of confounding in our study design. The SRA impacted vegetation was moister, and it is impossible to distinguish if the small rodents select moister habitats or if they modify the habitat to be moister. The moister environment can be the reason to the higher N- and P contents we detected in SRA impacted Si-rich grasses over the whole season (Figure 3), still, the effect of SRA on N and P content in leaves were retained in models both with and without moisture as additive predictor.

When season was not included in the analysis both LUA and SRA indicated to be moister (see result part). The study design is based on randomly chosen exclusion of LUA. Hence, it is more likely that larger herbivore activity modified the soil's capacity to hold moisture. In turn this show the herbivores capacity to modify abiotic factors. Moreover, the abiotic factors did not impact the model outcome when we included them in the analysis (Appendix C, Table C3). Likewise, the herbivore activity impact of the grasses nutrient content responses showed the same pattern across all sites despite the environmental differences (Appendix C, Table C3). Hence, the abiotic factors connected to site characteristics, are not likely to impact the short-term herbivore activity impact on the grasses nutrient response.

Conclusion

In this study we show how different sized mammalian herbivores in the sub-arctic tundra ecosystem impact the nutrient dynamics in Si-rich grasses differently.

We found that the winter activities by small rodents cause a significant increase of Nitrogen (N) and Phosphorous (P) content (% of dry weight) in the Si-rich grasses. This positive short-term effect is most likely the effect of nutrient addition to the soil via faeces and urine (McKendrick et al 1980; Jonasson 1992). Also we found reindeer grazing to reduce Silicon (Si) content, possibly by keeping them in younger stages, and as such decrease their effectiveness to absorb Si (Bañuelos & Obeso 2000; Rafi & Epstein). This indicates that leaf Si content in Si-rich grasses in the sub-arctic tundra is most likely not induced by direct herbivore grazing, but rather reduced. However, when small rodents have been active in the meadow during winter, and the reindeer continuous the grazing during summer, the quality of Si-rich grasses, in terms of their N, P and Si content is lower. Possibly this opposite response in nutrient content when both herbivores are active in the meadow habitats as opposed only either one herbivore alone, is caused by selective grazing by reindeer for the most palatable Si-rich grasses, leaving the less palatable ones behind.

The ability of the herbivores and their interactions to affect the quality of the Si-rich grasses in their habitats, are likely of consequence to other environmental factors such as decomposition rates and nutrient cycling, in turn modifying the growing conditions for the Si-rich grasses and other plants in the meadows.

Accordingly, depending on when the herbivore is active in the meadow, and if it is only one or both herbivores, the quality of the Si-rich grasses differs. This creates a landscape with a mosaic of Si-rich grasses with different quality. Hence, to better understand the mosaic of Si-rich grasses quality in the habitat, we have to consider the identity of the herbivore and the timing of the activity, as well as the combined effect of different herbivores activities throughout the season.

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Appendix

Appendix A

NIRS calibration models

For more details of NIRS calibration models, Contact persons: Kari Anne Bråthen (kari.brathen@uit.no) and Xabier Ancin (x.ancin@gmail.com)

Nutrient concentration

The spectra from the 4 mm adapter NIRS scans calculated with models for the 16 mm adapter for predicting Nitrogen, Phosphorous (Bråthen & Murguzur, *Unpublished*) and Silicon concentration (% of dry weight) (Smis et al 2014) were corrected for the downscaling to 4 mm (Bråthen & Murguzur, *Unpublished*) using following equations:

Predicted Nitrogen * 0.58264 + 1.18784

Predicted Phosphorous * 1.54597 - 0.13939

Predicted Silicon * 1.25177 + 0.68631

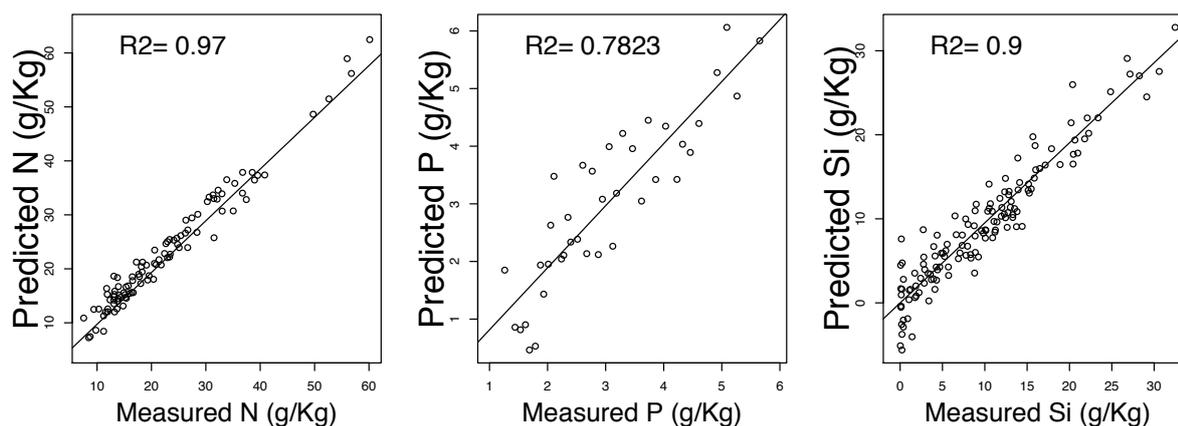


Figure A1 Applicability of NIRS for predicting Silicon (Si), Nitrogen (N) and Phosphorous (P) content (% of dry weight) of leaves of a range of plant species, data are from validating datasets (Bråthen & Murguzur, *Unpublished*; Smis et al 2014).

Species discrimination model

To assure the species specified, we ran the whole data-set through a species discrimination model (Bråthen & Murguzur, *Unpublished*). The model was based on 4 mm adapter scans from species we were sure of. The NIRS spectra were applied to the species discrimination model to predict *Calamagrostis spp.*, *Deschampsia cespitosa*, *Nardus stricta*. The species discrimination model is a two-model system, answering yes or no to e.g. “is this a *Nardus stricta*?” for each spectrum (Table A2). To classify the leaf’s probability to be a *Nardus stricta* the average outcome based on all spectra of the leaf was calculated (referred to as score). The scores for each leaf were evaluated using the rules in Table A1. To avoid converting a field classified non-Si-rich grass species, e.g. *Poa spp.*, into a Si-rich grass species, we used the species-specific Si content summary by Smis et al (2014) as a guideline.

Table A1 Rules to verify Si-rich grass species from the summarized species-specific scores (see above) calculated from the species discrimination model (Bråthen & Murguzur, *Unpublished*). Smis et al (2014) summary of Silicon content (% of dry weight) in Si-rich grass species was used as a guideline.

Field classified species	Verified species	Score <i>Cal. spp.</i>	Score <i>Des. ces.</i>	Score <i>Nar. str.</i>	Silicon content % of dry weight
<i>Calamagrostis spp.</i>	<i>Cal. spp.</i>	>0.83	<0.5	0	>0.29
<i>Deschampsia cespitosa</i>	<i>Cal. spp.</i>	>0.83	<0.5	0	>0.29
<i>Poa spp.</i>	<i>Cal. spp.</i>	>0.9	<0.5	0	>0.29
<i>Deschampsia cespitosa</i>	<i>Des. ces.</i>	0	>0.75	0	>0.34
<i>Calamagrostis spp.</i>	<i>Des. ces.</i>	<0.5	>0.75	0	>0.34
<i>Poa spp.</i>	<i>Des. ces.</i>	<0.5	>0.83	0	>0.34
<i>Nardus stricta</i>	<i>Nar. str.</i>	0	<0.13	>0.75	>0.55

Table A2 Species discrimination model validation. Two models, model EARTH and GLOBAL predicting Yes or No to species identity (column), compared to true species identity (row).

Species	Model	EARTH		GLOBAL	
	True spp	No	Yes	No	Yes
<i>Calamagrostis spp.</i>	No	167	2	166	4
	Yes	1	81	2	79
<i>Nardus stricta</i>	No	202	0	202	0
	Yes	0	49	0	49
<i>Deschampsia cespitosa</i>	No	197	1	183	5
	Yes	0	53	3	60

Appendix B

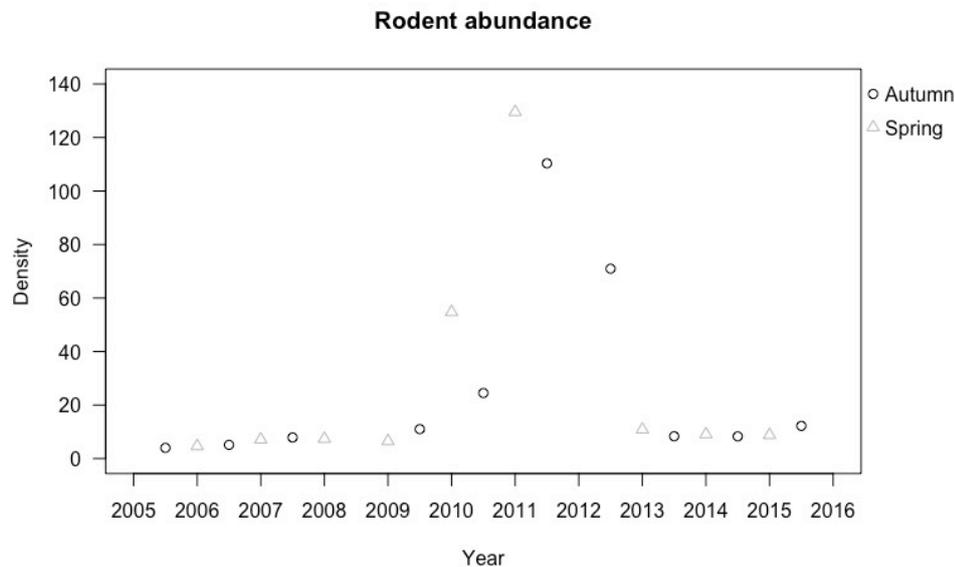


Figure B1 Small rodent abundance, based on observed records in COAT-sites at Ifjordfjellet located in proximity to our study sites (COAT). Grey triangles are spring abundance and black circles are autumn abundance.

Appendix C

Linear Mixed Effects models outcome and raw-data overview.

Table C1 Overview of Linear Mixed Effects model parameters and sample size and sample distribution for models including different effects of species, site and abiotic factors. Species- and season-specific effect sizes of larger ungulates activity (LUA), small rodents winter activity (SRA) and their interaction, are gained by having the different species and seasons holding the intercept. See Table C2 and Table C3 for model outcome specifics.

Model	Parameter distribution		Seasonal observation distribution			Observations	
	Range	Species	Early	Mid	Late	Tot. n	Species
M1	All sites	<i>Nardus stricta</i>	51	80	63	545	194
M2	All sites	<i>Deschampsia cespitosa</i>	22	36	7	545	65
M3	All sites	<i>Calamagrostis spp.</i>	67	135	84	545	286
M4	All sites	All species	140	251	154	545	
M5	All sites	All species	140	251	154	545	
M6	Summer	All species	108	192	124	424	
Model	Linear Mixed Effects model					Observations	
	Fixed effects					Random effects	
M1	SRA *LUA *Season *Species + Reindeer range					Site/Plot/Date	
M2	SRA *LUA *Season *Species + Reindeer range					Site/Plot/Date	
M3	SRA *LUA *Season *Species + Reindeer range					Site/Plot/Date	
M4	SRA *LUA *Season +Species + Reindeer range					Site/Plot/Date	
M5	SRA *LUA *Season +Species +Reindeer range +pH +Soil moisture +Soil's N					Site/Plot/Date	
M6	SRA *LUA *Season +Species					Site/Plot/Date	

Table C2 Overview of model outcomes for species-specific responses in leaf Silicon (Si), Nitrogen (N) and Phosphorous (P) contents (% of dry weight) to effects of larger ungulates activity (LUA) and small rodents winter activity (SRA) and their interactions (L*S) for Early-, Mid- and Late season, across all sites. The effects of predictors are presented as the model's estimated standardized coefficient mean value (Est.) and with an approximately 95% Confidence interval ($\pm 2SE$). Estimates marked with ** are significantly different ($p < 0.050$) and * indicate a trend of difference ($0.1 > p > 0.05$). Model type (see Table C1), total sample size (n), and species-specific sample size (within parenthesis) along with the nutrient in response are represented for each model. For all models the intercept is no SRA and no LUA.

Model		<i>Nardus stricta</i> (M1) n= 545(194)			<i>Deschampsia cespitosa</i> (M2) n= 545(65)			<i>Calamagrostis spp.</i> (M3) n= 545(286)		
		DF	Est.	$\pm 2SE$	DF	Est.	$\pm 2SE$	DF	Est.	$\pm 2SE$
Early				n= (57)			n= (22)			n= (67)
Si	Int.	280	1.003	0.552	280	-0.394	0.663	280	-0.082	0.519
	LUA	280	-0.119	0.545	280	-0.725	0.940	280	-0.358	0.497
	SRA	36	-0.372	0.670	36	-0.064	0.911	36	-0.408	0.606
	L*S	280	0.300	0.806	280	0.891	1.335	280	0.239	0.731
N	Int.	280	-0.344	0.489	280	0.727	0.601	280	0.535	0.455
	LUA	280	0.152	0.507	280	0.290	0.903	280	0.133	0.470
	SRA	36	0.720	0.647**	36	0.312	0.879	36	0.986	0.587**
	L*S	280	-0.163	0.754	280	0.229	1.290	280	-0.340	0.691
P	Int.	280	-0.421	0.504	280	0.627	0.603	280	0.446	0.449
	LUA	280	-0.160	0.516	280	0.866	0.906*	280	0.070	0.475
	SRA	36	0.550	0.630*	36	0.569	0.868	36	0.774	0.570**
	L*S	280	0.125	0.765	280	-1.275	1.299*	280	-0.145	0.697
Mid				n= (80)			n= (36)			n= (135)
Si	Int.	280	0.402	0.516	280	-1.222	0.680	280	-0.764	0.464
	LUA	280	-0.301	0.445	280	-0.069	0.855	280	0.092	0.338
	SRA	36	-0.086	0.543	36	0.424	0.814	36	0.027	0.445
	L*S	280	0.581	0.646*	280	0.041	1.068	280	0.187	0.508
N	Int.	280	-0.678	0.449	280	-0.903	0.622	280	-0.211	0.394
	LUA	280	-0.230	0.417	280	0.229	0.815	280	0.021	0.317
	SRA	36	0.575	0.521**	36	1.046	0.782**	36	0.726	0.432**
	L*S	280	0.189	0.604	280	-1.008	1.012**	280	-0.462	0.479*
P	Int.	280	-0.325	0.464	280	0.053	0.602	280	0.693	0.390
	LUA	280	-0.205	0.423	280	0.233	0.820	280	-0.042	0.321
	SRA	36	0.360	0.499*	36	0.941	0.767**	36	0.548	0.404**
	L*S	280	0.018	0.614	280	-0.847	1.020*	280	-0.382	0.485
Late				n=(63)			n= (7)			n= (84)
Si	Int.	280	0.790	0.551	280	0.754	1.148	280	0.292	0.491
	LUA	280	-0.366	0.541	280	-1.707	1.897*	280	-0.214	0.431
	SRA	36	0.314	0.583	36	-1.037	1.421	36	-0.287	0.516
	L*S	280	0.605	0.723*	280	2.763	2.556**	280	-0.027	0.640
N	Int.	280	-1.367	0.487	280	-1.790	1.084	280	-0.335	0.425
	LUA	280	0.088	0.507	280	1.716	1.850*	280	0.320	0.408
	SRA	36	1.243	0.563**	36	2.433	1.364**	36	0.765	0.501**
	L*S	280	-0.404	0.676	280	-2.064	2.464*	280	-0.752	0.604**
P	Int.	280	-0.670	0.490	280	-0.814	1.094	280	0.390	0.415
	LUA	280	0.119	0.514	280	1.887	1.849**	280	-0.091	0.412
	SRA	36	0.605	0.544**	36	1.939	1.361**	36	0.667	0.479**
	L*S	280	-0.540	0.686	280	-2.730	2.476**	280	-0.284	0.610

Table C3 Overview of model outcomes for site-specific responses in leaf Silicon (Si), Nitrogen (N) and Phosphorous (P) concentrations (% of dry weight) to effects of larger ungulates activity (LUA) and small rodents winter activity (SRA) and their interactions (L*S) for Early-, Mid- and Late season, for all species and with or without covariates. The effects of predictors are presented as the model's estimated standardized coefficient mean value (Est.) and with an approximately 95% Confidence interval ($\pm 2SE$). Estimates marked with ** are significantly different ($p < 0.050$) and * indicate a trend of difference ($0.1 > p > 0.05$). Model type (see Table C1), total sample size (n), season-specific sample size (within parenthesis) along with the nutrient in response is represented for each model. For all models the intercept is no SRA and no LUA.

Model		Summer reindeer range (M4) n= 424			All sites (M5) n= 545			All sites + covariates (M6) n= 545		
		DF	Est.	$\pm 2SE$	DF	Est.	$\pm 2SE$	DF	Est.	$\pm 2SE$
Early				n= (108)			n= (140)			n= (140)
Si	Int.	260	0.934	0.337	302	-0.053	0.501	296	0.749	2.623
	LUA	260	-0.247	0.371	302	-0.309	0.344*	296	-0.323	0.355*
	SRA	21	-0.284	0.509	36	-0.328	0.447	36	-0.328	0.462
	L*S	260	0.255	0.570	302	0.316	0.505	296	0.326	0.514
N	Int.	260	0.036	0.365	302	0.600	0.386	296	3.268	2.397
	LUA	260	0.104	0.385	302	0.115	0.325	296	0.087	0.331
	SRA	21	0.618	0.499**	36	0.736	0.444**	36	0.733	0.438**
	L*S	260	-0.235	0.593	302	-0.161	0.478	296	-0.205	0.479
P	Int.	260	0.036	0.365	302	-0.461	0.410	296	1.585	2.125
	LUA	260	0.104	0.385	302	0.042	0.322	296	0.093	0.327
	SRA	21	0.618	0.499**	36	0.632	0.412**	36	0.677	0.409**
	L*S	260	-0.235	0.593	302	-0.151	0.473	296	-0.248	0.474
Mid				n= (192)			n= (251)			n= (251)
Si	Int.	260	0.210	0.305	302	0.282	0.483	296	0.061	2.613
	LUA	260	-0.045	0.295	302	-0.043	0.260	296	-0.045	0.261
	SRA	21	-0.003	0.412	36	0.043	0.367	36	0.066	0.377
	L*S	260	0.254	0.425	302	0.270	0.376	296	0.282	0.378
N	Int.	260	-0.757	0.331	302	-0.904	0.359	296	2.516	2.386
	LUA	260	0.067	0.307	302	-0.013	0.246	296	-0.019	0.243
	SRA	21	0.609	0.385**	36	0.707	0.361**	36	0.645	0.351**
	L*S	260	-0.500	0.441**	302	-0.405	0.356**	296	-0.421	0.352**
P	Int.	260	-0.657	0.310	302	-0.422	0.380	296	1.717	2.114
	LUA	260	-0.003	0.294	302	-0.047	0.244	296	-0.057	0.241
	SRA	21	0.453	0.360**	36	0.535	0.325**	36	0.455	0.321**
	L*S	260	-0.329	0.423	302	-0.348	0.353**	296	-0.357	0.348**
Late				n= (124)			n= (154)			n= (154)
Si	Int.	260	1.099	0.340	302	1.179	0.501	296	0.964	2.619
	LUA	260	-0.410	0.379**	302	-0.340	0.335**	296	-0.329	0.337*
	SRA	21	-0.223	0.461	36	-0.121	0.415	36	-0.107	0.423
	L*S	260	0.545	0.523**	302	0.362	0.475	296	0.370	0.478**
N	Int.	260	-1.120	0.368	302	-1.209	0.384	296	2.175	2.394
	LUA	260	0.282	0.394	302	0.279	0.318*	296	0.240	0.314
	SRA	21	0.984	0.445**	36	1.017	0.414**	36	0.992	0.400**
	L*S	260	-0.669	0.542**	302	-0.673	0.449**	296	-0.717	0.444**
P	Int.	260	-0.936	0.349	302	-0.722	0.399	296	1.376	2.122
	LUA	260	0.003	0.377	302	0.056	0.314	296	0.012	0.310
	SRA	21	0.646	0.422**	36	0.705	0.380**	36	0.670	0.371**
	L*S	260	-0.503	0.519*	302	-0.475	0.445**	296	-0.503	0.439**

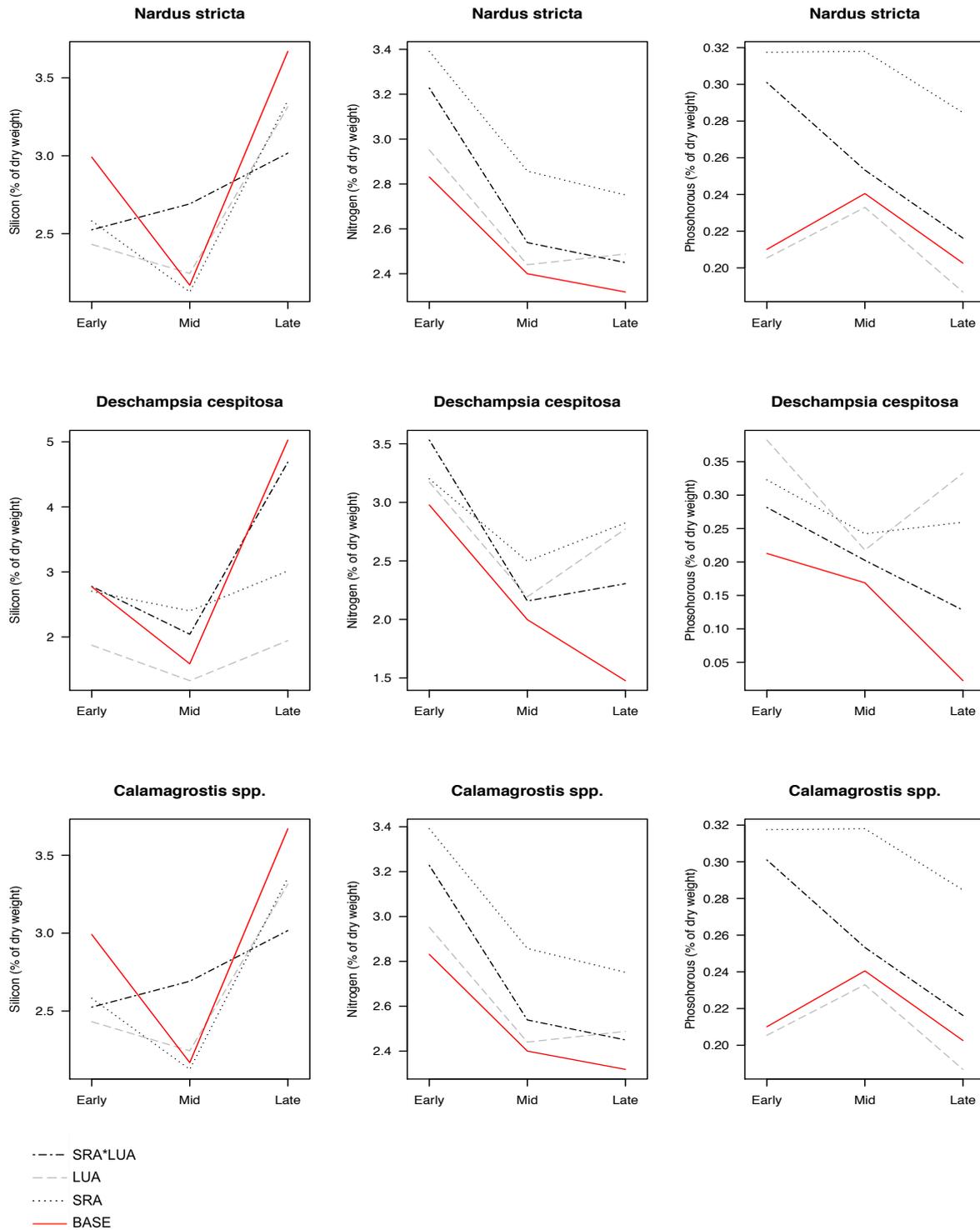


Figure C1 Mean of raw-data nutrient leaf content (% of dry weight) of leaf Silicon (Si), Nitrogen (N) and Phosphorous (P) over the season for each herbivore treatment for each Si-rich grass species. Red BASE line is no herbivore activity, i.e. no LUA and no SRA (BASE), larger ungulate activity (LUA), small rodents winter activity (SRA) and both herbivores activity (LUA*SRA). See Table C4 for mean values of raw data.

Table B4 Overview of species-specific means of raw-data leaf Silicon (Si), Nitrogen (N) and Phosphorous (P) concentration (% of dry weight) for each Si-rich grass species within each season (early, mid, late), for each herbivore treatment, no herbivore activity (BASE), larger ungulate activity (LUA), small rodent winter activity (SRA) and both herbivores activity (LUA*SRA). The statistical results from the species-specific Linear Mixed Effects model (Table C2) are marked ** for significantly different and * indicates a trend. See Figure C1 for graphical overview.

Season	Species	Raw-MEAN content (% of dry weight)				
		BASE	LUA	SRA	LUA*SRA	
Silicon	Early	<i>Calamagrostis spp.</i>	2.991	2.431	2.582	2.525
		<i>Deschampsia ces.</i>	2.773	1.873	2.702	2.778
		<i>Nardus str.</i>	4.567	4.404	3.933	4.331
	Mid	<i>Calamagrostis spp.</i>	2.169	2.245	2.126	2.691
		<i>Deschampsia ces.</i>	1.587	1.328	2.401	2.042
		<i>Nardus str.</i>	3.693	3.289	3.527	4.053
	Late	<i>Calamagrostis spp.</i>	3.670	3.315	3.355	3.017
		<i>Deschampsia ces.</i>	5.028	1.944*	3.015	4.687**
		<i>Nardus str.</i>	4.211	3.698	4.680	4.928*
Nitrogen	Early	<i>Calamagrostis spp.</i>	2.831	2.952	3.391**	3.228
		<i>Deschampsia ces.</i>	2.978	3.174	3.201	3.533
		<i>Nardus str.</i>	2.340	2.408	2.608**	2.601
	Mid	<i>Calamagrostis spp.</i>	2.400	2.440	2.858**	2.539*
		<i>Deschampsia ces.</i>	1.998	2.193	2.497**	2.158**
		<i>Nardus str.</i>	2.109	1.961	2.392**	2.336
	Late	<i>Calamagrostis spp.</i>	2.319	2.488	2.751**	2.450*
		<i>Deschampsia ces.</i>	1.477	2.773	2.825**	2.306**
		<i>Nardus str.</i>	1.670	1.746	2.398**	2.199
Phosphorous	Early	<i>Calamagrostis spp.</i>	0.210	0.205	0.317*	0.301
		<i>Deschampsia ces.</i>	0.213	0.382*	0.323*	0.282
		<i>Nardus str.</i>	0.065	0.037	0.131*	0.126
	Mid	<i>Calamagrostis spp.</i>	0.241	0.233	0.318**	0.253
		<i>Deschampsia ces.</i>	0.169	0.218	0.242**	0.202*
		<i>Nardus str.</i>	0.082	0.048	0.132*	0.105
	Late	<i>Calamagrostis spp.</i>	0.203	0.187	0.285**	0.216
		<i>Deschampsia ces.</i>	0.022	0.333**	0.260**	0.128**
		<i>Nardus str.</i>	0.034	0.045	0.114**	0.059